Arnold van der Valk
Editor

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Contents

Quantitative classification and carbon density of the forest vegetation in Lüliang Mountains of China

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Abstract Forests play a major role in global carbon (C) cycle, and the carbon density (CD) could reflect its ecological function of C sequestration. Study on the CD of different forest types on a community scale is crucial to characterize in depth the capacity of forest C sequestration. In this study, based on the forest inventory data of 168 field plots in the study area (E 111°30′–113°50′, N 37°30′–39°40′), the forest vegetation was classified by using quantitative method (TWINSPAN); the living biomass of trees was estimated using the volume-derived method; the CD of different forest types was estimated from the biomass of their tree species; and the effects of biotic and abiotic factors on CD were studied using a multiple linear regression analysis. The results show that the forest vegetation in this region could be classified into 9 forest formations. The average CD of the 9 forest formations was 32.09 Mg ha^{-1} in 2000 and 33.86 Mg ha^{-1} in 2005. Form. *Picea meyeri* had the highest CD (56.48 Mg ha^{-1}), and Form. *Quercus liaotungensis* + *Acer mono* had the lowest CD (16.14 Mg ha^{-1}). Pre-mature forests and mature forests were very important stages in C sequestration among four age classes in these formations. Forest densities, average age of forest stand, and elevation had positive relationships with forest CD, while slope location had negative correlation with forest CD.

Keywords TWINSPAN · Carbon density · Volume-derived method · Forest vegetation · China

Introduction

Forests play a major role in global carbon (C) cycle (Dixon et al. 1994; Wang 1999) because they store 80% of the global aboveground C of the vegetation and about 40% of the soil C and interact with atmospheric processes through the absorption and respiration of CO_2 (Brown et al. 1999; Houghton et al. 2001a, b; Goodale and Apps 2002). Enhancing C sequestration by increasing forestland area has been suggested as an effective measure to mitigate elevated atmospheric carbon dioxide (CO_2) concentration and hence contribute toward the prevention of global warming (Watson 2000). Recent researches

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focus mainly on carbon storage of forest ecosystem on landscape or regional scale (Fang et al. 2001; Hiura 2005; Zhao and Zhou 2006). Many studies have shown that the C sequestration abilities of different forests change considerably, which can be well explained by their CD values (Wei et al. 2007; Hu and Liu 2006). Meanwhile the C storage of forests may change substantially with forest ecosystems on a community scale. This type of moderate-scale research into the C storage of forests, however, has been rarely conducted.

Many methods have been used to estimate the biomass of forest vegetation (Houghton et al. 2001a, b). Among them, the volume-derived method has been commonly used (Brown and Lugo 1984; Fang et al. 1996; Fang and Wang 2001). Forest volume production reflects the effects of the influencing factors, such as the forest type, age, density, soil condition, and location. The forest CD estimated from forest biomass will also indicate these effects. Zhou et al. (2002) and Zhao and Zhou (2005) improved the volume-derived method by hyperbolic function, but the method has not been used to estimate forest CD on the moderate scale.

The Lüliang Mountains is located in the eastern part of the Loess Plateau in China, where soil and water losses are serious. To improve ecological environment there, the Chinese government has been increasing forestland by carrying out "The Three-North Forest Shelterbelt Program," "The Natural Forest Protection Project," and "The Conversion of Cropland to Forest Program" since 1970s. Previous studies on the forest vegetation in this region focus mainly on the qualitative description of its distribution pattern (The Editing Committee of Shanxi Forest 1984). The objectives of this study were (1) to classify the forest vegetation on Lüliang Mountains using quantitative classification method (TWINSPAN) (Zhang et al. 2003; Zhang 2004); (2) to estimate the CD of different forest types through biomass based on the modified volume-derived method (Zhou et al. 2002) and to clarify the distribution pattern of forest CD in this region; and (3) to quantify the contribution of biotic and abiotic factors (including average forest age, density, soil thickness, elevation, aspect, and slope) to forest CD based on a multiple linear regression analysis. The results would provide basic data for further study of forest C storage pattern in this region.

Methods

Study region

The study was conducted in the middle-north of Lüliang Mountains (E 111°30′–113°50′, N 37°30′–39°40′) with its peak (Xiaowen Mountain) 2831 m above sea level (asl). The temperate terrestrial climate is characterized by a warm summer, a cold winter, and a short growing season (90–130 days) with a mean annual precipitation of 330–650 mm and a mean annual temperature of 8.5°C (min. monthly mean of −7.6°C in January and max. monthly mean of 22.5°C in July). The soils from mountain top to foot are mountain meadow soil, mountain brown soil, mountain alfisol cinnamon soil, and mountain cinnamon soil (The Editing Committee of Shanxi Forest 1984).

There are two national natural reserves in this region with Luya Mountain National Nature Reserve in the north and Pangquangou National Nature Reserve in the south, in which *Crossoptlon mantchuricum* (an endangered bird species), *Larix principis-rupprechtii* forest, and *Picea* spp. (*P. meyeri* and *P. wilsonii*) forest are the key protective targets.

Based on the system of national vegetation regionalization, this area was classified into the warm-temperate deciduous broad-leaved forest zone. With the elevation rising, vegetation zone are, respectively, deciduous broad-leaved forest, needle-broad-leaved mixed forest, cold-temperate coniferous forest, and subalpine scrub-meadow.

Data collection

The forest inventory data from a total of 168 field plots in 2000 and 2005 were used in this study. These permanent plots (each with an area of 0.0667 ha) were established systematically based on the grid of 4 km × 4 km across the forestland of 2698.85 km^2 in 1980s under the project of the forest survey of the Ministry of Forestry of P. R. China (1982), in which the data, such as tree species, diameter at breath height of 1.3 m (DBH), the average height of the forest stand, and the average age of the forest stand had been recorded along with the data of location, elevation, aspect, slope degree, slope location, and soil depth. For trees with ≥ 5 cm DBH, the values of their DBH were included in the inventory.

TWINSPAN classification

A total of 26 tree species had been recorded in the 168 plots. The importance values (IV) for every tree species in each plot were calculated using the following formula:

$$\mathrm{IV} = (\text{Relative density} + \text{Relative dominance} + \text{Relative frequency})/300$$

where relative density is the ratio of the individual number for a tree species over the total number for all tree species in a plot, relative dominance is the ratio of the sum of the basal area for a tree species over the total basal area of all tree species in a plot, and the relative frequency is the percentage of the plot number containing a tree species over the total plot number (168) in this inventory. Based on the matrix of IVs of 26 × 168 (species × plots), the forest vegetation can be classified into different formations using the two-way indicator-species analysis (TWINSPAN) (Hill 1979).

Estimation of biomass and CD

The volume production of an individual tree could be obtained in the volume table (Science and Technology Department of Shanxi Forestry Bureau 1986) according to its DBH. The volume of a species (V) was the sum of its individual tree's volume in a plot. The total living biomass (B) (Mg ha^{-1}) of a species in a plot was calculated as:

$$B = \frac{V}{a + bV} \qquad (1)$$

where V represents the total volume (m^3 ha^{-1}) of a species in a plot, a (0.32–1.125) and b (0.0002–0.001) are constants (Zhou et al. 2002). The constants for most of the tree species in this study were developed by Zhao and Zhou in 2006 (Table 1).

Table 1 Parameters of biomass calculation for dominant species in this study

Species	Parameters in equation			
	a	b	n	R^2
Larix principis-rupprechtii	0.94	0.0026	34	0.94
Pinus tabulaeformis	0.32	0.0085	32	0.86
Picea meyeri	0.56	0.0035	26	0.85
Platycladus orientalis	1.125	0.0002	21	0.97
Pinus armandii	0.542	0.0077	17	0.73
Populus davidiana	0.587	0.0071	21	0.92
Betula platyphylla	0.975	0.001	14	0.91
Quercus liaotungensis	0.824	0.0007	48	0.92

In regard to companion tree species in this study, their biomass estimation was based on the parameters of above known species according to their morphological similarity, i.e., *Pinus bungeana* is referred to the parameters of *Pinus armandii*; *Ulmus pumilla* and *Tilia chinensis* to those of *Quercus liaotungensis*; and *Acer mono* and the rest of broad-leaved species to those of *Populus davidiana*.

Forest CD (Mg ha^{-1}) was calculated as:

$$CD = B \times C_c \qquad (2)$$

where B is the total living biomass of tree species in a plot; C_C is the average carbon content of dry matter, which is assumed to be 0.5, though it varies slightly for different vegetation (Johnson and Sharpe 1983; Zhao and Zhou 2006).

Effects of influencing factors

The qualitative data of the aspect and slope location were first transformed into quantitative data to quantify their effects on forest CD. According to the regulations of the forest resources inventory by the Ministry of Forestry (1982), the aspect data were transformed to eight classes starting from north (from 338° to 360° plus from 0° to 22°), turning clockwise, and taking every 45° as a class: 1 (338°–22°, north aspect), 2 (23°–67°, northeast aspect), 3 (68°–112°, east aspect), 4 (113°–157°, southeast aspect), 5 (158°–202°, south aspect), 6 (203°–247°, southwest), 7 (248°–292°, west aspect), and 8 (293°–337°, northwest aspect). The slope locations in the mountains were transformed to 6 grades: 1 (the ridge), 2 (the upper part), 3 (the middle part), 4 (the lower part), 5 (the valley), and 6 (the flat).

A multiple linear regression model was used to analyze the effects of biotic and abiotic factors on forest CD, assuming a significant effect if the probability level (P) is <0.05:

$$\hat{Y} = a + b_1 X_1 + b_2 X_2 + b_3 X_3 + \ldots + b_k X_k \theta \qquad (3)$$

where a is a constant, b_1, b_2, b_3, and b_k are regression coefficients. $\hat{Y}$ represents CD and X_1, X_2, X_3, X_4, X_5,

X_6, and X_7 represent forest density (X_1), average age (X_2), elevation (X_3), slope location (X_4), aspect (X_5), slope degree (X_6), and soil depth (X_7) in each plot, respectively. Here forest density is the individual number of all tree species per area in a plot, and forest age is the average age of dominant trees in the plot.

Results

Forest formations from TWINSPAN

According to the 4th level results of TWINSPAN classification, the 168 plots were classified into 9 formations (Table 2), which were named according to Chinese Vegetation Classification system (Wu 1980). The dendrogram derived from TWINSPAN analysis is shown in Fig. 1. The basic characteristics of species composition, structure along with its environment for each formation are described as follows:

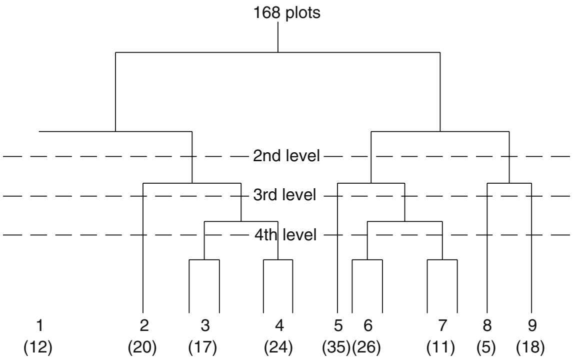

Fig. 1 Dendrogram derived from TWINSPAN analysis. *Note*: 1. Form. *Larix principis-rupprechtii*; 2. Form. *Picea meyeri*; 3. Form. *Betula platyphylla;* 4. Form. *Populus davidiana*; 5. Form. *Pinus tabulaeformis*; 6. Form. *Pinus tabulaeformis* + *Quercus liaotungensis*; 7. Form. *Quercus liaotungensis*; 8. Form. *Pinus bungeana* + *Platycladus orientalis*, and 9. Form. *Quercus liaotungensis* + *Acer mono*. The number of plots for each formation is shown between the brackets

1. Form. *Larix principis-rupprechtii* (Form. 1 for short, the same thereafter): *L. principis-rupprechtii* was the dominant tree species of the cold-temperate coniferous forest in north China. It grew relatively faster with fine timber. Therefore it was a very important silvicultural tree species at middle-high mountains in this region. This type of forest distributed vertically from 1610 m to 2445 m above sea level, and common companion species were *Picea meyer*i and *P. wilsonii* in the tree layer.
2. Form. *Picea meyeri* (Form. 2): *P. meyeri* forest belonged to cold-temperate evergreen coniferous forest. Its ecological amplitude was relatively narrow with a range of vertical distribution from 1860 m to 2520 m. *Betula platyphylla* and *Picea wilsonii* appeared commonly in this forest.
3. Form. *Betula platyphylla* (Form. 3): *B. platyphylla* was one of main tree species in this region and occupied the land at moderate elevation (1700–2200 m). In the tree layer, *Populus*

Table 2 The structure characteristics of 9 forest formations and their environmental factors

Form	Density (No./ha)	Age (Year)	Coverage (%)	Slope location	Elevation (m)	Slope (°)	Aspect	Soil depth (cm)
1	849.3 ± 121.8	40.0 ± 5.4	54 ± 8.7	2.7 ± 0.1	1610–2445	19.1 ± 1.1	4.1 ± .6	56.4 ± 5.1
2	869.6 ± 179.1	55.4 ± 4.8	62 ± 8.3	2.3 ± 0.2	1860–2520	19.6 ± 2.2	4.7 ± 0.6	50.6 ± 5.9
3	774.3 ± 57.8	45.5 ± 5.3	45 ± 4.1	2.6 ± 0.2	1700–2200	21.6 ± 1.9	4.2 ± 0.8	48.7 ± 3.3
4	1071.9 ± 124.4	31.6 ± 2.6	41 ± 6.3	3.5 ± 0.2	1350–1997	23.0 ± 1.6	4.1 ± 0.6	49.2 ± 6.2
5	770.9 ± 139.7	54.7 ± 2.6	49 ± 5.7	2.9 ± 0.2	1360–2010	23.9 ± 2.2	2.9 ± 0.5	41.0 ± 4.1
6	756.2 ± 87.7	60.9 ± 3.7	46 ± 4.2	2.6 ± 0.2	1235–1820	29.4 ± 2.3	3.7 ± 0.4	34.2 ± 4.1
7	731.3 ± 154.7	56.8 ± 6.2	46 ± 7.4	3.0 ± 0.3	1452–2010	25.9 ± 2.1	3.4 ± 0.8	53.2 ± 3.7
8	1589.2 ± 616.2	53.8 ± 3.8	41 ± 2.5	2.6 ± 0.5	1250–1270	26.6 ± 3.5	3.6 ± 0.7	34.0 ± 7.1
9	910.3 ± 136.8	51.3 ± 4.6	51 ± 7.3	3.4 ± 0.2	1350–1660	23.2 ± 2.5	4.8 ± 0.5	39.4 ± 4.4

Note: 1. Form. *Larix principis-rupprechtii*; 2. Form. *Picea meyeri*; 3. Form. *Betula Platyphylla*; 4. Form. *Populus davidiana*; 5. Form. *Pinus tabulaeformis*; 6. Form. *Pinus tabulaeformis* + *Quercus liaotungensis*; 7. Form. *Quercus liaotungensis*; 8. Form. *Pinus bungeana* + *Platycladus orientalis*; 9. Form. *Quercus liaotungensis* + *Acer mono* *davidiana* and *Larix principis-rupprechtii* were the companion species.

4. Form. *Populus davidiana* (Form. 4): *P. davidiana* was a pioneer tree species in the north secondary forest. This forest appeared at moderate elevation (1350–1997 m) and on southerly aspect. Tree species were plentiful in it, including *Pinus tabulaeformis*, *Quercus liaotungensis*, and so on.
5. Form. *Pinus tabulaeformis* (Form. 5): *P. tabulaeformis* (Chinese pine) was a main dominant tree species of the warm-temperate coniferous forest in north China. The Chinese pine forest was a dominant forest type in Shanxi Province (The Editing Committee of Shanxi Forest 1984). In the study region, it occupied the land at moderate elevation (1360–2010 m).
6. Form. *Pinus tabulaeformis* + *Quercus liaotungensis* (Form. 6): this forest was present at low to moderate elevation (1200–1800 m) on south-faced aspect.
7. Form. *Quercus liaotungensis* (Form. 7): the *Q. liaotungensis* forest was a typical warm-temperate deciduous broad-leaved forest and a main broad-leaved forest type in north China. *Q. liaotungensis* mainly distributed at middle-low elevation (1400–2000 m) in the middle-north of Lüliang Mountains.
8. Form. *Pinus bungeana* + *Platycladus orientalis* (Form. 8): there was relatively a few *Pinus bungeana* + *Platycladus orientalis* mixed forest appearing at the lower elevation of 1200 m on northerly aspect where environmental condition was characterized by drought, infertility, and cragginess.
9. Form. *Quercus liaotungensis* + *Acer mono* (Form. 9): in the low elevation (1300–1660 m), *Q. liaotungensis* was always mixed with other broad-leaved tree species, such as *Acer mono*, *Prunus armeniaca*, and so on. Most of these trees were light-demanding and drought-tolerant species.

Biomass

According to the national guidelines for forest resource survey (The Ministry of Forestry 1982), each forest formation can be divided into five age classes (young, mid-aged, pre-mature, mature, and post-mature). Since there was only one plot where the post-mature age class forest occurred, which belonged to *P. davidiana* Form., the rest of plots fell into four age classes (Fig. 3).

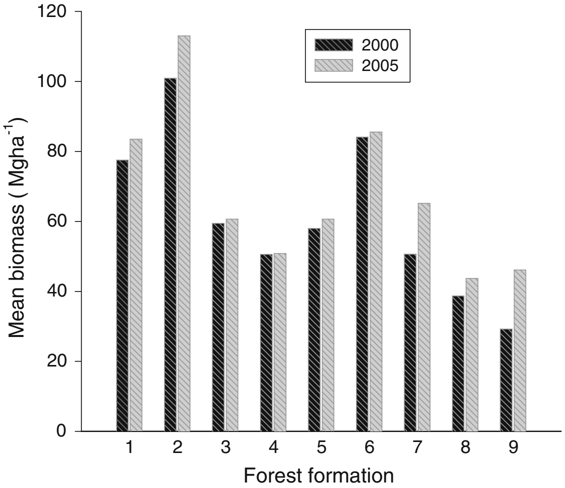

Fig. 2 The mean biomass of each formation in 2000 and 2005 (Mg ha^{-1})

According to Eq. 1 and the parameters of each species (Table 1; Zhao and Zhou 2006), the biomass of each age class for 9 formations were calculated, and the average biomasses of each formation are shown in Fig. 2. The average biomass in 2005 was slightly higher than that in 2000.

There was a wide range of change in the values of mean biomass among the 9 formations. For instance, in 2005, the highest value of biomass (112.97 Mg ha^{-1}) was observed in Form. 2; next to Form. 2 were Form. 6 (85.51 Mg ha^{-1}) and Form. 1 (83.49 Mg ha^{-1}); in the middle level were Form. 3 (60.64 Mg ha^{-1}), Form. 5 (60.61 Mg ha^{-1}), and Form. 7 (65.14 Mg ha^{-1}); and the lower values of biomass were found in Form. 4 (50.80 Mg ha^{-1}), Form. 8 (43.69 Mg ha^{-1}), and Form. 9 (46.12 Mg ha^{-1}).

Carbon density

The overall average values of carbon density (CD) for the 9 formations were 32.09 Mg ha^{-1} in 2000 and 33.86 Mg ha^{-1} in 2005, respectively, and the average values of CD for these formations ranged from 23.06 Mg ha^{-1} for Form. 9 to 56.48 Mg ha^{-1} for Form. 2.

The CD among different age classes changed considerably (Fig. 3), and showed an increased trend

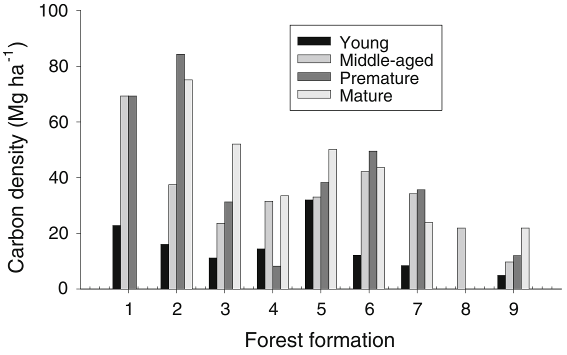

Fig. 3 The carbon density of 9 forest formations in Lüliang Mt. in 2005 (Mg ha^{-1}). *Note*: There is no mature age class in Form. 1, and there is only a single middle-aged class in Form. 8

from the young class to pre-mature or mature class in most forest formations. The extremely low amount of CD in the pre-mature forest of Form. 4 resulted from the low biomass accumulation, which may be caused, according to field observations, by (1) the insect infestation which had occurred and led to the death of some trees in plots 155 and 164, and (2) the droughty habitats on southerly aspect where these two plots were located, and the wilt of some tree species like *Populus davidiana* was found.

In Form. 2, Form. 6, or Form. 7 the CD of mature forest was lower than that of the pre-mature forest due to the fact: *Larix principis-rupprechtii, Picea meyeri*, and *Pinus tabulaeformis* were main timber tree species in study region, and some of the mature trees in these formations may have been illegally cut down for timber use by some local residents.

Nevertheless, from the total percentage of the CD of pre-mature and mature classes over the total CD of all classes of each formation, it was found that the CD in these two classes accounted for 74.9% in Form. 2, 70.6% in Form. 3, 60.8% in Form. 5, 63.2% in Form. 6, 58.3% in Form. 7, and 70.0% in Form. 9. This indicated that pre-mature and mature forests were very important C sequestration stages in most formations.

Effects of biotic and abiotic factors on forest CD

Due to lack of some environmental data in some plots, a total of 157 plot data was used for regression analysis. Based on Eq. 3, a multiple linear regression equation between the forest CD $\left(\hat{Y}\right)$ and influencing factors was established:

$$\hat{Y} = -17.687 + 0.17X_1 + 0.108X_2 + 0.019X_3 - 1.182X_4 \tag{4}$$

The partial correlation coefficients were 0.475 ($P < 0.01$) for forest density (X_1), 0.288 ($P < 0.01$) for average age (X_2), 0.261($P < 0.01$) for elevation (X_3) and -0.178 ($P < 0.05$) for slope location (X_4), respectively. It indicated that forest density, average age of forest stand and altitude had positive correlation with CD; whereas slope location had negative correlation with CD. And aspect (X_5), slope degree (X_6), and soil depth (X_7) had no significant relationship with the CD. This suggested that the CD rose with the increase of forest density, average age, and altitude; and it decreased with the slope location change from 1 (the ridge) to 6 (the flat). The biggest partial correlation coefficient for forest density indicated that forest density had a stronger effect on the CD than the other factors.

Discussions

The results of quantitative classification (TWINSPAN) clearly reflected the vertical distribution patterns of forest vegetation in Lüliang Mountains. The warm-temperate deciduous broad-leaved forest (Form. *Quercus liaotungensis* + *Acer mono*) was distributed in the low mountain area, and *Pinus bungeana* + *Platycladus orientalis* mixed forest was located in this altitude range on the southern aspect where the habitat was droughty and infertile. The warm-temperate coniferous forest (Form. *Pinus tabulaeformis*) and the warm-temperate needle-broad-leaved mixed forest (Form. *Pinus tabulaeformis* + *Quercus liaotungensis*) were present in the lower-to-middle mountain area. And *Quercus liaotungensis* forest also occupied this range. Deciduous broad-leaved forests (Form. *Populus davidiana* and Form. *Betula platyphylla*) occupied the middle-to-high mountain range. Cold-temperate coniferous forests (Form. *Larix principis-rupprechtii* and Form. *Picea meyeri*) were distributed in the middle-to-high mountain area, in which the distribution range of Form. 1 was wider than Form. 2.

Considered together, the distribution patterns and biomass estimates of the forests in Lüliang Mountains revealed that the biomass tended to increase with the altitude rising. Of the 5 coniferous formations (including coniferous and broad-leaved mixed formations), the biomass increased from 43.69 Mg ha^{-1} for Form. 8 (1200 m asl), 60.61 Mg ha^{-1} for Form. 5 (1360–2010 m asl), 85.52 Mg ha^{-1} for Form. 6 (1200–1800 m asl), 83.49 Mg ha^{-1} for Form. 1 (1610–2445 m asl) to 112.97 Mg ha^{-1} for Form. 2 (1860–2520 m asl). Of the 4 broad-leaved formations, the biomass increased from 46.12 Mg ha^{-1} for Form. 9 (1300–1660 m asl) and 50.80 Mg ha^{-1} for Form. 4 (1350–1997 m asl) to 65.14 Mg ha^{-1} for Form. 7 (1400–2000 m asl) and 60.64 Mg ha^{-1} for Form. 3 (1700–2200 m asl). In addition, the average biomass (79.12 Mg ha^{-1}) of the 5 coniferous formations was greater than that (53.91 Mg ha^{-1}) of the 4 broad-leaved formations.

The average CD of forest vegetation of Lüliang Mountains was 33.86 Mg ha^{-1} in 2005. It was lower than the average level of 41.938 Mg ha^{-1} (Wang et al. 2001a, b), 44.91 Mg ha^{-1} (Fang et al. 2001), or 41.32 Mg ha^{-1} (Zhao and Zhou 2006) estimated for all forests in China. The lower CD in Lüliang Mountains can be explained by (1) low annual precipitation of 330–650 mm in this area (The Editing Committee of Shanxi Forest 1984) and (2) large proportion of young, middle-age, and premature forests (80%) and small proportion of mature and post-mature forests (20%) (Liu et al. 2000).

Different forest formations had various ability of carbon sequestration. In this study, the average CD (56.48 Mg ha^{-1}) of Form. *Picea meyeri* was higher than those of other forest formations. This may result from the higher average individual volume production of *Picea meyeri*. According to The Editing Committee of Shanxi Forest (1984), the average individual volume production at the age of 60 were 0.0056 m^3 $year^{-1}$ for *Picea meyeri*, 0.0031 m^3 $year^{-1}$ for *Larix principis-rupprechtii*, and 0.0030 m^3 $year^{-1}$ for *Pinus tabulaeformis*, respectively. The average CD (42.76 Mg ha^{-1}) of Form *Pinus tabulaeformis* + *Quercus liaotungensis* was close to the average level in China, and this type of mixed forest could be largely afforested in the lower-to-middle mountain of the Loess Plateau. Most of the stands of Form. *Larix principis-rupprechtii* forest were still at very young stage (at an average age of 40 years for all stands), so the CD (41.75 Mg ha^{-1}) of this Form. was relatively low. As Wang et al. (2001a, b) and Zhou et al. (2000) suggested, in the middle-to-higher mountain of the Loess Plateau, subalpine coniferous tree species, such as *Picea meyeri* should be primarily protected because they can sequestrate more C than other tree species.

Under conditions of global climate change, the impact of biotic and abiotic factors on forest carbon density is complex. Many factors have synergistic effect on forest carbon, and the influencing degree of those factors is different (Houghton 2002). The analysis of multiple linear regression showed that forest density, average age, and elevation had positive relations with forest CD, and slope location had negative correlation with it.

In a single species population, the function relationship between mean biomass of individual trees and density has long been an issue in dispute. Recently, Enquist and Niklas (2002) put forward that there is a power function relationship between biomass (or C) of individual tree and forest density. Therefore forest density is an important influencing factor on forest carbon. In this research, the regression analysis indicated that forest density had significantly higher effect on carbon density than other factors.

The significant effects of altitude and slope location on forest CD may be to some extent related to human disturbance. Along with the elevation rise or the slope location change from mountain foot to top, the human activities decreased, and the carbon accumulation of forest ecosystems increased. Therefore the forest CD tended to increase with elevation rise or slope location rise.

Due to the fact that the volume-derived method provides only the parameters of biomass calculation for dominant species, and lacks the parameters for companion species, the biomass estimation of companion species were based on the parameters of known species according to the morphological similarity between the companion species and the known species in this study (Table 1). This kind of approximation may result in inaccurate CD estimation. Besides, only the living biomass of trees was estimated, the biomass of shrubs, herbs, standing dead wood, and litter on the ground were not taken into account in this study. As Duvigneaued (1987) noted that the total litter biomass accounts for 2–7% of the total biomass of major biomes of the world, so this study presents primarily the basic CD results of the forest tree species in this area. Much detailed work, especially that of the total biomass and carbon storage of every forest formation, needs to be done in the future.

Conclusion

The forest vegetation in this area was quantitatively classified into 9 forest formations. They showed distinctly the vertical distribution patterns along elevation gradient in Lüliang Mountains. The average CD was 32.09 Mg ha^{-1} in 2000 and 33.86 Mg ha^{-1} in 2005, with the highest CD (56.48 Mg ha^{-1}) in Form. *Picea meyeri* and the lowest CD (16.14 Mg ha^{-1}) in Form. *Quercus liaotungensis* + *Acer mon*. Pre-mature and mature forests generally sequestrated more C than young and middle-aged forests. Forest density, average age of forest stand, and elevation had significantly positive relationships with forest CD, and slope location showed negative correlation with forest CD. The forest density had a higher effect on forest CD than other factors.

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References

Brown S, Lugo AE (1984) Biomass of tropical forests: a new estimate based on forest volumes. Science 223:1290–1293. doi:10.1126/science.223.4642.1290

Brown SL, Schroeder P, Kern JS (1999) Spatial distribution of biomass in forests of the eastern USA. For Ecol Manag 123:81–90

Dixon RK, Brown S, Houghton RA et al (1994) Carbon pools and flux of global forest ecosystems. Science 263:185–190. doi:10.1126/science.263.5144.185

Duvigneaued P (1987) La synthese ecologique (in Chinese, trans: Li Y). Chinese Science Press, Beijing, China

Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass portioning in seed plants. Science 295:1517–1520. doi:10.1126/science.1066360

Fang JY, Wang ZM (2001) Forest biomass estimates at regional and global levels, with special reference to China's forest biomass. Ecol Res 16:587–592. doi:10.1046/j.1440-1703.2001.00419.x

Fang JY, Liu GH, Xu SL (1996) Biomass and net production of forest vegetation in China (in Chinese with English abstract). Acta Ecol Sin 16:497–508

Fang JY, Chen AP, Peng CH et al (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. Science 292:2320–2322. doi:10.1126/science.1058629

Goodale CL, Apps MJ (2002) Forest sinks in the northern hemisphere. Ecol Appl 12(3):891–899. doi:10.1890/1051-0761(2002)012[0891:FCSITN]2.0.CO;2

Hill MO (1979) TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. Department of Ecology and Systematics, Cornell University, Ithaca

Hiura T (2005) Estimation of aboveground biomass and net biomass increment in a cool temperate forest on a landscape scale. Ecol Res 20:271–277. doi:10.1007/s11284-005-0042-0

Houghton RA (2002) Terrestrial carbon sinks-uncertain explanations. Biologist 49:155–160

Houghton JT, Ding Y, Griggs DJ (eds) (2001a) Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK

Houghton RA, Lawrence KT, Hackler JL et al (2001b) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimate. Glob Change Biol 7:731–746. doi:10.1046/j.1365-2486.2001.00426.x

Hu HF, Liu GH (2006) Roles of forest management in global carbon dioxide mitigation (in Chinese with English abstract). Chin J App Ecol 17(4):709–714

Johnson WC, Sharpe DM (1983) The ratio of total to merchantable forest biomass and its application to the global carbon budget. Can J Res 13:372–383

Liu GH, Fu BJ, Fang JY (2000) Carbon dynamics of Chinese forests and its contribution to global carbon balance (in Chinese with English abstract). Acta Ecol Sin 20(5):733–740

Ministry of Forestry (1982) Standards for forest resources survey. China Forestry Publishing House, Beijing, China

Science and Technology Department of Shanxi Forestry Bureau (1986) The compilation of forestry standards in Shanxi Province. Taiyuan, China

The Editing Committee of Shanxi Forest (1984) Shanxi Forest. Chinese Forestry Press, Beijing, China, pp 135–136

Wang XK (1999) Study on regional carbon cycle of forest ecosystem in China. Theses of committee of Synthesis Investigation of Natural Resources. Chinese Academy of Science, Beijing, China, p 123

Wang XK, Feng ZW, Ouyang ZY (2001a) The impact of human disturbance on vegetation carbon storage in forest ecosystems in China (in Chinese with English abstract). For Ecol Manag 148:117–123. doi:10.1016/S0378-1127(00)00482-5

Wang XK, Feng ZW, Ouyang ZY (2001b) Vegetation carbon storage and density of forest ecosystems in China(in Chinese with English abstract). Chin J App Eco 12(1):13–16

Watson RT (2000) Land use, land-use change, and forestry: a special report of the IPCC. Cambridge university Press, Cambridge, p 377

Wei HD, Ma XQ, Liu AQ et al (2007) Review on carbon cycle of forest ecosystem (in Chinese with English abstract). Chin J of Eco-Agric 15(2):188–192

Wu ZY (1980) Chinese vegetation. Science Press, Beijing, China

Zhang JT (2004) Quantitative ecology. Science Press, Beijing, China

Zhang F, Zhang JT, Zhang F (2003) Pattern of forest vegetation and its environmental interpretation in Zhuweigou, Lishan mountain nature reserve (in Chinese with English abstract). Acta Ecol Sin 23:421–427

Zhao M, Zhou GS (2005) Estimation of biomass and net primary productivity of major planted forests in China based on forest inventory data. For Ecol Manag 207:295–313. doi:10.1016/j.foreco.2004.10.049

Zhao M, Zhou GS (2006) Carbon storage of forest vegetation in China and its relationship with climatic factors. Clim Change 74:175–189. doi:10.1007/s10584-006-6775-0

Zhou YR, Yu ZL, Zhao SD (2000) Carbon storage and budget of major Chinese formations (in Chinese with English abstract). Acta Phytoecol Sin 24:518–522

Zhou GS, Wang YH, Jiang YL, Yang ZY (2002) Estimating biomass and net primary production from forest inventory data: a case study of China's *Larix* forest. For Ecol Manag 169:149–157. doi:10.1016/S0378-1127(02)00305-5

Effects of introduced ungulates on forest understory communities in northern Patagonia are modified by timing and severity of stand mortality

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Abstract Natural disturbances such as fires, windstorms, floods, and herbivory often act on plant communities, affecting their structure and the abundance and composition of their species. Most research has focused on the effects of single disturbances on plant communities whereas the synergistic effects of several disturbances have received less attention. In this study, we evaluated how timing and severity of tree mortality modified plant use by introduced deer and early post-mortality successional trajectories in northern Patagonian conifer forests. We sampled understory composition and deer use in *Austrocedrus chilensis* (ciprés de la cordillera) forest stands undergoing varying timing and severity of forest mortality as reconstructed using dendroecological techniques. In addition, we evaluated the effect of fallen logs on plant composition and deer use of plants by monitoring areas of massive dieback where fallen logs had been removed for fire hazard reduction, and nearby control areas not subjected to such removal. Stepwise regression analyses showed that history and severity of tree mortality strongly influence plant composition and deer use of plants. For deer use (with pellet counts and browsing index as response variables), results showed a positive relationship with degree of stand mortality and a negative relationship with cover of fallen logs. Similarly, cover of unpalatable shrub species was explained by canopy mortality history, whereas cover of palatable shrub species was positively associated with severity of canopy mortality. In areas where fallen logs had been removed, pellet counts were six times higher than those in control areas. Though total shrub species cover was similar between log removal and control areas, proportion of unpalatable shrubs increased in areas where fallen logs had been removed. In conclusion, deer use of plants was strongly limited by tall fallen logs, allowing palatable species to establish and grow. Fallen log removal accelerated deer entrance and changed understory composition toward more browse-resistant and unpalatable species. These results underscore the importance of considering the dynamics (timing, severity, and extent) of fallen woody debris influencing understory herbivory and post-disturbance succession. In addition, experimental results underpin the importance of maintaining snags and large woody debris in disturbed landscapes where salvage logging is a routine procedure.

Keywords *Austrocedrus chilensis* · Browsing · Disturbance · Exotic deer · Forest decline

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Introduction

Coarse-scale disturbances such as fires, snow avalanches, windstorms, droughts, and insect defoliation strongly influence the rate and direction of plant succession. These disturbances release limiting resources, triggering vegetation changes that attract herbivores searching the landscape for patches of high-quality forage (Jefferies et al. 1994). On the other hand, the heterogeneous matrix of dead woody debris left after forest disturbances can strongly limit and control herbivore movement (Thomas et al. 1979; Hanley et al. 1989; Nyberg 1990). Thus, plant communities will likely reflect a complex synergism of disturbance characteristics that affect plant performance directly by releasing limiting resources (Pickett and White 1985) and indirectly by modifying herbivore foraging patterns (Stuth 1991).

Although forests are highly dynamic systems subjected to natural disturbances of different scales, relatively few studies have addressed how large herbivores, such as ungulates, differentially use and impact vegetation of sites affected by forest disturbances of varying severity and timing (Wisdom et al. 2006). Ungulates generally exert minor influences on the structure and function of mature forest stands (Russell et al. 2001). However, their effect following a disturbance can determine the trajectory of the system among alternative states (Hobbs 1996; Russell et al. 2001). We hypothesized that depending on the severity and timing of the disturbances, physical and biotic conditions at disturbed sites may alter deer behaviour, thus changing their role in modifying plant succession. We predict that recent sudden, massive forest dieback events such as windstorms may create a mosaic of highly inaccessible microsites composed of a tight network of fallen logs and branches and will be dominated by palatable plants. Older, less severe or more chronic patterns of tree mortality, by contrast, may allow more accessibility, will show signs of higher deer use and will be dominated by unpalatable plants.

Forests of northern Patagonia, particularly on Isla Victoria, are ideal for evaluating forest mortality–herbivory interactions. Here, extensive stands of *Austrocedrus chilensis* (D. Don.) Pic. Serm. & Bizarri (ciprés de la cordillera) are being affected by “mal del ciprés”, a syndrome caused by a poorly known agent (Filip and Rosso 1999; La Manna and Rajchenberg 2004; Greslebin and Hansen 2006) that causes root death and standing mortality followed by mass canopy collapse owing to root weakening and increased susceptibility to windthrow. At the landscape scale, poor soil drainage controls the occurrence of patches of standing dead trees of diverse sizes plus logs and fallen branches on the forest floor that appear interspersed in a matrix of healthy forest (La Manna et al. 2008; Fig. 1a). Interacting with the understory and tree saplings in these forests, there are also abundant introduced cervids, mostly red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) (Simberloff et al. 2003). *Austrocedrus* forests are heavily used by introduced deer owing to high forage availability and provision of winter cover (Relva and Caldiz 1998; Barrios Garcia Moar 2005). In addition, extensive removal of downed slash and fallen logs along roads for fire hazard mitigation (Fig. 1b) offers a unique large-scale manipulative experimental setting in which to test possible mechanisms involved in this interaction between mortality and herbivory.

Here, we present results that combine dendroecological techniques for determining timing and severity of past mortality with standard vegetation and herbivore use assessments that preliminarily underscore the importance of stand decline history on understory vegetation structure and composition. In addition, we experimentally demonstrate the impact of fallen obstacles on herbivory by deer as a key mechanism in modifying the strength of herbivory effects on vegetation.

Methods

Study site

The study was conducted in a 2 × 4 km area of evergreen conifer *Austrocedrus* forest on northern Isla Victoria, Nahuel Huapi National Park, Argentina (40°57′S; 71°33′W; Fig. 2). Within the study area, we sampled for tree mortality reconstructions, deer use and vegetation censuses in four areas of ca. 1 ha each representing forests with contrasting history and severity of stand mortality (Criollos, Larga, Redonda, Pseudotsuga, Fig. 2, Table 1).

Isla Victoria is an island running NW to SE that comprises 3,710 ha, with a varied topography that

Fig. 1 Photographs showing massive mortality of *Austrocedrus chilensis* forests with standing dead trees, logs and fallen branches (**a**) and adjacent areas where logs and fallen branches were removed (**b**) on Isla Victoria, northern Patagonia

includes flat, shallow valleys, and elevations of up to 1,025 m. Mean annual rainfall is 1,700 mm (Barros et al. 1988), mostly occurring during winter (June to September). Soils are allophanic (derived from volcanic ashes), sandy, permeable, and rich in organic matter and acid pH (Koutché 1942). Isla Victoria is covered mainly by southern beech pure *Nothofagus dombeyi* forests, pure *Austrocedrus* forests, and mixed *N. dombeyi-Austrocedrus* forests. *Lomatia hirsuta*, *Maytenus boaria*, *Nothofagus antarctica*, *Luma apiculata*, *Myrceugenia exsucca*, and *Dasyphyllum diacanthoides* are subdominant tree species in these forests. The understory includes palatable shrubs such as *Aristotelia chilensis*, *Maytenus chubutensis*, *Ribes magellanicum*, *Schinus patagonicus*, and *Chusquea culeou* as well as unpalatable shrubs such as *Berberis* spp. and *Gaultheria* spp. The herbaceous layer includes native species such as *Uncinia* sp. and exotics such as *Cynoglosum creticum* and *Digitalis purpurea*. Species nomenclature follows Ezcurra and Brion (2005).

Historical disturbances consist of extensive fires that occurred during European settlement resulting in 80- to 120-year-old postfire-cohorts (Veblen and Lorenz 1987). These forests have scarce regeneration because the dominant tree species are not shade tolerant, although sporadic regeneration can occur in small tree-fall gaps (Veblen et al. 1989). Since 1948, when the first observation was recorded on Isla Victoria (Havrylenko et al. 1989), and extending over the island and the region with geographically varying intensities, the main present disturbance pattern is *mal del ciprés Austrocedrus* mortality.

Superimposed on the pattern of disturbance by fires and dieback are the effects of introduced herbivores. In 1916, red deer (*Cervus elaphus*), axis deer (*Axis axis*), and fallow deer (*Dama dama*) were successfully introduced to the island. At present, red deer and fallow deer are extremely abundant, while axis deer is apparently extinct on the island. By 1959, exotic deer densities on the island were estimated to be 40 individuals/km^2 (Anziano 1962), and recent estimates indicate densities of 26 individuals/km^2 (Relva unpubl.). Average red deer density throughout the present distributional range in Patagonia has been estimated at about 2 individuals/km^2 (Flueck et al. 2003); however, these authors also state that in favourable conditions densities may reach 100 deer/km^2 (ecotonal habitat) and 40–50 deer/km^2 (steppe habitat). Exotic deer have significantly modified the forests on Isla Victoria, reducing cover by palatable species, such as *Aristotelia chilensis* (Veblen et al. 1989), and delaying the growth of *Austrocedrus* and *Nothofagus dombeyi* seedlings and saplings to adult size (Veblen et al. 1989; Relva and Veblen 1998).

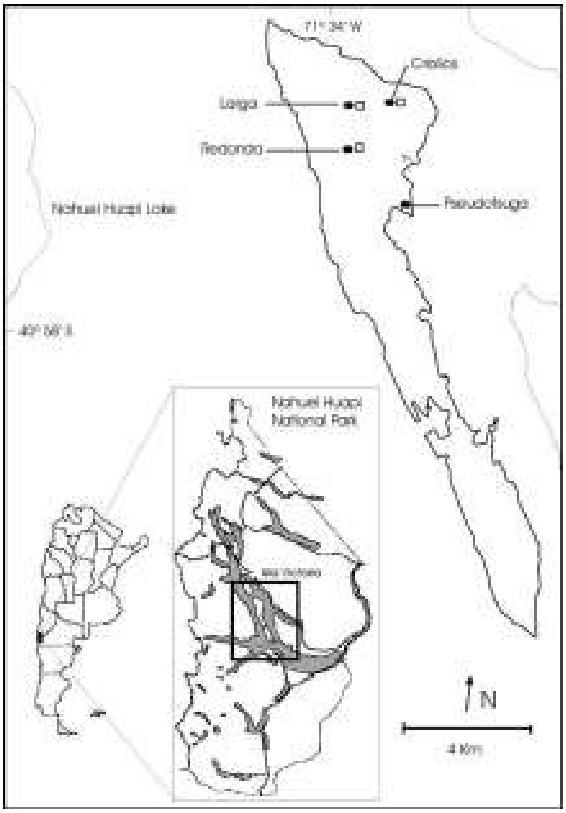

Fig. 2 Location of *Austrocedrus chilensis* forest stands studied on Isla Victoria, Parque Nacional Nahuel Huapi, Argentina. Closed circles denote control areas and open squares denote log removal areas. See Table 1 for stand characteristics

Field sampling

Mortality assessments

In each area we used dendroecological techniques (Stokes and Smiley 1968) to reconstruct the timing and duration of tree mortality events. In each area, in fifteen 314 m^2 plots we cored the closest live tree to the centre of the plot at ca. 50 cm with increment borers to determine dates of growth release related to *mal del ciprés* mortality and/or associated windthrow from neighbour trees. Dead standing, wind-snapped, and uprooted trees were sampled by cutting partial cross-sections at the base of each individual to date the year of death. All samples were sanded with successive grades of sandpaper to obtain an optimal view of annual rings. Ring widths in tree cores and cross-sections were measured to the nearest 0.01 mm using a Henson computer-compatible radial increment-measuring device. Disturbance dates were determined on living trees by detecting growth release events. In this study, we define release events as occurring when the tree-ring width of five contiguous years increased more than 150% compared to the preceding 5 years growth (Kitzberger et al. 2000a). The growth release frequencies were quantified in 10-year periods by calculating the number of individuals that underwent growth release in a period relative to total individuals present in that period. Dates of death of dead-standing and downed trees were established using the standard visual skeleton plots method (Stokes and Smiley 1968) in combination with the COFECHA cross-dating program (Holmes 1983). This program statistically analyses the correlation between pieces of undated (floating) tree-ring series and master series dated independently. For cross-dating, Cerro Los Leones (International Tree Ring Data Bank, http://www.ngdc.noaa.gov/paleo/treering.html) was used as the master tree ring chronology.

Vegetation and deer use

In each area we sampled forest structure, understory abundance and composition, and deer use with 15 concentric plots of variable sizes placed systematically every 20 m along three parallel lines that were located in relatively homogeneous areas, each approximately 50 m apart from adjacent lines. Forest structure was sampled in fifteen 314 m^2 circular plots, in which we measured diameters of adult trees (>4 cm at breast height) in four categories: living, uprooted dead, standing dead, and snapped dead tree. Understory abundance and composition were surveyed in fifteen 100 m^2 circular plots in which we visually estimated cover by individual species of tree saplings (height >10 cm and dbh <4 cm), shrubs, and herbs. In each 100 m^2 circular plot, we also counted and measured tree sapling height and assessed seedling abundances (height <10 cm) by counting within four 1 m^2 plots randomly distributed throughout the 100 m^2 understory plots. We measured the tallest shrub of each species and used a scale according to Allen and McLennan (1983) to assess the degree of browsing on saplings and shrubs. This scale distinguishes: 0, no evidence of browsing; (1) slightly browsed (one or two branches browsed); (2)

Table 1 Forest characteristics of *Austrocedrus chilensis* study areas and effects of mortality on Isla Victoria, Parque Nacional Nahuel Huapi, Argentina

	Area			
	Pseudotsuga	Criollos	Larga	Redonda
Latitude (S)	40°54′	40°53′	40°53′	40°53′
Longitude (W)	71°32′	71°32′	71°33′	71°33′
Annual precipitation (mm)	1600–1800	1600–1800	1600–1800	1600–1800
Elevation (m asl)	800	825	800	850
Aspect	NE	NE	NE	NE
Basal area live[a] (%)	46.4	21.1	26.8	25.7
Basal area dead standing (%)	24.2	21.6	18.6	20.6
Basal area uprooted (%)	35.0	58.1	54.0	50.3
Basal area snapped (%)	6.2	5.4	7.4	5.3
Total basal area (m^2/ha)	62.6 (9.5)[a]	125 (11.1)	133.4 (11.2)	173 (14.9)
Age of live trees (years)	56 (4.6) $n^b = 14$	116 (5.3) $n = 9$	75 (9.9) $n = 13$	103 (9.5) $n = 13$
Dead tree age (year)	52 (4.2) $n = 11$	104 (6.1) $n = 12$	116 (11.5) $n = 14$	134 (5.6) $n = 15$
Mortality initiation	1980	1980–1990	1970	1970–1980
Year of first death recorded	1972	1965	1933	1969

[a] Values are means with standard errors in parentheses

[b] Number of sampled trees

moderately browsed (more than two branches browsed), and (3) heavily browsed (most branches browsed). Pellet groups were counted using a 10 m^2 circular plot placed in each study station. Degree of browsing and pellet group counts were used as an index of animal use (Mayle et al. 1999). The degree of site accessibility to deer was estimated by measuring the maximum height of logs and fallen branches, and by estimating their cover as was done in the understory plots.

Fallen tree-removal experiment

To evaluate the effects of fallen trees on deer–vegetation interactions, we performed a blocked sampling design at control areas (Criollos, Redonda, and Larga) and three nearby (<200 m away) areas from which all downed dead trees had been removed in 1994, 1997, and 1998, respectively (hereafter, removal treatment). There were two different control (non-removal) areas: (1) areas with more than two downed trees (hereafter, non-removal treatment), and (2) naturally open areas between fallen trees (hereafter, non-removal open treatment). Each treatment was sampled in stratified manner using fifteen 20 m^2 circular plots. Variables describing forest structure, understory abundance and composition, and animal use were recorded in a similar fashion to those described at the beginning of this section.

Data analyses

We investigated the interaction among forest mortality, deer use, and understory traits through multiple stepwise regression. One set of regression analyses was performed to determine the minimum set of variables related to forest mortality and understory traits that allow us to predict deer use (pellet group counts and degree of browsing as dependent variables). A second regression analysis determined the variables related to forest mortality and deer use that can explain the abundance of palatable and unpalatable shrubs species in the understory. Independent variables related to forest mortality were: (i) history: according to dendroecological data forest stands that were categorized as recent (1, death dates peaking in the 1980s) and old (2, death dates peaking in the 1970s), and (ii) severity: expressed as basal area of live, uprooted, standing dead and snapped trees, and cover of fallen branches. Variables related to understory traits were herb cover, tree sapling cover, and cover of unpalatable and palatable shrubs.

Effects of fallen tree removal on plant community and deer use were evaluated by ANOVA using areas as experimental units and triplets of log removal/log non-removal/non-removal open treatments as blocks. Differences in means between treatments were based on post-hoc tests. In all statistical analyses, counts (numbers of pellet groups) and measures (heights) were log-transformed, and proportions (understory cover) were arcsine-transformed when needed to achieve normality and homoscedasticity.

Results

Timing and severity of tree mortality

Growth release patterns in surviving trees and frequency patterns of death dates suggest differences in timing and severity of mortality occurred within the study area. Larga showed the longest and most uniform history of mortality with death dates and releases starting in the 1950s, peaking in the 1970s, and extending into the 1980s (Fig. 3). Redonda showed evidence of mortality starting mainly in the 1960s and peaking in the 1970s, while at Criollos, mortality started in the 1970s and peaked in the 1980s and 1990s. Similar to Criollos, but with less severity, Pseudotsuga had mortality starting in the 1970s and peaking in the 1980s (Fig. 3). At Criollos, 80% of the dated uprooting occurred in a relatively distinct period during the 1980s and 1990s. By contrast, uprooting during that same period accounted for 40% and 50% of downed trees at Redonda and Larga, respectively, thus suggesting a more gradual process of canopy collapse. During the 1990s, dead trees in massive mortality stands (Criollos, Redonda, and Larga) were mostly uprooted (Fig. 3). Ring width patterns of these uprooted trees indicated the existence of growth release events in a large percentage of trees (50, 75, and 100% at Larga, Criollos, and Redonda, respectively). This fact suggested that wind-induced uprooting occurred after canopy opening owing to mortality of dead standing trees and/or uprooting of neighbouring trees.

Criollos, Redonda, and Larga were on average the stands affected the longest and most severely by *mal del cipre´s* mortality and subsequent windthrow (Table 1). Around 25% of the basal area consisted of live trees, whereas 50–60% of the basal area consisted of downed, uprooted trees. By contrast, Pseudotsuga, which was the youngest stand (Table 1), suffered lower overall levels of mortality and subsequent tree fall with ca. 45% of tree basal area alive and ca. 35% of the basal area on the ground. Percentages of wind-snapped and standing dead trees were relatively uniform among stands (Table 1).

Predictors of deer use and shrub composition

The multiple regression analyses showed that deer use was positively related to the history of stand mortality (stands with older mortality are used more heavily) and negatively related to branch cover. Thirty-five percent of the variance in the number of deer pellets was explained by the history of stand mortality (+, $P < 0.01$) and fallen branch cover (−, $P < 0.01$) (model: $F = 6.44$; df = 4,48; $P = 0.0031$). Similarly, 32% of the variance in the degree of browsing on plants was explained by the history of stand mortality (+, $P < 0.05$) and fallen branch cover (−, $P < 0.05$) (model: $F = 2.99$; df = 7,45; $P = 0.011$). By contrast, no single vegetation variable significantly explained deer use.

Composition of understory vegetation was also explained mostly by history and severity of stand mortality. Fifty percent of the variance in cover of unpalatable shrub species was positively related to history of stand mortality (stands with older mortality have higher cover of unpalatable shrubs, $P < 0.001$), while the degree of browsing was negatively related to cover of unpalatable shrubs ($P < 0.05$) (model: $F = 9.38$; df = 5, 47; $P = 0.001$). Cover of palatable species was related only to basal area of uprooted trees, a measure of mortality severity ($P < 0.05$) (model: $F = 4.46$; df = 3, 49; $P = 0.00756$), explaining 21% of the variance in palatable species cover.

Effects of fallen trees on deer use and vegetation

As expected, uprooted basal area ($F = 112.8$, df = 2, $P < 0.001$, Table 2) and branch cover on the ground ($F = 37.16$, df = 2, $P = 0.001$) in the fallen tree removal treatment were lower than those found in the

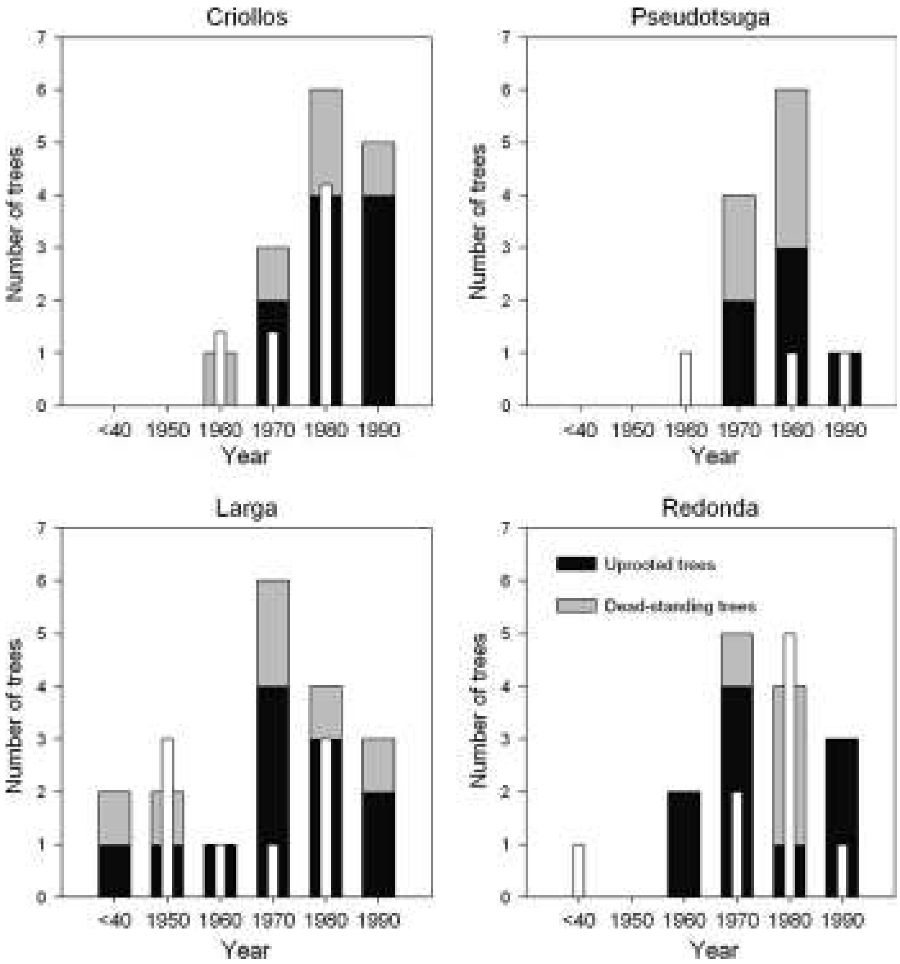

Fig. 3 Frequency of tree death dates by cause (wide bar) and frequency of live tree releases (narrow bar) at the study sites

non-removal treatment. In the treatment in which fallen trees had been removed and in the naturally open treatment, deer pellet number ($F = 75.1$, df = 2, $P < 0.001$) and browsing ($F = 23$, df = 2, $P = 0.002$, Table 2) were higher than in the adjacent treatment in which fallen trees had not been removed. Total shrub cover was similar among removal and non-removal treatments ($F = 3.99$, df = 2, $P = 0.079$). However, the proportion of palatable shrub species—such as *Aristotelia chilensis*, *Ribes magellanicum*,

Table 2 Mean (and SE) of different variables measured in fallen tree removal and non-removal treatments

	Uprooted basal area ($m^2/20\ m^2$)	Branch cover (%)	Number of pellet group	Browsing index	Palatable shrub cover (%)	Non-palatable shrub cover (%)	Herb cover (%)
Fallen tree removal treatment	0.03 (0.02) a	26.28 (2.82) a	6.31 (1.29) a	1.43 (0.11) a	6.00 (3.50) a	34.01 (7.85) a	40.8 (19.9) a
Non-removal treatment	0.63 (0.05) b	78.61 (4.94) b	0.11 (0.04) b	0.56 (0.13) b	50.84 (2.78) b	18.24 (5.5) b	19.56 (10.16) a
Naturally open treatment	0.15 (0.02) c	21.07 (3.82) a	5.67 (0.81) a	1.54 (0.06) a	3.12 (1.84) a	30.52 (7.74) a	62.52 (19.33) a

Different lowercase letters indicate significant differences among different treatments at $P < 0.05$ (ANOVA and post-hoc Tukey Tests). Statistical analyses were conducted on the transformed values of variables, but original values are shown in the table

Maytenus boaria—was significantly higher in the non-removal treatment compared with the removal treatment and the naturally open treatment ($F = 41.53$, df = 2, $P = 0.001$). Conversely, cover by unpalatable shrubs—such as *Berberis* spp.—was 15.8% and 12.3% higher in the removal treatment and naturally open treatment, respectively, than in non-removal treatment ($F = 38.75$, df = 2, $P = 0.001$, see Appendix). No significant differences were found in total herb cover among the three treatments ($F = 1.73$, df = 2, $P = 0.25$, Table 2).

Discussion

Timing and severity of tree mortality

Austrocedrus areas with moderate mortality (ca. 65% of basal area dead) are relatively open, young, and accessible forest with most trees alive or standing but dead. In contrast, where mortality exceeds 75% of basal area, many trees lie on the ground forming an inaccessible tangled mass of logs and branches several meters high. Mortality levels in this study are similar to those found by Loguercio and Rajchenberg (2004) but higher than those found by La Manna et al. (2006) for forests with similar stand structure in southwestern areas of Río Negro and in the nearby province of Chubut.

Two temporal factors are important in the interaction between mortality and herbivores that may affect plant communities: (1) the timing of canopy opening (i.e., increase in light levels to understory plants) and (2) the timing of canopy collapse (i.e., decreasing accessibility to herbivores). These stages do not necessarily coincide. Dendroecological techniques allowed us to differentiate both processes. In our system, most trees were attacked by root fungi, lost foliage, and remained standing until root rot made the trunk unstable and the tree fell. This was evidenced in ring growth patterns of downed trees by a strong suppression before and at the time of death. Additional unattacked trees fell because the lack of surrounding canopy trees made them susceptible to wind-throw. This was evidenced in downed trees by strong radial growth release (suggesting that trees were not infected) before sudden death by snapping or uprooting. In both cases, canopy opening may not result in understory blocking for several years or even one or two decades. This time lag between canopy opening and understory physical blocking may have an impact on understory composition. During early phases of the decline process, the understory receives light but there is also substantial herbivore pressure. Therefore shade-intolerant plants that are resistant to herbivores or are dispersed by them may benefit. In our system, such as species may be *Uncinia* sp., which dominated recently dead forest, is light-demanding, and is dispersed in deer fur. The initial density of the stand may have been important determinants of how fast the canopy collapsed after mortality began. In our study, in all dense areas (Criollos, Larga, and Redonda) uprooting has been the main cause of mortality process for the past three decades. The death dates in our study are similar to those registered by Cali (1996), who worked in two mainland *Austrocedrus* stands close to our study sites.

Interactive effects of forest mortality and deer use on plant communities

Our results indicate that fallen logs with a high density of branches strongly limited deer accessibility to certain microsites and created natural exclosures and safe sites for palatable plant establishment and growth. Pulido et al. (2000) found a similar relationship between presence of a native camelid, *Lama guanicoe* (guanaco), and slash in a managed *Nothofagus pumilio* forest in Tierra del Fuego (southern Argentina). Rebertus et al. (1997) found that browsing by guanaco was negatively correlated to the blowdown area of *N. pumilio* forest in Tierra del Fuego. In blowdown areas above 5 hectares, guanaco browsing was restricted to the periphery. Similarly, Cavieres and Fajardo (2005) found in old-growth stands of *N. pumilio* that guanaco damage was higher in small gaps than in the bigger ones. On the other hand, postfire coarse woody debris has been found to provide *Populus tremuloides* refugia from red deer browsing in Yellowstone National Park (Ripple and Larsen 2001). On the contrary, Bergquist and Örlander (1998) found that *Picea abies* browsed by moose did not vary in sites with different amounts of slash on the forest floor. Similarly, Kupferschmid and Bugmann (2005) found that fallen trees do not constitute a barrier to chamois (*Rupicapra rupicapra*) browsing *Picea abies* saplings. According to Thomas et al. (1979), a depth of dead and fallen material higher than 0.6 m substantially limits deer use of the area, and when the depth is high enough to make deer jump, the energetic cost of locomotion increases dramatically (Hanley et al. 1989; Nyberg 1990). Another complementary explanation for deer to avoid areas with deep slash is that they would not be able to escape easily if a predator does attack (White et al. 2003).

In our study, the negative relationship between the amount of fallen logs and the deer use was clearly manifested when slash was removed. The number of deer pellet groups found where slash had been removed was six times the number found in control areas. As a result of this heavier use, after only 4 years of the treatment, understory composition changed dramatically toward more unpalatable and browse-resistant species in the slash-removal treatments.

The positive relationship between deer use and time since peak mortality suggests that with time, fallen trees lose decomposing branches, and accessibility increases. In the early stages, shrubs would be not abundant except for *Aristotelia chilensis*, a shade-intolerant, tall shrub (Muñoz and González 2006) that is highly palatable and consumed by deer (Anziano 1962; Veblen et al. 1989; Relva and Veblen 1998; Relva and Caldiz 1998). In areas with recent or severe mortality, *A. chilensis* was observed growing between logs and fallen branches. This spatially aggregated distribution in herbivore-free refuges (i.e. safe sites where individuals grow and reproduce successfully, far from the browsing range of the herbivores) located in grazing areas was also observed by Vázquez (2002a), who also found that this type of distribution influenced the mechanisms of pollination of this species. Positive association between certain species of plants with coarse debris has been noted in other forest systems in which windstorms were generally predominant and produced great amounts of dead material on the forest floor (Allan et al. 1997; Peterson and Pickett 2000; de Chantal and Ganström 2007). However, the strong positive relationship between *A. chilensis* and fallen branches could additionally be a response to improved recruitment conditions, as shown in other species (Schreiner et al. 1996). In areas with the oldest mortality (Redonda and Larga) and in microsites from which logs had been removed, deer use increased, and shrub composition changed toward less palatable species or browse-resistant ones such as *Berberis* spp. Both *B. buxifolia* and *B. darwinii*, which are common in *Austrocedrus* forests, are dominant in intensely grazed areas (Rebertus et al. 1997; Vázquez 2002b; Gallopin et al. 2005). *Berberis* spp. and other spiny shrubs may act as nurse plants of other species, by physically protecting more palatable plants from herbivores (De Pietri 1992) and/or improving abiotic conditions to facilitate establishment and growth of tree seedlings (Kitzberger et al. 2000b). In our study site, we have found no saplings of *Austrocedrus* in recently and severely disturbed forest. This could be because of the high cover of light-demanding herbs, *Uncinia* sp. and *Digitalis purpurea*, in early post-disturbance stages that could be negatively affecting tree seedling recruitment or due to low seed production by overmature trees. By contrast, in areas with less severe mortality, *Austrocedrus* seedlings and saplings are a dominant component of the understory (see Appendix). Because *Austrocedrus* is a shade-intolerant species, the canopy opening produced by less severe mortality probably explains this abundant tree regeneration despite heavy use of canopy gaps by deer (Veblen et al. 1989; Relva and Veblen 1998).

The spatially and temporally heterogeneous nature of forest mortality interacting with large herbivores may shape complex mosaics of vegetation. Prediction of plant community composition and structure should move forward from approaches that emphasize disturbances modifying abiotic resources for plant regeneration or plant–animal interactions toward spatially explicit approaches that integrate plant performance and animal behaviour within the context of a dynamic forest landscape.

This study underpins the importance of maintaining snags and large woody debris for the role in providing safe sites for tree and understory regeneration, a management policy that should also extend to disturbed landscapes where salvage logging is a routine procedure.

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Appendix

Mean cover (%) and standard error of vascular species recorded in fifteen 100 m^2 plots in the study areas

	Area			
	Criollos	Pseudotsuga	Larga	Redonda
Tree species				
Austrocedrus chilensis		2.83 (1.31)		
Lomatia hirsuta		0.68 (0.29)		1.69 (1.06)
Luma apiculata	1.5 (1)	1.69 (0.99)	1.87 (0.99)	16.79 (5.66)
Maytenus boaria	0.01 (0.01)	0.01 (0.01)		0.01 (0.01)
Nothofagus dombeyi	0.17 (0.17)	1.69 (0.99)		1.08 (1.07)
Pseudotsuga menziesii[a]		1.34 (0.33)		
Shrub species				
Aristotelia chilensis	6.34 (2.68)	0.35 (0.23)	3.21 (2.47)	4.14 (1.60)
Azara lanceolata		0.01 (0.01)		0.01 (0.01)
Berberis darwinii	2.51 (0.94)	3.2 (1.27)	39.5 (7.47)	20.36 (5.73)
Budleja globosa	0.18 (0.17)	0.01 (0.01)		0.01 (0.01)
Colletia hystrix		0.18 (0.17)		0.02 (0.01)
Gaultheria spp.		2.67 (2.49)		0.54 (0.28)
Maytenus chubutensis		0.03 (0.01)		0.19 (0.18)
Ribes magellanicum	0.36 (0.22)	0.21 (0.18)	0.17 (0.17)	0.57 (0.28)
Rosa rubiginosa[a]				0.01 (0.01)
Schinus patagonicus	0.01 (0.01)	4.36 (1.45)		5.56 (1.68)
Herb species				
Acaena ovalifolia			0.01 (0.01)	0.01 (0.01)
Adiantum chilense				0.01 (0.01)
Alstroemeria aurea		0.01 (0.01)		0.01 (0.01)
Blechnum spp.	0.17 (0.17)			
Carex spp.		0.01 (0.01)		0.01 (0.01)
Cynanchum diemii	0.53 (0.26)	3.67 (1.22)		0.54 (0.28)
Cynoglossum creticum[a]	2.51 (1.33)	1.38 (1.00)	15.51 (4.32)	1.27 (1.07)
Digitalis purpurea[a]	30.17 (6.76)		13.01 (3.67)	7.16 (2.78)
Galium aparine[a]		0.34 (0.23)		0.21 (0.18)
Vicia nigricans		0.02 (0.01)	0.01 (0.01)	0.01 (0.01)
Mutisia spp.	1 (1)	0.045 (0.01)		2.87 (2.67)
Rumex acetosella[a]	0.02 (0.01)		0.01 (0.01)	0.2 (0.18)
Rumohra adiantiformis				0.01 (0.01)
Uncinia spp.	67.83 (6.8)	1.53 (1.00)	3.02 (1.29)	33.93 (6.74)
Grasses	0.01 (0.01)			

[a] Denotes exotic species

References

Allan C, Stewart G, Allen R (1997) Long term influences of deer browsing on forest health and conservation values of the Kaweka Range. Final Report Lincoln University and WWF, Canterbury

Allen RB, McLennan MJ (1983) Indigenous forest survey manual: two inventory methods. New Zealand For Serv FRI Bulletin no. 48

Anziano AF (1962) Acción de los animales sobre la flora. Anales de Parques Nacionales, Administración de Parques Nacionales. Tomo IX:107–112

Barros VR, Cordon VH, Moyano C, Mendez R, Forquera JC, Pizzio O (1988) Carta de precipitación de la zona oeste de las provincias de Río Negro y Neuquén. Primera contribución (1972–1981). Facultad de Ciencias Agrarias. Universidad Nacional del Comahue, Cinco Saltos

Barrios Garcia Moar MN (2005) Patrones de daño, uso actual y tendencia histórica de la abundancia de ciervos introducidos en bosques nativos de Isla Victoria, Patagonia, Argentina. Licenciate Dissertation. Universidad Nacional del Comahue, Bariloche, Argentina

Bergquist J, Örlander G (1998) Browsing damage by roe deer on Norway spruce seedlings planted on clearcuts of different ages. 1. Effect of slash removal, vegetation development, and roe deer density. For Ecol Manage 105:283–293

Cali SG (1996) Austrocedrus: estudio de los anillos de crecimiento y su relación con la dinámica del "mal del ciprés" en el Parque Nacional Nahuel Huapi, Argentina. Licenciate Dissertation. Universidad Nacional del Comahue, Bariloche, Argentina

Cavieres LA, Fajardo A (2005) Browsing by guanaco (*Lama guanicoe*) on *Nothofagus pumilio* forest gaps in Tierra del Fuego, Chile. For Ecol Manage 204:237–248

de Chantal M, Ganström A (2007) Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. For Ecol Manage 250(1):3–8

De Pietri DE (1992) Alien shrub in a National Park: can they help in the recovery of natural degraded forest? Biol Conserv 62:27–130. doi:10.1016/0006-3207(92)90933-E

Ezcurra C, Brion C (2005) Plantas del Nahuel Huapi. Catálogo de la Flora Vascular del Parque Nacional Nahuel Huapi, Argentina

Filip GM, Rosso PH (1999) Cypress mortality (mal del ciprés) in the Patagonia Andes: comparison with similar forest disease and declines in North America. Eur J Forest Pathol 29:89–96. doi:10.1046/j.1439-0329.1999.00133.x

Flueck WT, Smith-Flueck JA, Naumann CM (2003) The current distribution of red deer (*Cervus elaphus*) in southern Latin America. Z Jagdwiss 49:112–119. doi:10.1007/BF02190451

Gallopin GC, Martín CE, Mermoz MA (2005) Impacto de la ganadería en la cuenca del río Manso Superior. Parte I: Bosque de Ñire con Laura. Anales de Parques Nacionales, Administración de Parques Nacionales. Tomo XVII:9–36

Greslebin A, Hansen E (2006) Novedades sobre el mal del ciprés. Patagonia For 12(1):11–14

Hanley TAR, Robbins CT, Spalinger DE (1989) Forest habitats and the nutritional ecology of Sitka black-tailed deer: a research synthesis with implications for forest management. USDA For Serv Res Pap PNW-GTR-230

Havrylenko M, Rosso PH, Fontenla S (1989) *Austrocedrus chilensis*: contribución al estudio de su mortalidad en Argentina. Bosque 10(1):29–36

Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manage 60(4):695–713. doi:10.2307/3802368

Holmes R (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull 43:69–75

Jefferies RL, Klein D, Shaver GR (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71:193–206. doi:10.2307/3546267

Kitzberger T, Veblen T, Villalba R (2000a) Métodos dendroecológicos y sus aplicaciones en estudios de dinámica de bosques templados de Sudamérica. In: Roig FA (ed) Dendrocronología en América Latina. EDIUNC, Universidad de Cuyo, Mendoza, Argentina, pp 17–78

Kitzberger T, Steinaker D, Veblen T (2000b) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology 81(7):1914–1924

Koutché V (1942) Estación Forestal de Puerto Anchorena, Isla Victoria; su organización y trabajos. Ministerio de Agricultura, Dirección de Parques Nacionales, Buenos Aires, Argentina

Kupferschmid A, Bugmann H (2005) Effect of microsites, logs and ungulate browsing on *Picea abies* regeneration in a mountain forest. For Ecol Manage 205:251–265

La Manna L, Rajchenberg M (2004) The decline of *Austrocedrus chilensis* in Patagonia, Argentina: soil features as predisposing factors. For Ecol Manage 190:345–357

La Manna L, Bava J, Collantes M, Rajchenberg M (2006) Características estructurales de los bosques de *Austrocedrus chilensis* afectados por "mal del ciprés" en Patagonia, Argentina. Bosque 27(2):135–145

La Manna L, Matteucci SD, Kitzberger T (2008) Abiotic factors related to the incidence of the *Austrocedrus chilensis* disease syndrome at a landscape scale. For Ecol Manage 256:1087–1095

Loguercio G, Rajchenberg M (2004) El "mal del ciprés" y la silvicultura del ciprés de la cordillera. In: Arturi MF, Frangi JL, Goya JF (eds) Ecología y Manejo de los Bosques de Argentina. EDULP, Universidad Nacional de La Plata, La Plata, Argentina

Mayle BA, Peace AJ, Gill RMA (1999) How many deer? A field guide to estimating deer population size. Field Book 18. Forestry Commission, Edinburgh

Muñoz A, González M (2006) *Aristotelia chilensis* (Mol) Stuntz. In: Donoso C (ed) Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología, Cuneo Ediciones, pp 166–172

Nyberg JB (1990) Interaction of timber management with deer and elk. In: Nyberg JB, Janz DW (eds) Deer and elk habitat as in coastal forests of Southern British Columbia. BC Ministry of Forests and Ministry of Environment, Special Report 5, pp 99–131

Peterson CJ, Pickett STA (2000) Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos 90:489–500. doi:10.1034/j.1600-0706.2000.900307.x

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando

Pulido FJ, Díaz B, Martínez Pastur G (2000) Incidencia del ramoneo del guanaco (*Lama guanicoe* Müller) sobre la regeneración temprana en bosques de lenga (*Nothofagus pumilio* (Poepp et Endl) Krasser) de Tierra del Fuego, Argentina. Investigación Agraria. Sistemas Recursos Forestales 9(2):381–394

Rebertus AJ, Kitzberger T, Veblen T, Roovers LM (1997) Blowdown history and landscape patterns in the Andes of Tierra del Fuego, Argentina. Ecology 78:678–692

Relva MA, Caldiz M (1998) Composición estacional de la dieta de ciervos exóticos en Isla Victoria, P.N. Nahuel Huapi, Argentina. Gayana (Zool) 62(2):101–108

Relva MA, Veblen T (1998) Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. For Ecol Manage 108:27–40

Ripple WJ, Larsen EJ (2001) The role of postfire coarse woody debris in Aspen regeneration. West J Appl For 16(2):61–64

Russell FL, Zippin DB, Fowler NL (2001) Effects of White-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. Am Midl Nat 146:1–26. doi:10.1674/0003-0031(2001)146[0001:EOWTDO]2.0.CO;2

Schreiner EG, Krueger KA, Happe PJ, Houston DB (1996) Understory patch dynamics and ungulate herbivory in old-growth forest of Olympic National Park, Washington. Can J Res 26:255–265. doi:10.1139/x26-029

Simberloff D, Relva MA, Nuñez M (2003) Introduced species and management of a *Nothofagus*/*Austrocedrus* forest. Environ Manage 31:263–275. doi:10.1007/s00267-002-2794-4

Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. The University of Chicago Press, Chicago

Stuth JW (1991) Foraging behaviour. In: Heitschmidt RK, Stuth JW (eds) Grazing management. An ecological perspective. Timber Press, Oregon, pp 65–83

Thomas JW, Black H, Scherzinger RJ, Pedersen RJ (1979) Deer and Elk. In: Thomas JW (ed) Wildlife habitats in managed forest. The Blue Mountains of Oregon and Washington. USDA For Serv Agriculture Handbook 553, pp 104–147

Vázquez D (2002a) Interaction among introduced ungulate, plants and pollinators: a field study in the temperate forest of Southern Andes. PhD Dissertation, University of Tennessee, Knoxville, Usa

Vázquez D (2002b) Multiple effects of introduced mammalian herbivores in a temperate forest. Biol Invasions 4:175–191. doi:10.1023/A:1020522923905

Veblen TT, Lorenz DC (1987) Post-fire stand development of *Austrocedrus -Nothofagus* forest in northern Patagonia. Vegetatio 71:113–126

Veblen T, Mermoz M, Martín C, Ramilo E (1989) Effects of exotic deer on forest regeneration and composition in northern Patagonia. J Appl Ecol 26:711–724. doi:10.2307/2404095

White CA, Feller MC, Bayley S (2003) Predation risk and the functional response of elk-aspen herbivory. For Ecol Manage 181:77–97

Wisdom MJ, Vavra M, Boyd JM, Hemstrom MA, Ager AA, Johnson BK (2006) Understanding ungulate herbivory-episodic disturbances effects on vegetation dynamics: knowledge gaps and management needs. Wildl Soc Bull 34(2):283–292. doi:10.2193/0091-7648(2006)34[283:UUHDEO]2.0.CO;2

Tree species richness and composition 15 years after strip clear-cutting in the Peruvian Amazon

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Abstract Although strip clear-cutting has a long history of use in the temperate zone, it was only recently introduced for timber extraction in tropical rain forests, where it is known as the Palcazú Forest Management System. In this system heterogeneous tropical forests are managed for native gap-dependent timber species by simulating gap dynamics through clear-cutting long, narrow strips every 40 years. As part of an assessment of the sustainability of this system, we evaluated the recovery of tree basal area, species richness, and composition after 15 years of regeneration on two strips (30 × 150 m) clear-cut in 1989 in Jenaro Herrera, Peru. Timber stocking and the effects of silvicultural thinning were assessed in both strips. The strips recovered 58–73% of their original basal area and 45–68% of their original tree species richness. Although both strips recovered more than 50% of their original composition, commercial species had lower basal areas and lower densities than in the forest before the clearing. Pioneer species with high basal areas remained dominant 15 years after the cutting. Silvicultural thinning in 1996 reduced the abundance of pioneer species in both strips, and increased the abundance of commercial species in one of the strips. Half of one strip was harvested by deferment-cut (only commercial trees >30 cm dbh and "other" species >5 cm dbh were cut); regeneration here had greater abundance of commercial species and lower abundance of pioneer species. The low stocking of commercial trees challenges the sustainability claims for this forest management system.

Keywords Natural forest management · Palcazú forest management model · Rarefaction · Sustainable management · Tropical rain forest

Introduction

Strip-clear cutting has extensively been used in the temperate zone for forest management (Thornton 1957; Smith 1986; Heitzman et al. 1999; Allison et al. 2003); Tosi (1982) and Hartshorn (1989a, 1995) introduced this system to manage tropical rainforests for timber extraction. The first implementation was in the Palcazú Valley in Peru, as part of a joint United States Agency for International Development (AID) and Peru Instituto Nacional de Desarrollo (INADE) development project (Tosi 1982; Hartshorn 1989a). As a result, Tosi's (1982) and Hartshorn's (1989a, 1995) strip clear-cutting system is also known as the Palcazú Forest Management System. In the Palcazú Forest Management System heterogeneous tropical

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forests are managed for native gap-dependent timber species by simulating gap dynamics through clear-cutting long, narrow strips (Hartshorn 1989a, 1995). In this system, upland forest is clear-cut into 30–40 m wide strips with a rotation of 30 to 40 years. The length of the strip varies and depends upon topography (Hartshorn 1989a).

In the Palcazú system, timber, regardless of species, is harvested and used locally (sawnwood, preserved roundwood, and charcoal) or sold to attain maximum value from the strips (Hartshorn 1989a; Gorchov et al. 1993). Animal traction is used to reduce soil compaction (Hartshorn 1989a; Gorchov et al. 1993). Natural regeneration of seeds and stump sprouts is permitted (Gorchov et al. 1993). Silvicultural treatments may also be applied in the regenerating strips to promote growth of desired species (Dolanc et al. 2003).

Initially, the Palcazú system was thought to be a sustainable alternative for timber extraction compared to uncontrolled logging or selective logging. Tosi (1982) and Hartshorn (1989a) predicted that non-commercial pioneer species would not regenerate well in this system because the strips were too narrow to allow sufficient sunlight, and commercial species would be well represented in the regeneration. Many tropical timber species are gap-dependent (Swaine and Whitmore 1988), and such gap-dependent species have rapid height and diameter growth (Lieberman et al. 1985).

Several studies, however, have questioned the sustainability of the Palcazú system (Simeone 1990; Cornejo and Gorchov 1993; Gram 1997; Southgate 1998). Rapid early regeneration with high tree species richness suggested that this system is ecologically sustainable (Hartshorn 1989a), but Gorchov et al. (1993) found that after one year of regeneration the composition of strips was mainly dominated by pioneer species of low commercial value. Thinning enhanced the growth rates of commercial stems 11 years after the cutting, but they still averaged <0.3 cm/year in diameter growth (Dolanc et al. 2003). Clearly, data are still needed for later stages of regeneration.

We studied tree regeneration after 15 years on two strips clear-cut in 1989 in the Peruvian Amazon in order to generate the first assessment of the ecological sustainability of the strip clear-cutting system. To assess the ecological sustainability of a forest management system one ought to assess the structural characteristics of a developing forest (basal area and biomass), community characteristics (species richness and composition), and functional characteristics (nutrient cycling and primary productivity). In this study, we focused on the recovery of tree basal area, species richness, and species composition 15 years after the cutting with values prior to the cutting. The criterion used to assess the ecological sustainability of this system was to evaluate whether these community descriptors had recovered to approximate pre-clearing levels. This criterion is based on the assumptions of sustainability for natural forest management; i.e., sustained timber yields can be produced while maintaining a high diversity (Bawa and Seidler 1998). A second objective was to determine stocking of commercial species in the strips 15 years after the cutting to assess timber regeneration in this system. A third objective was to determine if silvicultural thinning and harvesting by deferment-cut improved the recovery of structural and community descriptors in the strips.

Clear-cutting is the least severe anthropogenic disturbance when compared to cutting and burning for pasture or plantation establishment, and bulldozing for road building or development (Uhl et al. 1982). Thus, clear-cut stands tend to have a rapid increase in species richness a few years after logging (Hartshorn 1989a; Faber-Landgendoen 1992) and a faster richness recovery than stands cut and burned for pasture or bulldozed (Uhl et al. 1982). However, composition usually takes longer to recover (Finegan 1996; Guariguata and Ostetarg 2001). Thus, we expected greater recovery of basal area and species richness than of species composition. We also expected silvicultural thinning and deferment-cutting in the strips to improve the recovery of all of these structural and community descriptors.

Methods

Study site

This study took place at the Centro de Investigaciones Jenaro Herrera (CIJH S 4°53.95′ W 73°39.04′), 200 km south of Iquitos, Loreto, Peru. Mean annual temperature is 26.5°C and mean annual precipitation is 2521 mm (Spichiger et al. 1989). A relatively dry period occurs from June to August, but rainfall highly varies each month of the year (Ascorra et al. 1993; Rondon 2008). Soils are sandy-loam and the vegetation is considered lowland tropical rainforest on high terrace

(Spichiger et al. 1989). The families with highest densities on high terrace at CIJH are Sapotaceae, Leguminosae, Lecythidaceae, Chrysobalanaceae, Lauraceae, and Myristicaceae (Spichiger et al. 1996).

History of clear-cut strips in CIJH

Two 30 × 150 m strips (Fig. 1), 150 m apart, were clear-cut in 1989 in primary high terrace tropical rain forest at CIJH. The area had been selectively logged 15–20 years prior, but the forest maintained an intact canopy. The long axis of each strip was oriented north–south. Strip 1 was cleared in April–May, 1989 and strip 2 in October–November, 1989. Lianas and shrubs were cut before tree felling. Most trees >5 cm in diameter at breast height (dbh) were felled in each strip using directional felling to ensure that the trees cut landed in the strips (Gorchov et al. 1993). A few large trees (>28 cm dbh, $N = 5$ in strip 1 and $N = 13$ in strip 2) leaning out of the strips were not cut to avoid damage to the surrounding forest (Cornejo and Gorchov 1993). An experimental deferment-cut treatment cut was implemented in the south half of strip 2 (plots 1–10). In the deferment-cut treatment, only commercial trees ≥30 cm dbh and “other” species >5 cm dbh were harvested in 1989; the smaller trees of commercial species were left uncut ($n = 56$, 5–28 cm dbh) to grow for the next harvest (Cornejo and Gorchov 1993). All timber harvested was locally used or carried off site. A complete survey of the trees (≥5 cm dbh) was made during the 1989 felling for both strips (Cornejo and Gorchov 1993).

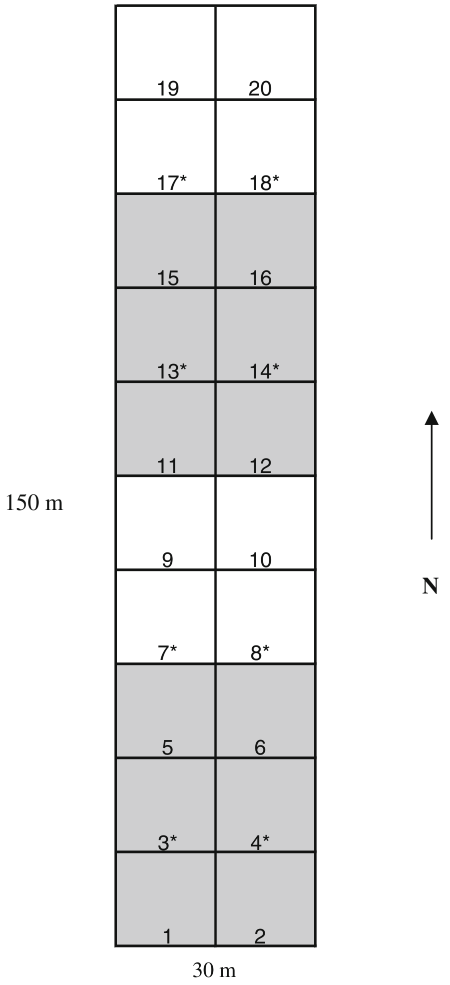

Fig. 1 Schematic of each of the two strips (30 × 150 m) at Centro de Investigaciones Jenaro Herrera, Peru. Twenty plots were marked in each strip (15 × 15 m). Plots thinned in 1996 are shaded. Plots with asterisk (*) were censused regularly for all saplings ≥2 m. Advanced regeneration and stump sprouts were censused throughout the strip. In strip 2, in the south half (plots 1 to 10), 56 commercial tree species (5–28 cm dbh) were left uncut as part of a deferment-cut treatment. Figure modified from Dolanc et al. (2003)

Each strip was divided into 20 15 × 15 m plots (Fig. 1), in which all stump sprouts and survivors (saplings not cut <5 cm dbh in 1989) were identified and tagged. Recruits (trees >2-m tall) were identified and censused on 8 out of the 20 plots in each strip. Censuses took place once a year during 1990–1994, 1996, and 2000. In addition, an experimental silvicultural thinning treatment took place in March 1996; pioneer trees (all *Cecropia* and trees <10-m tall of the genus *Alchornea* and the family Melastomataceae) were girdled by machete in portions of each strip (Fig. 1). Censuses carried out May–June, 2004 in strip 1 and June–July, 2005 in strip 2 provide the ‘post-clearing’ data analyzed here.

Tree identification

Tree identification was done in the field using Gentry (1993) and Spichiger et al. (1989, 1990). Voucher specimens were deposited at the CIJH herbarium, AMAZ, and MU. Voucher specimens of difficult taxa were brought for comparison to Missouri Botanical Garden (MOBOT). Several taxa were not identified to the species level in the pre-clearing (1989) period; identification for these taxa was only done to genus or family level. For analysis purposes, trees identified to the same genus or family, without species determination, were considered as one morphospecies. Some *Cecropia* species were difficult to identify to the species level, and they were grouped as one morphospecies for all richness comparisons.

Data analysis

Comparisons of tree basal area (BA), species richness, composition, and timber stocking were evaluated in strip 1 in 1989 (prior to cutting) vs. 2004, 15 years after cutting, and in strip 2, in 1989 (prior to the cutting) vs. 2005, 15 ½ years after cutting. In strip 2, all comparisons of community descriptors between the pre- and post-clearing period were carried out separately for the clear-cut and deferment-cut portions. We are aware that forests are not stable and community descriptors vary over time. In this study, we used the pre-clearing level (1989) as a reference of mature growth. All tree species richness and composition comparisons were done for trees >7.5 cm dbh since both strips had complete datasets per plot for these trees. Additional comparisons of richness and composition of trees ≥5 cm dbh between the post- and pre-clearing censuses were carried out for strip 2 (Rondon 2008), but these did not differ qualitatively from trees >7.5 cm dbh.

The effect of thinning and deferment-cut on structural and community descriptors

Before comparing structural and community descriptors in the pre- versus the post-clearing period, we tested the effect of silvicultural thinning in the post-clearing period in order to determine whether it was appropriate to pool thinned and unthinned plots. In strip 1, we used SAS proc GLM with thinning as a fixed factor and plots as replicates. For strip 2, we used a two-way ANOVA with two fixed factors, thinning and felling treatment (clear-cut versus deferment-cut), and their interaction. All analysis were done using SAS version 9.1, with $\alpha = 0.05$; ANOVA tables are reported in Rondon (2008). Statistical findings should be interpreted with caution since the 15 × 15 m plots within each strip were not independent.

Structural and community descriptors

Basal area (BA, m^2/ha) was calculated for trees >10 cm dbh for each strip at pre-clearing, one year after the clearing (1990), and 15 years post-clearing. The effect of thinning and deferment-cut was tested on per plot BA (m^2/plot). Calculations of BA are in Rondon (2008).

To compare tree species richness between the pre- and post-clearing censuses at equal sample sizes, sample-based rarefaction curves were obtained from EstimateS 7.5 (Colwell 2005). The 15 × 15 m plots were used as subsamples in each strip. Separate rarefaction curves were constructed for the clear-cut and deferment-cut portions in strip 2. Before constructing the rarefactions for the two different censuses, the effect of thinning and deferment-cut on tree species density (no. of species/plot) was tested using the post-clearing censuses of the strips.

Tree composition comparisons were done at the genus level because species identification may not have been consistent between censuses. Since the classic Sorensen index is sensitive to sample size and assemblages with numerous rare species (Chao et al. 2005), the abundance-based Sorensen index (*L*) was used to assess compositional similarity between censuses in the strips. Using EstimateS 7.5 (Colwell 2005), we calculated L, $L = 2UV/(U+V)$, where U and V are the total relative abundances of the shared species in samples 1 and 2 (Chao et al. 2005).

After determining if thinning and deferment-cut had an effect on L calculated between pre- and post-clearing censuses for each 15 × 15 m plots in the strips, we pooled the data for each strip (keeping clear-cut and deferment-cut halves of strip 2 separate) to assess the compositional change of the strips between censuses. In strip 1, L was recalculated for the entire strip between pre- and post- censuses ($N = 1$). In strip 2, L was recalculated separately for the deferment-cut ($N = 1$) and clear-cut ($N = 1$) portions of the strip. These values were compared with L between two mature forest stands: strip 1 and strip 2, both before the clearing (1989).

To calculate the relative abundances and basal area of commercial and pioneer species, trees >7.5 cm dbh in the strips were classified as commercial, pioneer, and "other" species (Table 1). Commercial species were those in genera valued for sawnwood at international and local markets based on data from the International Tropical Timber Organization (ITTO) from 1997 to 2005 (ITTO 1997–2005) and studies in the Peruvian Amazon (Peters et al. 1989; Pinedo-Vasquez et al. 1990). The list did not include species valued for roundwood or non-timber forest products.

Table 1 Commercial and pioneer taxa occurring in censused plots at CIJH with sources for commercial taxa

Commercial	Source	Commercial	Source
Annonaceae		Meliaceae	
Duguetia	2	Guarea	2, 3
Guatteria	2	Trichilia	2
Xylopia	2	Moraceae	
Apocynaceae		Brosimum	1, 2
Aspidosperma	1, 2	Clarisia	3
Macoubea	2	Myristicaceae	
Boraginaceae		Iryanthera	1, 2, 3
Cordia	1	Osteophloeum	2
Bignoniaceae		Virola	1, 2, 3
Tabebuia	1	Olacaceae	
Caryocaraceae		Heisteria	2
Caryocar	2	Sapotaceae	
Clusiaceae		Chrysophyllum	2
Calophyllum	2	Manilkara	1, 2
Combretaceae		Pouteria	2
Terminalia	1, 2	Simaroubaceae	
Fabaceae		Simarouba	1, 3
Dialium	2	Vochysiaceae	
Diplotropis	1	Vochysia	1
Hymenaea	1, 2	Erisma	1
Ormosia	1	*Pioneer*	
Parkia	2	Cecropiaceae	
Swartzia	2	Cecropia	
Lauraceae		Euphorbiaceae	
Aniba	2, 3	Alchornea	
Endlicheria	2, 3	Melastomataceae	
Licaria	3	All genera	
Mezilaurus	2		
Nectandra	1, 3		
Ocotea	1, 2, 3		
Persea	3		
Lecythidaceae			
Cariniana	1, 2		
Eschweilera	2		

Source: (1) ITTO 1997–2005; (2) Peters et al. 1989; (3) Pinedo-Vasquez et al. 1990

Taxa not appearing in commercial or pioneers were considered “others”. This table was modified from Dolanc et al. (2003)

We classified those taxa that made up the vast majority of pioneers in this system as “pioneer” species: the genera *Cecropia* (Cecropiaceae), *Alchornea* (Euphorbiaceae), and all genera in the Melastomataceae family (Dolanc et al. 2003). “Other” species were taxa that were not classified into one of the other two groups and taxa that were only identified to the family level ($N = 3$ morphospecies in strip 1 and $N = 8$ morphospecies in strip 2, both in 1989). “Other” species were a combination of fast growing species (e.g., *Inga*), successional species (e.g., *Protium*), and old growth species (e.g., *Mabea*). Since “other” species, grouped taxa of several life histories, this group was not statistically analyzed.

The relative abundance of commercial and pioneer species was calculated for each 15 × 15 m plot in both strips in the pre- and post-clearing censuses. The effect of thinning and deferment-cut was tested on the relative abundance of commercial species and pioneer species in the strips. Due to unequal variance of samples in testing the effect of thinning on commercial species in strip 1, additional analysis was done using Kruskal–Wallis test, a non-parametric test. This test did not differ qualitatively from the parametric analysis; thus, only the latter was reported here. For each strip, we used paired *t*-tests to determine whether the relative abundance of commercial and pioneer species for 15 × 15 m plots differed between censuses. We also calculated basal area of commercial, pioneer, and “other” species in both strips in the pre- and post-clearing censuses of each strip.

Stocking (no. of trees/ha) of commercial species was calculated for (1) small trees between 5 to 10 cm dbh, and (2) large trees >10 cm dbh, in the post- and pre-clearing censuses of each strip. We tested the effect of thinning and deferment-cut on the number of commercial stems per plot for each size class in the strips. To make timber stocking comparisons between censuses, for each size class the total number of stems/ha in the post-clearing period was calculated and compared to the pre-clearing period of each strip.

Results

After 15 years of regeneration, the advance regeneration (trees that survived the clearing in 1989) comprised 16 and 18% of the total tree regeneration (trees >5 cm dbh) of strips 1 and 2, respectively; stump sprouts comprised 3 to 6%, and recruits (apparently regenerating from seed) 81 to 76% (Table 2).

Table 2 Number of trees ≥5 cm dbh censused in both strips before the clearing (from Cornejo and Gorchov 1993) and after the clearing in 2004 for strip 1 and 2005 for strip 2 at CIJH, Peru

Categories	Strip 1	Strip 2
Pre-clearing (1989)		
No. of trees	662	619
No. of morphospecies	*248*	*228*
Post-clearing (2004–2005)		
Trees >5 cm dbh and not cut in 1989	3	52
Survivors (<5 cm dbh but >2 m tall in 1989)	131	108
Sprouts from stumps of trees ≥5 cm dbh in 1989	25	36
Recruits ≥5 cm dbh in 2004/2005	662	457
Total	821	653
No. of not identified taxa in the post-clearing	*1*	*2*
No. of species	*172*	*176*

Number of taxa is given in italics

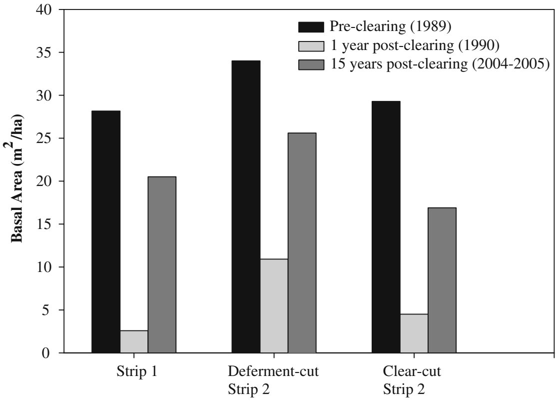

Fig. 2 Stand basal area (m^2/ha) of strip 1 and strip 2 before the clearing (1989), a year after the clearing (1990), and 15 years (2004) after the clearing (strip 1—2004, strip 2—2005)

Stand basal area

After 15 years of the first cutting, strip 1 and strip 2 recovered 73% (21 m^2/ha) and 58% (17 m^2/ha) of their original BA (Fig. 2), whereas the deferment-cut portion of strip 2 recovered 75% (26 m^2/ha) of its pre-clearing BA (Fig. 2). Silvicultural thinning did not affect 2004/2005 BA of trees >10 cm dbh in the strips (in strip 1, $F_{1,18} = 3.44$, $P = 0.080$, and in strip 2: $F_{1,16} = 0.55$, $P = 0.467$). In strip 2, neither felling (deferment-cut versus clear-cut, $F_{1,16} = 2.97$, $P = 0.104$) nor the interaction of thinning and felling ($F_{1,16} = 0.57$, $P = 0.461$) affected 2005 BA.

Tree species richness

Before clearing (1989), strip 1 had 422 trees >7.5 cm dbh, comprising 187 morphospecies (not all trees were identified to the species level in the pre-clearing censuses), whereas in 2004 there were 494 trees and 97 species. For strip 2, in 1989 there were 391 trees comprising 192 morphospecies compared to 410 trees and 109 species in 2005. Total number of trees and species ≥5 cm dbh found in 1989 and in the post-clearing censuses (2004/2005) of each strip are reported in Table 2.

In both strips silvicultural thinning did not affect the 2004/2005 tree species density (strip 1: $F_{1,18} = 1.85$, $P = 0.191$; strip 2: $F_{1,16} = 0.01$, $P = 0.926$); similarly, neither felling ($F_{1,16} = 0.32, P = 0.580$), nor the interaction of thinning and felling ($F_{1,16} = 0.08$, $P = 0.781$) affected the 2005 species density in strip 2. Fifteen years into the second rotation, strip 1 and the clear-cut portion of strip 2 recovered 47 and 45% of their pre-clearing richness, at equal sample sizes. The deferment-cut portions of strip 2 recovered 68% of its pre-clearing richness. Rarefaction curves for strip 1 and the clear-cut portion of strip 2 showed that species

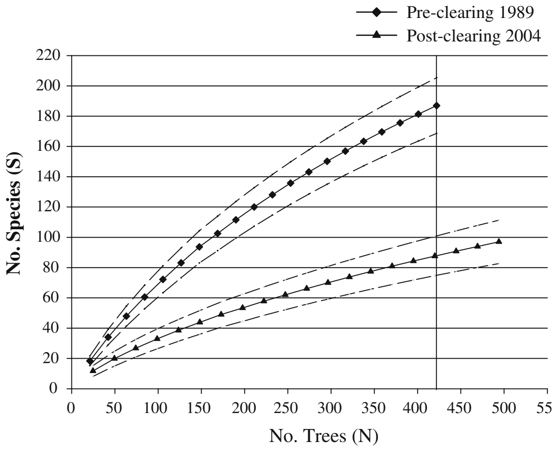

Fig. 3 Sample based rarefaction curves for 1989 ($N = 417$) and 2004 ($N = 494$) for trees >7.5 cm dbh in strip 1. Dotted lines are 95% CI. Number of samples was rescaled to number of individuals. Vertical line indicates species richness at equal sample sizes

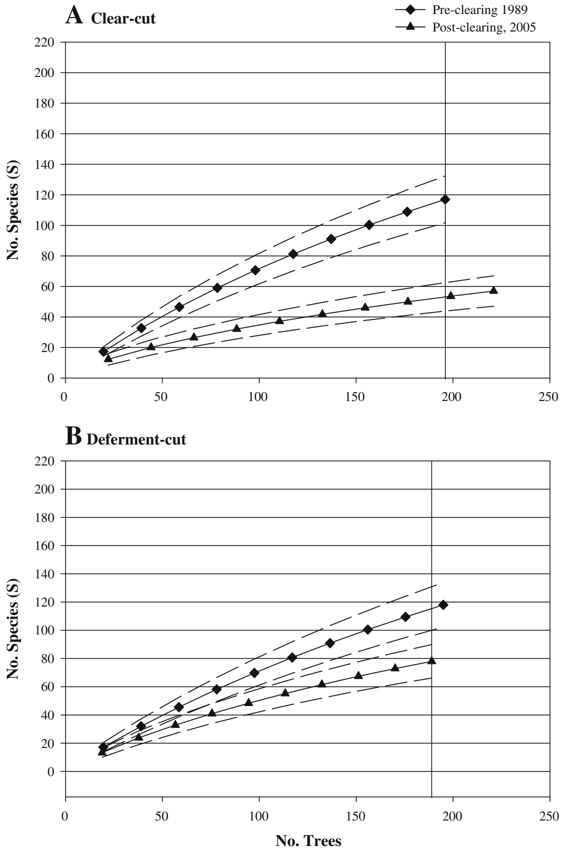

Fig. 4 Sample based rarefaction curves for the (**a**) clear-cut portion and (**b**) deferment-cut portion of strip 2 in 1989 and 2005 for trees >7.5 cm dbh. In the clear-cut portion, there were 196 trees in 1989 and 221 trees in 2005. In the deferment-cut portion, there were 195 trees in 1989 and 189 trees in 2005. Dotted lines are 95% CI. Number of samples was rescaled to number of individuals. Vertical line indicates species richness at equal sample sizes

richness was significantly lower in 2004/2005 than in 1989, as these curves diverged clearly and confidence intervals did not overlap (Figs. 3, 4a). In the deferment-cut portion of strip 2, rarefaction curves showed overlapping confidence intervals of species richness at smaller sample sizes ($N < 75$, Fig. 4b), but clearly diverged at greater sample sizes. Thus, species richness in the deferment-cut portion was also lower in 2005.

Tree composition

In 2004/2005, the strips had recovered more than 50% of the compositional similarity with the pre-clearing censuses. In strip 1, compositional similarity of 1989 vs. 2004 ($L = 0.828$) was slightly lower than compositional similarity of two mature stands ($L = 0.855$, Fig. 5). In strip 2, compositional similarity of 1989 vs. 2005 in the clear-cut ($L = 0.592$) and the deferment-cut portion ($L = 0.656$) was lower than the compositional similarity of two mature stands (Fig. 5). Thinning did not affect the compositional similarity of trees >7.5 cm dbh between 1989 and 2004 in strip 1 ($F_{1,18} = 3.78$, $P = 0.068$) or in strip 2 ($F_{1,16} = 0.39$, $P = 0.542$). In strip 2, neither felling treatment ($F_{1,16} = 1.03$, $P = 0.324$) nor the interaction of felling and thinning ($F_{1,16} = 0.72$, $P = 0.408$) significantly affected the compositional similarity between 1989 and 2005.

Commercial species

The relative abundance of commercial species was lower in 2004/2005 than in 1989 in strip 1 (thinned plots: $t = 6.44$, $P < 0.01$; unthinned plots: $t = 7.99$, $P < 0.01$), the clear-cut portions of strip 2 ($t = 5.83$, $P < 0.001$), and deferment-cut portions of strip 2 ($t = 3.56$, $P < 0.01$) (Fig. 6a). Strip 1 and the clear-cut portion of strip 2 recovered 25 and 43%, respectively, of the relative abundance of commercial species in the pre-clearing censuses, whereas the deferment cut portions of strip 2 recovered 67%.

Silvicultural thinning tripled the relative abundance of commercial species in one of the strips in 2004 ($F_{1,18} = 6.29$, $P = 0.022$). However, thinning did not significantly affect the relative abundance of commercial species in strip 2 ($F_{1,16} = 2.52$, $P = 0.132$). In strip 2, deferment-cut plots almost doubled the relative abundance of commercial species found in clear-cut plots ($F_{1,16} = 6.52$, $P = 0.021$), but the interaction of thinning and felling treatment ($F_{1,16} = 0.40$, $P = 0.534$) did not have an effect. In 1989, the BA of commercial species in strip 1 and the clear-cut portion of strip 2 were both about 14 m^2/ha, and in the deferment-cut portion of strip 2 was 18 m^2/ha. In 2004/2005 the BA of commercial species was 2 m^2/ha in strip 1 and 3 m^2/ha in the clear-cut portion of strip 2, 14 to 21% of their 1989 BA, whereas in the deferment-cut portion of strip 2 BA for these species was 6 m^2/ha, 33% of its 1989 BA (Fig. 7).

Pioneer species

Pioneer species were still abundant in 2004/2005, 65 and 62% of all trees (>7.5 cm dbh) belonged to

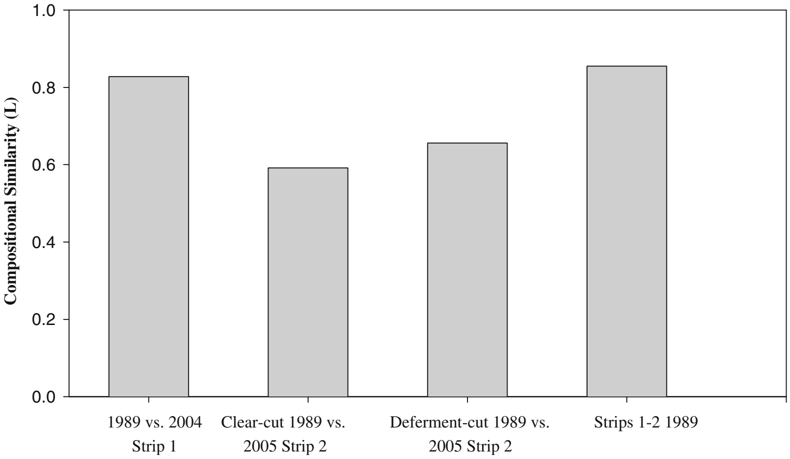

Fig. 5 Compositional similarity (L) of strip 1 between 1989 and 2004; clear-cut and deferment-cut halves of strip 2 between 1989 and 2005, and mature forest (strip 1 versus strip 2) in 1989 at the genus level, using the abundance-based Sorensen index

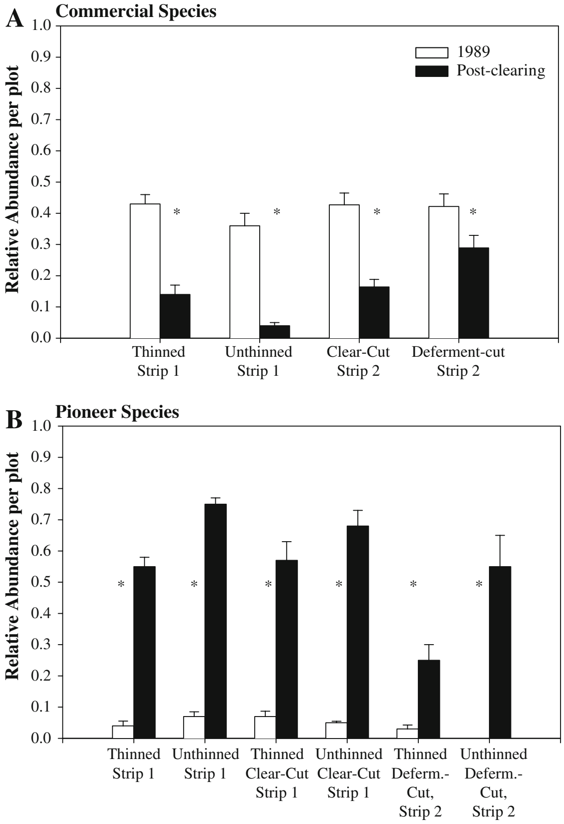

Fig. 6 (**a**) Mean (+SE) relative abundance of commercial species in thinned and unthinned 15 × 15 m plots of strip 1, and the clear-cut and deferment-cut plots of strip 2 in 1989 and post-clearing (2004, 2005) censuses. (**b**) Mean (+SE) relative abundance of pioneer species in thinned and unthinned plots of strip 1, and thinned and unthinned clear-cut, and deferment-cut plots of strip 2, in 1989 and post-clearing censuses. Asterisks (*) indicate significant difference between 1989 and post-clearing census

pioneer species in strip 1 and the clear-cut portion of strip 2, respectively. In the deferment-cut portion of strip 2 only 42% of the trees belonged to pioneer species. As expected the relative abundance of pioneer species was higher in 2004/2005 than in 1989 regardless of thinning treatment in strip 1 (thinned plots of strip 1: $t = 13.37$, $P < 0.001$; unthinned plots of strip 1: $t = 27.93$, $P < 0.001$), the clear-cut portion of strip 2 (thinned plots: $t = 8.32$, $P < 0.01$; unthinned: $t = 13.80$, $P < 0.01$), and the deferment-cut portion of strip 2 (thinned: $t = 3.45$, $P = 0.018$; unthinned: $t = 6.03$, $P < 0.01$, Fig. 6b). Silvicultural thinning and deferment-cutting both reduced the relative abundance of pioneer species. In 2004/2005 unthinned plots had 19 to 36% greater relative abundance of pioneer species than thinned plots in strip 1 and the clear-cut portion of strip 2; in the deferment-cut, unthinned plots doubled thinned plots in relative abundance of pioneer species (strip 1: $F_{1,18} = 21.10$, $P < 0.001$; strip 2: $F_{1,16} = 11.37$, $P < 0.01$). In strip 2, clear-cut plots had greater abundance of pioneers than the deferment-cut plots ($F_{1,16} = 10.41$, $P < 0.01$), and in some case doubled the amount of pioneers. However, the interaction of felling treatment and thinning ($F_{1,16} = 2.73$, $P = 0.118$) did not have an effect on pioneer species. In 1989 the BA of pioneer species in both strip 1 and the clear-cut portion of strip 2 were about 1 m^2/ha, compared to the deferment-cut portion of strip 2 which was about 0.2 m^2/ha. In 2004/2005, the BA of commercial species was 19 m^2/ha in strip 1 and 12 m^2/ha in the clear-cut portion of strip 2. The BA of commercial species of the

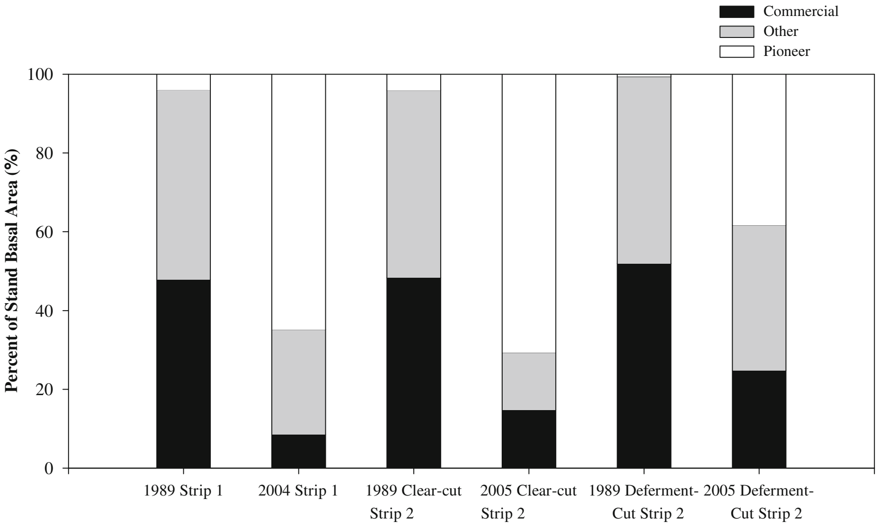

Fig. 7 Percent basal area of commercial, pioneer, and "other" species >7.5 cm dbh for strip 1 in 1989 and 2004, and in the clear-cut and deferment-cut portions of strip 2 in 1989 and 2005

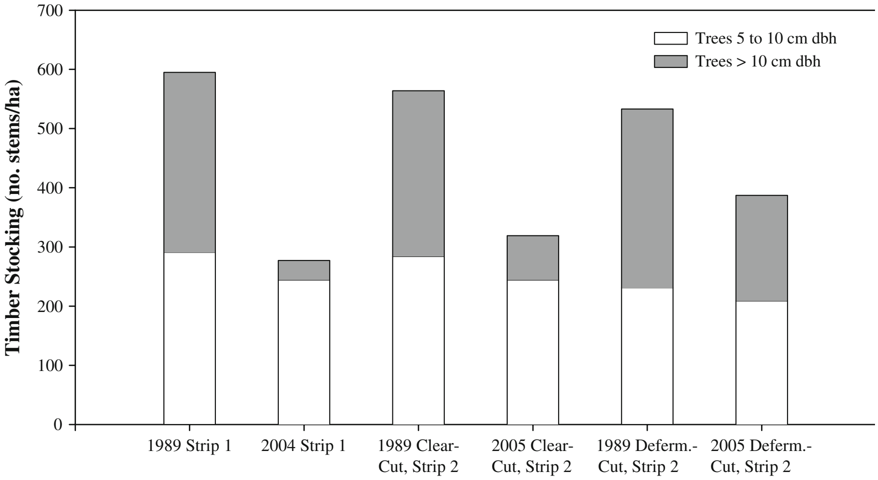

Fig. 8 Timber stocking (no. of commercial stems/ha) of small trees (5–10 cm dbh) and large trees (>10 cm dbh) in the pre-clearing (1989) and post-clearing period (2004/2005) for strip 1, and the deferment-cut and clear-cut portions of strip 2

deferment-cut portion of strip 2 was 10 m^2/ha in 2005. Figure 7 shows the percent BA of commercial, pioneer, and "other" species in 1989 and 2004/2005.

Stocking of commercial stems

In both strips, timber stocking of large stems (>10 cm dbh) was lower in 2004/2005 than in 1989 (Fig. 8). In strip 1, stocking of large commercial stems recovered 11% of its pre-clearing value (33 vs. 304 stems/ha). The clear-cut and deferment-cut portions of strip 2 recovered 27% (76 vs. 280 stems/ha) and 59% (178 vs. 302 stems/ha) of their pre-clearing stocking, respectively. Stocking of small stems (5 to 10 cm dbh) in 2004/2005 was similar to pre-clearing levels, and greater than stocking of large stems (Fig. 8). In both strips, the 1996 silvicultural thinning treatment did not affect the stocking of small (strip 1: $F_{1,18} = 2.50$, $P = 0.131$; strip 2: $F_{1,16} = 0.30$, $P = 0.590$) and large commercial stems (strip 1: $F_{1,18} = 1.68$, $P = 0.211$; strip 2: $F_{1,16} = 0.91$, $P = 0.355$) in 2004/2005. In 2005, the deferment-cut plots of strip 2 had greater than twice as much stocking of large commercial stems than the clear-cut plots ($F_{1,16} = 7.60$, $P = 0.014$), but similar stocking of small commercial stems ($F_{1,16} = 0.23$, $P = 0.637$, Fig. 8). The interaction of thinning and felling affected neither the stocking of small ($F_{1,16} = 0.80$, $P = 0.385$) nor large commercial stems ($F_{1,16} = 0.00$, $P = 0.961$).

Discussion

Basal area recovery

The recovery of a high percentage of stand BA 15 years after clear-cutting (73% in strip 1 and 58% in the clear-cut portion of strip 2) is consistent with rapid BA growth in the early years of secondary succession (Saldarriaga et al. 1988; Moran et al. 1996; Denslow and Guzman 2000), although this strongly depends on land use history and site productivity. BA of forest stands 12 to 18 years after clear-cutting for pulp in Colombia did not exceed 50% of old growth values (Faber-Landgendoen 1992). In Brazil, BA recovery 11 to 12 years after clear-cutting treatment was 50% of undisturbed forest and 60% of its pre-clearing value (Parrotta et al. 2002). Parrota et al. (2002) also compared BA recovery of different systems 11 to 12 years after harvesting. They found that high intensity harvesting or clear-cut (removal of 373 m^3, all above-ground biomass) had a lower BA recovery (50%) than moderate harvesting (trees $\leq$20 cm and $\geq$60 cm dbh for a total removal of 219 m^3) (68%), and low harvesting (trees $\geq$45 cm dbh for a total of 201 m^3) treatments (68%). Thus, the recovery of BA in this study was comparable to that reported for moderate harvest in Brazil (Parrotta et al. 2002) and somewhat higher than clear-cutting in Colombia (Faber-Landgendoen 1992).

Species richness recovery

The strips in the pre-clearing stage had high species richness: estimates reported in Table 2 underestimate the true richness since identification of some trees was done to morphospecies. Therefore, the extent to which species richness recovered after 15 years to pre-clearing values (47% in strip 1 and 45% in the clear-cut portion of strip 2) is probably slightly overestimated. Nevertheless, this was similar to the recovery 18 years after clear-cutting for pulp in Colombia, <50% of mature forest (trees $\geq$10 cm dbh, Faber-Landgendoen 1992). Less intensive harvesting systems, however, have greater species-richness recovery. Parrotta et al. (2002) reported lower species richness recovery of trees $\geq$15 cm dbh following clear-cut treatment (32%) versus moderate (59%) and low harvesting (94%) treatments after 11 to 12 years. In a dipterocarp forest in Borneo, Cannon et al. (1998) found that samples 8 years after selective logging (removal of 43% of stand BA) had as many tree species as unlogged forest.

Several studies have found that species richness tends to be more similar in secondary growth and old growth when smaller tree size classes are compared (Saldarriaga et al. 1988; Faber-Landgendoen 1992; Aide et al. 1996; Guariguata et al. 1997; Magnusson et al. 1999; Denslow and Guzman 2000; Parrotta et al. 2002; Peña-Claros 2003). We were not able to make such comparisons in our study due to incomplete pre-clearing datasets for smaller trees in both strips.

Composition recovery

While species richness increases in the early years of secondary succession, and takes only a few decades to reach old growth values when land use has not been severe and seed sources are close, composition of these forests remains different from old growth and may take longer to become similar to old growth stands (Finegan 1996; Guariguata and Ostetarg 2001). In our study, the strips recovered more than 50% of their pre-clearing composition at the genus level. If the analysis had been done at the species level, compositional similarities would have been lower, but genus-level analysis was conservative in the face of possible inconsistencies between censuses in some species identification, and is often done in studies of diverse tropical rainforests (e.g., Laurance et al. 2004). Despite this high composition recovery in the strips, the relative abundance and basal area of commercial and pioneer species were far from reaching pre-clearing levels.

Recruitment of commercial species after harvesting is difficult due to the different environmental conditions required by different species for regeneration. Although Swaine and Whitmore (1988) considered most commercial species gap-dependent, commercial seedlings have a broad range of shade-tolerances (Martini et al. 1994; Pinard et al. 1999). Out of 31 timber species (of high and low commercial value) studied by Pinard et al. (1999), 45% were shade intolerant and regenerated in forest edges and large gaps, 36% were shade-tolerant and regenerated in the understory, and 19% were in between the latter groups and regenerated under partial shade or small gaps. Similarly, Martini et al. (1994) classified timber species of the Brazilian Amazon.

Recruitment from seed was more important in our system than stump sprouts or advance regeneration. Sprouting of timber species in Amazonia is common; out of 305 timber species saplings, 87% of them produced sprouts following the breaking and crushing injuries associated with logging (Martini et al. 1994). In the strips, however, stump sprouts and the advance regeneration had a minor role in tree regeneration (Table 2) and the regeneration of commercial species. Although 41% of the stumps (>7.5 cm dbh) had one or more living sprouts, 10 months after cutting one of the strips (Gorchov et al. 1993), only four sprouting stumps in each strip (unpublished data) were of commercial value after 15 years. A high density of saplings (903/ha), belonging to mature forest trees, including many of commercial value, survived the clearing operation in 1989 (Gorchov et al. 1993), but 15 years later these only comprised a small percentage (16–18%) of the total regeneration in the strips, a little higher than the sprouting stumps.

Low seed input and/or high seed predation of commercial species could have lowered the recruitment of commercial species into the strips, resulting in low stocking and relative abundance of commercial trees in the strips 15 years later. Using seed traps aboveground, Gorchov et al. (1993) showed that very few large seeds, characteristic of timber species, were dispersed into the strips by birds or bats, one year after clear-cutting. Also, seeds of a valuable timber species, *Hymenaea courbaril*, were rarely moved by rodents into the interior of a strip, 10 to 30 months after the clearing (Gorchov et al. 2004). Predation of timber seeds (*Pouteria* sp.), was also greater in the strips than in the surrounding forest, 3 years after strip clear-cutting (Notman et al. 1996). Once established, commercial species compete for light with vines, lianas, and short-lived pioneer species that quickly colonize logged areas (Buschbacher 1990; Fredericksen and Mostacedo 2000; Pariona et al. 2003). As a result, growth and BA of commercial species often respond to logging less favorably than faster growing species of low commercial values (Silva et al. 1995; Kammesheidt 1998).

After 15 years of regeneration, timber stocking of small stems (5–10 cm dbh) in both strips was similar to pre-clearing levels. However, stocking of larger stems (>10 cm dbh) was low (33.3–75.5 stems/ha) and far from reaching pre-clearing levels (300 stems/ha, Fig. 8), and mature forest levels (233 stems/ha in Peters et al. (1989)), and lower than in a 50 year-old communal forest near Iquitos (125.5/ha for trees >25 cm dbh in Pinedo-Vasquez et al. 1990). This low stocking of large commercial stems in this system negatively affects the economic value projected for a potential second harvest after 25 years (Rondon 2008).

On the other hand, pioneers with large basal areas were still abundant in 2004/2005, 8 to 9 years after the thinning treatment. In the study of clear-cutting for pulp, pioneer species in a 12-year old forest comprised more than 50 to 60% of basal area and biomass (Faber-Landgendoen 1992); Parrotta et al. (2002) found that although tree floras within low, moderate, and intensive (clear-cut) harvesting treatments were broadly similar to those of undisturbed plots after 11 years; the clear-cut treatment was dominated by a higher proportion of short-lived early successional tree species, including *Cecropia* and *Vismia*.

One year after the clearing, the majority of the seedlings in the strip were a few bat (*Cecropia*)- and bird-dispersed (Melastomatace*ae* and *Alchornea triplinervia*) pioneer tree species (Gorchov et al. 1993). *Cecropia membranacea*, one of the species with the most seedlings in the strips, was also present in the seed bank; other tree seedlings, not represented in the seed bank, were attributed to the seed rain (Gorchov et al. 1993). Seeds from the seed bank as well as recently dispersed seeds contribute to the development of secondary forest. In a tropical forest of Mexico, all viable seeds of *Cecropia obtusifolia* were renewed from the soil almost every year; seed loss was mainly due to pathogen attack and high predation rates, but the seed bank was continually replenished by seed rain (Alvarez-Buylla and Martínez-Ramos 1990). It is very likely that the pioneer trees that currently dominate the strips depended on seed dispersal events that followed the clearing of the strips. One year after clearing one of the strips, bat- and wind-dispersed seeds accounted for more seed dispersal in the strip interior than bird-dispersed seeds, which arrived at high density within the forest or strip edge (Gorchov et al. 1993). Fifteen years after the felling, pioneer species comprised 65 and 62% of the trees in strip 1 and the clear-cut portion of strip 2, respectively.

Germination and establishment of short-lived pioneer species (such as *Cecropia*) can be reduced when residual vegetation and litter are present (Uhl et al. 1981; Putz 1983; Molofsky and Augspurger 1992). In this study, only slash <2.5 cm was left on site (Cornejo and Gorchov 1993). Although substantial, this amount of litter was apparently not sufficient to suppress germination and establishment of pioneer species.

In Jenaro Herrera, pioneer species such as *Cecropia*, *Alchornea, Miconia*, and *Vismia* spp. have been found to be dominant in 14 and 17-year old fallows (Baluarte Vásquez 1998). Dominance of few pioneers that established early in succession tends to "break up" within <25 years (Denslow and Guzman 2000). Senescence and mortality of these species will have a strong impact on the future biomass and stem density of secondary stands (Feldpausch et al. 2007). Thus, BA recovery in the strips is not likely to increase continuously over the next years unless there is higher growth of commercial and "other" species into larger size classes.

Silvicultural thinning

Liberation treatments such as thinning of lianas and pioneer species are commonly used to improve recruitment and tree growth (de Graaf et al. 1999; Guariguata 1999, 1997; Dolanc et al. 2003; Pariona et al. 2003). In this study, silvicultural thinning in 1996 was sufficient to significantly increase the 1996–2000 growth of commercial species (Dolanc et al. 2003), and to reduce 2004/2005 relative abundance of pioneer species of both strips, although pioneers were still abundant in the post-clearing censuses of both strips. Thinning also increased the relative abundance of commercial species significantly in one of the strips. However, thinning did not have an effect on basal area, compositional similarity, or timber stocking 8 to 9 years after the treatment application. The lack of effects of thinning on these community parameters might be because large *Alchornea* and melastomes that were not thinned, because some of the girdled pioneer trees did not die, and/or due to increased growth of the trees remaining in the thinned plots.

Deferment-cut

Deferment-cutting appeared to be more sustainable than clear-cutting. The deferment-cut portion of strip 2 had greater BA, species richness, and composition recovery than the clear-cut portion. The deferment-cut portion also had higher representation, stocking, and BA of commercial species, and a lower percentage of pioneers, than the clear-cut portion. This better recovery of the deferment-cut is consistent with the well documented role of remnant or residual vegetation in promoting recovery of species richness, tree density, and aboveground biomass (Guariguata and Ostetarg 2001; Parrotta et al. 2002; Chazdon 2003).

The Palcazú forest management system

Tosi (1982) and Hartshorn (1989a) proposed harvesting cycles of 30 to 40 years for the strip clear-cutting system. Tree regeneration in the two clear-cut strips, 15 years into the second harvesting, suggests that this system may not be ecologically sustainable, but this conclusion is tempered by replication constraints at the plot and site scale of this study.

Both strips showed some inherent variability in the pre- and the post-clearing censuses, especially in the recovery of commercial species. Predicting species richness and composition of the strips in the next 15 to 25 years would be difficult because this system would still be affected by variability in recruitment, growth, and mortality rates of commercial, pioneer, and "other" species due to biotic and abiotic factors. Thus far, 15 years into the regeneration, our results reveal that in this system regeneration of pioneer species exceed that of commercial species, even when the strips are surrounded by a matrix of old growth forest. In a forest managed by the strip clear-cutting system as it was originally proposed for the Palcazú, 44,000 ha would be under management for timber production (Hartshorn 1989b), and about half of the area would be cleared (Hartshorn 1989b); thus, eventually the surrounding matrix for many of the strips would be that of young growth. Therefore, the species that would thrive in these strips would be the ones that can reproduce within the cutting cycle of 30–40 year; i.e., pioneers. Contrary to predictions of Tosi (1982) and Hartshorn (1989a), pioneer species dominate the composition of the strips 15 years into the regeneration. Unless pioneer species have a high mortality rate in the coming years, and there is more recruitment of commercial and "other" species into the larger size classes, this system is not sustainable.

Two approaches could be taken to reduce the number of pioneer species in the strips. It is possible that cutting narrower strips (<30 m) in this system may reduce the amount of light entering the strip and thus, the germination and establishment of pioneer species. Periodic silvicultural thinning treatments may further reduce the abundance of pioneer species and further increase the establishment and growth of more commercial and “other” species in the strips.

We are aware that in the future high quality timber species will become scarce due to their high demand and strong extraction pressures. International markets will start accepting a broader range of lower quality timber species that are also gap-dependent, but this market will take some time to develop. In this study we were interested in studying the regeneration of timber species that already have an established market in order to assess the value of the strips in a potential second harvest.

From the economic perspective, composition in a forest management system has a great influence on the financial value of the next harvest. Relative abundance, stocking, and growth of commercial species will determine whether the second harvest (which is in the next 15–25 years) will be financially profitable. In order to fully assess the economic viability of this system, we have also investigated whether those few large commercial trees in the strips would reach marketable size in the next 25 years, in time for a second cutting (Rondon 2008).

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References

Aide TM, Zimmerman JK, Rosario M, Marcano H (1996) Forest recovery in abandoned cattle pastures along elevational gradient in Northeastern Puerto Rico. Biotropica 28:537–548. doi:10.2307/2389095

Allison TD, Art HW, Cunningham FE, Teed R (2003) Forty-two years of succession following strip clearcutting in a northern hardwoods forest in northwestern Massachusetts. For Ecol Manag 182:285–301. doi:10.1016/S0378-1127(03)00066-5

Alvarez-Buylla ER, Martínez-Ramos M (1990) Seed bank versus seed rain in the regeneration of a tropical pioneer tree. Oecologia 84:314–325

Ascorra CF, Gorchov DL, Cornejo F (1993) The bats from Jenaro Herrera, Loreto, Peru. Mammalia 57:533–552

Baluarte Vásquez J (1998) Composición floristica de los bosques secundarios de Jenaro Herrera, Loreto. Folia Amazonica 9:195–218

Bawa KS, Seidler R (1998) Natural forest management and conservation of biodiversity in tropical forests. Conserv Biol 12:46–55. doi:10.1046/j.1523-1739.1998.96480.x

Buschbacher RJ (1990) Natural forest management in the humid tropics: ecological, social, and economic considerations. Ambio 19:253–258

Cannon CH, Peart DR, Leighton M (1998) Tree species diversity in commercially logged Bornean rainforest. Science 281:1366–1368. doi:10.1126/science.281.5381.1366

Chao A, Chazdon LR, Colwell RK, Shen T (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol Lett 8:148–159. doi:10.1111/j.1461-0248.2004.00707.x

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspect Plant Ecol Evol Syst 6:51–71. doi:10.1078/1433-8319-00042

Colwell RK (2005) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL www.purl.oclc.org/estimates. Cited 24 Oct 2007

Cornejo F, Gorchov DL (1993) La tala rasa en fajas, el aprovechamiento integral del recurso y rendimiento económico: El caso de Jenaro Herrera, Loreto, Peru. Rev Forestal Peru 20:21–37

de Graaf NR, Poels RLH, Van Rompaey RSAR (1999) Effects of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. For Ecol Manag 124:123–135. doi:10.1016/S0378-1127(99)00057-2

Denslow JS, Guzman S (2000) Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. J Veg Sci 11:201–212. doi:10.2307/3236800

Dolanc C, Gorchov DL, Cornejo F (2003) The effects of silvicultural thinning on diversity and demography of trees regenerating in strip cuts in the Peruvian Amazon. For Ecol Manag 182:1–14. doi:10.1016/S0378-1127(03)00012-4

Faber-Langendoen D (1992) Ecological constraints on rain forest management at Bajo Calima, western Colombia. For Ecol Manag 53:213–244. doi:10.1016/0378-1127(92)90044-A

Feldpausch TR, da Conceicao Prates-Clark C, Fernandes ECM, Riha SJ (2007) Secondary forest growth deviation from chronosequence predictions in Central Amazonia. Glob Change Biol 13:967–979

Finegan B (1996) Patterns and process in neotropical secondary rain forests: the first 100 years of succession. Trends

Ecol Evol 11:119–124. doi:10.1016/0169-5347(96)81090-1

Fredericksen TS, Mostacedo B (2000) Regeneration of sawtimber species following selective logging in a Bolivian tropical forest. For Ecol Manag 131:47–55. doi:10.1016/S0378-1127(99)00199-1

Gentry AH (1993) A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru). Conservation International, Washington, DC, 895 pp

Gorchov DL, Cornejo F, Ascorra C, Jaramillo M (1993) The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio 107(108):339–349

Gorchov DL, Palmeirim JM, Jaramillo M, Ascorra C (2004) Dispersal of seeds of *Hymenaea courbaril* (Fabaceae) in a logged rain forest in the Peruvian Amazon. Acta Amazon 34:265–273. doi:10.1590/S0044-59672004000200014

Gram S (1997) Indian forestry in Latin American rain forests. Sustain Dev 5:21–29. doi :10.1002/(SICI)1099-1719(199703)5:1<21::AID-SD54>3.0.CO;2-I

Guariguata MR (1999) Early response of selected tree species to liberation thinning in young secondary forest in Northeastern Costa Rica. For Ecol Manag 124:255–261. doi:10.1016/S0378-1127(99)00072-9

Guariguata MR, Ostetarg R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manag 148:185–206. doi:10.1016/S0378-1127(00)00535-1

Guariguata MR, Chazdon RL, Denslow JS, Dupuy JM, Anderson L (1997) Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecol 132:107–120. doi:10.1023/A:1009726421352

Hartshorn GS (1989a) Application of gap theory to tropical forest management: natural regeneration on strip clearcuts in the Peruvian Amazon. Ecology 70:567–569. doi:10.2307/1940208

Hartshorn GS (1989b) Sustained yield management of natural forests. In: Browder JO (ed) Fragile lands of Latin America. Westview Press, London

Hartshorn GS (1995) Ecological basis for sustainable development in tropical forests. Annu Rev Ecol Syst 26:155–175. doi:10.1146/annurev.es.26.110195.001103

Heitzman E, Pregitzer KS, Miller RO, Lanasac M, Zuidema M (1999) Establishment and development of northern white-cedar following strip clearcutting. For Ecol Manag 123:97–104. doi:10.1016/S0378-1127(99)00025-0

ITTO (1997–2005) Annual review and assessment of the world timber situation. International Tropical Timber Organization, Yokohama

Kammesheidt L (1998) Stand structure and spatial pattern of commercial species in logged and unlogged Venezuelan forest. For Ecol Manag 109:163–174. doi:10.1016/S0378-1127(98)00245-X

Laurance WF, Oliveira AA, Laurance SG, Condit R, Nascimento HEM, Sanchez-Thorin AC et al (2004) Pervasive alteration of tree communities in undisturbed Amazonian forests. Science 248:171–175

Lieberman D, Lieberman M, Hartshorn GS, Peralta R (1985) Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. J Trop Ecol 1:97–109

Magnusson WE, de Lima OP, Quintiliano-Reis F, Higuchi N, Ferreira-Ramos J (1999) Logging activity and tree regeneration in an Amazonian forest. For Ecol Manag 113:67–74. doi:10.1016/S0378-1127(98)00418-6

Martini AMZ, de Rosa AN, Uhl C (1994) An attempt to predict which Amazonian tree species may be threatened by logging activities. Environ Conserv 21:152–161

Molofsky J, Augspurger CK (1992) The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73:68–77. doi:10.2307/1938721

Moran EF, Packer A, Brondizio E, Tucker J (1996) Restoration of vegetation cover in eastern Amazonia. Ecol Econ 18:41–54. doi:10.1016/0921-8009(96)00034-1

Notman E, Gorchov DL, Cornejo F (1996) Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed neotropical rain forest tree species. Oecologia 107:221–227. doi:10.1007/BF00328602

Pariona W, Fredeicksen TS, Licona JC (2003) Natural regeneration and liberation of timber species in logging gaps in two Bolivian tropical forests. For Ecol Manag 181:313–322. doi:10.1016/S0378-1127(03)00002-1

Parrotta JA, Francis JK, Knowles OH (2002) Harvesting intensity affects forest structure and composition in an upland Amazonian forest. For Ecol Manag 169:243–255. doi:10.1016/S0378-1127(01)00758-7

Peña-Claros M (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 35:450–461

Peters CM, Gentry AH, Mendelsohn O (1989) Valuation of an Amazonian rainforest. Nature 339:655–656. doi:10.1038/339655a0

Pinard MA, Putz FE, Rumíz D, Guzmán R, Jardim A (1999) Ecological characterization of tree species for guiding forest management decisions in seasonally dry forests in Lomerío, Bolivia. For Ecol Manag 113:201–213. doi:10.1016/S0378-1127(98)00426-5

Pinedo-Vasquez M, Zarin D, Jipp P, Chota-Inuma J (1990) Use-values of tree species in a communal forest reserve in Northeast Peru. Conserv Biol 4:405–416. doi:10.1111/j.1523-1739.1990.tb00315.x

Putz FE (1983) Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64:1069–1074. doi:10.2307/1937815

Rondon XJ (2008) Assessing the sustainability of strip clearcutting in the Peruvian Amazon. Dissertation, Miami University, Oxford, OH

Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. J Ecol 76:938–958. doi:10.2307/2260625

Silva JNM, de Carvalho JOP, do Lopes JCA, de Almeida BF, Costa DHM, de Oliveira LC, Vanclay JK, Skovsgaard JP (1995) Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. For Ecol Manag 71:267–274. doi:10.1016/0378-1127(94)06106-S

Simeone R (1990) Land use planning and forestry-based economy: the case of the Amuesha Forestry Cooperative. Tebiwa J Ida Mus Nat Hist 24:7–12

Smith DM (1986) The practice of silviculture, 8th edn. Wiley, New York

Southgate D (1998) Tropical Forest Conservation: An economic assessment of the alternatives in Latin America. Oxford University Press, Oxford, UK, 175 pp

Spichiger R, Meroz J, Loizeau PA, Stutz de Ortega L (1989) Contribución a la Flora de la Amazonía Peruana. Los Arboles del Arboretum Jenaro Herrera, vol 1. Conservatoire et Jardin Botaniques de Ginebra, Switzerland, 359 pp

Spichiger R, Meroz J, Loizeau PA, Stutz de Ortega L (1990) Contribución a la Flora de la Amazonía Peruana. Los Arboles del Arboretum Jenaro Herrera, vol 2. Conservatoire et Jardin Botaniques de Ginebra, Switzerland, 565 pp

Spichiger R, Loizeau PA, Latour C, Barriera G (1996) Tree species richness of a South-Western Amazonian forest (Jenaro Herrera, Peru, 73° 40′W/4° 54′S). Candollea 51:559–577

Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86. doi:10.1007/BF00044629

Thornton PL (1957) Effects of cutting methods on advance reproduction in two mature mixed coniferous swamps in Upper Michigan. J For 55:448–451

Tosi JA (1982) Sustained yield management of natural forests. Consultant report for USAID/Peru. Tropical Science Center. San Jose. Costa Rica, 53 pp

Uhl C, Clark K, Clark H, Murphy P (1981) Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. J Ecol 69:631–649. doi:10.2307/2259689

Uhl C, Jordan C, Clark K, Clark H, Herrera R (1982) Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. Oikos 38:313–320. doi:10.2307/3544671

Changing relationships between tree growth and climate in Northwest China

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Abstract Recently, several studies have shown changing relationships between tree growth and climate factors, mostly in the circumpolar north. There, changing relationships with climate seem to be linked to emergent subpopulation behavior. Here, we test for these phenomena in Northwest China using three tree species (*Pinus tabulaeformis*, *Picea crassifolia*, and *Sabina przewalskii*) that had been collected from six sites at Qilian Mts. and Helan Mts. in Northwest China. We first checked for growth divergence of individual sites and then investigated the relationship between tree growth and climate factors using moving correlation functions (CF). Two species, *Pinus* and *Sabina*, from two sites clearly showed growth divergence, not only in the late twentieth century as reported in other studies, but also over nearly the whole record. In divergent sites, one chronology shows more stable relationships with climate factors (usually precipitation). In non-divergent sites, nearly all relationships either vary in strength or become non-significant at one point. While this might possibly be related to increased stress on some trees due to increasing temperature, the exact causes for this shift in sensitivity remain unclear. We would like to highlight the necessity for additional studies investigating possible non-stationary growth responses of trees with climate, especially at sites that are used for climate reconstruction as our sites in Northwest China.

Keywords Growth divergence · Northwest China · Paleoreconstruction · Tree line · Tree ring

Introduction

Global warming is a great concern to human populations, as it has been shown to bring many threats, such as heat waves and warmer weather, spreading disease, earlier spring arrival, plant and animal range shifts and population declines, sea level rise, and frequent disaster (Greenough et al. 2001; Kahn 2005; Webster et al. 2005; Shepherd and Wingham 2007; IPCC 2007). In order to evaluate whether current global warming is unprecedented or not, it is essential to put this warming into a long-term perspective. Due to the limited time interval of instrumental climate records, many natural proxies have been used to conduct paleoclimatic reconstructions. Tree rings have been

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widely used to reconstruct the variability of many climate factors (e.g., temperature, precipitation), due to their annual resolution, wide spatial distribution, and the possibility of using simple linear models of climate–tree growth relationships that seem to be easily verified and calibrated (Hughes 2002).

It is generally assumed in dendroclimatological studies that the approximate relationship between tree growth and the limiting climate factor is stable over time (Fritts 1976). However, many recent studies have reported problems with this assumption. Either formerly temperature sensitive tree ring chronologies have lost or decreased in temperature sensitivity (Jacoby et al. 1996, 2000; Briffa et al. 1998a, b; Smith et al. 1999; Solberg et al. 2002), increased in sensitivity (Knapp et al. 2001; Wilmking et al. 2005), or even changed from positive to negative temperature sensitivity or vice versa (Wilmking et al. 2004, 2008).

In addition, temperature reconstructions in the northern hemisphere based on tree rings are often not able to follow the documented temperature increase in recent decades, thus leading to a widening gap (a divergence) between the temperature curve and the tree ring-based temperature reconstruction. D'Arrigo et al. (2008) has recently termed this phenomenon the "divergence problem" in northern forests.

Meanwhile, even trees growing at the same site showed not only opposite response relationships with climate factors, but also diverging long-term growth trends in the late twentieth century, possibly diluting the climate signal when averaged to site chronologies (Wilmking et al. 2004, 2005; Driscoll et al. 2005; Pisaric et al. 2007). These growth trend differences have also been called "diverging." In order to avoid possible confusion, we will use the term "growth divergence" for differences in growth trends between trees and "divergence problem" for the underestimation of recent temperatures by tree ring-based climate reconstructions.

Neither the real reasons causing (1) the shift in tree growth response to temperature (or possibly other environmental factors), (2) the diverging between recorded and reconstructed temperature, and (3) the diverging growth trends between neighboring trees nor the interaction between those three challenges are known. Some possible mechanisms have been proposed to explain these shifts in tree growth–climate relationships, such as temperature-induced drought stress (Jacoby and D'Arrigo 1995; Barber et al. 2000; Lloyd and Fastie 2002), non-linear thresholds, or time-dependent responses to recent warming (D'Arrigo et al. 2004; Wilmking et al. 2004; Sergio et al. 2007), delayed snowmelt and related changes in seasonality (Vaganov et al. 1999), air pollution (Wilson and Elling 2004; Yonenobu and Eckstein 2006), and differential growth/climate relationships inferred for maximum, minimum and mean temperatures (Wilson and Luckman 2002, 2003). In addition, there are also some other potential causes, for example, end effects during chronology development and biases in instrumental target data and its modeling (Cook and Peters 1997; Melvin 2004; Hoyt 2006; D'Arrigo et al. 2008).

Whatever the reasons for the growth divergence or the divergence problem are, these phenomena seem to be limited to the high latitudes of the northern hemisphere (D'Arrigo et al. 2008). But do these divergences and changes in climate sensitivity only appear in the circumpolar northern latitudes or do they exist worldwide? Here, we try to better understand the magnitude and extent of these phenomena by testing several sites in northwest China.

In northwest China, tree rings (width, isotopes, density) have been widely used in dendroclimatological studies at the alpine tree line (e.g., Yuan et al. 2003; Zhang and Wu 1997; Shao et al. 2004, 2005; Gao et al. 2005). Several climate reconstructions have been conducted in the Qilian Mts. (Zhang and Wu 1996; Wang et al. 2001; Gou et al. 2001) and the Helan Mts. (Liu et al. 2004, 2005), some extending back over 1,000 years (Kang et al. 2002). However, no study has yet considered testing for growth divergence or the stability of the relationship between tree growth and climate over time in this region. A better understanding of the tree growth responses to climate in northwest China during the last century, however, is important not only for regional paleoclimatic studies but also for forest carbon uptake simulations and future forest planning.

Materials and method

Study area

For this study, we sampled three regionally dominating tree species (two sites each) in the Qilian Mts. and Helan Mts.: (1) *Pinus tabulaeformis*, (2) *Sabina przewalskii*, and (3) *Picea crassifolia*. The Qilian Mts. and Helan Mts. are two prominent mountains in

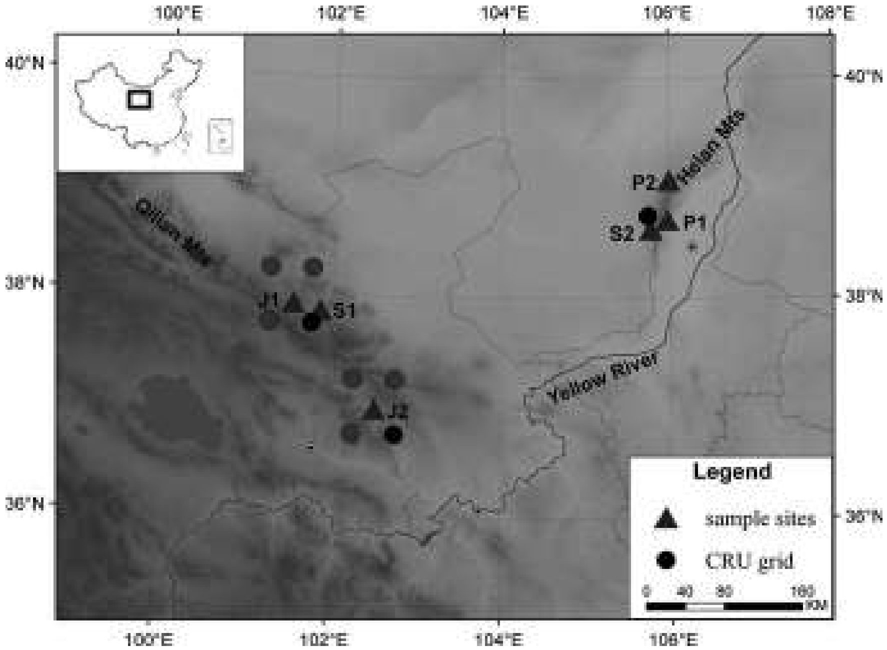


Fig. 1 Map of the sampling sites (▲) in eastern Qilian Mts. and Helan Mts., as well as of the nearby grid data (●) from CRUTS2.1 (37°75′ N, 101°75′ E; 36°75′ N, 102°75′ E; 38°75′ N, 105°75′ E). The gray dots indicate the grid cells around the sampling sites that showed similar results

Northwest China (Fig. 1). Each of them has its own typical topography and typical atmospheric systems. The Qilian Mts., located on the northern edge of the Tibet Plateau, have several peaks over 4,000 m, which create a strong rain shadow effect for monsoons coming from the southeast. Our study area is situated in the eastern part of the Qilian Mts., a transitional area between temperate monsoons and continental climate. There, *Picea* and *Sabina* are two typical and widespread conifer species. The Helan Mts. are located in north central China, where the arid northwest areas meet the Loess Plateau. They extend over 200 km from south to north, but only 15–60 km from east to west with peak elevations between 2,000 and 3,000 m a.s.l. Located along the northwest margin of the East Asian Summer Monsoon, the Helan Mts. act as a barrier to the penetration of monsoon rainfall into northwest China. *Pinus* and *Picea* are two typical and widespread species in Helan Mts.

Climate data

Most of the meteorological stations in Northwest China were set up after 1950 and thus provide only a short climatic record. As a consequence, we used gridded data from the high-resolution 0.5° × 0.5° gridded climate dataset CRUTS2.1 (Mitchell and Jones 2005) instead of the measured data for our analysis, fully aware that relationships between tree ring parameters and CRU data are usually weaker than with nearby station data, mostly because of the large scale smoothing applied in the CRU datasets (Mitchell and Jones 2005). In order to evaluate the quality of gridded data over time, a 10-year moving standard deviation (SD) was employed. The moving SD of precipitation data has an abrupt change around 1934, indicating a possible problem with the precipitation data prior to 1934. The moving SD of temperature is stable over the whole time period. Therefore, in this study we used only gridded data from 1934 to 2000 (1934 to 1999 for sites of Helan Mts.).

The climate data of the nearest CRU grid cells were used in this study for the calculations of climate–growth relationship, since the relationships between chronologies and climate data of the four grid cells around the sample sites were similar (data not shown).

Tree ring sampling and cross dating

Increment cores of trees in the Qilian Mts. were collected in October 2000. A total of 29 cores were taken from 16 living *Picea* trees growing between 2,600 and 2,900 m a.s.l. near the lower tree line and were herein named S1. All sampled trees were healthy and growing on an east-facing slope with moist soil (if compared to the other sampling sites). From 23/22 *Sabina* trees 41/39 cores were taken at two sites taken from the east Qilian Mts. and named J1 and J2. All cores were taken from healthy trees growing at the upper limit of the forest at an elevation of about 2,930–3,100 m a.s.l. with thin gray cinnamonic soil.

The increment cores of Helan Mts. were collected in October 1999. A total of 35 cores were taken from 18 living *Picea* trees growing above 2,500 m a.s.l. at west slope of Helan Mts. and were named S2. From 40/25 *Pinus* trees growing 68/41 cores were taken above 2,000–2,300 m a.s.l. at two sites from Helan Mts. and named P1 and P2. P1 and P2 are at the east and west slopes of the Helan Mts., respectively. The soil at both sites was thin and rocky. The dominant tree species in both forest sites was *Pinus*, typically found growing at an elevation between 1,900 and 2,350 m a.s.l. (Table 1).

Tree rings were processed and cross-dated with standard dendrochronological techniques (Cook and Kairiukstis 1990). Ring width was measured on a Velmex system with a precision of 0.001 mm. The program COFECHA (Holmes 1983) was employed to check the quality of visual cross-dating.

Tree ring data processing

Divergent growth trends over time and chronology development

First, we used the raw data to calculate the growth trend of each tree for the last 40 years using linear regression. All series at each site were classified into two groups: one with increasing growth trend (slope, $b > 0$) and the other with decreasing growth trend ($b < 0$) (Pisaric et al. 2007). All series were then standardized with the program ARSTAN (Cook 1985) using conservative negative exponential or linear regression. Due to the failure of conservative detrending in a few series (Table 2), they were standardized with the Hugershoff growth curve.

Chronologies based on the groups were built using traditional methods. Since we used raw data to judge the growth trend, the two chronologies (one with increasing and one with decreasing growth trend) were combined into one chronology, if the two groups showed a similar trend after detrending.

Table 1 Site information

Site	Species	Latitude (N)	Longitude (E)	Elevation (m)	Slope
S1	*Picea crassifolia*	37.87°	101.53°	2600–2900	East-facing
S2		38.63°	105.78°	2500	North-facing
P1	*Pinus tabulaeformis*	39.08°	106.08°	2600	North west-facing
P2		38.72°	105.98°	2400	North west-facing
J1	*Sabina przewalskii*	37.93°	101.53°	2930–3100	South-facing
J2		36.59°	102.31°	~3100	South-facing

Table 2 Statistics of the eight chronologies. Hug., series detrended by Hugershoff growth curve

Site	Sub-chro.	Sample size (cores/trees)	Hug.	Time interval	MS	AC	R_{bt}	EPS	EPS > 0.85
S1	S1	29/16	2	1840–2000	0.430	−0.124	0.601	0.945	1900
S2	S2	35/18	2	1869–1999	0.351	−0.006	0.496	0.811	1920
P1	P1I	8/6	0	1742–1999	0.648	−0.004	0.583	0.854	1850
	P1D	60/38	6	1700–1999	0.566	−0.067	0.615	0.988	1820
P2	P2	41/25	7	1739–1999	0.696	−0.013	0.694	0.983	1819
J1	J1I	18/13	0	1288–2000	0.351	−0.007	0.256	0.857	1865
	J1D	22/14	0	1590–2000	0.304	−0.034	0.248	0.868	1875
J2	J2	39/22	4	1740–2000	0.422	−0.043	0.341	0.952	1852

MS, Mean sensitivity; AC, first-order autocorrelation; R_{bt}, the mean interseries correlation; EPS, the expressed population signal and the year from when EPS is consistently greater than 0.85

Several descriptive statistics, commonly adopted in dendrochronology, were used to compare chronologies. These statistics include the mean sensitivity (MS) and SD (to assess the high-frequency variations), the first-order serial autocorrelation (AC) (to detect eventual persistence retained after the standardization), the mean correlation between trees (R_{bt}), and the expressed population signal (EPS) (to estimate the amount of year-to-year growth variations shared among trees of the same chronology). In order to visualize the apparent growth divergence over time, we subtracted the detrended tree ring width indices of the increasing chronology from the decreasing chronology where applicable.

Climate–growth relationships and their stability over time

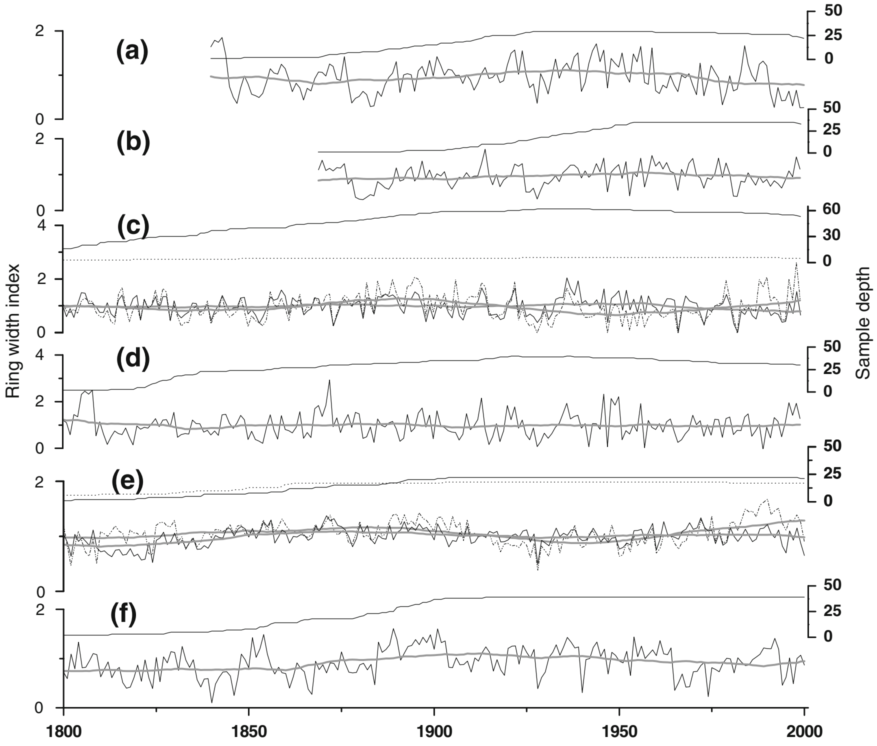
After dividing all series into groups of increasing and decreasing growth trends and chronology building, we tested each resulting chronology for its climate–growth relationship. First, simple correlation functions (CF) were employed. We then tested the stationary and consistency of these climate–tree growth relationships over time using moving CF (DENDROCLIM2002, Biondi and Waikul 2004). A moving CF employs a fixed number of years progressively slid across time to compute the correlation coefficients (Biondi 1997). Considering the length of recorded data and the reliability of sample size, we chose 48 years as the moving interval for each calculating analysis. Moving CFs produce a temporal set of coefficients for each predictor and coefficients not significant at the 95% confidence level are changed to zero. Here, we just present the results of the moving correlations in detail because the moving CFs not only include the results obtained from simple correlation analysis, but also provide a dynamic perspective on the evolution of tree responses to climate over time.

Results

Growth divergence and chronologies

After calculating growth trends for all trees, we found that sites J1 and P1 each contained one group with increasing and one with decreasing growth trends. Hence, they were separated for chronology building (Fig. 2) and subsequently termed J1D and

Fig. 2 The standard ring-width chronologies, 48-year smoothing (thicker line), and their corresponding sample depth, (**a**) S1; (**b**) S2; (**c**) P1, dashed line P1I and continuous line P1D; (**d**) P2; (**e**) J1, dashed line J1I and continuous line J1D; (**f**) J2



P1D (for decreasing) and J1I and P1I (for increasing). Trees from the other four sites did not divide into groups and thus showed no growth divergence and were subsequently combined into one chronology per site, resulting in a total of eight chronologies from the six sites. Time spans of the chronologies were different and we chose a fixed common period 1900–2000 to compare the quality of different chronologies. MS and first-order serial AC varied from 0.304 to 0.696 and from −0.004 to −0.124, respectively. All sites (except S1) exhibited low serial AC in their mean chronologies (in Table 2), which was mostly removed after autoregressive modeling of single series. Two useful parameters for evaluating the quality of a chronology are the mean interseries correlation (R_{bt}, varied from 0.248 to 0.694) and the EPS (varied from 0.811 to 0.988). The EPS values of the chronologies are greater than 0.85 except for S2, which has a 0.983 EPS value during 1920 and 1999, but low value during 1900 and 1920, since most trees of this site were younger than 100 years. The two *Sabina* sites (J1 and J2) had lower R_{bt} and EPS values, but all EPS values were above the accepted cut-off of 0.85 (Wigley et al. 1984).

Smoothing the chronologies with a 48-year spline showed that the two sub-chronologies from a site (J1D and J1I; P1D and P1I) had a very similar short-term variation but different long-term trends (Fig. 2).

Influence of climate and the stability of the tree ring growth–climate relationships

Regional influences of climate on tree growth

Most chronologies show a strong, consistent, and positive relationship with precipitation during the current growth season (Fig. 3). June precipitation was the key variable for tree growth in both mountain ranges. The strength of the positive correlations, however, varied over time except for J1D and J2.

Climate–growth relationships of each species

First noticeable in the *Pinus* chronologies is the high climate sensitivity of P1I chronology, which shows significant correlation with several climate parameters. P1D and P2 have quiet similar relationships but less significant than P1I. The *Pinus* trees are generally limited by growth season (especially June) precipitation, but this relationship weakened and is not significant in recent years. September temperature of the growing season and October precipitation of the previous year had influence on all *Pinus* chronologies with a positive relationship, but the relationships are not stable during the calculated time period. During the growing season, temperature seems to play a limited role for tree growth with negative relationships, for example, in August and March. These relationships are not stable over time. In P1I, two stable positive relationships between tree growth and prior October and December started from early 1980 and became stronger and stable in recent time. Also, in P1I, there is a noticeable phenomenon that the precipitation seems to affect growth of P1I moving forward from July to May over time.

The *Sabina* chronologies are not consistent with each other. At the J1 site, both J1D and J1I have a strong negative correlation with June temperature, but while this relationship in both chronologies weakened over time, it recently dropped to non-significant in J1I. This weakening of the negative correlation with June temperature in J1I is concurrent with an emergent positive correlation with June precipitation. The positive correlations with prior November and December temperature and negative correlation with the precipitation of August and September in J1I also became stable and significant during the second half of the record. In J1D, the negative relationships with temperature of January and February gradually became stronger. At the J2 site, May temperature and September temperature affected tree growth with negative and positive relationships, previous December temperature started to affect tree growth with a significant positive relationship, which became stronger in the late twentieth century.

In S1, the relationships between tree growth and current September temperature and June precipitation are positive, but the relationships dropped to non-significant at the end of the record. Instead, a negative relationship between the S1 chronology and several monthly temperatures became significant at the end of the record. S2 has mainly stationary significant positive correlations with prior October and current June precipitation over time.

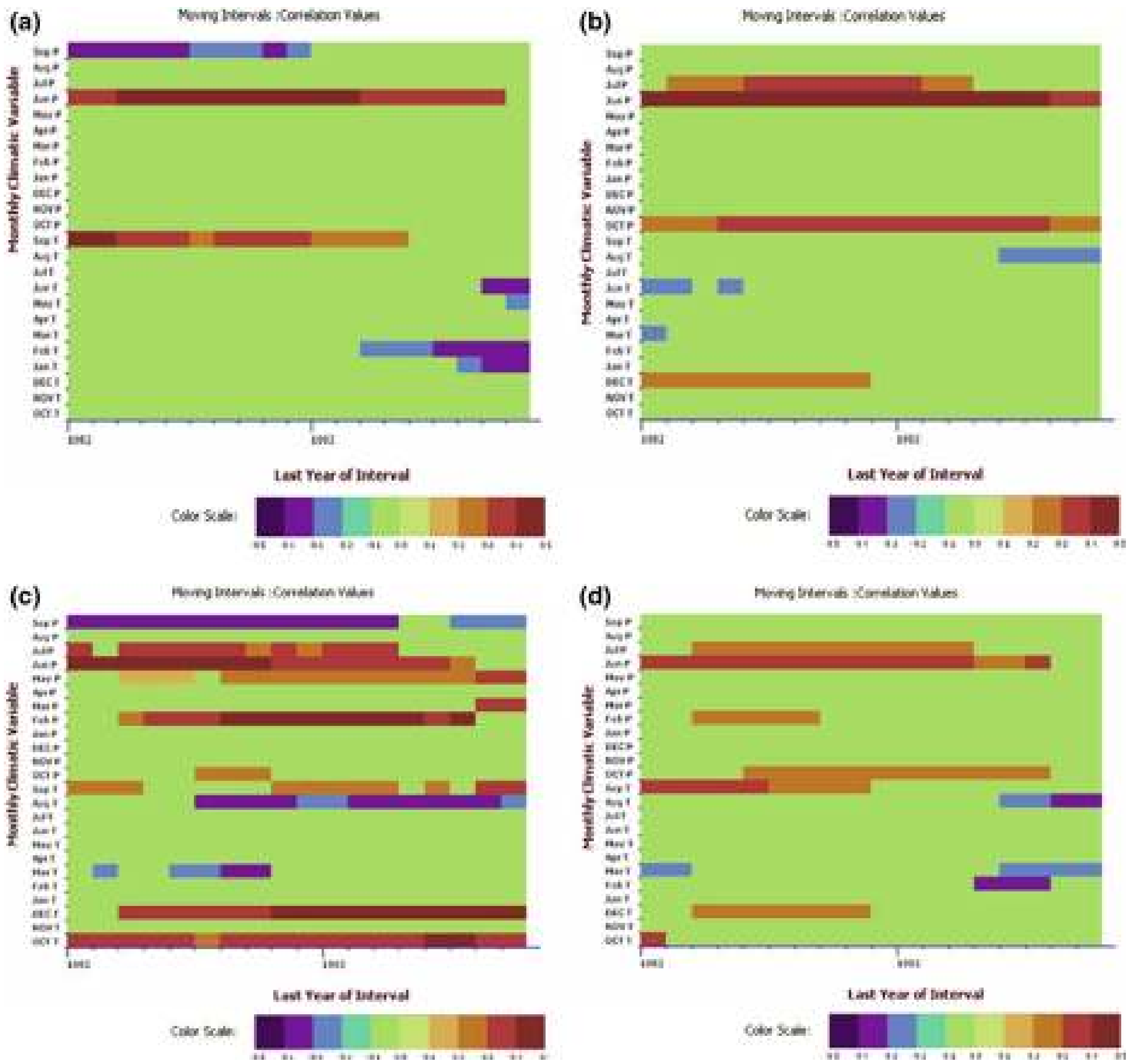


Fig. 3 Moving correlations between climate variables (monthly mean temperature (T) and monthly total precipitation (P)) and tree ring chronologies (**a**) S1; (**b**) S2; (**c**) P1I; (**d**) P1D; (**e**) P2; (**f**) J1I; (**g**) J1D; (**h**) J2. Previous year October—current year September were used in the analyses

Seasonalized pattern

For different seasons, trees from different sites (except J1D and S2) display similar relationships with temperature and precipitation (Table 3). In previous year's autumn and early winter (from October to December), there is a positive relationship between tree growth and both temperature and precipitation. During winter, early spring, and summer, trees have similar negative relationships with temperature but some positive relationships with precipitation. The response pattern to precipitation was generally opposite to the correlations with temperature during growing season (May, June, July) and September.

Discussion

Recent studies show several problems with the development of tree growth–climate relationships, e.g.,

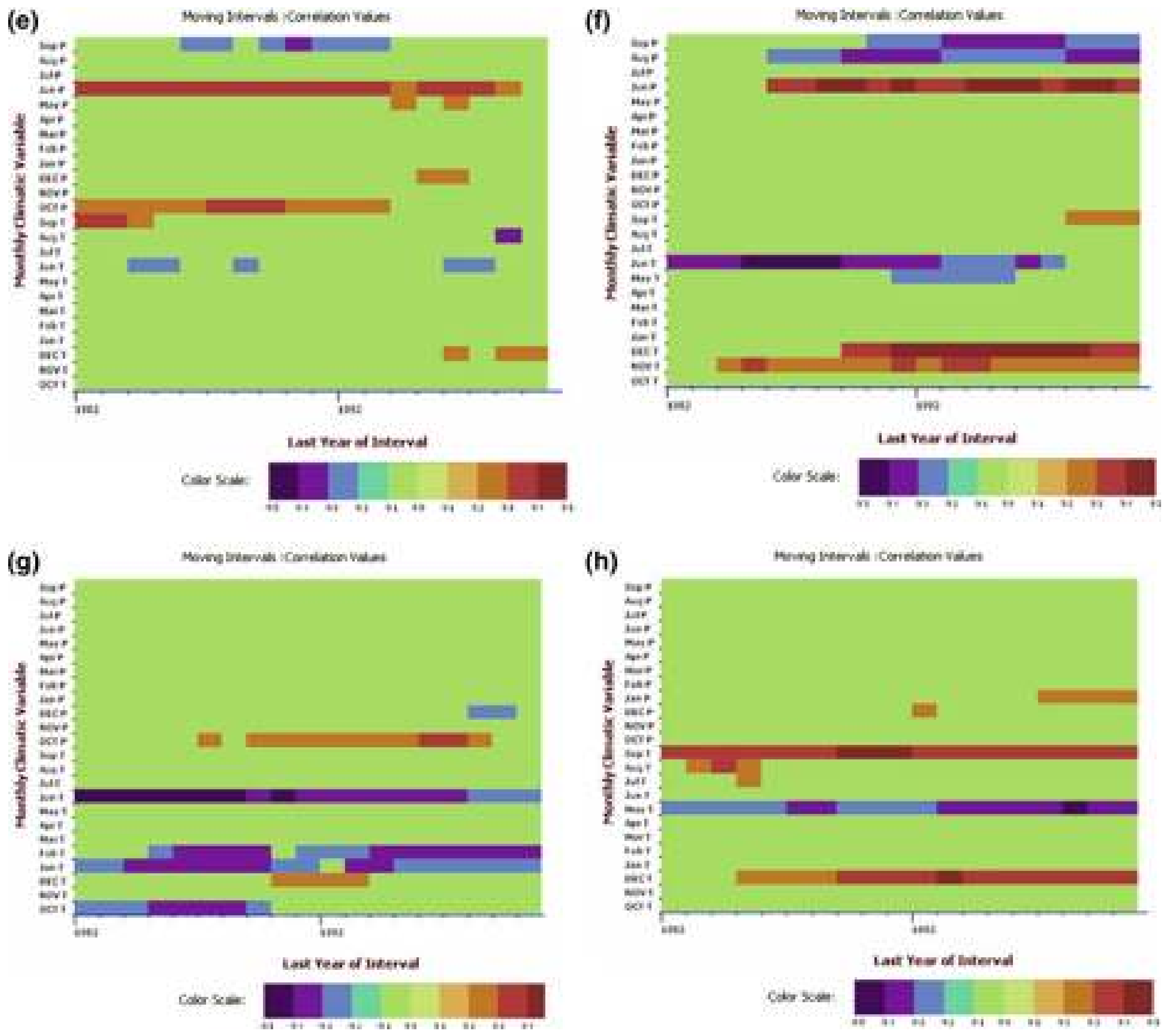


Fig. 3 continued

growth divergence of subpopulations (Wilmking et al. 2004, 2008), the "divergence problem" or underestimation of current temperatures by tree ring-based climate reconstructions (D'Arrigo et al. 2008) and changing relationships between tree growth and temperature variability (e.g., Carrer and Urbinati 2006), most of them occurring circumpolar at high northern latitudes. Here, we present evidence of growth divergence and instability of tree growth–climate relationships in three conifer tree species in northwest China. Two species (*Sabina* and *Pinus*) at two different sites show subpopulation behavior with growth divergence but the other sites do not. The growth divergences at these sites appeared not only in late twentieth century but also about 1920 (Fig. 4) in both species at similar times but with differing amplitude. The largest divergences occurred in *Sabina* in the late twentieth century but in *Pinus* during the 1920s. The growth divergence here is different from the growth divergences shown in other studies (Wilmking et al. 2005; Pisaric et al. 2007), which only reported growth divergence in the late twentieth century. Unfortunately, our sample size of different sites is inadequate to comprehensively address the question, if the growth divergence observed in this study is the result of a specific combination of site factors, such as elevation, slope, and exposure.

Table 3 The signs of significant moving correlation coefficients between chronologies and monthly climate factors (mean temperature T and total precipitation P)

	T								P							
	P1I	P1D	P2	S2	S1	J1I	J1D	J2	P1I	P1D	P2	S2	S1	J1I	J1D	J2
P-Oct	+	+					−		+	+	+	+			+	
P-Nov						+										
P-Dec	+	+	+	+		+	+	+			+				−	+
Jan					−		−									+
Feb		−			−		−		+	+						
Mar	−	−		−					+							
Apr																
May					−	−		−	+		+					
Jun			−	−	−	−	−		+	+	+	+	+	+		
Jul								+	+	+		+				
Aug	−	−	−	−				+						−		
Sep	+	+	+		+	+		+	−		−		−	−		

All correlation coefficients were calculated based on a 48-year time interval and previous year October (P-Oct)—current year September were used in the analysis

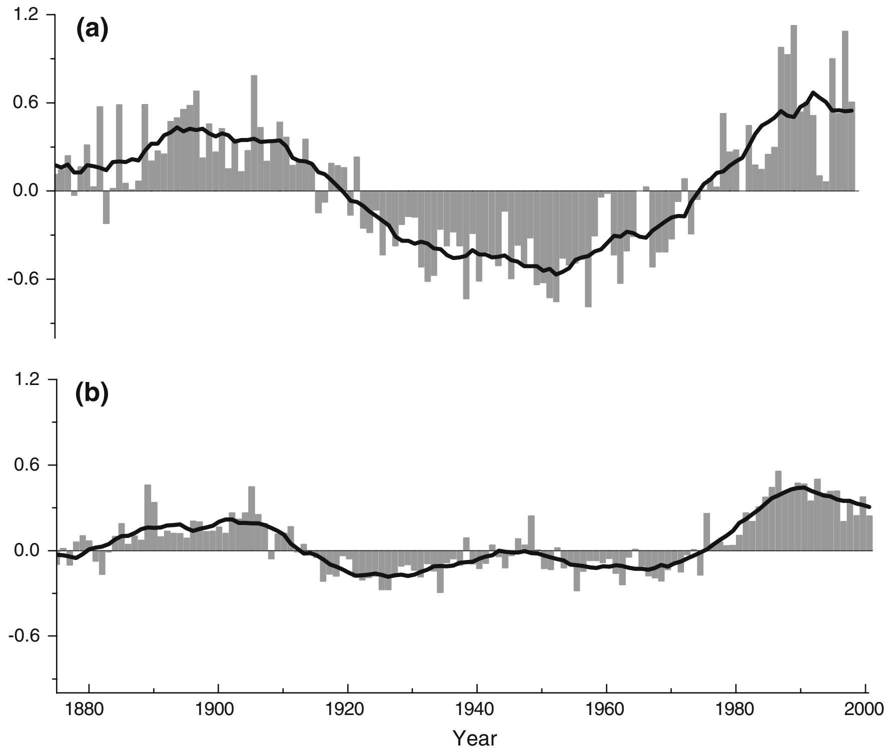


Fig. 4 An index of growth divergence in P1 (**a**) and J1 (**b**) shows similar trends but different amplitudes over the period 1934–1999. The thick lines are 11-year smoothing lines

Although the growth responses to climate revealed by most chronologies support the common fact that growing season (especially June) precipitation is the main limiting factor for tree growth, there are still other phenomena: (1) Positive correlations between tree growth and previous year autumn temperature suggest that the warm October condition likely support trees to keep carbohydrate storage and perhaps increased foliage or wood production in the subsequent growing season (Julian 2000; Schaberg et al. 2000). Previous studies indicate that temperate conifers have a positive carbon gain in warm winter days when their leaves are not frozen (Chabot and Hicks 1982; Havranek and Tranquillini 1995). (2) Negative relationship with temperature and positive relationship with precipitation during winter and early spring (from January to March) might indicate the protection of snow cover at high elevation. At the alpine timberline, Oberhuber (2004) found that trees show a tendency to suffer from enhanced desiccation during winter and early spring periods with insufficient snow depth because of increased transpiration rates of needles and shoots, photo inhibitory stress, and short-term fluctuations in shoot temperatures. (3) The warm autumn of the current year also has a strong effect on tree growth in most species. Trees seem to grow better during the warmer autumn. According to Shi et al. (2008), temperature could play an important role on tree ring formation at the end of the growing season in arid and semi-arid areas by prolonging the growing season.

The instable relationships over time between tree growth and climate factors might have been caused by different combination of climate factors (e.g., temperature and precipitation). Recent studies indicate that there is an ongoing warming and drying trend for all seasons in north central China (Wang and Zhou 2005; Zhai et al. 2005; Ma and Fu 2006). Individual trees (especially *Pinus* and *Sabina*) might have become more sensitive to micro-site differences, resulting in the breakdown of the uniform growth behavior at the sites and subsequent differing growth trends and climate sensitivity. One example is that the chronologies with increasing trend show more stable positive correlation with June precipitation than the chronologies with decreasing growth trend. The high correlations with prior winter and autumn of the current year appeared in both increasing chronologies during the calculated time period, indicating that those trees could take advantage of the available conditions better than trees of the decreasing chronology. However, the decreasing trees started to become more sensitive to the temperature during the late spring and early summer, which could be induced by more desiccation through increasing evaporation before the arrival of the summer monsoon (Ding 1994). Furthermore, the positive correlation with precipitation, gradually moving forward from July to May in the P1I chronology, might also indicate the drying trend in the early growth season.

Conclusion

Recent studies discussed three major challenges to the field of dendroclimatology, (1) changing relationships between tree growth with climate over time, (2) emerging sub-chronology behavior at sites formerly considered suitable to build one chronology, and as a possible result, (3) the "divergence problem" or underestimation of recent warming trends by tree ring-based climate reconstructions. Many of these studies were conducted either in the boreal zone or at altitudinal tree limit in Europe. Here, we present evidence of the first two phenomena in mid-latitude NW China. Diverging growth trends were found in *Pinus* and *Sabina* sites but not in *Picea* sites. The correlations between tree growth with climate factors at most sites are instable over time, as also indicated by switches from significant to non-significant or vice versa relationships with climate factors at different periods of the record. Non-divergent sites have more stationary relationships with climate factors than chronologies from divergent sites. There, decreasing chronologies show more stable relationships with climate than increasing chronologies, which are more sensitive to climate factors, indicated by higher correlation scores.

For the future, we see a major need for additional work at two fronts: (1) to test more regions and species for the phenomena of changing climate–growth relationships over time and (2) to better understand the mechanisms affecting growth from the level of the individual tree to the population through time. Only then can we safely proceed to use tree rings as robust source of paleoclimatic information.

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References

Barber V, Juday G, Finney B (2000) Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405:668–672. doi:10.1038/35015049

Biondi F (1997) Evolutionary and moving response functions in dendroclimatology. Dendrochronologia 15:139–150

Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput Geosci 30:303–311. doi:10.1016/j.cageo.2003.11.004

Briffa K, Schweingruber F, Jones P, Osborn T (1998a) Reduced sensitivity of recent tree growth to temperature at high northern latitudes. Nature 391:678–682. doi:10.1038/35596

Briffa K, Schweingruber F, Jones P, Osborn T, Harris I, Shiyatov S et al (1998b) Trees tell of past change climates: but are they speaking less clearly today? Philos Trans R Soc Lond B Biol Sci 353:65–73. doi:10.1098/rstb.1998.0191

Carrer M, Urbinati C (2006) Long-term change in the sensitivity of tree-ring growth to climate forcing in Larix decidua. New Phytol 170:861–872. doi:10.1111/j.1469-8137.2006.01703.x

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annu Rev Ecol Syst 13:229–259. doi:10.1146/annurev.es.13.110182.001305

Cook ER (1985) A time series approach to tree-ring standardization. PhD thesis, University of Arizona

Cook ER, Kairiukstis LA (1990) Methods of dendrochronology. Kluwer, Dordrecht

Cook ER, Peters K (1997) Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene 7:361–370. doi:10.1177/095968369700700314

D'Arrigo R, Kaufmann R, Davi N, Jacoby G, Laskowski C, Myneni R et al (2004) Thresholds for warming-induced growth decline at elevational treeline in the Yukon Territory. Global Biogeochem Cycles 18:GB3021. doi:10.1029/2004GBO02249

D'Arrigo R, Wilson R, Liepert B, Cherubini P (2008) On the "divergence problem" in northern forests: a review of tree-ring evidence and possible causes. Global Planet Change 60:289–305. doi:10.1016/j.gloplacha.2007.03.004

Ding YH (1994) Monsoon over China. Kluwer Academic Publisher

Driscoll W, Wiles G, D'Arrigo R, Wilmking M (2005) Divergent tree growth response to recent climatic warming, Lake Clark National Park and Preserve, Alaska. Geophys Res Lett 32:L20703. doi:10.1029/2005GL024258

Fritts HC (1976) Tree ring and climate. Academic Press, London

Gao SY, Lu RJ, Qiang MR (2005) Reconstruction of precipitation in the last 140 years from tree ring at south margin of the Tengger Desert, China. Chin Sci Bull 50(21):2487–2492. doi:10.1360/982005-363

Gou XH, Chen FH, Wang YJ, Shao XM (2001) Spring precipitation reconstructed in the east of the Qilian Mountain during the last 280 a by tree ring width. J Glaciol Geocryol 23(3):292–296 (in Chinese)

Greenough G, McGeehin M, Bernard SM (2001) The potential impacts of climate variability and change on health impacts of extreme weather events in the United States. Environ Health Perspect 109(Suppl. 2):191–198

Havranek M, Tranquillini W (1995) Physiological processes during their winter dormancy and their ecological significance. In: Smith WK, Hinkley TM (eds) Ecophysiology of coniferous forest. Academic Press, New York, pp 95–124

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Bull 43:69–78

Hoyt D (2006) Urban heat islands and land use changes. http://www.warwickhughes.com/hoyt/uhi.htm

Hughes MK (2002) Dendrochronology in climatology—the state of the art. Dendrochronologia 20:95–116. doi:10.1078/1125-7865-00011

IPCC Fourth AR (2007) Summary for policy makers In: Climate change 2007 Cambridge University Press, Cambridge

Jacoby GC, D'Arrigo R (1995) Tree-ring width and density evidence of climatic and potential forest change in Alaska. Global Biogeochem Cycles 9:227–234. doi:10.1029/95GB00321

Jacoby GC, D'Arrigo R, Davaajamts TS (1996) Mongolian tree rings and twentieth century warming. Science 273:771–773. doi:10.1126/science.273.5276.771

Jacoby GC, Lovelius N, Shumilov O, Raspopov O, Kurbainov J, Frank D (2000) Long-term temperature trends and tree growth in the Taymir region of northern Siberia. Quat Res 53:312–318. doi:10.1006/qres.2000.2130

Julian LH (2000) Effect of daily minimum temperature on photosynthesis in eastern Hemlock (*Tsuga canadensis* L.) in Autumn and Winter. Arct Antarct Alp Res 32(4):368–374. doi:10.2307/1552384

Kahn ME (2005) The death toll from natural disasters: the role of income, geography, and institutions. Rev Econ Stat 87(2):271–284. doi:10.1162/0034653053970339

Kang XC, Chen GD, Kang ES, Zhang QH (2002) Based tree rings data reconstruction over 1000-year streamflow of mountain pass in Heihe River. Sci China Ser Dokl Earth Sci 32(8):675–685

Knapp PA, Soule PT, Grissino MHD (2001) Detecting potential regional effects of increased atmospheric CO_2 on growth rates of western Juniper. Glob Change Biol 7:903–917. doi:10.1046/j.1365-2486.2001.00452.x

Liu Y, Shi JF, Shishov V (2004) Reconstruction of May–July precipitation in the north Helan Mountain, Inner Mongolia since AD 1726 from tree-ring late-wood widths. Chin Sci Bull 49(4):405–409. doi:10.1360/03WD0409

Liu Y, Cai QF, Shi JF (2005) Seasonal precipitation in the south-central Helan Mountain region, China, reconstructed from tree-ring width for the past 224 years. Can J For Res 35(10):2403–2412. doi:10.1139/x05-168

Lloyd A, Fastie C (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Clim Change 52:481–509. doi:10.1023/A:1014278819094

Ma ZG, Fu CB (2006) Some evidence of drying trend over northern China from 1951 to 2004. Chin Sci Bull 51:2913–2925. doi:10.1007/s11434-006-2159-0

Melvin T (2004) Historical growth rates and changing climatic sensitivity of boreal conifers. Ph.D. thesis, Climatic Research Unit, East Anglia

Mitchell T, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int J Climatol 25:693–712. doi:10.1002/joc.1181

Oberhuber W (2004) Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. Tree Physiol 24:291–301

Pisaric M, Carey S, Kokelj S, Youngblut D (2007) Anomalous 20th century tree growth, MackenzieDelta, Northwest Territories, Canada. Geophys Res Lett 34:L05714. doi:10.1029/2006GL029139

Schaberg IG, Snyder MC, Shane JB, Donnelly JR (2000) Seasonal patterns of carbohydrate reserves in red spruce seedlings. Tree Physiol 20:549–555

Sergio R, Annie D, Tommaso A, Vinicio C (2007) Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia 152:1–12. doi:10.1007/s00442-006-0625-7

Shao XM, Huang L, Liu HB (2004) Reconstruction of precipitation variation from tree rings in recent 1000 years in Delingha, Qinghai. Sci China Ser Dokl Earth Sci 34(2): 145–153

Shao XM, Li EY, Huang L, Wang LL (2005) A 1437-year precipitation history from Qilian Juniper in the Northeastern Qinghai-Tibetan Plateau. PAGES News 13(2):14–15

Shepherd A, Wingham D (2007) Recent sea-level contributions of the Antarctic and Greenland ice sheets. Science 315(5818):1529–1532. doi:10.1126/science.1136776

Shi J, Liu Y, Vaganov EA, Li J, Cai Q (2008) Statistical and process-based modeling analyses of tree growth response to climate in semi-arid area of north central China: a case study of *Pinus tabulaeformis*. J Geophys Res 113:G01026. doi:10.1029/2007JG000547

Smith KT, Cufar K, Levanic T (1999) Temporal stability and dendroclimatology in silver fir and red spruce. Phyton Ann Rei Bot 39:117–122

Solberg BO, Hofgaard A, Hytteborn H (2002) Shifts in radial growth responses of coastal *Picea abies* induced by climatic change during the 20th century, central Norway. Ecoscience 9:79–88

Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400:149–151. doi:10.1038/22087

Wang Y, Zhou L (2005) Observed trends in extreme precipitation events in China during 1961–2001 and the associated changes in large-scale circulation. Geophys Res Lett 32:L09707. doi:10.1029/2005GL022574

Wang YJ, Chen FH, Gou XH, Du SY (2001) Study on response relationship between tree-ring and climate factors and climate reconstruction in middle region of Qilianshan Mountains. J Desert Res 21(2):135–140 (in Chinese)

Webster PJ, Holland GJ, Curry JA, Chang HR (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309(5742):1844–1846. doi:10.1126/science.1116448

Wigley TL, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J Clim Appl Meteorol 23:201–213. doi :10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

Wilmking M, Myers-Smith I (2008) Changing climate sensitivity of black spruce in a peatland-forest landscape in interior Alaska. Dendrochronologia. doi:10.1016/j.dendro.2007.04.003

Wilmking M, Juday GP, Barber VA, Zald HSJ (2004) Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biol 10:1724–1736. doi:10.1111/j.1365-2486.2004.00826.x

Wilmking M, D'Arrigo R, Jacoby G, Juday G (2005) Divergent growth responses in circumpolar boreal forests. Geophys Res Lett 32:L15715. doi:10.1029/2005GLO23331

Wilson R, Elling W (2004) Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. Trees Struct Funct 18:19–28. doi:10.1007/s00468-003-0273-z

Wilson R, Luckman BH (2002) Tree-ring reconstruction of maximum and minimum temperatures and the diurnal temperature range in British Columbia, Canada. Dendrochronologia 20(3):257–268. doi:10.1078/1125-7865-00023

Wilson R, Luckman BH (2003) Dendroclimatic reconstruction of maximum summer temperatures from upper tree-line sites in interior British Columbia. Holocene 13(6):853–863. doi:10.1191/0959683603hl663rp

Yonenobu H, Eckstein D (2006) Reconstruction of early spring temperature for central Japan from the tree-ring widths of Hinoki cypress and its verification by other proxy records. Geophys Res Lett 33:L10701. doi:10.1029/2006GL026170

Yuan YJ, Jin LY, Shao XM (2003) Variations of the spring precipitation day numbers reconstructed from tree rings in the Urumqi River drainage, Tianshan Mts. over the last 370 years. Chin Sci Bull 48(14):1507–1510. doi:10.1360/02wd0251

Zhai P, Zhang X, Wan H, Pan X (2005) Trends in total precipitation and frequency of daily precipitation extremes over China. J Clim 18:1096–1108. doi:10.1175/JCLI-3318.1

Zhang ZH, Wu XD (1996) The change and rapid shifts of moisture index and its annual variability since 1310 A.D. in Qilianshan area. Quat Sci 4:368–378 (in Chinese)

Zhang ZH, Wu XD (1997) Reconstruction of climate variation in the last 700 years in the Qi Lian Mountain area using tree-ring data. Chin Sci Bull 42(8):849–851 (in Chinese)

Does leaf-level nutrient-use efficiency explain *Nothofagus*-dominance of some tropical rain forests in New Caledonia?

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Abstract Tropical rain forests generally have a complex structure and a high diversity of species in their canopy, but in some rain forests the upper canopy is dominated by a single species. The factors controlling this dominance are uncertain. In New Caledonia, *Nothofagus* species dominate the upper canopy of some rain forests on ultramafic soils. Here we investigate whether leaf-level nutrient-use efficiency (NUE) could explain dominance by *Nothofagus*. We found no evidence of a competitive advantage in *Nothofagus* in terms of leaf-level NUE: *Nothofagus* species did not have lower leaf macronutrient concentrations, nor did they resorb more nutrients than co-occurring species on average. They did, however, have lower foliar Ni concentrations on average. Leaf decay rate across all species in a glasshouse-based trial correlated positively with foliar P and negatively with cell wall content, lignin:P, C:P, lignin:N, leaf toughness and tannin activity. Multivariate analysis suggested that total cell wall concentration exerted the strongest independent effect on variation among species in decomposition rate. Slow decomposition of *Nothofagus* leaf litter may facilitate continued dominance of the upper canopy by suppressing establishment and growth of co-occurring species or by promoting disturbance through fire, since disturbance has been suggested as necessary for regeneration and maintenance of dominance by *Nothofagus* species. However, the biological mechanisms allowing *Nothofagus* to achieve *initial* dominance of these post-disturbance forests are uncertain, and may still include *plant*-level NUE.

Keywords Decomposition · Litter · Monodominance · Resorption

Introduction

Tropical rain forests most often have a complex structure and diverse canopy composition. However, some have 50–100% of their upper canopy dominated by a single species, referred to as monodominance (Connell and Lowman 1989). These monodominant forests are not rare, occurring in all continents that support tropical rain forests (Hart et al. 1989), but are more common in some regions than others (Torti et al. 2001). The mechanisms promoting monodominance are still uncertain and may vary among forests.

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For example, monodominant forests are common in suboptimal environments, such as where poor substrate quality or severe climate prevail (Connell and Lowman 1989; Hart et al. 1989), but can also occur adjacent to mixed-canopy forest where there is no obvious spatial determinant (Read et al. 2006). Monodominant forests can be either early or late successional stages (Connell and Lowman 1989; Hart et al. 1989; Nascimento et al. 2007). Torti et al. (2001), investigating the cause of monodominance of *Gilbertiodendron dewevrei* in Congolese rain forests, suggested that it was the result of traits that modified the understorey, making it difficult for other species to co-exist. These suggested traits included adult plants casting a deep shade and litter layer, making it difficult for seedlings of other species to establish, with a leaf litter slow to decompose, potentially reducing nitrogen availability.

In New Caledonia, *Nothofagus* species dominate the upper canopy of some tropical rain forests on ultramafic soils. These stands are often contiguous with diverse mixed-canopy forests, also on ultramafic soils (Read et al. 2000, 2006). Comparison of *Nothofagus* forests and adjacent mixed rain forest showed little evidence of soil-mediated boundaries (Read et al. 2006) and the factors controlling the local boundaries of these *Nothofagus*-dominated forests are uncertain. It is likely that numerous factors contribute, but in apparent contrast to the *Gilbertiodendron* forests, preliminary data suggest that the *Nothofagus*-dominated stands, at least in the lowlands, are an *early* successional stage following disturbance such as fire or cyclone, potentially replaced by mixed rain forest in the absence of further disturbance (Read and Hope 1996; Read et al. 2006). Here, we focus on traits that might allow *Nothofagus* to dominate the upper canopy of these early (first generation) post-disturbance forests.

One of the key traits facilitating monodominance in this case may be a high nutrient-use efficiency (NUE). The ultramafic soils on which the *Nothofagus* forests grow in New Caledonia have high contents of heavy metals such as Ni, which can be toxic to plants, and low concentrations of macronutrients, particularly Ca, P and K (Jaffré 1992; Read et al. 2006). Plants have evolved characteristics to cope with low levels of soil nutrients, including efficient acquisition of nutrients, internal nutrient economy via redistribution and/or low nutrient requirements (Clarkson and Hanson 1980; Aerts and Chapin 2000). Plants that are efficient with respect to soil nutrients produce more growth per absorbed nutrients than inefficient ones, especially when nutrient supplies are low (Clarkson and Hanson 1980). Hence, NUE may be the key trait allowing *Nothofagus* species to dominate these forests on infertile soils.

This study aims to determine if *Nothofagus* species differ from co-occurring species in some components of leaf-level NUE. Leaf-level NUE, a component of whole-plant NUE, operates at three levels, the initial green leaf NUE (INUE), the leaf life span (LNUE) and post- or senesced leaf NUE (PNUE). Foliar nutrient concentration and resorption during senescence contribute to the efficiency with which nutrients are used in nutrient-limited environments (Vitousek 1984; Aerts and Chapin 2000). Resorption can also affect neighbouring plants by influencing rates of nutrient input to the system through decomposition, with lower litter nutrient concentrations commonly resulting in slower decomposition (Swift et al. 1979; Aerts and Chapin 2000; Hobbie and Vitousek 2000). Hence, resorption traits may influence the capacity of *Nothofagus* to dominate the canopy of early successional forests by increasing whole-plant NUE and growth rate, and prolong the period of dominance by decreasing access to nutrients for competing species with higher nutrient demands. We address the following specific questions: (1) Do *Nothofagus* species have lower foliar nutrient concentrations and higher resorption efficiency and proficiency than co-occurring species, suggesting a lower nutrient demand and high efficiency of use at the leaf level? (2) Do the leaves of *Nothofagus* species decompose more slowly than those of co-occurring species, thereby potentially affecting nutrient cycling and availability to other species? (3) What leaf traits contribute to variation in decomposition among these species? In particular, we examine the roles of litter nutrient content, cell wall, phenolics and leaf toughness.

Methods

Site selection and leaf collection

Four study sites were selected in *Nothofagus* forests in the southeast of the main island of New Caledonia

(Table 1), across a range of soils, altitudes and canopy compositions (described in Read et al. 2002, 2006). These evergreen forests experience an annual rainfall of ca. 1,800–3,500 mm, with a short drier season from September to November of variable severity and duration. All forests were on ultramafic soils, but those at Col de Mouirange were influenced by gabbro intrusions, having higher concentrations of Ca and slightly lower concentrations of Ni (Read et al. 2006). Leaves were collected in October–November 2005 from the dominant *Nothofagus* species at each site and 4–7 co-occurring canopy species, each from a different family (Table 1). Sites could generally not be replicated at each location and so trees form the replicates for within-site analyses. At maturity, these species occupy various levels of the forest canopy. Most of the selected species occupy the middle to upper canopy, with trunk diameters at breast height commonly exceeding 20 cm. The green leaves sampled were the most recent fully expanded and hardened leaves with an age <1 year. Senesced leaves were selected if they were yellow or red (not brown), with no evidence of decay. Green and senesced leaves were collected from the same tree

Table 1 Species collected at each study site

Site and species	Measurements
Col de Mouirange Haut (CDMh): 22°12′ S, 166°40′ E, 320 m asl	
Nothofagus aequilateralis (Baum.-Bodenh.) Steenis (Nothofagaceae)	g, s, d
Agathis lanceolata Lindley ex Warb. (Araucariaceae)	g, s
Arillastrum gummiferum (Brongn. & Gris) Pancher ex Baill. (Myrtaceae)	g, s
Codia discolor (Brongn. & Gris) Guillaumin (Cunoniaceae)	g, s, d
Deplanchea speciosa Vieill. (Bignoniaceae)	g, s, d
Hibbertia lucens Brongn. & Gris ex Sebert & Pancher (Dilleniaceae)	g, s
Col de Mouirange Bas (CDMb): 22°12′ S, 166°41′ E, 250 m asl	
Nothofagus discoidea (Baum.-Bodenh.) Steenis	g, s, d
Acropogon dzumacensis (Guillaumin) Morat (Malvaceae)	g, s, d
Cerberiopsis candelabra var. *candelabra* Vieill. (Apocynaceae)	g, s, d
Crossostylis grandiflora Pancher ex Brongn. & Gris (Rhizophoraceae)	g, s, d
Diospyros parviflora (Schltr.) Bakh. f. (Ebenaceae)	g, s, d
Ficus austrocaledonica Bureau (Moraceae)	g, s, d
Storthocalyx chryseus Radlk. (Sapindaceae)	g, s
Dzumac: 22°3′ S, 166°28′ E, 940 m asl	
Nothofagus codonandra (Baill.) Steenis	g, s, d
Alphitonia neocaledonica (Schltr.) Guillaumin (Rhamnaceae)	g, s, d
Cryptocarya guillauminii Kosterm. (Lauraceae)	g, s, d
Flindersia fournieri Pancher & Sebert (Flindersiaceae)	g, s, d
Gastrolepis austrocaledonica (Baill.) Howard (Stemonuraceae)	g, s, d
Myodocarpus fraxinifolius Brongn. & Gris (Araliaceae)	g, s, d
Strasburgeria robusta (Vieill. ex Pancher & Sebert) Guillaumin (Strasburgeriaceae)	g, s, d
Styphelia pancheri (Brongn. & Gris) F. Muell (Ericaceae)	g, s, d
Col de Yaté: 22°10′ S, 166°54′ E, 340 m asl	
Nothofagus balansae (Baill.) Steenis	g, s, d
Calophyllum caledonicum Vieill. (Clusiaceae)	g, s, d
Elaeocarpus yateensis Guillaumin (Elaeocarpaceae)	g, s, d
Guettarda eximia Baill. (Rubiaceae)	g, s, d
Neoguillauminia cleopatra (Baill.) Croizat (Euphorbiaceae)	g, s, d
Planchonella kuebiniensis Aubrév. (Sapotaceae)	g
Semecarpus neocaledonica Engl. (Anacardiaceae)	g, s, d

Sites have been described in Read et al. (2000, 2006). The forest chosen at Col de Yaté contains *Nothofagus* but is not monodominant. Species nomenclature is taken from Jaffré et al. (2004). The ‘measurements’ column indicates the species included in analyses: g, green leaf traits; s, senesced leaf traits; d, decomposition study where possible, from sun-lit branches on forest edges or in large canopy gaps. Leaves of 4 of the 28 species, however, were collected from the forest floor (both green and senesced leaves) because of difficulty in collecting leaves from branches; therefore, their growth light environment is uncertain. However, these were trees of the uppermost forest canopy, and leaves were not likely to have been very heavily shaded. Leaves were only collected when they appeared fresh, as judged by colour and glossiness. Three to five replicate trees or collecting points were used for each species. Leaves used in chemical analyses were initially air-dried, then freeze-dried and ground to a powder in a ball mill.

Leaf traits

Macronutrient concentrations (N, P, K, Ca and Mg) were measured in green and senesced leaves, allowing determination of nutrient contents of functional leaves and of resorption. Resorption was measured as resorption efficiency and proficiency. Resorption efficiency (the percentage reduction of nutrients between green and senesced leaves) can indicate the degree to which nutrients are conserved in foliage, encompassing both nutritional demand and nutrient withdrawal by the plant, and resorption proficiency (the nutrient concentration of senesced leaves) indicates the absolute levels to which nutrients can be reduced in a plant, providing a measure of the degree to which selection has acted to minimise nutrient loss (Killingbeck 1996). Use of nutrient concentration per mass to estimate resorption efficiency may lead to errors due to changes in leaf mass caused particularly by resorption of compounds during senescence, but these errors are relatively small (Aerts 1996). Some error may also arise from the assumption of an identical constitution of senesced leaves when young to the green leaves sampled. We assume here that any such errors will be consistent across species. In addition to macronutrients, we measured Ni since it is potentially toxic and species vary in their capacity to exclude or tolerate this metal in their leaves (Baker 1981). Nitric acid digestion (USEPA Method 3050B) was used to extract macronutrients and metals (P, K, Ca, Mg and Ni are reported) from freeze-dried ground leaves prior to measurement by ICP-OES. C and N were determined by a Leco® CHN-2000 autoanalyser. All were expressed per unit leaf dry mass.

We measured other traits of senesced leaves suggested to affect decomposition rates (phenolics, cell wall content and toughness). "Total phenolics" were extracted in acetone following Cork and Krockenberger (1991), and assayed by the Prussian-Blue method (Price and Butler 1977) as modified by Graham (1992), with concentration expressed as gallic acid equivalents (GAE) per leaf dry mass. Tannins were extracted as for total phenolics, and tannin activity was estimated by the mass of protein precipitated using the Blue BSA (bovine serum albumen) method of Asquith and Butler (1985), with a bovine gamma globulin standard and was expressed per unit leaf dry mass. Cell wall content was measured as neutral detergent fibre (NDF, a measure of total cell wall, not including pectins), acid detergent lignin (ADL, a measure of lignin plus cutin) and cellulose, following Van Soest (1994).

Leaf toughness was measured on fresh hydrated green leaves, since differential water content among senesced leaves could confound interpretation. Toughness, measured as work to fracture, was determined for five leaves per species (within 24 h of collection) using a shearing test on a 5-mm-wide strip cut from one side of the leaf and sheared transversely at a random position along its length following Read and Sanson (2003). For *Calophyllum caledonicum*, which has closely spaced secondary veins perpendicular to the midrib, we cut across the veins rather then parallel to them. The force–displacement curve derived from each test was analysed by Leaf2000 software (M. Logan, Monash University). We calculated the work required to shear the leaf strip as the area under the force–displacement curve, expressed per unit strip width, and specific work to shear as the work to shear per unit strip thickness, with thickness measured by a digital micrometer. We measured specific leaf area (SLA) of senesced leaves, but for a few species for which leaves were scarce, we used green leaves (1–12% higher for species in which both leaf classes were measured).

Leaf decomposition experiment

Rates of leaf decomposition were determined by a glasshouse-based litter bag experiment, modified from Cornelissen (1996). Air-dried leaves were dried at 40°C for 48 h and weighed. Then, one or more leaf halves (depending on leaf size) were placed in a polyester litterbag with a mesh size of 1 mm. Individual bag size was determined by the size of the leaves to keep the individual leaf in contact with the substrate. Three to five replicate bags per species were used, depending on leaf availability. We compared leaf decomposition rates in packs of litter weighing 1–2 g with litterbags containing an individual leaf for seven species. Plastic planter bags ca. 20 × 10 cm were prepared 1 week prior to litterbag burial with 7-cm depth of commercial plant-based compost, and a thin layer of mixed decomposing leaf litter from the Monash University systems garden to ensure a range of soil microbes was present. One litter bag was placed in each pot in March 2006 and covered with 5 cm of compost. Pots were randomised in position in a glasshouse (mean daily maximum temperature of 26.1°C, with a minimum humidity of 75%) and watered twice daily to maintain moist conditions typical of rainforest. After 7 weeks, leaves in some additional 'trial' bags (checked every ca. 2 weeks to observe the rate of decomposition) were already highly decomposed. Therefore, litter bags in the main experiment were removed after 8 weeks so that differences among species in decomposition rate would be apparent. The leaves were lightly rinsed to remove extraneous material and dried at 40°C to constant mass. Samples were then weighed to determine percentage mass loss.

Data analysis

The data were analysed at two levels. First, *Nothofagus* species were compared with the average of other species (the average of the 4–7 species' means) across all sites using a randomised block design (sites as blocks). Any 'site' effects are potentially the result of differences in site growth conditions and/or differences in the suite of species. The data were then analysed separately for each site using a planned contrast between the dominant *Nothofagus* species and co-occurring species, i.e. comparing the average value of the *Nothofagus* species with the average of the means of the co-occurring species. We were only interested in large-scale trends, and so did not compare *Nothofagus* species to individual species at each site. Pearson correlation was used to investigate associations between decomposition rate and other leaf traits. *T*-tests were used to determine differences in decomposition rates between leaf packs and individual leaves. Principal components analysis (PCA) was used to summarise traits of senesced leaves suggested in earlier studies to affect decay rates. Hierarchical partitioning was used to determine independent contributions of traits to decomposition rate using the hier.part package v. 1.0–2 (Mac Nally and Walsh 2004) of R v. 2.5.1 (R Development Core Team 2004): I_{HP} indicates the percentage contribution of each trait (limited to 12 independent variables) to the total explained variance; rand.hp uses a randomisation test to compute *Z*-scores for tests of statistical significance, the latter based on an upper 0.95 confidence limit ($Z \geq 1.65$). In order to reduce the set of independent variables, we excluded SLA and Ni, which were not significantly correlated with decay rate, and cellulose, which was represented within the NDF variable. Due to rounding errors that can occur when more than nine independent variables are included (Walsh and Mac Nally 2007), we removed variables that did not consistently make a significant contribution in repeated analyses with variables entered in differing order (N, C:N and total phenolics). SYSTAT v. 11® was used for all other analyses. A critical value of $\alpha = 0.05$ was used for hypothesis tests.

Results

Macronutrient and Ni concentrations in green leaves

Within each site, there was ca. 2- to 8-fold variation in macronutrient concentrations among species, with most variation in K (3- to 4-fold), Ca (3- to 8-fold), Mg (2- to 7-fold) (Fig. 1) and Ca:Mg (4- to 8-fold) (Table 2). However, there were no significant differences in nutrient concentrations between *Nothofagus* species and the mean of co-occurring species across all sites (randomised block analysis, Fig. 1). High foliar N:P ratios suggested P-limitation in *Nothofagus* species and co-occurring species (Table 2). Foliar P concentration varied 2- to 3-fold among species at each site, but was lower in *Nothofagus* than the average of co-occurring species only at Col de Yaté (planned contrast of *Nothofagus* versus all other species) (Fig. 1). *Nothofagus* had higher N concentrations at Col de Mouirange than the average of co-

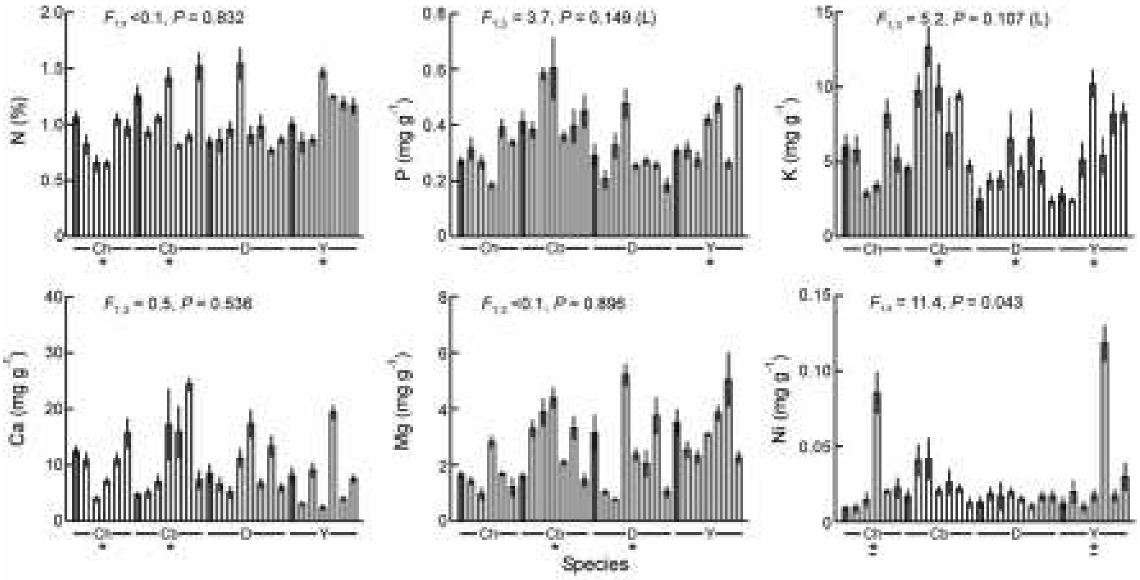

Fig. 1 Concentrations of macronutrients and Ni in green leaves at each site. Mean ± SE are given for each species, with *Nothofagus* species shown by filled bars. Species are given in the order shown in Table 1. Ch, Col de Mouirange Haut; Cb, Col de Mouirange Bas; D, Dzumac; Y, Col de Yaté. The results of randomised block ANOVA are given (L, data log-transformed for analysis). Asterisks indicate where there is a significant difference between *Nothofagus* and the mean of co-occurring species at a site (planned contrasts); a line below the asterisk indicates no significant difference after removal of an outlier

Table 2 Chemical ratios in green and senesced leaves of *Nothofagus* and other species

	Nothofagus species	Other species	$F_{1,3}$, P
N:P green	33 ± 2 (30–39)	30 ± 3 (18–49)	0.59, 0.499
N:P senesced	80 ± 30 (27–166)	63 ± 6 (25–128)	0.26, 0.647
Ca:Mg green	3.8 ± 1.4 (2.0–7.8)	5.2 ± 1.2 (0.8–19.6)	4.14, 0.135
Ca:Mg senesced (L)	5.7 ± 1.8 (3.4–11.1)	7.7 ± 2.3 (3.6–14.2)	4.86, 0.115
C:N sensesced	85 ± 4 (73–89)	90 ± 8 (51–177)	0.16, 0.715
C:P sensesced (L)	6,876 ± 2,714 (2,443–14,793)	5,479 ± 537 (2,540–12,221)	0.01, 0.952
Lignin:N sensesced	36 ± 7 (24–57)	28 ± 2 (11–53)	0.89, 0.414
Lignin:P sensesced (L)	3,491 ± 2,039 (933–9,583)	1,835 ± 90 (355–4,832)	0.16, 0.717

The data presented are mean ± SE (mass-based ratios) of *Nothofagus* (n = 4 species/sites) and other species (n = 4 sites, the value for each site being the average of 4 to 7 species' means). The range of species' means is given in brackets. ADL is given as 'lignin'. The results of randomised block analysis are given. L, log-transformed for analysis

occurring species, but lower N at Yaté (planned contrast, Fig. 1). At all sites except Col de Mouirange Haut (CDMh), K concentrations were lower in *Nothofagus* species than co-occurring species (planned contrasts, Fig. 1). Ca was lower in *Nothofagus* at Col de Mouirange Bas (CDMb), but higher at CDMh than co-occurring species, with no significant differences at Yaté and Dzumac (planned contrasts, Fig. 1). Mg concentrations and Ca:Mg were highly variable, with Mg higher and Ca:Mg (Table 2) lower in *Nothofagus* than co-occurring species at Dzumac, but Mg lower at CDMb (planned contrasts, Fig. 1). Ni levels varied 2- to 12-fold among species at each site, and were lower in *Nothofagus* species than the mean of co-occurring species across sites (Fig. 1, randomised block analysis), even after outliers were excluded ($\log_{10}$ Ni: $F = 32.8$, $P = 0.011$). However, Ni concentration was significantly lower in *Nothofagus* than co-occurring species only at CDMh and Yaté (but near-significant at CDMb: $P = 0.06$) (planned contrast, Fig. 1), but not after outliers were excluded. High Ni contents were recorded in *Codia discolor* and *Neoguillauminia cleopatra*, but no species showed evidence of hyperaccumulation (Ni > 1 mg g^{-1} foliar dry mass: Brooks et al. 1977). Comparison of sites for each element found differences only in foliar P concentrations (CDMb $>$ CDMh and Dzumac) (Fig. 1).

Macronutrient and Ni concentrations in senesced leaves

There were no significant differences in macronutrient concentrations (resorption proficiency) and ratios of senesced leaves between *Nothofagus* species and the mean of co-occurring species across all sites (randomised block analysis, Fig. 2, Table 2). All species, except *Crossostylis grandiflora*, *Alphitonia neocaledonica* and *Guettarda eximia*, had N proficiency below the 0.7% value suggested by Killingbeck (1996) as indicating high N proficiency, with only *Arillastrum gummiferum* having N concentrations at the 0.3% level suggested to represent 'ultimate' N-proficiency (the maximum level to which nutrients can be reduced). At CDMh, higher N was recorded in senesced *N. aequilateralis* leaves than the mean of co-occurring species, with no differences at other sites (Fig. 2). Trends in P concentration varied among sites, with higher P in *Nothofagus* than the mean of co-occurring species at Dzumac, but lower at CDMb. Only *N. discoidea* (Fig. 2) had high P proficiency (<0.04% P for evergreens: Killingbeck 1996), with no species reaching the ultimate proficiency of 0.01% (Killingbeck 1996). K in senesced leaves followed a similar pattern to green leaves, but was significantly lower in *N. codonandra* at Dzumac (Fig. 2). Ca and Mg were lower in senesced leaves of *N. discoidea* than co-occurring species at CDMb (Fig. 2). Ni concentrations were lower on average in senesced *Nothofagus* leaves across sites (Fig. 2).

Resorption efficiency ranged from 28% to 64% for N, 23% to 90% for P and 12% to 89% for K across species. There were no significant differences in resorption efficiency of N, P and K between *Nothofagus* and the mean of co-occurring species across all sites (Fig. 3), and no differences among sites ($P < 0.05$).

Foliar decomposition rates and leaf traits

There was 9-fold variation in mass loss among species, and leaves of *Nothofagus* species decomposed at less than half the rate of co-occurring species

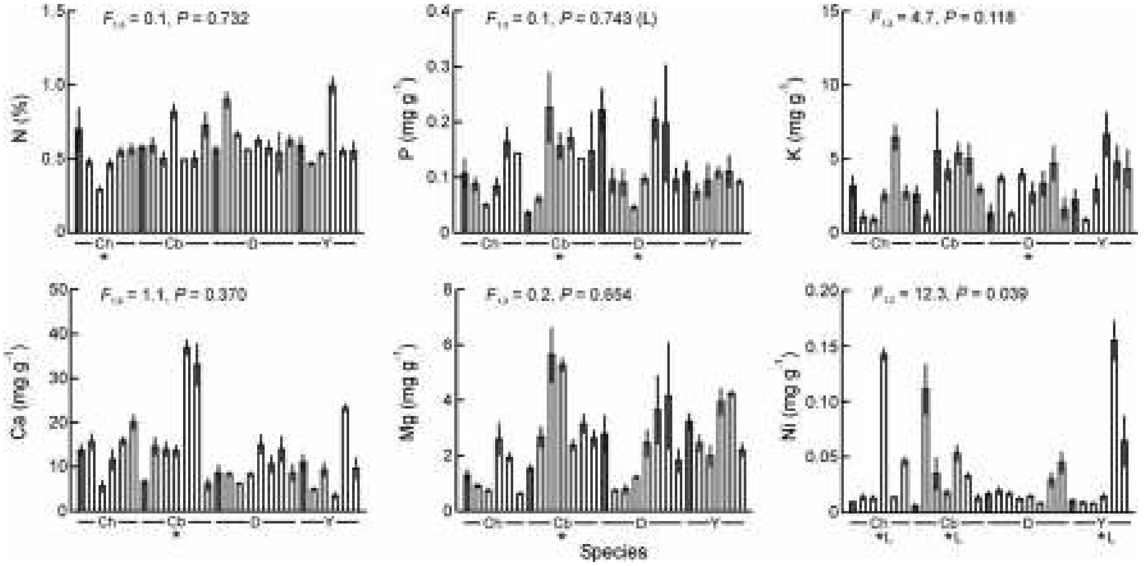

Fig. 2 Concentrations of macronutrients and Ni in senesced leaves at each site. Mean ± SE are given for each species, with *Nothofagus* species shown by filled bars. Abbreviations and results are given as in Fig. 1

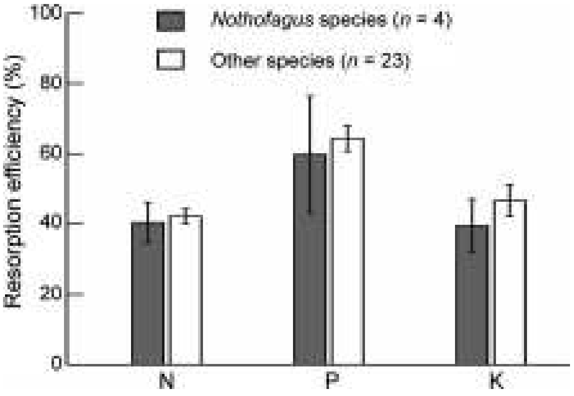

Fig. 3 Resorption efficiency of *Nothofagus* species and co-occurring species, averaging across the mean of species (±SE). Randomised block ANOVA indicated no significant effect of species (*Nothofagus* versus other species) or site. Species effects: N, $F_{1,3} = 0.2$, $P = 0.660$; P, $F_{1,3} = 0.2$, $P = 0.657$; K, $F_{1,3} = 2.2$, $P = 0.236$

on average (18% vs. 42% mass loss) (randomised block analysis, Fig. 4), with slower decomposition recorded in *Nothofagus* at CDMb and Dzumac (not at Yaté when the outlier was removed) (planned contrasts) (Fig. 4). Comparisons of single leaves with leaf packs showed either no difference (three species) or faster decay in single leaves (four species, $P < 0.05$).

Of the leaf traits commonly considered to influence decomposition rates (Table 3), only NDF differed significantly between *Nothofagus* and co-occurring species across sites (randomised block analysis, Figs. 2, 5, 6; Table 2). For other traits, differences were recorded between *Nothofagus* and the means of co-occurring species at some study sites, but not always consistently across sites. For example, leaf toughness (work to shear) was higher on average in *N. codonandra* than co-occurring species at Dzumac, but similar or lower in *Nothofagus* than co-occurring species at other sites (planned contrasts, Fig. 5). Leaf toughness per unit thickness (specific work to shear) was higher on average in *Nothofagus* than co-occurring species at Yaté and Dzumac, with no difference at the Col de Mouirange sites (Fig. 5). No difference was recorded for SLA (Fig. 5). Total phenolics and tannin activity were higher in *Nothofagus* than the average of co-occurring species at CDMb and Dzumac, but tannin activity was lower in

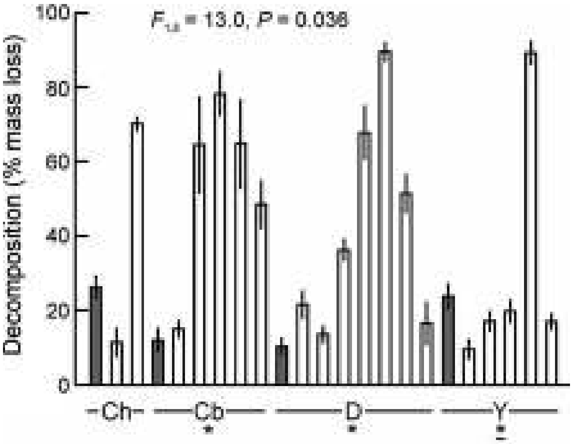

Fig. 4 Decomposition rates (given as percentage mass loss after 8 weeks) of *Nothofagus* species and co-occurring species at each site. Mean ± SE are given for each species, with *Nothofagus* species shown by filled bars. Abbreviations and results are given as in Fig. 1

Table 3 Relationships between decomposition rate (log-transformed) and traits of senesced leaves

Leaf trait	*R*	I_{HP}	*Z*
SLA	0.27		
Nitrogen	−0.03		
Phosphorus	0.50*	5.6	−0.03
Nickel	0.02		
C:N	−0.23		
C:P (L)	−0.56**	9.1	0.46
NDF	−0.78***	25.5	3.39*
ADL	−0.60**	8.7	0.52
Cellulose	−0.69***		
Lignin:N	−0.59**	7.7	0.21
Lignin:P (L)	−0.64***	10.3	1.17
Work to shear (L)	−0.48*	8.0	0.14
Specific work to shear (L)	−0.65***	13.9	1.26
Total phenolics	−0.32		
Tannin activity	−0.51*	11.1	0.90
PCA Component 1	−0.84***		
PCA Component 2	0.01		
PCA Component 3	0.16		

Values given are Pearson correlation coefficients (*R*) in the first column, with results of hierarchical partitioning analysis (I_{HP}, the independent contribution of each trait as a percentage of the explained variance, and the *Z*-score) in the second and third columns. Significance levels for *R* are given as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Significant *Z*-scores ($Z \geq 1.65$) are indicated by a single asterisk. Only nine variables were included in the final hierarchical partitioning analysis. L, log-transformed for analysis

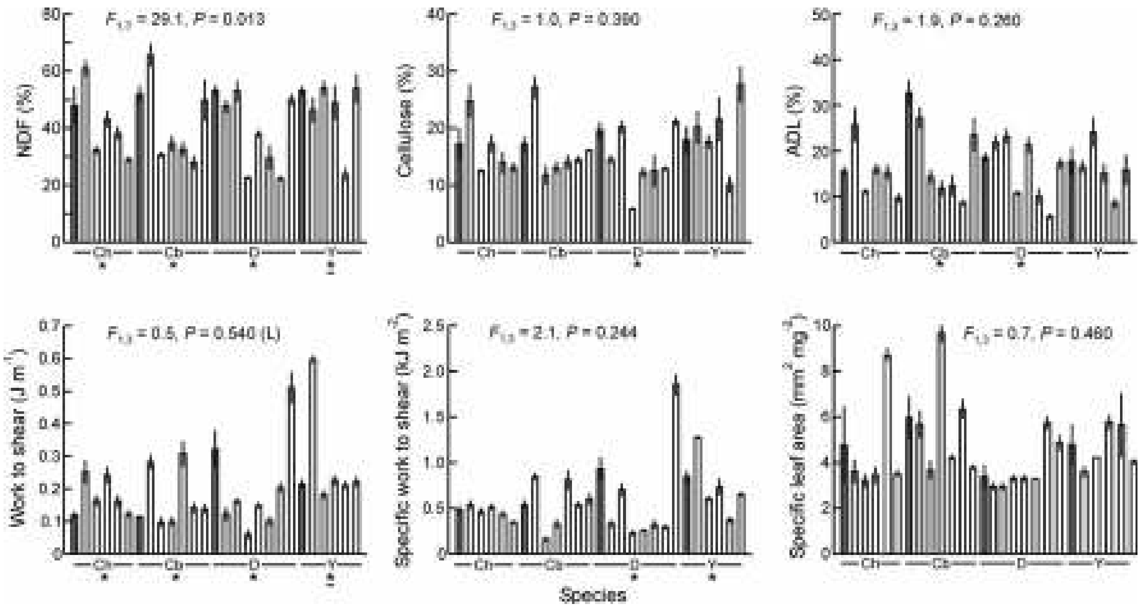

Fig. 5 Physical traits and cell wall components of leaves at each site. Traits were measured on senesced leaves except for mechanical traits, which were measured on green leaves, and SLA, which was measured on a mixture of green and senesced leaves. Mean ± SE are given for each species, with *Nothofagus* species shown by filled bars. Abbreviations and results are given as in Fig. 1

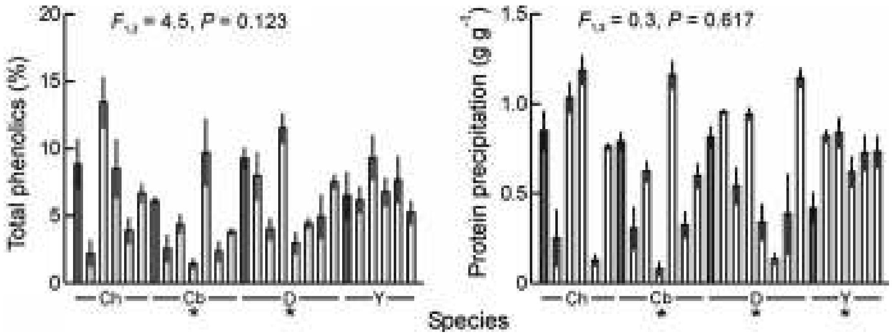

Fig. 6 Phenolic concentrations of senesced leaves at each site. Protein precipitation provides a measure of tannin activity. Mean ± SE are given for each species, with *Nothofagus* species shown by filled bars. Abbreviations and results are given as in Fig. 1

N. balansae than co-occurring species on average at Yaté (planned contrasts, Fig. 6). The C:N ratio was on average lower for *N. aequilateralis* at CDMh than co-occurring species, and *N. discoidea* had significantly higher C:P, lignin:N and lignin:P ratios at CDMb than co-occurring species (planned contrasts, data not presented). For all these traits, where there was a significant difference across or within sites, there was usually at least one other species with similar values to those of *Nothofagus*.

Leaf decomposition rates correlated positively with foliar P and negatively with measures of cell wall, lignin:N, lignin:P, C:P, tannin activity, work to shear and specific work to shear (Table 3). No correlations were recorded with SLA, N, C:N, Ni and total phenolics. PCA reduced the data to three main components explaining 69% of the variation among species (Fig. 7a). Lignin:P, lignin:N, ADL, NDF and C:P contributed most strongly to Component 1, C:N, N and SLA to Component 2, and work to shear, specific work to shear and cellulose to Component 3. The configuration plot of the first two components showed no clustering of *Nothofagus* species or of sites (Fig. 7a). Leaf decomposition rate correlated negatively with Component 1 (Fig. 7b), with more variation explained (71%) than by any individual variable (Table 3). Multiple regression showed that 82% of the variation in decomposition rate (log-transformed) was explained by the nine variables indicated in Table 3, but hierarchical partitioning indicated a significant independent contribution of only NDF (Table 3).

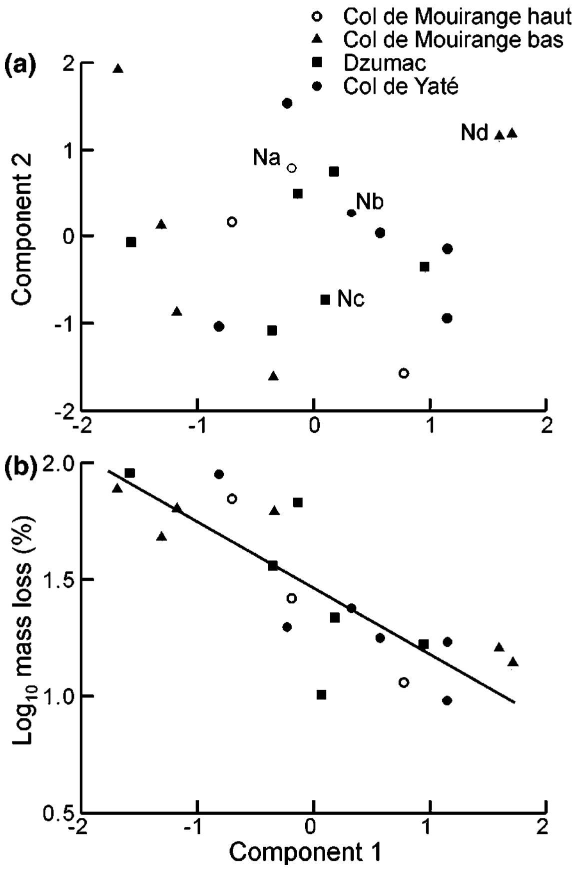

Fig. 7 PCA of the traits of senesced leaves. (**a**) The configuration plot of the first two component axes, and (**b**) the relationship between leaf decomposition rate and Component 1. The PCA was undertaken on the full set of variables given in Table 3. The *Nothofagus* species are shown by their initials in (**a**)

Discussion

Foliar element concentrations of green leaves

Foliar macronutrient concentrations were commonly on the low side of the range found in forests on ultramafic and non-ultramafic soils (Table 4), suggesting that the study species on average have high INUE. P appeared to be the limiting nutrient, with N:P ratios >16 (cf. Güsewell 2004) for all species, consistent with global trends suggesting that P-limitation is particularly common in tropical environments (Reich and Oleksyn 2004). However, in contrast to predictions, *Nothofagus* species did not have lower green-leaf nutrient concentrations (higher INUE) on average than co-occurring species for P or other nutrients, although K concentrations were lower in *Nothofagus* at three sites.

High levels of soil Ni have been recorded at these sites, but to a lesser extent at Col de Mouirange (Read et al. 2006). The degree of toxicity of Ni is site-dependant, with factors such as low soil pH and Ca concentrations influencing uptake (Proctor and Woodell 1975). Since Ca concentrations are low in these soils (Read et al. 2006), there is potential for Ni toxicity, particularly at Yaté and Dzumac. In addi-

Table 4 Foliar element concentrations (mg g^{-1}) of green leaves in rain forest species on ultramafic and non-ultramafic soils

	New Caledonian *Nothofagus*[a]	New Caledonian ultramafic[b]	Malaysian ultramafic[c]	Tropical rain forest non-ultramafic[d]
N	7.4–12.7	6.50–15.4	6.1–26.4	6.1–35.3
P	0.25–0.48	0.18–0.60	0.24–1.8	0.2–2.5
K	2.5–7.5	2.36–12.7	1.3–17.7	2.4–38.5
Ca	4.1–14.5	2.4–24.4	1.9–31.5	1.1–34.9
Mg	1.3–3.5	0.8–5.2	0.9–12.8	0.1–10.4
Ni	0.002–0.017	0.01–0.12	0.00–0.65	0.001–0.007

[a] From this study, Jaffré (1980) and Read et al. (2002)

[b] From this study, Jaffré (1980) (mean of 118–140 species), Enright et al. (2001) and Read et al. (2002)

[c] Proctor et al. (1989)

[d] Data from lowland to upper montane rain forests (Ovington and Olson 1970; Stark 1970; Tanner 1977; Grubb 1977; Thompson et al. 1992; Read et al. 2002; Plummer 2007), with few data available for Ni (Read et al. 2002; Plummer 2007)

tion, *Nothofagus* litter appears to be more acidic (pH 4) than that of mixed rain forest (ca. pH 5.5) (CDMh: McCoy 1991) and may increase Ni availability. Resistance to Ni toxicity is influenced by the ability to limit its uptake and transport, as well as tissue tolerance, each mechanism potentially incurring an energy cost. Foliar Ni content was quite variable among species in this study, but was generally at lower levels (7% of species with >0.05 mg g^{-1} Ni) than found in New Caledonian rain forests by Jaffré (1980) (58% of forest species on ultramafic soils >0.05 mg g^{-1} Ni), probably due largely to differences in soil and topographic situation between the studies. The low foliar concentration of Ni in *Nothofagus* species could be partly due to their ectomycorrhizae (VAM also weakly present in at least one species: Perrier et al. 2006). Mycorrhizal associations may play a crucial role in heavy metal tolerance in some plants (Baker and Walker 1989; Perrier et al. 2006), either due to general benefits conferred by the relationship (Meharg and Cairney 2000) or due to reduced metal uptake (Wilkinson and Dickinson 1995). If the ectomycorrhizal association reduces Ni uptake, it may provide an energetically efficient resistance mechanism. However, the low foliar Ni might be partly a consequence of the high cell wall fraction in *Nothofagus* species (Fig. 5), and so may not reflect trends among species in protoplasmic concentrations.

Post-leaf NUE—resorption efficiency and proficiency

Recycling of nutrients by decomposition and mineralisation is less efficient than resorption (Aerts and Chapin 2000), and we predicted that *Nothofagus* species would show higher PNUE than co-occurring species. Instead, resorption efficiency for N, P and K was highly variable across species, and the only significant difference was the higher resorption of P by *N. discoidea* at CDMb than co-occurring species. Low resorption rates of N (<50%) have been recorded in species with low green leaf concentrations (<1%), probably due to proportionately less leaf N being accessible for resorption (Diehl et al. 2003). Similarly, all species in this study had N concentrations below ca. 1.5%, with correspondingly low N resorption efficiency (<50%) in most species. P, like N, is fairly mobile in plants, but resorption was more variable among sites and species, suggesting lower reliance of some species on resorption even in a P-limited system. Most tropical rain forest species have mycorrhizae that are expected to increase substrate-P uptake, arbuscular mycorrhizae in most species (Connell and Lowman 1989; Smith and Read 1997) and ectomycorrhizae in *Nothofagus* (Read and Hope 1996) and some other monodominant trees (e.g. Connell and Lowman 1989; Newbery et al. 1997). It may be less energetically expensive for species to rely on substrate-available P than the resorption pathway if the mycorrhizal relationship is highly efficient (Newbery et al. 1997). The variation recorded in K resorption is not unusual as K is highly leachable, although leaching is likely to be lower on these infertile soils (Chapin 1980). Ca concentrations increased from green to senesced leaves (data not presented), as expected, given that Ca is not phloem-mobile (Chapin 1980).

Resorption proficiency may provide a better estimate of PNUE if plants control the minimum N and P concentrations of senesced leaves rather than the proportion of nutrients withdrawn (Killingbeck 1996; Aerts and Chapin 2000). N and P concentrations were low in senesced leaves of all species; most species had high resorption proficiency of N by Killingbeck's (1996) criterion, and all fell well within the range for highly proficient P resorption, further suggesting P-limitation. Levels of N and P were relatively low even compared with leaf litter from an ultramafic mountain in Sabah (means of 0.8 to 1.3 mg g^{-1} N and 0.17 to 0.26 mg g^{-1} P) (Proctor et al. 1989). However, there was no evidence of higher resorption proficiency in *Nothofagus*, except for high P-proficiency in *N. discoidea* at CDMb.

Differences in community-level traits can occur among sites due to both differences in species composition and effects of growth conditions on plant traits (phenotypic plasticity) (Richardson et al. 2005). In this study, differences among *Nothofagus* species, and in the trends between *Nothofagus* and co-occurring species among sites, may be due to either varying species composition or due to site effects on phenotypes. Killingbeck (1996) suggested that resorption is driven less by nutrient availability than by controls at the species level. Aerts and Chapin (2000) found no consistent phenotypic differences in resorption efficiency between low and high fertility conditions, and similarly, nutrient availability did not strongly affect resorption in a fertilisation experiment (Vitousek 1998). However, phenotypic variation has been recorded in green-leaf nutrient concentrations in *N. aequilateralis* among sites (Read et al. 2002). Hence, phenotypic variation may occur in resorption efficiency and proficiency.

Mg and Ni concentration of senesced leaves

The deciduous tree *Peltogyne gracilipes* forms monodominant forests on Mg-rich soils in Brazilian Amazonia and has high concentrations of Mg in both green and senesced leaves (Villela and Proctor 1999). Villela and Proctor (2002) suggested that pulses of Mg from decomposing leaves of *P. gracilipes* may be mildly toxic on these soils and linked to its monodominance if these levels of Mg suppress growth of less tolerant species. However, *Nothofagus* species on the New Caledonian ultramafic soils showed no evidence of consistent high concentrations of Mg and Ni in either green or senesced leaves; instead, levels of Ni in green and senesced leaves were lower on average than in co-occurring species. Hence, there is no evidence for the allelopathic mechanism of monodominance suggested for *Peltogyne*.

Litter decomposition rates and causal factors

Falling leaves typically account for more than 70% of all aboveground litter (Killingbeck 1996). Therefore, leaf decomposition has a large influence on nutrient recycling rates. In nutrient-poor habitats, such as studied here, leaf litter must represent a major pool of accessible nutrients that are deficient in the mineral soil. Litter quality appears to be the best determinant of decay rates in the tropics (Meentemeyer 1978; Aerts 1997), with both chemical and physical traits influencing its value as a nutrient resource to decomposers (Swift et al. 1979). N and P are often the most limiting nutrients (Heal et al. 1997; Aerts and Chapin 2000), but unlike some other studies in tropical rain forests (Santiago 2007), in this study, N did not correlate with decay rates, and P only weakly. On these severe soils, carbon:nutrient ratios may be of more relevance. C:N ratios exceeding 25:1 are considered to be high (Heal et al. 1997); for all of our study species, the mean C:N was above 50:1, but litter decay did not correlate with C:N, although it did with C:P. The largest quantitative demand by decomposers is the energy released from organic compounds, including cell wall polysaccharides (La Caro and Rudd 1985), but cell wall components can also provide a physical barrier to nutrients. We found that lignin:nutrient ratios were better predictors of decay rates than C:nutrient ratios, reflecting the influence of both nutrient limitation and the quality of carbon as an energy source (and barrier) to decomposers, lignin being highly recalcitrant to decay (Hammel 1997). Leaf decay was also negatively correlated with lignin concentration alone, consistent with some other studies (La Caro and Rudd 1985; Cornelissen 1996; Hobbie and Vitousek 2000). Lignin concentrations of our study species were not particularly high; the mean across all species was 16%, with none exceeding 35%, compared with the level of 50% considered likely to significantly retard litter decay rates (Mesquita et al. 1998), although Aerts (1997) found that low lignin concentrations could inhibit decay if there was a lack of specialised lignin-degrading organisms. However, in our study, the measure of total cell wall (NDF) correlated more strongly with decomposition rates than lignin.

Some secondary compounds can interact with the nutritional quality of litter to slow decay (Heal et al. 1997). Phenolics, in particular tannins, can suppress litter decomposition (Northup et al. 1998; Kraus et al. 2003), especially in the later stages of decay (Mesquita et al. 1998; Loranger et al. 2002). Consistent with this, tannin activity (but not total phenolics) was negatively correlated with litter decay rates in this study, but with no significant independent effect; a stronger effect may have been observed if the leaves of more species had decayed substantially. The physical characteristics of leaves can also affect litter decay rates (Swift et al. 1979). In particular, leaf mechanical properties have been found to correlate negatively with litter decomposition (Cornelissen et al. 1999). We measured leaf toughness as both work to shear and specific work to shear, but only the latter correlated with decomposition rates. However, it did not make a significant independent contribution to decomposition rates; its negative correlation with decomposition rate may be largely due to its positive correlation with NDF ($R = 0.64$, $P < 0.001$), but different results may have occurred if we had not excluded larger detritivores by the small mesh size. Even though only NDF made a significant independent contribution to variation in decomposition rates, the higher correlation of decomposition rate with the main component axis of the PCA than with any individual variables, and the high amount of variation explained when multiple variables were included in the regression model, is consistent with the influence of multiple factors in leaf decomposition, despite these apparently being minor individual contributions relative to NDF. The relatively low rate of *Nothofagus* leaf decay appears to be largely influenced by high cell wall content and ratios of lignin:N and lignin:P.

The decomposition experiment may not reflect rates of decay in nature. We attempted to mimic climatic conditions and to introduce a variety of soil biota, but the experiment is nevertheless artificial, and does not allow the complexity of interactions that exist in nature (e.g. Milton and Kaspari 2007). In addition, more detailed interpretation is precluded by using only a single harvest. More importantly, decay rates of individual leaves often exceeded those of leaf packs, not surprisingly as individual leaves had greater contact with the substrate and could be accessed more easily by decomposers. Interactions among species can also be important. Mixed litters can interact to affect decomposition rates of individual leaves, either positively or negatively (Gartner and Cardon 2004), with decomposition strongly controlled by traits of the dominant species (Hoorens et al. 2003). A study at Col de Mouirange found that in areas dominated by *N. aequilateralis*, the leaf litter was dominated by a large amount of undecomposed leaves and branch material of this species with a low pH (McCoy 1991). Our experiment found that leaf litter of *Nothofagus* was slow to decompose compared with co-occurring species, and together with the low pH of *Nothofagus* litter, must have a significant effect on nutrient cycling and availability in the monodominant forests.

Does leaf-level NUE influence monodominance of *Nothofagus*?

We found no evidence that leaves of *Nothofagus* species generally function at lower nutrient concentrations or are better on average at conserving scarce nutrients than co-occurring species. We note that our main analyses were limited in power by the low number of sites, and so, conclusions should be cautious. Within-site comparisons, however, showed high variability among species for many leaf traits, with no suggestion that *Nothofagus* species show consistent superior leaf-level NUE compared with other common canopy species. Some species that dominate tropical forest canopies produce leaf litter that is slow to decompose, e.g. *Gilbertiodendron dewevrei* in monodominant Congolese forest (Torti et al. 2001), and *Cecropia sciadophylla* in Amazonian secondary forest (Mesquita et al. 1998), and so is slow to release nutrients. Similarly, the litter of *Nothofagus* is relatively slow to decompose, but it is not clear whether this provides an advantage to *Nothofagus* species since there is no evidence to date of higher NUE than co-occurring species. However, the low decomposability of *Nothofagus* leaf litter may confer an advantage by slowing the establishment and growth of its competitors by other means: litter accumulation may change topsoil conditions by intercepting light and rain and the transfer of heat and water may be affected (Facelli and Pickett 1991), and the low pH may increase availability of Ni. In addition, succession may be delayed by effects of litter accumulation on fuel loads, increasing the probability of the forests burning during a severe dry season and potentially creating an environment suitable for *Nothofagus* regeneration. However, while these factors might explain the maintenance of dominance by delayed growth of competitors, or interruption of succession, they do not easily explain how *Nothofagus* achieves early dominance of these forests after disturbance. Other components of plant-level NUE, such as nutrient uptake rates and carbon gain per unit nutrient acquired, including effects of leaf lifespan (Aerts and Chapin 2000) and ectomycorrhizal relationships (Newbery et al. 1997; Smith and Read 1997; Aerts 2002; Erland and Taylor 2002), may be contributing to dominance by *Nothofagus* species. These warrant investigation in the context of understanding the mechanisms that promote monodominance by some species on severe soils.

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References

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? J Ecol 84:597–608. doi:10.2307/2261481

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449. doi:10.2307/3546886

Aerts R (2002) The roles of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Springer-Verlag, Berlin

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67. doi:10.1016/S0065-2504(08)60016-1

Asquith TN, Butler LG (1985) Use of dye-labeled protein as spectrophotometric assay for protein precipitants such as tannin. J Chem Ecol 11:1535–1544. doi:10.1007/BF01012199

Baker AJM (1981) Accumulators and excluders—strategies in the response of plants to heavy metals. J Plant Nutr 3:643–654

Baker AJM, Walker PL (1989) Ecophysiology of metal uptake by tolerant plants. In: Shaw AJ (ed) Heavy metal tolerance in plants: evolutionary aspects. CRC Press, Boca Raton, FL

Brooks RR, Lee J, Reeves RD, Jaffré T (1977) Detection of nickeliferous rocks by analysis of herbarium specimens of indicator plants. J Geochem Explor 7:49–57. doi:10.1016/0375-6742(77)90074-7

Chapin FS (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260. doi:10.1146/annurev.es.11.110180.001313

Clarkson DT, Hanson JB (1980) The mineral nutrition of higher plants. Annu Rev Plant Physiol 31:239–298. doi:10.1146/annurev.pp.31.060180.001323

Connell JH, Lowman MD (1989) Low-diversity tropical rain forests: some possible mechanisms for their existence. Am Nat 134:88–119. doi:10.1086/284967

Cork SJ, Krockenberger AK (1991) Methods and pitfalls of extracting condensed tannins and other phenolics from plants: insights from investigations on *Eucalyptus* leaves. J Chem Ecol 17:123–134. doi:10.1007/BF00994426

Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J Ecol 84:573–582. doi:10.2307/2261479

Cornelissen JHC, Pérez-Harguindeguy N, Diaz S, Grime JP, Marzano B, Cabido M et al (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytol 143:191–200. doi:10.1046/j.1469-8137.1999.00430.x

Diehl P, Mazzarino MJ, Funes F, Fontenla S, Gobbi M, Ferrari J (2003) Nutrient conservation strategies in native Andean-Patagonian forests. J Veg Sci 14:63–70. doi:10.1658/1100-9233(2003)014[0063:NCSINA]2.0.CO;2

Enright NJ, Rigg L, Jaffré T (2001) Environmental controls on species composition along a (maquis) shrubland to forest gradient on ultramafics at Mont Do, New Caledonia. S Afr J Sci 97:573–580

Erland S, Taylor AFS (2002) Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic environment. In: van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Springer-Verlag, Berlin

Facelli JM, Pickett STA (1991) Plant litter: its dynamics and effects on plant community structure. Bot Rev 57:1–32. doi:10.1007/BF02858763

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246. doi:10.1111/j.0030-1299.2004.12738.x

Graham HD (1992) Stabilization of Prussian Blue color in the determination of polyphenols. J Agric Food Chem 40:801–805. doi:10.1021/jf00017a018

Grubb PJ (1977) Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Annu Rev Ecol Syst 8:83–107. doi:10.1146/annurev.es.08.110177.000503

Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266. doi:10.1111/j.1469-8137.2004.01192.x

Hammel KE (1997) Fungal degradation of lignin. In: Cadisch G, Giller KE (eds) Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, UK

Hart TB, Hart JA, Murphy PG (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. Am Nat 133:613–633. doi:10.1086/284941

Heal OW, Anderson JM, Swift MJ (1997) Plant litter quality and decomposition: an historical overview. In: Cadisch G, Giller KE (eds) Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, UK

Hobbie SE, Vitousek PM (2000) Nutrient limitation of decomposition in Hawaiian forests. Ecology 81:1867–1877

Hoorens B, Aerts R, Stroetenga M (2003) Does initial litter chemistry explain litter mixture effects on decomposition? Oecologia 137:578–586. doi:10.1007/s00442-003-1365-6

Jaffré T (1980) Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie. Collection Travaux et Documents de l'ORSTOM no. 124, ORSTOM, Paris

Jaffré T (1992) Floristic and ecological diversity of the vegetation on ultramafic rocks in New Caledonia. In: Baker AJM, Proctor J, Reeves RD (eds) The vegetation of ultramafic (serpentine) soils. Intercept Ltd, Andover, UK

Jaffré T, Morat P, Veillon J-M, Rigault F, Dagostini G (2004) Composition et caractéristiques de la flore indigène de Nouvelle-Calédonie. Nouméa. 2nd ed. IRD Documents Scientifiques et Techniques II 4, pp 121

Killingbeck KT (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology 77:1716–1727. doi:10.2307/2265777

Kraus TEC, Dahlgren RA, Zasoski RJ (2003) Tannins in nutrient dynamics of forest ecosystems—a review. Plant Soil 256:41–66. doi:10.1023/A:1026206511084

La Caro F, Rudd RL (1985) Leaf litter disappearance rates in Puerto Rican montane rain forest. Biotropica 17:269–276. doi:10.2307/2388589

Loranger G, Ponge J-F, Imbert D, Lavelle P (2002) Leaf decomposition in two semi-evergreen tropical forests:

influence of litter quality. Biol Fertil Soils 35:247–252. doi:10.1007/s00374-002-0467-3

Mac Nally R, Walsh CJ (2004) Hierarchical partitioning public-domain software. Biodivers Conserv 13:659–660. doi:10.1023/B:BIOC.0000009515.11717.0b

McCoy S (1991) Edaphic controls influencing the distribution of *Nothofagus aequilateralis* on ultrabasic soils at the Col de Mouirange, New Caledonia. Honours Dissertation, Australian National University, Australia

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472. doi:10.2307/1936576

Meharg AA, Cairney JWG (2000) Co-evolution of mycorrhizal symbionts and their hosts to metal-contaminated environments. Adv Ecol Res 30:69–112. doi:10.1016/S0065-2504(08)60017-3

Mesquita RCG, Workman SW, Neely CL (1998) Slow litter decomposition in a *Cecropia*-dominated secondary forest of central Amazonia. Soil Biol Biochem 30:167–175. doi:10.1016/S0038-0717(97)00105-3

Milton Y, Kaspari M (2007) Bottom-up and top-down regulation of decomposition in a tropical forest. Oecologia 153:163–172. doi:10.1007/s00442-007-0710-6

Nascimento MT, Barbosa RI, Villela DM, Proctor J (2007) Above-ground biomass changes over an 11-year period in an Amazonian monodominant forest and two other lowland forests. Plant Ecol 192:181–191. doi:10.1007/s11258-007-9303-z

Newbery DM, Alexander IJ, Rother JA (1997) Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. Ecol Monogr 67:367–409

Northup RR, Dahlgren RA, McColl JG (1998) Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback? Biogeochemistry 42:189–220. doi:10.1023/A:1005991908504

Ovington JD, Olson JS (1970) Biomass and chemical content of El Verde lower montane rain forest plants. In: Odum HT, Pigeon RF (eds) A tropical rain forest. U.S. Atomic Energy Commission, Oak Ridge

Perrier N, Amir H, Colin F (2006) Occurrence of mycorrhizal symbioses in the metal-rich lateritic soils of the Koniambo massif, New Caledonia. Mycorrhiza 16:449–458. doi:10.1007/s00572-006-0057-6

Plummer A (2007) Decomposition rates of leaves on two contrasting soil types in a tropical rainforest—are the factors that control herbivory persistent and effective in reducing rates of decomposition? Honours Dissertation, Monash University

Price ML, Butler LG (1977) Rapid visual estimation and spectrophotometric determination of tannin content of sorghum grain. J Agric Food Chem 25:1268–1273. doi:10.1021/jf60214a034

Proctor J, Woodell SRJ (1975) The ecology of serpentine soils. Adv Ecol Res 9:255–366. doi:10.1016/S0065-2504(08)60291-3

Proctor J, Phillipps C, Duff GK, Heaney A, Robertson FM (1989) Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. II. Some forest processes. J Ecol 77:317–331. doi:10.2307/2260752

R Development Core Team (2004) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org. Accessed 3–6 August 2007

Read J, Hope GS (1996) Ecology of *Nothofagus* forests of New Guinea and New Caledonia. In: Veblen TT, Hill RS, Read J (eds) The ecology and biogeography of *Nothofagus* forests. University of Yale Press, New Haven

Read J, Sanson GD (2003) Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. New Phytol 160:81–99. doi:10.1046/j.1469-8137.2003.00855.x

Read J, Jaffré T, Godrie E, Hope GS, Veillon J-M (2000) Structural and floristic characteristics of some monodominant and adjacent mixed rain forest in New Caledonia. J Biogeogr 27:233–250. doi:10.1046/j.1365-2699.2000.00407.x

Read J, Ferris JM, Jaffré T (2002) Foliar mineral content of *Nothofagus* species on ultramafic soils in New Caledonia and non-ultramafic soils in Papua New Guinea. Aust J Bot 50:607–617. doi:10.1071/BT01091

Read J, Jaffré T, Ferris JM, McCoy S, Hope GS (2006) Does soil determine the boundaries of monodominant rain forest with adjacent mixed rain forest and maquis on ultramafic soils in New Caledonia? J Biogeogr 33:1055–1065. doi:10.1111/j.1365-2699.2006.01470.x

Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. Proc Natl Acad Sci USA 101:11001–11006. doi:10.1073/pnas.0403588101

Richardson SJ, Peltzer DA, Allen RB, McGlone MS (2005) Resorption proficiency along a chronosequence: responses among communities and within species. Ecology 86:20–25. doi:10.1890/04-0524

Santiago LS (2007) Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. Ecology 88:1126–1131. doi:10.1890/06-1841

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic Press, London

Stark N (1970) The nutrient content of plants and soils from Brazil and Surinam. Biotropica 2:51–60. doi:10.2307/2989789

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell, Oxford

Tanner EVJ (1977) Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. J Ecol 65:883–918. doi:10.2307/2259385

Thompson J, Proctor J, Viana V, Milliken W, Ratter JA, Scott DA (1992) Ecological studies on a lowland evergreen rain forest on Maraca Island, Roraima, Brazil. I. Physical environment, forest structure and leaf chemistry. J Ecol 80:689–703. doi:10.2307/2260860

Torti SD, Coley PD, Kursar TA (2001) Causes and consequences of monodominance in tropical lowland forests. Am Nat 157:141–153. doi:10.1086/318629

Van Soest PJ (1994) Nutritional ecology of the ruminant, 2nd edn. Comstock Publications, Ithaca, New York

Villela DM, Proctor J (1999) Litterfall mass, chemistry, and nutrient retranslocation in a monodominant forest on Maracá Island, Roraima, Brazil. Biotropica 31:198–211

Villela DM, Proctor J (2002) Leaf litter decomposition and monodominance in the *Peltogyne* forest of Maracá Island, Brazil. Biotropica 34:334–347

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298. doi:10.2307/1939481

Vitousek PM (1998) Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. Ecosystems 1:401–407. doi:10.1007/s100219900033

Walsh C, Mac Nally R (2007) The hier.part package. http://cran.r-project.org/doc/packages/hier.part.pdf

Wilkinson DM, Dickinson NM (1995) Metal resistance in trees: the role of mycorrhizae. Oikos 72:298–300. doi:10.2307/3546233

Dendroecological study of a subalpine fir (*Abies fargesii*) forest in the Qinling Mountains, China

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Abstract Dendroecological techniques were used to investigate the stand dynamics and the disturbance history of the subalpine fir forest in the Qinling Mountains of Shaanxi Province, China. The results indicated that 68% of the fir trees experienced 1–2 release events for a total of 10–29 (an average of 15.8) years, and 1–2 suppression events for a total of 10–27 (an average of 13.4) years before they reached canopy. Large number of *Abies fargesii* and *Betula albo-sinensis* recruitment coincided temporally with larger increases in the ring-width index from the 1830s to 1880s, suggesting occurrence of a major stand-wide disturbance during this time period. Few seedlings and saplings were found in the forest, and there was a dramatic decline in recruitment after 1890, probably because of the intensive cover of understory umbrella bamboo (*Fargesia spathacea*). Radial growth analyses indicated frequent canopy opening resulting from small-scale disturbances in the forest. Thus, the subalpine fir forest experienced frequent small-scale disturbances and infrequent large-scale disturbances in its developmental history, and these disturbances coupled with the understory umbrella bamboo might have influenced tree growth and species recruitment.

Keywords Growth release · Age distribution · Disturbance · Subalpine fir forest · The Qinling Mountains

Introduction

Forest's current structure, composition, and pattern are influenced by many factors over its developmental history, including disturbance, competitive interactions between trees, and microsite differences in resources (North et al. 2004). In fact, stand dynamics is an important subject of ecological research, and the studies on stand dynamics and developmental history have provided a substantial database of information on the regeneration ecology and population structure of forests, particularly in relation to canopy gaps (Namikawa 1996; Abrams et al. 1999). Reconstruction of forest history through identifying growth releases and tree recruitment is the primary information used to understand the ecosystem processes such as population dynamics, community structure and stand development (Taylor and Qin 1988; Taylor et al. 1996; Bergeron et al. 2002).

Over the past decades, dendroecological techniques have become an important tool in the studies

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of stand dynamics and ecological history (Fritts 1976; Fritts and Swetnam 1989; Nowacki and Abrams 1994), such as species recruitment patterns, periodicity and intensity of disturbances, and influences of climatic variation and extreme weather events (Henry and Swan 1974; Oliver and Stephens 1977; Foster 1988; Abrams and Orwig 1995; Abrams et al. 1995; Druckenbrod 2005). Tree rings present valuable and long-term records of tree growth in forest environments. Variations in tree-ring width can be used to reconstruct the occurrence of past forest disturbance and to speculate on the origin of the forest stand (Foster 1988; Lorimer and Frelich 1989; McClaran and Bartolome 1989; Veblen et al. 1994; Frelich 2002). As a result, coupling tree-ring chronologies and age structure have proven to be a particular robust approach for understanding long-term variation in forest dynamics and history (Foster 1988; Abrams and Orwig 1995; Abrams et al. 1999).

Disturbances in forested landscapes influence community structure, composition, and dynamics. Community response to disturbance varies widely and depends on the types, size, severity, and frequency of disturbance and species' life history attributes (Taylor et al. 1996). Large-scale disturbances (e.g. severe insect outbreaks, extreme climatic events, etc.) are usually visible on the mean ring-width chronology, while detection of medium- and small-scale disturbances needs more sophisticated methods of signal analysis (Rathgeber and Roche 2003). The moving average techniques allow us to derive the disturbance events that are associated with the medium-frequency signal and remove the high- and low-frequency signal (age and climatic effects) in a chronology (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Small-scale disturbances regularly cause tree-fall and branch breakage, thus creating canopy openings that trigger regeneration and increase of growth of suppressed trees in forests, i.e. growth release (Lorimer and Frelich 1989; Veblen et al. 1989; Schweingruber et al. 1990; Cao and Ohkubo 1999). Growth releases occur synchronously in neighbouring trees and show a slow decrease in the following years due to ageing or to closure of canopy (Veblen et al. 1991). So a disturbance that occurred in a stand can be identified by the growth releases of suppressed trees with an accuracy of a few years (Motta et al. 1999).

Abies fargesii is a subalpine tree species widely distributing in the Qinling Mountains of China. It occurs over a wide range in elevation and dominates the forests above 2,300 m a.s.l. in the Qinling Mountains. The subalpine fir forests remain undisturbed by human activities for more than a century in the Qinling Mountains (Zhang 1989). Thus, these forests represent a rare opportunity to study forest dynamics and developmental history for the subalpine conifer forests. However, a very little is known about the stand dynamics and developmental history of the subalpine fir forests in the Qinling Mountains, a biodiversity hotspot in China, due to insufficient research (Taylor and Qin 1988; Taylor et al. 1996). Understanding the forest dynamics and developmental history of the subalpine conifer forests is of great importance for the sustainable forestry.

In this study, we report the forest history and stand development of the subalpine fir forests in the Qinling Mountains of Shaanxi province, China. The primary objectives of this study are: (1) to describe the composition and structure of the subalpine fir forest; (2) to investigate the long-term patterns of species recruitment and radial growth variation; (3) to reconstruct the disturbance history of the forest using dendroecological evidence.

Methods

Study area

The study area is located in the Foping National Nature Reserve in the south aspect of the Qinling Mountains of Shaanxi Province, China (E107°49′, N33°42′) (Fig. 1). The Qinling Mountains run East–West and form the basin divider between China's two longest rivers, the Yellow River and the Yangtze River. The Qinling Mountains are situated in the transitional zone between two macroclimatic regimes (subtropical and warm-temperate zones), making it biologically rich area and sensitive to climatic change in China (Chen 1983). Elevation in the study area ranges from 980 to 2,838 m. The climate is characterized as subtropical with mild, wet summers and cold, dry winters. Annual precipitation ranges from 950 to 1,200 mm, most of which falls between July and September. Snow cover usually lasts five or more months (from November to March), and annual mean

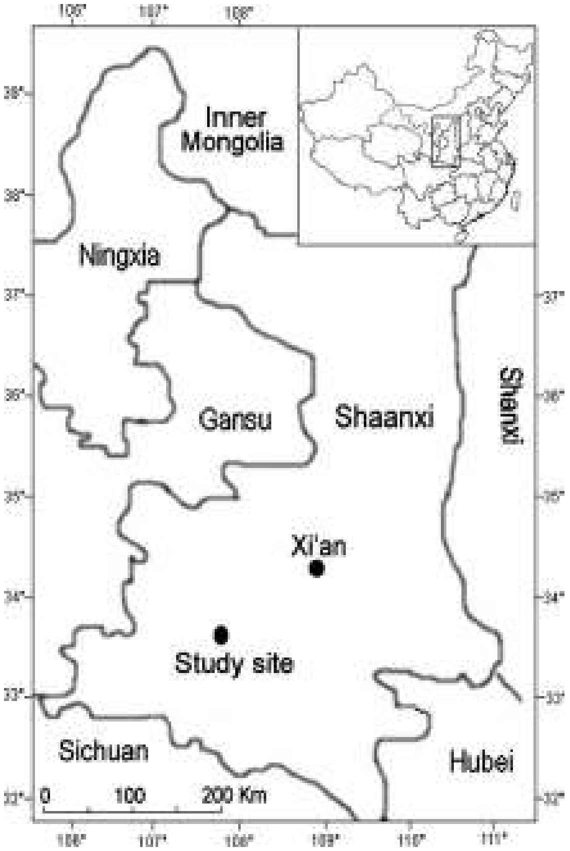


Fig. 1 Location of the study site in the Qinling Mountains of Shaanxi Province, China

temperature ranges from 6 to 11°C below 2,000 m and from 1 to 6°C above 2,000 m a.s.l. (Yue et al. 1999).

Conifers dominated by subalpine fir (*Abies fargesii*) occupy the area above 2,300 m in elevation, usually developing into mixed forests with birch (*Betula albo-sinensis*) or forming pure conifer forests in the study area. Umbrella bamboo (*Fargesia spathacea*) is a common understory species above 2,300 m. The mixed conifer and deciduous forests occur between elevations of 1,800 and 2,300 m. Patchy subalpine meadow also occurs above 2,600 m a.s.l. in this study area (Yue et al. 1999). Because of the limited accessibility, there have been no visible human activities in the region.

Field survey

In the summer of 2005, two transects of 20 m wide were established through the subalpine fir forest interior at the elevations of 2,360 and 2,450 m, respectively, which were orientated parallel to the isoline for a total length of 100 m. These transects were selected based on the criteria that there were similar habitats and species composition within and among transects and that the stands should represent the forest structure and composition in the study area.

Each transect was divided into five 20 × 20 m plots. Within each plot, all living trees (DBH $\geq$ 5 cm, measured at 1.37 m above ground) were labeled, counted and mapped with respect to a reference tree. Species, height, crown projection area and DBH were recorded. Increment cores were taken in the direction parallel to the slope contour using increment borers at the breast height. Trees of abnormal growth form (bent, twisted or hollow) were excluded from sampling. Usually one core per tree was taken, but for a few trees with unusable cores, additional cores were collected until a usable core was obtained. In total, 197 trees were cored (118 for *A. fargesii*, 46 for *B. albo-sinensis*, and 33 for the other species). Saplings and seedlings were counted by species in five 2 × 2 m quadrats within each of the 20 × 20 m plots. The cover of umbrella bamboo (*F. spathacea*) was estimated in the 2 × 2 m quadrats.

Radial growth analysis

All increment cores were air-dried, mounted, and sanded. The *Abies* cores were cross-dated using the signature year technique to identify the missing, partial, or false rings (Yamaguchi 1991). For cores, where the pith was missed, a graphical procedure was used to estimate their age (Villalba and Veblen 1997). Annual growth increments were measured to the nearest 0.01 mm with a tree ring-measuring device (Regent Instruments Inc., Quebec, Canada). The cores of *B. albo-sinensis* and other species were only used for age estimations. Recruitment was defined as the date when trees reached 1.37 m in height.

The percentage growth change filter (Lorimer and Frelich 1989; Nowacki and Abrams 1997) was applied to the fir tree ring series. The formulae $\%GCr = [(M_2 - M_1)/M_1] \times 100$ and $\%GCs = [(M_1 - M_2)/M_2] \times 100$ were used to identify growth release and suppression, respectively, where M_1 and M_2 are the preceding and subsequent 15-year ring-width mean, respectively. The minimum threshold of 100% for %GC was considered for event recognition, and the identified periods of release and suppression had to be at least 10 years to eliminate annual variations of radial growth. The criterion, coupled with tree canopy recruitment dates, was used to distinguish disturbance events from responses attributed to climatic factors (Lorimer and Frelich 1989; Abrams and Orwig 1996).

After cross-dating using signature years and the quality control program COFECHA (Holmes 1983), the raw ring widths from the oldest 30 fir cores were indexed using a detrending filter with a 10-year window (Guiot and Goeury 1996), and a mean indexed series was constructed. A site chronology was then developed using the oldest 30 fir cores. In addition, the tree-ring series at decadal intervals were used to reconstruct the disturbance history for the subalpine fir forest (Motta et al. 1999; Abrams et al. 2001; Bergeron et al. 2002; Druckenbrod 2005).

Results

Composition and size structure

The forest is comprised of nine tree species and is dominated by *A. fargesii* (47.86% importance value), *B. albo-sinensis* (19.66%), and *Acer maximowiczii* (9.13%) (Table 1). The six remaining species represent a combined relative importance value of 23%. The total density and basal area are 520 stems/ha and 68.31 m^2/ha, respectively. Tree regeneration was very sparse within the stand. Only 11 seedlings and 6 saplings, mainly *Acer maximowiczii* and *Prunus tomentosa*, were counted in the fifty 2 × 2 m quadrats (data not shown). Umbrella bamboo (*Fargesia spathacea*) with a height of 1.5–3.0 m averaged 95% cover in the understory.

The diameter-class structure showed a bell-shape distribution (Fig. 2). *Abies fargesii* occurred in all

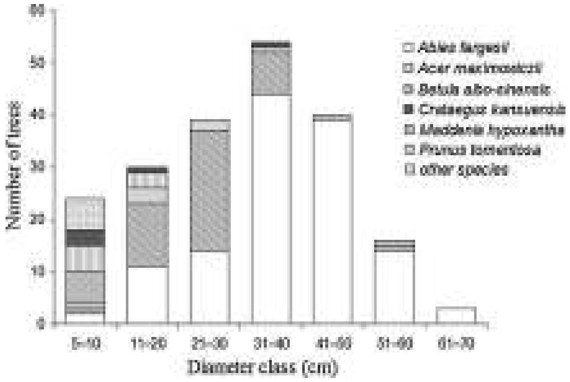


Fig. 2 Diameter (at 1.37 m above ground) distribution of tree species of the subalpine fir (*Abies fargesii*) forest in the Qinling Mountains of Shaanxi province, China. Other species include *Abelia macroptera*, *Sorbus koehneana*, and *Corylus tibetica*

Table 1 Species composition for the ten plots of the subalpine fir (*Abies fargesii*) forest in the Qinling Mountains of Shaanxi province, China

Species	Frequency	Density (stems/ha)	Dominance (m^2/ha)	Relative frequency	Relative density	Relative dominance	Importance value
Abies fargesii	10	317.5	40.85	22.73	61.06	59.80	47.86
Betula albo-sinensis	8	115.0	12.75	18.18	22.12	18.67	19.66
Acer maximowiczii	6	22.5	6.44	13.64	4.33	9.43	9.13
Maddenia hypoxantha	5	17.5	5.76	11.36	3.37	8.44	7.72
Prunus tomentosa	5	20.0	2.14	11.36	3.85	3.14	6.12
Crataegus kansuensis	4	12.5	0.27	9.09	2.40	0.40	3.96
Abelia macroptera	3	7.5	0.04	6.82	1.44	0.06	2.77
Sorbus koehneana	2	5.0	0.03	4.55	0.96	0.04	1.85
Corylus tibetica	1	2.5	0.01	2.27	0.48	0.02	0.92
Totals	44	520.0	68.31	100	100	100	100

Frequency is based on presence in the 10 sampled plots; density is based on the number of individuals; and dominance is based on basal area. Importance value is the average of relative frequency, relative density, and relative dominance (Cottam and Curtis 1956)

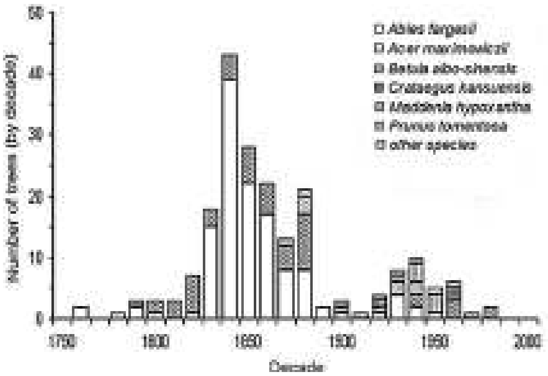


Fig. 3 Age class (at 1.37 m above ground) distribution of tree species of the subalpine fir forest (*Abies fargesii*) in the Qinling Mountains of Shaanxi province, China. Other species include *Abelia macroptera*, *Sorbus koehneana*, and *Corylus tibetica*

diameter classes and dominated the middle and larger diameter classes from 31 to 70 cm. In contrast, *Betula albo-sinensis* was in the relatively smaller diameter classes from 11 to 40 cm, and most of the remaining species were represented in the smaller diameter classes less than 20 cm.

Age structure

Based on the sample of 197 cored trees, the forest is uneven-aged (Fig. 3). Six fir trees are older than 200 years (239 years maximum at 1.37 m above ground). Long tree-ring series also exist for *B. albo-sinensis* (205 years old). A large number of *Abies fargesii* trees were recruited from the 1830s to 1880s with peak number in the 1840s. Few fir trees were recruited since the 1890s, and none after the 1950s. A large number of *Betula albo-sinensis* were recruited from the 1790s to 1880s, while very few after the 1880s. All recruitment of the rest species occurred in the 20th century with a few exceptions.

Release and suppression

The radial growth analysis indicated that 68% of the canopy fir trees ($n = 118$) showed periods of release and suppression. These trees experienced 1–2 (an average of 1.2) releases for 10–29 (an average of 15.8) years, and 1–2 (an average of 1.1) suppression for 10–27 (an average of 13.4) years (Table 2). There were average of 12.8 and 11.9 years for release and suppression period, respectively. The average ages for the first release and suppression were 45.2 (ranging from 15 to 124) and 60.5 (ranging from 15 to 119) years, respectively.

Table 2 Summary of growth release and suppression of canopy fir trees of the subalpine fir forest in the Qinling Mountains of Shaanxi province, China ($n = 118$)

	Mean	SD	Range
Release			
Numbers of release periods per core	1.2	0.4	1–2
Years of each release period	12.8	3.3	10–29
Years of release per core	15.8	5.8	10–29
Ages when the first release was identified	45.2	32.7	15–124
Suppression			
Numbers of suppression periods per core	1.1	0.3	1–2
Years of each suppression period	11.9	2.7	10–24
Years of suppression per core	13.4	4.8	10–27
Ages when the first suppression was identified	60.5	32.7	15–119

Growth releases occurred frequently over the past 240 years in the fir trees except the time periods of the 1770s to 1790s and the 1810s (Fig. 4). The number of trees showing releases was fairly low prior to 1840 because of the scarcity of fir trees greater than 180 years old. The number of trees showing releases each decade had generally remained constant after 1840, with the largest number in the 1940s and 1960s.

Dendroecology

Fir trees had an average growth rate of 1.14 mm/year, ranging from 0.11 mm/year to 3.67 mm/year. The

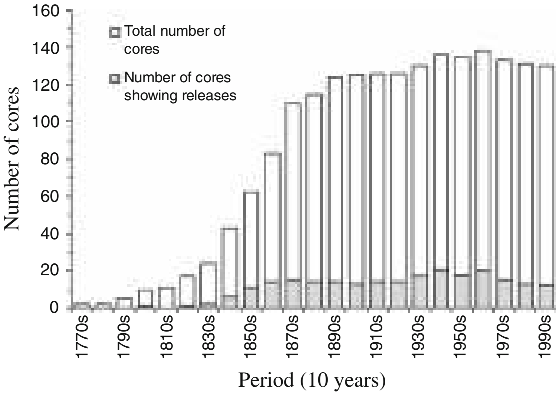


Fig. 4 Number of cores showing releases and total number of cores analyzed at 10-year intervals of the subalpine fir forest in the Qinling Mountains of Shaanxi province, China

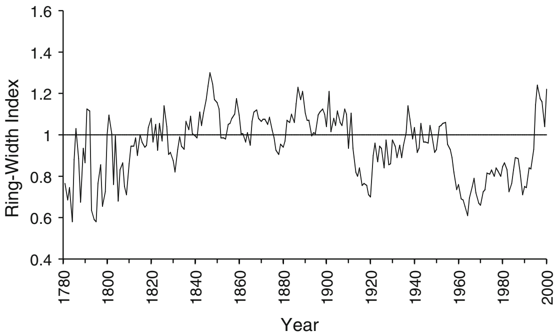
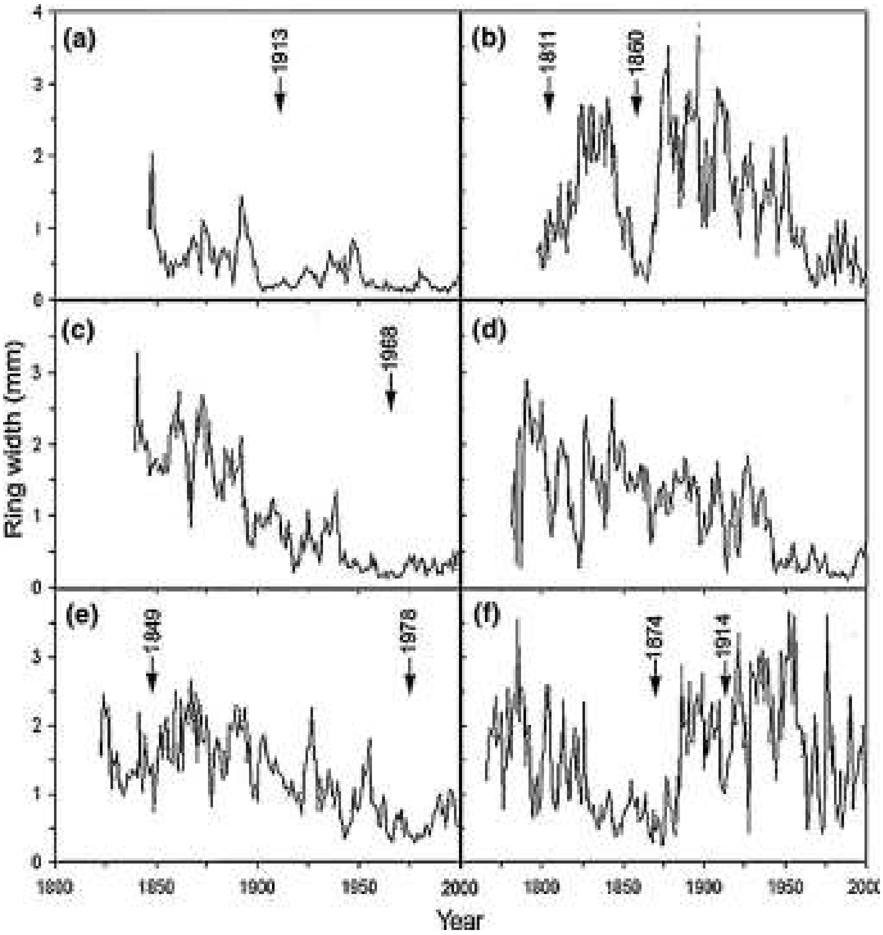


Fig. 5 Site chronology of *Abies fargesii* of the subalpine fir forest in the Qinling Mountains of Shaanxi province, China

ring-width index chronology for the oldest 30 fir trees indicated a period of generally high radial growth between 1836 and 1910 with a few exceptions (Fig. 5). Increases in radial growth also occurred in the time period of 1936–1954. The radial growth was substantially below average for most of the time period before 1835, and from 1911 to 1935 and 1955 to 1994.

Figure 6 illustrated variation in growth patterns and frequency of release dates of the representative fir trees. The timing of the releases reflected great variation among the individual trees, i.e. the releases were present only in individual cores (Fig. 6). The trees in Fig. 6a, c showed high early growth followed by a steep growth decline, characteristics of trees with gap origin followed by gap closure. The fir tree in Fig. 6b showed slow early growth followed by progressively higher growth before a dramatic increase of its growth rate in 1811, and then a peak growth was recognized after the release in 1860. The fir tree in Fig. 6d showed fairly consistent growth for more than 150 years before its growth began to decrease in 1938. The tree in Fig. 6f had major early growth, followed by a great decrease in growth for

Fig. 6 Individual tree-ring chronologies and release dates for six selected cores of the subalpine fir forest in the Qinling Mountains of Shaanxi province, China. *Arrows* indicate release dates



the next 60 years, and its growth rate drastically increased after a release in 1874, and then it experienced another release in 1914.

Discussion

The results of this study suggest that the existing fir and birch trees were primarily recruited in the subalpine fir forest between 1830 and 1890 in these plots on the Qinling Mountains. Prior to 1890, the forest was comprised of a large number of *A. fargesii*, *B. albo-sinensis*, and *Acer maximowiczii*, based on the current stand age distribution (Fig. 3). However, care must be taken, when explaining static age structure data because of difference in species mortality with various age and canopy classes and stand-history events (Johnson et al. 1994; Abrams et al. 2001). The oldest and the largest trees in our study sites are *Abies* species and the domination of the uneven-aged forest by *Abies* apparently dated back 200 years ago. The absence of *A. fargesii* trees older than 250 years in the subalpine fir forest may be attributable to their maximum life expectancy. *Prunus tomentosa*, *Maddenia hypoxanth*, *Crataegus kansuensis*, and the other species are companion species and have only invaded the forest recently.

A unique dendroecological feature of the *A. fargesii* stand is the association of the large recruitment pulse with high radial growth observed in the ring-width index chronology between 1830 and 1890 (Figs. 3 and 5). The forests were logged several times during the time period from the 1790s to 1870s, and most of the old trees were selectively cut in those logging activities (Zhang 1989). Logging may have greatly altered the composition and number of tree recruits in an old-grown forest (Abrams and Nowacki 1992; Nowacki and Abrams 1994; Orwig and Abrams 1999; Abrams et al. 2001). The several logging events may cause the sustained period of tree recruitment and the several increases in the ring-width index chronology from 1830 to 1890, culminating with a very large pulse around 1850 (Figs. 3 and 5). Prior to 1830, although *A. fargesii* recruitment in the subalpine fir forest was also associated with releases in the ring-width index chronology, e.g. 1789–1792, 1800–1802, and 1824–1827, the association between recruitment and high radial growth of fir trees might not be substantial due to the insufficient number of fir trees (Figs. 3 and 5). Catastrophic fire has been described as a pervasive disturbance in the coniferous forests of China (Wang 1961), while there are no recently burned stands in our study sites. Whether, natural disturbance events such as windstorms (Ren 1998) stimulated as much tree recruitment as the nineteenth logging is unknown, because of mortality in older fir trees.

Releases in radial growth indicate occurrence of disturbances almost over the developmental history of the fir forest (Fig. 4). While the 1770s to 1790s period without growth releases would perhaps be the stem exclusion stage for the fir forest (Oliver and Larson 1996). A series of release episodes are identified, but a very few of these releases are recorded in the same year (Figs. 4 and 6), indicating that the forest experienced frequent small-scale disturbances (such as tree-fall and branch breakage caused by windstorms, etc.) each of which impacted a relatively small number of trees in the stand development history (Abrams et al. 2001). Only a few major stand-wide disturbance events (such as logging activities, etc.) occurred in the subalpine fir forest according to the largest pulse in tree recruitment and the largest pulse in ring-width index chronology around the 1850s (Figs. 3 and 5). Thus, the subalpine forest experienced frequent small-scale disturbances and infrequent large-scale disturbances in its developmental history.

Tree recruitment after 1890 became infrequent, excluding a small pulse of recruitments between 1920 and 1960 (Fig. 3). Perhaps the intensive cover of understory umbrella bamboo (*Fargesia spathacea*) is responsible for the low frequency of seedling establishment. Bamboos, which are common understory plants in temperate and tropical forests, appear particularly effective in reducing tree regeneration where they achieve a high degree of dominance (Taylor and Qin 1988; Holz and Veblen 2006). In other subalpine forests with dense bamboo stands in China, Japan and South America (Franklin et al. 1979; Koyama 1984; Taylor and Qin 1988; Nakashizuka 1991; Taylor and Qin 1992; Taylor et al. 1996; Holz and Veblen 2006), bamboos with a 50% cover seem sufficiently to impede tree establishment and forest gaps fill slowly, and most regeneration of tree species occurs in canopy gaps caused by disturbances and such regeneration is sparse. In our study sites, the umbrella bamboo with a height of 1.5–3.0 m and a density of 70–140 stems/m^2 usually covers more than 85%, sometimes 100% of the understory of the subalpine fir forest (Ren 1998). As a result, it seems that regeneration of the *A. fargesii* population depends on the occurrence of large-scale disturbances in the Qinling Mountains (Ren 1998) or in areas of umbrella bamboo dieback (Taylor and Qin 1992; Namikawa 1996).

Patterns of tree recruitment in the subalpine fir forests of the Qinling Mountains appear to be similar to other subalpine forests in China, Japan and South America (Franklin et al. 1979; Koyama 1984; Taylor and Qin 1988; Nakashizuka 1991; Taylor and Qin 1992; Taylor et al. 1996; Holz and Veblen 2006). In these subalpine forests, bamboos reduce seedlings establishment and stands typically have few seedlings and saplings. Rapid vegetative growth of bamboos reduces space for other species within the community, and small-scale disturbances induce most trees' recruitment. Mass death of the bamboo understory following synchronized flowering is a large-scale disturbance, which increases space-related resources, especially light, that may allow for pulses of tree recruitment, otherwise tree recruitment is inhibited by the bamboo cover (Taylor and Qin 1988, 1992; Hiura et al. 1996; Abrams et al. 1999). However, there are no reports on bamboo die-off in the study area, which might contribute to the patterns of tree recruitment observed in this study. If the intensity of umbrella bamboo cover on tree regeneration does not lessen in the future, we anticipate very little opportunity for canopy recruitment in the subalpine fir forest in the Qinling Mountains.

Conclusions

The majority of the subalpine fir trees (68%) in the Qinling Mountains of China experienced 1–2 times of growth release and suppression before they reached canopy. A large number of *A. fargesii* and *B. albo-sinensis* were recruited from the 1830s to 1880s. In combination with frequent releases from radial growth analyses, it seems that tree growth and species recruitment have been influenced by the coupling of frequent small-scale disturbances and infrequent large-scale disturbances. There are very few seedlings and saplings in the forest, and canopy recruitment declined after 1890, probably as a result of the dense cover of understory umbrella bamboo (95%) which prevents tree recruitment in the subalpine fir forest.

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References

Abrams MD, Nowacki GJ (1992) Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bull Torrey Bot Club 119: 19–28

Abrams MD, Orwig DA (1995) Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. Oecologia 101:353–360

Abrams MD, Orwig DA (1996) A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau USA. J Ecol 84:353–363

Abrams MD, Orwig DA, DeMeo TE (1995) Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. J Ecol 83:123–133

Abrams MD, Copenheaver CA, Terazawa K, Umeki K, Takiya M, Akashi N (1999) A 370-year dendroecological history of an old-growth *Abies-Acer-Quercus* forest in Hokkaido, northern Japan. Can J For Res 29:1891–1899

Abrams MD, Copenheaver CA, Black BA, van de Gevel S (2001) Dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania USA. Can J Bot 79:58–69

Bergeron Y, Denneler B, Charron D, Girardin MP (2002) Using dendrochronology to reconstruction disturbance and forest dynamics around Lake Duparquet, northwestern Quebec. Dendrochronologia 20:175–189

Cao KF, Ohkubo T (1999) Suppression and release during canopy recruitment in *Fagus crenata* and *Acer mono* in two old-growth beech forests in Japan. Plant Ecol 145:281–290

Chen MR (1983) Climate and agriculture in the Qinling Mountains. Shaanxi People's Press, Xi'an (in Chinese)

Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. Ecology 37:451–460

Druckenbrod DL (2005) Dendroecological reconstructions of forest disturbance history using time-series analysis with intervention detection. Can J For Res 35:868–876

Foster DR (1988) Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire USA. J Ecol 76: 105–134

Franklin JF, Maeda T, Oshumi T, Matsui M, Yagia H, Hawk GM (1979) Subalpine coniferous forests of central Honshu, Japan. Ecol Monogr 49:311–334

Frelich LE (2002) Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, New York

Fritts HC (1976) Tree Rings and Climate. Academic Press, New York

Fritts HC, Swetnam TW (1989) Dendroecology: a tool for evaluating variations in past and present forest environments. Adv Ecol Res 19:111–188

Guiot J, Goeury C (1996) PPPBASE, a software for statistical analysis of paleoecological and paleoclimatological data. Dendrochronologia 14:295–300

Henry JD, Swan JMA (1974) Reconstructing forest history from live and dead plant material—an approach of the study of forest succession in southwest New Hampshire. Ecology 55:772–783

Hiura T, Sano J, Konno Y (1996) Age structure and response to fine scale disturbance of *Abies sachalinensis*, *Picea jezoensis*, *Picea glehnii*, and *Betula ermanii* growing under the influence of a dwarf bamboo understory in northern Japan. Can J For Res 26:289–297

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin 43:69–87

Holz CA, Veblen TT (2006) Tree regeneration responses to *Chusquea montana* bamboo die-off in a subalpine *Nothofagus* forest in the southern Andes. J Veg Sci 17:19–28

Johnson EA, Miyanishi K, Kleb H (1994) The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta-Picea engelmannii* forest. J Ecol 82:923–931

Koyama T (1984) Regeneration and coexistence of two *Aibes* species dominating subalpine forests in central Japan. Oecologia 62:156–161

Lorimer CG, Frelich LE (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can J For Res 19:651–663

McClaran MP, Bartolome JW (1989) Fire-related recruitment in stagnant *Quercus douglasii* populations. Can J For Res 19:580–585

Motta R, Nola P, Piussi P (1999) Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst) stands in Paneveggio (Trento, Italy). Glob Ecol Biogeogr 8:455–471

Nakashizuka T (1991) Population dynamics of coniferous and broad-leaved trees in a Japanese temperate mixed forest. J Veg Sci 2:413–418

Namikawa K (1996) Stand dynamics during a 12 year period in an old-growth, cool temperate forest in northern Japan. Ecol Res 11:23–33

North M, Chen J, Oakley B, Song B, Rudnicki M, Gray A, Innes J (2004) Forest stand structure and pattern of old-growth western Hemlock/Douglas-fir and mixed-conifer forests. For Sci 50:299–311

Nowacki GJ, Abrams MD (1994) Forest composition, structure, and disturbance of the Alan Seeger Natural Area, Huntingdon County, Pennsylvania. Bull Torrey Bot Club 121:277–291

Nowacki GJ, Abrams MD (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol Monogr 67:225–249

Oliver CD, Stephens EP (1977) Reconstruction of a mixed forest in central New England. Ecology 58:562–572

Oliver CD, Larson BC (1996) Forest Stand Dynamics (update edition). John Wiley and Sons Inc, New York

Orwig DA, Abrams MD (1999) Impacts of early selective logging on the dendroecology of an old-growth, bottomland hemlock-white pine-northern hardwood forest on the Allegheny Plateau. J Torrey Bot Soc 126:234–244

Rathgeber C, Roche P (2003) Spatio-temporal growth dynamics of a subAlpine *Pinus uncinata* stand in the French Alps. C R Biol 326:305–315

Ren Y (1998) Vegetation of Giant Panda's Habitat of the Qinling Mountains. Shaanxi Science and Technology Press, Xi'an (in Chinese)

Schweingruber FH, Eckstein D, Serre-Bachet F, Braker OU (1990) Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8:9–39

Taylor AH, Qin ZS (1988) Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong Natural Reserve, Sichuan, China. J Ecol 76:1204–1218

Taylor AH, Qin ZS (1992) Tree regeneration after bamboo die-back in Chinese *Abies-Betula* forests. J Veg Sci 3:253–260

Taylor AH, Qin ZS, Liu J (1996) Structure and dynamics of subalpine forests in the Wang Lang Natural Reserve, Sichaun, China. Vegetatio 124:25–38

Veblen TT, Hadley KS, Reid MS, Rebertus AJ (1989) Blowdown and stand development in a Colorado subalpine forest. Can J For Res 19:1218–1225

Veblen TT, Hadley KS, Reid MS (1991) Disturbance and stand development of a Colorado subalpine forest. J Biogeogr 18:707–716

Veblen TT, Hadley KS, Nel EM, Kitzberger T, Reid MS, Villalba R (1994) Disturbance regime and disturbance interactions in a Rock Mountains subalpine forest. J Ecol 82:125–135

Villalba R, Veblen TT (1997) Improving estimates of total tree ages based on increment cores samples. EcoSceince 4:535–542

Wang CW (1961) The Forests of China with a Survey of Grassland and Desert Vegetation. Maria Moors Cabot Foundation, Harvard University, Publication Series 5

Yamaguchi DK (1991) A simple method for cross-dating increment cores from living trees. Can J For Res 21:414–416

Yue M, Ren Y, Dang GD, Gu TQ (1999) Species diversity of higher plant communities in Foping Nature Reserve. Chinese Biodiversity 7:263–369 (in Chinese with English abstract)

Zhang YQ (1989) Shaanxi Forest. Xi'an Science and Technology Press, Xi'an (in Chinese)

A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (*Quercus suber* L.) trees in Southern Portugal

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Abstract The sprouting response types of 1,151 cork oak (*Quercus suber*) trees one and half years after a wildfire in southern Portugal were characterised. It was hypothesised that different response types should occur according to the following conceptual model: an increased level of damage (fire severity) on a sprouting tree that suffered a crown fire was expected to be reflected in a sequence of four alternative events, namely (a) resprouting exclusively from crown, (b) simultaneous resprouting from crown and base, (c) resprouting exclusively from base and (d) plant death. To assess whether the level of expected damage was influenced by the level of protection from disturbance, we explored the relationships between response types and tree size, bark thickness and cork stripping, using an information-theoretic approach. The more common response type was crown resprouting (68.8% of the trees), followed by plant death (15.8%), simultaneous resprouting from crown and base (10.1%) and basal resprouting (5.3%). In agreement with the conceptual model, trees which probably suffered a higher level of damage by fire (larger trees with thinner bark; exploited for cork) died or resprouted exclusively from base. On the other hand, trees that were well protected (smaller trees with thicker bark not exploited for cork) were able to rebuild their canopy through crown resprouting. Simultaneous resprouting from the crown and base was determined mainly by tree size, and it was more common in smaller trees.

Keywords Apical dominance · Mediterranean · Model · Mortality · Resource allocation · Resprouting · Severity

Introduction

Resprouting is an efficient mechanism through which many plants from the Mediterranean region recover above-ground biomass after they have suffered total crown consumption from a wildfire (Whelan 1995; Bond and van Wilgen 1996; Keeley 2006). Sprouting shoots can originate from dormant buds located above ground (axillary, branch epicormic or stem epicormic) or from the base of the plant (i.e. from the collar, roots or underground stems) (Bond and van Wilgen 1996; Miller 2000; Del Tredici 2001). Hereafter, these two sprouting modes will be referred to as 'crown' and 'basal' sprouting (Bond and van Wilgen 1996).

Bellingham and Sparrow (2000) presented a general model of resprouting responses as a function of increasing disturbance severity (severity defined as

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a measure of a plant′s perception of a disturbance event). This gradient of increasing severity was expected to create a sequence of hierarchical regenerative responses ranging from crown (e.g. axillary and branch epicormic) to basal sprouting, where the loss of one type of tissue (e.g. in twig) induces a regenerative response from the next level of hierarchy (e.g. twig axil on the branch) (Bellingham and Sparrow 2000). In their model, disturbance severity is expressed as proportion of above-ground biomass lost (Bellingham and Sparrow 2000). For one particular type of disturbance, wildfires, and in particular crown fires, often all the canopy foliage, buds and twigs are consumed (crown consumption). When this happens, severity will depend mainly on the fire intensity and the level of fire-protection mechanisms at the individual level (e.g. Bond and van Wilgen 1996). Although the hierarchical nature of sprouting responses presented in Bellingham and Sparrow′s model could also be expected in this situation, the fact that in a few studies sprouting responses at different hierarchical levels were simultaneously registered in the same individual plant (Trollope 1984, current study) suggests that the factors underlying response types will be more complex than just above-ground biomass lost.

In situations where wildfires caused total crown consumption in sprouting trees we allege that disturbances of differing levels of damage (severity), and corresponding sprouting responses, not necessarily organised as an hierarchical model, can still be recognised. These responses will be determined by the amount of bud damage in the twigs and branches, the level of damage to stem and root cambial tissue and the amount of below-ground reserves which determines how much carbohydrate reserves can be mobilised to rebuild the lost biomass (Chapin et al. 1990; Bond and van Wilgen 1996; Iwasa and Kubo 1997; Bellingham and Sparrow 2000) (Fig. 1). When the level of fire damage is low (e.g. caused by low fire intensity on trees with thicker bark, and where the stem cambium is not affected), the plant is expected to resprout from crown buds that survived the fire (Fig. 1a). If the level of damage is extreme (e.g. caused by high fire intensity on trees with thinner bark or where the stem cambium is damaged), the most likely outcome is plant death (Fig. 1d). At intermediate levels of severity two response types can be identified. If the level of damage is higher, all crown buds will be killed, either directly through heat or indirectly through the destruction of the vascular cambium in the stem, as the carbohydrate reserves that support sprouting are primarily stored in below-ground structures (Del Tredici 2001). Furthermore, apical dominance will be suppressed directly through bud destruction by heat or indirectly via damage to the cambium (Kozlowski 1971; Kozlowski et al. 1991; Miller 2000), and the tree is therefore expected to respond through basal resprouting (Fig. 1c). Alternatively, if the level of damage is not so severe, partial damage to the crown buds and cambium will cause weakened apical dominance (Kozlowski 1971) and at least some accessibility to below-ground reserves, thereby resulting in the simultaneous resprouting of the crown and base (Fig. 1b). Since the amount of carbohydrate, nitrogen and phosphorus resources that can be used for growth also determines the extent to which plants can resprout (Chapin et al. 1990), the observed resprouting patterns will therefore also be influenced, and plants with depleted below-ground resources may suffer higher levels of damage since they are unable to allocate enough energy to restore the lost biomass. An example of these above-mentioned four types of responses can be found in a study of *Acacia karroo* savanna by Trollope (1984), where different responses were related to tree size and fire intensity. However, no other examples were found in the literature where the

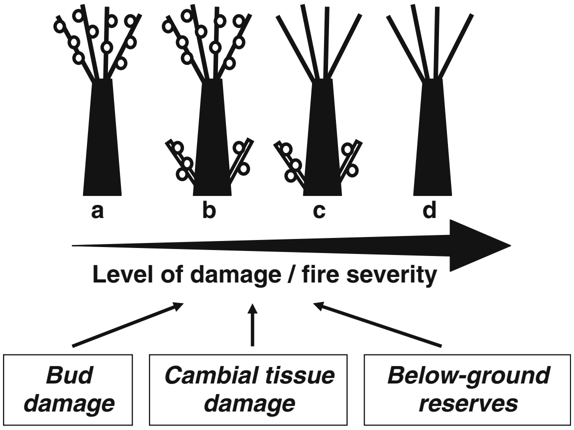

Fig. 1 A conceptual model of post-fire responses of a sprouting tree that suffered total crown consumption (combustion of leaves and twigs during a wildfire) in relation to a gradient of increasing level of damage/fire severity. (**a**) Crown sprouting, (**b**) simultaneous sprouting from crown and base, (**c**) basal sprouting, (**d**) plant death (for further explanations see text)

occurrence of different responses was registered and characterised for other tree species.

The cork oak *Quercus suber* L. is a very important tree species within the Mediterranean basin, both from an economic and ecological perspective (Silva and Catry 2006). The existence of a thick cork bark plays an important role in the capacity of this species to withstand the frequent occurrence of fire typical of Mediterranean climates (e.g. Pausas 1997; Moreira et al. 2007). Another feature of cork oak trees is the capacity of post-fire resprouting from the base and crown after complete defoliation, hence the species is a good model for studying the different response patterns previously described.

In general, there is little information available on the relative frequency of the different response types as well as the factors influencing these responses in cork oak. Previous studies (e.g. Cabezudo et al. 1995; Pausas 1997; Barberis et al. 2003; Catry et al. 2007; Moreira et al. 2007) focused mainly on the factors influencing post-fire survival, and showed the key role of cork stripping, cork thickness and tree size on determining oak survival. In this article, we hypothesise that these three variables also influence other post-fire response patterns (as described in Fig. 1) besides death, since they are expected to influence the level of resistance to fire and, consequently, the level of damage.

Cork stripping is a common operation that is normally performed after the tree attains a certain circumference at breast height (70 cm in Portugal). Cork is a valuable raw material for industry and is periodically removed with an axe by manually cutting along vertical and horizontal lines on the stem and thicker branches and stripping off cork planks (Pereira and Tomé 2004). After each cork stripping, the tree has the capacity to produce new cork bark by adding new layers of cork every year (Pereira and Tomé 2004), Moreira et al. (2007) showed that unstripped trees (with unharvested virgin cork) had higher survival rates than trees that had been exploited for cork (i.e. trees debarked at least once). These authors suggested that the higher survival rates of unstripped trees may be explained by the higher insulating properties of virgin cork (for a given bark thickness) and the absence of stress caused by cork extraction. In fact, cork extraction is a disturbance that has negative effects on tree health and growth (Costa et al. 2004). Thus, stripping probably requires a greater allocation of below-ground energy reserves that will subsequently not be available for investment in resprouting. Consequently, unstripped trees are expected to show lower levels of damage when compared to exploited trees since their buds are more protected and their below-ground reserves may be better preserved.

Cork thickness depends on the harvesting cycle and the time elapsed between harvesting events. Cork can only be harvested every 9–15 years (minimum 9 years according to Portuguese legislation), and several studies have shown that cork age (and thus thickness) is inversely related to post-fire mortality (e.g. Lamey 1893; Pampiro et al. 1992; Cabezudo et al. 1995; Pausas 1997; Barberis et al. 2003; Catry et al. 2007; Moreira et al. 2007). The thicker the bark, the lower the expected level of post-fire damage (again, buds and cambium are more protected from fire).

Barberis et al. (2003) and Moreira et al. (2007) provided evidence that trees with larger diameter at breast height (DBH) had a lower probability of survival. Possible explanation for this pattern include a likely higher amount of stripping damages, higher susceptibility to stress or diseases and higher frequency of poor management practices (e.g. deep ploughing, excessive pruning) in older trees (Costa et al. 2004; Moreira et al. 2007). A bigger tree that has suffered several damage events across its lifespan is therefore prone to higher levels of post-fire damage, mainly because of the lack of carbohydrate reserves to invest in resprouting (Iwasa and Kubo 1997).

The aim of this article is to explore the importance of tree size, bark thickness and cork stripping in determining the whole range of post-fire response types in cork oak. In particular we aimed to: (a) quantify the relative frequency of four different post-fire responses in burned cork oak trees 1.5 years after an intense wildfire and (b) explore whether stripping, bark thickness and tree size influenced each of the observed types of post-fire responses as hypothesised.

Methods

Study area and plot definition

The study area is located in “Serra do Caldeirão”, a mountain range in the Algarve province, southern Portugal. The climate is Mediterranean with an average annual temperature and rainfall of 16.6°C and 900 mm, respectively. The altitude ranges from 150 to 580 m above sea level. Soils consist mainly of shallow schist lithosols that have a low fertility and are prone to erosion. The landscape is characterised by vast expanses of cork oak forests ranging from areas with high tree cover, to "montados" that have scattered trees and an understory of crops or pastures. In the 2004 summer, an intense wildfire burned ca. 25,000 ha in this region. A 1×1 km^2 grid of points covering part of the burned area was used to define a 50 m-radius circle (sampling plot) around each point. Plots were checked in the field for accessibility and to confirm whether they had burned and were dominated by cork oak trees. A total of 40 plots were ultimately selected. Large within-plot variability in tree size and cork age (and consequently bark thickness) was common since cork debarking was not carried out simultaneously on all individual trees (for further details see Moreira et al. 2007).

Tree variables

Individual tree evaluation in the plots took place between December 2005 and April 2006, approximately 1.5 years after the fire. Trees were assessed along four 50-m strip transects departing from the plot centres at right angles. Given the very high density of young trees in many plots, only trees larger than ca. 9 cm DBH were measured. Approximately 30 trees per plot were assessed (mean ± s.e. of 28.8 ± 0.51, range = 14–30, $n = 40$) yielding a total of 1,151 individuals. For each tree, several variables were measured (see Moreira et al. 2007 for details); however, for the purposes of this article only the following variables are presented: (a) tree size (DBH, cm), taken as the average of two measurements at 1.3 m above ground level, (b) bark thickness (average thickness, cm) at breast height, calculated from four measurements using a bark gauge and (c) presence/absence of cork stripping in order to distinguish unstripped trees with virgin cork from exploited trees where cork debarking (stripping) had occurred at least once. The types of post-fire responses were also assessed and classified into four mutually exclusive categories: (a) dead trees (no resprouting from the base or crown), (b) trees that resprouted exclusively from the crown, (c) trees that resprouted exclusively from the base (thus with a dead stem) and (d) trees that resprouted from both the crown and base.

Data analysis

To examine the influence of tree variables on post-fire response types, an information theoretic approach was used based on the Akaike information criterion corrected for small sample sizes (AIC$_c$) (Burnham and Anderson 2002). This approach starts with the formulation of a series of models that rely on an understanding of the system being studied, followed by an assessment of how different putative models compare to the reality (Rushton et al. 2004). The suite of candidate models is compared using AIC$_c$, and the smaller the AIC$_c$ value the better the model fits the data.

Each of the four response types was modelled separately using a binary variable taking the value 1 for the specific response type and 0 for the remaining types. A generalised linear model with binomial error structure and a logit link function (McCullagh and Nelder 1989) was used to test a group of biologically plausible models, including separate models for each of the three variables (stripping, bark thickness, DBH) assumed to be biologically significant, and all possible combinations of these variables. Two interaction terms were also added to this list of variables: stripping × bark thickness, as previous analyses showed that we could expect different responses, for a given bark thickness, of unstripped or exploited trees (Moreira et al. 2007); and stripping × DBH, as the effects of tree size could also vary according to stripping status. This yielded four groups (one group per response type) of 27 models each, resulting from all combinations of these five variables. The smaller AIC$_c$ among the models in each group was used to identify the more parsimonious model (Burnham and Anderson 2002) for each response type.

The fit and predictive performance of the models with smaller AIC$_c$ was evaluated through the likelihood ratio statistic (full model χ^2) and by calculating the area under the receiver operating characteristics (ROC) curve (Saveland and Neueschwander 1990; Pearce and Ferrier 2000). This has the advantage of assessing model performance in a threshold-independent fashion, being independent of the prevalence of the several response types. The AUC varies between 0.5 (no discrimination ability) to 1 (perfect discrimination ability) (Pearce and Ferrier 2000). Usually, AUC values of 0.5–0.7 are taken to indicate low accuracy, values of 0.7–0.9 indicate useful applications and values above 0.9 indicate high accuracy (Swets 1988). The calculation of the AUC and standard error was based on a non-parametric assumption. For a better visualization of the expected probabilities of the fitted models, data from bark thickness and tree size were grouped into classes. The former was divided into three classes: ≤2 cm (33.8% of the trees), 2–4 cm (54.4%) and > 4 cm (11.8%). Tree size was also divided into three DBH categories: ≤20 cm (28.8% of the trees), 20–40 cm (58.5%) and> 40 cm (12.7%).

There was no correlation between bark thickness and DBH ($r = 0.021$, $n = 1151$, $P = 0.487$). However, exploited trees ($n = 859$) had significantly larger DBH than unstripped ones ($n = 292$) (mean ± s.e. of 30.7 ± 0.406 cm and 16.5 ± 0.253 cm, respectively, *t*-test, $t = 29.6$, $P < 0.001$), and had a slightly thinner bark (mean ± s.e. of 2.39 ± 1.289 cm and 2.93 ± 0.835, respectively, *t*-test, $t = 8.1$, $P < 0.001$).

Results

Response types

For the 1,151 sampled trees, the most common response type was resprouting exclusively from crown (68.8%, $n = 792$ trees), followed by death (15.8%, $n = 182$), simultaneous resprouting from the crown and base (10.1%, $n = 116$) and lastly, resprouting exclusively from the base (5.3%, $n = 61$).

Influence of predictor variables on response types

The more parsimonious model for tree death, among the set of models compared, is shown in Table 1 and Fig. 2. The probability of a tree dying increased if it had been exploited and had a larger DBH. Bark thickness was also a key variable but only if trees were exploited, in this case the probability of death increased as bark thickness decreased. Similarly to death, the model with the lowest AIC for resprouting only from base showed that this response type was also more likely in stripped trees (Table 1; Fig. 2). Bark thickness was an important variable in the case of stripped trees, and was negatively correlated to basal resprouting probability. The more parsimonious model for simultaneous resprouting from the base and crown (Table 1; Fig. 2) included only DBH, with larger trees being less likely to show this response type. Finally, resprouting exclusively from the crown was more likely in unstripped trees (Table 1; Fig. 2). For stripped trees, this resprouting type increased with bark thickness and decreased with DBH. Overall, model performance was low to moderate with AUC values ranging from 0.64 to 0.82.

Discussion

Differences in sprouting behaviour are important for understanding vegetation dynamics, extinction risks for threatened species and for defining management regimes for woody plants (Bond and Midgley 2003).

Table 1 Generalized linear models with the lowest AIC_c among the set of models compared, for each of the four post-fire response types in cork oak (death, resprouting exclusively from crown, resprouting exclusively from base, resprouting from both crown and base).

Variable	Death	Base only	Crown and base	Crown only
Stripping	1.645 ± 0.280	2.955 ± 0.440		−1.464 ± 0.278
Bark thickness				
DBH	0.031 ± 0.007		−0.055 ± 0.012	
Stripping × bark thickness	−0.688 ± 0.086	−1.272 ± 0.182		0.809 ± 0.075
Stripping × DBH				−0.016 ± 0.007
Constant	−2.722 ± 0.229	−3.570 ± 0.358	−0.842 ± 0.283	0.940 ± 0.130
Model χ^2	101.95	81.03	27.79	153.65
AUC	0.71 ± 0.022	0.82 ± 0.026	0.64 ± 0.026	0.70 ± 0.017

The variables entering each model (linear predictor), their coefficients (±s.e.), the model χ^2 and the area under the ROC curve (AUC ± s.e.) are shown for each response type. See Fig. 2 for model visualization. All model χ^2, variable coefficients and AUC values are significant ($P < 0.05$)

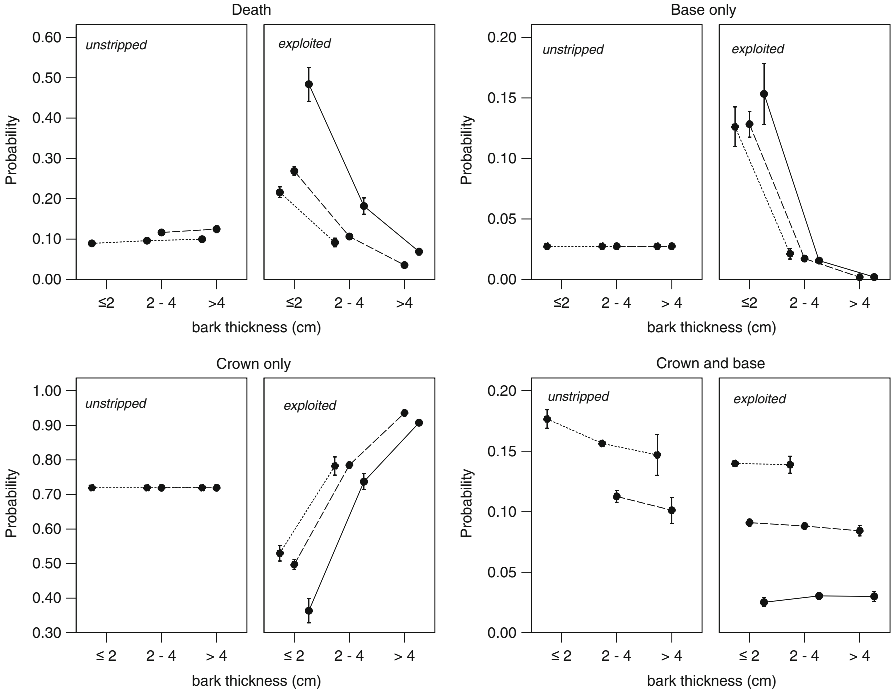

Fig. 2 Mean (±95% confidence intervals) of the predicted probability of each response type (dead, base only, crown and base, crown only), according to the GLM models shown in Table 1, for each combination of bark thickness and DBH classes. Unstripped and exploited trees correspond, respectively, to the left and right panels. The three DBH classes are shown by different line styles (——: >40 cm, - - - -: 20–40 cm, ·······: <20 cm)

Bellingham and Sparrow's (2000) model of resprouting response as a function of increasing disturbance severity assumes a hierarchical sequence of regenerative responses that depends on the proportion of the above-ground biomass lost. Here, a conceptual model is presented (Fig. 1) which can be applied to situations where a specific disturbance (fire) caused crown consumption on a tree with resprouting abilities. In this situation, different levels of damage are expected to create a sequence of response types where the hierarchical nature of sprouting type is not necessarily followed. These damage levels are assumed to be determined by the amount of damage to buds and cambial tissue, and by the available below-ground reserves that can be used to rebuild the lost biomass (e.g. Bond and van Wilgen 1996). Different levels of damage will cause four different types of post-fire responses that were identified in cork oaks in southern Portugal, 1.5 years after being burned in an intense wildfire. The majority of trees (ca. 70%) resprouted exclusively from the crown, which is expected to correspond to the lower level of damage. The second most common response category was death (16% of the trees), which corresponds to the highest level of damage. Response types expected to correspond to intermediate damage levels were less common: simultaneous resprouting of the crown and base was the third more common response type (10% of the trees), whereas the least common response type was resprouting only from the base (i.e. stem death) (5% of the trees).

The relationship between the expected level of damage and the degree to which a tree is protected from disturbance was also addressed. The focus was on three variables previously known to have an important impact on cork oak post-fire survival, namely cork stripping, bark thickness and tree size.

It was hypothesised that stripping would be a strong determinant of the expected level of post-fire damage to trees, since the process of extracting highly insulating virgin cork for the first time initialises major periodic stresses across the life span of a tree (e.g. Natividade 1950; Costa et al. 2004; Moreira et al. 2007). This is consistent with the result that stripping is positively correlated with the likelihood of response types with higher levels of damage (i.e. dead trees and resprouting from base), and was negatively related to the probability of crown resprouting (corresponding to lower levels of damage).

Bark thickness is a well-known determinant of post-fire survival in cork oak (e.g. Cabezudo et al.

1995; Pausas 1997; Barberis et al. 2003; Catry et al. 2007; Moreira et al. 2007). Insulating capacity increases with bark thickness (Dikinson and Johnson 2001), thereby providing a higher level of protection to both the buds and the living tissues in the vascular cambium from which resprouting closely depends. As expected, the thicker the bark the lower the probability of a greater level of damage (expressed in the negative correlation of this variable with dead and basal resprouting probability), and the higher the probability of a low level of damage (expressed in the positive correlation with crown resprouting probability). However, the effect of bark thickness on post-fire responses is expressed only in exploited trees, suggesting that trees with virgin cork have an additional degree of protection that appears independent of bark thickness, as previously discussed in Moreira et al. (2007).

The relationship between tree size (DBH) and level of protection from fire was hypothesised to be related to the amount of damage and to the availability of below-ground carbohydrate reserves that may be allocated to resprouting. To be able to sprout and support regrowth, a plant needs surviving meristems and stored carbohydrate reserves (Iwasa and Kubo 1997; Bond and Midgley 2001). Older plants should have larger below-ground reserves (Gurvich et al. 2005) and consequently a higher capacity to mobilise reserves in response to disturbance (Bellingham and Sparrow 2000). For example, Malanson and Trabaud (1988) found that a 9-year-old *Q. coccifera* resprouted more vigorously than a 3-year-old, presumably because the latter had less developed below-ground reserves. Other empirical studies, however, suggest that resprouting ability declines with age and that below-ground carbohydrate storage in larger trees may be invested in survival rather than growth (Bond and van Wilgen 1996; Bond and Midgley 2001). In the case of cork oak, once cork exploitation has begun, the older (and therefore larger) trees have probably experienced a higher number of stripping events and poor management practices (e.g. deep ploughing or excessive canopy pruning) (Natividade 1950; Costa et al. 2004; Silva and Catry 2006). Therefore, if below ground reserves are allocated to recover from damages accumulated across the plant's lifespan, they will be diverted from resprouting (Bellingham and Sparrow 2000; Chapin et al. 1990). Reduced vigour and survivorship of resprouting shrubs have been related to increasing disturbance frequency due to the impossibility of rebuilding or maintaining energy reserves in storage organs between consecutive disturbances (Bellingham and Sparrow 2000). Thus, it was hypothesised that bigger trees would be prone to higher levels of damage, and this was consistent with the fact that DBH was positively correlated with the likelihood of death, particularly in exploited trees. Bigger trees were also less likely to resprout from the crown, which also indicated a higher level of damage, and of simultaneous resprouting from the crown and base.

The fact that the models obtained had moderate predictive performance suggests that other variables, which may not be directly related to tree features, also contribute to the level of damage suffered by each individual. If these other factors had been taken into account, they would probably explain a larger proportion of variability in the observed patterns. For example, Moreira et al. (2007) showed that variables related to stand structure (e.g. tree density or understory vegetation height) and topographic location (slope and aspect) as well as indicators of fire severity (e.g. charring height) were significant predictors of cork oak mortality in the same study area. Other factors known to influence post-fire sprouting responses include site quality (López Soria and Castell 1992), disturbance frequency (Bond and Midgley 2001), fire season (Konstantidinis et al. 2006) and the existence of herbivory (Moreno and Oechel 1991).

The expected probabilities of the different response type models reflected the relative frequency of these types in the field. Thus, the more likely response type (the one with higher expected probability) for all possible combinations of stripping status, cork thickness and bark thickness was resprouting from crown. The only exception was when trees were exploited, had a very thin bark (<2 cm) and were very big (>40 cm DBH). This corresponds to the higher level of damage in our model, which is consistent with the fact that death was the most likely outcome (Fig. 2).

In summary, the influence of the studied variables on the post-fire response patterns of cork oak after fire were in agreement with the hypothesis that different levels of damage (and corresponding response types) may be found in sprouting trees where all the crown was destroyed by wildfire. We provided evidence that four different response types may occur, and that these are influenced by stripping status, bark thickness and tree size, which are probably related to the level of protection of buds and cambial tissue, and to the amount of below ground reserves available for the plant to invest in resprouting.

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References

Barberis A, Dettori S, Filigheddu MR (2003) Management problems in Mediterranean cork oak forests: post-fire recovery. J Arid Environ 54:565–569. doi:10.1006/jare.2002.1079

Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89:409–416. doi:10.1034/j.1600-0706.2000.890224.x

Bond WJ, van Wilgen BW (1996) Fire and plants. Chapman & Hall, London

Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51. doi:10.1016/S0169-5347(00)02033-4

Bond WJ, Midgley JJ (2003) The evolutionary ecology of sprouting in woody plants. Int J Plant Sci 164:103–114. doi:10.1086/374191

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach, 2nd edn. Springer, New York

Cabezudo B, Latorre A, Nieto J (1995) After fire regeneration in a *Quercus suber* forest in the South of Spain (Istan, Malaga). Acta Bot Malacitana 20:143–151

Catry FX, Rego FC, Bugalho MN, Lopes T, Silva JS, Moreira F (2007) Post-fire tree mortality and regeneration in a mixed forest: evaluating the cumulative impacts of herbivory. In: Rokich D, Wardell-Johnson, Yates C, Stevens J, Dixon K, McLellan R, Moss G (eds) Proceedings of the International Mediterranean Ecosystems Conference-Medecos XI 2007. Kings Park and Botanic Garden, Perth, Australia, pp 45–46

Chapin FS, Ernst-Detlef S, Mooney HA (1990) The ecology and economics of storage in plants. Annu Rev Ecol Syst 21:423–447. doi:10.1146/annurev.es.21.110190.002231

Costa A, Pereira H, Oliveira A (2004) The effect of cork-stripping damage on diameter growth of Quercus suber L. Forestry 77:1–8. doi:10.1093/forestry/77.1.1

Del Tredici P (2001) Sprouting in temperate trees: a morphological and ecological review. Bot Rev 67:121–140. doi:10.1007/BF02858075

Dikinson MB, Johnson EA (2001) Fire effects on trees. In: Johnson EA, Miyanishi K (eds) Forest fires: behaviour and ecological effects. Academic Press, New York, pp 477–525

Iwasa Y, Kubo T (1997) Optimal size of storage for recovery after unpredictable disturbances. Evol Ecol 11:41–65. doi:10.1023/A:1018483429029

Gurvich DE, Enrico L, Cingolani AM (2005) Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. Austral Ecol 30:789–796. doi:10.1111/j.1442-9993.2005.01522.x

Keeley J (2006) Fire severiy and plant age in postfire resprouting of woody plants in sage scrub and chaparral. Madrono 53:373–379. doi:10.3120/0024-9637(2006)53[373:FSAPAI]2.0.CO;2

Konstantidinis P, Tsiourlis G, Xofis P (2006) Effect of fire season, aspect and pre-fire plant size on the growth of *Arbutus unedo* L. (strawberry tree) resprouts. For Ecol Manag 225:359–367

Kozlowski TT (1971) Growth and development of trees, vol 1. Academic Press, New York

Kozlowski TT, Kramer PJ, Pallardy JG (1991) The physiological ecology of woody plants. Academic Press, San Diego

Lamey A (1893) Le chêne-liège, sa culture et son exploitation. Paris Nancy, Berger-Levrault et Cie éditeurs

López Soria L, Castell C (1992) Comparative genet survival after fire in woody Mediterranean species. Oecologia 91:493–499. doi:10.1007/BF00650321

Malanson GP, Trabaud L (1988) Vigour of post-fire resprouting by Quercus coccifera L. J Ecol 76:351–356. doi:10.2307/2260598

McCullagh P, Nelder JA (1989) Generalized Linear Models. Chapman and Hall, London

Miller M (2000) Fire autecology. In: Brown JK, Smith JK (eds) Wildland fire in ecosystems: effects of fire on flora. Gen Tech Rep RMRS-GTR-42, vol 2. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, US, pp 9–34

Moreira F, Duarte I, Catry F, Acácio V (2007) Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal. For Ecol Manag 253:30–37

Moreno JM, Oechel WC (1991) Fire intensity and herbivory effects on post-fire resprouting of Adenostoma fasciculatum in southern California chaparral. Oecologia 85:429–433. doi:10.1007/BF00320621

Natividade JV (1950) Subericultura. DGSFA, Lisboa

Pampiro F, Pintus A, Ruiu PA (1992) Interventi di recupero di una giovane sughereta percorsa da incêndio. In: Instituto de Promoción del Corcho (ed) Simpósio Mediterrâneo sobre Regeneración del Monte Alcornocal, Mérida, pp 174–177

Pausas J (1997) Resprouting of *Quercus suber* in NE Spain after fire. J Veg Sci 8:703–706. doi:10.2307/3237375

Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecol Modell 133:225–245. doi:10.1016/S0304-3800(00)00322-7

Pereira H, Tomé M (2004) Cork oak. In: Burley J, Evans J, Youngquist JA (eds) Encyclopedia of Forest Sciences. Elsevier, Oxford, pp 613–620

Rushton SP, Ormerod SJ, Kerby G (2004) New paradigms for modelling species distributions? J Appl Ecol 41:193–200. doi:10.1111/j.0021-8901.2004.00903.x

Saveland JM, Neueschwander LF (1990) A signal detection framework to evaluate models of tree mortality following fire damage. For Sci 36:66–76

Silva JS, Catry F (2006) Forest fires in cork oak (*Quercus suber*) stands in Portugal. Int J Environ Stud 63:235–257. doi:10.1080/00207230600720829

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293. doi:10.1126/science.3287615

Trollope WSW (1984) Fire in savanna. In: de Booysen PV, Tainton NM (eds) Ecological effects of fire in south African ecosystems. Springer Verlag, Berlin, pp 199–218

Whelan RJ (1995) The ecology of fire. Cambridge University Press, Cambridge

Non-woody life-form contribution to vascular plant species richness in a tropical American forest

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Abstract We provide total vascular plant species counts for three 1-ha plots in deciduous, semi-deciduous and evergreen forests in central Bolivia. Species richness ranged from 297 species and 22,360 individuals/ha in the dry deciduous forest to 382 species and 31,670 individuals/ha in the evergreen forest. Orchidaceae, Pteridophyta and Leguminosae were among the most species-rich major plant groups in each plot, and *Peperomia* (Piperaceae), *Pleurothallis* (Orchidaceae) and *Tillandsia* (Bromeliaceae), all epiphytes, were the most species-rich genera. This dominance of a few but very diverse and/or widespread taxa contrasted with the low compositional similarity between plots. In a neotropical context, these Central Bolivian forest plots are similar in total species richness to other dry

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deciduous and humid montane forests, but less rich than most Amazonian forests. Nevertheless, lianas, terrestrial herbs and especially epiphytes proved to be of equal or higher species richness than most other neotropical forest inventories from which data are available. We therefore highlight the importance of non-woody life-forms (especially epiphytes and terrestrial herbs) in Andean foothill forest ecosystems in terms of species richness and numbers of individuals, representing in some cases nearly 50% of the species and more than 75% of the individuals. These figures stress the need for an increased inventory effort on non-woody plant groups in order to accurately direct conservation actions.

Keywords Alpha diversity · Andean foothills forest ecosystem · Life-form diversity · Non-woody plants · Total species inventory

Introduction

Statements about the diversity of plant species in forest ecosystems are usually based on results from vegetation inventories that are mostly restricted to a certain plant subgroup. Woody species, usually trees and shrubs with diameter at breast height of ≥1 cm (e.g. the STRI 50-ha plots, Condit 1995), ≥2.5 cm (e.g. 0.1-ha transects, Gentry 1982) and ≥10 cm (e.g. Gentry 1988; Valencia et al. 1994; Smith and Killeen 1998), are the most commonly studied plant groups. In contrast, herbs (e.g. Poulsen and Balslev 1991; Poulsen and Nielsen 1995), lianas (Pérez-Salicrup et al. 2001; Mascaro et al. 2004) and epiphytes (Ingram et al. 1996; Arévalo and Betancur 2004; Benavides et al. 2005; Krömer et al. 2005) are less commonly used to characterize the diversity of vegetation types. These non-woody life-forms, however, have been shown to be of importance in the few assessments of tropical plant alpha diversity in which all vascular plants were counted (Whitmore et al. 1985; Gentry and Dodson 1987; Duivenvoorden 1994; Balslev et al. 1998; Galeano et al. 1998; Langenberger et al. 2006). The scarcity of such studies can be attributed to the difficulties associated with identification of more (and usually less well known) plant groups (restricting inventories to some life-form groups in the tropics is already a huge identification task) and the difficulty of collecting epiphyte specimens from the forest canopy. Whitmore and colleagues have undertaken the most comprehensive study of vascular plants to date in a Costa Rican rain forest. To accomplish their task of inventorying all species (including non-vascular plants), destructive sampling of a 10 m × 10 m plot was required (Whitmore et al. 1985).

The few full tropical plant inventories performed to date have focused on a single and homogeneous vegetation type, usually tropical lowland rain forests. Although some of these studies (e.g. Duivenvoorden 1994; Langenberger et al. 2006) inventoried plots and transects along edaphic and physiographic gradients, only two have inventoried and compared different vegetation types using a uniform sampling methodology throughout. Álvarez et al (2003) reported total vascular plant counts in three 0.1-ha plots in Amazonian, Chocoan and Andean forests in Colombia. This study, however, was not published formally, and epiphytes in the Amazonian plot were not sampled, restricting the total vascular plant count to the Chocó and Andean forest only. The other study by Gentry and Dodson (1987) compared three 0.1-ha plots in wet, moist and dry forests in Ecuador. The lack of standardized inventory methods hampers the quantitative comparison between both of these studies. The use of florulas could be an option to compare different forests (e.g. Gentry 1990), but the size of the areas studied and collection intensities are not uniform (Tobler et al. 2007).

We chose Central Bolivia, a region where four major biomes occur in close proximity to each other (humid and moist vegetation from Amazonia, seasonal subtropical lowland vegetation from the Chaco, subtropical highland vegetation from the Andes and seasonal vegetation of the Chiquitanía (Ibisch et al. 2003)), as our study region. We established within this complex biogeographic setting three permanent 1-ha plots. We used a uniform methodology along a humidity gradient from deciduous to evergreen forest, inventorying all vascular plants present. Our main objective was to quantitatively assess the relative importance of different life-form groups and taxa within the different vegetation types we surveyed and to compare our results with similar studies in the neotropical region.

Methods

Study area

The study was carried out at the Refugio Los Volcanes in Santa Cruz, Bolivia. Los Volcanes is a private reserve of approximately 300 ha. It is located about 18°06′ S and 63°36′ E and is adjacent to the southern border of Amboró National Park, directly on the transition from the humid inner tropics to the seasonally dry subtropics (Fig. 1a). The substrate of the study area consists primarily of red sandstone and locally of loamy sedimentary rocks (lutite). These red sandstones form cliffs several hundred metres high and are intersected by narrow valleys providing the area with dramatic scenery. Annual precipitation is about 1200–1500 mm, with most of the rainfall from October/November to March/April, but with high temporal variability.

The general vegetation of the area has been classified as ‘subhumid to humid deciduous forest of southeastern Amboró’ (Navarro et al. 1996) and is usually found at 900–1100 masl. Among the dominant tree species are *Aspidosperma cylindrocarpon* (Apocynaceae), *Cariniana estrellensis* (Lecythidaceae), *Cedrela lilloi* (Meliaceae), *Gallesia integrifolia* (Phytolaccaceae), *Pachystroma longifolium* (Euphorbiaceae), *Pogonopus tubulosus* (Rubiaceae) and *Tabebuia lapacho* (Bignoniaceae) (Navarro et al. 1996). Locally, however, vegetation types are determined by differences in topography, aspect and precipitation regimes that lead to ecologically relevant differences in water availability within the study area. Consequently, the dominant zonal vegetation is semi-deciduous forest (about 30–50% deciduous trees) mainly found on shaded south-facing slopes. Steep, sunny and north-facing slopes are occupied by deciduous forest (70–90% deciduous trees), whereas flat, shaded valleys with groundwater supply support evergreen forest (10–20% deciduous trees) (Fig. 1b).

Vegetation sampling

A permanent plot of 1 ha was established in each forest type (deciduous, semi-deciduous and evergreen) between 2002 and 2003. Each plot was subdivided into 25 adjacent 20 m × 20 m subplots. Plots where laid out in such a way as to include only the forest type under study, avoiding other forest types, young secondary vegetation and non-forest vegetation (e.g. rock outcrops). Thus, our plots are not the traditional square 100 m × 100 m inventory plots but have rather irregular shapes (Fig. 1c).

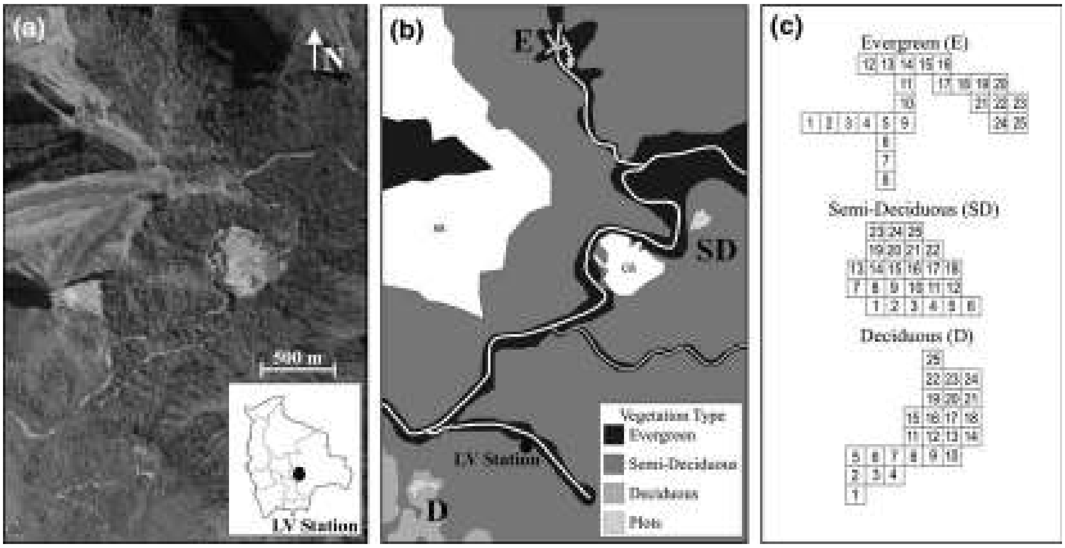

Fig. 1 Main vegetation types and plot shape and location in the study area. **a** Aerial photograph of the Refugio Los Volcanes area in central Bolivia, *inset* showing map of Bolivia and location of study area. **b** Schematic representation of the major vegetation types and geographical characteristics of the area, showing plot locations and orientation (ss: sandstone, ca: cleared area, LV Station: Los Volcanes Research Station). **c** Shape of inventory plots, where numbers denote subplots

All vascular plants in each plot were inventoried between 2002 and 2004, mainly in the season following the summer rains (i.e. May–August). J. Lendzion inventoried herbs, shrub and tree seedlings, E. I. Hennig epiphytes, D. Hoffmann lianas and V. Cardona, D. Soto and S. K. Herzog woody plants. For the herb inventories, we recorded all species with stem diameter below 1 cm. Additionally, we recorded all Cactaceae, Bromeliaceae and Costaceae below 1 m height and epiphytes on fallen branches. For lianas, we recorded all individuals, including Araceae, with a diameter of >1 cm at 1.3 m above soil level. All epiphytes were observed and counted. Collections of epiphytes were made either with a clipper pole or with the help of rope-climbing techniques. Binoculars were used to aid identification when they were too inaccessible to collect. Finally, we recorded all woody plants, excluding lianas, with diameter at breast height (dbh) of >1 cm.

Voucher specimens of all species were collected for later determination and are deposited at USZ (Santa Cruz) and LPB (La Paz), with a small subset of samples at the Göttingen Herbarium (GOET) (herbarium acronyms follow Holmgren and Holmgren 1998). Several sterile specimens could not be fully identified and were sorted into morphospecies. The final stage of data production was completed at USZ (by R. Linares-Palomino) by cross-checking all collected vouchers in order to unify morphospecies delimitations.

Data analysis

We used a conservative approach in calculating species numbers by lumping highly similar morphospecies into one group instead of considering them as several distinct species. The herb inventory, which included life-forms other than herbaceous plants, was split into terrestrial herbs, tree seedlings, shrub seedlings and epiphytes. Thus, terrestrial herbs formed a life-form group by itself in subsequent analyses. The other three subgroups were cross-referenced with the tree, shrub and epiphyte inventories and merged accordingly. We follow the TROPICOS and Flora of Bolivia online databases for nomenclatural purposes (both available at http://mobot.mobot.org/W3T/Search/vast.html and http://www.efloras.org/flora_page.aspx?flora_id=40, respectively). Despite much progress in the understanding of the phylogeny of extant ferns, familial composition and relationships are still unsatisfactorily solved (Smith et al. 2006; Schuettpelz and Pryer 2007). We therefore refrained from assigning our collections to families and treated all ferns and fern allies as a single taxon Pteridophyta.

We computed species accumulation curves based on the 20 m × 20 m subplots using Estimate*S* (Colwell 2005). Similarity between forest plots was evaluated by subtracting the Bray–Curtis distance between two forest plots from unity. Pair-wise Bray–Curtis distances (D_{BC}) were calculated in the vegan package for R (Oksanen et al. 2006; R Development Core Team 2006) using presence/absence data by $D_{BC} = 2a/(2a + b + c)$, where a is the total number of species present in both forest plots, b is the number of species present only in the first forest plot, and c is the number of species present only in the second forest plot (Magurran 2004). In order to compare the species richness of the Los Volcanes plots with that of other forests in the neotropics, we searched for other published full plant, epiphyte, liana, terrestrial herb and tree/woody plant inventories (Appendix 1) and plotted species accumulation curves for each forest type at Los Volcanes against the species richness data of the other studies.

Results

Taxonomic diversity

We recorded 80,352 individual plants belonging to 670 species (including morphospecies) on the three plots (Appendix 2). We were able to completely identify 52% of our collections to species level (341 species), an additional 25% could be assigned to genus (172 morphospecies) and 14% to family (95 morphospecies). Nine percent (62 morphospecies) could not be assigned to a family or lower taxon.

The most species-rich plots were in the evergreen and semi-deciduous forest, both of which had an almost identical number of species (381 and 382, respectively). The deciduous forest had 297 species. Of the 273 genera, most were recorded in the evergreen and semi-deciduous forest (190 and 185, respectively) compared to 162 genera in the deciduous forest. Of the 92 families, 75 were found in the evergreen, 72 in the semi-deciduous and 60 in the

Table 1 Number of families, genera and species of three 1-ha plots in Santa Cruz, Central Bolivia (A: angiosperms, P: pteridophytes)

	Total from the three forest plots			Deciduous forest plot			Semi-deciduous forest plot			Evergreen forest plot		
	A	P	Total	A	P	Total	A	P	Total	A	P	Total
Families	80	12	92	55	5	60	64	8	72	65	10	75
Genera	245	28	273	149	13	162	168	17	185	166	24	190
Species	617	53	670	279	18	297	353	29	382	337	44	381
Life-form												
Epiphyte	142			67			80			109		
Hemiepiphyte	9			1			4			8		
Liana	153			64			86			44		
Shrub	97			45			49			57		
Tree, liana	1			1			–			1		
Tree, shrub	39			17			16			20		
Terrestrial herb	79			30			42			57		
Tree	148			71			105			84		
Other	1			–			–			1		
Parasite	1			1			–			–		

Life-form composition values show the number of species assigned to each plant group

deciduous forest. The contribution of ferns and lycophytes ("pteridophytes") to species richness was higher in the evergreen forest than in the two other forest types (Table 1).

Of the 10 most species-rich families, seven were shared between all three plots, although with different ranking within each plot (Table 2). Taking all three plots together, the most species-rich families were Orchidaceae, pteridophytes, Leguminosae and Bignoniaceae. Orchidaceae, a family containing mostly epiphytic species, was by far the most species-rich in all plots. Pteridophytes, composed mostly of ground herbs, ranked second in the evergreen and semi-deciduous and fourth in the deciduous forest. Leguminosae, which was mainly composed of woody species in our plots, decreased in importance from the deciduous (second) to the evergreen forest (fourth). Absolute species numbers were similar in the evergreen forest and higher in the semi-deciduous forest as compared to the deciduous forest. Bignoniaceae (a family including liana, shrub and tree species), the third most important family in the deciduous forest, was the fourth most important family in the semi-deciduous forest (again with a higher species number) but was ranked only eighth in the evergreen forest. Only two other families were important in terms of species numbers, and these were shared by two forest types: Apocynaceae (mostly trees) present in the deciduous and semi-deciduous forest and Rubiaceae (shrubs and trees) present in the semi-deciduous and evergreen forest.

In contrast to families, only five species-rich genera were common to all three forest plots (*Peperomia*, *Pleurothallis*, *Tillandsia*, *Acalypha* and *Eugenia*). Of these, the three most species-rich genera were *Peperomia*, *Tillandsia* and *Pleurothallis*, although ranking varied between forest plots (Table 2).

Two species of *Tillandsia* had the highest numbers of individuals on all three plots (Table 2): *T. bryoides* had highest numbers in the deciduous forest, whereas *T. tenuifolia* had most individuals in the semi-deciduous and evergreen forests. The 10 species with highest number of individuals in the deciduous forest included epiphytes and terrestrial herbs (three species each) and shrubs and trees (two species each). The contribution of non-woody plants increased in the semi-deciduous forest, including epiphytes (four species), terrestrial herbs (three species) and one species each of shrubs, trees and lianas. Non-woody plant contribution was highest in the evergreen forest with six species of epiphyte, two species of terrestrial herb and one hemiepiphyte species dominating. Only one shrub species was included among the top 10.

Table 2 Most species-rich families and genera (number of species in parentheses) and most abundant species (number of individuals in parentheses)

Deciduous	Semi-deciduous	Evergreen	Total
Families (Pteridophyta is considered as one family)			
Orchidaceae (34, e)	Orchidaceae (45, e)	Orchidaceae (60, e)	Orchidaceae (85, e)
Leguminosae (20, t)	Pteridophyta (29, h)	Pteridophyta (44, h)	Pteridophyta (53, h)
Bignoniaceae (19)	Leguminosae (26, t)	Bromeliaceae (20, e)	Leguminosae (39, t)
Pteridophyta (18, h)	Bignoniaceae (23)	Leguminosae (20, t)	Bignoniaceae (35)
Bromeliaceae (16, e)	Rubiaceae (16)	Piperaceae (16)	Bromeliaceae (26, e)
Euphorbiaceae (13, s,t)	Bromeliaceae (15, e)	Rubiaceae (14)	Rubiaceae (23)
Piperaceae (12)	Sapindaceae (13)	Euphorbiaceae (12, s,t)	Euphorbiaceae (21, s,t)
Acanthaceae (12, h)	Euphorbiaceae (12, s,t)	Araceae (9, e)	Acanthaceae (20, h)
Apocynaceae (10, t)	Apocynaceae (11, t)	Moraceae (9, t)	Apocynaceae (18, t)
Myrtaceae (9, s,t)	Piperaceae (11)	Asteraceae (8)	Piperaceae (18)
Cactaceae (9)		Bignoniaceae (8)	
		Lauraceae (8, t)	
		Melastomataceae (8)	
Genera			
Peperomia (9)	*Tillandsia* (11)	*Tillandsia* (13)	*Tillandsia* (15)
Pleurothallis (8)	*Peperomia* (8)	*Pleurothallis* (10)	*Pleurothallis* (14)
Tillandsia (7)	*Pleurothallis* (8)	*Peperomia* (9)	*Peperomia* (11)
Acalypha (6)	*Forsteronia* (6)	*Epidendrum* (8)	*Acalypha* (10)
Forsteronia (6)	*Acalypha* (5)	*Acalypha* (7)	*Epidendrum* (9)
Acacia (5)	*Eugenia* (5)	*Begonia* (7)	*Forsteronia* (9)
Eugenia (5)	*Machaerium* (5)	*Piper* (7)	*Begonia* (8)
Machaerium (4)	*Philodendron* (5)	*Eugenia* (6)	*Eugenia* (7)
Epidendrum (4)	*Psychotria* (5)	*Ficus* (6)	*Ficus* (7)
Philodendron (4)	*Randia* (5)	*Thelypteris* (6)	*Piper* (7)
Ruellia (4)	*Thelypteris* (5)		
Species (number of individuals)			
Tillandsia bryoides (2410, e)	*Tillandsia tenuifolia* (2008, e)	*Tillandsia tenuifolia* (5576, e)	*Tillandsia tenuifolia* (8059, e)
Peperomia comarapana (1654, h)	*Piper callosum* (1132, s)	*Racinaea parviflora* (1879, e)	*Peperomia tetragona* (2549, e)
Rinorea ovalifolia (1534, s)	*Paspalum humboldtianum* (972, h)	*Vriesea maxoniana* (1745, e)	*Racinaea parviflora* (2426, e)
Petiveria alliacea (1056, s)	*Olyra fasciculata* (932, h)	*Blechnum occidentale* (1058, h)	*Tillandsia bryoides* (2410, e)
Peperomia tetragona (1012, e)	*Peperomia tetraphylla* (925, e)	*Philodendron camposportoanum* (837, e)	*Piper callosum* (2156, s)

Table 2 continued

Deciduous	Semi-deciduous	Evergreen	Total
Olyra fasciculata (986, h)	*Adiantum tetraphyllum* (800, h)	*Thelypteris dentata* (803, h)	*Vriesea maxoniana* (2120, e)
Acacia polyphylla (802, t)	*Peperomia tetragona* (789, e)	*Peperomia tetragona* (748, e)	*Olyra fasciculata* (2012, h)
Commelina erecta (777, h)	*Philodendron camposportoanum* (745, e)	*Lomagramma guianensis* (741)	*Philodendron camposportoanum* (2007, e)
Tillandsia streptocarpa (755, e)	*Piper* amalago (681, t)	*Peperomia aceroana* (735, e)	*Peperomia comarapana* (1678, h)
Coursetia brachyrhachis (522, t)	*Herreria montevidensis* (521, l)	*Piper callosum* (692, s)	*Commelina erecta* (1574, h)

The dominant life-form is indicated for families and individual species (e = epiphytic, h = terrestrial herb, s = shrub, t = tree, l = liana). Nomenclature follows TROPICOS and the Flora of Bolivia online databases (http://mobot.mobot.org/W3T/Search/vast.html and http://www.efloras.org/flora_page.aspx?flora_id=40, respectively)

Life-form composition

In the deciduous forest, trees, epiphytes and lianas contributed similar species numbers (22–24% of the total, Table 1). In the semi-deciduous forest, trees were slightly more species-rich than other life-forms (28%), followed by lianas (23%) and epiphytes (21%). The most species-rich life-form in the evergreen forest was epiphytes (29%), followed by trees (22%), shrubs (15%) and ground herbs (15%) (Table 1). Woody plants (including lianas and shrubs) contributed to approximately 66%, 57% and 54% of total species richness in the deciduous, semi-deciduous and evergreen forest plots, respectively. There was a highly significantly statistical difference between the proportions of life-forms in the three studied forest types (G-test, $G = 28.34$, $P = 0.0004$, df = 8).

Pearson correlation analyses among life-form richness patterns within each forest plot showed that tree species richness patterns were positively and significantly correlated with total plant species richness: deciduous forest $r = 0.67$ ($P = 0.0002$), semi-deciduous forest $r = 0.54$ ($P = 0.0049$), evergreen forest $r = 0.59$ ($P = 0.0021$). No other significant correlation could be detected between trees and other life-forms, except with shrubs in the semi-deciduous forest ($r = 0.51$, $P = 0.01$) and with lianas in the evergreen forest ($r = 0.53$, $P = 0.0064$). Apart from trees, lianas were the only other life-form that showed similar levels of positive and significant correlations with total plant species richness across the three plots: deciduous forest $r = 0.63$ ($P = 0.0007$), semi-deciduous forest $r = 0.66$ ($P = 0.0003$), evergreen forest $r = 0.54$ ($P = 0.0051$). Other positive significant correlations were detected in the evergreen forest plot between total plant species richness and epiphytes ($r = 0.60$, $P = 0.0017$) and terrestrial herbs ($r = 0.69$, $P = 0.0001$).

Similarity among plots

Similarity among plots was 0.46 between deciduous and semi-deciduous (155 species shared), 0.37 between deciduous and evergreen (125 species shared) and 0.57 between semi-deciduous and evergreen (216 species shared). We recorded 106 species occurring in all three plots. One hundred and twenty-three species were recorded only in the deciduous plot, 117 only in the semi deciduous plot and 146 only in the evergreen forest plot.

Discussion

Plot shape and its influence on species richness estimations

Spatial distribution patterns of plant species in tropical forests are influenced by niche assembly and/or random dispersal assembly processes acting at both local and landscape scales (Chave 2004; Gaston and Chown 2005; John et al. 2007), resulting in mostly clumped distributions (e.g. Condit et al. 2000). Within this scenario, plot shape has been documented to influence estimates of species richness, i.e. longer and narrower rectangular plots are prone to capture more species than square plots of similar area (Condit et al. 1996; Laurance et al. 1998). The differences, however, were found to be small and statistically non-significant in a study comparing tree species richness in 100 m × 100 m square plots versus 40 m × 250 m rectangular plots in Central Amazonia (Laurance et al. 1998). Given the patchy and fragmented nature of the deciduous and evergreen forests in our study area, it was impossible to survey the vegetation types in traditional square or rectangular plots. Rather, we tried to survey as environmentally homogeneous an area as possible, leading to our irregular plot shape design. There is little doubt that plot shape has influenced our results, especially those of the evergreen forest plot. The extent of this influence, however, seems to be small, since the species accumulation curves for all vascular plants together and for individual life-forms significantly decrease or level off when the hectare is completely surveyed, suggesting that sampling was representative in all three forest types.

Alpha diversity and plant density at Los Volcanes

Additional plant surveys across the entire Los Volcanes reserve (approx. 300 ha) have documented 65 species of pteridophytes (M. Kessler, unpublished data), of which 53 (82%) were recorded in the plots. The corresponding figures are 83% for Acanthaceae, 90% for Araceae, 84% for Bromeliaceae and 92% for Cactaceae. If these groups are considered to be representative of the total flora, then our plots contain roughly 80–90% of the vascular plant flora of Los Volcanes reserve, which would then be estimated to be around 740–840 species, corresponding to about 6.4–7.2% of the Bolivian vascular plant flora (estimated at 11,600 species, Jørgensen et al. 2006). Species that were not encountered in the plots are either forest species that are patchily distributed or non-forest species occurring on sandstone walls of the area, secondary vegetation on landslides, rock falls or along streams.

The impressive number of individuals of *T. tenuifolia* and *T. bryoides* in the Los Volcanes plots is not unique to these forests. Both have been documented as the characteristic and dominant species of some seasonal forests of Central and Southern Bolivia (Navarro 2001). Likewise, Bonnet (2006) and Bonnet et al. (2007) reported high densities and wide regional distribution for *T. tenuifolia* in Paraná, Brazil. They attributed the success of this species in humid and seasonal semi-deciduous forests to its small size (ca. 25 cm long, Smith and Downs 1977), the presence of plumose wind-dispersed diaspores, CAM metabolism, its atmospheric nutrient acquisition strategy (i.e. species that have no form of absorptive root system, in which the tank habit is lacking and where epidermal trichomes cover the whole shoot system and are entirely responsible for nutrient and water uptake, cf. Griffiths and Smith 1983) and the fact that this species usually forms dense monospecific associations with no explicit preference for some position on the phorophyte. Most of these factors are also true for *T. bryoides*, in particular the small size of the plants (usually no longer than 5 cm), their plumose diaspores (Smith and Downs 1977) and the formation of dense monospecific populations (Navarro 2001).

Los Volcanes plots in a neotropical context

To our knowledge, there is only one other study (Balslev et al. 1998) that includes an inventory of all vascular plants in 1 ha of tropical forest and is therefore directly comparable to our study (although the mentioned study inventoried trees and shrubs of 1–5 cm dbh only in a 0.49-ha subplot). In the Amazonian terra firme rain forest of Cuyabeno, Ecuador, a perhumid area with 3555 mm of annual rainfall and no dry season, Balslev et al. (1998) found

942 species of vascular plants in 88 families. Our plots contained between 297 and 382 species in 60–75 families/ha for the three forest types studied. This is clearly much lower than the Cuyabeno plot, but lower rainfall and strong seasonality set the forests at Los Volcanes apart from the Amazonian site. There were further differences in the relative contribution of different life-forms to overall species richness at both sites. At Cuyabeno, trees (which made up 50% of species) were clearly the most species-rich group, distantly followed by epiphytes (making up 18% of species) and shrubs and lianas (both making up 11% of species). At Los Volcanes, trees were the most species-rich life-form in the deciduous and semi-deciduous forest but contributed only 32% of all species. Epiphytes (including hemiepiphytes) and lianas (23% and 22% in the deciduous forest, 22% and 23% in the semi-deciduous forest, respectively) followed them closely. Shrubs were less important in these forests, contributing 13% and 15% of all species in the deciduous and semi-deciduous forest, respectively, and having percentages only slightly higher than terrestrial herbs (ca. 10%). The most striking difference is in the evergreen forest in which epiphytes (31%) were more species-rich than trees (27%).

For a more representative comparison of the Los Volcanes data with other neotropical sites, we constructed species accumulation curves for Los Volcanes that allowed comparisons with other surveys with plot sizes of up to 1 ha (Fig. 2). As Los Volcanes is found in a biogeographical transition zone and has high moisture variability between plots, our study plots cannot be easily assigned to any of the usual broad categories used for neotropical forests (lowland humid, montane humid, lowland dry, etc.). We therefore compared our richness counts with data from a wide range of other neotropical forest habitats.

Most inventories in lowland humid forests (mostly in Amazonia) have higher vascular plant, epiphyte, liana and terrestrial herb counts than any of the plots at Los Volcanes (Fig. 2). In contrast, plots inventoried in dry deciduous or humid montane forests have similar levels of species richness (Fig. 2). For example,

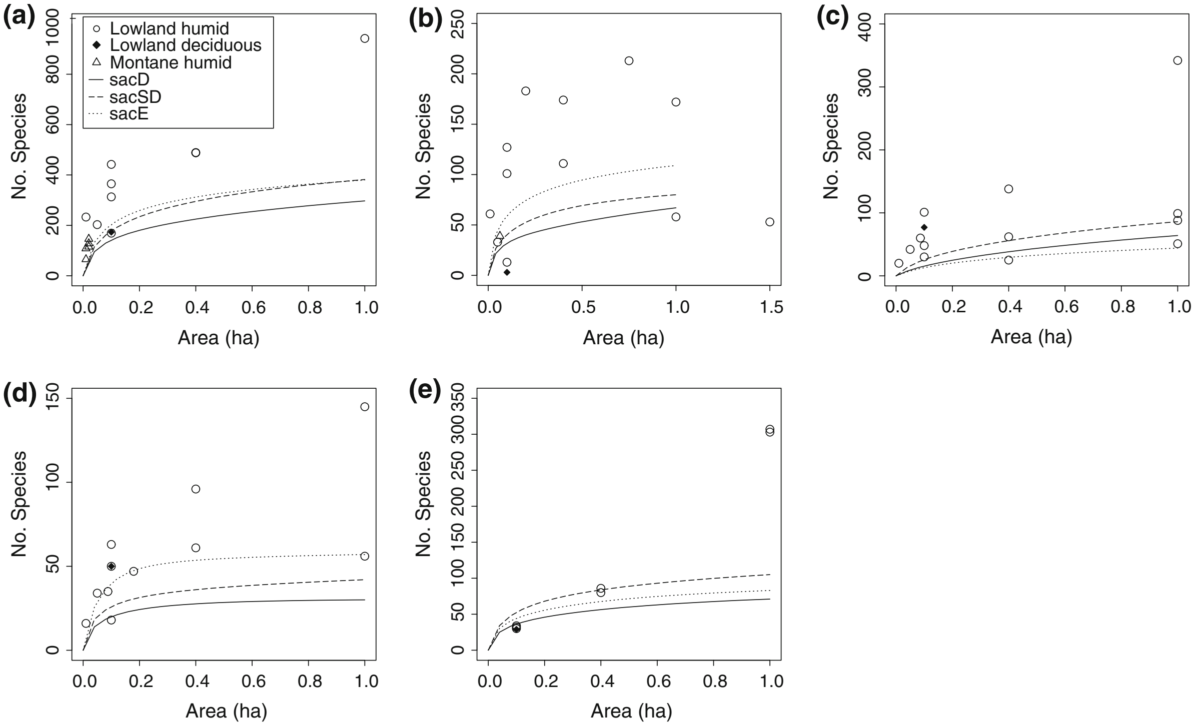

Fig. 2 Species accumulation curves (sac) for each forest type at Los Volcanes (D = deciduous, SD = semi-deciduous, E = evergreen) against species richness data of: **a** vascular plant counts, **b** epiphyte inventories, **c** liana inventories, **d** terrestrial herb inventories and **e** woody plant inventories in the neotropics. Symbols described in the *legend* apply to the entire figure. Note the different scales of the *x* and *y* axes. (Values for individual sites are provided in Appendix 1)

vascular plant counts at Los Volcanes are similar to those in the humid mountains of the Carrasco National Park (Ibisch 1996) and those in the deciduous forest of Capeira and moist forest of Jauneche in Ecuador (Gentry and Dodson 1987), at least at small plot sizes (Fig. 2a). Epiphytes are perhaps the best represented group at Los Volcanes. They are more diverse here than a humid forest plot in Ecuador (Jauneche, Gentry and Dodson 1987) and at least as diverse as the humid forest plots in French Guyana (Sinamary, Bordenave et al. 1998), Venezuela (Surumoni, Nieder et al. 2000) and interestingly also as the Chocoan forests in Caquetá (Colombia, Duivenvoorden 1994). They also have higher species richness than other deciduous forests and similar species richness as montane forests (Fig. 2b). Lianas have similar levels of species richness to several humid forests in Ecuador (Yasuní, Nabe-Nielsen 2001; Burnham 2004), Colombia (Nuqui and Coqui, Galeano et al. 1998) and Bolivia (Oquiriquia, Pérez-Salicrup et al. 2001). In contrast, the deciduous forest of Capeira in coastal Ecuador (Gentry and Dodson 1987) has a much higher species richness of lianas in smaller plots (Fig. 2c). Terrestrial herb counts are similar to other humid forests from Costa Rica (Whitmore et al. 1985), Panama (Royo and Carson 2005), French Guyana (Bordenave et al. 1998), Colombia (Galeano et al. 1998), Ecuador (Gentry and Dodson 1987; Poulsen and Balslev 1991) and Brazil (Costa 2004). The deciduous forest in Capeira (Gentry and Dodson 1987) again has a higher count of terrestrial herbs than any plot at Los Volcanes (Fig. 2d).

Tree species richness at Los Volcanes is similar to several other forest types in the neotropics. If only trees with dbh ≥10 cm are considered, the plots at Los Volcanes are similar to other deciduous forests in Bolivia and reach the lower end of species richness of 1-ha plots in humid and montane forests (Figs. 2e, 3). If we compare the overall richness of trees on the Los Volcanes plots (including those with dbh <10 cm) with several forest types inventoried by A. Gentry (0.1-ha transects using the exploded quadrat method, available at http://www.mobot.org/MOBOT/research/gentry/transect.shtml), the studied plots have higher species richness values than most dry deciduous forests in the neotropics. They have also values similar to the average species richness of humid montane forests but only reach the lower end of the species richness values of humid lowland forest (Fig. 3).

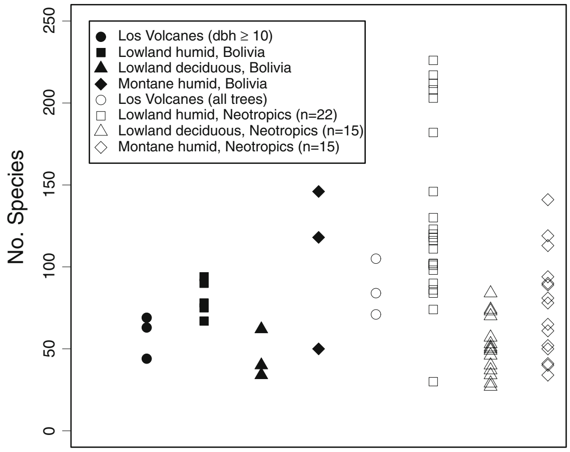

Fig. 3 Species richness values of woody plants and trees at Los Volcanes (LV) with dbh ≥10 cm compared against species richness data of other woody plant inventories (1 ha, dbh ≥10 cm) in Bolivia (filled symbols), and all trees inventoried at Los Volcanes compared to species richness data of woody plant inventories (0.1 ha, dbh ≥ 2.5 cm) in the neotropics (empty symbols)

Contribution of non-woody plant groups to overall plant species richness

Non-woody plants, and specifically epiphytes, have been highlighted by Gentry and Dodson (1987) as the most important plant group in terms of species richness and individual numbers in wet tropical rain forests in Ecuador, whereas tree species with dbh ≥10 cm were more or less equally well represented in dry, moist and wet forest. In the wet forest sampled by them, 35% of the species and 49% of the individuals were epiphytes. At Los Volcanes, epiphytes (including hemiepiphytes) included ca. 30% of the species and nearly 60% of the individuals in the evergreen forest plot. If terrestrial herbs are included, non-woody life-forms represent 45% of the species and more than 76% of the individuals. In the semi-deciduous and deciduous forest plots, figures are somewhat lower but still impressive. Epiphytes (including hemiepiphytes) comprised 22% and 23% of the species and 36% and 31% of the individuals on the semi-deciduous and deciduous forest plots, respectively. If terrestrial herbs are included, the figures are ca. 32% of the species in both forests and 58% and 52% of the individuals, respectively. Non-woody life-forms showed a consistent pattern across the different forest types and represented an important component of neotropical forests. This is certainly overlooked when plots are only sampled for trees. In contrast, trees with dbh ≥10 cm represented only 14%, 18% and 16% of the species and 2.4%, 2.5% and 1.7% of the individuals on our deciduous, semi-deciduous and evergreen forest plot, respectively.

Despite these facts, species richness and floristic data arising from tree inventories are often used (for want of better and more complete, but also usually more work-intensive, information) to characterize all the surrounding vegetation because they are the major structural element (e.g. ter Steege et al. 2000a; La Torre-Cuadros et al. 2007). While this may be enough to identify the major forest types, and indeed some studies in tropical forests do confirmed a positive correlation between the richness of the woody component of a forest and its accompanying non-woody component (e.g. Webb et al. 1967), there is also evidence that this is not a consistent pattern (Duivenvoorden and Lips 1995 in Colombia; ter Steege et al. 2000b in Guyana; Williams-Linera et al. 2005 in Mexico; Tchouto et al. 2006 in Cameroon). Our own data indicate that there is no consistent correlation between tree species richness and the other life-forms studied at Los Volcanes. The comparisons of inventories across the neotropics discussed above also show that forests with higher tree species richness do not necessarily contain higher species richness in non-woody life-forms. In a neotropical context, the forests at Los Volcanes may be poor in terms of tree species richness, but they do show remarkable species richness of lianas, terrestrial herbs and, especially, epiphytes, challenging even those of the most diverse forests of the continent, the Colombian Chocó.

We have shown that tree species richness alone does not always correlate with species richness patterns in other life-forms (although it consistently did so with total species richness across the three forest types studied, as did the species richness patterns of lianas). We thus advocate that more effort be put into non-woody plant inventories in order to better assess the biodiversity of an area and to allow more informed conservation decisions to be made.

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References

Álvarez E et al (2003) Conteo total de plantas vasculares en parcelas de 0.1 ha en Bosques de Amazonía, Chocó y los Andes de Colombia. In: Romero-Fernández L, Lucero-Mosquera H, Aguirre-Mendoza Z et al (eds) Libro de Resúmenes II Congreso de Conservación de la Biodiversidad en los Andes y la Amazonia y IV Congreso Ecuatoriano de Botánica. Editoral de la Universidad Técnica Particular de Loja, Loja, Ecuador, p 171

Arévalo R, Betancur J (2004) Diversidad de epífitas vasculares en cuatro bosques del sector Suroriental de la Serranía de Chiribiquete, Guayana Colombiana. Caldasia 26:359–380

Balslev H, Valencia R, Paz y Miño G et al (1998) Species count of vascular plants in 1-hectare of humid lowland forest in Amazonian Ecuador. In: Dallmeier F, Comiskey JA (eds) Forest biodiversity in North, Central and South America and the Caribbean: research and monitoring. Man and the biosphere series, vol 21. UNESCO and Parthenon, Lancashire

Benavides A, Duque A, Duivenvoorden J et al (2005) A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. Biodivers Conserv 14:739–758. doi:10.1007/s10531-004-3920-9

Bonnet A (2006) Caracterização fitossociológica das bromeliáceas epifíticas e suas relações com os fatores geomorfológicos e pedológicos da planície do Rio Iguaçu, Paraná, Brasil. Dissertation, Universidade Federal do Paraná, Brazil

Bonnet A, Curcio GR, Barddal ML et al (2007) Estratificação vertical de bromélias epifíticas na planície do rio Iguaçu, Paraná, Brasil. Rev Bras Biociencias 5:492–494

Bordenave BG, De Granville JJ, Hoff M (1998) Measurement of species richness of vascular plants in a neotropical rain forest in French Guiana. In: Dallmeier F, Comiskey J (eds) Forest biodiversity, research, monitoring and modelling: conceptual background and Old World case studies. Man and the biosphere series, vol 20. UNESCO and Parthenon, Paris

Burnham RJ (2004) Alpha and beta diversity of lianas in Yasuní National Park, Ecuador. For Ecol Manag 190:43–55. doi:10.1016/j.foreco.2003.10.005

Chave J (2004) Neutral theory and community ecology. Ecol Lett 7:241–253. doi:10.1111/j.1461-0248.2003.00566.x

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application published at: http://purl.oclc.org/estimates. Accessed 31 May 2007

Condit R (1995) Research in large, long-term tropical forest plots. Trends Ecol Evol 10:18–22. doi:10.1016/S0169-5347(00)88955-7

Condit RG, Hubbell SP, Lafrankie JV et al (1996) Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. J Ecol 84:549–562. doi:10.2307/2261477

Condit R, Ashton PS, Baker P et al (2000) Spatial patterns in the distribution of tropical tree species. Science 288:1414–1418. doi:10.1126/science.288.5470.1414

Costa FRC (2004) Structure and composition of the ground-herb community in a terra-firme Central Amazonian forest. Acta Amazon 34:53–59

Duivenvoorden JF (1994) Vascular plant species counts in the rain forests of the middle Caquetá area. Colombian Amazonia. Biodivers Conserv 3:685–715. doi:10.1007/BF00126860

Duivenvoorden JF, Lips JM (1995) A land ecological study of soils, vegetation and plant diversity in Colombian Amazonia. Tropenbos series 12. The Tropenbos Foundation, Wageningen

Galeano G, Suárez S, Balslev H (1998) Vascular plant species count in a wet forest in the Chocó area on the Pacific coast of Colombia. Biodivers Conserv 7:1563–1575. doi:10.1023/A:1008802624275

Gaston KJ, Chown SL (2005) Neutrality and niche. Funct Ecol 19:1–6. doi:10.1111/j.0269-8463.2005.00948.x

Gentry AH (1982) Patterns of neotropical plant species diversity. Evol Biol 15:1–84

Gentry AH (1988) Tree species richness of upper Amazonian forests. Proc Natl Acad Sci USA 85:156–159. doi:10.1073/pnas.85.1.156

Gentry AH (ed) (1990) Four neotropical rainforests. Yale University Press, New Haven

Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19:149–156. doi:10.2307/2388737

Griffiths H, Smith JAC (1983) Photosynthetic pathways in the Bromeliaceae of Trinidad: relations between life-forms, habitat preference and the occurrence of CAM. Oecologia 60:176–184. doi:10.1007/BF00379519

Holmgren PK, Holmgren NH (1998) Index herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/. Cited 20 May 2007 (continuously updated)

Ibisch PL (1996) Neotropische Epiphytendiversität, das Beispiel Bolivien. Martina-Galunder-Verlag, Wiehl

Ibisch PL, Beck SG, Gerkmann B et al (2003) Ecoregiones y ecosistemas. In: Ibisch PL, Mérida G (eds) Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación. Ministerio de Desarrollo Sostenible y Planificación, Editorial FAN, Santa Cruz

Ingram SW, Ferrell-Ingram K, Nadkarni NM (1996) Floristic composition of vascular epiphytes in a neotropical cloud forest, Monteverde, Costa Rica. Selbyana 17:88–103

John R, Dalling JW, Harms KE et al (2007) Soil nutrients influence spatial distributions of tropical tree species. Proc Natl Acad Sci USA 104:864–869. doi:10.1073/pnas.0604666104

Jørgensen PM, Ulloa C, Maldonado C (2006) Riqueza de plantas vasculares. In: Moraes M, Øllgaard B, Kvist LP et al (eds) Botánica Económica de los Andes Centrales. Universidad Mayor de San Andrés, Plural Editores, La Paz

Krömer T, Kessler M, Gradstein SR et al (2005) Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J Biogeogr 32:1799–1810. doi:10.1111/j.1365-2699.2005.01318.x

Langenberger G, Martin K, Sauerborn J (2006) Vascular plant species inventory of a Philippine lowland rain forest and its conservation value. Biodivers Conserv 15:1271–1301. doi:10.1007/s10531-005-2576-4

Laurance WF, Ferreira LV, Rankin-De Merona JM et al (1998) Influence of plot shape on estimates of tree diversity and community composition in Central Amazonia. Biotropica 30:662–665. doi:10.1111/j.1744-7429.1998.tb00106.x

La Torre-Cuadros MA, Herrando-Pérez S, Young KR (2007) Diversity and structural patterns for tropical montane and premontane forests of central Peru, with an assessment of the use of higher-taxon surrogacy. Biodivers Conserv 16:2965–2988. doi:10.1007/s10531-007-9155-9

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Oxford

Mascaro J, Schnitzer SA, Carson WP (2004) Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica. For Ecol Manag 190:3–14. doi:10.1016/j.foreco.2003.10.002

Nabe-Nielsen J (2001) Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. J Trop Ecol 17:1–19. doi:10.1017/S0266467401001018

Navarro G (2001) Contribución al conocimiento fitosociológico de la vegetación de epífitos vasculares del centro y sur de Bolivia. Rev Bol Ecol 10:59–79

Navarro G, Vargas I, Jardim A et al (1996) Clasificación y diagnóstico para la conservación de la vegetación de la región del Parque Nacional Amboró. Santa Cruz, Bolivia. Universidad Complutense, Fundación Amigos de la Naturaleza, Museo de Historia Natural Noel Kempff Mercado, Universidad Mayor de San Andrés and New York Botanical Garden, Santa Cruz

Nieder J, Engwald S, Klawun M et al (2000) Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Suromoni Crane Plot) of Southern Venezuela. Biotropica 32:385–396

Oksanen J, Kindt R, Legendre P et al (2006) vegan: Community Ecology Package version 1.8-3. http://cc.oulu.fi/~jarioksa/. Accessed 10 Oct 2006

Pérez-Salicrup DR, Sork VL, Putz FE (2001) Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33:34–47

Poulsen AD, Balslev H (1991) Abundance and cover of ground herbs in an Amazonian rain forest. J Veg Sci 2:315–322. doi:10.2307/3235922

Poulsen AD, Nielsen IH (1995) How many ferns are there in one hectare of tropical rain forest? Am Fern J 85:29–35. doi:10.2307/1547678

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, URL http://www.R-project.org

Royo AA, Carson WP (2005) The herb community of a tropical forest in central Panama: dynamics and impact of mammalian herbivores. Oecologia 145:66–75. doi:10.1007/s00442-005-0079-3

Schuettpelz E, Pryer KM (2007) Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon 56:1037–1050

Smith AR, Pryer KM, Schuettpelz E et al (2006) A classification for extant ferns. Taxon 55:705–731

Smith DN, Killleen TJ (1998) A comparison of the structure and composition of montane and lowland in the Serranía Pilon Lajas, Beni, Bolivia. In: Dallmeier F, Comiskey JA (eds) Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring. Man and the biosphere series, vol 21. UNESCO and Parthenon, Lancashire

Smith LB, Downs RJ (1977) Tillansioideae (Bromeliaceae). Flora Neotrop Monogr 4:663–1492

Tchouto MGP, de Boer WF, de Wilde JJFE et al (2006) Diversity patterns in the flora of the Campo-Ma'an rain forest, Cameroon: do tree species tell it all? Biodivers Conserv 15:1353–1374. doi:10.1007/s10531-005-5394-9

ter Steege H, Sabatier D, Castellanos H et al (2000a) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. J Trop Ecol 16:801–828. doi:10.1017/S0266467400001735

ter Steege H, Ek R, van Andel T (2000b) A comparison of diversity patterns of tree and non-tree groups. In: ter Steege H (ed) Plant diversity in Guyana. With recommendation for a protected areas strategy. Tropenbos series 18. Tropenbos Foundation, Wageningen

Tobler MW, Janovec J, Honorio E et al (2007) Implications of collection patterns of botanical specimens on their usefulness for conservation planning: an example of two neotropical plant families (Moraceae and Myristicaceae) in Peru. Biodivers Conserv 16:659–677. doi:10.1007/s10531-005-3373-9

Valencia R, Balslev H, Paz y Miño G (1994) High tree alpha-diversity in Amazonian Ecuador. Biodivers Conserv 3:21–28. doi:10.1007/BF00115330

Webb LJ, Tracey JG, Williams WT et al (1967) Studies in the numerical analysis of complex rain-forest communities: II. The problem of species-sampling. J Ecol 55:525–538. doi:10.2307/2257891

Whitmore TC, Peralta R, Brown K (1985) Total species count in a Costa Rican tropical rain forest. J Trop Ecol 1:375–378

Williams-Linera G, Palacios-Rios M, Hernández-Gomez R (2005) Fern richness, tree species surrogacy, and fragment complementarity in a Mexican tropical montane cloud forest. Biodivers Conserv 14:119–133. doi:10.1007/s10531-005-4053-5

Relationships between spatial configuration of tropical forest patches and woody plant diversity in northeastern Puerto Rico

Ileana T. Galanes · John R. Thomlinson

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Abstract The destruction and fragmentation of tropical forests are major sources of global biodiversity loss. A better understanding of anthropogenically altered landscapes and their relationships with species diversity and composition is needed in order to protect biodiversity in these environments. The spatial patterns of a landscape may control the ecological processes that shape species diversity and composition. However, there is little information about how plant diversity varies with the spatial configuration of forest patches especially in fragmented tropical habitats. The northeastern part of Puerto Rico provides the opportunity to study the relationships between species richness and composition of woody plants (shrubs and trees) and spatial variables [i.e., patch area and shape, patch isolation, connectivity, and distance to the Luquillo Experimental Forest (LEF)] in tropical forest patches that have regenerated from pasturelands. The spatial data were obtained from aerial color photographs from year 2000. Each photo interpretation was digitized into a GIS package, and 12 forest patches (24–34 years old) were selected within a study area of 28 km^2. The woody plant species composition of the patches was determined by a systematic floristic survey. The species diversity (Shannon index) and species richness of woody plants correlated positively with the area and the shape of the forest patch. Larger patches, and patches with more habitat edge or convolution, provided conditions for a higher diversity of woody plants. Moreover, the distance of the forest patches to the LEF, which is a source of propagules, correlated negatively with species richness. Plant species composition was also related to patch size and shape and distance to the LEF. These results indicate that there is a link between landscape structure and species diversity and composition and that patches that have similar area, shape, and distance to the LEF provide similar conditions for the existence of a particular plant community. In addition, forest patches that were closer together had more similarity in woody plant species composition than patches that were farther apart, suggesting that seed dispersal for some species is limited at the scale of 10 km.

Keywords Biodiversity · Landscape structure · Plant species composition · Tropical moist forests · Patch area · Patch shape

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Introduction

Human land-use practices and the accelerating rate of human population growth are negatively impacting ecosystems and landscapes on a global scale. Land-use change is projected to have the largest worldwide impact on biodiversity by the year 2100, especially in the tropics (Sala et al. 2000). Tropical forests are the world's richest in terms of species number; thus, their destruction is a major source of global loss of species (Lugo 1988; Brown and Lugo 1990; du Toit et al. 2004). The rate of humid tropical deforestation between 1990 and 1997 was approximately 5.8 million ha annually, and 2.3 million ha of forest was visibly degraded as observed in satellite imagery (Achard et al. 2002). According to McCloskey (1993), two-thirds of tropical forests have been fragmented and are especially vulnerable. Scattered and isolated forest patches of less than 100 ha are found in many tropical regions, restricting the dispersal capacity of organisms and reducing their habitat (Turner and Corlett 1996). Patch size is related positively to the presence of interior species (Grashof-Bokdam 1997; Bender et al. 1998). Thus, small forest patches may lack the interior conditions necessary for the survival of some species that require the remoteness from the surroundings or particular microclimate conditions (Kremen et al. 1994; Forman 1999). In addition, larger areas support larger populations, which are associated to lower extinction rates (Rosenzweig 1995). These forest patches need to be managed appropriately in order to prevent future species extinctions, given that the main goal of conservation management is to maintain species diversity (Coleman et al. 1996).

Spatial patterns at landscape scales may control the ecological processes that affect species richness and composition (Turner 1989; Haines-Young and Chopping 1996; Gustafson 1998; de Blois et al. 2002; Opdam et al. 2003). Studies have shown that the size, shape, and degree of connectivity of habitat patches influence patterns of species diversity and abundance due to the effects of spatial patterns on the dispersal, distribution, and persistence of species (Burkey 1988; Turner 1989; Bierregaard et al. 1992; Pearson 1993; Beier and Noss 1998; Gibbs 1998; Mazerolle and Villard 1999; Jeanneret et al. 2003; Waldhardt 2003). In addition, landscape-scale studies have shown that matrix attributes are important for the dispersal of plants. For example, flying seed dispersers and pollinators may use small fragments or solitary trees as "stepping stones" to move between forest patches (Tewksbury et al. 2002; Murphy and Lovett-Doust 2004; Turner 2005).

Conservation planning in anthropogenically fragmented landscapes must include a better understanding of biodiversity patterns and spatial relationships at a landscape scale (Wu and Hobbs 2002; Waldhardt 2003). However, there is little information on how plant species diversity and composition vary with changes in the parameters of landscape structure, especially in fragmented tropical habitats (Laurance et al. 1998; Metzger 1997, 2000; de Blois et al. 2002; McGarigal and Cushman 2002; Hernandez-Stefanoni 2006).

The purpose of this research was to determine how woody plant species diversity and composition of forest patches in northeastern Puerto Rico relate to spatial variables such as patch area and shape and the degree of connectivity or isolation between forested areas. Several questions that need to be addressed for the appropriate management and conservation of tropical forest patches were considered in this study: (1) Do forest patches near a reserve, which is a rich source of propagules, have a higher diversity of woody plants? (2) Do larger forest patches and/or patches with a convoluted shape have a higher diversity of woody plants? (3) Do forest patches with vegetation corridors and/or a vegetated buffer zone have greater woody plant diversity? (4) Which spatial variables are related to forest patches with similar woody plant species composition? (5) Do closer forest patches are more similar in species composition than forest patches farther apart?

The northeastern part of Puerto Rico was selected for this study, because the landscape in this location has become a mosaic of forest patches and corridors in a matrix of mixed urban and pasture, as a result of human intervention. These forest patches regenerated from pasturelands that were abandoned during the 1950s through the 1970s (Aide et al. 1995; Thomlinson et al. 1996; Chinea and Helmer 2003). During this period the economy of Puerto Rico shifted from an agrarian economy to an industrial one (Dietz 1986; Grau et al. 2003). Thus, the chosen site provided an excellent opportunity to study the spatial configuration of forest patches with more or less equal age of abandonment, similar land-use history and edaphic conditions. In addition, evolutionary factors that may affect species composition were minimized in this study because of the young age of the patches.

There is a need to consider these forest patches in conservation and management efforts because of their role in sustaining species diversity and as a source of propagules at a time of accelerating increase of urban development in this part of Puerto Rico (Helmer 2004; Lugo and Helmer 2004) and in many tropical areas of the world (Achard et al. 2002). In addition, subtropical moist forests in Puerto Rico are the least protected among the six ecological life zones found in this Caribbean island (only 3.2% are protected), and land development occurs mostly in this ecological zone (Helmer 2004; Lugo 2006).

Materials and methods

Study site

The northeastern part of Puerto Rico (between 18°22′ N, 65°47′ W and 18°17′ N, 65°57′ W) was selected for this study (Fig. 1). The study site includes part of the municipalities of Carolina, Canóvanas, and Río Grande and has an area of 28 km^2. It is adjacent to the northwestern part of the Luquillo Experimental Forest (LEF), a rainforest reserve of 11,491 ha. The studied forest patches are located in the subtropical moist forest life zone (Ewel and Whitmore 1973) and have a mean elevation ranging from 25 to 105 m above sea level. The soil of these forest patches is predominantly silty clay loam inceptisols (USDA Soil

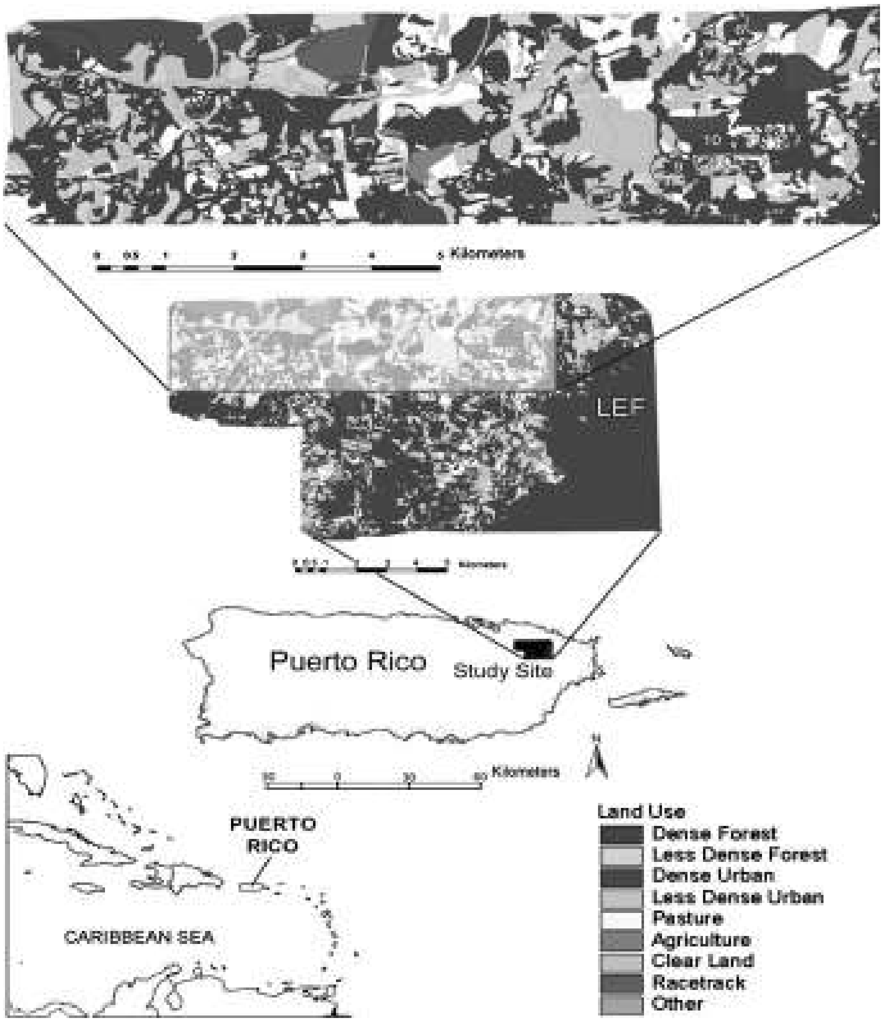

Fig. 1 Study site in northeastern Puerto Rico. The polygons, digitized from aerial photographs, represent land-use classes as shown in the legend. The 12 forest patches examined are marked by a circle. The Luquillo Experimental Forest (LEF) reserve is indicated

Conservation Service 1977). The mean annual rainfall ranges from 1,893 mm at Canóvanas to 2,506 mm at Río Grande, and the average annual temperature minimum and maximum at the Canóvanas Station are 23 and 30°C, respectively (Puerto Rico Station Data Inventory, NOAA/NWS cooperative observer network).

Aerial photo interpretation

The spatial configuration of the study site was obtained from true-color aerial photographs at a scale of 1:20,000 taken in year 2000. Land use was delineated on 10 of these 9 × 9 inch photographs. A mirror stereoscope was used to delineate polygons with a minimum mapping unit of 0.36 ha, equivalent to 3 × 3 mm on the photographs.

Each polygon was assigned one of eight land-use classes as follows: dense forest (80% or more of forest cover), less dense forest (between 80% and 20% of forest cover), agriculture, pasture, dense urban (80% or more of construction), less dense urban (less than 80% of construction), cleared land, and others (business, factories, stable buildings, poultry farms). The polygons were rectified and digitized into a geographical information system (ArcView version 3.2, ESRI 1999) (Fig. 1).

Selection of forest patches

Soil maps from the United States Department of Agriculture, Soil Conservation Service (1977) were used to determine the type of soil and topography for the studied forest patches. Aerial photographs taken in years 1936, 1964, 1971, 1981, and 1990 were used to determine the land-use history and age of these patches. Twelve dense forest patches (80% of forest cover or more) were selected according to the criteria of same soil type and similar topography, state of secondary succession (between 24 and 34 years since abandonment), and land-use history (sugar cane until the 1950s and then pasture). This was to minimize the effects of these factors on the species composition. In addition, each forest patch was classified according to the following seven spatial variables:

1. Patch size.
2. Patch shape, calculated with the Shoreline Development Index (SLD) (Patton 1975).
3. Mean elevation.
4. Distance to the LEF.
5. Isolation index (Whitcomb et al. 1981) within a 600-m radius from the center of the study patch. This radius was chosen because it assured that there was at least one other forest patch within the radius.
6. Percent of forest area (defined as polygons with >33% forest cover) within the matrix, in a buffer of 50 m radius around the forest patch. Forest area in the buffer was determined as the proportion of dots on a 1-mm grid transparent overlay that intercepted tree crowns on the aerial photo.
7. Connectivity: the number of vegetation corridors from each patch that connected to other forest patches. A corridor was defined as a continuous strip between patches that showed a distinct narrowing compared to a patch.

Forest patch sampling

Woody plant species composition (shrubs and trees $\geq$1 cm diameter and >1.3 m height) of the 12 study patches was determined by a systematic floristic survey. The survey consisted of several belt transects of 2 m × 50 m spaced regularly in the interior and at the edge of each patch, perpendicular to the topographic gradient. Cumulative species–area curves were constructed. Rarefaction curves based on individuals and samples were also created using the software package EstimateS, version 6 (Colwell 2000). These rarefaction and species–area curves aided in determining the number of transects needed to sample each forest patch; typically four to six transects were needed. Collected specimens of each species were identified in the University of Puerto Rico, Río Piedras herbarium, and voucher specimens were deposited.

Data analysis

Woody plant species diversity (i.e., species number and relative abundance or evenness) and species composition of the 12 study patches were related to patch size, patch shape, distance between each forest patch and the LEF, degree of isolation from other forest patches (within a 600-m radius), percent of forest in the matrix around the patch (within a buffer of 50 m radius), and number of vegetation corridors connected to other forest patches. Differences in woody plant species composition were also related to the geographic distance among the 12 forest patches.

Plant species diversity for each forest patch was measured using species richness (S) and the Shannon diversity index (H'). The relative importance of all the spatial variables in relation to species diversity was analyzed using a stepwise regression analysis of H' (dependent variable) against the spatial variables of each patch. This analysis has the advantage that it reduces the multicollinearity among the explanatory variables (Draper and Smith 1981). The analysis was repeated with species richness as the dependent variable.

Nonmetric multidimensional scaling (NMS) analysis (Mather 1976; Kruskal 1964) was used to compare dissimilarity among the study patches in relation to plant species composition and to correlate these dissimilarities with the spatial variables. The computer program PC-ORD version 3.18 (McCune and Mefford 1997) was used for multivariate analysis of the data. A two-way samples-by-species data matrix was constructed using the abundance values of each woody plant species within each forest patch. The data were relativized by the species maximum to reduce the coefficient of variation between species columns, in this case from 297% to 53%, well below the value of 100% that is considered to interfere with the multivariate analysis (McCune and Grace 2002). This adjustment tends to equalize rare and abundant species, giving more weight to rare species that are frequently encountered in tropical forests. An additional two-way samples-by-variables matrix was constructed, which contained the values of the spatial variables for each forest patch (Table 1). The ordination was done using the Sørensen dissimilarity coefficient (Bray and Curtis 1957).

The NMS analysis was run with a random starting configuration and stepping down in dimensionality from six axes to one axis. The number of runs with real data was 40 and with randomized runs was 50. The maximum number of iterations was 400 and the instability criterion was set to 0.00001. Based on the preliminary runs, the best starting configuration and dimensionality was selected for the final run; the number of real runs was set to 1 and the maximum number of iterations was set to 500.

A Mantel test (Mantel 1967) was performed to test the correspondence between the geographic distances (km) among the 12 forest patches and the Sørensen dissimilarity measures among the patches' woody plant species composition. The species abundance matrix used for this analysis was the same one used for the NMS analysis. An additional two-way samples-by-distance matrix was constructed, which contained the geographic distances (km) among the 12 forest patches. Mantel's asymptotic approximation (Douglas

Table 1 Forest patch spatial variables: area (ha), shape (SLD), distance (km) to Luquillo Experimental Forest (LEF), elevation (meters above sea level), isolation index (600 m radius), percent of forest area in the matrix (polygons >33% of forest cover, in a 50 m radius), and number of vegetation corridors connected to other forest patches; dependent variables: plant species richness (S) and Shannon diversity index (H')

Forest patch no.	Area (ha)	Shape SLD index	Dist. LEF (km)	Elevation (m)	Isolation index	Forest matrix (%)	No. of corridors	S	H'
1	33.3	1.5	11.9	45	3.33E-05	3.19	0	33	2.69
10	16.0	1.7	2.7	90	1.23E-04	23.5	2	25	2.03
9	15.6	2.2	2.8	95	3.69E-05	19.7	1	29	2.03
2	15.3	2.0	11.5	75	2.97E-05	34.0	0	23	2.26
6	15.1	2.1	3.9	25	2.17E-03	0.23	0	27	2.37
3	13.9	1.5	9.2	35	3.68E-04	55.5	0	16	1.51
4	11.4	1.5	7.8	50	7.14E-04	18.2	0	12	1.52
11	7.58	1.7	2.3	75	3.12E-05	21.0	4	17	1.92
7	7.26	2.1	3.4	45	1.69E-04	10.2	2	22	2.36
5	4.97	1.5	3.9	105	4.74E-03	27.4	1	16	1.63
12	4.05	1.6	2.2	80	7.89E-04	29.9	1	18	1.91
8	1.60	1.5	2.8	85	4.03E-03	0	0	13	1.48

and Endler 1982) was the method used to test the significance of the correlation between these two matrices.

Results

The total number of woody plant species found in the 12 forest patches (γ diversity) was 69 species from 4,713 individuals sampled. The percentage of native species was 80%, with an abundance of 92%. The three most abundant species were *Casearia guianensis* (Aubl.) Urb., *Tabebuia heterophylla* (DC.) Britton, and *Casearia sylvestris* Sw. (Appendix A).

The average species richness for each patch (α diversity) was 21 species. The amount of compositional variation in the 12 patches, or β_w diversity (Whittaker 1972), was 3.3. Values of $\beta_w < 1$ are considered low and $\beta_w > 5$ are considered high (McCune and Grace 2002). In this study each patch had, on average, 30% of the total number of species found.

The area of the forest patches ranged from 1.6 to 33.3 ha; the SLD index was from 1.5 to 2.2; the distance to the LEF varied from 2.2 to 11.9 km; the isolation index ranged from 2.23E-05 to 4.74E-03; the percentage of forest area in the matrix (50 m radius) ranged from 0% to 55.5%; and the number of vegetation corridors connected to other dense forest patches ranged from 0 to 4 (Table 1).

Pearson correlation analysis showed no significant correlations among five of the seven spatial variables studied. Area and distance to the LEF correlated positively ($r = 0.67$, $P = 0.02$), while the number of vegetation corridors and distance to the LEF correlated negatively, though it was marginally significant ($r = -0.58$, $P = 0.05$).

The Shannon diversity index (H') ranged from 1.48 to 2.69 (Table 1). The significant variables included in the stepwise regression model were area ($P = 0.01$) and shape ($P = 0.03$), both of which were positively correlated with H' (Table 2a). Patch area ($P = 0.0002$) and shape ($P = 0.01$) were also positively correlated with woody plant species richness, and distance to the LEF correlated negatively ($P = 0.04$) (Table 2b). There was no correlation with plant species number nor H' and the other spatial variables (number of vegetation corridors, degree of isolation, elevation, and percent of forest in the matrix in a 50-m radius).

In the NMS analysis, the final stress for a three-dimensional solution was 7.15. A value between 5 and 10 indicates a good ordination with no risk of drawing false inferences (Clarke 1993). In addition, the final instability criterion, which should be 0.0005 or less, was 0.00006. The cumulative coefficient of determination, R^2, for the three axes in the NMS ordination was 88%, and the orthogonality for axes 1 vs. 3 was 98%.

The NMS analysis (Fig. 2) showed that forest patches with similar woody plant species composition correlated with the area ($r^2 = 0.52$, $\tau = 0.55$) and shape ($r^2 = 0.28$, $\tau = -0.50$) of the forest patch, as well as distance to the LEF ($r^2 = 0.60$, $\tau = 0.55$). The patch elevation ($r^2 = 0.39$, $\tau = -0.40$) and the

Table 2 Results from stepwise regression analyses for (a) Woody-plant Shannon diversity index and (b) Woody-plant species richness in relation to seven spatial variables of 12 forest patches

Variable	Coefficient	STD error	Student's T	P	VIF
(a) Woody-plant Shannon diversity index vs. 7 spatial variables					
Constant	0.41338	0.48775	0.85	0.4187	
Area	2.906E-06	9.113E-07	3.19	0.0110	1.0
Shape	0.69314	0.27400	2.53	0.0323	1.0
$R^2 = 0.6640$					
Adjusted $R^2 = 0.5894$					
(b) Woody-plant species richness vs. 7 spatial variables					
Constant	−1.02108	5.03646	−0.20	0.8444	
Area	8.019E-05	1.199E-05	6.69	0.0002	2.0
Shape	9.12325	2.73923	3.33	0.0104	1.1
Distance to LEF	−6.907E-04	2.764E-04	−2.50	0.0370	2.0
$R^2 = 0.9070$					
Adjusted $R^2 = 0.8721$					

See Table 1 for definitions of the spatial variables

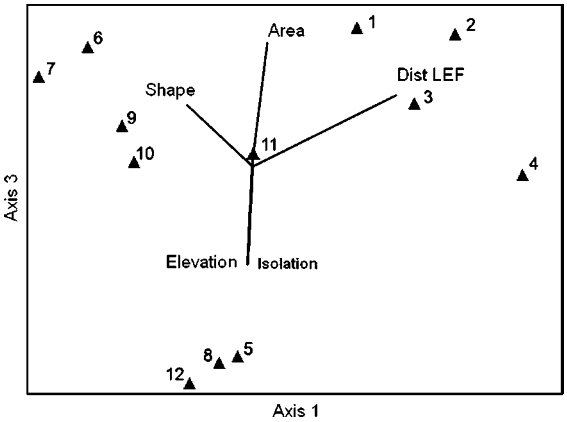

Fig. 2 NMS ordination joint plot of axes 1 and 3, for the 12 forest patches-by-plant species abundance matrix (trees and shrubs), in relation to seven spatial variables. The angles and lengths of the radiating vectors indicate the direction and strength of the relationships of the spatial variables with the ordination scores. See Table 1 for the definitions and values of the spatial variables

isolation index ($r^2 = 0.43$, $\tau = -0.42$) also correlated with the woody plant species composition. On the other hand, the woody plant species composition correlated weakly with the percent of forest area in the matrix around the patch (50 m radius) ($r^2 = 0.17$, $\tau = 0.27$) as well as the number of vegetation corridors of each forest patch that connected to other dense forest areas ($r^2 = 0.22$, $\tau = 0.27$).

The Mantel test demonstrated a strong positive correlation between the geographic distances (km) among the 12 forest patches and the Sørensen dissimilarity measures among the patches' woody plant species composition ($P = 0.000016$, Standardize Mantel statistic: $r = 0.57$).

Discussion

Our results show a link between the spatial configuration of tropical forest patches and the diversity and composition of woody plants. The area, shape, and distance to the LEF were the spatial variables that best explained the differences in plant species diversity and composition of the 12 forest patches studied. The area of the forest patches showed the strongest correlation with the species diversity and/or richness followed by patch shape and the distance to the LEF. On the other hand, the distance of forest patches to the LEF showed the strongest correlation with similar species composition followed by the patch area and shape.

The woody plant Shannon diversity and species richness were higher in larger patches, consistent with results from European landscapes (Honnay et al. 1999; Krauss et al. 2004; Økland et al. 2006). In addition, we found that patches near the LEF (a rich source of propagules) had higher woody plant species richness than more distant forest patches. However, we found no correlation between patch distance to the LEF and plant species diversity (Shannon index), which considers not only the number of species but also their relative abundance or species evenness. Similar results were found in the study of Chinea and Helmer (2003) in Puerto Rico, where species richness of trees in tropical forest patches was related to the distance to larger forest patches while Shannon index was not. One possible reason for these results is that while the LEF is a rich source of species, some of those species may have a low probability of recruitment in the forest patches studied, resulting in low evenness.

The literature contains few studies that consider the ecological effects of the shape of a patch (Forman 1999; Hernandez-Stefanoni 2006; Økland et al. 2006). Patch shape determines the proportion of edge habitat; i.e., more convoluted patches have more edge habitat than more compact patches of the same area. However, not all edge types may be suitable for species survival. Ratti (1988) observed that feathered edges provided greater vegetative complexity to birds than abrupt-edge habitats. He also found that birds were attracted to the vegetative diversity of edge habitats, but they experienced greater predator activity in the abrupt-edge habitats than in feathered edges.

Our study found that the more convoluted a forest patch is, the higher the woody plant species diversity and species number. These results agree with the results found by Økland et al. (2006) in Norway, where vascular plant species richness was positively related to patch shape complexity and patch area. Hernandez-Stefanoni (2006) also found a positive correlation with patch shape complexity and the diversity of tropical trees and shrubs. One plausible explanation for these observations is that a higher degree of convolution of a forest patch causes greater spatial heterogeneity due to the junction of two different habitats and to the complex patterns of turbulence and wind flow created by the lobes (Forman 1999; Turner 2005).

Habitat heterogeneity is strongly correlated to plant species richness, since it allows the coexistence of competing species (Burnett et al. 1998; Dufour et al. 2006). This environmental heterogeneity may have a positive feedback on diversity, since richer vegetation provides greater habitat heterogeneity and resources for other organisms, such as plant pollinators and seed dispersers, which may further increase the diversity of the vegetation (Ratti 1988; Wunderle 1997; Turner 2005; Dufour et al. 2006). Patch convolution also produces drift-fence and cove effects where the form of the patch enhances the interception of seeds, plant pollinators, and seed dispersers, increasing the species diversity of the patch (Forman 1999).

There was no correlation between other spatial variables (number of vegetation corridors, percent of forest in the matrix in a 50-m radius, and degree of isolation in a 600 m radius) and plant species richness or diversity. This is probably because woody plant dispersal is not affected significantly by a lack of nearby vegetation adjacent to a patch, since woody plants in Puerto Rico are dispersed mostly by flying animals (e.g., birds, bats) or by wind (Francis and Lowe 2002). Approximately 74% of the species sampled in this study are known to be dispersed by flying animals (mostly birds and, to a lesser extent, bats) and 10% by wind (Appendix A; T. Carlo 2007, personal communication, University of Washington, Seatle, WA; Francis and Lowe 2002).

In this study the dispersal limitation within a distance of 600 m was low, as was indicated by the isolation values and the β_w diversity obtained. These results suggest that the 12 forest patches, considered as a whole, were not sufficiently isolated from wooded areas to exhibit major limitations of seed dispersal at a scale of 600 m. Studies reviewed by Sork and Smouse (2006) showed that physical isolation does not prevent pollen flow at a distance of 1 km in tropical tree species, and seed flow into fragments was high even though there were few seed donors.

However, at a scale of 10 km some species do appear to be dispersal limited, because we found that forest patches near LEF had higher plant species richness than patches farther away. In addition, the Mantel test demonstrated that forest patches that were closer had more similarity in woody plant species composition, and as the geographic distance increased to a maximum of 10 km, the dissimilarity in species composition became greater. These results showed that distant sites (10 km apart) are less likely to share species than nearby sites, probably because seed dispersal for some species is limited at this scale (Hubbell 1979, 2001; Condit et al. 2002). Although in this study we selected forest patches with similar abiotic conditions, the differences in floristic composition as patches are more distant could also be due to slight differences in soil, temperature, or precipitation. However, Pyke et al. (2001) looked at samples in a lowland neotropical forest and found that distance affects plant species variation over relatively small scales (<5 km), which is close to the scale of our study, while climate and geology predicted differences in floristic composition at broader scales.

Patches that had similar area and shape had similar woody plant species composition (Fig. 2). Thus, the size and shape of a forest patch were important in providing conditions for the existence of particular species. Smaller or more convoluted patches have more habitat edge, proportional to the area, when compared to larger or less convoluted patches. These smaller patches may lack the interior conditions necessary for the survival of some species that require remoteness from their surroundings or particular microclimate conditions, for example, low temperature or high humidity (Kremen et al. 1994; Grashof-Bokdam 1997; Bender et al. 1998; Forman 1999). Normally, rare and specialist species are found in the interior of a forest patch, while most species that live in edge habitats are generalists and common. There are, however, indifferent species that can thrive in both interior and edge conditions (Grashof-Bokdam 1997; Bender et al. 1998; Krauss et al. 2004; Turner 2005).

Forest patches with similar distances to the LEF had similar woody plant species composition. Forest patches closer to the LEF are also closer to each other, allowing the sharing of species. On the other hand, forest patches near the LEF probably will have a different source of propagules than patches farther from the LEF. This can cause differences in shaping the composition of species that will be established in a forest patch.

The isolation index in a 600-m radius also correlated with similar woody plant species composition in the NMS analysis suggesting that the degree of isolation may cause differences in the kind of propagules that will arrive in these patches. The effectiveness of animal-mediated seed dispersal, which is the major form of dispersal in our study area, can be limited by the degree of isolation (Butaye et al. 2001; Wunderle 1997). Woody plant species composition also correlated with elevation in the NMS analysis. The mean elevation of the 12 forest patches varied from 25 to 105 m, a range of 80 m. Past studies have shown that tree species composition varies according to elevation, especially when the increments in altitude result in temperature decreases and increases in rainfall and cloud cover (White 1963; Crow and Grigal 1979; Weaver 1991; García-Martinó et al. 1996). However, these other studies examined increments in elevation over ranges of hundreds of meters, where noticeable differences in rainfall and temperature occur.

The number of vegetation corridors connecting the forest patches and the percentage of forest in the matrix (50 m radius surrounding the patch) correlated weakly with woody plant species composition, indicating that these factors did not significantly affect the woody plant species composition of the forest patches.

Conclusions

There are few studies that have examined the relationships between woody plant diversity and species composition in tropical forest patches and spatial variables at a landscape level. In this study we found that there was a strong correlation with the spatial configuration of tropical forest patches and the woody plant species diversity and composition in northeastern Puerto Rico. The variables that best explained the species diversity and/or richness were patch area and shape and the distance from the patch to the LEF reserve. Forest patch area, shape, and distance to the LEF also correlated with similar woody plant species composition. We also found that species composition dissimilarity increased with the geographic distance between patches at a scale of 10 km. These findings support the premise that there are strong associations between landscape elements and the ecological processes involved in shaping patterns of species diversity. The spatial configuration of forest patches (patch area and shape and distance among patches) contributes to the existence of a particular plant species composition and diversity. The results of this study shed light on possible explanations for the observed spatial patterns of woody plant species diversity and composition at landscape levels. These findings can be used for the effective management or restoration of forest patches and for the conservation of woody plant species, especially in highly fragmented landscapes.

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Appendix A

List of the 69 woody plant species, sampled in the 12 forest patches examined, with species abundance values, species origin, and mode of dispersal

Species (total: 69)	Origin	Abundance (total: 4,713)	Percent of abundance (%)	Mode of dispersal
Casearia guianensis	Native	1,458	30.94	Bird
Tabebuia heterophylla	Native	593	12.58	Wind
Casearia sylvestris	Native	566	12.01	Bird
Miconia prasina	Native	203	4.31	Bird
Andira inermis	Native	192	4.07	Bat
Syzygium jambos	Exotic	188	3.99	Bat

Appendix continued

Species (total: 69)	Origin	Abundance (total: 4,713)	Percent of abundance (%)	Mode of dispersal
Guapira fragrans	Native	185	3.93	Bird
Eugenia biflora	Native	144	3.06	Bird
Calophyllum antillanum	Native	142	3.01	Bat
Myrcia splendens	Native	96	2.04	Bird
Citharexylum spinosum	Native	89	1.89	Bird
Casearia decandra	Native	85	1.80	Bird
Inga laurina	Native	81	1.72	Gravity and bat
Spathodea campanulata	Exotic	76	1.61	Wind
Guarea guidonia	Native	71	1.51	Bird
Peltophorum pterocarpum	Exotic	57	1.21	Wind
Hura crepitans	Native	40	0.85	Capsule blow up
Cupania americana	Native	36	0.76	Bird
Ocotea leucoxylon	Native	36	0.76	Bird
Faramea occidentalis	Native	35	0.74	Bird
Zanthoxylum martinicense	Native	27	0.57	Bird
Ardisia obovata	Native	21	0.45	Bird
Hymenaea courbaril	Native	21	0.45	Gravity
Trichilia pallida	Native	21	0.45	Bird
Trichilia hirta	Native	20	0.42	Bird
Nectranda turbacensis	Native	20	0.42	Bird
Albizia procera	Exotic	19	0.40	Wind
Randia aculeata	Native	18	0.38	Bird
Chrysophyllum argenteum	Native	16	0.34	Bird
Miconia impetiolaris	Native	15	0.32	Bird
Cordia sulcata	Native	15	0.32	Bird and bat
Picramnia pentandra	Native	13	0.28	Bird
Cinnamomum elongatum	Native	9	0.19	Bird
Cordia collococca	Native	8	0.17	Bird
Petitia domingensis	Native	8	0.17	Bird
Artocarpus altilis	Exotic	8	0.17	Gravity and human
Mangifera indica	Exotic	7	0.15	Gravity and human
Tabernaemontana citrifolia	Native	6	0.13	Bird
Calophyllum inophyllum	Exotic	5	0.11	Bat
Ardisia solanacea	Exotic	4	0.08	Bird
Inga vera	Native	4	0.08	Bat
Clusia rosea	Native	4	0.08	Bird
Piper amalago	Native	3	0.06	Bat
Palicourea crocea	Native	3	0.06	Bird
Leucaena leucocephala	Native	3	0.06	Wind
Swietenia mahagoni × *macrophylla*	Exotic	3	0.06	Wind
Senna siamea	Native	3	0.06	Wind
Miconia racemosa	Native	3	0.06	Bird
Roystonea borinquena	Native	3	0.06	Bird
Adenanthera pavonina	Exotic	3	0.06	Gravity
Bursera simaruba	Native	3	0.06	Bird

continued

Species (total: 69)	Origin	Abundance (total: 4,713)	Percent of abundance (%)	Mode of dispersal
Coccoloba venosa	Native	3	0.06	Bird
Cecropia schreberiana	Native	2	0.04	Bird and bat
Gonzalagunia hirsuta	Native	2	0.04	Bird
Ficus citrifolia	Native	2	0.04	Bird and bat
Thespesia grandiflora	Endemic	2	0.04	Gravity
Spondias mombin	Native	1	0.02	Bird and bat
Margaritaria nobilis	Native	1	0.02	Capsule blow up
Coccoloba diversifolia	Native	1	0.02	Bird
Annona reticulata	Native	1	0.02	Gravity and human
Delonix regia	Exotic	1	0.02	Gravity
Tournefortia hirsutissima	Native	1	0.02	Bird
Psidium guajava	Native	1	0.02	Bird, bat, and human
Terminalia catappa	Exotic	1	0.02	Bat
Trema micrantha	Native	1	0.02	Bird
Piper jacquemontianum	Native	1	0.02	Bat
Vitex divaricata	Native	1	0.02	Bird
Annona muricata	Native	1	0.02	Gravity and human
Citrus × *aurantium*	Exotic	1	0.02	Gravity and human

Species origin	Abundance	Mode of dispersal of the 69 species examined
Native species: 80%	Native: 92%	Bird: 61%
Endemic species: 1.4%	Endemic: 0.04%	Bat: 13%
Exotic species: 8.8%	Exotic: 7.9%	Wind: 10%
		Other (e.g., gravity, human): 16%

References

Achard F, Eva HD, Stibig H, Mayaux P, Gallego J, Richards T et al (2002) Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002. doi:10.1126/science.1070656

Aide TM, Zimmerman JK, Herrera L, Rosario M, Serrano M (1995) Forest recovery in abandoned tropical pastures in Puerto Rico. For Ecol Manag 77:77–86. doi:10.1016/0378-1127(95)03576-V

Beier P, Noss RF (1998) Do habitat corridors provide connectivity? Conserv Biol 12:1241–1252. doi:10.1046/j.1523-1739.1998.98036.x

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533

Bierregaard RO Jr, Lovejoy TE, Kapos V, DosSantos AA, Hutchings RW (1992) The biological dynamics of tropical rainforest fragments. Bioscience 42:859–866. doi:10.2307/1312085

Bray JR, Curtis JT (1957) An ordination of the upland forest communities in southern Wisconsin. Ecol Monogr 27:325–349. doi:10.2307/1942268

Brown S, Lugo A (1990) Tropical secondary forests. J Trop Ecol 6:1–32

Burkey TV (1988) Extinction in nature reserves: the effect of fragmentation and of migration between reserves fragments. Oikos 55:75–81. doi:10.2307/3565875

Burnett MR, August PV, Brown JH Jr, Killingbeck KT (1998) The influence of geomorphological heterogeneity on biodiversity I. A patch-scale perspective. Conserv Biol 12:363–370. doi:10.1046/j.1523-1739.1998.96238.x

Butaye J, Jacquemyn H, Hermy M (2001) Differential colonization causing non-random forest plant community structure in a fragmented agricultural landscape. Ecography 24:369–380. doi:10.1034/j.1600-0587.2001.d01-193.x

Chinea JD, Helmer EH (2003) Diversity and composition of tropical secondary forests recovering from large-scale clearing: results from the 1990 inventory in Puerto Rico. For Ecol Manag 180:227–240. doi:10.1016/S0378-1127(02)00565-0

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Coleman WG, Mattice J, Brocksen RW (1996) Soulé's conservation biology as the foundation for econometric ecosystem management. Conserv Biol 10:1494–1499. doi:10.1046/j.1523-1739.1996.10061494.x

Colwell RK (2000) EstimateS: statistical estimation of species richness and shared species from samples. Version 6. User's guide and application published at http://purl.oclc.org/estimates

Condit R, Pitman N, Leigh EG Jr, Chave J, Terborgh J, Foster RB et al (2002) Beta-diversity in tropical forest trees. Science 295:666–669. doi:10.1126/science.1066854

Crow TR, Grigal DF (1979) A numerical analysis of arborescent communities in the rain forest of the Luquillo Mountains, Puerto Rico. Vegetatio 40:135–146

de Blois S, Domon G, Bouchard A (2002) Landscape issues in plant ecology. Ecography 25:244–256. doi:10.1034/j.1600-0587.2002.250212.x

Dietz JL (1986) Economic history of Puerto Rico: institutional change and capitalist development. Princeton University Press, New Jersey

Douglas ME, Endler JA (1982) Quantitative matrix comparisons in ecological and evolutionary investigations. J Theor Biol 99:777–795. doi:10.1016/0022-5193(82)90197-7

Draper NR, Smith H (1981) Applied regression analysis, 2nd edn. Wiley, New York

du Toit JT, Walker BH, Campbell BM (2004) Conserving tropical nature: current challenges for ecologists. Trends Ecol Evol 19:12–17. doi:10.1016/j.tree.2003.09.018

Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. Ecography 29:573–584

ESRI (1999) ArcView geographic information system, version 3.2. Environmental Systems Research Institute, Inc, Redlands

Ewel JJ, Whitmore JL (1973) The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Research Paper ITF-018, US Department of Agriculture Forest Service. International Institute of Tropical Forestry, Puerto Rico

Forman RT (1999) Land mosaics, the ecology of landscape and regions. Cambridge University Press, Cambridge

Francis JK, Lowe CA (2002) Bioecología de árboles nativos y exóticos de Puerto Rico y las Islas Occidentales. US Department of Agriculture, Forest Service International Institute of Tropical Forestry, Puerto Rico

García-Martinó AR, Warner GS, Scatena FN, Civco DL (1996) Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. Caribb J Sci 32:413–424

Gibbs JP (1998) Amphibian movements in response to forest edges, roads, and streambeds in southern New England. J Wildl Manag 62:584–589. doi:10.2307/3802333

Grashof-Bokdam C (1997) Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. J Veg Sci 8:21–28. doi:10.2307/3237238

Grau HR, Aide TM, Zimmerman JK, Thomlinson JR, Helmer E, Zou X (2003) The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. Bioscience 53:1159–1168. doi:10.1641/0006-3568(2003)053[1159:TECOSA]2.0.CO;2

Gustafson EJ (1998) Quantifying landscape spatial pattern: what is the state of the art? Ecosystems (NY, Print) 1:143–156. doi:10.1007/s100219900011

Haines-Young R, Chopping M (1996) Quantifying landscape structure of landscape indices and their application to forested landscapes. Prog Phys Geogr 20:418–445. doi:10.1177/030913339602000403

Helmer EH (2004) Forest conservation and land development in Puerto Rico. Landsc Ecol 19:29–40. doi:10.1023/B:LAND.0000018364.68514.fb

Hernandez-Stefanoni JL (2006) The role of landscape patterns of habitat types on plant species diversity of a tropical forest in Mexico. Biodivers Conserv 15:1441–1457. doi:10.1007/s10531-005-0598-6

Honnay O, Hermy M, Coppin P (1999) Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. Biol Conserv 87:73–84. doi:10.1016/S0006-3207(98)00038-X

Hubbell SP (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299–1309. doi:10.1126/science.203.4387.1299

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Jeanneret P, Schüpbach B, Luka H (2003) Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. Agric Ecosyst Environ 98:311–320. doi:10.1016/S0167-8809(03)00091-4

Krauss J, Klein AM, Steffan-Dewenter I, Tscharntke T (2004) Effects of habitat area, isolation, and landscape diversity on pant species richness of calcareous grasslands. Biodivers Conserv 13:1427–1439. doi:10.1023/B:BIOC.0000021323.18165.58

Kremen C, Merelender AM, Murphy DD (1994) Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. Conserv Biol 8:388–397. doi:10.1046/j.1523-1739.1994.08020388.x

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115–129. doi:10.1007/BF02289694

Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79:2032–2040

Lugo AE (1988) Estimating reductions in the diversity of tropical forest species. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, DC

Lugo AE (2006) Conservación de recursos. In: López Marrero TM, Villanueva Colón N (eds) Atlas ambiental de Puerto Rico. La Editorial Universidad de Puerto Rico, San Juan, pp 124–130

Lugo AE, Helmer E (2004) Emerging forests on abandoned land: Puerto Rico's new forests. For Ecol Manag 190:145–161. doi:10.1016/j.foreco.2003.09.012

Mantel N (1967) The detection of disease clustering and generalized regression approach. Cancer Res 27:209–220

Mather PM (1976) Computational methods of multivariate analysis in physical geography. Wiley, London

Mazerolle MJ, Villard MA (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6:117–124

McCloskey M (1993) Note on the fragmentation of primary rainforest. Ambio 22:250–251

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Oregon

McCune B, Mefford MJ (1997) PC-ORD for windows: multivariate analysis of ecological data, version 3.18. MjM Software, Gleneden Beach

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345. doi:10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2

Metzger JP (1997) Relationships between landscape structure and tree species diversity in tropical forests of South-East Brasil. Landsc Urban Plan 37:29–35. doi:10.1016/S0169-2046(96)00367-2

Metzger JP (2000) Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. Ecol Appl 10:1147–1161. doi:10.1890/1051-0761(2000)010[1147:TFGRAL]2.0.CO;2

Murphy HT, Lovett-Doust J (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105:3–14. doi:10.1111/j.0030-1299.2004.12754.x

Økland RH, Bratli H, Dramstad WE, Edvardsen A, Engan G, Fjellstad W et al (2006) Scale-dependent importance of environment, land use and landscape structure for species richness and composition of SE Norwegian modern agricultural landscapes. Landsc Ecol 21:969–987. doi:10.1007/s10980-006-0005-z

Opdam P, Verboom J, Powels R (2003) Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. Landsc Ecol 18:113–126. doi:10.1023/A:1024429715253

Patton DR (1975) A diversity index for quantifying habitat edge. Wildl Soc Bull 394:171–173

Pearson SM (1993) The spatial extent and relative influence of landscape level factors in wintering bird populations. Landsc Ecol 8:3–18. doi:10.1007/BF00129863

Puerto Rico Station Data Inventory NOAA/NWS Cooperative Observer Network. http://www.ncdc.noaa.gov/oa/climate/stationlocator.html. Accessed 17 Dec 2005

Pyke CP, Condit R, Aguilar S, Hernández A (2001) Floristic composition across a climatic gradient in neotropical lowland forest. J Veg Sci 12:533–566. doi:10.2307/3237007

Ratti JT (1988) Preliminary test of the ecological trap hypothesis. J Wildl Manag 52:484–491. doi:10.2307/3801596

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Sala OE, Chapin FSIII, Armesto JJ, Berlow E, Bloomfield J, Dirzo R et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. doi:10.1126/science.287.5459.1770

Sork VL, Smouse PE (2006) Genetic analysis of landscape connectivity in tree populations. Landsc Ecol 21:821–836. doi:10.1007/s10980-005-5415-9

Tewksbury JJ, Levey DJ, Haddad NM (2002) Corridors affect plants, animals, and their interactions in fragmented landscape. Proc Natl Acad Sci USA 99:12923–12962. doi:10.1073/pnas.202242699

Thomlinson JR, Serrano MI, López TM, Aide TM, Zimmerman JK (1996) Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). Biotropica 28:525–536. doi:10.2307/2389094

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197. doi:10.1146/annurev.es.20.110189.001131

Turner MG (2005) Landscape ecology: what is the state of the science? Ann Rev Ecol Evol 36:319–344. doi:10.1146/annurev.ecolsys.36.102003.152614

Turner IM, Corlett RT (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol Evol 11:330–333. doi:10.1016/0169-5347(96)10046-X

United States Department of Agriculture Soil Conservation Service in Cooperation with the University of Puerto Rico College of Agricultural Sciences (1977) Soil survey of Humacao area of eastern Puerto Rico. USDA-NRCS, Humacao Field Office, Humacao

Waldhardt R (2003) Biodiversity and landscape-summary, conclusions and perspectives. Agric Ecosyst Environ 98:305–309. doi:10.1016/S0167-8809(03)00090-2

Weaver PL (1991) Environmental gradients affect forest composition in the Luquillo mountains of Puerto Rico. Interciencia 16:142–151

Whitcomb RF, Robbins CS, Lynch JF, Whitcomb BL, Klimkiewicz MK, Bystrak D (1981) Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess RL, Sharpe DM (eds) Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, pp 125–205

White HH (1963) Variation of stand structure correlated with altitude, in the Luquillo mountains. Caribb For 24:46–52

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251. doi:10.2307/1218190

Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landsc Ecol 17:355–365. doi:10.1023/A:1020561630963

Wunderle JM Jr (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. For Ecol Manag 99:223–235. doi:10.1016/S0378-1127(97)00208-9

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Abstract The Changbaishan Nature Reserve (CNR) is the largest protected temperate forest in the world. It was established in 1960 to protect the virgin Korean pine (*Pinus koraiensis*) mixed hardwood forest, a typical temperate forest of northeast China. Studies of vascular diversity patterns on the north slope of the CNR mountainside forest (800–1700 m a.s.l.) were conducted in 1963 and in 2006. The aim of this comparison was to assess the long-term effects of the protected status on plant biodiversity during the intervening 43 years. The research was carried out in three forest types: mixed coniferous and broad-leaved forest (MCBF), mixed coniferous forest (MCF), and sub-alpine coniferous forest (SCF), characterized by different dominant species. The alpha diversity indicted by species richness and the Shannon–Wiener index were found to differ for the same elevations and forest types after the 43-year interval, while the beta diversity indicated by the Cody index depicted the altitudinal patterns of plant species gain and loss. The floral compositional pattern and the diversity of vascular species were generally similar along altitudinal gradients before and after the 43-year interval, but some substantial changes were evident with the altitude gradient. In the tree layer, the dominant species in 2006 were similar to those of 1963, though diversity declined with altitude. The indices in the three forest types did not differ significantly between 1963 and 2006, and these values even increased in the MCBF and MCF. However, originally dominant species, such as *Pinus koraiensis*, tended to decline, the proportion of broad-leaved trees increased, and the species turnover in the succession layers showed a trend to shift to higher altitudes. The diversity pattern of the understory fluctuated along the altitudinal gradient due to micro-environmental variations. A comparison of the alpha diversity indices among the three forest types reveals that the diversity of the shrub and herb layer decreased, and some rare and medicinal species disappeared. Meteorological records show that climate has changed significantly in this 43-year intervening period, and information collected from another field survey found that the most severe human disturbances to the CNR forests stemmed from the exploitation of Ginseng roots and Korean pine nuts.

Keywords Alpha diversity · Beta diversity · Forest ecosystem change · Global warming · Human activity · Nature preserve

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Introduction

Biodiversity patterns are the combined result of the interior processes of the plant community and external conditions. The hierarchy in forest plant species diversity is established by the interaction between the canopy and the understory layers. Gaps in the main story are initially filled by succession trees growing up from seedlings, and these gaps may naturally persist for a long time (Whitmore 1998; Chapin et al. 2002). Species richness gradients are always determined by natural environmental gradients, such as altitude, temperature, seasonal variations, and geological conditions (Rosenzweig 1995; Begon et al. 1996; Körner 2000). Diversity pattern gradients on individual mountains are simpler to understand and work with than those in more extensive regional, national, continental, or global ranges, because of the shorter geographical distances involved and the similarity of climatic zones in mountains (Körner 2000; Buker 2003). However, altitudinal patterns of plant species diversity have long been in contention due to variations in research domains and sampling methods (He and Chen 1997; Buker 2003; Bhattarai et al. 2004).

Emissions from fossil fuels are increasing, and the effect of human activity on the environment is intensifying. Changes in global and local climate, and in land use, have become the major factors affecting natural diversity patterns, and such changes are resulting in noticeable shifts in natural forest distribution and biodiversity loss (Whitmore 1998; Dupouey et al. 2002; Carey and Alexander 2003; Parmesan 2006). Hence, the establishment of nature reserves with the aim of rescuing critical ecosystems and endangered species has focused on the relationships between biodiversity, warming climate, and human impacts (Mouillot et al. 2000; Hooper et al. 2005; Fang et al. 2006). Ecologists continue to study the long-term maintenance of global biodiversity in various ecosystems (Halpin 1997; Anderson and Inouye 2001; Defries et al. 2005; Chapman et al. 2006). Such long-term surveys can assess whether current ecosystem conservation strategies suitably address the impact of climate change on biodiversity and species distribution (Phillips et al. 1998; Scott et al. 2001; Clark 2002).

The ecological responses of vegetation to recent climate change have been reviewed by Parmesan (2006), who pointed out the serious shortage of studies on the biological impact of climate change on mountain plant patterns, especially in Asia. The summer temperatures in northeastern China have increased 0.15°C per decade during the past 50 years, which is higher than the global average warming rate (Li et al. 2005). The existence of so few studies of floral shift along the elevation gradients of mountainsides has been attributed to the absence of historical data. Long-term records of field observations are necessary for assessing the trends in ecosystems affected by environmental change and human activities, especially within the framework of surveying permanent plots (Grabherr et al. 1994; Anderson and Inouye 2001; Clark 2002; Moiseev and Shiyatov 2003; Pauli et al. 2007).

The Changbaishan Nature Reserve (CNR) was founded in 1960 to protect the virgin Korean pine (*Pinus koraiensis*) mixed hardwood forest, a temperate forest type typical of those found in northeastern China (Tao 1994; Yang and Xu 2003; Stone 2006). The CNR is the largest protected temperate forest in the world and is home to endangered Siberian tigers (*Panthera tigris altaica*), valuable species of Ginseng (*Panax ginseng* C.A. Mey), and the Korean pine (*P. koraiensis*).

Due to its quality, the wood of the Korean pine has high commercial value, while the Korean pine seeds are an important food source for the rodent wildlife of the forest ecosystem. A study conducted 43 years ago systematically characterized the distribution pattern of vegetation in the CNR (Chen 1963; Chen et al. 1964; Zhou and Li 1990) and identified five natural vertical vegetation zones along the elevation gradient (Chen et al. 1964; Wang et al. 1980; Zhao et al. 2004): (1) a mixed coniferous and broad-leaved forest zone (MCBF) (below 1100 m a.s.l.), dominated by *Pinus koraiensis*, *Acer mono*, *Tilia amurensis*, *Ulmus davidiana* var. *japonica*, *Quercus mongolica*, etc.; (2) a mixed coniferous forest zone (MCF) (1100–1500 m a.s.l.), dominated by *P. koraiensis*, *Picea jezoensis* var. *komarovii*, *Abies nephrolepis*, *Larix olgensis* var. *changpaiensis*, etc.; (3) a sub-alpine coniferous forest zone (SCF) (1500–1800 m a.s.l.), dominated by *Picea jezoensis* var. *komarovii*, *Larix olgensis* var. *changpaiensis*, and *Abies nephrolepis*; (4) a birch forest zone (BF) (1800–2100 m a.s.l.), dominated by *Betula ermanii*; (5) a tundra zone (above 2100 m a.s.l.), dominated by *Rhododendron aureum*, *R. redowskianum*, *Vaccinium uliginosum* var. *alpinum*, etc. (Fig. 1).

Although tree cutting was prohibited around the time the natural reserve was founded, the forest is still threatened by warming temperatures and by human activities under the canopy, such as tourism and the collecting of pine nuts (Chen and Wang 1999). Although the forest has been monitored by field investigations and satellite imagery during the past 10–28 years (Zhang et al. 1994; Liu 1997; Jin et al. 2005; Liu et al. 2005; Li et al. 2006), no long-term survey comparing the diversity patterns in the 1960s to the present status of CNR had been conducted before the study reported here. In 1963, Chen et al. (1964) investigated the flora with the aim of characterizing the major forests in various vertical zones on the north slope of the CNR. Fortunately, a set of original plot records from that survey of the CNR has been preserved.

The aim of the this study was to determine whether significant differences have occurred in terms of the forest biodiversity patterns of vascular plant species on the north slope of the CNR by comparing the field observations made in 1963 with those of 2006. Analysis and discussion of the possible reasons for this change, involving global warming and human activities, is relevant to any assessment of the long-term protective effects of the CNR and to planning future management strategies.

Methods

Study area

The CNR covers an area of 196,456 ha and is located in Jilin Province, northeastern China. This region is situated on the border between China and North Korea. The major factor affecting the weather is the monsoon. The area is characterized by a mountain climate, with dry and windy springs, short and rainy summers, cool and foggy autumns, and cold and long winters; there are decreasing temperatures with increasing elevation, abundant precipitation that increases along altitudinal gradients, and strong winds with a prevailing direction to the west–south–west (WSW) (Chi et al. 1981) (Table 1).

The research was carried out in a mixed coniferous and broad-leaved forest (MCBF), a mixed coniferous forest (MCF), and a sub-alpine coniferous forest (SCF), three of the natural vertical vegetation zones identified in the earlier study, on the north slope of Changbaishan Mountain (800–1700 m a.s.l.). The map coordinates of the investigation area are 127°55′ E–128°08′ E, 42°04′ N–42°23′ N (Fig. 1). The topography is very moderate, ranging from 800 to 1700 m a.s.l., with slopes of <15°.

Human activities in these three forest types have been reduced since the establishment of the CNR, though some disturbances still occur. The different elevations with their plant compositions are variously affected by a range of human activities, such as gathering pine seeds, collecting herbs, and tourism (Table 1). Of the three forest types mentioned above, the MCF has been impacted the most by these activities, the SCF the least.

According to the climatic records of the Songjang meteorological station (721.4 m a.s.l.; 42°25′ N/128°07′ E), located on the northern edge of the CNR (Fig. 2), climate trends have changed during the 45 years from 1960 to 2005. Annual average temperatures have fluctuated and gradually increased about 0.37°C per decade. The temperature values recorded after 1985 are higher than preceding ones and than the 45-year average (2.7°C). Precipitation has fluctuated around the 45-year average (680.5 mm), without any apparent trend.

Field surveying

Based on the records of Chen et al. (1964), we repeated the 1963 field survey in 2006, using the same methods and at the same locations. The plots were chosen according to the 1963 plot records, which contained information on elevation, landforms, slope gradients, slope directions, and dominant species in each forest type.

The field observations of the 1963 survey were carried out from June to August and the 2006 survey from July to August. In order to achieve comparable results, we utilized the same sampling method as the 1963 inventory. From the 63 plots sampled in 1963, we chose 52 plots (20 × 20 m) with clear location records and distinct geographic characteristics. A minimum of two plots were sampled in each 100-m altitudinal interval, and ten plots were chosen in each forest type (Table 1).

Each plot contained four sub-plots (10 × 10 m) for surveying trees, four shrub sub-plots (10 × 10 m), and four herb sub-plots (1 × 1 m). The plot positions were determined by GPS, which also recorded the

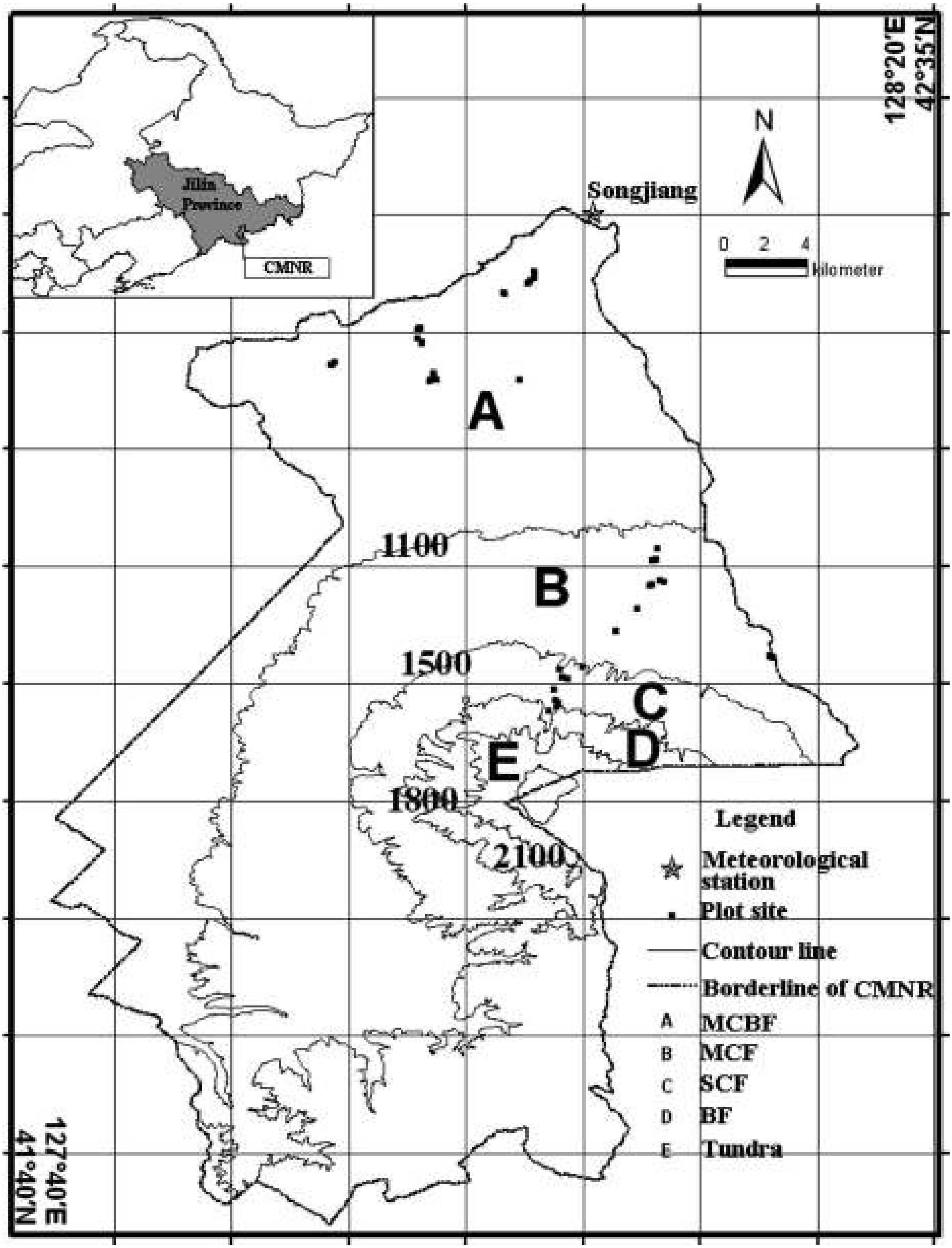


Fig. 1 Map of the research area and vegetation zone according to altitude in the Changbaishan Nature Reserve (CNR)

Table 1 Altitude, temperature, precipitation, and plot characteristics of the survey area along the northern slope of Changbaishan Mountain

Altitude (m)	Annual mean temperature[a] (°C)	Annual precipitation[a] (mm)	Forest type[b]	Human activity[c]	Number of plots
800	2.32	703.62	MCBF	A, B	13
900	1.81	728.95			10
1000	1.29	755.19			3
1100	0.78	782.37	MCF	A, B, C	5
1200	0.27	810.53			6
1300	−0.24	839.70			3
1400	−0.75	869.92			2
1500	−1.26	901.23	SCF	B, C	2
1600	−1.78	933.67			4
1700	−2.29	967.28			4

[a] Data from Chi et al. 1981

[b] MCBF, a mixed coniferous and broad-leaved forest zone; MCF, a mixed coniferous forest zone; SCF, a sub-alpine coniferous forest zone

[c] A, collecting Korean pine nuts; B, collecting herbs and medicinal plant materials; C, tourism

elevation, topography, and other background information. All living trees with height $\geq$1.3 m in the tree sub-plots were tallied by species and DBH (diameter at breast height). The canopy was divided into a main story (DBH $\geq$ 8 cm) and succession layer (DBH < 8 cm) (Hao 2000), representing the main composition and the future trend of the forest ecosystem, respectively. In the shrub and herb sub-plots, records of every stem were organized by species or species group, abundance, coverage, and average height.

Data analysis

Altered Important Value

The Altered Important Value (AVI, Ma et al. 1995) was used to measure the relative importance of the plant species in the community. The AIV values were determined as follows:

$$\mathrm{AIV(tree\ layer)} = \frac{\text{Relative dominance} + \text{Relative abundance} + \text{Relative height}}{3} \times 100\%$$

$$\mathrm{AIV(shrub/herb\ layer)} = \frac{\text{Relative coverage} + \text{Relative abundance} + \text{Relative height}}{3} \times 100\%$$

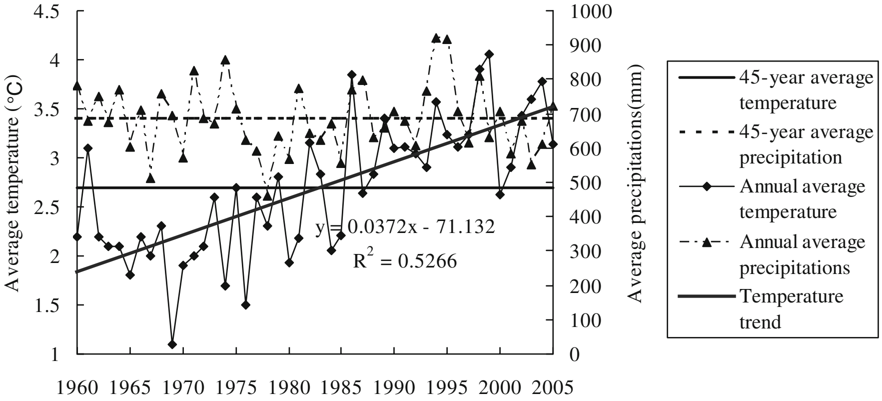
Alpha diversity index

Species richness (S) and the Shannon–Wiener index (H), both based on the AIV, were used to measure plant species diversity and to show the distribution pattern of plant diversity within plots at the same altitude. These two indices were calculated for the canopy (DBH $\geqq$ 8 cm), succession (DBH < 8 cm), shrub, and herb layers. Species richness was determined as the total number of species in each plot. The values of the Shannon–Wiener index are generally defined as follows (Ma 1994; Ma and Liu 1994; Shang 2002):

$$H = -\sum_{i=1}^{s} p_I \ln p_I$$

where s is the total number of species in a plot, and p_I is the AIV corresponding to the species.

Fig. 2 Changes in the annual average temperature and precipitation at Songjiang in the CNR from 1960 to 2000



The *t* test was used to assess the differences in the Shannon–Wiener index (*H*) mean values for each plot of the three forest types between the two surveys.

Beta diversity index

Species turnover diversity, indicated by the Cody index (β_c), was calculated as the gain and loss of species between neighboring altitudes according to the formula proposed by Wilson and Shmidam (1984):

$$\beta_c = \frac{g(H) + l(H)}{2}$$

where $g(H)$ and $l(H)$ are the number of species gained and lost, respectively, between two neighboring elevation intervals (100 m). In this study, the Cody index (β_c) was used to illustrate the spatial patterns of species change along the altitudinal gradient.

The researchers who conducted the 1963 survey did not plan to analyze the beta diversity, so the plot numbers varied within each altitudinal interval (e.g. two plots at 1400 m a.s.l., and 13 plots at 800 m a.s.l.). The situation is different with the general sampling design using the same sample size at every elevation (Fosaa 2004; Chao et al. 2005; Harborne et al. 2006). The minimum total area of each elevation plot (800 m^2) was far larger than the minimum sample area in the temperate zone. Hao (2000) concluded that the sampling areas are 64 m^2 in the CNR and that the Cody index (β_c) is therefore credible.

To avoid any bias caused by the different sample areas, we calculated the same year β_c to determine whether there was any significant difference between the two methods: (1) based on the different areas, including all plots at each elevation; (2) based on the same number of plots at each elevation, randomly selecting two plots at each 100-m interval.

The paired *t* test results of β_c by these two methods using the 1963 and 2006 data showed that all *t* test values were <1 ($P > 0.05$); thus, there were non-significant differences between varied sample areas. As in Heegaard's (2004) research, we demonstrated that the main factor influencing the beta diversity was not the sampling area or habitat size, but the ecological gradients and increased distances. Thus, we concluded that the method based on the different sampling areas could be used to measure the beta diversity in the study.

Results

Altitudinal gradient patterns of plant diversity in 1963 and 2006

Floral composition

The 1963 survey found 202 species, 144 genera, and 61 families of vascular plants, comprising 38 tree species, 37 shrub species, and 127 herb species, within the altitude range between 800 and 1700 m a.s.l. The numbers of species had slightly declined by 2006, when we found 196 species, belonging to141 genera and 58 families, comprising 37 tree species, 37 shrub species, and 122 herb species.

Alpha diversity pattern

The patterns of species richness and the Shannon–Wiener index along altitudinal gradients in 2006 are similar to those of 1963, except in the succession layer (Fig. 3).

Figure 3a, c shows that species richness in the tree layer and the Shannon–Wiener index in the main story decreased along altitude. The least square linear regression analysis is given in Table 2. The curve in 2006 has the nearly same shape as that of 1963 but, in general, there is more richness in 2006 than 1963. Both results show three peaks in species richness and Shannon–Wiener index, all of which are located in the central part of the three forest types. The first is at 900 m a.s.l. for 1963 and at 1000 m a.s.l. for 2006; the second occurs between 1200 and 1300 m a.s.l. for the two periods; the third is at 1500 m a.s.l. for 1963 and 1600 m a.s.l. for 2006. Above an altitude of 900 m a.s.l. for the 1963 survey and 1000 m a.s.l. for the 2006 survey, the Shannon–Wiener index decreases more or less monotonically up to 1700 m a.s.l.

It can be seen that the diversity pattern of the understory layer (shrub and herb layers) in 2006 still has the same shape as in 1963, but is less rich. The diversity tends to decrease along the altitudinal gradient (Fig. 3b, e, f). The indices fall from peaks at 800 m a.s.l. to troughs at 1200 or 1300 m a.s.l., then increase again to peaks at 1400 or 1500 m a.s.l., finally decreasing with elevation. A linear regression between the Shannon–Wiener index values and altitude was used for the shrub layer (Table 2).

In contrast to the main story, the Shannon–Wiener index of the succession layer is distinct for the two surveys (Fig. 3d). The index for 1963 generally shows a decreasing trend for the main story, with peaks at 900 and 1500 m a.s.l. In contrast, the decreasing trend of the under tree layer in 2006 is similar to that of the succession layer, with a lower value at 1200 m a.s.l.

Beta diversity pattern

Figure 4 shows the beta diversity patterns (Cody index) along the altitudinal gradient for 1963 and 2006. All beta diversity declined sharply with increasing elevation. The beta diversity patterns of the two surveys differ only for the succession layer, with similar trends seen for the other canopies and all of its species.

The beta diversity pattern of the main story shows two peaks (1000–1100 m a.s.l. and 1400–1500 m

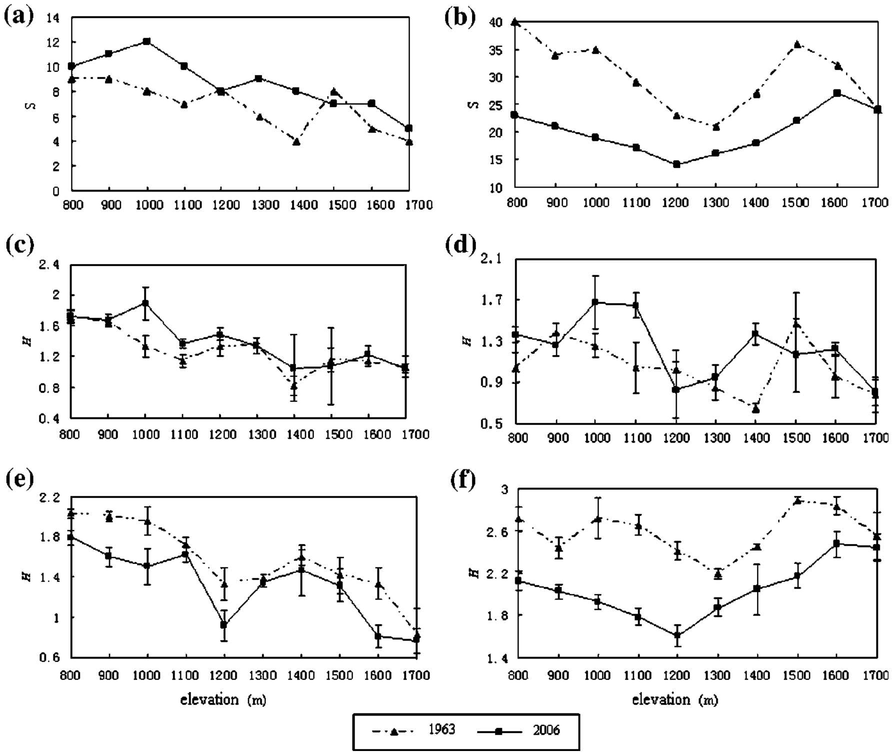


Fig. 3 Patterns of change in forest alpha diversity along the altitudinal gradient in 1963 and 2006. **a** Species richness in tree layer, **b** species richness in understory, **c–f** Shannon–Wiener index in main story **c**, success layer **d**, shrub layer **e**, and herb layer **f**

Table 2 A comparison of the linear relations between species richness and altitude in 1963 and 2006

Diversity index	Canopy	1963			2006		
		Regression parameters[a]		r	Regression equation[a]		r
		B	A		B	A	
Species richness	Tree layer	−0.0051 (−0.0082, −0.00195)	13.164 (9.139, 17.188)	−0.80	−0.0062 (−0.0088, −0.0037)	16.503 (13.257, 19.749)	−0.89
Shannon-Wiener index	Main story (canopy)	−0.0007 (−0.0013, −0.0005)	2.123 (1.988, 2.971)	−0.77	−0.0009 (−0.0011, −0.0002)	2.480 (1.540, 2.707)	−0.88
	Succession layer	−0.0003 (−0.0012, 0.0002)	1.462 (0.972, 2.779)	−0.39	−0.0005 (−0.00098, 0.0003)	1.875 (0.632, 2.292)	−0.51
	Shrub layer	−0.0011 (−0.0015, −0.0004)	2.969 (1.761, 3.263)	−0.90	−0.001 (−0.0016, −0.0007)	2.512 (2.391, 3.547)	−0.80

[a] The regression model is $y = \mathrm{B} \times x + \mathrm{A}$ ($n = 10$, x = elevation m a.s.l., y = alpha biodiversity index). The confidence probability of the regression parameters B and A is 95%. The confidence limits are in parenthesis following the parameters (lower bound, upper bound)

a.s.l.) for 1963 and 2006 (Fig. 4a). In the 800–1000 m a.s.l. interval, the Cody index increases gradually to a peak at 1000–1100 m a.s.l., decreases to its lowest level, and then fluctuates between 1100 and 1400 m a.s.l. until reaching a second peak. The index value at low elevation is greater than that at high elevation.

The beta diversity patterns in the succession layer fluctuate along the altitudinal gradient with three peaks and troughs, as shown in Fig. 4b. Peaks in the 1963 data occur at 900–1000, 1200–1300, and 1500–1600 m a.s.l.; troughs occur at 1100–1200, 1300–1400, and 1600–1700 m a.s.l. Peaks in the 2006 data occur at 1000–1100, 1400–1500, and 1600–1700 m a.s.l., while the troughs occur at 900–1100, 1100–1300, and 1500–1600 m a.s.l.

Figure 4c, d shows a similar trend for the understory layer and all its species. Comparing the trends of the 1963 and 2006 data, the lower Cody index for both years are at 1100–1300 m a.s.l., while peaks appear at 1000–1100 and 1400–1500 m a.s.l. for 1963 and at 900–1000 and 1500–1600 m for 2006.

Changes in the three forest types

Changes in species composition

The dominant tree species in the canopy and the succession layer are given in Tables 3 and 4, which show that the dominant species in 2006 were generally similar to those of 1963. Nevertheless, some important changes in species status occurred in the three forest types during the time interval between studies.

In the MCBF (800–1100 m a.s.l.), *Pinus koraiensis* was still the predominant tree, but the AIV declined from 27 to 19%. The proportion of broad-leaved tree species increased, so that *Quercus mongolica* became the newly dominant tree.

In the MCF (1100–1500 m a.s.l.), the AIV of *Abies nephrolepis* increased, although those of other needle-leaved trees (e.g. *Larix olgensis* var. *changpaiensis* and *Pinus koraiensis*) lost their once dominant status. The proportion of broad-leaved tree species increased (e.g., *Acer mono* and *Betula platyphylla*).

In the SCF (1500–1700 m a.s.l.), *Picea jezoensis* var. *komarovii* and *A. nephrolepis* took each others place, with the AIV of *A. nephrolepis* being 44%. Broad-leaved tree species were also added.

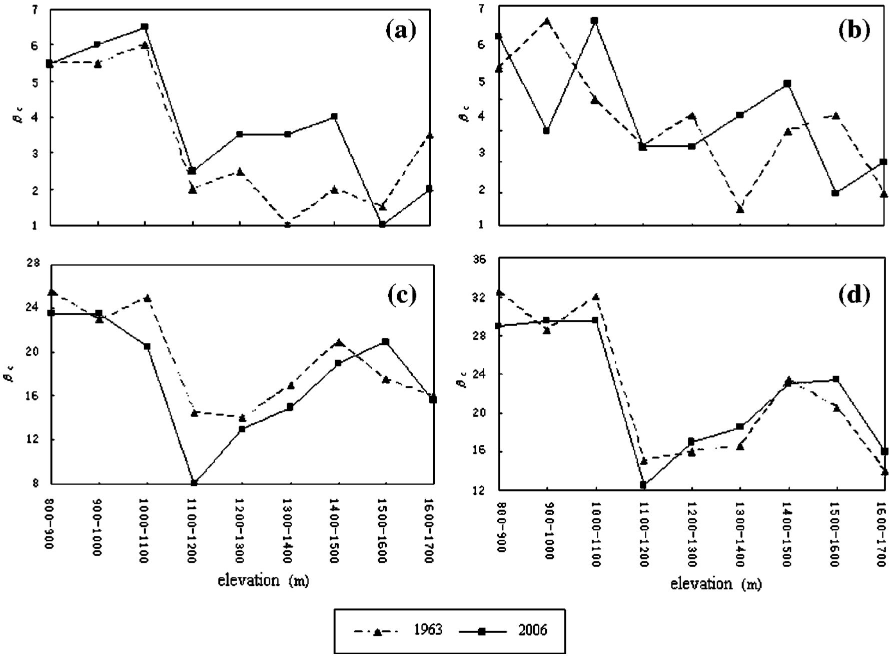


Fig. 4 Patterns of change in forest beta diversity along an altitudinal gradient in 1963 and 2006. **a** Canopy, **b** succession layer, **c** understory, **d** all plant species

As shown in Table 3, the AIV of the succession layer and the status of the broad-leaved tree species in MCBF and MCF all increased. There were broad-leaved trees together with the dominant species in the succession layer of the MCBF (Table 4).

Alpha diversity change

Table 5 enumerates the species richness and the Shannon–Wiener index for the different forest types of the two surveys. The trends of the changes were nearly the same in the MCBF and MCF, but they differed in the SCF.

The indices of the tree layer (the canopy and succession layer) do not differ significantly between the 1963 and 2006 data sets. The values of the canopy indices increased 5 and 13% in the MCBF and MCF, respectively, but are almost equal for the SCF. The indices of the succession layer increased more than 20% in the MCBF and MCF and by 5% in the SCF.

The diversity of the shrub and herb layers significantly decreased in the three forest types, except in SCF shrub layer. In the MCBF and MCF, species richness in the shrub layer decreased slightly, and the Shannon-Wiener index of both fell

Table 3 Comparisons of the composition of dominant species[a] in the canopy of the three forest types between the 1963 and 2006 surveys

Forest type	Year	Components of tree species (DBH $\geq$ 8 cm) and AIV ($\times$100)[b]
MCBF	1963	PK 27 + AM 15 + AN 13 +TA 10 + AP 8 + Others 27
	2006	PK 19 + AM 13 + AN 12 + QM 10 + TA 8 + Others 38
MCF	1963	LO 29 + PK 26 + AN 25 + PJ 11 + Others 9
	2006	AN 27 + LO 22 + PK 22 + PJ 6 + Others 23
SCF	1963	LO 39 + PJ 34 + AN 19 + Others 8
	2006	AN 44 + PJ 26 + LO 13 + Others 17

Only trees with a DBH (diameter at breast height) $\geq$ 8 cm were counted. AIV, Altered Important Value

[b] AN,*Abies nephrolepis*; LO, *Larix olgensis* var. *changpaiensis*; PJ, *Picea jezoensis* var. *komarovii*; PK, *Pinus koraiensis*; QM, *Quercus mongolica*; AM, *Acer mono*; AP, *A. pseudo-sieboldianum*; TA, *Tilia amurensis*

about 15%, while 1963 species richness had decreased by over 40% and the Shannon-Wiener index by over 20% by 2006. There is no statistically significant decrease in the shrub layer of the SCF, and the diversity of its herb layer decreased less than 12%.

Discussion

Effective conservation in the CNR

Floral composition

The establishment of the CNR has prevented the forest communities from experiencing large disturbances, such as clear cutting and land-use change (Liu 1997; Yang and Xu 2003; Liu et al. 2005), as clearly shown by our comparisons of field data from 1963 and 2006. The total number of species recorded in 2006 were only slightly less than those counted in 1963 and, in general, similar patterns were found in the floral composition of the tree layer. As seen in this analysis, the species compositions of the dominant trees in the tree layer were generally the same in both surveys. The succession layer represents the future canopy of the forest following long-term growth (Lertzman 1992; Whitmore 1998; Chapman et al. 2006). Consequently, the results of this investigation indicate that biodiversity conservation has been effective in the CNR.

Other investigators of the CNR have reported similar results in terms of these three forest types. Zhao et al. (2004) described the composition and structure of communities on the northern slope of Changbai Mountain based on TWINSPAN classification. They found that three community groups existed within the altitude range from 700 to 1780 m a.s.l. The MCBF, containing the dominant tree species, such as *Pinus koaiensis*, is the most important forest type in China (Wu 1980; Zhou and Li 1990); the MCF, located between two other forest types, represents a transitional zone (Zhao et al. 2004); the SCF is typical of alpine forests. Thus, the vegetation zones in this area are suitable for carrying out the kind of long-term monitoring and research reported in our study.

General diversity pattern between 1963 and 2006

The general comparability of altitudinal diversity patterns between the CNR surveys of 1963 and 2006 is evident, as are the analogous patterns within the specific elevation intervals (Shao 1999; Hao 2000; Zhao et al. 2004). The species richness and Shannon–Wiener indices decreased in the tree layer and the understory with increasing altitude. A higher species turnover was apparent at lower elevations. Hence, the conservative effects of the CNR cannot be doubted.

The causes of the changes in plant diversity are complex, involving various ecological gradients and floral interactions. In lower mountains, the presence of more broad-leaved tree species is due to the abundance of growth resources and warmer temperatures (Lopes Valle de Britto Rangel and Felizola Diniz-Filho 2003) (Bhattarai et al. 2004; Stromberg 2007). Competition resulting from the complex interactions between plant species and disturbances caused by animals are also seen to be further reasons for higher diversity (Vázquez and Givnish 1998; Pauli et al. 2007). The decline in forest tree diversity with elevation may be related to decreased temperature gradient, seasonal length, and/or nutritive material (Körner 2000; Fosaa 2004).

In terms of species–area relationships (Rosenzweig 1995; Hill and Curran 2001), fewer species were expected in the higher part of Changbai Mountain because the amount of available habitat area decreases. Nevertheless, the three peaks of the diversity curves did occur in the tree layer at the mid-elevation of each forest type and are consistent with the hypothesis of a mid-domain effect (MDE) (Colwell and Lees 2000). There are boundary constraints of species dispersal at the ecotone, but more overlap of species ranges and species inter-connection occurs in the middle of habitats because they are the centers of shared geographic domains (Bhattarai et al. 2004; Pauli et al. 2007).

In contrast to the tree layer, the lower values of the diversity patterns for the understory appeared at mid-elevation (1200 or 1300 m a.s.l.) and the peaks at the boundary between different forest types. These observations seem to contradict the MDE. Such a situation has been noted by other researchers and is interpreted as resulting from the different processes that influence species richness across an altitudinal

Table 4 Comparisons of composition of dominant species[a] in the succession layers of the different forest types between 1963 and 2006 surveys

Forest type	Year	Component of tree species (DBH < 8 cm) and AIV (× 100)[b]
MCBF	1963	AU 23 + AP 17 + AM 16 + SR 12 + ATF 6 + Others 26
	2006	AU 23 + AM 18 + SR 13 + AP 11 + AK 6 + Others 29
MCF	1963	AN 52 + PJ 16 + ATM 11 + AU 7 + AB 6 + Others 8
	2006	AN 48 + ATM 11 + PJ 10 + LO 6 + SP 6 + Others 19
SCF	1963	AN 41 + PJ 38 + AU 7 + AK 6 + Others 8
	2006	AN 45 + AU 13 + BE 8 + PJ 6 + Others 14

[a] Only trees with a DBH < 8 cm were counted

[b] AN, *Abies nephrolepis*; LO, *Larix olgensis* var. *changpaiensis*; PJ, *Picea jezoensis* var. *komarovii*; BE, *Betula ermanii*; SP, *Sorbus pohuashanensis*; AB, *Acer buergerianum*; AK, *A. komarovii*; AM, *A. mono*; AP, *A. pseudo-sieboldianum*; ATF, *A. triflorum*; ATM, *A. tegmentosum*; AU. *A. ukurunduense*; SR, *Syringa reticulata* var. *mandshurica*

gradient (Ricklefs 1987; Hao 2000; Pearman and Weber 2007). The environmental patterns of the understory plants are more sensitive to micro-environmental variations with elevation, which do not always concur with those of woody plants (Bhattarai et al. 2004; Bergman et al. 2006; Freestone and Inouye 2006). In the mid-domain, the continuous tree canopies provided homogeneous habitats for shrubs and herbs, while at the ecotone between one vegetation zone and another, greater species diversity is explained as resulting from more gaps and greater heterogeneity (Shao 1999; Fosaa 2004; Zhao et al. 2004).

The higher beta diversity at lower elevations, indicating a higher degree of species turnover, is generally interpreted to be the result of warmer, more nutrient-rich conditions, and also supports the conjecture that lowland forests may be more diverse because they contain more space for species–area relationships (MacArthur 1972; Rosenzweig 1995; Vázquez and Givnish 1998). Species turnover peaks cluster around 1000–1100 and 1400–1500 m a.s.l. These patterns overlap the boundaries between two forest types. This could be explained simply as a loss of species in lower altitudes and a gain in the higher ones. Beta diversity thus illustrates the degree of habitat compensation (Ma et al. 1995; Fosaa 2004; Zhao et al. 2004).

Long-term changes in the CNR

Changes in species composition

Despite effective conservation in the CNR, this forest ecosystem is under pressure from the impact of climate change and social economic development, and a degree of instability is evident in the composition and diversity patterns of these forests. Some rare herb species have disappeared, such as *Adonis amurensis*, *Jeffersonia dubia*, and *Goodyera repens*. The predominance of needle-leaved tree species, such as *Pinus koraiensis*, has declined, while the broad-leaved tree species have expanded into higher altitude communities in both the main story and the succession layer. This trend was predicted using observational data and modeling by Yang and Xu (2003). The reasons for this change were ascribed to the combined effect of climate change and local human activities, an assumption that is supported by observed changes in the diversity pattern, as discussed below.

Changes in the succession layer

Because it is the main force driving the changes in the forest ecosystem, the succession layer is arguably the most important part of a forest (Whitmore 1998). Unlike the Shannon–Wiener and Cody indices for the canopy, those for the succession layer were distinct in the two surveys. The alpha diversity pattern changed from a decreasing trend in 1963 to a trend that deceases with elevation in 2006. As the increasing proportion of broad-leaved trees seems to be a signal of global warming (Yang and Xu 2003; Thuiller et al. 2006), it may be presumed that the species in the succession layer became more environmentally sensitive, as did the understory layers. Thus, the spatial pattern altered with the gradual change of the habitat gradient and the available resources resulting from

Table 5 Plant diversity dynamics of the three forest types on Changbai Mountain in terms of changes in the canopy layer between the 1963 and 2006 surveys

Forest type:		MCBF				MCF				SCF			
Canopy layers:		Main story	Success layer	Shrub layer	Herb layer	Main story	Success layer	Shrub layer	Herb layer	Main story	Success layer	Shrub layer	Herb layer
S^b	1963	6	5	10	26	5	5	6	19	4	5	5	26
	2006	8	6	8	13	7	6	6	11	5	4	5	20
H^c	1963	1.64 (0.05)	1.12 (0.09)	2.01 (0.03)	2.61 (0.07)	1.21 (0.07)	0.94 (0.11)	1.48 (0.08)	2.46 (0.06)	1.11 (0.06)	0.99 (0.14)	1.14 (0.17)	2.73 (0.10)
	2006	1.73 (0.05)	1.36 (0.07)	1.68* (0.06)	2.07* (0.05)	1.37 (0.06)	1.17 (0.14)	1.26* (0.10)	1.77* (0.06)	1.11 (0.09)	1.04 (0.10)	0.89 (0.14)	2.40* (0.08)

* Significantly different at $P < 0.05$

[a] Canopy layer: Main story and success, shrub, and herb layers

[b] *S*, Species richness

[c] *H*, Shannon-Wiener index, including mean (standard error of mean given in parenthesis) of same forest types

climate change (Nogués-Bravo et al. 2007; Pauli et al. 2007). The underlying factor for the decreased resilience in the succession layer could be human impact from continuous harvesting and tourist activities under the canopy (Whitmore 1998; Buker 2003).

The shift in vegetation belts to higher elevations due to global warming, as demonstrated in this study, has also been reported from experimental research and modeling (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006), but it has not been found in field investigations. With the expansion of broad-leaved tree species into higher altitude communities, the beta diversity in the succession layer also showed a trend to move to higher altitudes. The peaks in beta diversity in 1963 were at 900–1000, 1200–1300, and 1500–1600 m a.s.l; in 2006, the peaks had shifted upwards 100–200 m, with the peaks occurring at 1000–1100, 1400–1500, and 1600–1700 m a.s.l. Figure 5 shows that after moving 100 m a.s.l. upwards from the 1963 original beta diversity pattern (Fig. 5a), the first peak joints (Fig. 5b); moving up 200 m a.s.l., the second peak joints. The higher the jointed point, the longer the time needed. This results illustrates that global warming is likely to have a more severe impact on higher altitudes, where the adaptive capacities of species are lower (Nogués-Bravo et al. 2007; Pauli et al. 2007). Based on our results, climate change has already had a profound effect on forest patterns in the CNR.

Changes in the three forest types

The keystone species, such as dominant species in the tree layer and highly sensitive herb species, are those that respond most rapidly to external factors. Such effects extend to the entire community through the interactions between plants (Mitchell et al. 1999; Klanderud and Totland 2005). Hence, the changes in the three forest types can be studied by analyzing the unique features of the species, the composition of the community, the degree of diversity, climate change, and human impact factors.

The changes that occurred in the MCBF and MCF are nearly the same. The species richness, Shannon–Wiener index, and proportion of broad-leaved species in the tree layer increased from 1963 to the present. This trend was consistent with the RPMKPF modeling result of a primarily mixed broad-leaved Korean

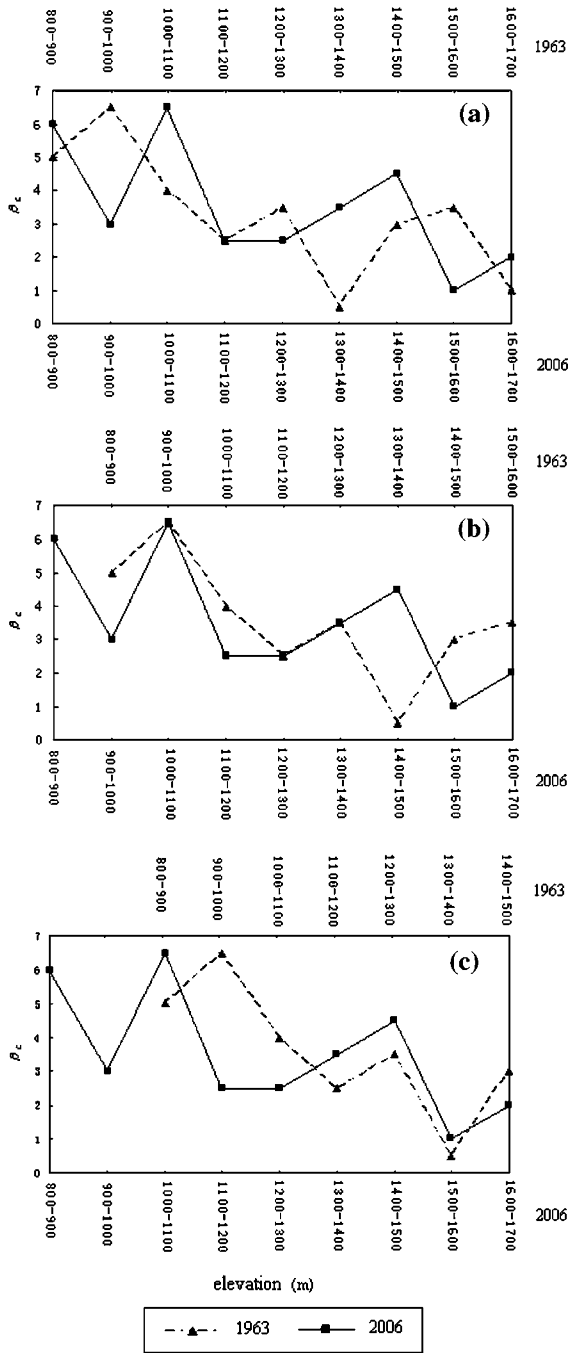


Fig. 5 Upward-shifting trends in forest beta diversity along an altitudinal gradient in 1963 and 2006. **a** Original status, **b** the 100-m upward shift from the 1963 beta diversity pattern, **c** the 200-m upward shift from the 1963 beta diversity pattern

pine forest under pressure from a combination of climate change and human activities (Chen and Li 2004). The reduction of *Pinus koraiensis*' dominant status and alpha diversity in the understory would also support this result. The collecting of pine nuts has dramatically affected the regeneration of the Korean pine by depleting the seed bank (Wu and Han 1992), while collecting herbs for food and medicinal purposes has heavily disturbed the understory layer (Chen and Wang 1999). Global warming could exacerbate this situation. Miles et al. (1983) used a Markov chain to simulate the future status of Korean pine. The results showed that the broad-leaved trees, especially *Quercus mongolica*, which is more adapted to drought conditions, would replace the Korean pine with increasing climate change (Zhang 1983; Tao 1994). In our study, we found that *Quercus mongolica* had become the newly dominant species by 2006.

Human impact in the SCF is relatively light and concentrated. There are no disturbances other than tourism, the effects of which are focused on certain areas and along the tourist path. Thus, the change in alpha diversity in the SCF is the lowest of the three forest types (Huston 2005). In the future, however, the impact on the SCF may intensify due to economic development (Ohl et al. 2007). After all, the broad-leaved trees have invaded the succession layer, and the diversity of the herb layer has decreased significantly. Human impact on the shrub and herb layers of forests often escape the notice of forest managers, because of the delayed or long-term effects (Hooper et al. 2005; Bergman et al. 2006).

Conclusions

The absence of significant changes in the diversity patterns of vascular plant species with altitude indicates the effectiveness of the conservation measures that have been in force in the CNR during the 43 years since the 1963 survey. The prohibition of tree cutting helped to preserve the tree layer. However, global warming has caused an increase in the proportion of broad-leaved trees, while human activity in the forest, such as tourism and the collecting of pine nuts, has disturbed the understory plants and the succession layer of trees. The goal of our study was to provide guiding principles for the preservation of biodiversity (Hill and Curran 2001). Regulations and policies for conservation should be strengthened in the interest of reversing the deteriorating trends in the forest communities of the CNR.

Due to the limits of the 1963 survey, we were not able to cover the higher vegetation zones of the birch forest and tundra zone. These two tree line ecotones should show close relationships with environmental variation (Moiseev and Shiyatov 2003). Thus, incomplete sampling may result in some spurious diversity patterns (Lomolino 2001; Bhattarai et al. 2004) and make it difficult to confirm the shift to higher altitudes of the plant life in those zones. However, we have made some inferences as to what may happen and have proposed a number of issues that should be studied in future investigations.

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References

Anderson JE, Inouye RS (2001) Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol Monogr 71(4):531–556

Begon M, Harper JL, Townsend CR (1996) Ecology: individuals populations and communities. Blackwell Scientific, Oxford

Bergman E, Ackerman JD, Thompson J, Zimmerman JK (2006) Land-use history affects the distribution of the saprophytic Orchid *Wullschlaegelia calcarata* in Puerto Rico's Tabonuco Forest. Biotropica 38(4):492–499. doi:10.1111/j.1744-7429.2006.00167.x

Bhattarai KR, Vetaas OR, Grytnes JA (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. J Biogeogr 31:389–400

Buker A (2003) Inselbergs in a changing world-global trend. Divers Distrib 9:375–385. doi:10.1046/j.1472-4642.2003.00035.x

Carey C, Alexander MA (2003) Climate change and amphibian decline: is there a link? Divers Distrib 9:111–121. doi:10.1046/j.1472-4642.2003.00011.x

Chao A, Chazdon RL, Colwell RK, Shen T-J (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol Lett 8:148–159. doi:10.1111/j.1461-0248.2004.00707.x

Chapin S III, Matson PA et al (2002) Principles of terrestrial ecosystem ecology. Springer, New York

Chapman RA, Heitzman E, Shelton MGD (2006) Long-term change in forest structure and species composition of an upland oak forest in Arkansas. For Ecol Manage 236:85–92. doi:10.1016/j.foreco.2006.08.341

Chen LZ (1963) Study on the structure of *Picea jezoensis* forest on the western slope of Changbai Mountains. Acta Phytoecol Geobot Sin 1(1–2):69–80

Chen LZ, Wang ZW (1999) The impact of human alteration on ecosystem diversity principles. Zhejiang Science and Technology Press, Zhejiang

Chen LZ, Bao XC et al (1964) Major forests in various vertical zones on northern slope of Changbai Mountains of Jilin Province. Acta Phytoecol Geobot Sin 2(2):207–225

Chen XW, Li BL (2004) Tree diversity change in remaining primary mixed-broadleaved Korean pine forest under climate change and human activities. Biodivers Conserv 13:563–577. doi:10.1023/B:BIOC.0000009490.57334.0a

Chi ZW, Zhang FS, Li XY (1981) Preliminary analysis on the climate of the Changbai Mountain area. Res For Ecosyst 2:179–186

Clark DA (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. Ecol Appl 12(1):3–7. doi:10.1890/1051-0761(2002)012[0003:ATFAIC]2.0.CO;2

Colwell RK, Lees DC (2000) The mid-domain effect: geometric constrains on the geography of species richness. Trends Ecol Evol 15:70–76. doi:10.1016/S0169-5347(99)01767-X

Defries R, Hansen A, Newton A, Hansen M (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. Ecol Appl 15(1):19–26. doi:10.1890/03-5258

Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land on forest land use on forest soils and biodiversity. Ecology 83(11):2978–2984

Fang JY, Wang ZH, Zhao SQ, Li YK, Yu D, Ni LY, Liu HZ, Da LJ, Tang ZY, Zheng CY (2006) Biodiversity changes in the lakes of the Central Yangtze. Front Ecol Environ 4(7):369–377. doi:10.1890/1540-9295(2006)004[0369:BCITLO]2.0.CO;2

Fosaa AM (2004) Biodiversity pattern of vascular plant species in mountain vegetation in the Faroe Islands. Divers Distrib 10(3):217–223. doi:10.1111/j.1366-9516.2004.00080.x

Freestone AL, Inouye BD (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. Ecology 87(10):2425–2432. doi:10.1890/0012-9658(2006)87[2425:DLAEHS]2.0.CO;2

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature 369:448. doi:10.1038/369448a0

Halpin PN (1997) Global climate change and natural-area protection: management responses and research directions. Ecol Appl 7(3):828–843. doi:10.1890/1051-0761(1997)007[0828:GCCANA]2.0.CO;2

Hao ZQ (2000) Analysis of plant community diversity and their gradient patterns on the northern slope of Changbai Mountain, Northeast China. PhD thesis. Chinese Academy of Sciences, P.R. China

Harborne AR, Mumby PJ, Hedley JD, Zychaluk K, Blackwell PG (2006) Modeling the beta diversity of coral reefs. Ecology 87(11):2871–2881. doi:10.1890/0012-9658(2006)87[2871:MTBDOC]2.0.CO;2

He JS, Chen WL (1997) A review of gradient changes in species diversity of land plant communities. Acta Ecol Sin 17(1):91–99

Heegaard E (2004) Trends in aquatic macrophyte species turnover in Northern Ireland—which factors determine the spatial distribution of local species turnover? Glob Ecol Biogeogr 13:97–408. doi:10.1111/j.1466-822X.2004.00119.x

Hill JL, Curran PJ (2001) Species composition in fragmented forests: conservation implications of changing forest area. Appl Geogr 21:157–174. doi:10.1016/S0143-6228(01)00002-9

Hooper DU, Chapin FSIII, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, SetÄlÄ H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75(1):3–35. doi:10.1890/04-0922

Huston MA (2005) The three phases of land-use change: implications for biodiversity. Ecol Appl 15(6):1864–1878. doi:10.1890/03-5281

Jin YH, Li DQ et al (2005) Quantitative dynamics on natural regeneration of secondary forest during the restoration period in Changbai Mountain area. Natural Sciences Edition. J Nanjing For Univ 29(5):65–68

Klanderud K, Totland Ø (2005) Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology 86(8):2047–2054. doi:10.1890/04-1563

Körner C (2000) Why are there global gradients in species richness? Mountains might hold the answer. Trends Ecol Evol 15:513–514. doi:10.1016/S0169-5347(00)02004-8

Lertzman KP (1992) Patterns of gap-phase replacement in a subalpine, old-growth forest. Ecology 73:657–669. doi:10.2307/1940772

Li J, Gong Q et al (2005) Climatic features of summer temperature in northeast China under warming background. Chin Geogr Sci 15(4):337–342. doi:10.1007/s11769-005-0022-x

Li XB, Wang XP et al (2006) Influence of human disturbance on community structure and tree species diversity of secondary forest on northern slope of Mt. Changbai. Sci Silae Sin 42(2):105–110

Liu QJ (1997) Structure and dynamics of the subalpine coniferous forest on Changbai Mountain, China. Plant Ecol 132:97–105. doi:10.1023/A:1009705319128

Liu QJ, Li XR et al (2005) Monitoring forest dynamics using satellite imagery-a case study in the natural reserve of Changbai Mountain in China. For Ecol Manage 210:25–37. doi:10.1016/j.foreco.2005.02.025

Lomolino MV (2001) Elevation gradients of species-density: historical and prospective views. Glob Ecol Biogeogr 10:3–13. doi:10.1046/j.1466-822x.2001.00229.x

Lopes Valle de Britto Rangel TF, Felizola Diniz-Filho JA (2003) Spatial patterns in species richness and the geometric constraint simulation model: a global analysis of mid-domain effect in Falconiformes. Ecologica 24(4); 203–207

Ma KP (1994) The measurement of community diversity. I: The measurement of α diversity. Chin Biodivers 2(3): 162–168

Ma KP, Liu YM (1994) The measurement of community diversity. II: The measurement of α diversity. Chin Biodivers 2(4):231–239

Ma KP, Huang JH et al (1995) Plant community diversity in Dongling Mountain, Beijing, China. II. Species richness, evenness, and species diversities. Acta Ecol Sin 15:268–277

MacArthur RH (1972) Geographical ecology. Harper and Row, New York

Miles J, French DD, Xu Z (1983) The primary researcher on the forest succession status of mixed conifer and broadleaved forest in north slop of Changbai Mountain. Res Forest Ecosyst 3:54–72.

Mitchell RJ, Zutter BR, Gjerstad DH, Glover GR, Wood CW (1999) Competition among secondary–successional pine communities: A field study of effects and responses. Ecology 80(3):857–872

Moiseev PA, Shiyatov SG (2003) The use of old landscape photographs for studying vegetation dynamics at the treeline ecotone in the Ural Highlands, Russia. In: Nagy L, Grabherr G, KÖrner C, Thompson DBA (eds) Alpine biodiversity in Europe. Springer, Berlin, pp 423–436

Mouillot D, Titeux A, Migon C, Sandroni V, Frodello, JP, Viale D (2000) Anthropogenic influences on a Mediterranean Nature Reserve: modelling and forecasting. Environ Model Assess 5:185–192. doi:10.1023/A:1011533811237

Nogués-Bravo D, Araújo MB, Martinez-Rica JP, Errea MP (2007) Exposure of global mountain systems to climate warming during the 21st Century. Glob Environ Change 11(7):420–428

Ohl C, Krauze K, Grünbühel C (2007) Towards an understanding of long-term ecosystem dynamics by merging socio-economic and environmental research Criteria for long-term socio-ecological research sites selection. Ecol Econ 63:383–391. doi:10.1016/j.ecolecon.2007.03.014

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669. doi:10.1146/annurev.ecolsys.37.091305.110100

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. doi:10.1038/nature01286

Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. Glob Change Biol 13:147–156. doi:10.1111/j.1365-2486.2006.01282.x

Pearman PB, Weber D (2007) Common species determine richness patterns in biodiversity indicator taxa. Biol Conserv 138:109–119. doi:10.1016/j.biocon.2007.04.005

Phillips OL, Malhi Y, Higuchi N, Laurance WF, Nunez PV et al (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282:439–442. doi:10.1126/science.282.5388.439

Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171. doi:10.1126/science.235.4785.167

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60. doi:10.1038/nature01333

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Scott JM, Davis FW, McGhie G, Wright RG (2001) Nature reserves: Do they capture the full rang of American's biological diversity? Ecol Appl 11(4):999–1007. doi:10.1890/1051-0761(2001)011[0999:NRDTCT]2.0.CO;2

Shang YC (2002) Ordinary ecology. Beijing University Press, Beijing

Shao B (1999) Specie diversity in the sub alpine spruce-fir forest community on the north slope of MT. Changbai. Acta Phytoecol Sin 23[Suppl]:47–57

Stone R (2006) A threatened nature reserve breaks down Asian borders. Science 313:1379–1380. doi:10.1126/science.313.5792.1379

Stromberg JC (2007) Seasonal reversals of upland-riparian diversity gradients in the Sonoran Desert. Divers Distrib 13:70–83

Tao Y (1994) Revolution and succession trends of forest vegetation in Changbai Mountain. Res For Ecosyst 7:173–184

Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Divers Distrib 12:49–60. doi:10.1111/j.1366-9516.2006.00216.x

Vázquez GJA, Givnish TJ (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. J Ecol 86:999–1020. doi:10.1046/j.1365-2745.1998.00325.x

Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC et al (2002) Ecological responses to recent climate change. Nature 416:389–395. doi:10.1038/416389a

Wang Z, Xu ZB, Li X, Peng DS, Tan ZX (1980) The main forest type and their structure characteristics (I). Res For Ecosyst 1:25–42

Whitmore TC (1998) Potential impact of climatic change on tropical rain forest seedlings and forest regeneration. Clim Change 39:429–438. doi:10.1023/A:1005356906898

Wilson MV, Shmidam A (1984) Measuring beta diversity with presence–absence data. J Ecol 72:1055–1064. doi:10.2307/2259551

Wu YG, Han JX (1992) The analysis of community structure and nature succession pattern of Korea pine. Res For Ecosyst 6:14–23

Wu ZY (1980) The vegetation of China. Science and Technology Press, Beijing

Yang X, Xu M (2003) Biodiversity conservation in Changbai Mountain biosphere reserve, northeastern China: status, problem, and strategy. Biodivers Conserv 12:883–903. doi:10.1023/A:1022841107685

Zhang SY (1983) Study on succession pattern of secondary forest in Changbai Mountain. Res For Ecosyst 3:44–53

Zhang YP, Guo XF et al (1994) Study on tree dynamics of shrub-broadleaved Korean Pine Forest in Changbai Mountain. Res For Ecosyst 7:48–53

Zhao SQ, Fang JY et al (2004) Composition, structure and species diversity of plant communities along an altitudinal gradient on the northern slope of Mt. Changbai, Northeast China. Chin Biodivers 12(1):164–173

Zhou YL, Li SY (1990) Forests of China. Science Press, Beijing

Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA

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Abstract Disturbance regimes in many temperate, old growth forests are characterized by gap-scale events. However, prior to a complex stage of development, canopy gaps may still serve as mechanisms for canopy tree replacement and stand structural changes associated with older forests. We investigated 40 canopy gaps in secondary hardwood stands on the Cumberland Plateau in Tennessee to analyze gap-scale disturbance processes in developing forests. Gap origin, age, land fraction, size, shape, orientation, and gap maker characteristics were documented to investigate gap formation mechanisms and physical gap attributes. We also quantified density and diversity within gaps, gap closure, and gap-phase replacement to examine the influence of localized disturbances on forest development. The majority of canopy gaps were single-treefall events caused by uprooted or snapped stems. The fraction of the forest in canopy gaps was within the range reported from old growth remnants throughout the region. However, gap size was smaller in the developing stands, indicating that secondary forests contain a higher density of smaller gaps. The majority of canopy gaps were projected to close by lateral crown expansion rather than height growth of subcanopy individuals. However, canopy gaps still provided a means for understory trees to recruit to larger size classes. This process may allow overtopped trees to reach intermediate positions, and eventually the canopy, after future disturbance events. Over half of the trees located in true gaps with intermediate crown classifications were *Acer saccharum*, *A. rubrum*, or *Liriodendron tulipifera*. Because the gaps were relatively small and close by lateral branch growth of perimeter trees, the most shade-tolerant *A. saccharum* has the greatest probability of becoming dominant in the canopy under the current disturbance regime. Half of the gap maker trees removed from the canopy were *Quercus*; however, *Acer* species are the most probable replacement trees. These data indicate that canopy gaps are important drivers of forest change prior to a complex stage of development. Even in relatively young forests, gaps provide the mechanisms for stands to develop a complex structure, and may be used to explain patterns of shifting species composition in secondary forests of eastern North America.

Keywords Canopy gaps · Disturbance · Forest development · Mixed hardwoods · Succession · Tennessee

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Introduction

All forest ecosystems are subject to natural disturbance events that shape species composition and stand structure. In many forest types, gap-scale disturbance processes are the dominant disturbance mechanisms. Thus, canopy gap characteristics and forest response have been studied in forests throughout eastern North America to elucidate patterns, and processes of gap-scale disturbances and forest vegetation dynamics. The overwhelming majority of canopy gap studies, however, have been conducted in old growth remnants (e.g., Lorimer 1980; Barden 1981; Runkle 1982; Cho and Boerner 1991; Runkle 2000). Throughout the Eastern Deciduous Forest Region, most forested land supports secondary stands (secondary referring to all non-primeval forests prior to a complex stage of development) composed of mixed hardwood species (Cowell 1998; Rebertus and Meier 2001). Few studies have analyzed gap-scale disturbances and forest response in secondary forests (but see Clebsch and Busing 1989; Dahir and Lorimer 1996; Wilder et al. 1999; Yamamoto and Nishimura 1999), and no such research has been conducted in mixed hardwood stands on the Cumberland Plateau.

Undoubtedly, forest disturbance dynamics differ between old growth remnants and mature secondary stands. Differences in disturbance characteristics are attributed to variations in species composition, biomass arrangement, and tree-age distribution. As forests mature, the distance between large individuals increases. Tree crowns separate into distinct categories, creating a more complex vertical structure, and species composition shifts to favor later-successional species (Goebel and Hix 1996; Oliver and Larson 1996; Goebel and Hix 1997). Forest response to disturbance events likely differs between old growth and secondary stands, because of differences in stand structure and species composition, and also because of the ages of the oldest trees, as older trees are less able to respond to increase in available resources resulting from disturbance events (Fritts 2001).

In old growth forests, the spacing between large individuals is greater than in secondary forests. Thus, when a canopy tree is removed from an old growth stand, the size of the canopy gap created should be larger than a comparable disturbance during earlier stages of forest development (Clebsch and Busing 1989; Spies et al. 1990; Tyrell and Crow 1994; Runkle 1998; Yamamoto and Nishimura 1999). Because canopy gaps are generally larger in old growth remnants, many of the gaps in these forests close by the height growth of subcanopy individuals rather than lateral crown expansion of perimeter trees (Runkle 1982). This gap-replacement process creates forests with complex age and size structures, and patchy species composition in the canopy (Lorimer 1980; Runkle 1982; Yetter and Runkle 1986; Runkle and Yetter 1987). Although canopy gaps in secondary forests are hypothesized to be smaller in size, they may still act as a mechanism for canopy tree replacement, and stand structural changes associated with older forests (Clebsch and Busing 1989; Wilder et al. 1999; Taylor and Lorimer 2003; Cole and Lorimer 2005).

The overarching goal of our study was to document the influence of localized, natural disturbance events on the development of secondary hardwood stands during the understory reinitiation stage of development. Our research was driven by four major questions. *Question* 1: What are the patterns and processes of canopy gap formation prior to a complex stage of forest development? We hypothesized that most canopy gaps would be created by uprooted stems, as windthrow has been widely reported from many old growth stands and visual observation of the forest revealed uprooted trees. *Question* 2: What percentage of the forest is occupied by canopy gaps and what are the shape, size, and age distributions for gaps in developing stands? We hypothesized that the land fraction of the forest in gaps would be within the range of variability reported from old growth stands, but the forest would contain a higher density of smaller gaps relative to older stands. *Question* 3: Do small canopy disturbances influence density and diversity patterns in secondary stands? We hypothesized that larger gaps would support a higher number of individuals as well as higher levels of diversity because they should contain more microsite heterogeneity, and the likelihood of documenting rare species should increase by sampling a larger spatial area. *Question* 4: How do the gaps close, and what effects do they have on composition and structure in developing stands? We hypothesized that most gaps would close by lateral crown expansion rather than height growth of subcanopy individuals and would cause the structure of the forest to move from a high density of small trees to a lower density of larger individuals, more typical of older stands.

Methods

Study area

The study was conducted in the Pogue Creek Natural Area (PCNA) located in Fentress County, Tennessee, in the north-central portion of the state (Fig. 1). The PCNA is a 1,505 ha reserve managed by the State of Tennessee, Department of Environment and Conservation, Division of Natural Areas. The PCNA is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The underlying geology consists of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked Groups (Smalley 1986). The area has irregular topography (Fenneman 1938) characterized by long, narrow to moderately broad ridges and narrow to moderately broad valleys (Smalley 1986). Soils are acidic, highly leached, and low in fertility (Francis and Loftus 1977; Smalley 1982; USDA 1995; Hart 2007). Depth to bedrock varies from 1 to 1.8 m and slope gradients range from 15% to 60%. The elevation of the study plots ranged from 260 to 490 m amsl.

Climate is classified as humid mesothermal with moderately hot summers and short-mild to moderately cold winters (Thornthwaite 1948). Local topography strongly influences microclimatic conditions. The average frost-free period is 160 days (from early-May to late-October) and the mean annual temperature is 13°C. The July average is 23°C and the January average is 2°C (USDA 1995). The area receives steady precipitation during the year with no distinct dry season. Mean annual precipitation is 137 cm and mean annual snowfall is 50 cm (USDA 1995). Late spring and summer are characterized by heavy rains that are often accompanied by moderate

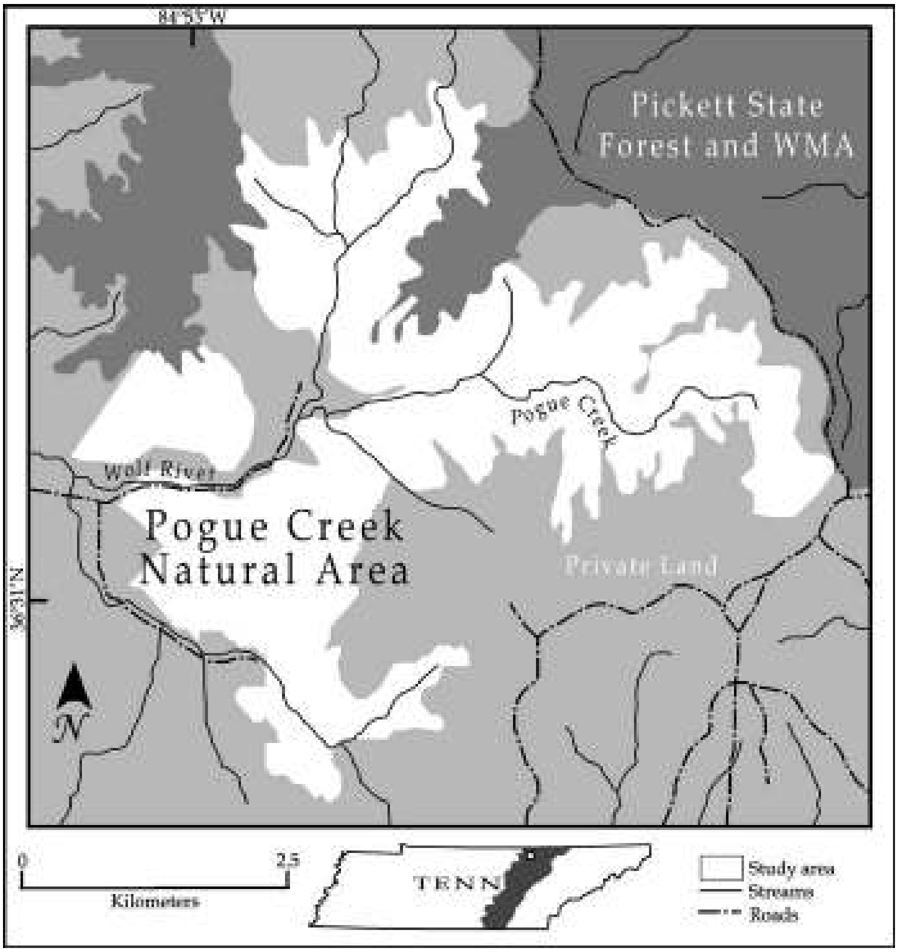

Fig. 1 Map of the Pogue Creek Natural Area, Fentress County, Tennessee. Shaded portion of the Tennessee inset map is the Cumberland Plateau physiographic section

to severe thunderstorms and strong winds (Smalley 1982).

Braun (1950) classified the area as part of the Cliff Section of the Mixed Mesophytic Forest Region, but local topography influences forest composition and true mesophytic species only dominate on protected sites. Regionally, forests are intermediate between mixed mesophytic and *Quercus–Carya* types (Hinkle 1978; Hinkle 1989; Hinkle et al. 1993). Forest vegetation patterns of the PCNA were quantified by Hart and Grissino-Mayer (2008). The forest was dominated by *Carya ovata*, *Quercus rubra*, *Q. alba*, and *Q. montana*. The sparse sapling layer was dominated by *Acer saccharum*. The forest was established in the late 1920s after the cessation of local logging operations. From field observations and investigation of 17 tree cross sections from a previous study, no signs of fire or other large-scale disturbance events were evident since the anthropogenic disturbances of the 1920s (Hart 2007). *Castanea dentata* Marsh was a forest component prior to the arrival of *Cryphonectria parasitica* (Murrill) M.E. Barr (chestnut blight). The blight reached the Cumberland Plateau in the 1920s, and by the end of the 1930s, most *C. dentata* in the region were dead. Thus, the loss of the species roughly coincided with stand initiation.

Field sampling

Canopy gaps ($n = 40$) were located along transects throughout the reserve using the line intersect method (Runkle 1982; Runkle 1985; Veblen 1985; Runkle 1992). Gaps were defined as environments where a visible void space existed in the main forest canopy, leaf height of the tallest stems was less than three-fourths the height of the adjacent canopy, and gap makers were present. We did not use a minimum gap size threshold to document the full range of canopy gaps. Transects were established parallel to slope contour beginning at randomly selected points throughout the forest. All transects were located along mid-slope positions. We sampled at mid-slope positions, because the mid-slope forests of the reserve are indicative of slope forests of the greater Cumberland Plateau region and the majority of forested land in the reserve occurs along mid-slopes. Total transect length and transect length in expanded (boundary defined by the base of surrounding canopy trees (Runkle 1981)) and true (area unrestricted from above) canopy gaps were documented by recording the number of paces across each. The fraction of land area in canopy gaps was calculated by dividing the transect distance in gaps by total transect length (Runkle 1985; Runkle 1992). At each gap, physical site characteristics, including percent slope, aspect, and elevation, were recorded . When walking transects through a forest, large gaps are more likely to be encountered than relatively small gaps, and sampling estimators have been created to correct for sampling bias (see De Vries 1974; Pickford and Hazard 1978). However, values obtained with the use of estimator equations and those obtained by simply dividing transect distance in gaps by total transect length are similar (Runkle 1985).

Gap area was determined for expanded and true gaps by, measuring length (largest distance from gap edge to gap edge) and width (largest distance perpendicular to the length). These measurements were fitted to the formula of an ellipse (Runkle 1985; Runkle 1992). Although gap shapes can be highly variable (Ferreira de Lima 2005), most gaps at the PCNA had elliptical shapes, which is common for forests of the southern Appalachian Highlands (Runkle 1982; Runkle 1992; Clinton et al. 1994). Thus, fitting the measurements to the formula of an ellipse was appropriate for this study.

Canopy gaps can be created by several different mechanisms that remove overstory trees. Biotic and abiotic forest conditions can be modified differently by canopy disturbances that are caused by different gap formation mechanisms. Differences between gap origins may also influence forest response. In order to analyze these patterns, gap formation mechanisms were classified into one of the three categories (snag, uprooted stem, or snapped stem) according to gap origin (Clinton et al. 1993). The number of trees involved in gap formation was also recorded to document the abundance of single-tree versus multi-tree events.

Gap maker trees were taxonomically classified to quantify any species-specific overstory mortality patterns and possible composition changes associated with small canopy disturbances. We measured gap maker diameter at breast height (dbh, ca. 1.4 m above the surface or root collar for downed individuals) and length. Basal area (m^2) was calculated for all gap makers that could be accurately measured and totaled by gap, to determine the amount of basal area lost per disturbance event. This information may be used to document the amount of biomass naturally removed from a stand through gap-scale processes. Direction of gap maker fall relative to slope (i.e., down, across, or up slope) was also recorded and all gap makers were placed into one of four decay classes (1–4, with 4 being the most decayed) following criteria adapted from McCarthy and Bailey (1994).

In each gap, we recorded species, crown class, and diameter of all trees ≥5 cm dbh to characterize forest gap vegetation. Crown class categories (dominant, codominant, intermediate, and overtopped) were visually assessed based on the amount and direction of intercepted light (Oliver and Larson 1996). The location of each of these individuals was also recorded as being in either an expanded or true canopy gap. All saplings (woody stems ≥1 m height, <5 cm dbh) in the expanded gap area were tallied by species to characterize gap regeneration patterns. The number of perimeter trees with dominant or codominant positions in the canopy was documented for each gap, to analyze the number of trees required to complete the canopy surrounding gaps, and the number of canopy individuals with the potential to close the void space through lateral crown expansion.

Tree core samples were collected to aid in the documentation of gap age. A minimum of nine trees were cored (mean = 18.6) per gap resulting in the collection of 742 cores. Tree core samples or cross sections were also collected from all gap makers that were not in an advanced state of decay (intact bark and no sapwood degradation), to aid with gap age determination and to document the seasonal timing of gap events, based on the amount of xylem produced during the last year of growth. Dating the seasonality of tree death and gap formation illustrates a new approach in dendroecology.

Data analyses

Tree core and cross section samples were prepared and processed for dating using the methods outlined in Stokes and Smiley (1996). The samples were air-dried, glued to wooden mounts, and sanded to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002) before tree rings were dated with the aid of a stereo zoom microscope. All tree cores were visually analyzed for radial growth releases to document gap age. In order to document gap maker death dates, tree rings were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all sampled gap makers. The measurement series were visually compared to a reference *Quercus* chronology developed by Hart and Grissino-Mayer (2008) for the site. We confirmed the graphical crossdating of all gap maker tree-ring series using the computer software COFECHA, a quality-control program that uses segmented time series correlation analyses to confirm the placements of all tree rings (Holmes 1983; Grissino-Mayer 2001). In COFECHA, we tested consecutive 50-year segments (with 25-year overlaps) on each undated gap maker series to the reference *Quercus* chronology. Once statistically confirmed, we assigned calendar years to all tree rings in each individual undated measurement series. All gap ages were confirmed using gap maker decay classifications.

Canopy gaps can be caused by the removal of a single tree or a small cluster of trees. Because single-tree gaps may result from the death of a large canopy tree and multi-tree gaps may result from the deaths of relatively small trees, the amount of basal area lost between single- and multi-tree gaps was statistically analyzed using a two-tailed *t*-test. This information may be useful to analyze the quantity of basal area lost by small canopy disturbance events and applied to harvesting techniques that may mimic natural disturbance processes.

The rate of gap formation and closure may be balanced or may vary through time. Non-parametric correlation techniques were used to analyze the relationship between land fraction in gaps and gap age. Gaps may be caused by a variety of formation mechanisms that differ in the way overstory vegetation is removed, and the mechanism of canopy tree removal may influence gap size. In order to determine, if a relationship existed between gap size and gap origin, data were analyzed using a one-way ANOVA. A Tukey honestly significant difference (HSD) test was used to compare mean expanded and true gap sizes across origin categories to determine if gap size varied by gap formation mechanism.

Length and width of gaps were measured in the field. Ratios were calculated for length to width (L:W) of expanded and true gaps to document gap shape characteristics. This information is useful to understand the variation in the shape of gaps created by the disturbance and has implications for forest response and microenvironmental changes within the gap environment.

For each gap, density and diversity (H') measures were calculated for saplings, trees, and total stems (all woody stems $\geq$1 m height) to document forest response to canopy disturbances. Gap size is believed to influence stem density and diversity. Correlation coefficients were calculated to determine if a relationship existed between gap size and density of individuals in gaps. Regression techniques were then used to model gap size and density relationships. In order to analyze the relationship between expanded gap area and diversity patterns, correlation coefficients were calculated for sapling, tree, and total stem diversity.

Canopy gaps can close by crown expansion of perimeter trees at canopy level or by the height growth of understory individuals. The likely closure mechanism, either by height growth or lateral crown expansion, of each gap was recorded in the field to document changes in forest structure following the removal of canopy trees. Probable gap successors, which are the individuals that will likely fill the canopy void, can often be determined in the field (Barden 1979; Barden 1980; White et al. 1985; Yamamoto and Nishimura 1999). The documentation of replacement trees is useful to project the future composition of the stand and to analyze the influence of canopy gaps on forest succession. In order to quantify recruitment following overstory removal, crown class distributions were constructed for all trees located in true gap environments for the 15 most dominant species with canopy potential. These measures may be used to document future canopy trees and recruitment patterns associated with gap-scale disturbance processes.

Results

Gap formation patterns and processes

Of the 40 gaps sampled, 8 (20%) were created by snags, 16 (40%) were created by uprooted stems, and 16 (40%) were created by snapped stems. Eventually, snag trees will fall, generally during mild to severe wind events, possibly causing further disturbance to the forest. It is possible that a gap created by a snag, subsequently blown down, was classified incorrectly. However, measures were taken to avoid this issue, such as documenting the decay class of gap makers and noting the position of the gap maker relative to other downed logs. The number of gap maker trees involved with opening the canopy ranged from one to four. The majority (78%) of the canopy gaps involved the death of only one individual. Of the nine multi-tree gaps, six (66%) resulted from uprooted stems including the gap that consisted of the removal of four canopy individuals, while the three other multi-tree gaps resulted from snapped boles.

We identified 50 gap maker trees in the 40 canopy gaps studied. Most gap makers ($n = 36$, 72%) could be identified to the species level; however, 4 (8%) could only be identified to genus and 10 (20%) were too decayed to be taxonomically classified. Of the 36 gap makers that could be identified to species, 12 different species were represented. The most common species that caused canopy gap formation was *Quercus montana* ($n = 8$). At the genus level, 50% of all gap makers were *Quercus*.

Diameter was measured at ca. 1.4 m above the surface or root collar for 46 gap makers. Diameter measurements could not be collected for four gap makers that were in a state of advanced decay. Average gap maker diameter at breast height was 38.38 cm ± 11.6 (SD). The minimum diameter of a gapmaker was 19.5 cm and the maximum was 70 cm. The gap maker with a diameter of 19.5 cm was involved in a multi-tree uprooting event that also included the death of an individual with a diameter of 28 cm. Average basal area lost per gap was 0.16 $\text{m}^2 \pm 0.10$ (SD). The minimum removed was 0.05 m^2 and the maximum was 0.52 m^2. Multi-tree gaps (mean $= 0.24\ \text{m}^2 \pm 0.13$ (SD)) resulted in a larger amount ($P < 0.01$) of basal area lost compared to single-tree events (mean $= 0.14\ \text{m}^2 \pm 0.08$ (SD)).

Age was determined for all canopy gaps by the identification of radial growth releases, crossdating the gap makers to document death dates, field observation, and gap maker decay classification. Gap ages ranged from 1 to 17 years with a mean of 7 years. Multiple gaps occurred in 13 years. The highest frequency of gap events during any one year was five, which occurred during 3 years (1999, 2002, and 2003).

Gap seasonality was determined for 17 gaps by examining the amount of xylem produced during the last year of growth. Other gapmakers were too decayed for this analysis. Of these 17 events, only one occurred during the dormant season. For the dormant season gap, the latewood portion of the last ring was complete and buds were still present on the tree. All other gap makers had partial rings, indicating that the gap events occurred during the growing season. Because the majority of these individuals had already completed the production of earlywood prior to death, we surmise that these events occurred in the middle or later part of the growing season.

Gap fraction and physical characteristics

Total transect length was 4.47 km, with 15% of the total length in expanded gaps and true gaps, and 6% in true canopy gaps only. When percentage values were standardized at the hectare level, 1,500 m^2/ha were in expanded gaps and 600 m^2/ha were in true gap environments. Total transect length in true canopy gaps was plotted by gap age to analyze patterns of gap formation and closure (Fig. 2). The largest amount of land area in true canopy gaps occurred in gaps that were 2 years of age and no gap area occurred in gaps aged 5, 6, 14, 15, or 16 years. A significant negative relationship existed, where older gaps occupied a smaller amount of land area relative to younger gaps.

Average expanded gap area was 213.34 $m^2 \pm$ 108.44 (SD). The maximum expanded gap area was 587.91 m^2 and the minimum was 47.10 m^2. Average true gap area when sampled was 42.78 $m^2 \pm$ 40.16 (SD), with a maximum of 157.84 m^2 and a minimum of 1.14 m^2. The size of expanded gaps created by uprooted stems was significantly larger than that of gaps created by snags (Fig. 3). No other size differences between gap origins were significant.

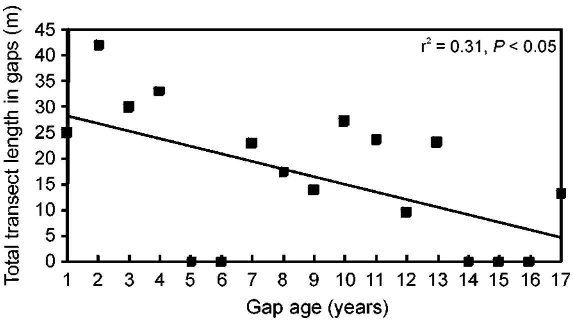

Fig. 2 Relationship between land fraction in true canopy gaps and gap age in the Pogue Creek Natural Area in Tennessee

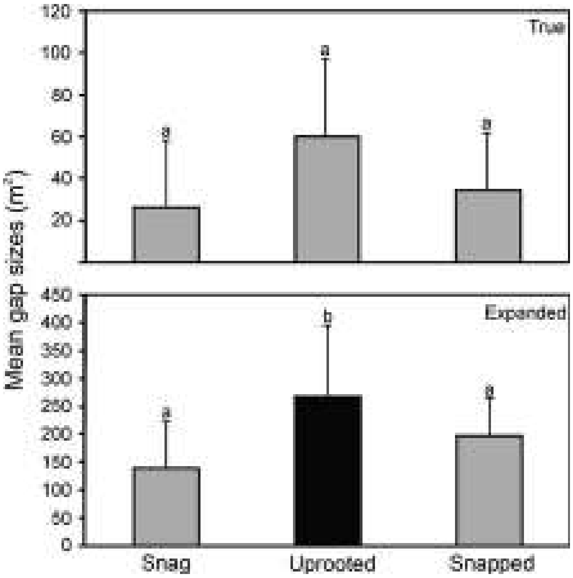

Fig. 3 Mean sizes of expanded and true canopy gaps by gap origin with standard deviations. Solid bar and different letter indicate a significant ($P < 0.05$) difference between gap origins as detected by ANOVA and Tukey's post-hoc testing

The average L:W ratio of expanded gaps was 1.58:1, with a maximum of 3.60:1 and a minimum of 1.01:1. Thus, the average expanded gap was 58% longer than it was wide. Similar patterns were observed for true gap areas, for which the mean ratio was 2.58:1. The maximum length of true gaps was 475% the width. The minimum L:W patterns of expanded and true gaps revealed circular over ellipsoidal shapes.

Density and diversity within gaps

The mean number of canopy trees that bordered gaps was 6.38 ± 1.79 (SD). The maximum number of perimeter trees was 12, and minimum number of trees required to complete the canopy around a gap was 4. In general, larger canopy gaps were bordered by a higher number of canopy trees relative to smaller gaps.

The average number of saplings in expanded gaps was 54.48 ± 28.47 (SD) with a maximum of 144 and a minimum of 13 (Fig. 4). The mean number of trees in expanded gaps was 22.73 ± 7.99 (SD) with a maximum of 44 and minimum of 11 individuals. The average number of all stems $\geq$1 m height in expanded gaps was 74.20 ± 34.14 (SD). The highest number of stems in an expanded gap was 188 and the

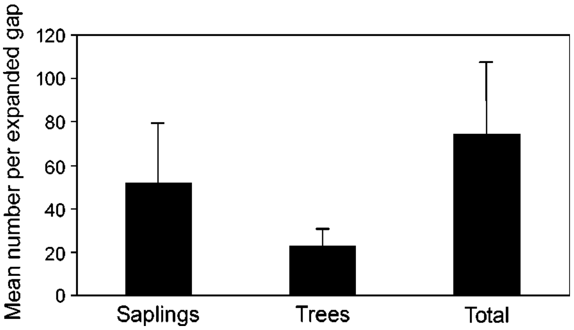

Fig. 4 Mean number of saplings (≥1 m height, <5 cm dbh), trees (≥5 cm dbh), and total stems (all stems ≥1 m height) with standard deviations in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee

lowest number of individuals was 28. The highest values for saplings and trees occurred in the same gap that was 10 years old and caused by the uprooting of four trees.

The sum of all saplings in all expanded gaps was calculated by species and standardized at the hectare level to document sapling establishment, and possible species recruitment in gap environments. The most abundant species in the sapling layer of expanded gaps was *Acer saccharum* followed by *Fagus grandifolia* and *Acer rubrum* (Table 1). Together these three species comprised almost 69% of all saplings in expanded gaps.

Acer saccharum represented 29.18% of all trees in true canopy gaps followed by *A. rubrum* and *Liriodendron tulipifera* (Table 2). Collectively, these three species represent over half of all trees in true canopy gaps. Dominance (based on basal area) was also calculated for all canopy gap trees. The most dominant species were *A. saccharum* and *A. rubrum* (Table 2). The *Acer* species were followed by a second tier of species that included *L. tulipifera* and *Carya ovata*. No other species represented more than 6% of the basal area. Species and diameter of all snags in true canopy gaps were also recorded. A total of 40 snags were documented and mean snag diameter at breast height was 10.89 cm ± 6.21 (SD). Of the 40 snags within true gaps, 12 different species were represented with *A. rubrum*, *A. saccharum* and *Q. montana* being the most common ($n = 8$ for all species).

Table 1 Density of saplings (≥1 m height, <5 cm dbh) in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee

Species	Density/ha	Relative density
Acer saccharum Marsh.	863.63	35.70
Fagus grandifolia Ehrh.	474.70	19.62
Acer rubrum L.	327.83	13.55
Asimina triloba (L.) Dunal	168.03	6.95
Magnolia acuminata (L.) L.	158.63	6.56
Fraxinus americana L.	88.13	3.64
Liriodendron tulipifera L.	49.35	2.04
Oxydendrum arboreum (L.) DC.	48.18	1.99
Cornus florida L.	37.60	1.55
Ulmus rubra Muhl.	31.73	1.31
Nyssa sylvatica Marsh.	30.55	1.26
Cercis canadensis L.	29.38	1.21
Tilia heterophylla Vent.	12.93	0.53
Aesculus flava Ait.	11.75	0.49
Carpinus caroliniana Walt.	8.23	0.34
Ilex opaca Ait.	8.23	0.34
Magnolia tripetala L.	8.23	0.34
Quercus montana Willd.	8.23	0.34
Carya ovata (P. Mill.) K. Koch	5.88	0.24
Ostrya virginiana (P. Mill.) K. Koch	5.88	0.24
Sassafras albidum (Nutt.) Nees	5.88	0.24
Ailanthus altissima (Mill.) Swingle	4.70	0.19
Betula lenta L.	4.70	0.19
Diospyros virginiana L.	4.70	0.19
Quercus alba L.	4.70	0.19
Ulmus alata Michx.	3.53	0.15
Amelanchier laevis Weig.	2.35	0.10
Carya tomentosa (Poiret) Nutt.	2.35	0.10
Quercus rubra L.	2.35	0.10
Ulmus americana L.	2.35	0.10
Hamamelis virginiana L.	1.18	0.05
Magnolia macrophylla Michx.	1.18	0.05
Morus rubra L.	1.18	0.05
Quercus velutina Lam.	1.18	0.05
Total	2419.33	100.00

Expanded canopy gaps contained 34 different species in the sapling layer. Mean sapling diversity (H') was 1.43 ± 0.42 (SD) (Fig. 5). Maximum sapling layer diversity was 2.22 and the minimum was 0.78. Total species richness of the tree layer was 28. Average diversity of all trees in expanded gaps was 1.90 ± 0.35 (SD) with maximum and minimum values of 2.44 and 1.20, respectively. Mean total diversity of all stems ≥1 m height was 1.95 ± 0.36

Table 2 Density and dominance measures for all trees (stems ≥5 cm dbh) in true canopy gaps in the Pogue Creek Natural Area in Tennessee

Species	Density/ha	Relative density	Dominance (m^2/ha)	Relative dominance
Acer saccharum	807.30	29.18	0.59	24.34
Acer rubrum	391.95	14.16	0.32	13.15
Liriodendron tulipifera	251.55	9.09	0.23	9.37
Carya ovata	146.25	5.29	0.21	8.68
Oxydendrum arboreum	146.25	5.29	0.14	5.91
Fagus grandifolia	175.50	6.34	0.13	5.48
Tilia heterophylla	122.85	4.44	0.10	4.15
Carya tomentosa	81.90	2.96	0.09	3.58
Carya glabra (P. Mill.) Sweet	64.35	2.33	0.08	3.38
Nyssa sylvatica	99.45	3.59	0.08	3.25
Fraxinus americana	70.20	2.54	0.07	2.95
Quercus alba	5.85	0.21	0.07	2.85
Cornus florida	111.15	4.02	0.06	2.59
Quercus montana	40.95	1.48	0.05	1.94
Magnolia acuminata	52.65	1.90	0.03	1.44
Quercus rubra	23.40	0.85	0.03	1.40
Ulmus rubra	40.95	1.48	0.03	1.16
Cercis canadensis	35.10	1.27	0.02	0.89
Carya cordiformis (Wangenh.) K. Koch	17.55	0.63	0.02	0.67
Ostrya virginiana	23.40	0.85	0.02	0.66
Diospyros virginiana	11.70	0.42	0.01	0.51
Sassafras albidum	11.70	0.42	0.01	0.49
Prunus serotina Ehrh.	5.85	0.21	0.01	0.31
Aesculus flava	5.85	0.21	0.01	0.25
Ulmus alata	5.85	0.21	0.00	0.21
Betula lenta	5.85	0.21	0.00	0.17
Magnolia tripetala	5.85	0.21	0.00	0.13
Ulmus americana	5.85	0.21	0.00	0.10
Total	2767.05	100.00	2.41	100.00

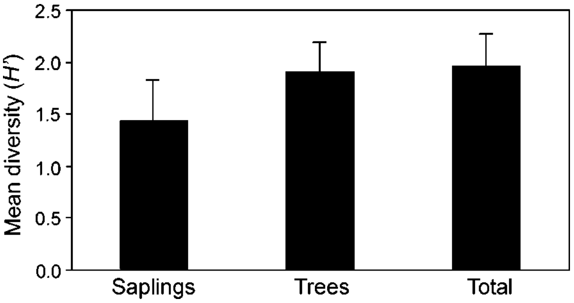

Fig. 5 Mean diversity for saplings (≥1 m height, <5 cm dbh), trees (≥5 cm dbh), and total stems (all stems ≥1 m height) with standard deviations in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee

(SD). The highest total diversity value was 2.46 and the lowest was 1.17. Interestingly, diversity patterns differed by category (i.e., sapling, tree, and total). For example, the gap with the lowest sapling diversity was not the same gap with the lowest tree diversity. However, the gap with the highest sapling and highest total woody stem diversity values was an exception.

Significant positive relationships were found for the number of saplings ($r = 0.54$, $P = 0.0003$), trees ($r = 0.73$, $P < 0.0001$), and total stems ($r = 0.62$, $P < 0.0001$) (Fig. 6). However, the largest gap did not contain the highest number of stems, which

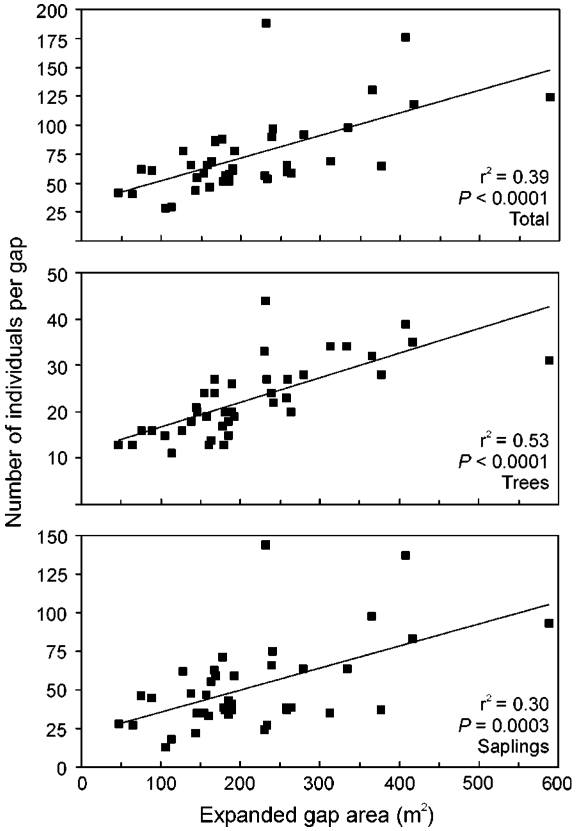

Fig. 6 Relationships between the number of saplings (≥1 m height, <5 cm dbh), trees (≥5 cm dbh), and total stems (all stems ≥1 m height) and expanded gap area in the Pogue Creek Natural Area in Tennessee

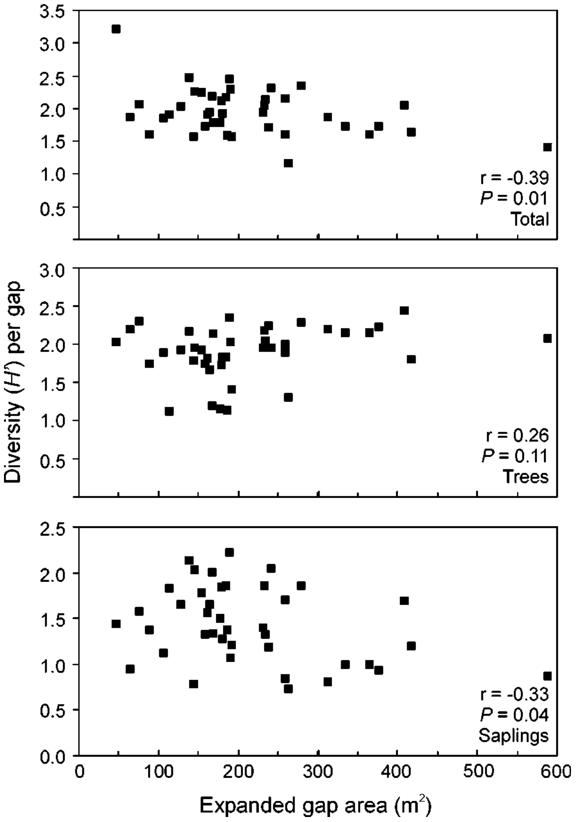

Fig. 7 Relationships between diversity values for saplings (≥1 m height, <5 cm dbh), trees (≥5 cm dbh), and total stems (all stems ≥1 m height) and expanded gap area in the Pogue Creek Natural Area in Tennessee

occurred in a gap of an intermediate size class (188 individuals/231.97 m^2). A weak negative relationship existed between sapling diversity and gap size ($r = -0.33$, $P = 0.04$) (Fig. 7). A similar pattern was also observed for total stem diversity ($r = -0.39$, $P = 0.01$). Tree diversity showed no relationship to expanded gap size. Shannon diversity (H') is a dimensionless index such that gap size would not bias the diversity measure.

Gap closure and recruitment

Of the 40 gaps studied, 10 were projected to close by height growth of understory individuals and the remaining 30 gaps were projected to close by lateral branch growth of canopy trees surrounding the voids. Mean expanded area of gaps likely to close via the height growth of understory trees was 285.13 m^2 ± 137.58 (SD), which was ca. 34% greater than the mean expanded area for all 40 gaps (213.34 m^2). The gap with the largest expanded area (587.91 m^2) was projected to close by understory height growth. However, a relatively small gap (153.59 m^2) was also projected to close by height growth of a subcanopy individual.

Of the 10 successor trees documented, five species were represented (*A. saccharum*, *A. rubrum*, *C. ovata*, *Q. montana*, and *Quercus alba*). *Acer rubrum* was the most common gap successor ($n = 3$) followed by *A. saccharum* ($n = 2$), *C. ovata* ($n = 2$), *Q. montana* ($n = 2$), and *Q. alba* ($n = 1$). *Acer saccharum* represented 28.7% of trees with intermediate positions of all 15 selected species within true gap environments (Table 3). *Acer saccharum* was followed by *A. rubrum* (13.45%) and *L. tulipifera* (13.45%), a noted gap-phase species. Collectively, these three species represented 55.6% of the intermediate trees from the 15 selected species. A similar

Table 3 Crown class distributions for all trees (stems ≥5 cm dbh) in 40 true canopy gaps in the Pogue Creek Natural Area in Tennessee

Species	Overtopped		Intermediate	
	Density	Relative density	Density	Relative density
Acer saccharum	72	36.36	64	28.70
Acer rubrum	37	18.69	30	13.45
Liriodendron tulipifera	13	6.57	30	13.45
Carya ovata	4	2.02	21	9.42
Tilia heterophylla	11	5.56	10	4.48
Oxydendrum arboreum	16	8.08	9	4.04
Fraxinus americana	3	1.52	9	4.04
Carya glabra	1	0.51	9	4.04
Fagus grandifolia	21	10.61	8	3.59
Carya tomentosa	5	2.53	8	3.59
Quercus alba	1	0.51	8	3.59
Quercus montana	1	0.51	6	2.69
Nyssa sylvatica	12	6.06	5	2.24
Quercus rubra	0	0.00	4	1.79
Carya cordiformis	1	0.51	2	0.90
Total	198	100.00	223	100.00

pattern was observed for overtopped positions, with *A. saccharum* being the most abundant (36.36%) followed by *A. rubrum* (18.69%) and *F. grandifolia* (10.61%).

Discussion

Gap formation patterns and processes

The majority (80%) of the gaps documented originated from uprooted or snapped stems. Other studies have also found these mechanisms to be the most common means of gap formation in the southern Appalachians (Barden 1979; Barden 1981; Romme and Martin 1982; Runkle 1982). However, Clinton et al. (1993) found snag gaps to be more prevalent following drought in secondary forests of the Appalachian Highlands in North Carolina. Based on the means by which canopy trees were removed, we speculate that wind is the dominant disturbance agent in the forest as strong winds have the potential to uproot trees and snap boles. Wind also has the potential to alter forest composition and structure by blowing down snag trees. Standing dead trees are often removed by mild to severe wind events, but the potential for snags to be blown down varies by site conditions (Jans et al. 1993). Further, snags that eventually fall likely alter the forest differently than gaps that are caused rapidly (Franklin et al. 1987; Krasny and Whitmore 1992; Clinton et al. 1994). The eventual fall of a snag may cause additional forest disturbance, possibly with a greater magnitude than the initial event. Also, the bole and branches of standing dead trees may block sunlight from reaching the understory, thereby, facilitating gap closure by perimeter trees rather than subcanopy individuals.

The percentage of single-tree gaps (78% of gaps sampled) was within the range of what has been reported from old growth forests of the eastern USA (Runkle 1990). Of the multi-tree disturbance events, most were caused by uprooted stems. Windthrow gaps have the potential to cause more site modification than gaps caused by other mechanisms, because as the root network is lifted, microtopography (pits and mounds) and soil characteristics are also modified (Clinton et al. 1994; Beckage et al. 2000).

Average diameter of gap maker trees was 38.38 cm at breast height and the average diameter of canopy trees (dominant and codominant crown classes) that surrounded gaps was 38.83 cm ± 6.04 (SD). This result is contrary to what has been reported for old growth forests of the southern Appalachians, where gap makers were significantly larger than border trees (Runkle 1998). This pattern may be related to the age of the forest. In second growth forests, canopy trees are within a narrower diameter range as their age (and diameter) structure is not complex. Thus, in mature second growth forests, size does not indicate that one individual is more likely to be removed from the canopy than another. Also, the smallest gap maker was just 19.5 cm dbh, but was a component of a multi-tree gap with another individual of 28 cm. Although both of these individuals were below the average size for gap makers, the removal was enough to open the canopy and modify the forest.

Of the 17 disturbance events with known seasonality, one occurred during the growing season. Most growing season deaths occurred after the formation of earlywood cells but before the completion of latewood cells. We interpret the amount of xylem produced during the last year of growth to indicate that the majority of the canopy disturbance events occurred during the middle or later part of the growing season. The timing of death combined with the primary origins of formation (uprooted and snapped stems) indicated that strong winds associated with frontal and convection storms may be the major agents that disrupt the forest. Severe wind events in the region are associated with thunderstorms that occur ca. 55 days per year, usually during late-spring and summer (Smalley 1982). Documenting the season of gap formation is important because the time of year a gap forms may influence the ability of residual trees to exploit the additional resources (Runkle 1989). Gaps that form during the growing season may expose shade-developed leaves to changes in environmental conditions. When light levels increase, expanding leaves and leaves produced in the new environment may acclimate to high-light conditions. Fully shade-developed leaves are not able to change their anatomy to acclimate to modifications in the light regime. Thus, fully shade-developed leaves may undergo a period of photoinhibition after gap events (Kozlowski 1957; Naidu and DeLucia 1997). Plastic species that periodically flush throughout the growing season may be best suited to take advantage of the increased resources of the gap environment (Kozlowski and Pallardy 1997). Gap seasonality may be especially important in secondary forests, where gaps are generally small and relatively short-lived.

Gap fraction and physical characteristics

The fraction of land area in expanded gaps and true gaps is within the range of what has been reported elsewhere in the Eastern Deciduous Forest Region (Runkle 1982; Beckage et al. 2000). Based on gap fraction and mean gap size, we conclude that the secondary forest supported a higher number of gaps compared to older stands throughout the region. Thus, we propose that during the understory reinitiation stage of development, forests support a higher density of smaller gaps, but similar total land area in gap environments compared to stands in a complex developmental stage. The fraction of land area in gaps was highest for younger gaps and generally decreased with increased gap age. This pattern was expected because older gaps have had a longer time to be filled. No gaps were documented over 17 years of age. From this, we propose that most gaps in the forest are filled within 20 years of formation, but many are likely filled within shorter periods. Hart and Grissino-Mayer (2008) statistically analyzed radial growth releases attributed to canopy disturbances in *Quercus* individuals from the PCNA and found mean release durations of only 4 years. Thus, we speculate that most gaps are short-lived in these secondary hardwood stands, and that the increase in available resources is generally not sustained for more than 4 years.

In general, L:W patterns were similar for expanded and true gaps as both had ellipsoidal shapes. The shape of the disturbed canopy area is largely a function of the mechanism of tree death and architecture of the gap maker. Circular gap shapes resulted from canopy disturbances related to snags rather than uprooted or snapped stems. Trees that remained standing after their death did not fall, and remove vegetation in a linear pattern starting at the base of the tree as is normal for treefall disturbances. The majority (55%) of the gaps were oriented downslope from the base of the tree, while 40% were oriented across slope and 5% of the trees fell up slope. Thus, most canopy disturbances resulted in ellipsoidal shaped gaps that were oriented perpendicular to slope contours. The shape, size, slope, orientation, height of surrounding forest, residual plants, and post-treefall debris of canopy gaps, as well as latitudinal position, are important in determining the microenvironmental conditions of the disturbed area (Poulson and Platt 1989; Runkle 1989). These physical gap characteristics may be useful if forest management plans have a goal of mimicking natural disturbance processes.

Density and diversity within gaps

Significant positive relationships were documented between expanded gap size and the number of saplings, trees, and total stems. Although, this result may seem expected, a significant positive relationship between gap size and stem number does not always occur (Runkle 1982). Larger gaps may be the result of high intensity events with few residual trees, may be characterized by abiotic conditions (e.g., full sunlight and high temperatures) not conducive to the growth of forest interior species, and may support increased herbivory. Interestingly, in our study, the largest gap did not support the highest number of stems, which occurred in an intermediate size gap. The density measures analyzed were for expanded gap areas. Individuals in the entire area of an expanded gap do not benefit from increased resources such as light. Because the true gap area gets smaller with time since the disturbance, gap age may play an important role in the number of individuals that inhabit a gap site (Runkle 1982; Clinton et al. 1994). Also, the number of individuals within the gap should decrease through self-thinning processes as they compete to reach the canopy.

We hypothesized that larger gaps would support higher diversity values. By containing more surface area, larger gaps have the potential to contain more site heterogeneity and microsites that may favor certain species over others. However, only weak relationships existed between diversity and gap size and two of the relationships (saplings and total stems) were negative. Perhaps, gap size is not as important to diversity as the physical site characteristics of the gap or the biotic assemblage of the gap prior to formation. It is also possible that the gaps sampled in this study (and those in other secondary forests of similar age) were not large enough for the pattern to manifest. Although canopy gaps should increase biological diversity, this pattern does not necessarily occur at the gap-level, but at the stand-level, where a collection of different sized and aged canopy gaps across a variety of sites may support species that are otherwise absent or sparse under the closed forest canopy.

Gap closure, recruitment, and succession

No clear species-specific patterns were observed with gap successors, indicating that the location of an individual within the gap and its vertical crown position prior to the disturbance may be the most important factors that determine how the gap is closed, and by what species. As further evidence of this point, radial-growth response of understory individuals has been shown to be related to position within a canopy gap (Tryon et al. 1992).

Species composition of gaps is a good predictor of future forest composition (Runkle and Yetter 1987). Three species (*A. saccharum*, *F. grandifolia*, and *A. rubrum*) represented 69% of all saplings in expanded gaps. Because saplings represent the pool of individuals that may be recruited to larger size classes following disturbance events, we hypothesize that *Acer* species and *F. grandifolia* will become more abundant in intermediate, and eventually, canopy positions under the current disturbance regime. There is a greater likelihood that individuals of these species will be able to exploit current and future gap events, because they are so abundant in the sapling layer.

We projected that the majority of the canopy gaps would close by lateral crown expansion rather than height growth of understory individuals. However, even gaps that close by lateral branch growth still provide a means for understory trees to recruit to larger size classes. This process may allow overtopped trees to reach intermediate positions, and eventually, the canopy following future disturbance events. Trees already in intermediate positions may expand their crowns to become dominant or codominant in the canopy. Over half of all trees located in true gaps with intermediate crown classifications were *A. saccharum*, *A. rubrum*, or *L. tulipifera*.

Acer species and *L. tulipifera* have the greatest potential to recruit in gaps based on density, dominance, and crown class measures. It is interesting that species with such different life history characteristics were well represented in canopy gaps, and employ different strategies to reach canopy level. *Acer saccharum* is very shade-tolerant and has the ability to persist in the understory of a closed canopy while maintaining the ability to rapidly respond to increased light (Canham 1988; Tryon et al. 1992). *Acer rubrum* is classed as moderately shade-tolerant and can exist in the understory of a relatively closed canopy until the formation of gaps when the species has also been shown to quickly respond to increased resources (Wallace and Dunn 1980). In general, the life history characteristics of the *Acer* species may be classed as conservative. Both *A. saccharum* and *A. rubrum* can establish in at least relatively shaded conditions and wait for the formation of small canopy gaps to recruit to larger size classes and higher canopy positions. In contrast to the *Acer* species, *L. tulipifera* is disturbance obligate. The species is shade-intolerant and cannot exist under a closed forest canopy. However, *L. tulipifera* is capable of quickly responding to increased resources when they become available and is a common component in forests with disturbance regimes that consist of small localized events (Buckner and McCracken 1978; Wallace and Dunn 1980; Orwig and Abrams 1994; Busing 1995; Lafon 2004).

Shade-intolerant species, such as *L. tulipifera*, must reach the canopy in one gap event, because once the gap closes, they will not be able to survive under the canopy (Hibbs 1982; Runkle and Yetter 1987; Cole and Lorimer 2005; Webster and Lorimer 2005). Thus, in forests with a disturbance regime characterized by small localized events, there are few opportunities for shade-intolerant species to exist (Runkle 1998). Shade-tolerant species are more likely to be present in a gap when they form; thus, they are generally more likely to recruit or reach the canopy in small gaps (Henry and Swan 1974; Dahir and Lorimer 1996; McClure et al. 2000; Taylor and Lorimer 2003). Gaps of a larger size, however, may allow time for germinants to establish and recruit. Because of its rapid growth, *L. tulipifera* can reach the canopy in gaps of ca. 400 m^2 and larger (Busing 1994; Busing 1995). Although gaps of that size were documented in this study, we do not think *L. tulipifera* will reach the canopy at any of the gap sites before closure. The majority of the gaps documented will close by lateral branch growth before understory individuals can reach the canopy. Although individuals are recruited to larger size classes and higher vertical positions in these gaps, it will take multiple disturbance events for most subcanopy individuals to reach the main canopy level. Because it will generally take multiple events for individuals to be recruited to the canopy, shade-tolerant *A. saccharum* and moderately-tolerant *A. rubrum* are the species most likely to attain canopy dominance under the current disturbance regime. Interestingly, half of the canopy gaps were caused by the removal of a *Quercus* individual, but *Acer* species represented a large proportion of trees likely to either reach the canopy or recruit to larger size classes. These data indicate a likely shift in composition if gap processes continue to remove *Quercus* from the canopy and provide the means for *Acer* recruitment.

Conclusions

Canopy gaps obviously have an important influence on forest composition and structure. However, little information is available on natural gap-scale disturbances in secondary hardwood forests. By analyzing gap formation mechanisms, physical gap characteristics, and forest response to canopy gaps, we can gain a better understanding of the role of gap-scale disturbance processes in the development of hardwood forests. This study showed that disturbances that involved the death of a single tree or a small cluster of trees were common events throughout secondary stands on the Cumberland Plateau in Tennessee. The fraction of the forest in canopy gaps was within the range reported from old growth remnants throughout the region. However, gap size was smaller in the developing stands indicating that secondary forests contain a higher density of smaller gaps. These localized disturbances modified biomass arrangement and tree-age distribution patterns as they allowed for crown expansion of canopy trees, recruitment of understory individuals, and in some instances, establishment of new germinants. Thus, canopy gaps provide the mechanism for forests to develop a complex size and age structure indicative of older stands. Gap-scale processes may also be used to help explain shifting species composition that has been widely reported throughout the Central Hardwood Forest Region of the eastern US. Half of the canopy gaps documented in this study were caused by the removal of a *Quercus* individual, but *A. saccharum*, *A. rubrum*, and *L. tulipifera* were the most likely species to capture canopy gaps. The gaps documented favored the very shade-tolerant *A. saccharum* because most gaps were small, and multiple overstory removal events would be required for trees to reach the main canopy level. In conclusion, this study demonstrated that natural disturbance processes have significant influences on forest development and successional patterns. Thus, small-scale disturbance events must be considered when developing long-term forest management plans.

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References

Barden LS (1979) Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. Oecologia 44:141–142. doi:10.1007/BF00346412

Barden LS (1980) Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos 35:16–19. doi:10.2307/3544722

Barden LS (1981) Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. Oikos 37:205–209. doi:10.2307/3544466

Beckage B, Clark JS, Clinton BD et al (2000) A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Can J For Res 30:1617–1631. doi:10.1139/cjfr-30-10-1617

Braun EL (1950) Eastern deciduous forests of North America. Blakiston, Philadelphia

Buckner E, McCracken W (1978) Yellow-poplar: a component of climax forests? J For 76:421–423

Busing RT (1994) Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. Vegetatio 115:19–27

Busing RT (1995) Disturbance and the population dynamics of *Liriodendron tulipifera*: simulations with a spatial model of forest succession. J Ecol 83:45–53. doi:10.2307/2261149

Canham CD (1988) Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69:786–795. doi:10.2307/1941027

Cho D, Boerner REJ (1991) Canopy disturbance patterns and regeneration of *Quercus* species in two old-growth forests. Vegetatio 93:9–18

Clebsch EEC, Busing RT (1989) Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. Ecology 70:728–735. doi:10.2307/1940223

Clinton BD, Boring LR, Swank WT (1993) Canopy gap characteristics and drought influence in oak forests of the Coweeta Basin. Ecology 74:1551–1558. doi:10.2307/1940082

Clinton BD, Boring LR, Swank WT (1994) Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influence of topographic position and evergreen understory. Am Midl Nat 132:308–319. doi:10.2307/2426587

Cole WG, Lorimer CG (2005) Probabilities of small-gap capture by sugar maple saplings based on height and crown growth data from felled trees. Can J For Res 35:643–655. doi:10.1139/x04-210

Cowell CM (1998) Historical change in vegetation and disturbance on the Georgia Piedmont. Am Midl Nat 140:78–89. doi:10.1674/0003-0031(1998)140[0078:HCIVAD]2.0.CO;2

Dahir SE, Lorimer CG (1996) Variation in canopy gap formation among developmental stages of northern hardwood stands. Can J For Res 26:1875–1892. doi:10.1139/x26-212

De Vries PG (1974) Multi-stage line intersect sampling. For Sci 20:129–133

Fenneman NM (1938) Physiography of Eastern United States. McGraw-Hill Book Company, New York

Ferreira de Lima RA (2005) Gap size measurement: the proposal of a new field method. For Ecol Manag 214:413–419. doi:10.1016/j.foreco.2005.04.011

Francis JK, Loftus JS (1977) Chemical and physical properties of the Cumberland Plateau and Highland Rim forest soils. USDA, Forest Service, Research Paper SO-138

Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecosystem process. Bioscience 37:550–556. doi:10.2307/1310665

Fritts HC (2001) Tree rings and climate. Blackburn Press, Caldwell, New Jersey

Goebel PC, Hix DM (1996) Development of mixed-oak forests in southeastern Ohio: a comparison of second and old-growth forests. For Ecol Manag 84:1–21. doi:10.1016/0378-1127(96)03772-3

Goebel PC, Hix DM (1997) Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. Ecoscience 4:327–339

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree Ring Res 57:205–221

Hart JL (2007) A multi-scale analysis of disturbance dynamics in hardwood forest communities on the Cumberland Plateau, USA. Dissertation, University of Tennessee, Knoxville

Hart JL, Grissino-Mayer HD (2008) Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. For Ecol Manag 255:1960–1975

Henry JD, Swan JMA (1974) Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772–783. doi:10.2307/1934413

Hibbs DE (1982) Gap dynamics in a hemlock-hardwood forest. Can J For Res 12:522–527. doi:10.1139/x82-081

Hinkle CR (1978) The relationship of forest communities and selected species to edaphic and topographic factors on the Cumberland Plateau of Tennessee. Dissertation, University of Tennessee, Knoxville

Hinkle CR (1989) Forest communities of the Cumberland Plateau of Tennessee. J Tenn Acad Sci 64:123–129

Hinkle CR, McComb WC, Safely JM Jr, Schmalzer PA (1993) Mixed mesophytic forests. In: Martin WH, Boyce SG, Echternacht AC (eds) Biodiversity of the Southeastern United States: upland terrestrial communities. Wiley, New York, pp 203–253

Holmes RL (1983) Computer assisted quality control in tree-ring dating and measurement. Tree Ring Bull 43:69–78

Jans L, Porter L, van Rompaey RSAR et al (1993) Gaps and forest zones in tropical moist forest in Ivory Coast. Biotropica 25:258–269. doi:10.2307/2388784

Kozlowski TT (1957) Effect of continuous high light intensity on photosynthesis of forest tree seedlings. For Sci 3:220–224

Kozlowski TT, Pallardy SG (1997) Physiology of woody plants, 2nd edn. Academic Press, San Diego

Krasny ME, Whitmore MC (1992) Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. Can J For Res 22:139–143. doi:10.1139/x92-019

Lafon CW (2004) Stand dynamics of a yellow-poplar (*Liriodendron tulipifera* L.) forest in the Appalachian

Mountains, Virginia, USA. Dendrochronologia 22:43–52. doi:10.1016/j.dendro.2004.09.002

Lorimer CG (1980) Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169–1184. doi:10.2307/1936836

McCarthy BC, Bailey DR (1994) Distribution and abundance of coarse woody debris in a managed forest landscape. Can J For Res 24:1317–1329

McClure JW, Lee TD, Leak WB (2000) Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For Ecol Manag 127:181–189. doi:10.1016/S0378-1127(99)00129-2

Naidu SL, DeLucia EH (1997) Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. Tree Physiol 17:367–376

Oliver CD, Larson BC (1996) Forest stand dynamics, update edition. Wiley, New York

Orvis KH, Grissino-Mayer HD (2002) Standardizing the reporting of abrasive papers used to surface tree-ring samples. Tree Ring Res 58:47–50

Orwig DA, Abrams MD (1994) Contrasting radial growth and canopy recruitment patterns in Liriodendron tulipifera and Nyssa sylvatica: a gap-obligate versus gap-facultative tree species. Can J For Res 24:2141–2149. doi:10.1139/x94-276

Pickford SG, Hazard JW (1978) Simulation studies on line intersect sampling of forest residue. For Sci 24:469–483

Poulson TL, Platt WJ (1989) Gap light regimes influence canopy tree diversity. Ecology 70:553–555. doi:10.2307/1940202

Rebertus AJ, Meier AJ (2001) Blowdown dynamics in oak-hickory forests of the Missouri Ozarks. J Torrey Bot Soc 128:362–369. doi:10.2307/3088668

Romme WH, Martin WH (1982) Natural disturbance by tree-falls in old-growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky. In: Muller RN (ed) In: Proceedings of the central hardwood forest conference. University of Kentucky, Lexington, pp 367–383

Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041–1051. doi:10.2307/1937003

Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of the eastern United States. Ecology 63:1533–1546. doi:10.2307/1938878

Runkle JR (1985) Comparison of methods for determining fraction of land area in treefall gaps. For Sci 31:15–19

Runkle JR (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. Ecology 70:546–547. doi:10.2307/1940199

Runkle JR (1990) Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. Can J For Res 20:632–641. doi:10.1139/x90-085

Runkle JR (1992) Guidelines and sample protocol for sampling forest gaps. USDA, Forest Service, Pacific Northwest Research Station, GTR 283, Portland

Runkle JR (1998) Changes in southern Appalachian canopy tree gaps sampled thrice. Ecology 79:1768–1780

Runkle JR (2000) Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology 81:554–576

Runkle JR, Yetter TC (1987) Treefalls revisited: gap dynamics in the southern Appalachians. Ecology 68:417–424. doi:10.2307/1939273

Smalley GW (1982) Classification and evaluation of forest sites on the mid-Cumberland Plateau. USDA, Forest Service, Southern Research Experiment Station, GTR SO-38, New Orleans, Louisiana

Smalley GW (1986) Classification and evaluation of forest sites on the northern Cumberland Plateau. USDA, Forest Service, Southern Research Experiment Station, GTR SO-60, New Orleans, Louisiana

Spies TA, Franklin JF, Klopsch M (1990) Canopy gaps in Douglas-fir forests of the Cascade Mountains. Can J For Res 20:649–658. doi:10.1139/x90-087

Stokes MA, Smiley TL (1996) An introduction to tree-ring dating. University of Arizona Press, Tucson

Taylor SO, Lorimer CG (2003) Loss of oak dominance in dry-mesic deciduous forests predicted by gap capture methods. Plant Ecol 167:71–88. doi:10.1023/A:1023975026261

Thornthwaite CW (1948) An approach toward rational classification of climate. Geogr Rev 38:55–94. doi:10.2307/210739

Tryon EH, Lanasa M, Townsend EC (1992) Radial growth response of understory sugar maple (*Acer saccharum*) surrounding openings. For Ecol Manag 55:249–257. doi:10.1016/0378-1127(92)90104-H

Tyrell LE, Crow TR (1994) Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75:370–386. doi:10.2307/1939541

USDA (1995) Soil survey of Fentress and Pickett Counties. USDA, Soil Conservation Service, Tennessee

Veblen TT (1985) Forest development in tree-fall gaps in the temperate rain forest of Chile. Natl Geogr Res 1:162–183

Wallace LL, Dunn EL (1980) Comparative photosynthesis of three gap phase successional tree species. Oecologia 45:331–340. doi:10.1007/BF00540201

Webster CR, Lorimer CG (2005) Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. Ecol Appl 15:1245–1262. doi:10.1890/04-0763

White PS, MacKenzie MD, Busing RT (1985) Natural disturbance and gap-phase dynamics in southern Appalachian spruce-fir forests. Can J For Res 15:233–240. doi:10.1139/x85-041

Wilder CM, Holtzclaw FW Jr, Clebsch EEC (1999) Succession, sapling density and growth in canopy gaps along a topographic gradient in a second growth east Tennessee forest. Am Midl Nat 142:201–212. doi:10.1674/0003-0031(1999)142[0201:SSDAGI]2.0.CO;2

Yamamoto S, Nishimura N (1999) Canopy gap formation and replacement pattern of major tree species among development stages of beech (*Fagus crenata*) stands, Japan. Plant Ecol 140:167–176. doi:10.1023/A:1009713002039

Yetter TC, Runkle JR (1986) Height growth rates of canopy gap tree species in southern Appalachian gaps. Castanea 51:157–167

Plurality of tree species responses to drought perturbation in Bornean tropical rain forest

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Abstract Drought perturbation driven by the El Niño Southern Oscillation (ENSO) is a principal stochastic variable determining the dynamics of lowland rain forest in S.E. Asia. Mortality, recruitment and stem growth rates at Danum in Sabah (Malaysian Borneo) were recorded in two 4-ha plots (trees $\geq$ 10 cm *gbh*) for two periods, 1986–1996 and 1996–2001. Mortality and growth were also recorded in a sample of subplots for small trees (10 to <50 cm *gbh*) in two sub-periods, 1996–1999 and 1999–2001. Dynamics variables were employed to build indices of drought response for each of the 34 most abundant plot-level species (22 at the subplot level), these being interval-weighted percentage changes between periods and sub-periods. A significant yet complex effect of the strong 1997/1998 drought at the forest community level was shown by randomization procedures followed by multiple hypothesis testing. Despite a general resistance of the forest to drought, large and significant differences in short-term responses were apparent for several species. Using a diagrammatic form of stability analysis, different species showed immediate or lagged effects, high or low degrees of resilience or even oscillatory dynamics. In the context of the local topographic gradient, species' responses define the newly termed perturbation response niche. The largest responses, particularly for recruitment and growth, were among the small trees, many of which are members of understorey taxa. The results bring with them a novel approach to understanding community dynamics: the kaleidoscopic complexity of idiosyncratic responses to stochastic perturbations suggests that *plurality*, rather than neutrality, of responses may be essential to understanding these tropical forests. The basis to the various responses lies with the mechanisms of tree-soil water relations which are physiologically predictable: the timing and intensity of the next drought, however, is not. To date, environmental stochasticity has been insufficiently incorporated into models of tropical forest dynamics, a step that might considerably improve the reality of theories about these globally important ecosystems.

Keywords Dynamics · Ecosystem · El Niño · Resilience · Stem growth · Tree mortality

Introduction

Tropical rain forests are highly dynamic and responsive ecosystems. Their physical structure and processes may remain relatively stable over time, but species composition is thought to constantly fluctuate around a quasi-equilibrium or change slowly in the

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long-term (Huston 1979, 1994). Perturbations drive these dynamics, and earlier ideas of equable tropical conditions have given way to the view that climate is indeed variable, particularly on the scale of decades to centuries (Newbery et al. 1999a). Droughts are the major cause of perturbation across much of South-East Asia, and are probably a main determinant of forest structure and tree species composition, in particular in Borneo. They are often associated with the El Niño Southern Oscillation (ENSO) cycle (Trenberth 1997; Trenberth and Hoar 1997; McPhaden 1999; Cane 2005). The last strong drought in Borneo was in 1997/1998 and prior to that 1982/1983 (Walsh 1996a, b; Walsh and Newbery 1999).

Global change scenarios for the tropics expect climate to become more unstable this century with more frequent and intense droughts (Hulme and Viner 1998; Timmermann et al. 1999). Not all models, however, predict more ENSO activity (Timmermann et al. 2004; Cane 2005; McPhaden et al. 2006; Meehl et al. 2007) although the risk of droughts is expected to increase during future El Niño events (Christensen et al. 2007), and this could have serious implications for forest management. Tropical rain forests appear to exist in variously complex and overlapping states of recovery from past perturbations, whether singular or multiply clustered, recent or from the distant past (Newbery et al. 1999a, b; Newbery and Lingenfelder 2004). Measuring how these forests respond to the perturbations could lead to valuable models of how changes in drought frequency and intensity affect their future. It might also allow a rethinking in tropical rain forest dynamics with broader considerations for rain forest conservation.

Forests in parts of Borneo are apparently still recovering from a very strong drought c. 130 years ago (Newbery et al. 1992; Walsh and Newbery 1999) with tree species appearing well adapted to the several less-severe intervening events (Gibbons 1998; Newbery et al. 1999b; Gibbons and Newbery 2003; Newbery and Lingenfelder 2004). Setbacks in forest biomass temporarily destabilize the ecosystem, but over centuries a form of dynamic equilibrium is presumably attained. Uncertain though is how far from this equilibrium are these forests due to the 1997/1998 and earlier droughts, and whether they have a high enough resilience to recover before the next one (Newbery and Lingenfelder 2004).

In Central America, intensification of the 1982/1983 dry season by the ENSO that year, together with a regional trend of decreasing rainfall since 1965, have been shown to affect tree mortality and forest population change, and account for species' geographical distributions (Condit et al. 1995, 1996, 2004; Engelbrecht et al. 2007). This situation contrasts in interesting ways to that of Borneo with its regionally steady environment punctuated by occasional strong drought. Indeed when generally comparing drought effects worldwide, it is important to place these usual periods of large water deficit within the context of any long-term regular (annual or supra-annual) patterns characterizing the regional climate.

This paper reports on the impact of this 1997/1998 drought on lowland dipterocarp rain forest dynamics in the Danum Valley Conservation Area, Sabah, Malaysia (Marsh and Greer 1992), a site c. 70 km inland of the north-eastern coast of Borneo. With precise enumeration data over a 15-year period, collected before and after the drought on a large sample of trees, changes to the most abundant species and estimated ecosystem resilience are quantified. An omnibus test of the null model that there were no species-specific responses at the community level was performed. An attempt of this kind for tropical ecosystem dynamics has to our knowledge not hitherto been made. Finally, a new concept of rain forest dynamics emerging from this work is presented.

Climate

Meteorological data have been recorded at Danum Valley Field Centre (DVFC, 152 m a.s.l.) since July 1985. Monthly mean temperatures ranged 1.8°C about an annual mean temperature of 26.8°C, while the mean daily range was 8.6°C. The highest temperature was recorded in April 1992 with 36.5°C, the lowest in January 1993 with 16.5°C. Relative humidity varied between 95.3% at 08:00 and 78.3% at 14:00. These values are typical of equatorial rainforest locations (Walsh 1996b).

Mean annual rainfall (±SE) across complete years 1986–2003 was 2,825 ± 110 mm with a range from 1,918 mm in 1,997–3,539 mm in 2003. During the study period of 1986 to 2001 mean annual rainfall was

2,787 ± 115 mm. Annual monthly rainfall (±SE) from July 1985 to December 2003 was 235 ± 13 mm ranging from 158 mm in April to 312 mm in January. For the study period the corresponding mean was 232 ± 13 mm. Mean rainfall in the month of April was significantly different from the annual monthly mean from 1985 to 2003 (Mann–Whitney *U*-test: $P = 0.006$), varying from 11 mm in 1998—the lowest monthly value on record—to 433 mm in 1999, the wettest month of that year. With 701.2 mm of rain, December 2003 was the wettest month on record at Danum. Although rainfall in the months of April and July/August on average was well below the annual monthly mean, rainfall fluctuated considerably between years as well as between months. There is no clear dry season indicating that Danum has a generally aseasonal tropical climate.

Since the start of meteorological data collection, Danum experienced 38 droughts, defined as periods with running 30-day rainfall total (R_{30}) < 100 mm for rain forests not short of water (Brünig 1969; Malhi and Wright 2004). These include two ENSO-related drought events in 1991/1992(–1994) and in 1997/1998. Before that, in 1982/1983, a strong ENSO-event affected Sabah (Beaman et al. 1985; Woods 1989) and may have had effects at Danum. Very strong droughts have been recorded in the late 19th and early 20th centuries at regional scales throughout Sabah (Walsh 1996a, b). In 1997/1998 drought effects on forest vegetation were reported to be stronger in Sarawak (Nakagawa et al. 2000; Potts 2003).

Methods

Antecedent rainfall history

For rain forest vegetation that is not short of water, water stress is assumed to set in when the monthly mean rainfall drops below 100 mm, the estimated value for evapotranspiration in the tropics (Brünig 1969, 1971; Walsh 1996b; Walsh and Newbery 1999; Malhi et al. 2002; Malhi and Wright 2004). For the daily rainfall data available, this threshold can be applied to R_{30}, the 30-day running total of rainfall. Droughts can be assessed by calculating an intensity index that takes into account the deficit (R_{30}–100) and the drought duration (Newbery and Lingenfelder 2004).

This approach, however, neglects the rainfall preceding the 30-day periods. A period of rainfall below 100 mm that had low rainfall in the months before would, assuming that the soil water reservoir was already depleted, likely be more severe for the trees than such a period with high rainfall preceding it, in which case water would probably be still available from storage in the soil (Malhi and Wright 2004; R. P. D. Walsh, pers. comm.). Water stress caused by a deficit in soil water tends to affect the forest immediately (in <15 days), but some time is required (c. 60 days in a central Amazonian rain forest) for the soil to be recharged with water after a dry season (Malhi et al. 2002).

Antecedent rainfall history was brought into the calculation of drought intensity in the following way. Across the 18.5 years for which data were available, Julian-day rainfall was averaged to give mean values of what the vegetation might ‘expect’—the annual distribution of rainfall to which its species have generally been subjected. This was termed the mean daily rainfall, *MDR* (Fig. 1). The difference between the actual and mean daily rainfall (*ADR*–*MDR*), the daily rainfall anomaly (*DRA*), was accumulated across 90, 180 and 365 days prior to each day (the accumulated rainfall anomaly, *ARA*). For any one day *ARA* gave the sum of rainfall across the selected period that was a deficit or a surplus to the expected average for that period.

Plots and enumerations

Two permanent plots were set up and first enumerated in 1985–1986. They lie 0.8 km NW of Danum Valley Field Centre, 0.3 km apart on gently undulating terrain at c. 200–250 m asl. Each plot has dimensions 100 m × 400 m (total area = 8 ha). Eight 40 m × 40 m subplots were selected in a stratified random manner within each plot in 1998 (area = 2.56 ha), half on lower slopes (<12 m elevation) and half on ridges (≥25 m). For further information about the site and the plots see Newbery et al. (1992, 1996) and Newbery and Lingenfelder (2004).

Plots were enumerated in (1) August 1985–December 1986, (2) November 1995–February 1997 and (3) February 2001–February 2002; and subplots alone in December 1998–March 1999. All trees

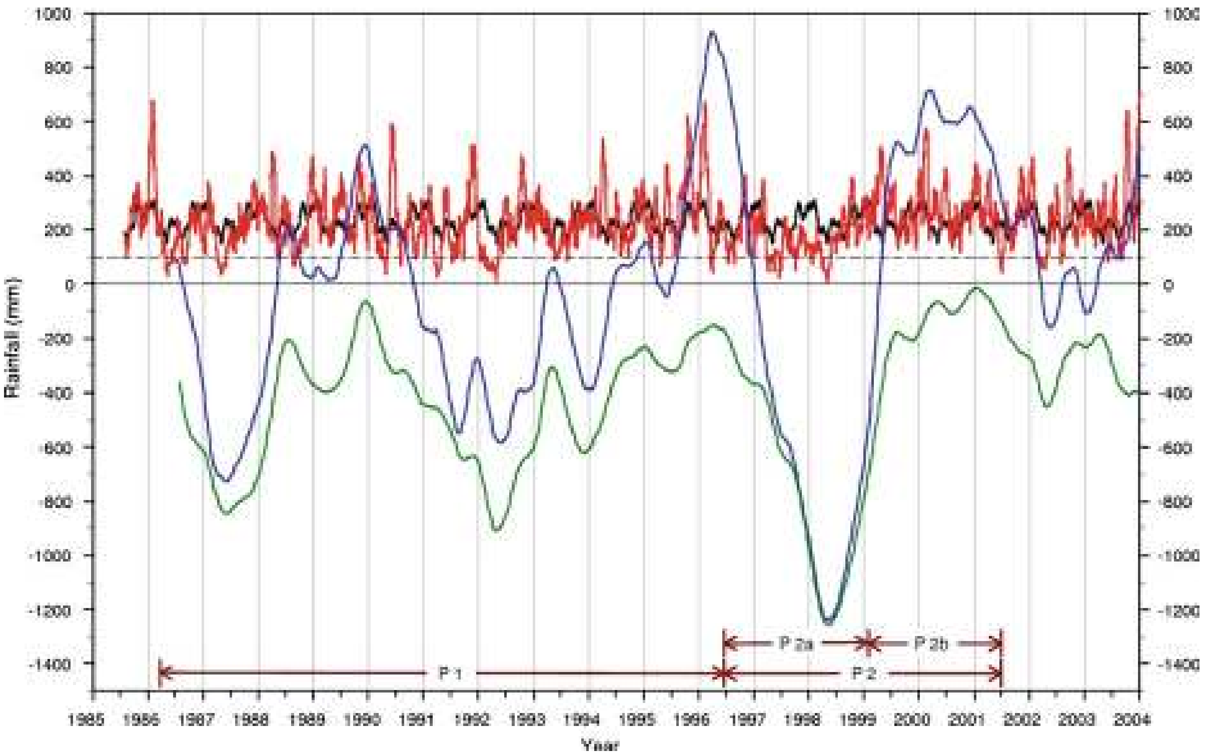

Fig. 1 Accumulated rainfall anomalies (*ARA*) with conditions applied at Danum, 1985–2003: R_{30} of mean daily (*MDR*; black line) and actual (*ADR*; red) rainfall, ARA_{365} (blue) and accumulation only when $R_{30} < 232$ mm ($CARA_{232}$; dark green); dashed reference at 100 mm (see text for explanations). Smoothing algorithm used a negative exponential function with sampling proportion equal to 0.02 (smoothing showed not all of the individual shorter and milder drought events as defined but was nevertheless preferred over the raw data for clarity). Intervals between plot measurements are shown as periods P1 and P2, and sub-periods P2a and P2b

≥10.0 cm stem *gbh* (girth at breast height) or 3.18 cm *dbh* (diameter), were measured for *gbh* (above buttresses where these occurred), mapped and identified at each plot census; deaths were recorded, and recruits enumerated, in 1996 and 2001. In subplots trees 10 to <50 cm *gbh* (small trees) were remeasured, and deaths recorded: in 1999 limited resources did not permit the measurement and identification of recruits. In 1996–2001 a system of identifying suitable trees for valid growth rate estimates was introduced. Plots 1 and 2 had 17,942, 17,265 and 16,623 trees ≥10 stem *gbh* in 1986, 1996 and 2001, respectively, of correspondingly 450, 466 and 489 species. With 98% of trees identified to named species, 2% stayed at unnamed but distinct taxa. Voucher material is held at the Rijksherbarium (Leiden) and the Sabah Forest Department Herbarium (Sepilok, near Sandakan).

At the plot level all measured trees were considered. The intervals 1986–1996 and 1996–2001 were designated periods P1 (10.0 years) and P2 (5.0 years), respectively. At the subplot level only small trees were considered at the four dates: recruits in 1996 and 2001 were omitted. Period P2 was subdivided into sub-periods P2a (1996–1999, 2.6 years) and P2b (1999–2001, 2.4 years; see Fig. 1). Further, for all trees three size classes were defined: small, 10 to <50; medium, 50 to <100 and large ≥ 100 cm *gbh*; and for small trees four 10 cm *gbh* classes.

Species selection

As many species had too few individuals to permit reliable analysis, those 34 with $n \geq 100$ trees, in both plots together, in either 1986, 1996 or 2001 were selected. This gave $n \geq 60$ valid trees per species for growth estimates. Newbery et al. (1999) give the basis for these sample sizes. These abundant species represented on average 60% of all trees enumerated in 1986–1996–2001. For the subplots, the 22 species each with $n \geq 50$ small trees in 1986 were selected: they represented on average 53% of the populations.

Dynamics rates

Annualized rates (% year^{-1}) of mortality (m_{a}) and recruitment (r_{a}) were based on the numbers of trees that died (n_d) or recruited (n_r) relative to those at the start of intervals (n_{start}) and mean time intervals (t) per species:

$$m_{\mathrm{a}} = \left(1 - \left(1 - \frac{n_d}{n_{\mathrm{start}}}\right)^{\frac{1}{t}}\right) \cdot 100$$

$$r_{\mathrm{a}} = \left(\left(1 + \frac{n_r}{n_{\mathrm{start}}}\right)^{\frac{1}{t}} - 1\right) \cdot 100$$

were derived (Sheil et al. 1995; Alder 1996). Calculations of mortality and recruitment rates on the plot or subplot level, or for different species and size classes, used the mean time intervals of each individual group. Regressors, trees that decreased in size to < 10 cm *gbh* but remained alive (Lingenfelder 2005), were not considered in the present analysis. Confidence limits of means (95%) of m_{a} were found using an approximation based on the F-distribution (Alder 1996; Nelson 1982). Recruitment was based on the size of each period's starting population because the dynamics of the forest was in a state of strong disequilibrium over the 15 years recorded. Using final population sizes (i.e. the numbers of survivors), as have Phillips et al. (1994), would have led to the estimate of r_{a} being confounded by the effect of the drought on m_a.

Annualized mortality rate, m_a, in period P1 was adjusted to a 5.0-year basis (to equate period P2) following the correction procedure of Newbery and Lingenfelder (2004). The approach was based on the earlier theoretical analysis of Sheil and May (1996). Correction factors (i.e. the numbers by which the original values of m_{a} must be multiplied) for the rates of all trees in the plots, and for their size classes (small, medium and large) were correspondingly 1.04 (1.03, 1.08 and 1.10). In an analogous way, for small trees in subplots, the correction factors for period P1 and sub-periods 2a and 2b were 1.11, 0.83 and 0.85, respectively. These last values were also applied to the 10-cm *gbh* size classes of small trees without differentiation. The correction procedure assumes that the major source of heterogeneity within tree populations lies with species-specific differences in m_a. A similar correction procedure for r_{a} is unknown.

Relative (*rgr*; mm m^{-1} year^{-1}) stem growth rates were calculated from *gbh* at the start and the end of an interval for valid trees, based on time intervals of each tree.

$$rgr = \frac{(\ln(gbh_{\mathrm{end}}) - \ln(gbh_{\mathrm{start}}))}{t} \cdot 10^3$$

For a growth rate to be valid between enumerations the previous point of measurement on the stem should not have moved (due a problem at the old point) or been lost (e.g. due to tree breakage), and the stem was in an optimal condition (i.e. no new buttress growth; no cracks, splits or embedded lianas in, or excrescences or termites on, the bark; absence of deformations such as strong fluting or hollowness, a pronounced oval cross-section or spiral form; and not based on relascopic measurement—a few very large trees). A bootstrapping procedure using $N = 2{,}000$ runs found the means and 95% confidence limits to *rgr* (with GenStat 7/8, Payne 2000).

Drought response index

Percentage response to drought (R_{D}) of a dynamic rate variable, v, was calculated as the difference in v between periods P1 and P2 (v_1, v_2) relative to the weighted mean of the rates in these periods. The rate in P1 received double the weight of that in P2 to reflect the relative interval lengths of 10.0 and 5.0 years:

$$R_{\mathrm{D}\_1,2} = ((v_2 - v_1) \cdot 300)/(2v_1 + v_2)$$

R_{D} had a minimum of -150% when v_2 was 0, and a maximum of 300% when v_1 was 0. The R_{D} for m_{a} was multiplied by -1 so that decreases in m_{a} indicated positive responses, in a similar manner to increases in r_{a} and *rgr*. A new composite index *cmp* was constructed using squares of loadings on the first axis of a principal component analysis as linear coefficients (m_{a} -0.587, r_{a} -0.451 and *rgr* -0.672):

$$R_{\mathrm{D}\_cmp} = 0.345 \cdot R_{\mathrm{D}\_m_{\mathrm{a}}} + 0.203.R_{\mathrm{D}\_r_{\mathrm{a}}} + 0.452.R_{\mathrm{D}\_rgr}$$

(correlation-based; $\lambda = \{0.42, 0.32, 0.26\}$).

Percentage response to drought was found for P1–P2a ($R_{\mathrm{D}\_1,2a}$), P2a–P2b ($R_{\mathrm{D}\_2a,2b}$), and P1–P2b ($R_{\mathrm{D}\_1,2b}$), using m_{a} or *rgr* as variable v. Sub-periods P2a and P2b were each taken to be c. 2.5 years in duration so that the relative weights for P1 and either P2a or P2b would be 4 to 1:

$$R_{\mathrm{D}\_1,2a} = ((v_{2a} - v_1) \cdot 500)/(4v_1 + v_{2a})$$

$$R_{\mathrm{D}\_1,2b} = ((v_{2b} - v_1) \cdot 500)/(4v_1 + v_{2b})$$

$$R_{\mathrm{D}\_2a,2b} = ((v_{2b} - v_{2a}) \cdot 200)/(v_{2a} + v_{2b})$$

Of the 22 species, *Reinwardtiodendron humile* was outlying because of its highly negative growth rates which strongly biased the weighted mean across species. In one case, m_{a} for *Lophopetalum becarrianum*, both v_1 and v_2 were 0 and $R_{\mathrm{D}\_2a,2b}$ was also set to 0. With results for r_{a} lacking, a composite index was not calculated for the subplot-recorded species.

Randomization and multiple testing

To test whether species differed from one another significantly, more than would be expected had their dynamics variables been completely randomly distributed across trees of all species, a Monte Carlo approach was taken. Randomization simply removed species identity. For P1 and P2, deaths were re-assigned across all trees at random, to the same extent as was recorded. Samples equal in size to those of the 34 species' populations (with a further all-other-species sample) were randomly selected without replacement (FORTRAN77 program with NAG20 algorithms), and m_{a} and R_{D} calculated. The procedure was repeated a recommended $N = 5{,}000$ times (Manly 1997), and exact probabilities found as twice the percentile of the tail of the ranked values more extreme than that observed. Values of r_{a} were simulated in the same way, but for *rgr* all values were re-allocated at random across valid samples sizes. Individual randomized values of *cmp* were found as for the recorded data, and because they were weighted means of $j = 3$ variables it was necessary to re-scale them by multiplying by $\sqrt{j}$, and to re-adjust means to their original values.

To derive an overall test for the whole community individual species' tests needed to be combined as a 'family'. Family-wise error rate (FWER) tests of significance were achieved with the sequentially rejective procedure of Holm (1979) applying Sidák's adjustment to the Bonferroni α-level, and by finding the Benjamini–Hochberg false discovery rate (FDR) (Westfall and Young 1993; Benjamini and Hochberg 1995). The Holm procedure was applied to the values of *rgr*, but not m_a, of the 22 species of small trees in the subplots. For both 34- and 22-species data sets, the Bernoulli formula was applied to find the minimum numbers of species required to reject the null hypothesis of no family response at $\alpha = 0.05$, these being based on the lowest Bonferroni critical *P*-values allowed by the FDR for the four variables separately (Moran 2003).

Sidak's adjustment to the level of individual hypothesis rejection ($\alpha' = 1 - (1 - \alpha)^{1/k} = 0.001508$; $\alpha = 0.05$, $k = 34$) was used because it more powerful than that of Bonferroni ($\alpha' = 0.05/k = 0.001471$) yet it maintains a strong family-wise error rate (Westfall and Young 1993). The $N = 5{,}000$ randomizations allowed a lowest *P*-value of 0.0002 to be detected, which is well below α' in either case above. As a consequence, ranking could result in ties at this lowest level or simple multiples of it. In these cases, whilst the family-wise *P*-value at each step was the maximum of the previous and currently considered step, adjusted α'-values were averaged across ties (Appendix 3).

Stability analysis

Building upon the concepts of classical stability thinking, a diagrammatic approach was developed to highlight the different species' modes of response. Graphing $R_{\mathrm{D}1-2b}$ against $R_{\mathrm{D}1-2a}$ permitted an evaluation of each species' trajectory. The four quadrants (numbered clockwise) showed which species remained positive (1) or negative (3), and which switched from being positive to negative (2) or vice versa (4), between P2a and P2b. Diagonal lines, where Δ ($= \mathrm{R}_{\mathrm{D}1-2b}/R_{\mathrm{D}1-2a}$) was either 1 or −1 represented no change between sub-periods, or a change in the opposite direction of the same magnitude, respectively. Subdividing, octants defined regions of stability and instability; numbered again clockwise they represented four types of response behaviour: destabilizing non-recovery ($1'$, $5'$; either increasingly positive or negative; $\Delta > 1$), stabilizing recovery ($2'$, $6'$; reduced positive and negative; $0 < \Delta > 1$), stabilizing oscillation ($3'$, $7'$; positive switching to negative of less magnitude and the converse; $-1 < \Delta > 0$) and destabilizing oscillation ($4'$, $8'$; positive switching to negative of greater magnitude and the converse $\Delta < -1$).

Results

Antecedent rainfall history

Values of *accumulated rainfall anomalies* across 90, 180 (not shown—see Lingenfelder 2005) and 365 days (ARA_{365}) ran roughly in parallel, with the 1 year curve having the strongest amplitudes both in rainfall deficit and surplus (Fig. 1). Accumulation of anomalies across 1 year is assumed to adequately reflect the water conditions and to reveal the severity of drought events by reflecting depletion or saturation of soil water content quantitatively rather than simply stating whether it was below or above a certain threshold value. With this approach, immediate strong rainfall deficits ($R_{30} < 100$ mm) as well as the ecologically more meaningful long-term (365-day) deficits are being picked up.

Definition of events

Forest on soil that was already water-saturated would not be able to make use of more rainfall, the excess running off or draining away. Whilst accumulating rainfall as *DRA* when R_{30} was < 100 mm would have been one possibility, the preferred solution took *DRA*-values when rainfall was below *MDR* (the average R_{30} of *MDR* being 232.2 mm), i.e. when the forest received less water than 'expected' (Fig. 1). Both 'conditional accumulations' ($CARA_{100}$, $CARA_{232}$) highlighted the main droughts at Danum during the period of climate records.

If a low precipitation event is taken to have occurred when ARA_{365} was < 0 (events were allowed to be interrupted by up to 8 days without breaking continuity), 19 such events occurred at Danum between July 1985 and December 2003 (Appendix 1). Six events were less than 10 days in duration. The longest-lasting event was that in 1990–1993, followed by 1997–1998, 1986–1988 and 1993–1994. Drought intensity can thus be expressed as the sum of all daily rainfall anomalies (total *DRA*) within an event, the deficit in rainfall derived from the antecedent rainfall history (*DEFARH*).

Neglecting $R_{30} > 232$ mm ($CARA_{232}$), the 1997–1999 event was severest with $DEFARH = -1{,}846$ mm, followed by the 1990–1993 one with $DEFARH = -1{,}567$ mm (Appendix 1). In conclusion, between July 1985 and December 2003 three drought events were shown to be strong. Most severe was the one centred on 1998, followed by those centred on 1992 and 1987. The longest drought-free period by far was between April 1999 and March 2002.

Spectral analysis

The power spectral density function (or 'spectrum') was derived for several of the variables (Chatfield 2004; S-Plus 6 2001 version 7.0). Plots of $\log_{10}$ of spectral value versus $\log_{10}$ of frequency have characterizing slopes ranging from ~ 0 through -1 to ~ -2, these being commonly referred to as white, pink and brown noise, respectively (Steele 1985; Vasseur and Yodzis 2004). Results: *ADR*, -0.161; *DRA*, -0.153; R_{30}, -1.91; ARA_{365}, -1.96; $CARA_{100}$, -2.19; $CARA_{232}$, -1.98.

Forest dynamics

Overall response

Between periods P1 and P2, for all trees in plots, annualized mortality (m_a) and recruitment (r_a), and stem relative growth rate (*rgr*), increased by 45% (interval-corrected 25%), 12% and 12%, respectively (Table 1). Changes in the weighted means of the 34 most abundant species were very similar. Between period P1 and sub-period P2a, for small trees in subplots, m_a increased by 41% (interval-corrected 6%) but *rgr* decreased by 38%; and between period P1 and sub-period P2b the corresponding changes were increases of 51% (16%) and 11%. Thus, whilst m_a increased during the drought (P2a) and continued to rise slightly afterwards (P2b), *rgr* had a substantial decrease followed by a larger overcompensating increase. The weighted means of the 22 most abundant species at this level showed a similar response for m_a, but a stronger one for *rgr* (Table 1).

Table 1 Mortality (m_a), recruitment (r_a) and stem relative growth (rgr) rates for all (≥10 cm *gbh*) and small (10 to <50 cm *gbh*) in plots and subplots, respectively, over all individuals of all species

	m_a (% year^{-1})	r_a (% year^{-1})	rgr (mm m^{-1} year^{-1})
All trees/plots			
P1	1.59 (1.87)	1.24	11.14
P2	2.30 (2.34)	1.39	12.48
Small trees/subplots			
P1	1.54 (1.70)	1.31	10.85
P2a	2.17 (1.81)	–	6.79
P2b	2.32 (1.97)	–	13.36

Mortality values in parenthesis are 5.0-year interval corrected rates

Size class analysis

For all trees in the main plots the difference in m_a between periods P1 and P2 increased with tree size, and the R_{D1-2} became increasingly negative (Fig. 2a). Across the smaller size classes, for small trees in the subplots, trends were not apparent except in the 30–40 cm *gbh* class where m_a increased across periods and sub-periods (Fig. 2b). By contrast, for all trees in plots, rgr decreased roughly in parallel across size classes in periods P1 and P2 (Fig. 2c), but within the smaller size classes of small trees in subplots there was a strong change in relative differences between periods and sub-periods. In the lowest 10–20 cm *gbh* size class the decrease in rgr from period P1 to sub-period 2a, and the increase from sub-periods 2a to 2b, was much greater than in the highest 40–50 cm *gbh* class. The R_{D1_2a} and R_{D2a_2b}, respectively, increased and decreased in a linear manner with *gbh* (Fig. 2d).

Species dynamics

Plot and period scales

Between periods P1 and P2, the forest, as shown by the most abundant 34 species, became more dynamic (Table 2). Sample sizes are given in Appendix 2. Thirty-one species increased, and three decreased in m_a between P1 and P2 (Table 2). Species differed

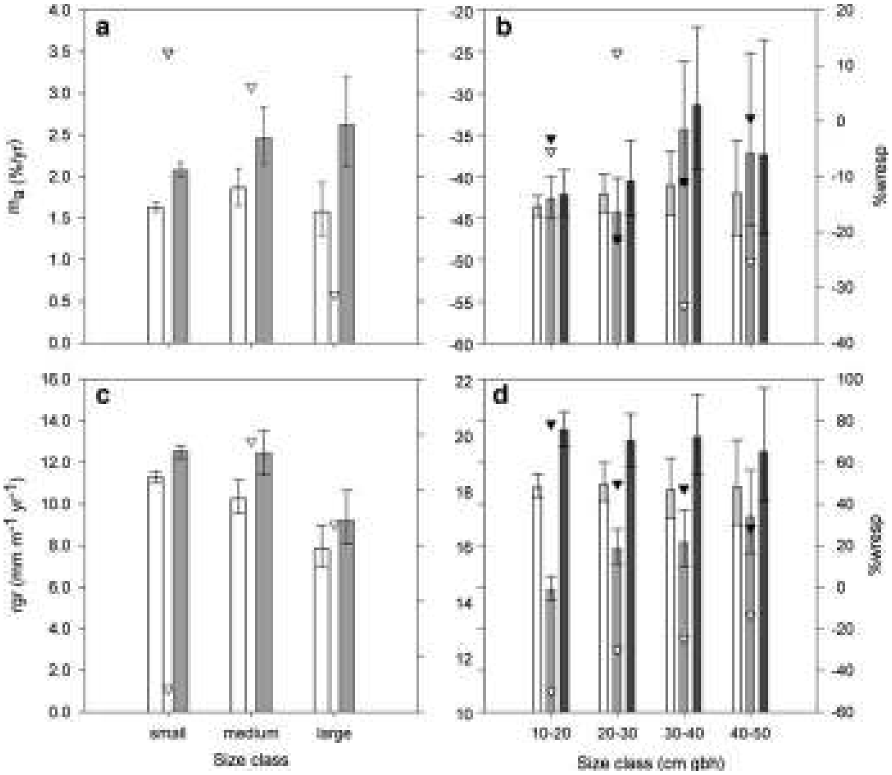

Fig. 2 Annualized mortality (m_a) (**a**, **b**) and relative stem growth (rgr) (**c**, **d**) rates for all trees within three size classes (see text for definitions) in the main plots (**a**, **c**) for periods P1 (open bars) and P2 (grey bars), and for small trees within four smaller size classes in the subplots (**b**, **d**) for period 1 (open bars), and sub-periods P2a (light grey bars) and P2b (dark grey bars) at Danum. Error bars indicate 95% confidence limits. Weighted percent changes (% wresp) are shown by inverted triangles: P1–P2 and P1–P2a (open) and P2a–P2b (closed)

Table 2 Mortality (m_a; % year^{-1}), recruitment (r_a; % year^{-1}) and relative (*rgr*; mm m^{-1} year^{-1}) growth rates in periods P1 and P2 for the 34 most abundant species within plots at Danum

Code	Species	m_a		r_a		*rgr*	
		P1	P2	P1	P2	P1	P2
aj	*Alangium javanicum* Koord.	1.27	3.45	0.86	2.45	7.99	6.99
an	*Antidesma neurocarpum* Miq.	3.20	3.64	1.12	1.17	3.01	5.56
af	*Aporosa falcifera* Hook. f.	1.74	2.00	0.74	0.00	12.12	10.61
as	*Ardisia sanguinolenta* Blume	1.14	1.87	1.79	2.68	11.24	11.33
bt	*Baccaurea tetrandra* Müll. Arg.	1.06	1.46	0.40	1.06	8.10	7.59
bl	*Barringtonia lanceolata* (Ridl.) Payens	0.29	1.41	0.68	1.07	5.47	7.11
cs	*Chisocheton sarawakanus* Harms	1.16	1.48	0.87	0.52	12.06	11.88
cc	*Cleistanthus contractus* Airy Shaw	1.17	1.26	0.67	1.64	6.89	9.60
dr	*Dacryodes rostrata* (Blume) H. J. Lam	0.75	1.26	0.26	0.00	7.97	6.64
dm	*Dimorphocalyx muricatus* (Hook. f.) Airy Shaw	1.05	1.07	0.59	0.85	5.43	8.00
dc	*Dysoxylum cyrtobotryum* Miq.	1.65	1.43	0.69	0.62	17.63	15.91
fs	*Fordia splendidissima* (Blume ex Miq.) J. R. M. Buijsen	1.13	1.88	1.76	1.95	10.21	12.22
gk	*Gonystylus keithii* Airy Shaw	0.77	1.11	1.17	1.51	11.34	14.22
kl	*Knema latericia* Elmer	0.22	0.49	1.96	0.36	12.24	13.02
ln	*Lithocarpus nieuwenhuisii* (Seem.) A. Camus	1.01	1.24	0.47	0.68	15.30	17.87
lc	*Litsea caulocarpa* Merr.	2.45	3.88	2.56	1.88	16.26	20.36
lo	*Litsea ochracea* Boerl.	1.73	4.33	0.95	1.47	13.54	11.05
lb	*Lophopetalum beccarianum* Pierre & Ridl.	0.79	0.88	2.01	1.23	15.24	18.95
mk	*Madhuca korthalsii* H. J. Lam	0.58	1.22	1.11	1.06	10.65	12.21
mp	*Mallotus penangensis* Müll. Arg.	1.23	1.57	2.35	2.34	11.74	14.94
mw	*Mallotus wrayi* King ex Hook. f.	1.55	1.99	1.21	1.59	9.10	11.58
mc	*Maschalocorymbus corymbosus* (Blume) Bremek.	3.67	3.53	1.39	2.17	8.24	9.90
pm	*Parashorea malaanonan* Merr.	1.91	2.82	0.65	0.59	14.03	14.84
pl	*Pentace laxiflora* Merr.	1.28	3.45	1.08	0.45	21.03	20.54
pc	*Polyalthia cauliflora* Hook. f. & Thomson	1.29	1.42	0.56	1.22	5.01	6.58
pr	*Polyalthia rumphii* Merr.	0.96	1.02	0.82	0.98	11.95	14.03
ps	*Polyalthia sumatrana* King	1.14	1.19	1.04	0.88	15.50	17.15
px	*Polyalthia xanthopetala* Merr.	2.82	4.79	1.76	0.00	9.50	10.20
rh	*Reinwardtiodendron humile* (Hassk.) D. J. Mabberly	2.59	4.13	0.71	1.20	6.19	6.43
sf	*Shorea fallax* Meijer	2.35	3.25	2.52	1.84	17.97	15.75
sj	*Shorea johorensis* Foxworthy	4.01	5.12	1.32	1.98	38.35	29.71
sp	*Shorea parvifolia* Dyer	3.71	4.67	1.32	3.11	43.78	37.41
se	*Syzygium elopurae* (Ridl.) Merr. & L. M. Perry	1.42	1.77	0.51	0.00	5.66	6.17
st	*Syzygium tawaense* (Merr.) Masam.	1.37	2.44	1.00	0.00	13.41	15.39
	Means						
	Unweighted	1.60	2.31	1.15	1.19	12.77	13.28
	Weighted*	1.55	2.11	1.22	1.38	11.08	12.34

Families are found in Appendix 2(a)

* By the number of trees per species at the start of each period

considerably in annualized mortality rate (m_a) with ranges of 0.22–4.01 widening to 0.49–5.12% year^{-1} between P1 and P2 (Table 2). Weighted average m_a in P2 was 36% higher than P1. During both periods, 21 species had lower, and 13 species had higher, than average m_a. Across the 34 species, m_a was significantly correlated between periods ($r = 0.850$, df = 32, $P < 0.001$).

For annualized recruitment rate (r_a) species also ranged widely from 0.26–2.56 in P1 to 0.00–3.11% year^{-1} in P2. Fourteen species decreased and 20 increased in r_a between P1 and P2. Weighted mean r_a was only slightly (0.17% year^{-1}) higher in P2 than P1. The r_a was also significantly correlated between periods ($r = 0.445$, df = 32, $P = 0.008$). Mean turnover increased from 1.37 to 1.75% year^{-1} between periods, and mean difference between m_a and r_a widened from 0.46 to 1.12% year^{-1}.

Twenty-three species had higher relative growth rate (*rgr*) in P2 than P1, and eleven lower *rgr*. Weighted mean *rgr* increased by 11%, although ranges in *rgr* contracted slightly from 3.0–43.8 to 5.6–37.4 mm m^{-1} year^{-1} (Table 2). Across species, ln(*rgr*) was strongly positively correlated between periods ($r = 0.943$, df = 32, $P < 0.001$). The m_a, r_a and *rgr* were only weakly to marginally significantly positively inter-correlated, however ($r = 0.214$ to 0.348, df = 32, $P = 0.043$ to 0.225). The mean m_a of the 34 species was lower than that for all trees in the plots, whilst for r_a and *rgr* the means were closer (Table 1).

Subplot and sub-period scales

Within the subplots, of the 22 most common species (Table 3; sample sizes in Appendix 2), individual species' mortality rates (m_a), which had a range of 0.55 to 3.86% year^{-1} in P1, became more variable in

Table 3 Annualized mortality (m_a; % year^{-1}) and relative growth rates (*rgr*, mm m^{-1} year^{-1}) in period P1 and sub-periods P2a and P2b for the 22 most abundant species within subplots at Danum

Code	Species	m_a			*rgr*		
		P1	P2a	P2b	P1	P2a	P2b
af	*Aporosa falcifera*	0.85	1.17	1.35	12.80	5.42	9.52
as	*Ardisia sanguinolenta*	1.28	1.45	2.59	12.35	4.88	13.59
bt	*Baccaurea tetrandra*	1.27	1.12	2.07	8.37	3.92	12.49
cc	*Cleistanthus contractus*	1.24	1.23	1.30	7.81	4.03	14.93
dr	*Dacryodes rostrata*	0.72	3.54	1.74	7.49	6.99	9.06
dm	*Dimorphocalyx muricatus*	0.95	1.78	0.37	5.26	3.72	16.54
dc	*Dysoxylum cyrtobotryum*	2.10	2.90	1.16	20.28	12.56	18.76
fs	*Fordia splendidissima*	0.99	2.31	3.09	9.52	5.99	12.22
lc	*Litsea caulocarpa*	2.32	7.39	3.04	18.20	11.58	18.23
lo	*Litsea ochracea*	1.43	1.58	5.83	16.98	8.08	10.19
lb	*Lophopetalum beccarianum*	0.57	0.00	0.00	15.11	14.32	24.39
mk	*Madhuca korthalsii*	0.55	0.72	1.70	10.35	7.71	12.44
mp	*Mallotus penangensis*	1.47	1.41	0.00	12.10	8.35	13.87
mw	*Mallotus wrayi*	1.49	2.00	1.99	9.08	5.73	14.83
mc	*Maschalocorymbus corymbosus*	3.86	3.44	8.28	8.44	4.45	11.80
pl	*Pentace laxiflora*	2.31	4.14	2.72	16.03	9.03	16.41
pc	*Polyalthia cauliflora*	1.28	1.41	2.03	4.77	2.63	7.37
pr	*Polyalthia rumphii*	1.00	0.00	3.59	8.60	6.81	17.91
ps	*Polyalthia sumatrana*	1.06	2.70	2.31	17.54	15.18	23.57
px	*Polyalthia xanthopetala*	3.06	9.96	4.01	11.17	9.01	12.50
rh	*Reinwardtiodendron humile*	3.18	4.06	4.45	4.97	−2.46	7.84
sf	*Shorea fallax*	2.10	4.57	4.76	17.51	6.80	8.67
	Means						
	Unweighted	1.59	2.68	2.65	11.60	7.03	13.96
	Weighted*	1.52	2.26	2.26	10.11	6.08	14.11

* As Table 2

subperiods P2a and P2b where two species each had zero mortality, and maximum values were 10.0 and 8.3% year^{-1}, respectively (Table 3). Sixteen of the 22 species showed increases in m_a in P2a compared to P1. Six species decreased in m_a. Between P2a and P2b, 12 species increased and nine species decreased in m_a; and one species remained at zero mortality. Weighted mean m_a increased between P1 and P2a by 50% but then did not change in P2b. For *rgr* all species decreased between P1 and P2a, and all increased between P2a and P2b (Table 3).

Hypothesis testing of species' responses

Each set of 34 species' *P*-values from the randomization tests of $R_{D\_1,2}$, for m_a, r_a, *rgr* and *cmp*, were ranked from smallest to largest separately. The condition of a one-step procedure for multiple (simultaneous) testing that *P*-values be uniformly distributed was tested with the χ^2-statistic (df = 4) on frequencies in five bins of 0.2 between 0 and 1 (expected frequency in each = 6.8). The observed distributions were significantly non-uniform for r_a ($\chi^2 = 37.47$, $P <<0.0001$) and *cmp* ($\chi^2 = 21.59$, $P < 0.001$), but not for m_a ($\chi^2 = 4.53$, $P > 0.3$) and *rgr* ($\chi^2 = 5.41$, $P > 0.2$). Holm's sequential step-down procedure (Holm 1979) was used accordingly.

There existed a very low degree of logical interdependence between values when randomizing (without replacement) across species, i.e. one dead tree or recruit allocated to any one of the 34 species cannot be allocated to any of the others, or a high or low *rgr* value allocated to one species cannot be given to another species. The means (±SE) of the 528 pair-wise Pearson correlation coefficients ($N = 5{,}000$ simulated values) for each of the four variables, and the percentage variance accounted for by principal components analysis (based on *r*) on the first three axes, showed that the correlations involved were in fact negligible (Appendix 3).

For the 22 species of small trees in the subplots testing of responses for m_a was restricted. In an appreciable percentage of the randomization runs double-zero cases for the numbers of dead trees meant that R_D could not be found, and substitution of so many results with $R_D = 0$ would have been unsatisfactory. Furthermore, many species (15/22 with zero r_a -values c. 50–800 times out of 5,000) had 95%, and often 99%, upper and lower confidence limits at the maximum or minimum of R_D possible, and so rejection of the individual-species' null hypotheses was largely impossible.

Species' response indices

Plot and period scales

Most species had increased R_D-values for m_a in P2 compared to P1, about equal numbers had increases and decreases in r_a, two-thirds increases in stem *rgr*, and two-thirds decreases in *cmp* (Fig. 3). The randomization tests followed by family-wise error rate adjustment highlighted one significant ($P < 0.01$) negative case for m_a (*Barringtonia lanceolata*) and one positive case for *rgr* (*Dimorphocalyx muricatus*) (Fig. 3a, c). For r_a, five species (*Aporosa falcifera*, *Dacryodes rostrata*, *Polyalthia xanthopetala*, *Syzygium elopurae* and *S. tawaense*) showed significantly ($P < 0.01$) negative responses, one other (*Knema latericia*) less so ($P < 0.05$); two species (*Cleistanthus contractus* and *Baccaurea tetrandra*) responded significantly and positively ($P < 0.05$) (Fig. 3b). Of 34 species, only one (*D. muricatus*) showed a significant *cmp* response (positive, $P < 0.01$; Fig. 3d).

Allowing for a ≤ 5% false discovery rate (FDR), the analysis revealed just three further significant ($P < 0.05$) cases for r_a (negative—*Pentace laxiflora*, positive—*Polyalthia cauliflora* and *Shorea parvifolia*), and for *rgr* ($P < 0.01$) one more (positive—*Mallotus wrayi*) (Fig. 3b, c). The rate of increase in R_D per ranked-species (linear regression line) was highest for r_a (7.57%), less for m_a (3.59%) and lowest for *rgr* (1.90%), with *cmp* between m_a and *rgr* (2.47%). The R_{D1_2} of m_a, r_a and *rgr* were not significantly correlated with one another ($r = 0.047$ to 0.132, df = 32, $P > 0.25$). Mean m_a of the 34 species was lower than that of all trees in the plots, whilst for r_a and *rgr* it was close (Fig. 3). Note that among the positively responding species one, aj, in Fig. 3b was not significant because its sample size was the smallest of all species ($n = 101$), compared with the four significant species ($n = 206 - 324$): see Appendix 2 for full range of sample sizes. Applying the Bernoulli formula, a minimum of $k = 2$, 5, 3 and 2 (out of 34) individually significant results would have been needed to meet a family-wise level of $\alpha = 0.05$. On this basis r_a qualified with

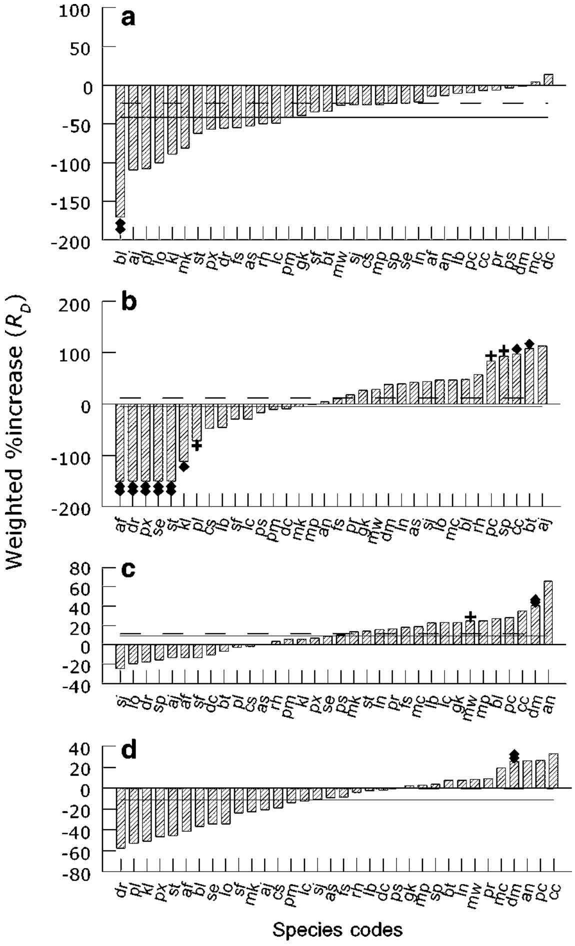

Fig. 3 Weighted percent changes between periods P1 (1986–1996) and P2 (1996–1999) in **a** mortality (m_a, inverted scale), **b** recruitment (r_a), **c** relative growth rate (*rgr*) and **d** a composite index (*cmp*) of the three variables, ranked for the 34 most common species in the main plots at Danum: solid line, weighted mean of the 34 species; dashed line, the overall values for all trees in plots. Codes for species are explained in Table 2. Species significance, determined by randomization tests and family-wise adjusted probability levels, is signified by number of diamonds over/under bars: two, $P \leq 0.01$; one, $P \leq 0.05$; and none, ns or $P > 0.05$. Crosses above bars indicate species additionally significant ($P \leq 0.05$) after controlling for false discovery rate

eight strong and three protected cases, but not m_a, *rgr* and *cmp*.

Subplot and sub-period scales

Within subplots three-quarters of the 22 species showed an increase in R_D-values for m_a in P2a and in P2b compared to P1: between P2a and P2b increases balanced decreases (Fig. 4a–c). Despite the wide range in responses none could be shown to be significant ($P \leq 0.05$). All species had lower *rgr* in P2a than P1, all higher *rgr* in P2b than P2a which led to three-quarters with higher *rgr* in P2b than P1 (Fig. 4d–f). Randomization tests showed just one species with a significantly ($P \leq 0.01$) reduced *rgr* between P1 and P2a (*R. humile*), two with similarly significant increases between P2a and P2b (*R. humile*, *D. muricatus*) and P1 and P2b (*D. muricatus*, *Mallotus wrayi*), and one decrease ($P \leq 0.05$) in the last (*Shorea fallax*). Allowing for the FDR level led to no further significant cases.

Rates of increase in R_D with ranked species (outlier *R. humile* excluded) were similar for R_{D1-2a}, R_{D2a-2b} and R_{D1-2b} using m_a (11.8, 12.9 and 12.7 respectively), but increased for *rgr* (3.10, 4.97 and 6.61). Again, R_D for m_a and *rgr* were not significantly correlated within each of the (sub-) periods ($r = -0.103$ to 0.284, df = 20, $P \geq 0.20$). R_{D1-2a} and R_{D2a-2b} were significantly negatively correlated for m_a ($r = -0.497$, $P = 0.019$) and *rgr* ($r = -0.854$, $P < 0.001$); and conversely R_{D1-2b} and R_{D2a-2b} significantly positively so for m_a ($r = 0.735$, $P < 0.001$) and *rgr* ($r = 0.428$, $P = 0.047$): R_{D1-2a} and R_{D1-2b} being insignificantly correlated for m_a and *rgr* ($P > 0.45$). Mean m_a of the 22 species was very close to that for all trees in the plots, although for *rgr* it differed slightly (Fig. 4). Applying the Bernoulli formula again, a minimum of $k = 2$, 2 and 3 out of 22 individually significant results were needed to qualify for family-level significance. This requirement was met for *rgr* in sub-periods 2a–2b and period 1—sub-period 2b (Appendix 3).

Since m_a remained insignificant at the family level when the less conservative FDR procedure was applied to the 34 species, and the relationship between m_a and size (*gbh*) within the small trees was weak, it may be reasonably inferred that differences at the 22 species level would be insignificant too. Mortality was also likely to have shown much less response that *rgr* when moving from a 5.0-year to a 2.5-year period.

Between-scales correlation

The 16 subplots were nested stratified random subsamples of the plots. Selecting the dynamics variables for the same 22 species studied at the subplot level

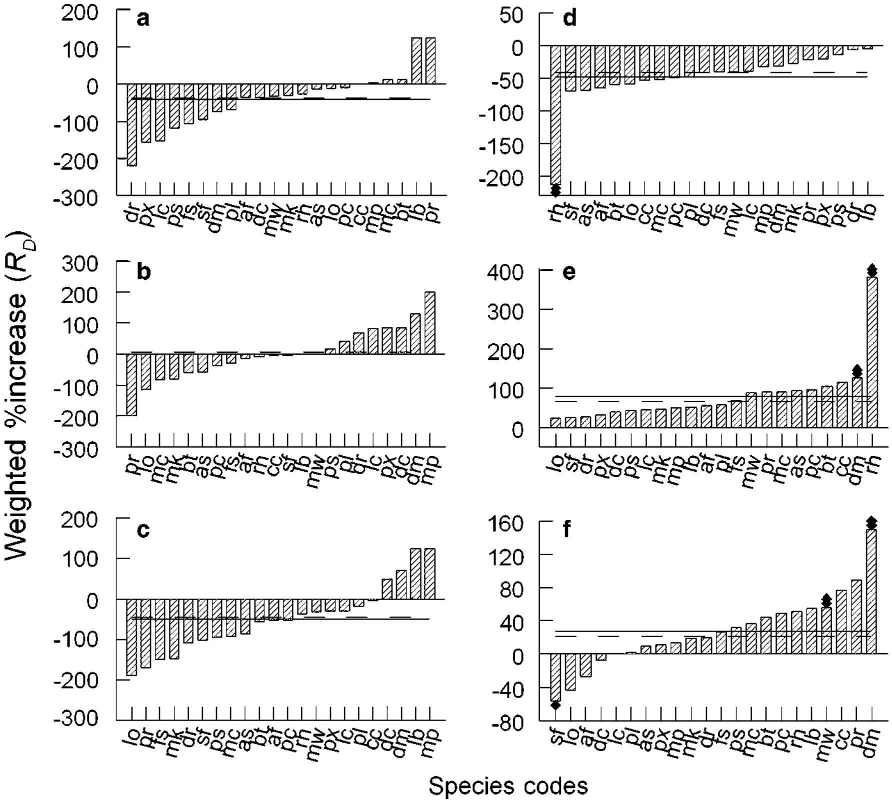

Fig. 4 Weighted percent changes in **a**–**c** mortality rate (m_a, inverted scale) and **d**–**f** relative growth rate (*rgr*) between period P1 (1986–1996) and sub-periods P2a (1996–1999) and P2b (1999–2001), as (**a** and **d**) P1–P2a, (**b** and **e**) P2a–P2b and (**c** and **f**) P1–P2b; ranked for the 22 most common species in the subplots at Danum. Lines, significance levels and species codes as in Fig. 3

from the 34 used at the plot level, the trends across species were in good agreement. Mortality rate and *rgr* for P1 were each strongly correlated between the subplot and plot levels ($r = 0.912$ and 0.919 respectively), and correspondingly so were mean rates of P2a and P2b at the subplot level and those for P2 at the plot level ($r = 0.877$ and 0.782). The correlation between $R_{\mathrm{D}1\text{–}2}$ and the average of $R_{\mathrm{D}1\text{–}2a}$ and $R_{\mathrm{D}1\text{–}2b}$ for the 22 of 34 species at the subplot level were significant for m_a ($r = 0.468$, df $= 20$, $P = 0.028$) and for *rgr* ($r = 0.646$, $P < 0.001$) indicating that the subplot sampling was a good representation of the plot for the species' responses also. Correlations between *rgr* in period P1, and $R_{\mathrm{D}1\text{–}2}$ for *rgr*, for 21 species in the subplots (rh omitted again) with the subsequent m_a in sub-periods P2a and P2b, and $R_{\mathrm{D}1\text{–}2a}$, $R_{\mathrm{D}1\text{–}2b}$ and $R_{\mathrm{D}2a\text{–}2b}$, were all insignificant ($r = -0.332$ to 0.224, df $= 19$, $P = 0.13$ to 0.94).

Stability analysis

Analysis for m_a, showed that octants 2′ and 3′ were unoccupied, most species fell in 4′–6′, and a few in 1′, 7′ and 8′ (Fig. 5a)—a wide range of trajectory dynamics. For *rgr*, 1′–5′ were empty, most species were in 7′ and 8′ and a few in 6′ (Fig. 5b)—a largely stabilizing response. Octants 1′ up to 4′ may be described, respectively, as over-enhanced, enhanced, not enhanced and under-enhanced, whilst 8′ down to 5′ as over-recovered, recovered, not recovered and under-recovered. Thus, in terms of m_a most species either did not recover or they under-recovered, whilst in terms of *rgr* most species recovered or over-recovered. The species that 'benefited' from, or were promoted by, the drought were in 1′ and 8′, while those that suffered or were disadvantaged were in 4′ and 5′. Four species (if *Dimorphocalyx muricatus* very close to the line is allowed) were thus promoted in terms of m_a and eight (including *Polyalthia cauliflora* on the line) in terms of *rgr* (Fig. 5). One species, *Cleistanthus contractus*, had zero change in m_a and therefore appeared resistant.

Post-drought response in growth was strongest for understorey species. Across the 16 species which were > 0.75 composed of very small (10 to <30 cm *gbh*) stems, $R_{\mathrm{D}2a\_2b}$ and $R_{\mathrm{D}1\_2b}$ for *rgr* increased

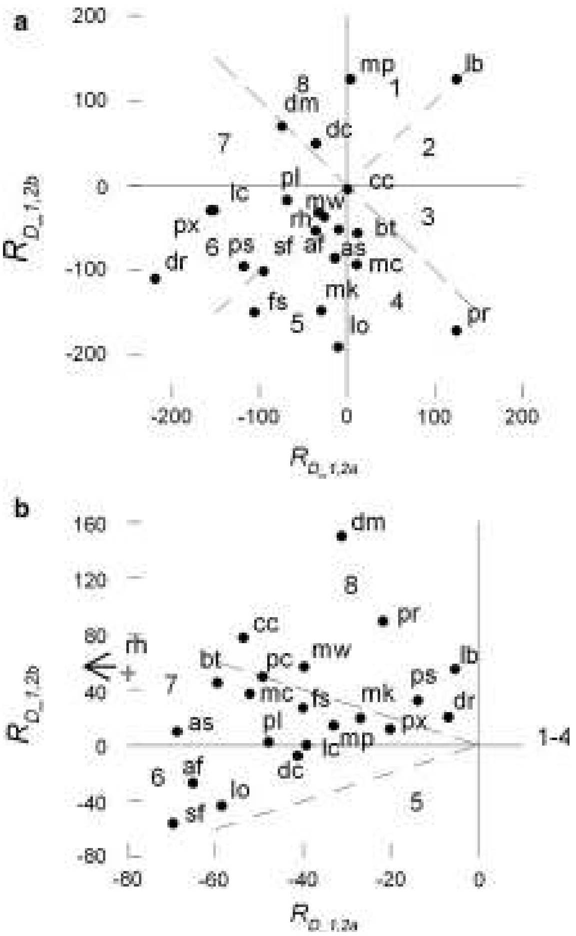

Fig. 5 Weighted percent changes of **a** mortality rate (m_a, inverted scale) and **b** relative growth rate (*rgr*), between period P1 (1986–1996) and sub-period P2a (1996–1999) plotted against the same between period P1 and sub-period P2b (1999–2001) for the 22 most common species in the subplots at Danum. Codes for species are explained in Table 2; rh has an *x*-axis value of −213. Octant numbers 1′–8′ are shown without primes

significantly with this proportion ($F = 15.9$ and 5.22, $\mathrm{df} = 1,\ 14$; $P = 0.001$ and 0.038; resp.; Fig. 6) although for R_{D1_2a} the relationship was not significant ($F = 0.38$, $P = 0.55$).

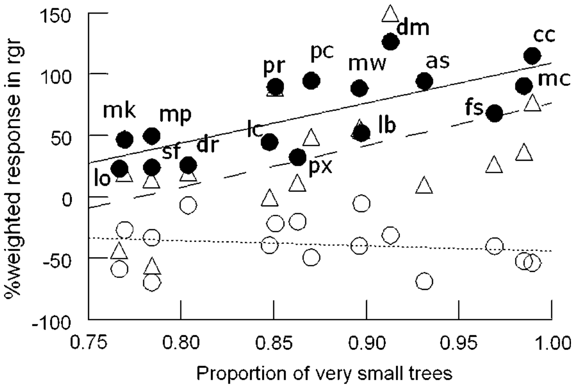

Fig. 6 Weighted percent changes (R_D) in relative stem growth rate (*rgr*) between period P1 and sub-period P2a (open circles), sub-periods P2a and P2b (closed circles) and period P1 and sub-period P2b (open triangles) regressed against the proportion of very small trees, *pvs* (10–30 cm *gbh*) for those 16 species in the subplots at Danum which had ≥ 0.75 of their small-tree stems in this size class. $R_{D1\text{–}2a} = -1.5 - 42.5\ pvs$; $R_{D2a\text{–}2b} = -216 + 325\ pvs$; and $R_{D1\text{–}2b} = -265 + 342\ pvs$ (see text for statistics). Extrapolated $R_{D1\text{–}2a}$ and $R_{D1\text{–}2b}$ lines cross at $pvs = 0.685$. Codes for species (upper line) are explained in Table 2; codes for other lines may be found by down projection

Discussion

Resilience of the tree community

During the 1997/1998 ENSO the rainfall in April reached an exceptionally low value. Based on the concept of antecedent rainfall history, the conditional accumulated rainfall deficit also then fell to its lowest level during the period of recording, highlighting the importance of the 1997/1998 event (Fig. 1). The 1982/1983 event (Walsh 1996a, b; Walsh and Newbery 1999; Newbery and Lingenfelder 2004) may have affected Danum to a similar extent and less extreme lows (relevant to the period of forest measurements here) were found in 1987 and 1992.

Drought evidently perturbed, but did not disturb, the forest at Danum: its effect on tree mortality was quite small overall. The forest community, nevertheless, showed a high resilience to the 1997/1998 event, with immediate negative *rgr* responses followed by recovery. This suggests that interspecific variation in drought responses may be driving community dynamics. Recruitment of about a third of the common species decreased or increased significantly within 5 years: mortality, however, appeared to be much less species-specific. Using family-wise statistical procedures, the forest community overall was shown to have been significantly affected. The ‘family’ is the community in the present context.

The interpretation is that stochastic environmental variation in accumulated rainfall deficit primarily controls tree growth rate (through a limitation in water supply); and recruitment is growth-dependent because saplings advance into the smallest size class enumerated. Species differ in susceptibility to increasing deficit because of their differences in morphology and physiology (Gibbons and Newbery 2002). In this way the dynamics of the forest and its tree community interactions are largely reducible to, and understandable in terms of, the plant-environment physical processes in operation.

Drought is a complex factor and the physical variables behind it can have a distinctive signal. Spectral analysis showed that raw rainfall values from Danum displayed white noise (low and high frequencies evenly distributed) yet the various accumulated drought indices all indicated brown noise with a higher proportion of contributions from low frequencies. On this basis realizations of rainfall depletion are stochastic in nature. Only long-term measurements that capture forest dynamics before and after an event for several years are therefore likely to provide sufficient relevant information.

Because the driving water deficit variable is stochastic, none of the species can 'tune in' to regular cycles and each is continually experiencing immediate and lagged effects of the perturbations. Neighbourhood competitive interactions would also be expected to be undergoing continual change. This leads to complex yet predictable dynamics in the short-to-medium term (10–50 years), which—if stationarity holds—might be expected to average out towards quasi-constant structural and species composition in the longer term (50–200 years).

The conditional accumulated rainfall anomaly variable represents what the tree is likely to experience over time. Arguably, relatively high as opposed to low antecedent rainfall will, respectively, buffer, or make more susceptible, the forest over those months preceding a period of strong rainfall deficit. Such a formulation has not hitherto been made for trees, let alone tropical ones. This is illustrated by the inferred weak effect in 1991/1992 versus strong effect of drought in 1997/1998. Better growing conditions presumably lead to more stored water which allows trees to ameliorate the drought effect.

Perturbation response niche

Species-specific responses were very different which leads here to the idea of a perturbation response niche. Different species having greater-than-average restrictions in growth and reduced recruitment in drought periods would be expected to compensate in the wetter inter-event periods; those enhanced by, or over-compensating to, the drought are likely at competitive disadvantage in the wetter periods (currently under test). Further, differentiation of the niche would be emphasized by the effect of topography acting through soil water relations, i.e. ridges being drier than lower slopes. The concept is somewhat akin to the regeneration niche of Grubb (1977) where in the former case time is more important, whilst in the latter it is space.

The new results accord well with the spatial distributions of the common understorey species across the two plots with respect to topography. *Dimorphocalyx muricatus*, *Cleistanthus contractus* and *Lophopetalum beccarrianum*, in decreasing order of importance, cluster and are associated on drier ridge locations at Danum (Newbery et al. 1996). The first showed strong positive *rgr* and *cmp* responses to drought perturbation (Figs. 3, 4), the second positive r_a, *rgr* and *cmp*, and the third reduced mortality responses—as did *Polyalthia rumphii* and *Mallotus penangensis* (Fig. 3). Additionally, *Polyalthia cauliflora* showed a positive increase in r_a (Fig. 2). Those mentioned are the six species in the outer sector or octant 8′ in Fig. 5b, and it underlines the likely central driving role of *rgr* in species' dynamics in response to drought. Three addenda are: (1) for the seven species with negative r_a we have no explanation at present; (2) *Mallotus wrayi*, the ubiquitous numerically dominant species, responded positively to drought in terms of *rgr*; (3) *Reinwardtiodendron humile* is a potential drought phytometer. Importantly, all those species just discussed are understorey taxa (Newbery et al. 1992, 1996, 1999a, b).

No correlation at the species level between *rgr* in period P1 and m_a in subperiods P2a and P2b was detectable, suggesting that faster or slower growing species were neither more nor less affected by the drought. Species appeared to respond over time in a highly idiosyncratic manner, each species with its own trajectory.

That larger trees died more often than smaller ones under drought meant that a moderate degree of random canopy opening followed the defoliation observed and evidenced by a large increase in small end branch abscission (Walsh and Newbery 1999). The drought-adapted small-stemmed understorey species (many in the Euphorbiaceae) were able to benefit from the temporarily increased light levels. This in part corroborates the understorey facilitation hypothesis (Newbery et al. 1999; Newbery and Lingenfelder 2004), which proposes that drought-tolerant or drought-avoiding understorey species in some Bornean rain forests nurse saplings and small trees of the drought-sensitive canopy species (particularly of the canopy-forming Dipterocarpaceae), through the crucial dry periods. The saplings of the canopy species are thought to be protected from the direct light and drier conditions caused by canopy opening.

Complex forest dynamics driven by perturbations

The most remarkable general result from this study is that the common species at least show highly specific and different dynamics from one another. Furthermore, different species responded differently to drought, to varying degrees, sooner or later after the event, and with more or less extent of recovery. The oscillating dynamics of several species is what might be expected of a system that is moderately perturbed and returning to an equilibrium (Botkin and Sobel 1975; DeAngelis and Waterhouse 1987; Ives 1995). The impression of all these changing patterns of dynamics and their interactions can be likened to a kaleidoscope. The challenge is to find the attractor which bounds the system: this may be the topographic gradient.

The results do not sit well though with the suppositions of the recently debated neutral theory of biodiversity for tropical forests (Hubbell 2001, 2005, 2006). In that thesis equivalence of species and individuals, and random mortality, lead to weakly diffuse competitive interactions and a slow non-adaptive drift in species composition over time. That species could be so ecologically and evolutionary similar has been often challenged (Chave 2004; Bell 2005; Purves and Pacala 2005; Bell et al. 2006): the theory says any differences that do occur are of little consequence. Under the neutral theory the patterns of species' responses and dynamics recorded at Danum would presumably be labelled as 'random'; which seems highly implausible to us given the supporting ecological information on forest structure and tree physiology (Gibbons 1998; Gibbons and Newbery 2002), and the topographic gradient effect on species patterning (Newbery et al. 1996).

There is then an underlying structure to the forest community at Danum, which is determined to a large degree by the species-specific dynamic responses to perturbation. This tends to refute neutrality and species equivalence, rather the forest at Danum functions on the basis of *plurality* of species' responses. A further serious and over-looked problem with the neutral theory is that it assumes a constant environment. This too seems not to be the case at Danum, and is arguably unlikely to be realistically so anywhere, including the tropics.

A possible alternative to the descriptive neutral theory (which in any case is very difficult to test directly, if at all) is to take a dynamic ecosystems approach (Shugart 1998) in which testable mechanisms and processes may allow understanding of structural equilibria (or dis-equilibria) in multi-species population dynamics with reference to a measured stochastically varying environment (May 1974; Ives and Carpenter 2007). It has been shown theoretically that a stochastic environment can result in community stability (Chesson 1982; Chesson and Huntly 1997), and possibly a plurality of responses might play an important role. One caveat to the present work, however, is that only one ENSO event was followed. Predicting and testing for similar patterns of response after future events will be valuable.

This new postulate does not attempt to explain species diversity per se but aims primarily at quantifying, and finding the limits to, complex forest community dynamics. Rare species, for which data will be always insufficient to make reliable estimates of dynamics parameters, could be treated as being neutral (i.e. as indeterminate), whilst the common species, for which estimates can be made reliably a non-neutral way (determinate), could be followed over time using physical, physiological and statistical models.

Apart from large historical disturbances, stochastic droughts perturb the forest at Danum on a short time scale and the forest appears to accommodate them by being resilient. This may work up to a certain threshold of frequency and intensity, one to which the main constituent species are avoidance- or tolerance-adapted. But if, as a result of prognosticated climatic change, droughts were to increase, then higher tree mortality rates and longer periods of restricted growth would be expected to ensue, the latter inevitably lowering critically the recruitment of many species to the extent that they may not recover in the shortened inter-drought periods; and hence an end-effect change in forest structure and species composition. With the continuing long-term observations at Danum, it might soon be possible to model different scenarios with statistical confidence, and on that basis take the necessary measures to conserve the lowland tropical rain forests of Borneo in its original and natural form of a mosaic of perturbed and, it seems, resilient ecosystems.

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Appendix 1

Climate

The low precipitation events at Danum 1985–2003

Event[a]	Start	End	Duration (d)	*DEFARH* (mm)[b]
1	8/30/86	5/1/88	610	−905.1
2	11/7/88	12/7/88	31	−38.1
3	2/13/89	2/20/89	8	−7.5
4	3/29/89	5/13/89	44	48.9
5	6/1/89	6/6/89	6	n.a.[c]
6	10/23/90	3/23/93	883	−1,566.9
7	6/18/93	6/3/94	351	−357.3
8	6/15/94	6/23/94	9	−65.8
9	9/15/94	9/23/94	5	−17.8
10	10/25/94	11/1/94	6	−28.5
11	4/2/95	5/27/95	56	−8.6
12	6/29/95	8/13/95	44	−91.8
13	1/18/97	4/15/99	818	−1,846.0
14	3/18/02	6/26/02	101	−25.4
15	7/10/02	9/2/02	54	21.7
16	11/1/02	11/25/02	23	−73.9
17	12/4/02	3/26/03	112	−126.4
18	6/27/03	6/29/03	3	9.8
19	9/3/03	9/26/03	24	17.0

[a] When $ARA_{365} < 0$

[b] (Total *DRA*) when $ARA_{365} < 0$ and $R_{30} < 232$ mm

[c] $\mathrm{ARA}_{365} < 0$ but $\mathrm{R}_{30} > 232$ mm across all 6 days

Appendix 2

Trees

Appendix 2(a) Sample sizes at the start of the periods P1 and P2 (n_{86}, n_{96}) and corresponding numbers of valid trees (nv_{P1}, nv_{P2}) for the calculation of annualized mortality (m_a; % year^{-1}) and recruitment (r_a; % year^{-1}) rates, and relative (rgr; mm m^{-1} year^{-1}) growth rates, in periods P1 and P2 for the 34 most abundant species (and their families) at Danum

Species	Family*	m_a and r_a		rgr	
		n_{86}	n_{96}	nv_{P1}	nv_{P2}
Alangium javanicum	Alan	101	91	69	60
Antidesma neurocarpum	Euph	119	100	77	70
Aporosa falcifera	Euph	261	238	157	143
Ardisia sanguinolenta	Myrs	568	591	430	444
Baccaurea tetrandra	Euph	250	233	189	168
Barringtonia lanceolata	Lecy	141	147	129	120
Chisocheton sarawakanus	Meli	155	150	116	105
Cleistanthus contractus	Euph	289	273	223	212
Dacryodes rostrata	Burs	153	145	130	118
Dimorphocalyx muricatus	Euph	840	801	667	645
Dysoxylum cyrtobotryum	Meli	170	155	129	122
Fordia splendidissima	Legu	520	543	394	414
Gonystylus keithii	Thym	121	126	104	101
Knema latericia	Myri	141	166	128	140
Lithocarpus nieuwenhuisii	Faga	125	115	94	70
Litsea caulocarpa	Laur	322	319	197	215
Litsea ochracea	Laur	163	147	115	95
Lophopetalum beccarianum	Cela	234	267	200	221
Madhuca korthalsii	Sapo	508	532	433	429
Mallotus penangensis	Euph	204	233	172	196
Mallotus wrayi	Euph	2,268	2,207	1,781	1,723
Maschalocorymbus corymbosus	Rubi	403	335	245	243
Parashorea malaanonan	Dipt	149	133	111	93
Pentace laxiflora	Tili	240	214	163	145
Polyalthia cauliflora	Anno	324	302	271	258
Polyalthia rumphii	Anno	141	138	119	119
Polyalthia sumatrana	Anno	222	221	192	186
Polyalthia xanthopetala	Anno	241	223	172	156
Reinwardtiodendron humile	Meli	262	221	166	140
Shorea fallax	Dipt	371	395	264	298
Shorea johorensis	Dipt	197	157	82	72
Shorea parvifolia	Dipt	206	170	124	104
Syzygium elopurae	Myrt	134	120	100	97
Syzygium tawaense	Myrt	124	120	85	74
Totals		10,667	10,328	8,028	7,796

* Family abbreviations; Alan, Alangaceae; Anno, Annonaceae; Burs, Burseraceae; Cela, Celastraceae; Dipt, Dipterocarpaceae; Euph, Euphorbaceae; Faga, Fagaceae; Laur, Lauraceae; Lecy, Lecythidaceae; Legu, Leguminosae; Meli, Meliaceae; Myrs, Myrsinaceae; Myrt, Myrtaceae; Rubi, Rubiaceae; Sapo, Sapotaceae; Thym, Thymelaceae; Tili, Tiliaceae

Appendix 2(b) Sample sizes at the starts of period P1 (n_{86}) and sub-periods P2a and P2b (n_{96}, n_{99}) and corresponding numbers of valid trees (nv_{P1}, nv_{P2a}, nv_{P2b}) for the calculation of annualized mortality rates (m_a; % year^{-1}), and relative growth rates (rgr, mm m^{-1} year^{-1}), for the 22 most abundant species within subplots at Danum

Species	m_a			rgr		
	n_{86}	n_{96}	n_{99}	nv_{P1}	nv_{P2a}	nv_{P2b}
Aporosa falcifera	74	65	62	57	54	57
Ardisia sanguinolenta	166	138	130	125	114	109
Baccaurea tetrandra	76	66	62	57	52	55
Cleistanthus contractus	118	103	97	85	75	86
Dacryodes rostrata	58	54	48	51	45	40
Dimorphocalyx muricatus	276	250	236	227	209	213
Dysoxylum cyrtobotryum	53	41	36	39	32	32
Fordia splendidissima	157	134	122	119	105	101
Litsea caulocarpa	105	72	56	66	52	46
Litsea ochracea	60	49	45	47	42	35
Lophopetalum beccarianum	71	66	63	64	60	56
Madhuca korthalsii	112	103	98	97	89	86
Mallotus penangensis	57	48	45	48	44	44
Mallotus wrayi	713	612	573	569	517	493
Maschalocorymbus corymbosus	120	80	71	65	58	52
Pentace laxiflora	58	36	31	34	27	26
Polyalthia cauliflora	123	108	104	104	97	94
Polyalthia rumphii	53	48	47	46	45	41
Polyalthia sumatrana	50	43	36	45	35	31
Polyalthia xanthopetala	59	42	32	41	30	26
Reinwardtiodendron humile	76	55	48	49	42	40
Shorea fallax	85	64	55	62	51	43
Totals	2,720	2,277	2,097	2,097	1,875	1,806

Appendix 3

Tests

Appendix 3(a) Means (±SE) of 34-spp pair-wise correlations ($n = 528$) for each of four dynamics variables and % variance accounted for by first three axes of corresponding principal components analyses

	Coefficient r	1*	2	3
m_a	−0.014358 ± 0.000732	3.48	3.41	3.35
r_a	−0.014434 ± 0.000738	3.49	3.43	3.41
rgr	−0.014838 ± 0.000778	3.49	3.39	3.35
cmp	−0.014510 ± 0.000777	3.55	3.42	3.37

* % Var. = 100/34 = 2.94 had all axes been equal

Appendix 3(b) Species which had significant differences in their dynamics variables from random expectation adjusted for multiple hypothesis testing: 34 species in plots

Variable	Species codes#	Holm (Sidak) adjusted P	Family-wise P
m_a	bl	0.001508	0.0068
r_a	af, dr, px,se, st	0.001605	0.0068
	kl	0.001767	0.0116
	bt,cc	0.001804	0.0220
rgr	dm	0.001508	0.0068
cmp	dm	0.001508	0.0068

species codes are those of Table 2 in the main text

The Benjamini-Hochberg step-up FDR procedure gave the same results as the Holm step-down one for m_a and cmp; but for r_a three further species were significant: pc, pl and sp (adjusted $P = 0.0132$, 0.0147 and 0.0162 resp.), and for rgr there was one further case: mw (adjusted $P = 0.0029$). Note that mw was ranked 4th highest yet was significant (unlike pr and cs) due to its very much larger population size (maximum in Appendix 2)

Appendix 3(c) Species which had significant differences in their *rgr* from random expectation adjusted for multiple hypothesis testing: 22 species in subplots

Period	Species codes#	Holm (Sidak) *P*	Family-wise *P*
P1-P2a	rh	0.002329	0.0044
P2a-P2b	rh	0.002329	0.0044
	dm	0.002440	0.0042
P1-P2b	dm	0.002329	0.0044
	mw	0.002440	0.0084
	sf	0.002500	0.0400

\# Species codes are those of Table 2 in main text

The FDR procedure resulted in the same results, i.e. no additionally significant species

Appendix 3(d) Bonferroni minimum *P*-critical values from the step-down FDR procedure which are used in the Bernoulli formula

1. P1 − P2: m_{a}, 0.0002; r_{a}, 0.0152; *rgr*, 0.0024; *cmp*, 0.0024
2. *Rgr*: P1 − P2a, 0.0002; P2a − P2b, 0.0002; P1 − P2b, 0.0020

References

Alder D (1996) Growth modelling for mixed tropical forests. Forestry Papers No. 30. (Oxford Forestry Institute, Oxford. Beaman RS, Beaman JH, Marsh CW, Woods PV (1985) Drought and forest fires in Sabah in 1983. Sabah Soc J 8:10–30

Bell G (2005) The co-distribution of species in relation to the neutral theory of community ecology. Ecology 86:1757–1770. doi:10.1890/04-1028

Bell G, Lechowicz MJ, Waterway MJ (2006) The comparative evidence relating to functional and neutral interpretations of biological communities. Ecology 87:1378–1386. doi:10.1890/0012-9658(2006)87[1378:TCERTF]2.0.CO;2

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B 57:289–300

Botkin DB, Sobel MJ (1975) Stability in time-varying ecosystems. Am Nat 109:625–646. doi:10.1086/283034

Brünig EF (1969) On the seasonality of droughts in the lowlands of Sarawak (Borneo). Erdkunde 2:127–133

Brünig EF (1971) On the ecological significance of drought in the equatorial wet evergreen (rain) forest of Sarawak (Borneo). In: Flenley JR (ed) Transactions of the 1st symposium on Malesian ecology. Geography Department, University of Hull, UK, pp 66–97

Cane MA (2005) The evolution of El Niño, past and future. Earth Planet Sci Lett 230:227–240. doi:10.1016/j.epsl.2004.12.003

Chatfield C (2004) The analysis of time series, 6th edn. Chapman and Hall, London, UK

Chave J (2004) Neutral theory and community ecology. Ecol Lett 7:241–253. doi:10.1111/j.1461-0248.2003.00566.x

Chesson PL (1982) The stabilizing effect of a random environment. J Math Biol 15:1–36. doi:10.1007/BF00275786

Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am Nat 150:519–553. doi:10.1086/286080

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, et al. (2007) Regional climate projections, Chap. 11. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt K, et al. (eds.), Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK, pp 847–940

Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol Monogr 65:419–439. doi:10.2307/2963497

Condit R, Hubbell SP, Foster RB (1996) Changes in tree species abundance in a neotropical forest: impact of climate change. J Trop Ecol 12:231–256

Condit R, Aguilar S, Hernandez A, Perez R, Lao S, Angehr G et al (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Nino dry season. J Trop Ecol 20:51–72. doi:10.1017/S0266467403001081

DeAngelis DL, Waterhouse JC (1987) Equilibrium and non-equilibrium concepts in ecological models. Ecol Monogr 57:1–21. doi:10.2307/1942636

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL et al (2007) Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–82. doi:10.1038/nature05747

Gibbons JM (1998) Water relations, phenology and drought adaptation of understorey trees in tropical lowland rain forest. PhD thesis, University of Stirling, Scotland, UK

Gibbons JM, Newbery DM (2003) Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. Plant Ecol 164:1–18. doi:10.1023/A:1021210532510

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev Camb Philos Soc 52:107–145. doi:10.1111/j.1469-185X.1977.tb01347.x

Holm S (1979) A simple sequential rejective multiple test procedure. Scand J Stat 6:65–70

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, USA

Hubbell SP (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. Funct Ecol 19:166–172. doi:10.1111/j.0269-8463.2005.00965.x

Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. Ecology 87:1387–1398. doi:10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2

Hulme M, Viner D (1998) A climate change scenario for the tropics. Clim Change 39:145–176. doi:10.1023/A:1005376007729

Huston MA (1979) General hypothesis of species diversity. Am Nat 113:81–101. doi:10.1086/283366

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK

Ives AR (1995) Measuring resilience in stochastic systems. Ecol Monogr 65:217–233. doi:10.2307/2937138

Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. Science 317:58–62. doi:10.1126/science.1133258

Lingenfelder M (2005) Rain forest dynamics and response to drought in a Bornean primary lowland dipterocarp forest. PhD thesis. University of Bern, Switzerland. http://www.stub.unibe.ch/download/eldiss/05lingenfelder_m.pdf

Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. Philos T R Soc B 359:311–329. doi:10.1098/rstb.2003.1433

Malhi Y, Pegoraro E, Nobre AD, Pereira MGP, Grace J, Culf AD et al (2002) Energy and water dynamics of a central Amazonian rain forest. J Geophys Res-Atmos 107:D20–D34. doi:10.1029/2001JD000623

Manly B (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London, UK

Marsh CW, Greer AG (1992) Forest land-use in Sabah, Malaysia: an introduction to the Danum Valley. Philos T R Soc B 335:331–339. doi:10.1098/rstb.1992.0025

May RM (1974) Stability and complexity in model ecosystems. Princeton University Press, Princeton, USA

McPhaden MJ (1999) Genesis and evolution of the 1997–98 El Niño. Science 283:950–954. doi:10.1126/science.283.5404.950

McPhaden MJ, Zebiak SE, Glantz MH (2006) ENSO as an integrating concept in earth science. Science 314:1740–1745. doi:10.1126/science.1132588

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, et al. (2007) Global climate projections, Chap. 10. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt K, et al. (eds) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK, pp 747–845

Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405. doi:10.1034/j.1600-0706.2003.12010.x

Nakagawa M, Tanaka K, Nakashizuka T, Ohkubo T, Kato T, Maeda T et al (2000) Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. J Trop Ecol 16:355–367. doi:10.1017/S0266467400001450

Nelson W (1982) Applied life data analysis. Wiley, NewYork, USA

Newbery DM, Lingenfelder M (2004) Resistance of a lowland rain forest to increasing drought intensity in Sabah, Borneo. J Trop Ecol 20:613–624. doi:10.1017/S0266467404001750

Newbery DM, Campbell EJF, Lee YF, Ridsdale CE, Still MJ (1992) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. Philos T R Soc B 335:341–356. doi:10.1098/rstb.1992.0026

Newbery DM, Campbell EJF, Proctor J, Still MJ (1996) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. Vegetatio 122:193–220. doi:10.1007/BF00044700

Newbery DM, Clutton-Brock TH, Prance GT (1999a) Changes and disturbance in tropical rainforest in South-East Asia. Imperial College Press, London, UK

Newbery DM, Kennedy DN, Petol GH, Madani L, Ridsdale CE (1999b) Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. Philos T R Soc B 354:1763–1782. doi:10.1098/rstb.1999.0519

Payne RW (ed) (2000) GENSTAT reference manual. Lawes Agricultural Trust, Rothamsted, UK

Phillips OL, Hall P, Gentry AH, Sawyer SA, Vásquez R (1994) Dynamics and species richness of tropical rain forests. Proc Natl Acad Sci USA 91:2805–2809. doi:10.1073/pnas.91.7.2805

Potts MD (2003) Drought in a Bornean ever-wet rain forest. J Ecol 91:467–474. doi:10.1046/j.1365-2745.2003.00779.x

Purves DW, Pacala SW (2005) Ecological drift in niche-structured communities: neutral pattern does not imply neutral process. In: Burslem DRFP, Pinard M, Hartley S (eds) Biotic interactions in the tropics. Cambridge University Press, Cambridge, UK, pp 103–138

Sheil D, May RM (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. J Ecol 84: 91–100. doi:10.2307/2261703

Sheil D, Burslem DFRP, Alder D (1995) The interpretation and misinterpretation of mortality rate measures. J Ecol 83: 331–333. doi:10.2307/2261571

Shugart HH (1998) Terrestrial ecosystems in changing environments. Cambridge University Press, Cambridge, UK

S-Plus 6 (2001) Guide to statistics. Insightful Corporation. Seattle, Washington, USA

Steele JH (1985) A comparison of terrestrial and marine ecological systems. Nature 313:355–358. doi:10.1038/313355a0

Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398:694–697. doi:10.1038/19505

Timmermann A, Jin FF, Collins M (2004) Intensification of the annual cycle in the tropical Pacific due to greenhouse warming. Geophys Res Lett 31:L12208. doi:10.1029/2004GL019442

Trenberth KE (1997) The definition of El Niño. Bull Am Meteorol Soc 78:2771–2777. doi:10.1175/1520-0477(1997)078<2771:TDOENO>2.0.CO;2

Trenberth KE, Hoar TJ (1997) El Niño and climate change. Geophys Res Lett 24:3057–3060. doi:10.1029/97GL03092

Vasseur DA, Yodzis P (2004) The color of environmental noise. Ecology 85:1146–1152. doi:10.1890/02-3122

Walsh RPD (1996a) Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. J Trop Ecol 12:385–407

Walsh RPD (1996b) Climate. In: Richards PW (main author) The tropical rain forest: an ecological study. Cambridge University Press, Cambridge, UK, pp 159–236

Walsh RPD, Newbery DM (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. Philos T R Soc B 354:1869–1883. doi:10.1098/rstb.1999.0528

Westfall PH, Young SS (1993) Resampling-based multiple testing. Wiley, New York, USA

Woods P (1989) Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. Biotropica 21:290–298. doi:10.2307/2388278

Red spruce forest regeneration dynamics across a gradient from Acadian forest to old field in Greenwich, Prince Edward Island National Park, Canada

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Abstract Red spruce forests have declined considerably throughout their range in the past decades. As agricultural fields are abandoned and land becomes available for reforestation, the possibility arises for red spruce forests to expand onto them. This study addresses the potential for red spruce forests to expand onto adjacent old fields in Greenwich, Prince Edward Island National Park, Canada. We examined red spruce distribution and abundance, plant species diversity and changes in community composition along a gradient from the interior of red spruce forests out towards the centre of adjacent old fields. Examining the patterns of red spruce distribution and abundance revealed that, where cultivation and logging have been abandoned recently in the fields and forests, regeneration is limited to the forest stands, but in the sites with older fields and forests, regeneration extends into and is more vigorous in the fields. Although species diversity varied from forest to field only for the tree and shrub layers, important changes occurred in the ground species composition. There is no evidence yet that the herbaceous species present in the forest stands will colonise the old fields. The results suggest that both environmental differences among sites and length of time since the fields were abandoned explain red spruce regeneration patterns. In order to more accurately assess the potential for red spruce regeneration in old fields, long-term monitoring of the production, dispersal and viability of red spruce seeds from adjacent forests and of the constraints to seedling establishment and survival in old fields will be needed.

Keywords Regeneration · Red spruce · Abandoned fields · Plant community · Diversity

Introduction

Descriptions of the patterns and processes of succession abound in the ecological literature. However, since successional trajectories are contingent upon site-specific conditions, generalisations from one site cannot necessarily be applied to another (Pickett et al. 2001). For example, agricultural and logging disturbances can have similar initial impacts, but the regeneration dynamics following them can differ significantly. This is because successional patterns depend on the nature of the disturbance, on the life history strategies of each species involved and on the outcomes of the interactions among the species and

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their environment (Pickett et al. 2001). This study focuses on the red spruce (*Picea rubens* Sarg.) regeneration in agricultural fields after their abandonment.

Agricultural practices such as tilling, flattening, clearing and planting greatly disturb the soil layer, resulting in a field ground environment that differs considerably from a forest ground environment. Soil mycorrhizal colonisation (Barni and Siniscalco 2000), organic matter and nitrogen content (Richter et al. 2000), nutrient availability and the condition of the surface horizon (Pickett et al. 2001) change significantly in agricultural soil. In most cases, the conversion of forested land to agricultural land leads to the elimination of the forest herbs (Ramovs and Roberts 2003). Additional practices that influence succession include spreading manure (Pickett et al. 2001), fertilisation (Richter et al. 2000) and ploughing (Pickett et al. 2001; Ramovs and Roberts 2003), as well as post-agricultural management such as pasturing (Howard and Lee 2002).

Recolonisation, whether in forest ecosystems or in agricultural ecosystems, depends heavily on: (1) the reproductive strategies of the species in question, such as its mode of dispersal, (2) the spatial features of the available site, such as its size and its distance from the seed source, (3) the environmental characteristics of the new site and (4) the interactions between the species (Bazzaz 1996; Li and Wilson 1998; Yao et al. 1999; Meiners et al. 2000, 2002; Pickett et al. 2001; Howard and Lee 2002).

Red spruce is an eastern North American tree species that regenerates from wind-dispersed seed. Although its seedlings and saplings can persist upwards of 50 years in the shade, its seeds are seldom viable for longer than 1 year (see, Sullivan 1993 for a review of red spruce ecology). In a forest environment that is not too disturbed, red spruce seedlings and saplings can be preserved as advance regeneration during logging and dominate forest regeneration later (Greene et al. 1999; Reyes and Vasseur 2003). Conversely, in an agricultural setting, seed dispersal from sufficiently stocked, nearby sources of reproductive trees will be necessary for natural colonisation.

Red spruce is an important but declining component of eastern North American forests, and it is a species characteristic of mature Acadian forests (Loo and Ives 2003). Atmospheric pollution, acid deposition (Johnson et al. 1992; McLaughlin et al. 1987) and deforestation (White and Cogbill 1992) are the principal causes of its decline throughout its range. Late-successional species, including red spruce, have declined in abundance and age in Prince Edward Island as a result of selective forest exploitation and clearing for agriculture. Consequently, the forest composition has shifted to higher frequencies of balsam fir (*Abies balsamea* (L.) P. Mill.), red maple (*Acer rubrum* L.), white spruce (*Picea glauca* A. Dietr.), white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) (Loo and Ives 2003 describe the pre-settlement and current Acadian forest in detail). For these reasons, it is important to monitor and protect red spruce in Prince Edward Island.

This study assesses the species composition along a gradient from red spruce forests to adjacent, recently abandoned agricultural fields in order to better understand the structure of the red spruce population and its regeneration dynamics. Our study examines (1) spatial variation of red spruce abundance and density from the forest into the field, (2) the influence of adjacent forests on red spruce abundance in the old fields and (3) the influence of historical disturbance on species composition.

Methodology

Study sites

The study sites were located in Prince Edward Island National Park (hereafter PEINP). In 1996, the park acquired new land, including several agricultural fields (Rennie et al. 1997). The cessation of agricultural disturbances (as of 2001 or earlier) on these fields raised the possibility for adjacent red spruce forests to expand onto them, and thus raised the possibility to study the potential and mechanisms of such regeneration.

Using aerial photographs from 1997 (scale 1:4,000, provided by PEINP, flight line A31757, No. 51-52 and 80-83), all the sites in the Greenwich section of the park where forests and old fields occurred adjacent to one another, unseparated by barriers (such as roads or footpaths), were located. These potential sites were then visited to determine whether they met the following criteria: (1) red spruce is present in the tree layer; (2) the soil drainage and texture are similar in all sites; (3) the forest edge of each site is oriented in roughly the same direction; and (4) the forest stand is large enough for a full vegetation survey (105 m along the edge, >50 m deep). In addition, sites with high presence of white spruce were avoided.

Four sites were selected. They were all situated on well-drained Orthic Humo-Ferric Podzols of the Charlottetown map unit (soil classification map provided by PEINP, Greenwich, 2003). The topography at the sites is gently rolling. The forest edges at all sites are oriented roughly east-west. The mean annual temperature of Prince Edward Island is about 5.5°C; the summer mean is 15°C and the winter mean is −3.5°C (Environment Canada 2005). The frost-free period averages 130 days per year between late May and early October (Atlantic Climate Centre 2004). The mean annual precipitation ranges from 900 to 1,150 mm (Environment Canada 2005).

The four sites differ in their land use histories and in some associated characteristics (Table 1). Just before they were abandoned, the old field portions of the four sites were used to grow hay, especially timothy (*Phleum pratense* L.). Prior to that, they were also used to grow potatoes (Lajeunesse 2004,

Table 1 Descriptive characteristics and histories of the four study sites in Greenwich, Prince Edward Island National Park

	Site 1	Site 2	Site 3	Site 4
Percentage of red spruce				
Trees[a]	60	78	17	93
Saplings[b]	39	94	8	89
Aerial photo[c]				
1935				
Forest	Logged, hedgerow	Closed canopy	Logged	Logged
Field	Cultivated	Cultivated	Cultivated	Unclear
1958				
Forest	Logged	Closed canopy	Logged	Closed canopy
Field	Cultivated	Cultivated	Cultivated	Cultivated
1974				
Forest	Partially logged	Closed canopy	Regenerating	Closed canopy
Field	Cultivated	Cultivated	Cultivated	Cultivated
1990				
Forest	Closed canopy	Closed canopy	Closed canopy	Closed canopy
Field	Cultivated	Cultivated	Cultivated	Cultivated
1997				
Forest	Closed canopy	Closed canopy	Closed canopy	Closed canopy
Field	Abandoned	Sapling dotted	Cultivated (hay)	Sapling dotted
2000				
Forest	Closed canopy	Closed canopy	Closed canopy	Closed canopy
Field	Abandoned	Sapling dotted	Cultivated (hay)	Sapling dotted
Approximate forest age	13–29 years	over 68 years	13–29 years	±45 years
Approximate number of years since field abandonment	13	13	<3	13
Forest classification[d]	Old-field white spruce	Old-field white spruce	Disturbed hardwood	Old-field white spruce

[a] DBH ≥ 10 cm

[b] DBH < 10 cm, height>1 m

[c] Scales: 1935–1990 (1:<17,500); 1997 (1:4,000); 2000 (1:17,500)

[d] Source: Forest classification map provided by PEINP, Greenwich, 2003

personal communication). Site 3 is the only one where red spruce is not the most dominant species in the tree and sapling layers of the forested component; in this site, red maple (55%) dominates the tree layer and a mixture of *Amelanchier* spp. (35%) and red maple (31%) dominate the sapling layer.

Species identification

Red spruce was differentiated from white and black spruce (*Picea mariana* (P. Mill.) B.S.P.) morphologically, mostly using twig hair characteristics. Since red spruce was far more abundant than white and black spruce in the tree and sapling layers of the study sites and their surroundings, seedlings were assumed to be red spruce. Since white spruce saplings sometimes have sparse twig hair (Jablanczy 1964), it is possible that some red spruce saplings in this study might have been misidentified. It is important to note that trees identified as red spruce in our sites were most likely red spruce × black spruce hybrids (Mosseler 2004, personal communication); morphological features are not reliable for distinguishing pure spruce from hybrid spruce (Nkongolo et al. 2003). For simplicity, and because we do not know the degree of hybridisation of the individual trees or stands, in this study we refer to the probable red spruce × black spruce hybrids simply as red spruce.

Survey plot design

Each of the four sites was 105 m wide (parallel to the forest edge) and 110 m long (perpendicular to the forest edge). We defined the forest edge as the conspicuous boundary between the forest and the field, regardless of the age of the trees. The width included a 20 m buffer zone on each side. The sites comprised five transects oriented perpendicular to the forest edge and spaced 15 m apart. From a zero point at the forest edge, each transect extended 50 m into the forest and 60 m into the field. Eight 5 m × 5 m quadrats, each spaced 10 m apart, lined the west side of each transect at the following distances from the forest edge: (1) +45 to 50 m, (2) +30 to 35 m, (3) +15 to 20 m, and (4) 0 to +5 m in the forest; (5) −10 to 15 m, (6) −25 to 30 m, (7) −40 to 45 m and (8) −55 to 60 m in the field. These distances are termed as positions in the remaining of this article; the positions are identified by the above number in brackets, which designates the distance that follows it. Each 5 m × 5 m quadrat contained two embedded 1 m × 1 m quadrats, one centered against the west edge and one centered against the east edge.

Data collection

In each 5 m × 5 m quadrat, we surveyed the mature trees (DBH $\geq$ 10 cm), the saplings (DBH $<$ 10 cm, height $\geq$ 1 m) and the shrubs (height $\geq$ 1 m). In the 1 m × 1 m quadrats, we surveyed the herbaceous layer, including tree seedlings and shrubs shorter than 1 m. For the trees and saplings, we counted the number of stems of each species; for the shrubs and herbs, we estimated the percent cover for each species. The survey began in July 2003 and ended in September 2003. Since the survey began in July, that year's cohort of spruce seedlings had already germinated (the vegetation in the plots was surveyed only once). This survey design is adapted from the Ecological Monitoring and Assessment Network's Terrestrial Vegetation Biodiversity Monitoring Protocols (Roberts-Pichette and Gillespie 1999) and from Reyes (2002) and Reyes and Vasseur (2003). All species were identified using Gleason and Cronquist (1991) and Roland (1998) and species names were updated according to the Integrated Taxonomic Information System database (2005, http://www.itis.usda.gov/).

Statistical analyses

Univariate analyses

Three diversity indices (species richness (r), the Shannon–Weiner index (h') and Simpson's index (d)) for mature trees, saplings, shrubs and herbs, as well as red spruce and balsam fir tree and sapling abundances were calculated at the position level (the average of the data from the five quadrats at the same distance from the forest edge within a site). Species for which there were only one or two observations might have skewed the data so we removed them from the data set, except in the shrub layer where most species occurred only once or twice. The data were not normally distributed according to Kolmogorov–Smirnov and Shapiro–Wilk tests and they could not be transformed to meet the conditions for normality; therefore, they were tested for significant differences among the positions and among the sites using Kruskal–Wallis tests with $\alpha = 0.05$. In order to locate the differences when the null hypothesis was rejected, a post priori multiple comparison tests designed to follow Kruskal–Wallis tests was used (Post Hoc for Kruskal; macro available on StatSoftInc 2006). All univariate analyses were performed using SPSS 11.0, except the nonparametric multiple comparisons which were performed using STATISTICA, Version 6 (StatSoft, Inc 2001).

We used 2 × 2 contingency tables to analyse the relationships among red spruce seedling, sapling and tree occurrences. Chi-square tests were followed with contingency and uncertainty coefficient calculations. Contingency coefficients measure the degree of association between the variables. Uncertainty coefficients measure the proportional reduction of error in the prediction of one variable when another is known. Quadrat level correlations between red spruce tree and sapling abundances were examined using Spearman rank correlation tests.

Multivariate analyses

In order to assess the similarities in forest and field species composition in our sites, community level changes in vegetation composition across the forest-field gradient were examined with detrended correspondence analysis (DCA) using CANOCO 4.02. 'Species' data were stem counts for the tree and sapling analysis and percent cover for the herb and shrub analysis. The 'downweighting of rare species' option was selected to prevent infrequently occurring species from exerting too strong an influence on the analysis (ter Braak and Šmilauer 1998). CANOCO gives the option to add a supplementary environmental variable to an ordination by projecting its data onto the existing ordination axes. This way, that variable does not influence the calculation of the axes, but its relation to the other variables in the ordination can still be interpreted from the results. In our analyses, we used position relative to the forest edge as a supplementary environmental variable. The actual DCA axes represent hypothetical gradients along which the maximum variability in species composition is explained (ter Braak and Šmilauer 1998).

Results

In the four sites surveyed, there were a total of seven species present in the tree layer (DBH ≥ 10 cm), nine species in the sapling layer (DBH < 10 cm and height ≥ 1 m), eight species in the shrub layer (height ≥ 1 m) and 71 species in the herbaceous layer. The relative abundances of each tree and sapling species are presented in Table 2. Only red spruce and balsam fir saplings were present in the field portions of the sites, and only two of the sites

Table 2 Relative abundances of the species (trees (DBH ≥ 10 cm) and saplings (DBH < 10 cm)) in each site

	Site 1		Site 2		Site 3		Site 4	
	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings
Abies balsamea	0.29	0.25	0.21	0.06	0.05	0.02	0.04	0.09
Acer rubrum	0.00	0.03	0.00	0.00	0.55	0.31	0.00	0.00
Amelanchier sp.	0.00	0.00	0.00	0.00	0.07	0.35	0.00	0.00
Betula papyrifera	0.11	0.24	0.01	0.00	0.00	0.01	0.00	0.00
Picea glauca	–	0.01	–	0.00	–	0.00	–	0.00
Picea mariana	0.00	0.00	0.00	0.00	0.07	0.04	0.03	0.02
Picea rubens	0.60	0.39	0.78	0.94	0.17	0.08	0.93	0.89
Populus tremuloides	0.00	0.00	0.00	0.00	0.10	0.19	0.00	0.00
Prunus pennsylvanica	–	0.07	–	0.00	–	0.01	–	0.00
N	70	71	111	400	42	108	101	45

– indicates no stems with DBH ≥ 10 cm

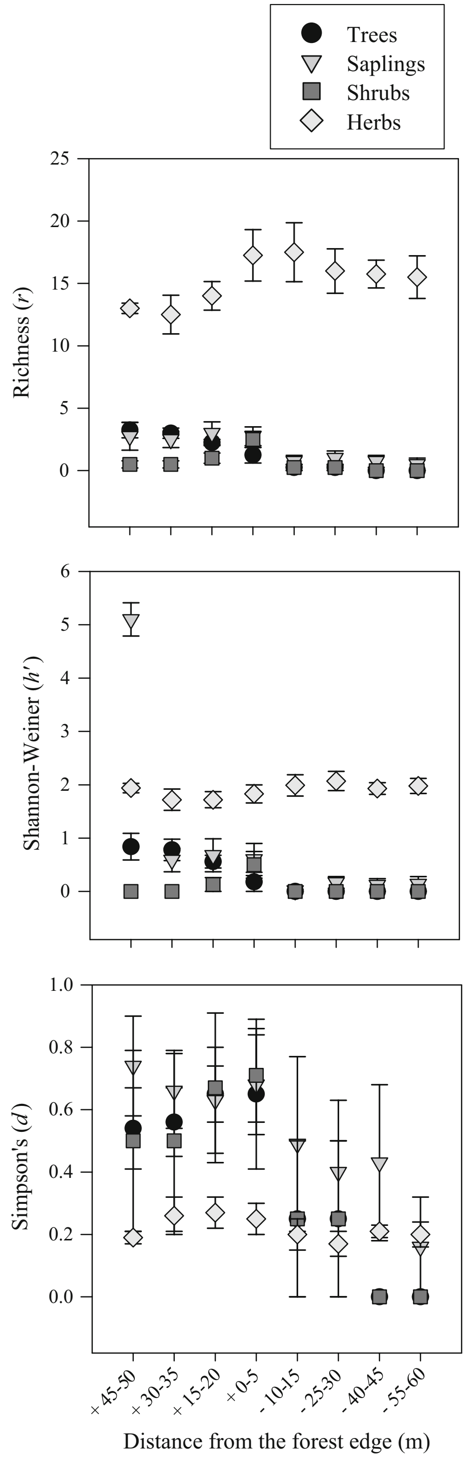


Fig. 1 Mean species richness (*r*) and mean value for Shannon–Weiner index (h') and Simpson's Index (*d*) ± standard error for each vegetation layer at eight positions relative to the forest edge; $N = 4$ (one index per position per site)

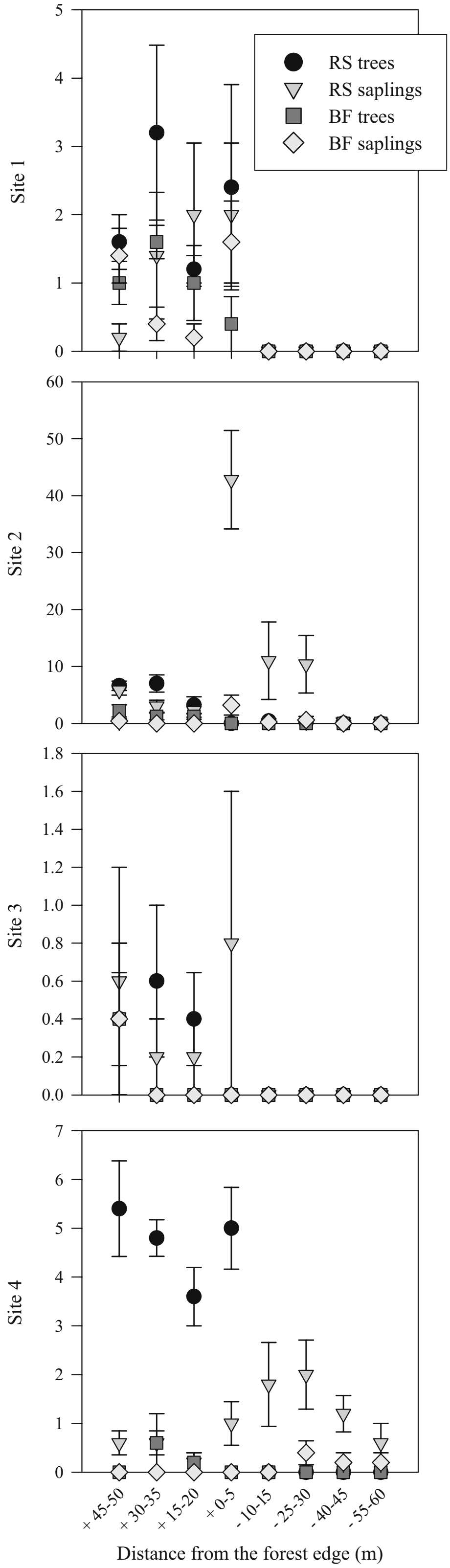
had saplings in their fields. Trees and saplings of all other species were present only in the forest portions of the sites.

Five diversity variables varied significantly along the distance gradient relative to the forest edge (Kruskal–Wallis, $N = 32$, df = 7): *r* trees ($X^2 = 25.353$, $P = 0.001$), h' trees ($X^2 = 25.477$, $P = 0.001$), *d* trees ($X^2 = 14.896$, $P = 0.037$), *r* shrubs ($X^2 = 17.220$, $P = 0.016$) and h' shrubs ($X^2 = 17.896$, $P = 0.012$) (Fig. 1). The results suggest that the significant variation lies between forest and field. As expected, nearly all the trees were located in the forest. The shrub layer species diversity was highest at the forest positions near the edge (Fig. 1). Only *d* for the sapling layer differed significantly among sites ($X^2 = 18.419$, df = 3, $P = 0.001$), with sites 1 and 3, and sites 2 and 4 as two homogenous subsets (Fig. 1).

Red spruce distribution

Red spruce tree ($X^2 = 90.561$, df = 7, $P < 0.001$) and sapling ($X^2 = 18.664$, df = 7, $P = 0.009$) abundance differed significantly with the distance from the forest edge (Fig. 2). Mean red spruce tree stem density was 1,100 stems/ha in the forest and 0 stems/ha in the field; maximum density was 1,600 stems/ha at position 2 (30–35 m into the forest). Mean red spruce sapling stem density was 1,600 stems/ha in the forest and 700 stems/ha in the field; maximum density was 4,700 stems/ha at position 4 (0–5 m into the forest) and it rapidly declined to 1,200 stems/ha by position 6 (25–30 m into the field).

Sites differed significantly in red spruce tree abundance ($X^2 = 16.466$, df = 3, $P = 0.001$), with subsets defined as sites 1, 2, and 3 together and sites 1, 2, and 4 together. Testing site differences using only forest data (the field data were removed from the set because of the dominance of zeroes), three subsets were identified. Sites 1 and 2, and sites 2 and 4 were grouped together, leaving site 3 separate ($X^2 = 34.476$, df = 3, $P < 0.001$). The number of red spruce saplings also varied significantly between sites ($X^2 = 39.951$, df = 3, $P < 0.001$). Sites 1 and 3, sites 1 and 4, and sites 2 and 4 formed three homogenous subsets. Saplings have not begun to colonise the fields of sites 1 and 3. Despite their similarities in abundance, sites 2 and 4 differed in sapling distribution; it was



◀ **Fig. 2** Mean stem count and standard error of red spruce and balsam fir trees and saplings in each site at eight positions relative to the forest edge; positive distances are in the forest and negative distances are in the field. For each distance at each site, $N = 5$ plots (5 m × 5 m)

more even in the field of site 4 and patchier in the field of site 2. Red spruce regeneration was most abundant in site 2 (Fig. 2).

Red spruce trees occurred in 37.5% of the 160 surveyed quadrats and red spruce saplings occurred in 40.6% of the quadrats. There is a relationship between red spruce tree and sapling occurrence (Pearson $X^2 = 17.621$, df = 1, $P < 0.001$); however, the association is not very strong (contingency coefficient = 0.315; symmetric uncertainty coefficient = 0.083, $P < 0.001$). The abundances of red spruce trees and saplings were also significantly correlated (Spearman rank correlation coefficient (r_s): 0.299, $P < 0.001$).

Red spruce seedlings (height < 1 m) occurred in 16.3% of the 160 quadrats, always where red spruce sapling abundance was the highest. The relationship between red spruce seedlings and saplings (Pearson $X^2 = 29.452$, df = 1, $P < 0.001$; contingency coefficient = 0.394, symmetric uncertainty coefficient = 0.173, $P < 0.001$) was stronger than the one between saplings and trees. There was no significant relationship between seedling and tree occurrences (Pearson $X^2 = 2.755$, df = 1, $P = 0.097$). Separating the occurrence data into forest and field quadrats gives the following stocking rates (percentage of quadrats with at least one occurrence): in the forest, 18.8% for seedlings, 53.8% for saplings and 72.5% for trees; in the field, 13.8% for seedlings, 27.5% for saplings and 2.5% for trees.

Balsam fir is the only other tree species to have begun colonising the old fields. Its abundance and distribution are presented in Fig. 2. Balsam fir was less abundant than red spruce in the tree and sapling layers everywhere except at position 1 (45–50 m into the forest) in site 1. Mean balsam fir tree stem density was 245 stems/ha in the forest and 0 stems/ha in the field; maximum density was 360 stems/ha at position 1. Mean balsam fir sapling stem density was 190 stems/ha in the forest and 40 stems/ha in the field; maximum density was 480 stems/ha at position 4. Balsam fir trees were present in 16% of the quadrats and saplings were present in 14% of the quadrats.

Vegetation gradient

DCA results exposed the strong field/forest distinction in the species composition of our study sites, as well as the distinction between the species composition of site 3 and that of the other sites. In the tree and sapling layer ordination (Fig. 3), the four samples belonging to the forest portion of site 3 are clustered on the left of the diagram near the abundance optima for red maple, trembling aspen and *Amelanchier* sp. All other forest samples are positioned between the abundance optima for balsam fir and red spruce trees, with no particular order in the positions. All the field samples (that were not void of saplings) are clustered around the optimum for red spruce saplings on the right side of the diagram. The eigenvalue of the first axis was 0.850 and that of the second axis was 0.259; the cumulative percentage of variance in the species data explained was 35.4% for the first axis and 46.2% for the second. The sum of all eigenvalues was 2.399. The eigenvalue calculated for position relative to the forest edge as a supplementary environmental variable was 0.344.

In the herbaceous and shrub layer ordination (Fig. 4), all the forest species and samples are positioned on the left of the diagram, while all the field species and samples are positioned on the right of the diagram. Forest positions and species are loosely ordered from forest interior to edge from the left of the diagram to the centre, except for the four samples belonging to site 3 at the far left. Species exclusive to or most abundant in site 3 include *Kalmia angustifolia* L., *Vaccinium angustifolium* Ait., *Gaultheria procumbens* L., and *Nemopanthus mucronatus* (L.) Loes. Among the field species, grasses are scattered at the top of the diagram. There is no apparent ordering within the field positions. The eigenvalue of axis 1 was 0.943 and that of axis 2 was 0.361. The cumulative percentage of variance in the species data explained was 24.4% for the first axis and 33.8% for the second. The sum of all eigenvalues was 3.858. The eigenvalue calculated for position relative to the forest edge as a supplementary environmental variable was 0.702.

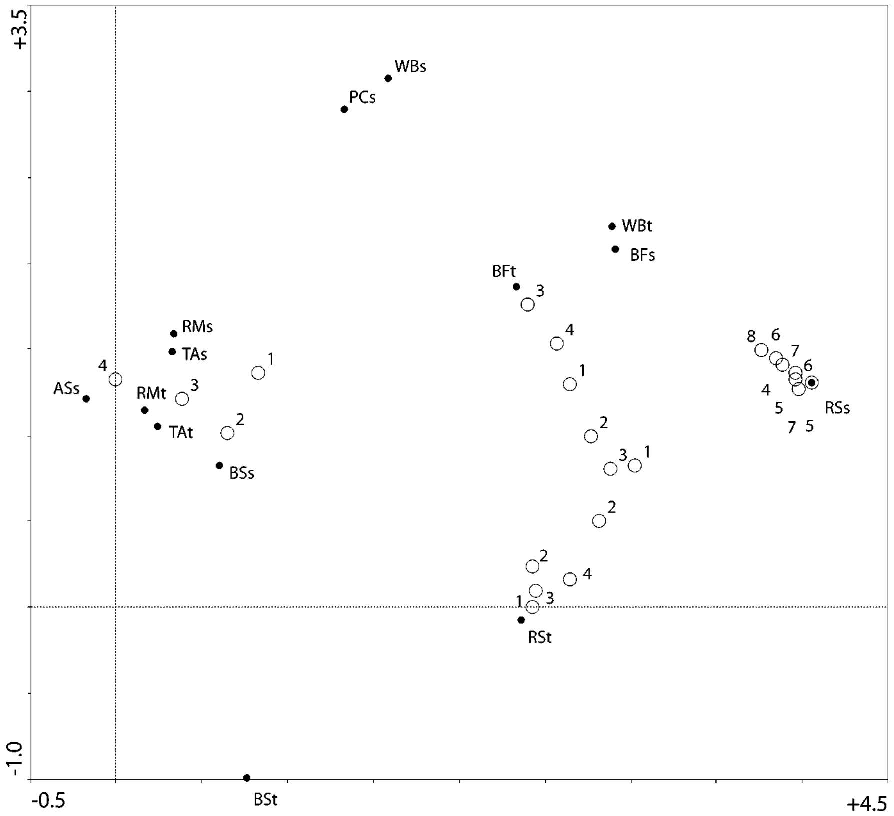


Fig. 3 Detrended correspondence analysis biplot of the species surveyed in the tree and sapling layers at the four study sites. Circles represent samples, which are labelled with their position numbers. Position numbers refer to the distance from the forest edge, with position 1 beginning in the forest interior and position 8 ending furthest into the field. The full species names corresponding to the species codes are in Appendix 1

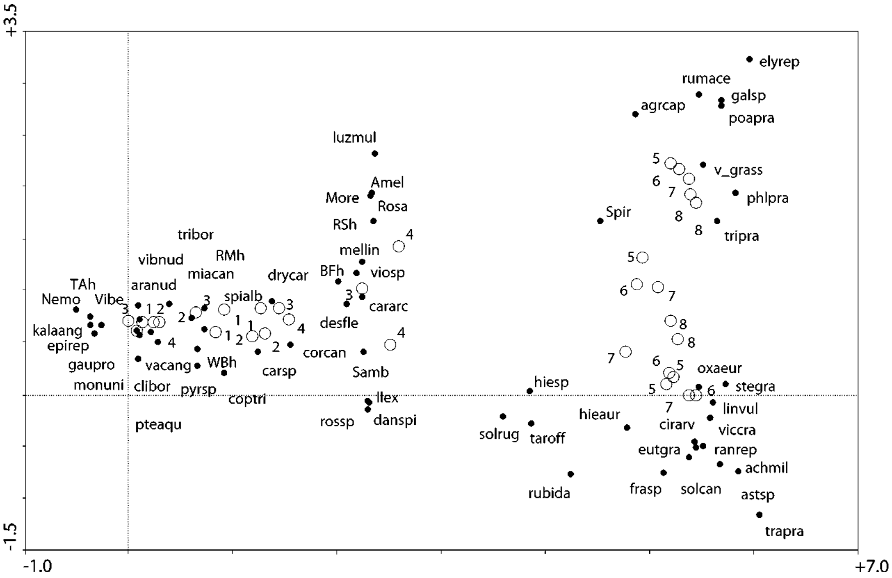


Fig. 4 Detrended correspondence analysis biplot of the species surveyed in the herbaceous and shrub layers at the four study sites. Circles represent samples, which are labelled with their position numbers. Position numbers refer to the distance from the forest edge, with position 1 beginning in the forest interior and position 8 ending furthest into the field. The full species names corresponding to the species codes are in Appendix 1. Forest edge

Discussion

Red spruce populations appeared to be capable of slowly expanding into at least some of the abandoned fields. Saplings, mostly of red spruce, have begun to colonise the fields of the two sites with the older forests, but species in the herbaceous layer did not overlap between forest and field. The fields of the two sites with the younger forests had no saplings in the year of our survey. This suggests that the time since abandonment has been too short for significant change in the fields. Even after 54 years of succession following clearcutting in an Acadian forest, Moola and Vasseur (2004) found no evidence that pre-harvest forest species composition was returning. Among the species which they found to have the greatest difficulty in recovering after clearcutting, the following are also present in our forest sites: *Aralia nudicaulis*, *Coptis trifolia*, *Maianthemum canadense*, *Monotropa uniflora* and *Trientalis borealis*.

Red spruce regeneration density in our sites was lower than in studies conducted on harvested forest stands. For example, Roy et al. (2000) inventoried red spruce regeneration 3 years after clearcutting (80 m × 120 m stripcuts) with protection of advance growth in southern Quebec and recorded densities between 900 and 5,000 stems/ha; their stocking rates were 13–75%. Prévost and Pothier (2003) measured a mean of 200 stems/ha in unscarified clearcuts and 17,000 stems/ha in scarified sites (the densities in this study included both red and white spruce). In Nova Scotia, Reyes (2002) found very high red spruce regeneration densities with means of 34,000 seedlings/ha as far as 110 m into the cut and 76,000 seedlings/ha between 0 and 20 m from the forest edge, 3 and 4 years after the cut. The seedlings in these studies came from both advance regeneration and from seeds dispersed after the harvest. The differences in the densities found in our study compared to those following forest harvesting, as well as the importance of advance regeneration as a seedling source in harvested sites, confirm that recovery of forest stands on agricultural lands cannot be compared to forest regrowth after logging. In addition, the red spruce seeds from our sites had a germination rate of 0.004% (Cavallin and Vasseur, in press). This low germination rate might have resulted from the high occurrence of hybridisation between red and black spruce on Prince Edward Island (Mosseler 2004, personal communication) and suggests a limited ability for natural regeneration.

The species diversity indices suggest that, other than for the tree layer, diversity did not vary significantly from forest to field. Nonetheless, the pattern we observed in herbaceous species richness approached the one in Meiners and Pickett (1999), where species richness increased across the forest-field gradient to a peak 40 m into the field and then declined. Despite the continuity in species diversity, species composition greatly differs between habitats.

Red spruce was the dominant regenerating tree species along the forest-to-field gradient in all sites except site 3. A significant cover of both hardwoods and *Kalmia angustifolia* in site 3 could explain the competitive difficulty for red spruce seedling establishment. Ericaceous species, especially *Kalmia angustifolia*, can be inhibitory to spruce establishment (Yamasaki et al. 1998; Mallik 2001). Hardwoods also can compete considerably with spruce seedling growth (Lautenschlager 1991; Roy et al. 2000; Prévost and Pothier 2003). Site-specific information about past disturbances, other than the logging and farming visible in the aerial photos, was not available, but it is possible that the currently forested portion of site 3 received a different treatment from the other sites in the past and thus is undergoing a different successional path. Modifications to the environment such as adding fertilisers to the soil, tree harvesting and burning all create conditions favouring *Kalmia* growth and spread (Mallik 1994, 1996).

Moreover, the dominance of red spruce trees in the other three sites provides a greater seed source for maintaining the species in the forest and for reforesting the fields. In fact, the percentage contribution of red spruce to the tree composition is much higher in these three sites (60–93%) than it is in the three forest types in which it typically occurs in Prince Edward Island (4.6–17.3%) (Sobey and Glen 2002). Dibble et al. (1999) regarded the presence of seed-bearing red spruce trees as a very important indicator of red spruce regeneration habitat. We indeed found the presence and abundance of red spruce saplings to be significantly correlated with those of mature red spruce. Balsam fir was the only other tree species colonising the old fields. Its lower abundance suggests that red spruce could dominate the future old field forests as well.

In conclusion, our results suggest that red spruce forests have the potential to serve as sources for reforesting adjacent old fields. However, this regeneration will be slow, raising two choices concerning park management: the fields can be left to reforest slowly and naturally or they can be artificially reforested to speed up the process. Further research into the constraints to red spruce establishment and persistence in old fields will be needed to develop a restoration plan favouring natural regeneration. Alternately, red spruce can be grown naturally in fields from seedlings (Beaulieu et al. 1989), but its susceptibility to drought and winter desiccation can limit its success (Beaulieu et al. 1989; Blum 1990). Further monitoring would be needed to better understand this option as well.

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Appendix 1

Species names corresponding to the codes in Figs. 3 and 4

Trees: subscripts t, s and h indicate tree layer, sapling layer and herbaceous layer, respectively.

BF	*Abies balsamea* (L.) P. Mill.
RM	*Acer rubrum* L.
AS	*Amelanchier* sp. Medik.
WB	*Betula papyrifera* Marsh.
BS	*Picea mariana* (P. Mill.) B.S.P.
RS	*Picea rubens* Sarg.
TA	*Populus tremuloides* Michx.
PC	*Prunus pensylvanica* L. f.
Shrub layer	
Amel	*Amelanchier* sp. Medik.
Ilex	*Ilex verticilata* (L.) Gray
More	*Morella pensylvanica* (Mirbel) Kartesz, comb. nov. ined.
Nemo	*Nemopanthus mucronatus* (L.) Loes.
Rosa	*Rosa* sp. L.
Samb	*Sambucus racemosa* L.
Spir	*Spiraea alba* Du Roi
Vibe	*Viburnum nudum* var. *cassinoides* (L.) Torr. & Gray
Herbaceous layer	
achmil	*Achillea millefolium* L.
elyrep	*Elymus repens* (L.) Gould
agrcap	*Agrostis capillaris* L.
aranud	*Aralia nudicaulis* L.
astsp	*Aster* sp. L.
cararc	*Carex arctata* Boott ex Hook.
carsp	*Carex* sp. L.
cirarv	*Cirsium arvense* (L.) Scop.
clibor	*Clintonia borealis* (Ait.) Raf.
coptri	*Coptis trifolia* (L.) Salisb.
corcan	*Cornus canadensis* L.

Appendix continued

danspi	*Danthonia spicata* (L.) Beauv. ex Roemer & J.A. Schultes
desfle	*Deschampsia flexuosa* (L.) Trin.
drycar	*Dryopteris carthusiana* (Vill.) H.P. Fuchs
epirep	*Epigaea repens* L.
frasp	*Fragaria* sp. L.
galsp	*Galium* sp. L.
gaupro	*Gaultheria procumbens* L.
hieaur	*Hieracium aurantiacum* L.
hiesp	*Hieracium* sp. L.
kalaang	*Kalmia angustifolia* L.
linvul	*Linaria vulgaris* P. Mill.
luzmul	*Luzula multiflora* var. *acadiensis* Fern.
mellin	*Melampyrum lineare* Desr.
miacan	*Maianthemum canadense* Desf.
monuni	*Monotropa uniflora* L.
oxastr	*Oxalis stricta* L.
phlpra	*Phleum pratense* L.
poapra	*Poa pratensis* L.
v_grass	Poaceae (vegetative)
pteaqu	*Pteridium aquilinum* (L.) Kuhn
pyrsp	*Pyrola* sp. L.
ranrep	*Ranunculus repens* L.
rossp	*Rosa* sp. L.
rubida	*Rubus idaeus* L.
rumace	*Rumex acetosella* L.
solcan	*Solidago canadensis* L.
eutgra	*Euthamia graminifolia* var. *graminifolia* (L.) Nutt.
solrug	*Solidago rugosa* P. Mill.
spialb	*Spiraea alba* Du Roi
stegra	*Stellaria graminea* L.
taroff	*Taraxacum officinale* G.H. Weber ex Wiggers
trapra	*Tragopogon pratensis* L.
tribor	*Trientalis borealis* Raf.
tripra	*Trifolium pratense* L.
vacang	*Vaccinium angustifolium* Ait.
vibnud	*Viburnum nudum* var. *cassinoides* (L.) Torr. & Gray
viccra	*Vicia cracca* L.
viosp	*Viola* sp. L.

References

Atlantic Climate Centre (2004) The climate of Prince Edward Island. http://atlantic-web1.ns.ec.gc.ca/climatecentre/. Accessed 28 July 2006

Barni E, Siniscalco C (2000) Vegetation dynamics and arbuscular mycorrhiza in old-field successions of the western Italian Alps. Mycorrhiza 10:63–72. doi:10.1007/s005720000059

Bazzaz FA (1996) Recruitment in successional habitats: general trends and specific differences. In: Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge

Beaulieu J, Corriveau A, Daoust G (1989) Productivité et stabilité phénotypique de l'épinette rouge au Québec. For Chron 65:42–48

Blum BM (1990) Red spruce. In: Burns RM, Honkala BH (eds) Silvics of North America. United States Department of Agriculture, Forest Service, Washington, DC

Cavallin N, Vasseur L (2008) Potential for red spruce (*Picea rubens* Sarg.) establishment from natural seed dispersal in old fields adjacent to forest stands. Plant Ecol (in press). doi:10.1007/s11258-008-9409-y

Dibble AC, Brissette JC, Hunter ML Jr (1999) Putting community data to work: some understory plants indicate red spruce regeneration habitat. For Ecol Manag 114:275–291. doi:10.1016/S0378-1127(98)00359-4

Environment Canada (2005) Narrative descriptions of terrestrial ecozones and ecoregions of Canada. http://www.ec.gc.ca/soer-ree/. Accessed 28 July 2006

Gleason HA, Cronquist A (1991) Manual of vascular plants of northeastern United States and adjacent Canada. New York Botanical Garden, Bronx, NY, USA

Greene DF, Zasada JC, Sirois L, Kneeshaw D, Morin H, Charron I et al (1999) A review of the regeneration dynamics of North American boreal forest tree species. Can J For Res 29:824–839. doi:10.1139/cjfr-29-6-824

Howard LF, Lee TD (2002) Upland old-field succession in southeastern New Hampshire. J Torrey Bot Soc 129:60–76. doi:10.2307/3088683

Hughes JW, Bechtel DA (1997) Effect of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. Can J For Res 27:2088–2096. doi:10.1139/cjfr-27-12-2088

Jablanczy A (1964) Identification of black, red and white spruce seedlings. Canada Department of Forestry Publication No. 1039. Queen's Printer, Ottawa

Johnson AH, McLaughlin SB, Adams MB, Cook ER, DeHayes DH, Eagar C et al (1992) Synthesis and conclusions from epidemiological and mechanistic studies of red spruce decline. In: Eagar C, Adams MB (eds) Ecology and decline of red spruce in the eastern United States. Springer, New York

Lautenschlager RA (1991) Red raspberry ecology and the effect of raspberry and other forest brush on white spruce growth. CFRU Information Report, College of Forest Resources, Maine Agricultural Experiment Station, University of Maine, Orono, ME, USA

Li X, Wilson SD (1998) Facilitation among woody plants establishing in an old field. Ecology 79:2694–2705

Loo J, Ives N (2003) The Acadian forest: historical condition and human impacts. For Chron 79:462–474

Mallik AU (1994) Autecological response of *Kalmia angustifolia* to forest types and disturbance regimes. For Ecol Manag 65:231–249. doi:10.1016/0378-1127(94)90173-2

Mallik AU (1996) Effect of NPK fertilizations on *Kalmia angustifolia*: implications for forest disturbance and conifer regeneration. For Ecol Manag 81:135–141. doi:10.1016/0378-1127(95)03659-8

Mallik AU (2001) Black spruce growth and understory species diversity with and without sheep laurel. Agron J 93:92–98

McLaughlin SB, Downing DJ, Blasing TJ, Cook ER, Adams HS (1987) An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United States. Oecologia 72:487–501. doi:10.1007/BF00378973

Meiners SJ, Pickett STA (1999) Changes in community and population responses across a forest-field gradient. Ecography 22:261–267. doi:10.1111/j.1600-0587.1999.tb00501.x

Meiners SJ, Handel SN, Pickett STA (2000) Tree seedling establishment under insect herbivory: edge effects and inter-annual variation. Plant Ecol 151:161–170. doi:10.1023/A:1026509529570

Meiners SJ, Pickett STA, Handel SN (2002) Probability of tree seedling establishment changes across a forest-old field edge gradient. Am J Bot 89:466–471. doi:10.3732/ajb.89.3.466

Moola FM, Vasseur L (2004) Recovery of late-seral vascular plants in a chronosequence of post-clearcut forest stands in coastal Nova Scotia, Canada. Plant Ecol 172:183–197. doi:10.1023/B:VEGE.0000026326.09137.06

Nkongolo KK, Deverno L, Michael P (2003) Genetic validation and characterization of RAPD markers differentiating black and red spruces: molecular certification of spruce trees and hybrids. Plant Syst Evol 236:151–163. doi:10.1007/s00606-002-0236-7

Pickett STA, Cadenasso ML, Bartha S (2001) Implications from the Buell-Small Succession Study for vegetation restoration. Appl Veg Sci 4:41–52

Prévost M, Pothier D (2003) Partial cuts in a trembling aspen-conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can J For Res 33:1–15. doi:10.1139/x02-147

Ramovs BV, Roberts MR (2003) Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. Ecol Appl 13:1682–1700. doi:10.1890/02-5237

Rennie F, Curley R, Ristau C, Robichaud H, MacQuarrie K, MacNeill R et al (1997) Proposed addition of the Greenwich Dunes area to Prince Edward Island National Park. Inventory and assessment of resource information and park development concepts. Submitted to the Greenwich Steering Committee

Reyes GL (2002) Chapter 2: red spruce regeneration. Factors affecting vegetation re-establishment patterns following clearcutting of coastal red spruce-balsam fir stands in southwestern Nova Scotia. Thesis, Dalhousie University, Halifax

Reyes G, Vasseur L (2003) Factors influencing deer browsing damage to red spruce (*Picea rubens*) seedlings in coastal red spruce-balsam fir stands of southwestern Nova Scotia. For Ecol Manag 186:349–357. doi:10.1016/S0378-1127(03)00303-7

Richter DD, Markewitz D, Heine PR, Jin V, Raikes J, Tian K et al (2000) Legacies of agriculture and forest regrowth in the nitrogen of old-field soils. For Ecol Manag 138:233–248. doi:10.1016/S0378-1127(00)00399-6

Roberts-Pichette P, Gillespie L (1999) Terrestrial vegetation biodiversity monitoring protocols. EMAN Occasional Paper Series, Report No. 9. Ecological Monitoring Coordinating Office, Burlington, Ontario

Roland AE (1998) Roland's flora of Nova Scotia, 3rd edn, Revised by Zinck M. Nimbus Publishing and Nova Scotia Museum, Halifax, NS, Canada

Roy V, Ruel J-C, Plamondon AP (2000) Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. For Ecol Manag 129:253–267. doi:10.1016/S0378-1127(99)00170-X

Sobey DG, Glen WM (2002) The forests of Prince Edward Island: a classification and ordination using multivariate methods. Can Field Nat 116:585–602

StatSoft, Inc. (2001) STATISTICA (data analysis software system). Version 6. Tulsa, Oklahoma

StatSoft, Inc. (2006) STATISTICA visual basic programs. http://www.statsoft.com/downloads/maintenance/svbprograms.html. Accessed 27 June 2006

Sullivan J (1993) *Picea rubens*. In: Fire effects information system. Rocky Mountain Research Station, Fire Sciences Laboratory (Producer), U.S. Department of Agriculture, Forest Service. http://www.fs.fed.us/database/feis/. Accessed 15 Feb 2006

ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to Canoco for windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY

White PS, Cogbill CV (1992) Spruce-fir forests of eastern North America. In: Eagar C, Adams MB (eds) Ecology and decline of red spruce in the eastern United States. Springer, New York

Yamasaki SH, Fyles JW, Egger KN, Titus BD (1998) The effect of *Kalmia angustifolia* on the growth, nutrition, and ectomycorrhizal symbiont community of black spruce. For Ecol Manag 105:197–207. doi:10.1016/S0378-1127(97)00285-5

Yao J, Holt RD, Rich PM, Marshall WS (1999) Woody plant colonization in an experimentally fragmented landscape. Ecography 22:715–728. doi:10.1111/j.1600-0587.1999.tb00521.x

Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest

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Abstract To examine whether the Janzen–Connell mechanism applies to temperate forests, seedling survival and causes of mortality were investigated at two distances (beneath, far) from conspecific adults and at two densities (high, low) at each distance for seedlings ($n = 7935$) of eight tree species co-occurring in a hardwood forest. Six of the eight species showed distance- and/or density-dependent seedling mortality mainly caused by diseases and rodents. In four of the five species primarily killed by disease (i.e. damping-off, blight, rot, powdery mildew), the infectivity (probability of infection by the disease) and/or the virulence (proportion of seedlings killed to those infected by the disease) were higher beneath than far from conspecific adults. These findings suggest that host specificity and/or spatially heterogeneous activity of natural enemies play an important role in the reciprocal replacement of tree species, maintaining species diversity in temperate forests.

Keywords Disease · Herbivore · Host specificity · Janzen–Connell mechanism · Species diversity

Introduction

Attempts to understand the coexistence and replacement of plant species in natural communities have focussed on biotic interactions (Dinoor and Eshed 1984; Burdon 1991; Coley and Barone 1996; Wright 2002). In forest communities, Janzen (1970) and Connell (1971) hypothesised that host-specific natural enemies such as pathogens and vertebrate and invertebrate herbivores can maintain a high diversity of tree species if they are more likely to damage and kill juveniles growing at high densities or close to conspecific adults. This high mortality might, in turn, liberate areas for colonisation and recruitment by other tree species and thereby contribute to the maintenance of high local diversity. To evaluate the extent to which the Janzen–Connell mechanism leads to species coexistence, it is important to examine how many tree species co-occurring within a forest community exhibit these types of mechanisms (Bell et al. 2006). If most tree species within a forest show distance- and/or density-dependent juvenile mortality, the reciprocal replacement of tree species would be promoted, resulting in a higher probability of tree species co-existence within the forest. However, most studies of the Janzen–Connell mechanism have

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focused on a single tree species in forest communities of tropical (see references in Wright 2002; Gilbert 2002, 2005; Marquis 2005; Freckleton and Lewis 2006) and temperate regions (Packer and Clay 2000; Masaki and Nakashizuka 2002; Tomita et al. 2002; Seiwa et al. 2008). Several community-level studies have also analysed the distance- and/or density-dependent mortality of juveniles for a substantial number of tree species co-occurring within a forest community in tropical (e.g. Wills et al. 1997; Harms et al. 2000; Peters 2003; Webb et al. 2006) and temperate forests (Streng et al. 1989; Jones et al. 1994; Hille Ris Lambers et al. 2002), but most of these studies did not identify the killing agents (but see Augspurger 1984). In field conditions, competition and adult interference may also affect juvenile mortality; thus, the killing agents must be identified to apply this mechanism (Janzen 1970; Clark and Clark 1984). To elucidate whether the Janzen–Connell mechanism mediates species diversity in temperate forests, we conducted a field experiment investigating both the killing agents that cause seedling mortality and their manner of attack (i.e. distance or density dependency or both) for eight tree species co-occurring in a temperate forest.

In both tropical and temperate forests, tree juveniles are usually attacked by a variety of natural enemies, such as pathogens and invertebrate and vertebrate herbivores, and the enemies show a variety of means of attack. For example, invertebrate and vertebrate herbivores usually kill juveniles in the density- and/or distance-dependent manner (e.g. Maeto and Fukuyama 1997; Wada et al. 2000; reviewed by Marquis 2005), although relatively fewer evidences have been reported in vertebrate herbivores (Akashi 1997; Tomita et al. 2002; Silman et al. 2003; Wyatt and Silman 2004). On the other hand, juvenile mortality from pathogens is better predicted by distance from mature trees than by juvenile density (Augspurger and Kelly 1984; Packer and Clay 2000; Masaki and Nakashizuka 2002; Tomita et al. 2002; Gallery et al. 2007). Although several exceptions have been observed (e.g. Bell et al. 2006; reviewed by Freckleton and Lewis 2006), results of these studies suggest that the manner of attack differs among types of natural enemies. However, in forests, juvenile density is often correlated with distance from conspecific adults (Packer and Clay 2000; Seiwa et al. 2008), leading to misunderstandings of the manner of attack of each agent. Thus, to explicitly distinguish the effects of density from those of distance, it is necessary to independently manipulate density and distance in the field (Clark and Clark 1984). To clarify whether natural enemies have a specific mode of attack, comparative studies are required for several tree species co-occurring within a forest community.

Host-specificity of natural enemies is crucially important to apply the Janzen–Connell hypothesis (Janzen 1970; Packer and Clay 2000; Gilbert 2005; Freckleton and Lewis 2006; Seiwa et al. 2008). In individual forest communities, seedlings of several species coexist in a spatially complex understorey community that is generated by overlapping seed shadows of the adults. If herbivores or pathogens attack in a distance- or density-dependent manner without host specificity, all tree seedlings co-occurring with the focal species (even under heterospecific adults) would also be affected by generalist pathogens when total seedling density is high. Several studies have recently examined the virulence of pathogens beneath parents that more strongly affect seedlings through negative feedback mechanisms or local adaptation, not only in herbaceous and grassland communities (Bever 1994; Bever et al. 1997; Mills and Bever 1998; Lively and Dybdahl 2000; Sicard et al. 2007) but also in forest communities (Packer and Clay 2000, 2004; Hood et al. 2004; Reinhart et al. 2005; Seiwa et al. 2008). If locally adapted parasites infect a maximum number of local hosts depending on the host population density (Kirchner and Roy 2002; Dybdahl and Storfer 2003), disease infectivity and consequent seedling mortality will be higher beneath compared with far from conspecific adults. On the other hand, several authors have noted that disease infectivity does not always correspond to disease lethality (Kirchner and Roy 2002; Dybdahl and Storfer 2003), probably because of differences in the extent of local adaptation or intensity of negative feedback. Therefore, information regarding the virulence as well as infectivity of pathogens may provide more accurate estimates of host specificity. However, in field conditions, a variety of disease symptoms are often observed, even within a single seedling of an individual tree species, and each symptom may also involve a variety of fungal species (e.g. Garcia-Guzman and Dirzo 2001; Schafer and Kotanen 2004), pointing to the difficulty in testing host specificity for all diseases by inoculation or sterilisation methods. Here, for convenience, we classified the diseases causing seedling mortality into four predominant symptoms (i.e. damping-off, blight, rot and powdery mildew), and we evaluated the host specificity of these diseases for seedlings of five tree species that are killed primarily by disease by investigating the difference in pathogenicity beneath and far from conspecific adults. Specifically, we addressed (i) how and what natural enemies attack the seedlings of each of the eight tree species co-occurring within a forest community; (ii) differences in the manner of attack among the natural enemies; (iii) host specificity of the predominant diseases; and (iv) the potential validity of the Janzen–Connell mechanism mediating species diversity in a temperate forest.

Materials and methods

Study site and species

This study was conducted in the reserve area (ca. 168 ha) of an experimental forest at the Field Science Centre of Tohoku University in northeastern Japan (38°48′ N, 140°44′ E, altitude 500–610 m). Mean monthly temperatures ranged from 1.0°C (January) to 22.5°C (August) in 2004. Mean annual temperature and rainfall were 11.0°C and 1563 mm, respectively. Trees in the reserve area have re-established after clear-cutting 60 years ago, and the area has been protected from human activity as a forest reserve for at least last 40 years. The canopy layer was dominated by *Fagus crenata* and *Quercus serrata* as mosaic patches, and the total basal area of the two species was approximately 20% (Terabaru et al. 2004). In this study, eight deciduous broadleaf tree species that were common in this forest were selected as focal plants: *Prunus grayana*, *Cornus controversa*, *Magnolia obovata*, *Fraxinus lanuginosa*, *Acer mono*, *Castanea crenata*, *F. crenata*, and *Q. serrata.* As these species belong to different genera, we hereafter refer to them by their genus names.

Experimental design and demographic censuses

Three adult trees were selected for each study species in a 30-ha area within the reserve. For each species, individual adults were isolated from each other and were at least 50 m from the nearest conspecific adult. In each species, we selected two distance intervals: 0–3 m (beneath) and 25–50 m (far) from each adult tree, representing non-dispersed fruits and fruits dispersed far from the adults, respectively (Masaki et al. 1994; Akashi 1997; Maeto and Fukuyama 1997; Tomita et al. 2002; Seiwa et al. 2008; Yamazaki and Seiwa, unpublished data). For each adult tree, four and eight quadrats (35 × 45 cm) were randomly established within the 0–3 m (beneath) and 25–50 m (far) ranges, respectively. Exceptions were *Prunus*, *Fraxinus* and *Castanea*, for which the far quadrats were established 50–75 m from conspecific adults, because there were few flat areas near the adults. Within the far ranges for each species, each far quadrat was located under non-conspecific adult trees. In both *Fagus* and *Quercus*, four quadrats were established at each of the two distance intervals. Before the seeds were sown, naturally fallen seeds were removed from the both litter and soil layer of approximately 3 cm in depth in each quadrat.

In 2003, fresh seeds were collected in the experimental forest from more than three canopy trees for each of six species (*Prunus*, *Cornus*, *Magnolia, Fraxinus*, *Acer* and *Castanea*) or from the ground under more than three adult trees for each of *Fagus* and *Quercus*. *Fagus* seeds were collected from forests 100 km north of the study area, because 2003 was a non-mast year in the study forest. Seeds were floated in water to eliminate non-viable seeds. The number of seeds sown in each quadrat differed among species according to the density of naturally falling seeds or newly emerged seedlings (Maeto and Fukuyama 1997; Masaki and Nakashizuka 2002; Tomita et al. 2002; Seiwa et al. 2008). The number of seeds sown in each high- and low-density quadrat was 200 and 30 for *Prunus*, *Cornus* and *Fraxinus*, 100 and 20 for *Acer*, 50 and 10 for *Magnolia*, *Fagus* and *Quercus*, and 45 and 6 for *Castanea*, respectively. The total number of seeds sown was 18,738. To avoid severe seed predation by mammals and jays during the winter, the quadrats were covered by 0.3 × 0.3-cm mesh nets buried to a depth of 10 cm. The height of the nets was 10 cm. These nets were removed when seedlings started to emerge during the following spring.

In each quadrat, all newly emerging seedlings were tagged and monitored for survivorship, causes of mortality, and disease symptoms and signs.

Measurements started on 7 April 2004, immediately after snow melt, and were repeated weekly or biweekly until 9 November, and then monthly for the remainder of the first growing season. The number of seedlings that emerged in each of the high- and low-density treatments in the quadrats is shown in Appendix 1.

Causes of seedling mortality

All causes of seedling mortality were investigated during the first growing season for all seedlings ($n = 7935$) that emerged in 2004. The causes were classified as follows: (1) disease: disease symptoms and signs were determined following Agrios (1997) and Horst (2001); (2) invertebrate herbivores: seedling death caused by predation of hypocotyls, leaves (more than 80% of the area) or roots; (3) vertebrate herbivores: severing of main stems by mammals such as wood mice, rabbits and Japanese serows. We distinguished symptoms of vertebrates from those of pathogens and invertebrates on the strength of the traces of mammals such as the shape of the teeth, cut edge, animal droppings and turned soil by mammals; (4) withering: drying and uprooting; and (5) physical damage: fallen branches and snow pressure.

Identification of disease types and isolation of fungi

Although more than one symptom or sign appeared on individual seedlings, each disease was quantified separately, and the most crucial symptom that affected the stem or largest proportion of leaves was regarded as the disease that caused seedling death. In this study, diseases that caused seedling death were classified into four predominant types as follows: (1) Damping-off: succulent stems became water-soaked, necrotic, and sunken near the soil line or at ground level. (2) Blight: primary symptoms were small round or irregular brown spots on leaves of *Prunus* and *Fraxinus*, dark brown spots on *Magnolia*, and black spots on *Cornus*, *Magnolia* and *Fraxinus*. The spots enlarged and coalesced to cover most of the individual leaves. Secondary symptoms were leaf defoliation or enlargement of lesions to stems, followed by stem die-back from the tip. (3) Rot: symptoms included softening, discoloration and disintegration of leaves, followed by stem die-back. (4) Powdery mildew: patches of white to greyish and powdery spots on leaf surfaces. Mildew first grew on young leaves, and then the top of the stem often died.

For each type of diseases, the disease infectivity, virulence and seedling mortality were calculated for all seedlings in each high-density quadrat at each distance for each species. Disease infectivity was defined as the proportion of seedlings infected to those emerged. Virulence was defined as the proportion of seedlings killed by the disease to those infected by the disease. Seedling mortality was defined as the proportion of seedlings killed by the disease to those emerged.

To determine how many and what pathogens caused the disease symptoms, individual fungi were identified. We sampled at least two or three diseased parts of or whole of the dead individuals at each measurement time. Approximately 10% of dead individuals were randomly chosen (Appendix 2), and the fungi were isolated immediately after sampling. Seedlings damaged by disease were dissected into small pieces of approximately 5 mm in length, submerged in 70% ethanol (v/v) for 30 s, and then surface sterilised for 60 s in a solution of 0.1% sodium hypochlorite (v/v). Samples were then rinsed in sterile distilled water and placed in corn meal agar (Nissui, Tokyo, Japan) and incubated at 20°C. Five to a month after inoculation, cultures were purified using single-spore isolation or by transforming small portions of the culture medium several times, including the advancing margin of the mycelia. Fungal morphotypes were described, and when possible, morphologically identified to genus.

Micro-environmental conditions

To estimate the environmental light conditions in which seedlings were growing, hemispherical photographs were taken with a fish-eye camera (Nikon, F8 mm) at a height of 0.3 m above the ground in each high- and low-density quadrat both beneath and far from conspecific adults on 6 August 2004. Canopy openness in each quadrat was calculated as the ratio of the open-to-closed portions of the canopy in the entire hemispherical area. Photographs were converted to computer data, and the photosynthetic photon flux density (PPFD) was computed using Gap Light Analyzer (GLA) version 2.0 (Frazer et al.

1999). Relative PPFD (rPPFD) was obtained by dividing PPFD in each canopy openness dataset by that under an obstructed sky. Soil water potential was also estimated using soil tensiometers (DIK-8331 pF meter, Daiki Rika Kogyo Co. Lid.) near each quadrat on 14 October 2004.

Data analysis

To evaluate differences in micro-environmental conditions (relative PPFD, %, soil moisture, pF values) between distances (beneath, far), one-way analysis of variance (ANOVA) was conducted separately for each species.

To examine whether the percentage of seedling survival depended on distance from conspecific adults and/or seedling density, survival time models based on a Weibull distribution were constructed for each species. To examine whether the probability of seedling death depended on distance, seedling density or the percentage of seedlings killed by each agent (disease, invertebrate herbivore, vertebrate herbivores, withering and physical damage), these factors were analysed using two-way ANOVA for each species. Prior to ANOVAs, the percentage values were arcsine transformed. Data for each quadrat at each distance were pooled across the two different densities.

Each of the three disease indices (disease infectivity, virulence and seedling mortality) was compared between distances (beneath versus far) using Wilcoxon tests for each disease symptom. In this analysis, data from high-density quadrats were used because of the small sample size in the low-density plots. Statistical analyses were performed using JMP version 4.0.5 (SAS Institute Inc., Cary, North Carolina).

Results

Micro-environmental conditions

There were few differences in rPPFD (%) and soil moisture (pF) between the two distances (beneath versus far) for most of the eight species studied (one-way ANOVA: $F < 0.37$, $P > 0.54$). As an exception, rPPFD was greater beneath compared with far from both *Castanea* and *Quercus* ($F > 16.3$, $P < 0.01$), whereas the reverse was true in *Fagus* ($F = 36.51$, $P < 0.01$). The pF value was greater beneath compared with far from *Prunus* ($F = 9.02$, $P < 0.05$).

Seedling survival

In all the species studied, seedling death occurred throughout the growing season, particularly during the rainy period from June to July (Fig. 1). For most species, seedling survival was usually lower beneath compared with far from conspecific adults, although data from *Castanea* were not significant (Table 1, Fig. 1). An exception was *Quercus*, in which the reverse was true. Seedling survival was significantly lower at high density relative to low density for *Magnolia*, *Fraxinus* and *Cornus* (marginal), whereas the reverse was true for *Fagus* (Table 1, Fig. 1). For the other four species, seedling survival did not differ between densities. An interaction between distance and density was only observed in *Cornus*, in which seedling survival was lower at high density than at low density beneath conspecific adults but did not differ between the two densities in the far treatment (Table 1, Fig. 1).

Causes of seedling mortality

In each species, seedlings were killed by a variety of agents. In particular, disease accounted for a larger proportion of seedling deaths compared to other agents (i.e. vertebrate and invertebrate herbivores, physical damage, withering) at both distances for *Prunus*, *Cornus*, *Magnolia, Fraxinus* and *Quercus* (Fig. 2). Two-way ANOVAs indicated that the proportion of seedlings dying due to disease was significantly higher beneath compared with far from conspecific adults for *Prunus*, *Cornus*, *Magnolia* and *Fraxinus*, whereas the opposite was true for *Quercus* (Table 2, Fig. 2). The proportion of seedlings dying due to disease was also higher at high density rather than low density for *Cornus*, *Fraxinus* and *Castanea*, whereas minimal differences were observed for the other five species (Table 2, Fig. 2). An interaction between distance and density was observed only for *Prunus*, in which the probability of death by disease did not differ between the two densities beneath adults but was higher at high density compared to low density in the far treatment (Fig. 2).

In *Fraxinus*, *Castanea* and *Fagus*, the proportion of seedlings killed by vertebrate herbivores was

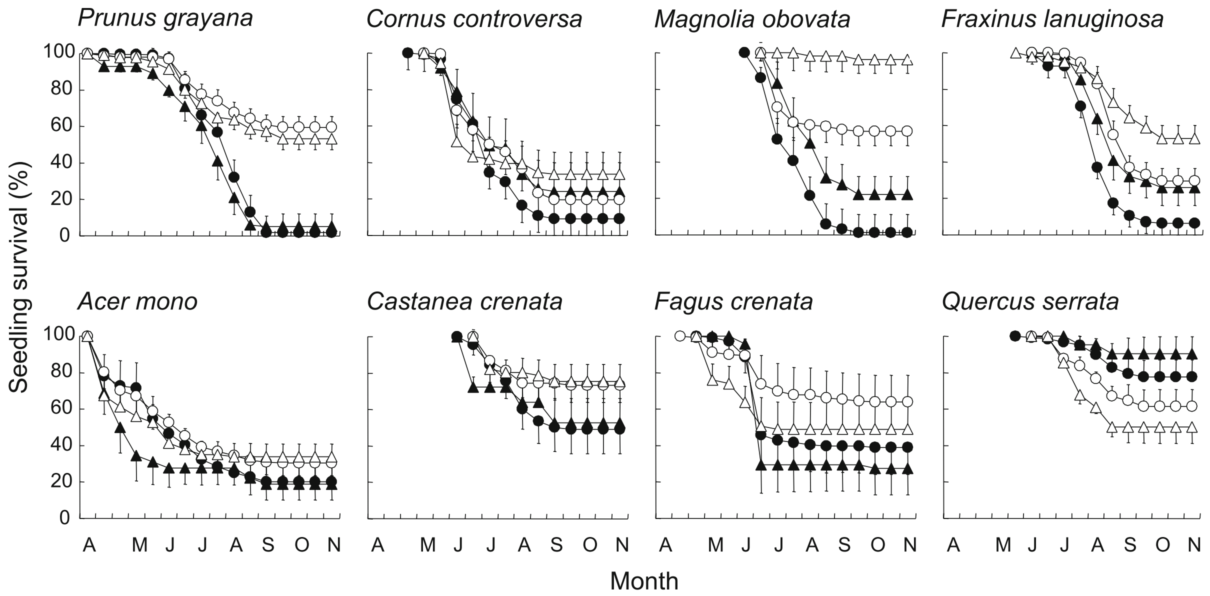

Fig. 1 Seedling survivorship from April to November 2004 for two density treatments (high and low) at two distances (beneath and far) from conspecific adult trees for eight deciduous broadleaf tree species. High (●) and low (▲) density beneath conspecific adults; high (○) and low (△) density far from conspecific adults

Table 1 Results of survival time analysis assessing the effects of distance (beneath or far) from conspecific adult trees, density (high or low) and their interaction on X^2 values for the eight study species

Species	Distance (D_i) d.f. = 1	Density (D_e) d.f. = 1	$D_i \times D_e$ d.f. = 1
Prunus grayana	93.53***	1.87	2.25
Cornus controversa	4.81*	$2.73^\dagger$	21.97***
Magnolia obovata	77.59***	20.61***	0.68
Fraxinus lanuginosa	121.27**	139.70**	1.84
Acer mono	4.52*	1.03	0.02
Castanea crenata	3.02	0.16	0.00
Fagus crenata	20.18***	5.61*	0.37
Quercus serrata	14.15***	0.20	1.83

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

higher beneath compared with far from conspecific adults (Table 2, Fig. 2), whereas the reverse was true for *Cornus*. In *Magnolia*, the probability of death by vertebrate herbivores was higher at high density relative to low density. For each of the other killing agents (invertebrate herbivores, withering and physical damage), few differences were observed between distances ($F < 0.007$, $P > 0.931$) or between densities ($F < 0.005$, $P > 0.947$) for all the species studied (Fig. 2).

Infectivity, virulence, and seedling mortality

For *Prunus*, *Cornus*, *Magnolia*, *Fraxinus* and *Quercus*, which were mainly killed by disease in a distant-dependent manner, seedling mortality was primarily caused by four predominant diseases (damping-off, blight, rot, powdery mildew), although several disease symptoms (e.g. sooty mould, rust, leaf spot) were also observed. Damping-off diseases were chiefly observed during the early growing season, particularly from seedling emergence to July, for all the species. Thereafter, foliar diseases (e.g. blight, rot, powdery mildew) were observed. The fungal genera *Colletotrichum*, *Phoma*, *Fusarium*, *Cylindrocarpon*, *Cladosporium* and *Alternaria* were isolated from samples of damping-off diseases, which were observed in all the species (Appendix 3). In samples of blight and rot, the genera *Colletotrichum*, *Phoma* and *Cladosporium* were primarily detected in dead seedlings (Appendix 3). In blight of *Cornus* and damping-off of *Fraxinus*, both infectivity and mortality were higher beneath compared with far from adults, but minimal differences in virulence were observed between the distances (Fig. 3). In contrast, in blights of *Prunus* and *Magnolia*, both virulence and mortality were higher beneath compared with far from adults, although few differences were observed

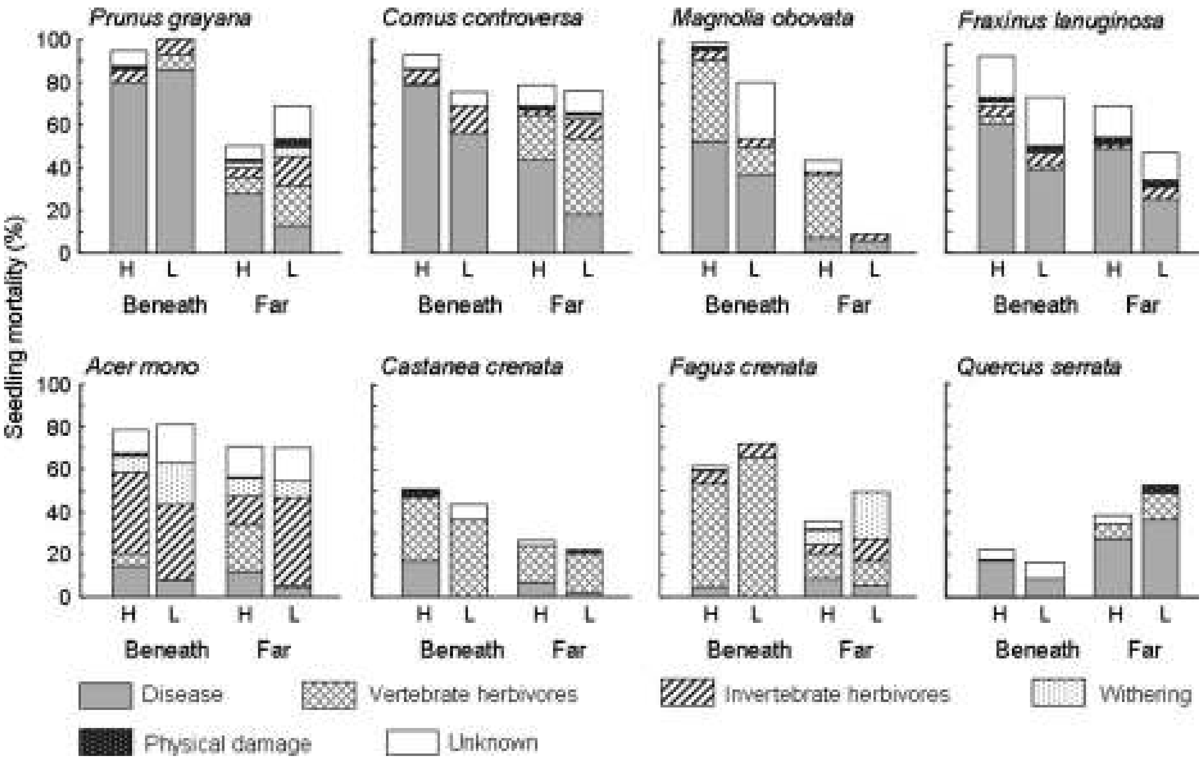

Fig. 2 Seedlings killed by each agent at two different densities (high, low) at two different distances (beneath, far)

Table 2 Results of two-way ANOVAs assessing the effects of distance (beneath and far) from conspecific adult trees, seedling density (high and low) and their interaction on *F* values of disease and vertebrate herbivores per species

Species	Factor causing death	Distance (D_i)	Density (D_e)	$D_i \times D_e$
Prunus grayana	Disease	127.45***	1.07	11.78**
	Vertebrate herbivores	0.68	0.68	0.01
Cornus controversa	Disease	26.42***	12.81**	0.09
	Vertebrate herbivores	8.44**	1.00	1.13
Magnolia obovata	Disease	15.56***	1.24	1.04
	Vertebrate herbivores	0.41	4.52*	0.06
Fraxinus lanuginosa	Disease	4.25*	10.26**	0.00
	Vertebrate herbivores	9.06**	0.11	0.01
Acer mono	Disease	0.53	2.19	0.02
	Vertebrate herbivores	1.10	2.28	0.90
Castanea crenata	Disease	0.91	5.28*	1.73
	Vertebrate herbivores	3.08†	0.56	0.40
Fagus crenata	Disease	3.34	2.06	0.05
	Vertebrate herbivores	21.36***	0.72	0.64
Quercus serrata	Disease	5.93*	0.01	1.28
	Vertebrate herbivores	3.24	0.20	0.31

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Degree of freedom for distance (D_i), density (D_e) and $D_i \times D_e$ = 1, 32, with exceptions of *Fagus* and *Quercus*, where D_i, D_e and $D_i \times D_e$ = 1, 20

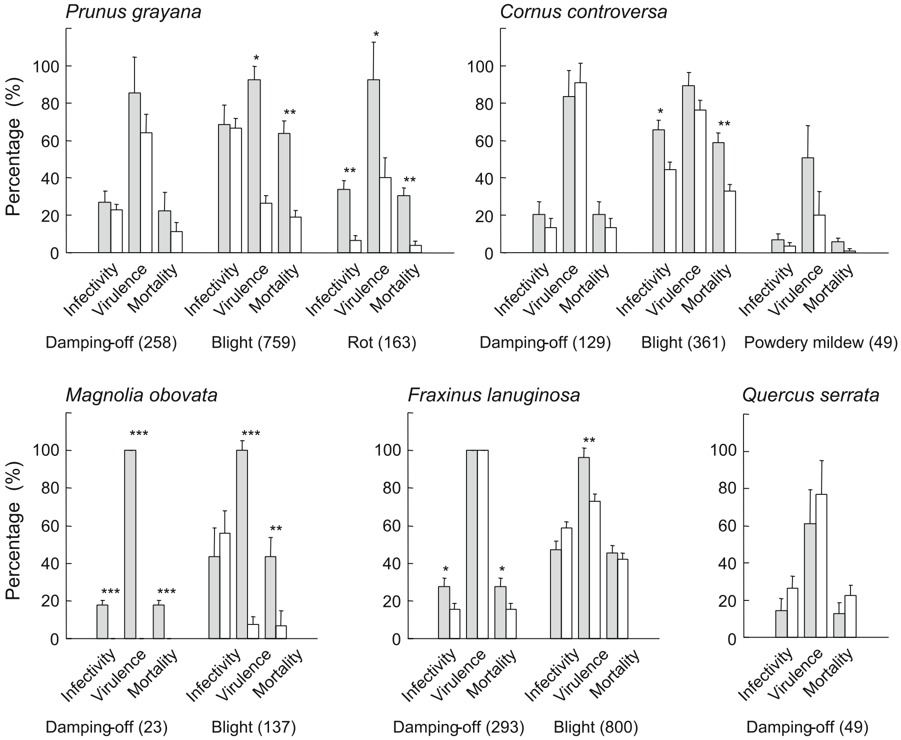

Fig. 3 Percentages of infectivity, virulence, and seedling mortality beneath (shaded bars) and far (open bars) from conspecific adults for four predominant diseases in five tree species. Only data for high-density plots are given. Error bars represent standard errors. Asterisks indicate significant differences between distances (Wilcoxon test * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Numbers in parentheses are total numbers of seedlings infected by each disease

in infectivity (Fig. 3). In rot of *Prunus* and damping-off of *Magnolia*, all the three indices (infectivity, virulence, mortality) were higher beneath compared with far from adults (Fig. 3). For all the three indices, few differences were observed between distances in damping-off diseases of *Prunus*, *Cornus* and *Quercus*, and in powdery mildew of *Cornus* (Fig. 3).

Discussion

Distance- and/or density-dependent seedling mortality by natural enemies

Our results clearly demonstrated that seedlings of temperate tree species are mainly killed by biotic agents, particularly diseases and vertebrate herbivores, in a positive distance-dependent and negative density-dependent manner, rather than by a deficiency of environmental resources such as light and soil moisture. These patterns were observed for six of the eight co-occurring study species and resulted in a greater proportion of seedling death beneath conspecific adults, particularly at higher seedling density. These findings strongly suggest that recruitment of heterospecific seedlings to the free space near conspecific adult trees is largely promoted in this temperate forest community. If such reciprocal replacements occur under adults of most common tree species co-occurring within individual forest communities, species diversity would be maintained (Janzen 1970). Although there are increasing evidences in the density- and/or distance-dependent mortality in juveniles including seed-to-sapling stages, this short-term study focused on only seedling stage. Because distance- and density-dependent reductions in performance accumulate as juveniles grow (Gilbert et al. 2001; Wright 2002; Packer and Clay 2003; Seiwa et al. 2008), further studies including seed-to-sapling stages and the spatial distribution of saplings are needed to confirm the Janzen–Connell mechanisms. Although the full extent of recruitment reductions near fruiting conspecifics may have been systematically underestimated, the results from this community-level study strongly suggest that the Janzen–Connell mechanism have the potential to affect species diversity in temperate as well as tropical forests.

In this study, *Quercus* was an exception to the Janzen–Connell hypothesis. Surprisingly, seedling mortality of *Quercus* was lower beneath compared with far from conspecific adults. Canopy trees of *Quercus* usually started to unfold their leaves approximately 1 month later than conspecific seedlings and other heterospecific canopy trees co-occurring at the study site (Yamazaki and Seiwa unpublished data). In temperate forests, tree seedlings with earlier leaf emergence compared to overstorey trees usually gain more favourable light prior to canopy closure, thereby producing large and sturdy seedlings that usually show high resistance to herbivores and disease compared with late emerging seedlings (Seiwa 1998). For seedlings of *Quercus*, such phenological advantages in acquiring spring light and escaping from natural enemies would enhance survival under conspecific adults compared with heterospecific trees. These traits suggest that phenological events may be one of the most important factors required to evaluate the validity of the Janzen–Connell hypothesis, especially in temperate forests.

Primary killing agents and the manner of attack

In this study, the most important killing agent clearly differed among species, according to seed size. Vertebrate herbivores (mainly rodents) were the major cause of mortality for the large-seeded species (*Castanea* and *Fagus*), whereas disease was most important for the small-seeded species (*Prunus*, *Cornus*, *Magnolia* and *Fraxinus*). This difference is probably due to the preference of rodents for large seeds (Jensen 1985; Seiwa and Kikuzawa 1996; Ostfeld et al. 1997). Predation usually occurred during the early growing season, when seed reserves remain in the cotyledons, prior to disease attack. Furthermore, large seeds may also produce sturdy seedlings that are more disease resistant, resulting in little damage from pathogens.

The manner of attack (distance or density dependency) did not differ between the two primary killing agents (disease and rodents), both of which usually exhibited distance dependence or a combined effect of both distant and density dependence in disease attack for two species (*Cornus* and *Fraxinus*). These results are in accordance with previous studies on disease attacks (Packer and Clay 2000; reviewed by Gilbert 2005; Bell et al. 2006; Seiwa et al. 2008), but not rodent predation (Tomita et al. 2002). For rodents, particularly wood mice (*Apodemus* spp.), the close proximity (1 m) of the quadrats between high- and low-density treatments may have promoted seed consumption even at low density, thus reducing the effects of density. Because the experiment was conducted in a non-mast year for the large-seeded study species, seed predation in low density quadrats may also have been promoted by the lack of naturally regenerating seedlings. To clarify the manner of attack by rodents, temporal fluctuations in seed crops and rodents should be considered. In contrast, distance-dependent disease attacks are primarily caused by crowding of disseminated seeds and seedlings beneath conspecific adults, which enhances cultures of soil microbial communities (Bever 1994; Packer and Clay 2000; Hood et al. 2004). In forest communities, a greater proportion of the seed crop is deposited below canopies of bird- or wind-dispersed species (Houle 1992; Clark et al. 2005). Approximately 80% of seeds were disseminated beneath a conspecific canopy without bird dispersal in *C. controversa* (Masaki et al. 1994).

Adult trees may also serve as leaf disease ‘incubators’, because diseases in the canopy are often shared by juveniles beneath conspecific adults (Gilbert 1995; Hood et al. 2004; Gallery et al. 2007). In this study, the foliar disease “blight” observed in seedlings was also observed in leaves of conspecific adults in *Cornus* (e.g. zonate leaf blight, grey mould), *Prunus* (e.g. *Monilinia* blight, angular leaf spot) and *Fraxinus* (brown leaf spot; Yamazaki and Seiwa, unpublished data). Because the majority of leaves fall in the vicinity of adults, infected leaves and spores accumulate beneath them. Foliar diseases strongly reduce the photosynthetic area of leaves and frequently destroy constructive tissues such as stems (Gilbert 1995). Such negative effects of foliar diseases, together with soil-borne pathogens, such as damping-off diseases, resulted in higher seedling mortality beneath conspecific adults. Subsequent studies of foliar disease in both seedlings and conspecific adult trees warrant further work following individual diseases.

Host specificity of predominant diseases

In our experiment, four predominant symptoms (damping-off, blight, rot, powdery mildew) were observed in the dead seedlings of the five tree species that exhibited distant-dependent mortality due to the disease. For each disease symptom, the higher infectivity and/or virulence beneath compared with far from conspecific adults strongly indicated the host specificity of the disease attack. In blight of *Cornus* and damping-off of *Fraxinus*, higher infectivity was observed beneath relative to far from conspecific adults, whereas virulence did not differ between distances. These patterns possibly suggest that higher seedling mortality due to these diseases beneath conspecific adults is likely due to greater abundance and/or infective activity of the pathogens beneath adult trees. In blights of both *Prunus* and *Magnolia*, infectivity did not differ between distances, but virulence was significantly higher beneath compared with far from adults. These results potentially indicate that pathogens causing blight were ubiquitous, but virulence was stronger beneath conspecific adults, resulting in higher seedling mortality beneath them. In rot of *Prunus* and damping-off of *Magnolia*, both infectivity and virulence were higher beneath compared with far from conspecific adults, suggesting that combined effects of pathogenicity caused higher seedling mortality beneath the adults. In *Prunus*, *Magnolia* and *Fraxinus*, more than two disease symptoms exhibited significant differences in pathogenicity between distances. Even though each disease attacks host seedlings independently, their combination may synergistically affect seedling mortality, resulting in distance-dependent seedling mortality for these study species.

Furthermore, fungal species of *Colletotrichum*, *Phoma*, *Fusarium*, *Cylindrocarpon*, *Cladosporium* and *Alternaria*, which were isolated from dead seedlings infected with damping-off, blight and rot, were observed in most of the eight species studied (Appendix 3). These fungal species are considered facultative pathogens, which originally exhibited wide host ranges (Agrios 1997; Horst 2001). Although little is known of the causal relationships between infectivity and host mortality in most of the individual fungal species, particularly for host tree species (but see Sahashi et al. 1995; Packer and Clay 2000; Augspurger and Wilkinson 2007; Seiwa et al. 2008), the observed distant-dependent attacks by the predominant diseases (including several fungi) may suggest that generalist pathogens with broad host ranges may cause seedling mortality in a host-specific manner in this forest community. Recently, Sicard et al. (2007) found that both infectivity and the degree of leaf damage by the pathogen *Colletotrichum lindemuthianum* differed among individual host populations and among host plants, because the pathogens were adapted to the local genotypes of the host plant. Our results, together with evidence of local adaptation (Sicard et al. 2007) and negative feedback (Packer and Clay 2004; Kotanen 2007), may suggest that some soil-borne pathogens are ubiquitous, but infectiousness and virulence of the pathogens are frequently higher beneath conspecific adults, because generalist pathogens sometimes adapt specifically to their local host populations (Bever 1994; Bever et al. 1997; Mills and Bever 1998; Lively and Dybdahl 2000). However, we compared pathogenicity between distances for predominant disease symptoms (including several fungi; Appendix 3), instead of individual fungi. To clarify the host specificity of individual pathogens, further experimental studies that include inoculation trials, fungicide experiments and molecular identification must be conducted (Gilbert 2005).

In conclusion, our study clearly revealed that biotic natural enemies (diseases and rodents) strongly influence seedling mortality in a distance-dependent manner for six of eight tree species co-occurring in a temperate forest. Comparisons of pathogenicity of diseases between distances from conspecific adults (i.e. four predominant disease symptoms) indicated that both soil-borne and foliar diseases may affect seedlings in a host-specific manner. These traits strongly suggest that the Janzen–Connell mechanism is important for maintaining local plant diversity in temperate as well as tropical forests.

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Appendices

Appendix 1 Number of seedlings emerged at two densities (high and low) and at two distances (beneath and far) from conspecific adult trees for the eight tree species studied

Species	Seedling density (m^{-2}, ± SE)			
	Beneath		Far	
	High	Low	High	Low
Prunus grayana	403.2 ± 28.5	48.7 ± 20.8	507.9 ± 67.0	57.6 ± 9.2
Cornus controversa	295.2 ± 49.6	59.3 ± 30.8	312.7 ± 63.8	68.3 ± 46.4
Magnolia obovata	143.9 ± 61.2	21.2 ± 14.8	161.5 ± 42.0	15.9 ± 8.5
Fraxinus lanuginosa	520.6 ± 36.1	117.5 ± 4.8	511.6 ± 84.7	118.0 ± 8.4
Acer mono	203.2 ± 51.4	22.2 ± 4.8	222.8 ± 46.7	46.9 ± 6.4
Castanea crenata	80.4 ± 16.4	13.8 ± 2.8	79.4 ± 8.7	19.0 ± 4.3
Fagus crenata	265.6 ± 29.6	37.0 ± 17.3	255.0 ± 8.5	50.8 ± 6.6
Quercus serrata	127.0 ± 14.9	25.4 ± 2.8	124.9 ± 5.7	17.0 ± 1.9

Appendix 2 The number of seedlings died and the number of seedlings for fungal isolations at two distances (beneath and far) from conspecific adults for the eight tree species

Host species	Beneath			Far		
	Number of dead seedlings	Number of seedlings for fungal isolations	Percentage	Number of dead seedlings	Number of seedlings for fungal isolations	Percentage
Prunus grayana	246	20	8.1	209	23	11.0
Cornus controversa	257	25	9.7	300	22	7.3
Magnolia obovata	88	9	10.2	4	1	25.0
Fraxinus lanuginosa	345	12	3.5	482	2	0.4
Acer mono	41	3	7.3	47	5	10.6
Castanea crenata	11	3	27.3	15	2	13.3
Fagus crenata	11	7	63.6	24	2	8.3
Quercus serrata	20	2	10.0	44	5	11.4

Percentages are defined as the proportion of seedlings for fungal isolations

Appendix 3 Description of disease symptoms and the isolated fungal genera at two distances (beneath and far) from conspecific adult trees for each tree species studied

Symptom	Genus of fungi	*Prunus grayana*		*Cornus controversa*		*Magnolia obovata*		*Fraxinus lanuginosa*		*Acer mono*		*Castanea crenata*		*Fagus crenata*		*Qurcaus serrata*	
		Beneath (5)	Far (15)	Beneath (7)	Far (5)	Beneath (3)	Far (1)	Beneath (3)	Far (1)	Beneath (5)	Far (5)	Beneath (6)	Far (2)	Beneath (7)	Far (5)	Beneath (2)	Far (4)
Damping-off	*Colletotrichum*	+	+	+	+	+	−	+	+	+	+	+	−	+	−	+	+
	Phoma	+	+	+	+	+	−	−	+	+	+	+	+	+	−	−	+
	Fusarium	+	+	−	+	+	−	−	−	+	+	−	−	+	−	−	−
	Cylindrocarpon	+	+	+	+	+	−	+	−	−	+	−	−	+	−	−	−
	Cladosporium	−	+	−	+	+	−	−	+	+	+	+	+	+	+	−	−
	Alternaria	−	+	−	+	−	−	−	−	+	+	+	−	+	−	+	−
	Cylindrocladium	−	−	−	−	−	−	−	−	+	−	+	−	−	−	+	+
	Trichoderma	+	+	+	+	−	−	−	−	−	−	−	−	−	−	+	−
	Mucor	+	+	+	+	−	−	+	−	−	−	−	+	−	−	−	−
	Idriella	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	+
	Arthrinium	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	+
	Rhizoctonia	−	+	−	−	+	−	−	−	−	−	+	−	−	−	−	−
	Epicoccum	+	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−
	Pythium	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−
	Penicillium	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
	Pestalotiopsis	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
	Gliocephalotrichum	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
	Scytalidium	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
	Mortierella	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
	Monochaetia	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
	Polyscytalum	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
	Dictyochaeta	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
	Unknown	+	+	−	−	+	−	−	−	+	+	+	−	+	+	+	+

Appendix 3 continued

Symptom	Genus of fungi	*Prunus grayana*		*Cornus controversa*		*Magnolia obovata*		*Fraxinus lanuginosa*	
		Beneath	Far	Beneath	Far	Beneath	Far	Beneath	Far
		(13)	(5)	(11)	(10)	(5)	(3)	(3)	(3)
Blight and die-back	*Colletotrichum*	+	+	+	+	+	+	+	+
	Phoma	+	+	+	+	+	+	+	+
	Cladosporium	+	+	+	+	−	−	+	−
	Alternaria	+	+	+	+	−	−	+	−
	Cylindrocarpon	+	+	−	+	+	−	+	−
	Cylindrocladium	+	+	+	+	+	+	−	−
	Fusarium	+	+	+	+	−	−	−	−
	Trichoderma	+	+	−	+	−	−	−	−
	Idriella	−	−	+	+	−	−	−	−
	Epicoccum	−	+	−	+	−	−	−	−
	Clonostachys	−	+	−	+	−	−	−	−
	Mucor	+	−	−	−	−	−	−	−
	Botrytis	−	−	+	−	−	−	−	−
	Pythium	−	−	+	−	−	−	−	−
	Aureobasidium	−	+	+	−	−	−	−	−
	Penicillium	+	+	−	−	−	−	−	−
	Curvularia	+	−	−	−	−	−	−	−
	Gliocladium	+	−	−	−	−	−	−	−
	Macrophoma	+	−	−	−	−	−	−	−
	Cladosporium	−	−	+	−	−	−	−	−
	Polyscytalum	−	−	−	+	−	−	−	−
	Unknown	+	−	−	−	−	−	−	+

Appendix 3 continued

		(2)	(3)
Rot	*Colletotrichum*	+	+
	Phoma	+	+
	Cladosporium	+	+
	Idriella	+	−
	Botrytis	+	−
	Alternaria	+	−
	Aureobasidium	+	−
	Epicoccum	+	−
	Unknown	+	−

Numerals in parenthesis are number of seedlings for fungal isolations

+, the presence of fungi isolated from diseased seedling; −, no isolation

References

Agrios GN (1997) Plant pathology, 4th edn. Academic Press, London

Akashi N (1997) Dispersion pattern and mortality of seeds and seedlings of *Fagus crenata* Blume in a cool temperate forest in western Japan. Ecol Res 12:159–165. doi: 10.1007/BF02523781

Augspurger CK (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712. doi:10.2307/1937766

Augspurger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61:211–217. doi:10.1007/BF00396763

Augspurger CK, Wilkinson HT (2007) Host specificity of Pathogenic *Pythium* species: implications for tree species diversity. Biotropica 39:702–708. doi:10.1111/j.1744-7429.2007.00326.x

Bell T, Freckleton RP, Lewis OT (2006) Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecol Lett 9:569–574. doi:10.1111/j.1461-0248.2006.00905.x

Bever JD (1994) Feedback between plants and their soil communities in an old field community. Ecology 75:1965–1977. doi:10.2307/1941601

Bever JD, Westover KM, Antonovics J (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. J Ecol 85:561–573. doi: 10.2307/2960528

Burdon JJ (1991) Fungal pathogens as selective forces in plant populations and communities. Aust J Ecol 16:423–432. doi:10.1111/j.1442-9993.1991.tb01072.x

Clark DA, Clark DB (1984) Spacing dynamics of a tropical rainforest tree, evaluation of the Janzen–Connell model. Am Nat 124:769–788. doi:10.1086/284316

Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86:2684–2694. doi:10.1890/04-1325

Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. Annu Rev Ecol Syst 27:305–335. doi: 10.1146/annurev.ecolsys.27.1.305

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: van der Boer PJ, Gradwell GR (eds) Dynamics of populations. Proceeding of the advanced study institute, Osterbeek, 1970. Centre for Agricultural Publication and Documentation, Wageningen, pp 298–312

Dinoor A, Eshed N (1984) The role and importance of pathogens in natural plant communities. Annu Rev Phytopathol 22:443–466. doi:10.1146/annurev.py.22.090184.002303

Dybdahl MF, Storfer A (2003) Parasite local adaptation: Red Queen versus Suicide King. Trends Ecol Evol 18:523–530. doi:10.1016/S0169-5347(03)00223-4

Frazer GW, Canham CD, Lertzman KP (1999) Gap light analyzer (GLA), Version 2.0. Copyright© 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York

Freckleton RP, Lewis OT (2006) Pathogens, density dependence and the coexistence of tropical trees. Proc R Soc Lond 273:2909–2916. doi:10.1098/rspb.2006.3660

Gallery RE, Dalling JW, Wolfe BT, Arnold AE (2007) The influence of seed source, habitat and fungi on *Cecropia* seed survival in two Neotropical forests. In: Dennis A, Green R, Schupp E, Westcott D (eds) Theory and its seed dispersal, application in a changing world. CABI Press, Wallingford, UK, pp 479–498

Garcıa-Guzman G, Dirzo R (2001) Patterns of leaf-pathogen infection in the understory of a Mexican rain forest: incidence, spatiotemporal variation, and mechanisms of infection. Am J Bot 88:634–645. doi:10.2307/2657063

Gilbert GS (1995) Rain forest plant diseases: the canopy—understory connection. Selbyana 16:75–77

Gilbert GS (2002) Evolutionary ecology of plant diseases in natural ecosystems. Annu Rev Phytopathol 40:13–43. doi:10.1146/annurev.phyto.40.021202.110417

Gilbert GS (2005) Dimensions of plant disease in tropical forests. In: Burslem DFRP, Pinard MA, Hartley SE (eds) Biotic interactions in the tropics. Cambridge University Press, Cambridge, pp 141–164

Gilbert GS, Harms KE, Hamill DN, Hubbell SP (2001) Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panamá. Oecologia 127:509–516. doi:10.1007/s004420000616

Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495. doi:10.1038/35006630

Hille Ris Lambers J, Clark JS, Beckage B (2002) Density-dependent mortality and the latitudinal gradient in species diversity. Nature 417:732–735. doi:10.1038/nature00809

Hood LA, Swaine MD, Mason PA (2004) The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest soil. J Ecol 92:816–823. doi:10.1111/j.0022-0477.2004.00917.x

Horst RK (2001) Wescott's plant disease handbook, 6th edn. Kluwer, Norwell

Houle G (1992) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. J Ecol 80:99–108. doi:10.2307/2261066

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528. doi:10.1086/282687

Jensen TS (1985) Seed–predator interactions of European beech (*Fagus silvatica* L.) and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. Oikos 44:149–156. doi:10.2307/3544056

Jones RH, Sharitz RR, Dixon PM, Segal DS, Schneider RL (1994) Woody plant regeneration in four floodplain forests. Ecol Monogr 64:345–367. doi:10.2307/2937166

Kirchner JW, Roy BA (2002) Evolutionary implications of host-pathogen specificity: fitness consequences of pathogen virulence traits. Evol Ecol Res 4:27–48

Kotanen PM (2007) Effects of fungal seed pathogens under conspecific and heterospecific trees in a temperate forest. Can J Bot Rev Can Bot 85:918–925. doi:10.1139/B07-088

Lively CM, Dybdahl MF (2000) Parasite adaptation to locally common host genotypes. Nature 405:679–681. doi:10.1038/35015069

Maeto K, Fukuyama K (1997) Mature tree effect of *Acer mono* on seedling mortality due to insect herbivory. Ecol Res 12:337–343. doi:10.1007/BF02529463

Marquis RJ (2005) Impacts of herbivores on tropical plant diversity. In: Burslem DFRP, Pinard MA, Hartley SE (eds) Biotic interactions in the tropics. Cambridge University Press, Cambridge, pp 328–346

Masaki T, Nakashizuka T (2002) Seedling demography of *Swida controversa*: effect of light and distance to conspecifics. Ecology 83:3497–3507

Masaki T, Kominami Y, Nakashizuka T (1994) Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. Ecology 75:1903–1910. doi:10.2307/1941595

Mills KE, Bever JD (1998) Maintenance of diversity within plant communities: soil pathogens as agents of negative feedback. Ecology 79:1595–1601

Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78:1531–1542

Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278–281. doi:10.1038/35005072

Packer A, Clay K (2003) Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. Ecology 84:108–119. doi:10.1890/0012-9658(2003)084[0108:SPAPSS]2.0.CO;2

Packer A, Clay K (2004) Development of negative feedback during successive growth cycles of black cherry. Proc R Soc Lond 271:317–324. doi:10.1098/rspb.2003.2583

Peters HA (2003) Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. Ecol Lett 6:757–765. doi:10.1046/j.1461-0248.2003.00492.x

Reinhart KO, Royo AA, Van der Putten WH, Clay K (2005) Soil feedback and pathogen activity in *Prunus serotina* throughout its native range. J Ecol 93:890–898. doi:10.1111/j.1365-2745.2005.01028.x

Sahashi N, Kubono T, Shoji T (1995) Pathogenicity of *Colletotrichum dematium* isolated from current-year beech seedling exhibiting damping-off. Eur J Forest Pathol 25:145–151. doi:10.1111/j.1439-0329.1995.tb00329.x

Schafer M, Kotanen P (2004) Impacts of naturally-occurring soil fungi on seeds of meadow plants. Plant Ecol 175:19–35. doi:10.1023/B:VEGE.0000048096.00772.23

Seiwa K (1998) Advantages of early germination for growth and survival of seedlings of *Acer mono* under different overstorey phenologies in deciduous broad-leaved forests. J Ecol 86:219–228. doi:10.1046/j.1365-2745.1998.00245.x

Seiwa K, Kikuzawa K (1996) Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. Vegetation 123:51–64. doi:10.1007/BF00044887

Seiwa K, Miwa Y, Sahashi N, Kanno H, Tomita M, Ueno N, Yamazaki M (2008) Pathogen attack and spatial patterns of juvenile mortality and growth in a temperate tree, *Prunus grayana*. Can J Res 38:2445–2454. doi:10.1139/X08-084

Sicard D, Pennings PS, Grandclement C, Acosta J, Kaltz O, Shykoff JA (2007) Specialization and local adaptation of a fungal parasite on two host plant species as revealed by two fitness traits. Evol Int J Org Evol 61:27–41. doi:10.1111/j.1558-5646.2007.00003.x

Silman MR, Terborgh J, Kiltie R (2003) Population regulation of a dominant rain forest tree by a major seed predator. Ecology 84:431–438. doi:10.1890/0012-9658(2003)084[0431:PROADR]2.0.CO;2

Streng DR, Glitzenstein JS, Harcombe PA (1989) Woody seedling dynamics in an east Texas floodplain in forest. Ecol Monogr 59:177–204. doi:10.2307/2937285

Terabaru M, Yamazaki M, Kanou K, Suyama Y, Seiwa K (2004) Influence of topographic positions on tree distribution patterns in a temperate broad-leaved deciduous forest. Bull Integr Field Sci Cent 20:21–26 (In Japanese)

Tomita M, Hirubuki Y, Seiwa K (2002) Post-dispersal changes in the spatial distribution of *Fagus crenata* seeds. Ecology 83:1560–1565

Wada N, Murakami M, Yoshida K (2000) Effects of herbivore-bearing adult trees of the oak *Quercus crispula* on the survival of their seedlings. Ecol Res 15:219–227. doi:10.1046/j.1440-1703.2000.00343.x

Webb CO, Gilbert GS, Donoghue MJ (2006) Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. Ecology 87:S123–S131. doi:10.1890/0012-9658(2006)87[123:PSMSSA]2.0.CO;2

Wills C, Condit R, Foster RB, Hubbell SP (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proc Natl Acad Sci USA 94:1252–1257. doi:10.1073/pnas.94.4.1252

Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1–14

Wyatt JL, Silman MR (2004) Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. Oecologia 140:26–35. doi:10.1007/s00442-004-1554-y

Response of native Hawaiian woody species to lava-ignited wildfires in tropical forests and shrublands

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Abstract Wildfires are rare in the disturbance history of Hawaiian forests but may increase in prevalence due to invasive species and global climate change. We documented survival rates and adaptations facilitating persistence of native woody species following 2002–2003 wildfires in Hawaii Volcanoes National Park, Hawaii. Fires occurred during an El Niño drought and were ignited by lava flows. They burned across an environmental gradient occupied by two drier shrub-dominated communities and three mesic/wet *Metrosideros* forest communities. All the 19 native tree, shrub, and tree fern species demonstrated some capacity of postfire persistence. While greater than 95% of the dominant *Metrosideros* trees were top-killed, more than half survived fires via basal sprouting. *Metrosideros* trees with diameters >20 cm sprouted in lower percentages than smaller trees. At least 17 of 29 native woody species colonized the postfire environment via seedling establishment. Although the native biota possess adaptations facilitating persistence following wildfire, the presence of highly competitive invasive plants and ungulates will likely alter postfire succession.

Keywords Disturbance · *Dodonaea viscosa* · Fire adaptations · Hawaii · *Metrosideros polymorpha* · Sprouting

Introduction

Wildfires have a dramatic effect on Hawaiian landscapes (D'Antonio et al. 2000). Yet, little is known on the fire history of the Hawaiian Islands and its role in the evolution and development of Hawaiian ecosystems (Vogl 1969; Mueller-Dombois 1981, 2001; Smith and Tunison 1992). Studies of sediment cores collected in bogs and radiocarbon data from charcoal studies indicated that wildfires have occurred in Hawaii prior to European settlement (Mueller-Dombois 1981; Smith and Tunison 1992; Burney et al. 1995). The occurrence of natural ignition sources including lightning and volcanism (Vogl 1969; Tunison and Leialoha 1988) and continuous vegetation cover in many ecosystems (Wagner et al. 1999) further suggests that fire did occur historically and did influence the disturbance history of Hawaiian ecosystems.

Although there is a poor fire record, the response of native woody species to wildland fire provides insights into historical fire patterns because

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adaptations evolve within the context of each ecosystem's natural disturbance regime (Kauffman 1990). Species adaptations in ecosystems are linked to their capacity to survive, establish, and reproduce in the disturbance regime of their habitats (White and Pickett 1985). Examples of traits that promote survival of individuals following fire include: thick bark, protected buds from dense leaf bases, and sprouting from either epicormic or subterranean tissues. Adaptations that facilitate establishment of species or populations, but not the individual following fire include: fire-stimulated germination or flowering, seed storage on plants (e.g., serotinous cones), and wind-borne seeds (Kauffman 1990).

Many Hawaiian wet forest species possess characteristics frequently associated with long fire-return intervals (e.g., thin bark, buried seeds requiring heat or other disturbance to germinate, enhanced seedling establishment on downed wood, sprouting). Basal and epicormic sprouting following fire have been observed for *Metrosideros polymorpha,* a dominant Hawaiian tree species (Parman and Wampler 1977; Hughes et al. 1991; Tunison et al. 1995; D'Antonio et al. 2000). Another dominant native tree, *Acacia koa* has the capacity to sprout following disturbance (Tunison et al. 2001) and produces refractory seeds capable of surviving in the soils for decades until disturbance stimulates germination. The tree ferns *Cibotium glaucum* and *Sadleria cyathoides* survive and rapidly produce new fronds, presumably because the meristematic tissues are protected by frond scales (Smith and Tunison 1992).

Wind dispersal and capacity to establish on bare substrate is a common adaptation that facilitates invasion and establishment following disturbance such as fire (Kauffman 1990). *Metrosideros* has long-ranging and abundant wind-dispersed seeds (Drake 1992; Hatfield et al. 1996). Seedling recruitment has been observed following wildfire in *Metrosideros*-dominated wet forests (Tunison et al. 2001). In addition, the seeds of a dominant native shrub species in Hawaiian ecosystems, *Dodonaea viscosa,* were found to break dormancy following exposure to heat (Hodgkinson and Oxley 1990) and have also been found to germinate readily after fire (Hughes et al. 1991; Shaw et al. 1997; D'Antonio et al. 2000).

Although postfire response of many native Hawaiian species suggest that they may be adapted to disturbance, the majority of studies have been limited to the seasonally dry *Metrosideros* woodlands of Hawaii Volcanoes National Park (Hughes et al. 1991; Hughes and Vitousek 1993; Freifelder et al. 1998; Ley and D'Antonio 1998; D'Antonio et al. 2000; D'Antonio et al. 2001; Mack et al. 2001). Nonnative grass invasions during the past century have led to a dramatic increase in fire frequency and size in these dry woodlands (Smith and Tunison 1992). Rapid grass recovery or fine fuel re-accumulation following fire (Hughes et al. 1991) coupled with drier, windier microclimatic conditions (Freifelder et al. 1998) has led to additional fires creating a grass/fire cycle (D'Antonio and Vitousek 1992). Consequently, many previously native-dominated woodlands have been type converted to nonnative-dominated grasslands.

In contrast to the drier Hawaiian woodlands, few recorded fires have occurred and no studies have been conducted in the wetter *Metrosideros* forests with understories dominated by herbaceous species and tree ferns. The effects of fire are expected to differ from those in the dry woodlands because of differences in fuels and microclimatic conditions despite some similarity in species (e.g. *Metrosideros*). Although fires may have been infrequent historically, climate change, nonnative species invasions, and increasing human ignition sources are likely to result in more frequent larger fires in wet Hawaiian forests. Naturally ignited wildfires during particularly strong El Niño (ENSO), mediated droughts in 2002 and 2003 created an opportunity to examine fire effects in relatively intact wet forests as well as adjacent perturbed shrublands.

We hypothesized that native Hawaiian species would persist following fire through individual survival or establish from propagules in the postfire environment because these species evolved in a landscape subjected to a wide array of infrequent disturbance events (fires, volcanism, tropical storms, etc). We measured the response of native Hawaiian woody species and tree ferns for the first two years following the 2003 Luhi and Panauiki lava-ignited wildfires in five community types across an elevation/moisture gradient in Hawaii Volcanoes National Park. The specific objectives of this study were to: (1) examine the postfire survival rates and describe the mechanisms of persistence of native Hawaiian trees, tree ferns, and shrubs partitioned by species and size class; and (2) quantify native woody seedling establishment across this elevation/moisture gradient for the first two years following fire. Information from this study should provide insights regarding historic fire regimes in this area and native species' response to fire, and will assist managers in evaluating the potential threat of fire to native forest recovery in these unique communities.

Methods

Study site

This study was conducted at Hawaii Volcanoes National Park on the Island of Hawaii (19°20′11″ N and 155°7′29″ W). Elevation ranged from 350 m in the relatively dry shrub-dominated communities to 825 m in wet forest communities; all communities occurred within 5 km of each other. The study area was located over a very steep precipitation gradient from dry shrublands to wet forest and encompassed four distinct Holdridge life zones: subtropical basal moist forest, subtropical basal wet forest, subtropical lower mountain moist forest, and subtropical lower mountain wet forest (Tosi et al. 2001). Substrate across the gradient consisted of young (400 to 750 yr-old) pahoehoe lava flows with minimal topographic relief (Trusdell et al. 2005). Two basic soil types are present: the Kalapana series and the Makaopuhi series. Both series are very shallow to shallow soils formed in ash deposited over pahoehoe lava with 2–10% slopes, and are classified as Medial, ferrihydritic, isothermic, Lithic Udivitrands (well drained), and Hapludands (poorly drained). The shrub-dominated communities are on the Kalapana dry phase soils, the mesic forest communities are on Kalapana medial course sandy loam, and the wet forest community is on Makaopuhi very paragravelly muck (Jasper 2007).

Metrosideros polymorpha is the dominant forest tree across the elevation gradient, but ranges in percent canopy cover from <1% in the shrublands to >60% in the mesic forests. The study area contained five major plant communities (Ainsworth 2007). The *Dodonaea viscosa/Andropogon virginicus* community (350–450 m) was dominated by native *Dodonaea* in the shrub layer (~9,000 individuals/ha) with the nonnative perennial bunch grass *Andropogon* dominating the understory. A few trees (*Metrosideros*) were scattered across the landscape, but were primarily restricted to lava uplifts where past fires did not kill them. This community is located within the mapped boundaries of past wildfires that occurred in 1972 and 1992 and will be referred to hereafter as the "*Andropogon* shrubland."

The *Dodonaea/Nephrolepis multiflora* shrub-dominated community (450–550 m) is also dominated by *Dodonaea* in the shrub tier (~8,500 individuals/ha) with the nonnative fern *Nephrolepis multiflora* dominating the understory. Similar to the *Andropogon* shrubland, remnant *Metrosideros* trees are scattered throughout this community. This community will be referred to as the "*Nephrolepis* shrubland." While the tree component of these two communities is now sparse due to the recent fires, historic photos indicate that the area was characterized as relatively open *Metrosideros* woodlands with scattered shrubs and a mixed understory prior to the 1972 wildfire (Hawaii Department of Land and Natural Resources 1966).

We sampled the *Metrosideros/Nephrolepis multiflora* forest community (550–640 m) which is dominated by *Metrosideros* in the overstory (~700 individuals/ha) and the nonnative fern *Nephrolepis multiflora* in the understory. This community will be referred to as the "*Nephrolepis* forest." The *Metrosideros/Dicranopteris linearis* forest community (640–750 m) contains *Metrosideros* in the overstory (~850 individuals/ha) and the native, mat forming fern *Dicranopteris* in the understory. This community will be referred to as the "*Dicranopteris* forest." The wettest and highest elevation community sampled was the *Metrosideros/ Cibotium glaucum* forest community (700–850 m). This community has an open canopy overstory of *Metrosideros* (~500 individuals/ha) with a native tree fern *Cibotium glaucum* midstory (~2,800/ha) and the native fern *Dicranopteris* and nonnative grasses in the understory. This community will be referred to as the "*Cibotium* forest."

Fire history

Lava has been an ignition source in this area of the Park at least from 1916 to present (Gassaway et al. 2002). Multiple fires have occurred in the coastal lowlands in the last 30 years including a 1992 fire which burned the *Andropogon and Nephrolepis* shrublands. The Panauiki Fire (January, 2003) reburned over half (860 ha) of *Andropogon and Nephrolepis* shrublands between 60 and 670 m. In May 2003, the Luhi fire burned over 75% (2,000 ha) of the forested study area (National Park Service 2003). We established replicate plots ($n = 5$) in each of the five vegetation communities in the areas burned in the 2003 wildfires and unburned controls to determine tree and tree fern responses and the postfire seedling establishment.

Field methods

In the burned areas for each of the sampled communities, we established five randomly located 20 × 50 m permanent plots and measured the vegetation response one (2004) and two (2005) years following fire. Sample locations were selected based on composition and structure, elevation, fire history, and proximity to unburned sites. Unburned plots were sampled once—two years (2005) following fire except the *Nephrolepis* forest community which was sampled one year (2004) following fire. We selected unburned plots in each community type based on comparable elevation, and vegetation composition and structure. Flowering plant nomenclature followed that of Wagner et al. (1999), and tree fern nomenclature followed that of Palmer (2003).

We sampled trees, tree ferns, shrubs, and woody seedlings using a nested plot design. Individuals in the burned plots were recorded as sprouts if the live portion was attached to an older burned stem or root. Tree seedlings, defined as individuals less than 1.3 m tall, tree fern juveniles (those with fronds <50 cm long), and shrubs were measured in six subplots (1 × 5 m). Trees <10 cm diameter at breast height (dbh; 1.3 m in height) and tree ferns <10 cm in diameter at the point below past years frond shed were measured in six 2 × 10 m subplots. Trees >10 cm dbh and tree ferns with trunk diameters >10 cm were measured in the entire 20 × 50 m plot. Species with individuals that reached reproductive maturity within the first two years following fire were recorded.

Quantitative measures recorded for all trees, tree ferns, and shrubs included: plant mortality and mode of sprouting (basal if it originated from subterranean plant organs at the base of trees <50 cm above ground, and epicormic if it originated from dormant meristematic tissue in the bole or mainstems) (Kauffman 1990). For trees (>1.3 m tall) diameter at breast height (dbh) and crown mortality were recorded. For tree ferns (with fronds >50 cm long), basal diameter, trunk length, and crown mortality were recorded. From these data, percent crown mortality and individual plant death were calculated for all trees, tree ferns, and shrubs by species, and by diameter size class (<10, 10–20, >20 cm) for the dominant canopy (*Metrosideros*) and subcanopy (*Cibotium*) species. Tree fern survival was also analyzed by length class (<1, 1–2, >2 m).

Analysis

Native Hawaiian woody species and tree ferns were grouped according to Rowe's (1981) plant response classification system which incorporates life history traits of species and characteristics of fire regimes. The five categories include: invaders (high dispersal ability), evaders (long lived propagules stored in the soil), avoiders (shade tolerant and slow invaders following fire), resisters (thick bark or an anomalous arrangement of mertistematic tissues that facilitates fire survival), and endurers (capacity to sprout from dormant surviving meristematic tissues) (Rowe 1981). Species often have multiple or changing adaptations and therefore can fit into more than one category. This universal life-form classification is a useful way to examine species response to fire on a per site basis because categories incorporate the influence of environmental factors (Agee 1993).

The sampling unit used in analysis for all the parameters was the 20 × 50 m plot. Average values were calculated per plot and used in analysis for vegetation parameters that were sampled in subplots (e.g., seedlings, small trees, and tree ferns). *Metrosideros* percentage survival and population structure were analyzed as two factor ANOVA's with tree diameter size class, community, and size class × community as fixed effects. Differences among plant communities were compared using Tukey's multiple comparison tests. Tree count data used to examine population structure were log base 10 transformed (log + 1) to equalize variance. ANOVA and *t*-test analyses were performed at an $\alpha = 0.10$ in order to increase the power $(1 - \beta)$.

Differences in *Cibotium* survival among size classes were compared using nonparametric tests (Kruskal–Wallis Rank Test and Wilcoxon Rank Test for pair-wise comparisons). Nonparametric tests were also used to detect differences in native species seedling density between treatments and years (unburned vs. two year postfire) for each community.

Results

Sprouting response

Wildland fire resulted in greater than 95% crown mortality of the dominant *Metrosideros* trees. There were remarkably few unburned islands within the fire perimeters. Despite the near complete crown mortality, many individuals of the native Hawaiian species survived fire across the elevation gradient via vegetative sprouting. Nineteen tree, shrub, and tree fern species were observed to have survived fire primarily through basal spouting (Table 1). In addition to sprouting from the base or root crown, scattered individuals of three woody species, *Dodonaea*, *Metrosideros,* and *Santalum paniculatum*, were also observed to have sprouted from epicormic tissues. Postfire reproduction of surviving individuals can be rapid as we observed fruiting or spore production of individuals of all tree fern and shrub species within the first two years following fire (Table 1). In addition, two tree species, *Hedyotis terminalis* and *Santalum* were also observed to be fruiting during the second postfire year.

Despite high crown mortality, more than half (57%) of the 911 individual *Metrosideros* trees sampled in the burned communities survived fire through basal sprouting. Survival significantly differed among diameter classes, where trees with larger diameters (>20 cm) were less likely to sprout following fire than those with smaller diameters ($P = 0.05$; Fig. 1). The influence of plant size on survival was most pronounced in the *Dicranopteris* forest community, where >70% of the smaller trees (<10 cm and 10–20 cm dbh) and only 38% of the larger trees (>20 cm dbh) survived fire ($P = 0.02$).

The postfire survival of *Metrosideros* (all sizes combined) differed among communities where survival was 71% in the *Dicranopteris* community, 48% in the *Cibotium* community and 52% in the *Nephrolepis* forest community ($P = 0.07$). However, we found no difference in survival among communities when controlling for differences among size classes by using a two factor ANOVA with size class and community ($P = 0.36$; Fig. 1). Differences in survival among communities were related to differences in *Metrosideros* population structure among communities ($P < 0.01$; Fig. 2). The population structure of the *Dicranopteris* and *Nephrolepis* forest communities was composed of smaller individuals with greater than 75% of *Metrosideros* trees in the smallest size class (<10 cm dbh). In contrast, in the *Cibotium* forest <30% of the trees were in the smallest size class and over 50% in the largest size class (>20 cm dbh).

Tree ferns survived the fires in very high percentages (>86%; N = 1,195 *Cibotium* tree ferns sampled). While existing foliage of tree ferns were killed by fire, the individuals were observed to rapidly refoliate from the apical meristems that were apparently protected from lethal temperatures by the bark, and leaf bases. Tree fern size affected rates of survival where smaller sized individuals (<10 cm diameter) had lower (42%) survival than the larger classes (10–20 cm and >20 cm diameter; Fig. 3). In the largest size class >90% of the individual's possessed live fronds one year postfire ($P < 0.01$). Although there was a difference ($P < 0.10$) in survival between the two larger diameter classes, this difference is probably not ecologically meaningful considering that survival was extremely high (>90%) in both classes. For *Cibotium* individuals >10 cm in diameter, no difference in survival was detected among trunk length classes (<1 m, 1–2 m, >2 m; $P = 0.38$).

Seedling response

There were a total of 29 native woody species and tree ferns that were found on the entire study area, and seedlings or juveniles of 17 were found to occur in the postfire plots (Table 1). Seedlings of 10 species were found only in burned areas while seedlings of three species were found only in unburned sites and seven species were found in both burned and unburned sites. The majority of species found in the burn following fire were present both as seedlings and as sprouts including four tree, six shrub, and two tree fern species. Of the five species present, only as seedlings, two were tree species and three were shrub species. For three shrub species, *Clermontia hawaiiensis*, *Lythrum maritimum*, and *Sida fallax* no individuals (living or dead) were found in the study area suggesting that these species either dispersed into the area from outside or had been present only as

Table 1 Native woody species and tree ferns that survived fire and/or established from seed in the postfire environment

Species	Life form	Individual survival			Postfire
		Apical	Basal	Epicormic	Seedlings
Broussaisia arguta	Shrub		X		
Cheirodendron trigynum	Tree				X
Cibotium glaucum	Tree fern	X*			X
Cibotium menziesii	Tree fern	X*			
Clermontia hawaiiensis	Shrub				X
Coprosma menziesii	Shrub		X*		X
Dodonaea viscosa	Shrub		X*	X*	X*
Hedyotis terminalis	Tree		X*		X
Ilex anomala	Tree		X		X
Leptecophylla tameiameiae	Shrub		X*		X
Lythrum maritimum	Shrub				X
Melicope clusiifolia	Tree		X		X
Melicope radiata	Tree				X
Metrosideros polymorpha	Tree		X	X	X
Myrsine lessertiana	Tree		X		
Myrsine sandwicensis	Tree		X		
Osteomeles anthyllidifolia	Shrub		X*		
Pipturus albidus	Shrub				X*
Psychotria hawaiiensis	Tree		X		
Sadleria cyatheoides	Tree fern	X*			X
Santalum paniculatum	Tree		X*	X*	
Scaevola chamissoniana	Shrub		X*		
Sida fallax	Shrub				X*
Vaccinium calycinum	Shrub		X*		X
Vaccinium reticulatum	Shrub		X*		X
Total		3	16	3	17

Mode of survival was recorded as apical for tree ferns and basal or epicormic sprouting for tree and shrub species. Asterisks denote species with individuals that fruited or flowered within two years following fire

propagules in the soil seed bank. Growth and maturation from seed was rapid for *Dodonaea*, *Pipturus albidus*, and *Sida fallax*. Individuals of these three species were observed to have flowered within the first two postfire (and post germination) years.

There were no differences in shrub species seedling densities when comparing between unburned and burned sites for any community (Table 2) except for the common shrub *Dodonaea*. *Dodonaea* seedlings had dramatically higher densities in burned, compared to unburned sites. For example, in the *Andropogon* shrubland, the second postfire year *Dodonaea* density was 3,333/ha in the unburned and 12,333/ha in burned sites ($P = 0.16$). Similarly in the *Nephrolepis* shrubland, *Dodonaea* seedlings densities were 5,733/ha in the unburned sites, but densities were almost 8-fold greater in burned sites of this community (45,267/ha) two years postfire ($P = 0.01$). In the forest communities, *Dodonaea* was not encountered in the unburned sites (Table 2), but did establish from seed in low densities in the burned sites of the *Nephrolepis* (200/ha; $P = 0.07$), *Dicranopteris* (67/ha; $P = 0.43$), and *Cibotium* (267/ha; $P = 0.18$) forest communities.

The relatively low seedling densities of rare tree and tree fern species did not differ between unburned and burned sites within each community type (Table 2). However, for the canopy dominant species, *Metrosideros*, seedling density did differ between burned and unburned sites within the three forest communities. Only one seedling was found in the unburned plots, but two years following fire many more seedlings were found in the burned plots of the *Nephrolepis* (667/ha; $P = 0.06$) and *Dicranopteris* (267/ha; $P = 0.07$) forests (Fig. 4). Alternatively, in

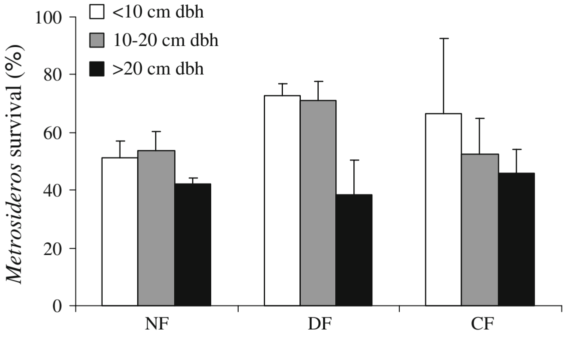

Fig. 1 Postfire survival (%) via sprouting of *Metrosideros polymorpha* individuals in the three sampled forest communities 12 months following fire at Hawaii Volcanoes National Park (NF = *Nephrolepis* forest; DF = *Dicranopteris* forest; and CF = *Cibotium* forest). Survival differed by diameter size class (dbh) across the three forest communities ($P = 0.04$), with the greatest mortality in the largest size class. Survival did not differ among communities when controlling for size class ($P = 0.36$) and no interaction was detected (Size × Community: $P = 0.59$). Data are means +1 SE

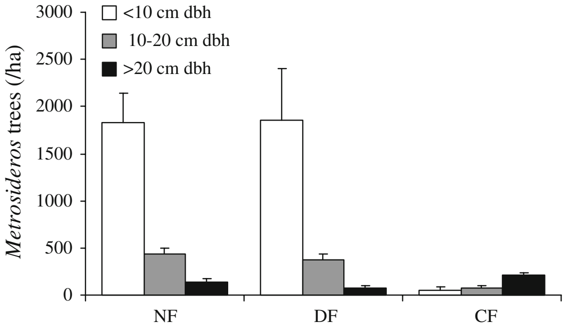

Fig. 2 The population structure of *Metrosideros polymorpha* in the three different forest communities at Hawaii Volcanoes National Park. Structure differed among the three forest communities ($P < 0.01$; NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest). Data are means ±1 SE. A total of 911 trees were measured

the *Cibotium* forest seedling density was high (8,267/ha) in the unburned sites, whereas in the burned sites two years postfire seedling density was significantly lower (733/ha; $P = 0.09$; Fig. 4). Juveniles of the subcanopy dominant tree fern species, *Cibotium glaucum*, were more abundant in the burned *Cibotium* forest two years following fire (3,200/ha) than the unburned forest (400/ha), but this difference was not significant ($P = 0.16$) due to high variation among plots.

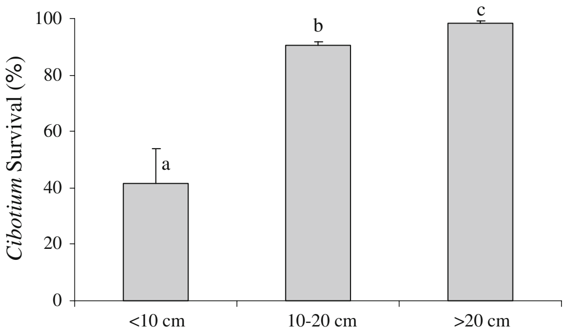

Fig. 3 *Cibotium glaucum* survival by diameter class in the *Cibotium* forest community ($P < 0.01$). The greatest mortality was found to occur in the smallest size class. Data are means +1 SE. Letters indicate significant differences. A total of 1195 tree ferns were measured

Discussion

Previous observations of postfire sprouting have been made for many of the species present in this study (Warshauer 1974; Parman and Wampler 1977; Tunison et al. 1994, 1995; D'Antonio et al. 2000). Yet this study is the first study to quantify survival and mortality rates and how survival differed by species, size class, and plant communities across an elevation gradient. These findings are particularly relevant because context (e.g. community type, elevation, fire characteristics, invasive species, post fire competition, etc) may greatly influence species response to fire (Kauffman 1990; Kauffman and Martin 1990, Sampaio and Kauffman 1993). Given the characteristics of the relatively wet climate and the relatively low incidence of lightning, naturally occurring fires were likely a rare occurrence in native Hawaiian wet forests. However, we observed that native Hawaiian woody plants in this study possessed several adaptations that facilitated fire survival.

The majority of species were characteristic of "endurers" (i.e. they were top-killed, but sprouted after fire; Table 3). Nearly all tree and shrub sprouts originated from the base or root crown where bark tends to be the thickest and where soils provide a great deal of insulation (Agee 1993). Tree ferns were characteristic of "resistors" in that above ground tissues and plant structures survived fire and refoliated within a few months following fire (Table 3). *Cibotium* and *Sadleria* fern species have been observed to recover following wildfires (1969–1973) in the region (Warshauer 1974), but the high

Table 2 Native shrub, tree, and tree fern seedling densities in unburned (U) and burned (B) sites two years following fire for the three forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest)

Species	NF		DF		CF	
	U	B	U	B	U	B
Shrub species						
Coprosma menziesii	0	0	67 (67)	0	133 (133)	67 (67)
Dodonaea viscosa	0	* 200 (82)	0	67 (67)	0	267 (163)
Labordia hedyosmifolia	0	0	0	0	67 (67)	0
Leptecophylla tameiameiae	67 (67)	0	0	67 (67)	0	0
Pipturus albidus	0	0	0	67 (67)	0	67 (67)
Vaccinium calycinum	0	0	0	0	133 (82)	67 (67)
Vaccinium reticulatum	0	0	0	67 (67)	0	0
Tree species						
Cheirodendron trigynum	0	0	0	0	133 (82)	0
Hedyotis terminalis	0	0	0	67 (67)	0	0
Ilex anomala	0	0	0	67 (67)	0	133 (82)
Melicope clusiifolia	0	0	0	0	400 (245)	1000 (350)
Melicope radiate	0	0	0	0	0	67 (67)
Metrosideros polymorpha	67 (67)	* 667 (236)	0	* 267 (125)	8267 (3165)	* 733 (386)
Myrsine lessertiana	0	0	0	0	267 (125)	* 0
Myrsine sandwicensis	0	0	133 (82)	0	0	0
Tree fern species						
Cibotium glaucum	0	0	0	333 (333)	400 (323)	3200 (1948)
Sadleria cyatheoides	0	0	0	67 (67)	0	0

Mean densities per hectare are reported with standard errors in parentheses. Asterisks denote significant differences ($P < 0.10$) between unburned and burned sites for each community

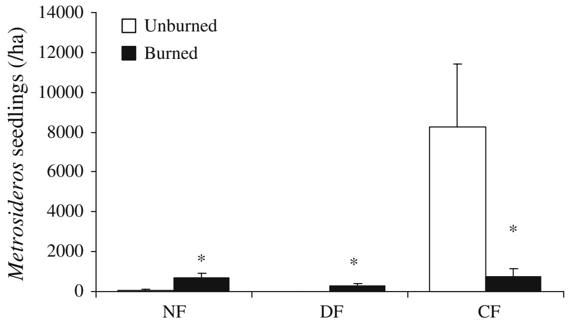

Fig. 4 *Metrosideros polymorpha* seedling density in unburned and burned sites two years following fire in the forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest and CF = *Cibotium* forest). Means +1 SE are reported and asterisks denote significant differences between treatments for each community

degree of survival (>90%) of these tree ferns has not been previously quantified. In Australia, tree ferns (*Cyanea* spp.) have also been reported to recover rapidly following disturbance including fire (Ough and Murphy 2004). We attribute the high survival of tree ferns to their unique morphology in which the meristematic tissues were protected from lethal temperatures by the thick fibrous bark, live tissues embedded within the main stem, and cover by green frond bases. Survival of species with this suite of morphological traits would be increased with increasing trunk diameter as was observed in this study.

In rare cases, some woody species including *Metrosideros*, *Santalum paniculatum*, and *Dodonaea* were also observed to regenerate from epicormic buds along the stem and in the crown. Vegetative sprouting from trunks of *Metrosideros* individuals has also been observed to occur following tree-fall in unburned wet forests (Drake and Mueller-Dombois 1993). Sprouting from aboveground tissues provides a competitive advantage in terms of rapid recovery of leaf area over individuals sprouting from the base or establishing from seed (Agee 1993). However, in this study,

Table 3 Native woody species and tree fern plant adaptations that facilitate survival following fire in tropical wet forests and shrublands of Hawaii Volcanoes National Park, Hawaii

Adaptation	Trait	Species
Resistors	Protected meristems	Tree ferns (3):
		Cibotium glaucum, Cibotium menziesii, Sadleria cyathoides
Endurers	Sprouters	Trees (8):
		Hedyotis terminalis, Ilex anomala, Melicope clusiifolia, Metrosideros polymorpha, Myrsine lessertiana, Myrsine sandwicense, Psychotria hawaiiensis, Santalum paniculatum
		Shrubs (8):
		Broussaisia arguta, Coprosma menziesii, Dodonaea viscosa, Leptecophylla tameiameiae, Osteomeles anthyllidifolia, Scaevola chamissoniana, Vaccinium calycinum, Vaccinium reticulatum
Invaders	Wind-borne seeds	Tree ferns (2):
		Cibotium glaucum and *Sadleria cyathoides*
		Trees (5):
		Cheirodendron trigynum, Hedyotis terminalis, Ilex anomala, Melicope clusiifolia, Metrosideros polymorpha
		Shrubs (10):
		Clermontia hawaiiensis, Coprosma menziesii, Dodonaea viscosa, Leptecophylla tameiameiae, Lythrum maritimum, Melicope radiate, Pipturus albidus, Sida fallax, Vaccinium calycinum, Vaccinium reticulatum
Evaders	Soil seed bank	Shrubs (2):
		Dodonaea viscosa[a] and *Osteomeles anthyllidifolia*[a]

[a] Hughes and Vitousek 1993

Adaptations follow that of Rowe (1981). Numbers in parentheses are the total number of species where the specific trait was observed

epicormic sprouting was very rare (<1% of individuals), presumably because temperature extremes and durations during the fire reached lethal levels to kill epicormic buds present beneath the thin scaly bark of the *Metrosideros*.

Rapid maturation and reproductive effort following fire is also an adaptation facilitating persistence and establishment following fire (Kauffman 1990). All the eight shrub and the three tree fern species that survived fire vegetatively had individuals that reached sexual maturity (i.e., were observed to be fruiting or produced spores) within two years following fire (Table 1). In addition, two tree species *Hedyotis terminalis* and *Santalum* also had sprouts that reached sexual maturity during the second postfire year. The majority of reproducing *Santalum* originated from previously burned basal or root sprouts, suggesting that flowering for this species was fire enhanced.

Specific characteristics promoting survival in an individual plant will often change with age (Kauffman 1990). Size class distribution of the dominant tree and tree fern species influenced rates of survival. We found that postfire survival rates of *Metrosideros* decreased with increasing size. Tunison et al. (1995) observed that *Metrosideros* survival following fire appeared to be inversely correlated with tree size. Conversely, in the dry *Metrosideros* woodlands D'Antonio et al. (2000) found mortality to be independent of size class. Although increased mortality with age and size has been documented in other tree species such as *Quercus* spp. (Griffin 1980), the loss of sprouting capacity usually signifies a shift in the mode of survival to a general thickening of the bark tissue to protect cambial and meristematic tissues (Kauffman and Martin 1990). In this study, the stem and crown of *Metrosideros* trees were extremely sensitive because of the thin-barked nature of all individuals in all size classes. This heat sensitivity of aboveground tissues of *Metrosideros* was exemplified by the near complete crown mortality and paucity of epicormic sprouting following fire. Based on these findings, predicted increases in fire frequency associated with climate change responses (e.g., warmer temperatures, greater frequency, and severity of El Niño events; IPCC 2007) may limit structural complexity and increase dominance of nonnative species as has already occurred at lower elevations.

In addition to the individual species adaptations to fire, context-specific factors such as pre-fire population, vegetation structure, weather conditions, fire behavior, and fuel consumption may greatly influence individual survival (Agee 1993; D'Antonio et al. 2000). Survival of *Metrosideros* was the greatest in the *Dicranopteris* forest community (71%). Differences in *Metrosideros* population structure between the *Dicranopteris* and *Cibotium* communities partially explain the lower survival in the *Cibotium* community (48%). The *Cibotium* community appears to be a later successional forest with a greater proportion of trees in the largest size class (Fig. 2) which had a lower number of surviving/sprouting individuals. Many explanations as to why the trees are larger in the *Cibotium* community as compared to the *Dicranopteris* community are possible (e.g., older substrate age; less historical disturbance from humans, ungulates, and plants; moister microclimatic conditions; and/or differences in soil ash content).

Total survival of *Metrosideros* in the *Nephrolepis* forest community (52%) was also significantly lower than in the *Dicranopteris* (71%) community ($P = 0.02$), but population structures of these two young forests were similar (Fig. 2). These data suggest that the difference in survival may be related to differences in fire severity (i.e., fuel consumption or fire intensity). In the burned *Dicranopteris* forest community, the quantity of unconsumed residual surface fuels was greater than that of the other two communities suggesting lower fuel consumption. Lower fuel consumption would result in lower heat flux around the base of the trees and could explain the higher survival observed in this community. In the coastal lowlands and seasonal submontane zones of Hawaii Volcanoes National Park, D'Antonio et al. (2000) observed that individual mortality was greater for native Hawaiian woody species in sites where fuel consumption was the highest.

In the burned landscape, about the same number of native Hawaiian plant species were encountered as seedlings (17) as surviving individuals from sprouts (19). Two tree (*Cheirodondron trigynum* and *Melicope radiata*) and four shrub species (*Clermontia hawaiiensis*, *Lythrum maritimum*, *Pipturus albidus*, and *Sida fallax*) were observed to be obligate seeders (i.e., no vegetative survival by sprouting). It is not surprising that many native species can be classified as "invaders" (i.e. those that disperse onto the site following fire) according to Rowe's (1981) classification (Table 3). Mueller-Dombois (1987) also characterized *Metrosideros* as an early successional tree species that colonized new volcanically derived substrates or gaps created by tree falls while remaining dominant in mature wet forest communities.

Species with seeds that can survive fire in the soil seed back or on individual plants are classified as "evaders" (Table 3). Some of the seedlings detected following fire in this study may also have originated from the soil seed bank, but the relative importance of the seed bank is unknown. Hughes and Vitousek (1993) found that some native Hawaiian shrub species retain the capacity to germinate following exposure to high-temperature treatments (120°C for 5 min) including *Osteomeles* and *Dodonaea*.

Seedling establishment following fire differed among species and among communities across the elevation gradient of this study (Table 2). Fewer *Metrosideros* seedlings were found in the burned *Cibotium* forest as compared to those in the unburned *Cibotium* forest (Table 2). Lower *Metrosideros* seedling density in the burned plots is not likely because of limited seed source considering the proximity to unburned forests and the dispersal capabilities of these small wind-blown seeds. The majority of *Metrosideros* seedlings found in the unburned forest had established on moss covered tree fern nurse logs. Although tree fern trunks were abundant in the burned sites, mosses were burned off during the fire, and conditions on the trunks were presumably drier and less favorable for *Metrosideros* establishment.

The short-term changes in *Metrosideros* seedling density following fire in this study do not necessarily indicate differences in the future forest because this site is not likely seed limited as *Metrosideros* is well suited for establishing in canopy gaps (Drake 1992; Hatfield et al. 1996). Drastically lower seedling density in the burned *Cibotium* forest (733/ha) may be inconsequential because the density of 2-year old seedlings was still much greater than the canopy density. In addition, higher light conditions in the burned forest presumably will result in a higher likelihood of reaching the canopy than those seedlings in the unburned forest (Burton and Mueller-Dombois 1984).

In contrast to the *Cibotium* forest, *Metrosideros* seedling recruitment appeared to be enhanced by fire in the *Nephrolepis* and *Dicranopteris* forests where seedling densities were greater in burned sites than unburned sites (Table 2). Sampling other disturbed sites, Restrepo and Vitousek (2001) found that *Metrosideros* seedling establishment was greater on recent (4 to 17-year old) landslides than undisturbed mesic forests on the Island of Hawaii. Because the *Nephrolepis* and *Dicanopteris* forest communities are younger and lack woody and tree fern nurse logs, the dense herbaceous fern understory in the unburned sites may limit light and space for seedling establishment. Fire temporarily removed understory barriers and allowed for seedling establishment. The fact that, seedling densities remain lower in these communities than the *Cibotium* forest even following fire, supports the idea that seedling establishment across the study area is facilitated by tree fern nurse logs.

The native shrub *Dodonaea viscosa* was the only woody species present in all the five communities following fire. *Dodonaea* colonized the postfire environment through dispersal (i.e. seeds are enclosed in wind-borne bracts) and from the soil seed bank where temperatures during fire scarify the seeds (Hodgkinson and Oxley 1990). Therefore, *Dodonaea* possesses traits characteristic of evaders, invaders, and endurers (Table 3).

In the three forest communities of this study, no *Dodonaea* shrubs were found in the unburned sites and those in the burned sites had established from seed presumably from offsite colonization (i.e. neighboring shrubland communities). In the shrubland communities, however, *Dodonaea* individuals both sprouted and established from seed. This species had higher seedling densities in burned areas than in unburned areas. It is also one of three native woody species to reach sexual maturity from seed within two postfire years. Other fire studies at Hawaii Volcanoes National Park found that *Dodonaea* seedlings were abundant in burned mesic forest and shrublands (Warshauer 1974), submontane sites (Hughes et al. 1991; Hughes and Vitousek 1993; D'Antonio et al. 2000), and coastal lowlands (D'Antonio et al. 2000).

Many of the native Hawaiian woody species and tree ferns in this study area possessed traits that facilitated or ensured the persistence of individuals and/or species following fire. As would be expected the effects of fire differed among species; populations, and vegetation communities. The majority of woody species demonstrated the capacity to sprout, thus conferring these plants with advantages over individuals that rely solely on seeds for establishment in the postfire environment. It is unclear whether these are evolutionary adaptations to fire or causal adaptations of traits derived in response to other disturbances common in the region (volcanism, landslides, hurricanes, etc.). These adaptations may not be sufficient to insure dominance of native species in the future as the presence of invasive plant and nonnative ungulate species coupled with changes in climate may dramatically alter postfire succession and dominance in these ecosystems.

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References

Agee J (1993) Fire ecology of pacific northwest forests. Island Press, Washington, DC

Ainsworth A (2007) Interactive influences of wildfire and nonnative species on plant community succession in Hawaii Volcanoes National Park. Oregon State University, Corvallis, OR

Burney D, DeCandido R, Burney L et al (1995) A holocene record of climate change, fire ecology and human activity from montane Flat Top Bog, Maui. J Paleolimnol 13:209–217. doi:10.1007/BF00682765

Burton P, Mueller-Dombois D (1984) Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. Ecology 65:779–791. doi:10.2307/1938050

D'Antonio C, Vitousek P (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

D'Antonio C, Hughes F, Vitousek P (2001) Factors influencing dynamics of two invasive C4 grasses in seasonally dry Hawaiian woodland. Ecology 82:89–104

D'Antonio C, Tunison J, Loh R (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. Austral Ecol 25:507–522

Drake D (1992) Seed dispersal of *Metrosideros polymorpha* (Myrtaceae): a pioneer tree of Hawaiian lava flows. Am J Bot 79:1224–1228. doi:10.2307/2445048

Drake D, Mueller-Dombois D (1993) Population development of rain forest trees on a chronosequence of Hawaiian lava flows. Ecology 74:1012–1019. doi:10.2307/1940471

Freifelder R, Vitousek P, D'Antonio C (1998) Microclimate change and effect on fire following forest-grass conversion in seasonally dry tropical woodland. Biotropica 30:286–297. doi:10.1111/j.1744-7429.1998.tb00062.x

Gassaway L, Tunison J, Loh R (2002) Kupukupu Fire Hawaii Volcanoes National Park: burned area emergency rehabilitation plan. Hawaii Volcanoes National Park, Hawaii

Griffin J (1980) Sprouting in fire-damaged valley oaks, Chews Ridge, California. In: Ecology, management, and utilization of California Oaks. General Technical Report PSW-44. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture:216–219

Hatfield J, Link W, Dawson D et al (1996) Coexistence and community structure of tropical trees in a Hawaiian montane rain forest. Biotropica 28:746–758. doi:10.2307/2389061

Hawaii Department of Land and Natural Resources (1966) Aerial photo series of Hawaii Island. Air Survey Hawaii, Honolulu

Hodgkinson K, Oxley R (1990) Influences of fire and edaphic factors on germination of the arid zone shrubs. Aust J Bot 38:269–279. doi:10.1071/BT9900269

Hughes F, Vitousek P (1993) Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawaii. Oecologia 93:557–563. doi:10.1007/BF00328965

Hughes F, Vitousek P, Tunison J (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawaii. Ecology 72:743–746. doi:10.2307/2937215

IPCC (2007) Summary for policymakers. In: Parry M, Canziani J, Palutikof P, van der Linden P, Hanson C (eds) Climate change 2007: impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, 7–22

Jasper C (2007) Soil survey of Island of Hawaii. USDA-NRCS. U.A. Gov. Print. Office, Washington, DC (in press)

Kauffman B (1990) Ecological relationships of vegetation and fire in Pacific Northwest Forests. In: Walstad J, Radosevich S, Sandberg D (eds) Natural and prescribed fire in the Pacific Northwest Forests. Oregon State University Press, Corvallis

Kauffman JB, Martin RE (1990) Sprouting shrub response to varying seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. For Sci 36:748–764

Ley R, D'Antonio C (1998) Exotic grass invasion alters potential rates of N fixation in Hawaiian woodlands. Oecologia 113:179–187. doi:10.1007/s004420050366

Mack M, D'Antonio C, Ley R (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C4 grasses in Hawaii. Ecol Appl 11:1323–1335

Mueller-Dombois D (1981) Fire in tropical ecosystems. In: Mooney H, Bonnicksen T, Christiansen N Jr et al. (eds) Proceedings of the conference in fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26, Washington DC, National Park Service

Mueller-Dombois D (1987) Forest dynamics in Hawaii. Trends Ecol Evol 2:216–220

Mueller-Dombois D (2001) Biological invasion and fire in tropical biomes. In: Galley K, Wilson T (eds) Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the First National Congress on fire ecology, prevention, and management. Miscellaneous publication no. 11, Tall Timbers Research Station, Tallahassee, pp 112–121

National Park Service (2003) Fire history map for Hawaii Volcanoes National Park. Pacific West Region, Honolulu

Ough K, Murphy A (2004) Decline in tree-fern abundance after clearfell harvesting. For Ecol Manage 199:153–163

Palmer D (2003) Hawaiì's ferns and fern allies. University of Hawaiì Press, Honolulu

Parman T, Wampler K (1977) The Hilina Pali fire: a controlled burn exercise. Technical Report 18, Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu

Restrepo C, Vitousek P (2001) Landslides, alien species, and the diversity of a Hawaiian montane mesic ecosystem. Biotropica 33:409–420

Rowe J (1981) Concepts of fire effects on plant individuals and species. In: Wein R, Maclean D (eds) The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York

Sampaio E, Kauffman J (1993) Effects of different fire severities on coppicing of Caatinga vegetation in Serra Talhada, PE, Brazil. Biotropica 25:452–460. doi:10.2307/2388868

Shaw R, Castillo J, Laven R (1997) Impacts of wildfire on vegetation and rare plants with the Kipuka Kalawamauna endangered plant habitat area, Pohohakuloa Training Area, Hawaii. In: Greenlee J (ed) Proceedings: first conference on fire effects on rare and endangered species and habitats conference. International Association of Wildland Fire, Coeur d'Alene, ID, pp 253–264

Smith C, Tunison J (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. In: Stone C, Smith S, Tunison J (eds) Alien plant invasions in native ecosystems of Hawaii: management and research. Cooperative National Park Resources Studies Unit, Honolulu, pp 394–408

Tosi J, Watson V, Bolanos R (2001) Life zone map of Hawaii. Based on the world life zone system of L.R. Holdridge. UTM grid zone designation 40. Tropical Science Center, San Jose, Costa Rica

Trusdell F, Wolfe E, Morris J (2005) Digital database of the geologic map of the island of Hawaii. DS 144. U.S. Geological Survey, Reston, VA

Tunison J, D'Antonio C, Loh R (2001) Fire and invasive plants in Hawaii Volcanoes National Park. In: Galley K, Wilson T (eds) Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the First National Congress on fire ecology, prevention, and management. Miscellaneous publication no. 11, Tall Timbers Research Station, Tallahassee, pp 122–131

Tunison J, Leialoha J (1988) The spread of fire in alien grasses after lightning strikes in Hawaii Volcanoes National Park. Hawaii Bot Soc 27:102–109

Tunison J, Leialoha J, Loh R et al (1994) Fire effects in the coastal lowlands Hawaii Volcanoes National Park. Cooperative National Park Resources Study Unit, Technical Report no. 88, Cooperative Agreement CA 8007-2-9004. University of Hawaii Press, Honolulu

Tunison J, Loh R, Leialoha J (1995) Fire effects in the submontane seasonal zone Hawaii Volcanoes National Park. Cooperative National Park Resources Study Unit, Technical Report no. 97, Cooperative Agreement CA 8007-2-9004. University of Hawaii Press, Honolulu

Vogl R (1969) The role of fire in the evolution of the Hawaiian flora and vegetation. In: Tall Timbers Fire Ecology Conference, vol 9, pp 5–60

Wagner W, Herbst D, Sohmer S (1999) Manual of the Flowering Plants. Revised edition. Bishop Museum, Honolulu

Warshauer F (1974) Biological survey of Kealakomo and vicinity affected by 1969–1973 lava generated wildfires, Hawaii Volcanoes National Park. Hawaii Volcanoes National Park, Hawaii

White P, Pickett S (1985) Natural disturbance and patch dynamics: an introduction. In: Pickett S, White P (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York

Evaluating different harvest intensities over understory plant diversity and pine seedlings, in a *Pinus pinaster* Ait. natural stand of Spain

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Abstract Although modern forestry takes into consideration the analysis of the effects of forest management on plant structure, diversity and seedlings, little is known about how those parameters respond to harvest techniques in the Mediterranean region. We investigated the effect of three different harvest intensities, respect to uncut controls, on understory plant species functional groups, richness, diversity and pine seedlings in a natural Maritime pine stand in Spain, three years after harvesting. The harvest treatments produced a reduction of the number of *Pinus pinaster* seedlings and woody species cover, and an increase of species richness (total and of annual species) and plant cover of annual species respect to control plots (CO). The Shannon diversity values showed no differences between treatments. These results emphasize that the tree harvest treatments analyzed are not suitable for the management of this *P. pinaster* stand. Otherwise, the reduction of pine seedling density by harvest treatments and the changes in richness and cover of functional groups would not induce the natural regeneration of this stand maintaining the understory plant layer.

Keywords Anthropogenic disturbance · Herbaceous layer · Mediterranean ecosystem · Silviculture · Woody species

Introduction

One of the major challenges for modern forestry is to combine conservation of biodiversity and ecosystem functioning with wood production and other values (Hummel 2003; Decocq et al. 2004; Nagai and Yoshida 2006; Newmaster et al. 2007). These general principles will obviously need to be achieved using adequate management practices (Kimmins 2004). It is generally assumed that management practices, and especially harvesting, modulate simultaneously the availability of different types of resources (e.g. light, water and soil nutrients; Decocq et al. 2004). As a result, understory species diversity and flora, which play a fundamental role in the structure and function of ecosystems (Roberts and Gilliam 1995; Newmaster et al. 2007), become quite affected (Hughes and Fahey 1991; Zenner et al. 2006). Therefore, the

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knowledge of the effects of different harvest disturbances on understory plant layer is an essential element to implement sustainable management of forest landscapes (Halpern and Spies 1995; Roberts and Gilliam 1995; Fahey and Puettmann 2007).

Maritime pine (*Pinus pinaster* Ait.) is a natural forest species characteristic of the western Mediterranean basin, mainly distributed over the Iberian Peninsula, France and Italy (Alía et al. 1996). Traditionally, *P. pinaster* in central Spain has been used for resin production and soil protection against mobile continental dunes (Bravo-Oviedo et al. 2007), with wood production as secondary objective. An important step towards ecologically sound wood production procedures is to test different management alternatives (i.e. harvest intensities) to induce the natural revegetation of these stands. At the same time, these alternatives should always contribute to maintain the landscape and ecological protection functions, mushrooms production and biodiversity of the stands (Oria de Rueda 2003), while sustainable wood and resin production is obtained.

The effect of forest management on plant diversity and flora is complex and more difficult to generalize than it was originally thought (Tárrega et al. 2006), underlining the importance of studying plant and diversity responses for different forest types and harvest techniques (Gilliam 2002). Moreover, most published studies concern managed forests in North America, whose history and tradition radically differ from Europe (Decocq et al. 2004), and particularly from the Mediterranean region (Scarascia-Mugnozza et al. 2000). The aim of this study, therefore, is to investigate the effects of three harvest intensities, relative to untreated control areas, on understory species richness, diversity, functional groups (life forms) and *P. pinaster* seedlings, and their relation to the remaining basal area and canopy cover of a natural maritime pine stand in semi-arid Mediterranean conditions in Spain, three years after harvest. We hypothesized that: (1) the number of *P. pinaster* seedlings in such semi-arid Mediterranean conditions would be reduced by harvest intensity, (2) the functional groups (annual and perennial herbs and woody species) cover and richness would be affected by harvest treatments, and (3) the understory plant richness and diversity would be markedly affected by harvest intensity.

Methods

Study area

This study was conducted in a flat natural Maritime pine forest located in the Segovia province (Cuellar, 757 m a.s.l.; 41°22′N, 4°29′W; Central Spain). The original stand density was 140 stems/ha, tree age ranges from 80 to 100 years and silvicultural practice is based on natural regeneration following a shelterwood system adapted to resin production. The climate is semi-arid Mediterranean, with a mean annual temperature of 11.2°C, a mean annual rainfall of 461 mm and dry period from the middle of June to the middle of September (M.A.P.A 1987). The soils are sandy siliceous of Quaternary age (Junta de Castilla y León 1988), and the vegetation of the area is dominated by *Pinus pinaster* with some isolated trees of Stone pine (*Pinus pinea* L.) and crop fields.

Treatments

About 16 continuous hectares of natural Maritime pine were selected in a ca. 15,000 ha of forest to delimit twelve 70 × 70 m permanent plots. To record the variation caused by silviculture treatments rather than to site variability, the selected hectares shared the same abiotic conditions, forest structure and vegetation composition. After plots were established two variables were recorded for all trees with diameter at breast height greater than 7.5 cm found inside the plots: diameter at breath height (DBH; cm), and crown diameters (m). The DBH and crown diameters were measured in order to obtain the basal area (BA) and the canopy cover (%) as informative parameters of the light conditions for ground vegetation (Härdtle et al. 2003). Three levels of harvest intensity with three replicates for each one were applied over nine of the permanent plots: (1) 25% of basal area removed (close plots, H25), (2) 50% of basal area removed (open plots, H50), and (3) 100% of basal area removed (clear-cut plots; CC). All treatments were randomly allocated on these nine plots, whereas the remaining three permanent plots were used as control units (CO) not receiving any treatment during the study. Harvesting was carried out manually with handsaw once all trees selected for cutting were marked according to the basal area removal criteria. The trees were harvested using a silvicultural criterion to facilitate the natural regeneration, i.e. trees showing disease or physical damage were removed first, followed by the smaller trees and finally by others with larger diameters, to increase the amounts of low- and mid-story shade. Moreover, harvesting was designed to distribute residual overstory canopies as uniform as possible inside every particular harvest plot (H25, H50). The sampling of DBH and crown diameters was carried out in summer 2003, whereas the harvest operations were made in autumn 2003.

Understory vegetation sampling

To sample understory vegetation in each of 12 permanent plots, 20 quadrats of 1 × 1 m were placed using simple random sampling design (Krebs 1999). However, in order to evade edge effect the first 10 m from the plot edge were avoided. In each quadrat, the cover (%) of all vascular plant species present and the number of *P. pinaster* seedlings (criteria = maximum 3-years old) were estimated visually by the same observer in May 2006.

Data analyses

Diversity of understory plant communities was assessed using the Shannon index (H′) (Shannon and Weaver 1949) with logs to base 2, and its two components, richness (S) and evenness (J′) (Pielou 1969). Shannon diversity and richness were calculated on two scales, similar to Tárrega et al. (2006): (1) on small scale (per quadrat or m^2), alpha diversity or microcosmic diversity (Magurran 2004); and (2) on a community scale for each plot (4,900 m^2), plot gamma diversity or macrocosmic diversity (from the joint consideration of the 20 samples carried out for each studied plot). Evenness, however, was calculated only on a community scale. By using the comparison of both types of diversity, beta diversity or spatial heterogeneity was calculated: S_β by the Whittaker (in Magurran 2004) formula, $S_\beta = (S/S_\alpha) - 1$, and H_β' as the difference between H′ and the average of H_α' (Margalef 1972). The number of *P. pinaster* seedlings is referred to the total number of seedlings in the 20 quadrats of each plot.

To evaluate the significance of different harvest treatments, relative to controls, on the number of *P. pinaster* seedlings, functional groups cover and richness (annual herbs, perennial herbs and woody species), species richness (S), evenness (J′) and diversity values (H_α', H_β', H′, S_α and S_β), one-way analyses of variance (ANOVA) were applied followed by Tukey's HSD tests to enable pairwise comparisons of means ($P < 0.05$). In all cases, the inspection of residuals was carried out to check for normality and homoscedasticity. Nevertheless, when variables do not meet normality and variance assumptions, data were transformed using arcsine squared-root transformation for binomially distributed variables (i.e. plant cover) and squared-root transformation for count data (i.e. richness) (Zar 1996).

In order to determine possible relationships among the 13 variables analyzed, a Pearson's correlation matrix was constructed considering: canopy cover, basal area, number of *P. pinaster* seedlings, number of woody species, number of perennial and annual herbs and J′, H_α', H_β', H′, S_α, S_β and S. A Principal components analysis (PCA) was used to summarize the relationships among treatments and the variables as a whole. Data for the 13 variables used in PCA were standardized prior to analysis, to correct for different measuring units.

Results were expressed as mean ± standard error and all statistical computations were implemented in the R software environment (version 2.7.0; R Development Core Team 2008).

Results

P. pinaster seedlings

The density of *P. pinaster* seedlings found in the plots was lower than 3.3 seedlings/m^2, however, significant differences among harvest intensities were found ($F_{[3,8]} = 23.4$, $P < 0.001$; Fig. 1). Untreated control plots (CO) showed the greatest number of seedlings per plot (66 ± 13.5), clear cut plots (CC) the lowest (1 ± 0.58), and H25 and H50 treated plots an intermediate number (16 ± 8.5 and 8 ± 1.8, respectively).

Functional groups (life forms)

Annual species dominated, in number and cover, the understory plant communities in the four treatments

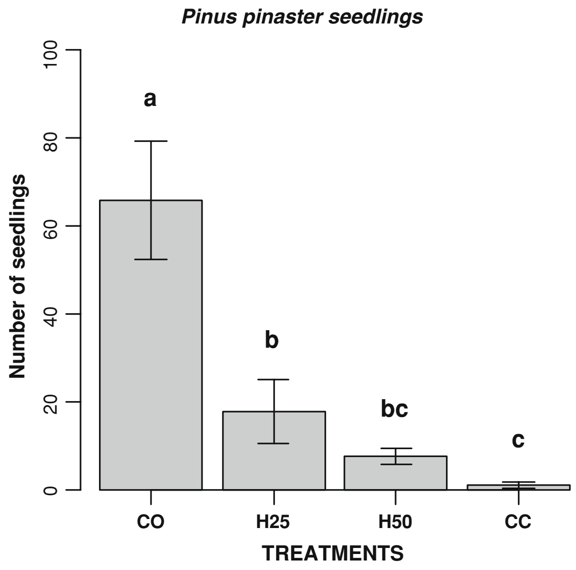


Fig. 1 Comparison of the number of *P. pinaster* seedlings per plot (total number of seedlings in the 20 quadrats of each plot) among treatments (mean ± SE). CO: control plots; H25: 25% of basal area removed (close plots); H50: 50% of basal area removed (open plots); CC: 100% of basal area removed (clear cut). Different letters above the bars indicate significant differences ($P < 0.05$) by Tukey's test

(Fig. 2). Annual cover was similar in the tree treated areas (H25, H50 and CC), ranging between 37 and 41%, and significantly greater than in the untreated CO ($F_{[3,8]} = 16.59$, $P < 0.001$; Fig. 2a). On the contrary, the cover of woody species was significantly greater in the CO than in the CC and open plots (H50) ($F_{[3,8]} = 7.01$, $P = 0.013$), where it hardly reached a 2%. The cover of perennial herbs only differed between the CC and open plots (H50) ($F_{[3,8]} = 5.36$, $P = 0.026$).

Annual species number significantly varied with harvest intensity. Clear cut plots (CC), with maximum values (41 ± 1.78), followed by open plots (H50; 31 ± 0.33) showed significantly greater values than control plots (CO) ($F_{[3,8]} = 23.21$, $P < 0.001$; Fig. 2b). Perennial species number was also significantly greater in the clear cut plots (CC) than in the rest ($F_{[3,8]} = 7.3$, $P = 0.011$; Fig. 2b), whereas the number of woody species did not differ with harvest intensity ($F_{[3,8]} = 0.58$, $P = 0.647$).

Richness and diversity

The small scale richness (S_α) varied between 12 and 17 species/m^2 in control and clear cut plots, respectively, but not differed significantly among treatments ($F_{[3,8]} = 2.54$, $P = 0.130$; Fig. 3a). In contrast, species richness on a community scale (S), which ranged between 37 and 62 species per treatment, showed significantly greater values in CC plots than in the remainder ($F_{[3,8]} = 16.86$, $P < 0.001$; Fig. 3a). In spite of that, Shannon diversity index, that showed high values in the four treatments (H′ always above 4.2; Fig. 3b), did not differ significantly with harvest intensity ($F_{[3,8]} = 0.28$, $P = 0.835$), due to a reduction of evenness; thus, no statistically significant differences between treated plots (H25, H50 and CC) and controls (CO; Fig. 3d) were found. There were also no significant differences in spatial heterogeneity among harvest intensities (Fig. 3c).

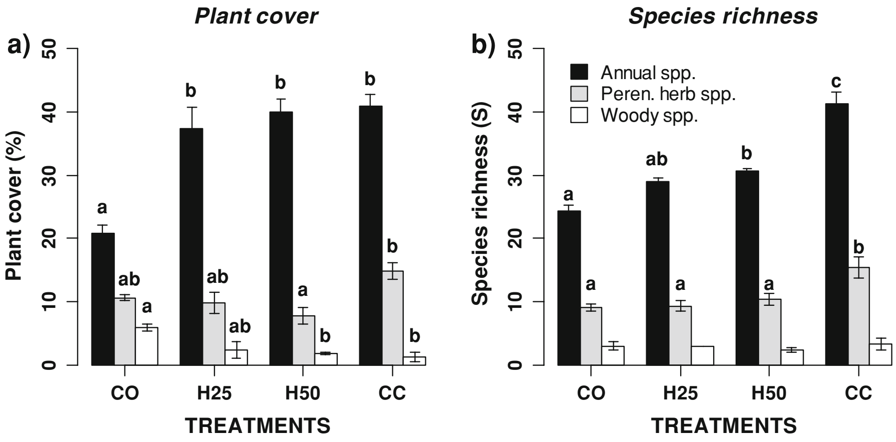
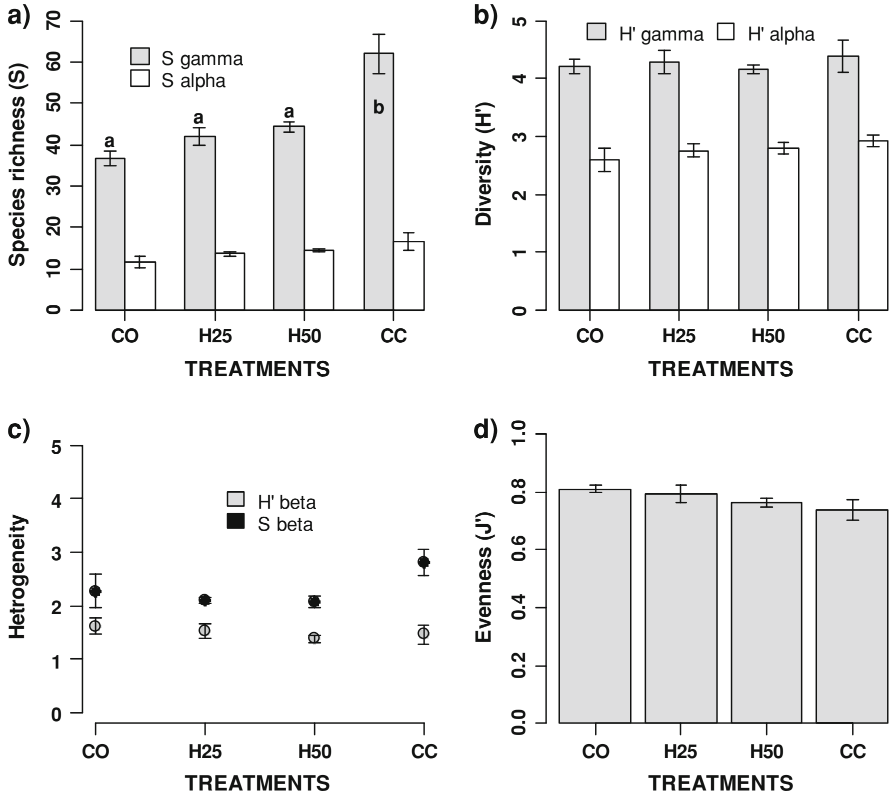


Fig. 2 Comparison of annual, perennial herbaceous and woody species cover and richness among treatments (mean ± SE). See Methods or Fig. 1 caption for treatment description. Different letters above the bars indicate significant differences among treatments ($P < 0.05$) by Tukey's test

Fig. 3 Comparison of different richness (**a**), Shannon diversity (**b**), heterogeneity (**c**) and evenness (**d**) values among treatments (mean ± SE). See Methods or Fig. 1 caption for treatment description. Different letters above the bars indicate significant differences among treatments ($P < 0.05$) by Tukey's test



Relationship between variables

The correlation analysis carried out to determine the relationship among the 13 variables analyzed (Table 1) showed that basal area, canopy cover and *P. pinaster* seedlings were negatively correlated with different richness values (S, S_α and S_β), and to the number of perennial and annual herbs. However, in general those parameters were not correlated with diversity values (H′, H_α' and H_β'). The Shannon diversity (H′) showed a significant positive correlation with H_α', H_β' and J′, the number of perennial herbs and woody species. The number of *P. pinaster* seedlings was negatively correlated with annual species number and positively with basal area.

The PCA performed for the joint comparison of all the variables produced an ordination of plots with the first two axes accounting for 78% of the total variance. The first component explained 55% of variance and was strongly positively correlated with S, S_α, H_α', and number of perennial and annual herbs, on the contrary it was strongly negatively correlated with basal area, canopy cover and number of *P. pinaster* seedlings (Table 2). The second component explained an additional 23% and showed only positive correlation with diversity (H′ and H_β'), evenness (J′) and woody species number (Table 2). In the ordination diagram, the first axis ordered the sites according to their treatment, increasing harvest intensity from the left to the right (Fig. 4). Controls (CO) were located on the left associated with greater basal area and lower richness. Close plots (H25) were located near controls and open plots (H50) in intermediate position. However, clear cuts (CC) appeared on the right without basal area and greater species number. The second axis was related to diversity gradient, increasing diversity, evenness and woody species number to the positive end, and produced a separation between plots within the same treatment.

Discussion

The results illustrate that three harvest treatments applied over a natural stand of Maritime pine in Spain

Table 1 Pearson correlation matrix between richness, diversity and functional groups richness

	S_γ	S_α	S_β	H'_γ	H'_α	H'_β	J'	As	Ps	Ws	Pp	Cc	Ba
S_γ	1												
S_α	**0.85**	1											
S_β	0.41	−0.13	1										
H'_γ	0.53	**0.71**	−0.20	1									
H'_α	**0.60**	**0.83**	−0.30	**0.66**	1								
H'_β	0.06	0.04	0.05	**0.60**	−0.21	1							
J'	−0.32	0.00	−0.57	**0.63**	0.15	**0.66**	1						
As	**0.94**	**0.72**	0.50	0.26	0.52	−0.21	−0.57	1					
Ps	**0.92**	**0.79**	0.37	**0.59**	**0.59**	0.14	−0.19	**0.79**	1				
Ws	0.46	0.54	−0.07	**0.72**	0.33	**0.58**	0.42	0.28	0.36	1			
Pp	**−0.67**	**−0.73**	0.01	−0.26	**−0.65**	0.35	0.38	**−0.72**	−0.55	0.03	1		
Cc	**−0.83**	−0.52	**−0.69**	−0.19	−0.29	0.06	0.55	**−0.86**	**−0.79**	−0.12	0.50	1	
Ba	**−0.86**	**−0.59**	**−0.61**	−0.19	−0.40	0.18	**0.58**	**−0.90**	**−0.81**	−0.10	**0.60**	**0.98**	1

As: annual species number; Ps: perennial species number; Ws: woody species number, Pp: number of *P. pinaster* seedlings, Cc: canopy cover and Ba: basal area. In bold type are significant correlations at $P < 0.05$

Table 2 Correlation coefficients of plot scores along axes 1 and 2 and the 13 variables used in the principal components analysis (PCA)

	Axis 1	Axis 2
S_γ	**0.98**	0.12
S_α	**0.82**	0.46
S_β	0.43	−0.55
H'_γ	0.45	**0.87**
H'_α	**0.61**	0.46
H'_β	−0.06	**0.65**
J'	−0.41	**0.87**
Annual species number	**0.96**	−0.16
Perennial herbs species number	**0.90**	0.18
Woody species number	0.32	**0.72**
Number of *Pinus pinaster* seedlings	**−0.74**	0.04
Canopy cover	**−0.88**	0.28
Basal area	**−0.93**	0.29
Eigenvalues	8.17	3.47
Explained variance	55%	23%

In bold type are significant correlations at $P < 0.01$

influenced on species richness, annual herbs and woody species cover, and reduced the number of *P. pinaster* seedlings. These results were in agreement with previous studies that have documented how overstory alterations conditioned the post-disturbance response of understory vegetation (Ramovs and Roberts 2003).

P. pinaster seedlings

An important result was that the three harvest intensities reduced the number of *P. pinaster* seedlings in comparison with control plots; thus the first hypothesis is accepted. The reduction in the number of established seedlings from control to clear cut plots was correlated positively with basal area and negatively with annual species number. Therefore, this reduction may be caused by a combination of factors: (1) a decrease of seed inputs caused by the elimination of trees in treated plots in comparison with controls; (2) a reduction of canopy cover, which undoubtedly changed understory microclimate (Aussenac 2000), increasing the radiation intensity during summer and reducing the water availability for seedlings and their viability (Castro et al. 2004; Gómez-Aparicio et al. 2005; Calvo et al. 2008) and (3) competition for water and nutrients between coniferous seedlings and annual species (Peltzer et al. 2000), since annuals were able to dry up the upper soil layer leading to seedling mortality, especially during the early period of seedling development (Sternberg et al. 2001). Indeed, those factors could be highly emphasized by the intense summer droughts detected in the study area at 2004–2006 periods. Especially over treated plots, because temperature and moisture stress are lower in the presence of an overstory cover (Pérez and Moreno 1998; Aussenac

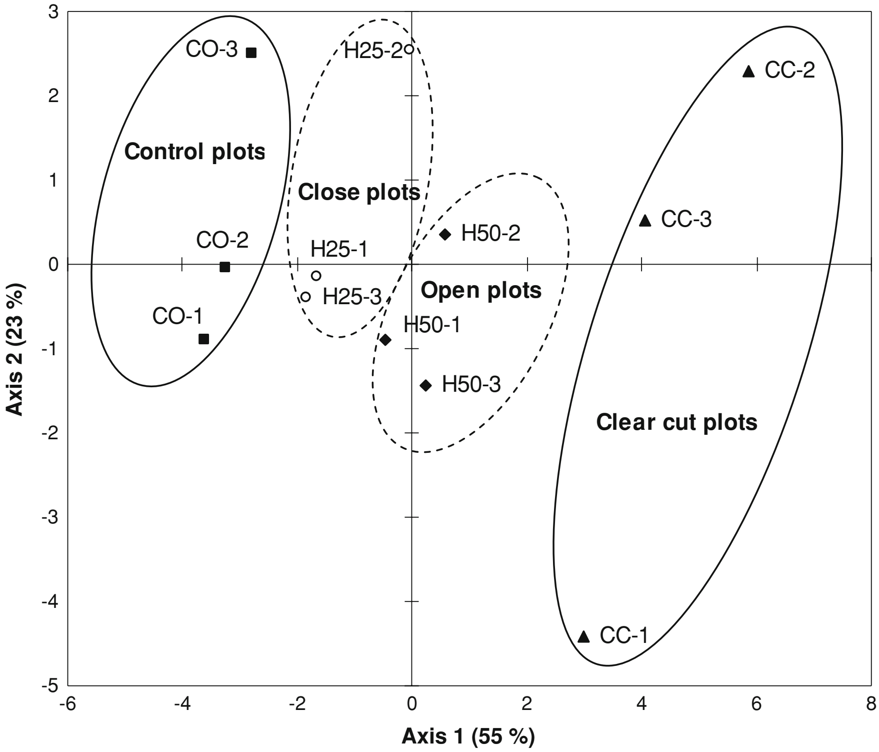


Fig. 4 First two axes of the PCA ordination of different harvest intensity plots. See Methods or Fig. 1 caption for treatment description. The number after the treatment abbreviation indicates the number of replicate

2000). The relative importance of each of these possible explanations required further investigation.

In any case, the density of seedlings found in this stand three years after harvest is very low, even in controls (3.3 seedlings/m^2), compared with 8 seedlings/m^2 recommended to ensure natural regeneration (Luis-Calabuig et al. 2002). Therefore, artificial reintroduction of seeds or seedlings may be a suitable option to increase the seedling density (Pausas et al. 2004), with the objective of facing up to the survival loss caused by inter-specific competition (Eshel et al. 2000), and water availability by summer droughts (Gómez-Aparicio et al. 2005), which would become normal in this area in near future as a consequence of climate change (Intergovernmental Panel on Climate Change (IPCC) 2007).

Functional groups (life forms)

The harvest treatments, in comparison with controls, influenced the richness of annual and perennial herbs and plant cover of annual herbs and woody species, thus the second hypothesis is partially accepted.

Different studies have reported that harvesting increases potential growing space in the understory (Newmaster et al. 2007), and the relative availability of resources (Fredericksen et al. 1999), especially light (Zenner et al. 2006), improving the conditions for establishment of early colonizer species (Newmaster et al. 2007). Not surprisingly, our results provided similar patterns, with an increase of annual species richness and cover along the harvest intensity gradient (from controls to clear-cuts).

In these semi-arid Mediterranean forests, with three months of summer drought, harvesting generates habitats with a strong seasonal stress and with understory vegetation dominated by annuals. Under these conditions, perennial species establish themselves with difficulty compared to annuals whose life cycle is adapted to this seasonal stress (Madon and Médail 1997). At the same time, and as we said previously, the pine seedling establishment may be reduced by the great cover development of annual species through inter-specific competition (Eshel et al. 2000).

On more disturbed plots (clear-cut), with greater solar radiation intensity during summer, species richness of perennial herbs showed greater values than on control plots. This may be caused because the new established species were characteristic of

Mediterranean open sites (e.g. *Cynodon dactylon* or *Armeria arenaria*), in accordance with previous research findings in recent clear-cut stands (Roberts and Gilliam 1995; North et al. 1996).

Woody species showed an opposite pattern, maintaining their species richness and decreasing in cover along the harvest intensity gradient (from controls to clear-cuts). Woody species were more abundant in sites with higher tree cover, as in control and close (H25) plots, than in clear-cut and open (H50) plots. It is possible that the partial shade provided by trees may alleviate the harsh environmental factors prevailing under full-sun environments (Alrababah et al. 2007), enhancing the woody species growth. However, under the most severe treatments, although woody species richness was similar to control plots, the physical destruction of existing woody species by the harvest operations (Newmaster et al. 2007), linked to the marked seasonal stress may cause their cover reduction.

The different responses of annual and perennial herbs, and woody species richness along the harvest treatments supports the hypothesis of Peet's (1978), who found different response patterns of plant species richness for different structural groups (woody and herbs).

Richness and diversity

The influence of harvest is clear only in the case of richness, therefore the third hypothesis is partially accepted. Three years after harvesting, understory plant richness was higher in treated plots than in controls, although differences were significant only for the most severe disturbance treatment (clear-cutting). At the same time, plant richness had negatively significant relationship with basal area, suggesting an increase in richness as harvest intensity increases, as observed in similar studies in temperate forest (Fredericksen et al. 1999; Götmark et al. 2005; Zenner et al. 2006). Harvesting increased species richness because of the colonization of annuals and some perennial herbs (Swindel et al. 1983; Götmark et al. 2005), which were favoured by the modification of the stand habitat-conditions (Jobidon 1990).

Despite the positive influence of harvesting on species richness showed in this study, no differences with control plots on the understory Shannon diversity values were found, as in other studies in temperate forest (Gilliam et al. 1995; Gilliam 2002; Krzic et al. 2003). The relative high Shannon diversity values reached under all treatments indicated that plant communities after harvesting were not dominated by just a few species (Krzic et al. 2003). On the contrary, these results did not suggest that an increase in harvest intensity did not influence the understory species layer. Peltzer et al. (2000) found that plant diversity did not change when increasing the intensity of silvicultural disturbances, but a higher number of herb species appeared. These results are consistent with our findings of increasing annual and perennial herbs richness with harvest intensity.

The Shannon index (H') is affected by species richness and evenness (Westman 1990). As previously explained, richness increased as harvest intensity increases, whereas evenness decreased, resulting in no changes in the Shannon diversity index (H'). This suggest that in control plots the relative abundance of species is more similar than in treated plots (H25, H50 and CC), in which some of new species tend to be relatively uncommon or rare (Small and McCarthy 2002).

The separation between different harvest treatments was clearly connected with basal area, canopy cover and *P. pinaster* seedlings reduction, and with the increase of richness (S and S_α) and herbs richness (annual and perennial). This indicates that the elimination of tree cover favoured the establishment of new herbs species, which increased their cover by the addition of more species, rather than by the growth increase of a few of them (Gilliam 2002). In contrast, diversity (H' and H_β'), evenness and woody species number were related with differences between plots of the same treatment, rather than with differences between harvest treatments. These results emphasize the difficulty in making general conclusions of the effects of harvest treatments (disturbances) on diversity, supporting the conclusions of Gilliam (2002) and Tárrega et al. (2006).

Finally, our results emphasize that the tree harvest treatments assessed are not suitable for the management of this *P. pinaster* stand. Otherwise, the reduction of pine seedling density and the changes in richness and cover of functional groups by harvest treatments would not induce the natural regeneration of this stand, maintaining the understory plant layer. Managers must realize that even controls would have problems to ensure natural regeneration, because the pine seedling density reached in three years is not enough to guarantee it. Therefore, further investigations are needed to assess seedling establishment limiting factors, the effectiveness of reintroduction of pine seeds or seedlings and other silvicultural alternatives (i.e. single tree selection or nurse plant strategies) to achieve adequate management practices, including wood production, with respect to ecosystem functioning.

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References

Alía R, Martín R, de Miguel J, Galera RM, Agúndez D, Gordo J et al (1996) Regiones de procedencia *Pinus pinaster* Ait. DGCN, Madrid

Alrababah MA, Alhamad MA, Suwaileh A, Al-Gharaibeh M (2007) Biodiversity of semi-arid Mediterranean grasslands: impact of grazing and afforestation. Appl Veg Sci 10:257–264. doi:10.1658/1402-2001(2007)10[257:BOSMGI]2.0.CO;2

Aussenac G (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences of silviculture. Ann Sci 57:287–301. doi:10.1051/forest:2000119

Bravo-Oviedo A, del Río M, Montero G (2007) Geographic variation and parameter assessment in generalized algebraic difference site index modeling. For Ecol Manag 247:107–119

Calvo L, Santalla S, Valbuena L, Marcos E, Tárrega R, Luis-Calabuig E (2008) Post-fire natural regeneration of *Pinus pinaster* forest in NW Spain. Plant Ecol. doi:10.1007/s11258-007-9362-1

Castro J, Zamora R, Hódar JA, Gómez JM (2004) Seedling establishment of boreal tree species (*Pinus sylvestris*) at its southern most distribution limit: consequences of being in a marginal Mediterranean habitat. J Ecol 92:266–277. doi:10.1111/j.0022-0477.2004.00870.x

Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A et al (2004) Plant diversity in a managed temperate deciduous forest: understory response to two silvicultural systems. J Appl Ecol 41:1065–1079. doi:10.1111/j.0021-8901.2004.00960.x

Eshel A, Henig-Sever N, Ne'eman G (2000) Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession. Plant Ecol 148:175–182. doi:10.1023/A:1009880416760

Fahey RT, Puettmann KJ (2007) Ground-layer disturbance and initial conditions influence gap partitioning of understory vegetation. J Ecol 95:1098–1109. doi:10.1111/j.1365-2745.2007.01283.x

Fredericksen TS, Ross BD, Hoffman W, Morrison ML, Beyea J, Johnson B, Lester MB, Ross E (1999) Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For Ecol Manag 116:129–139

Gilliam FS (2002) Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA. For Ecol Manag 155:33–43

Gilliam FS, Turril NL, Adams MB (1995) Herbaceous-layer and overstory species in clear-cut and mature Appalachian hardwood forests. Ecol Appl 5:947–955. doi:10.2307/2269345

Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL (2005) Canopy vs soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. J Veg Sci 16:191–198. doi:10.1658/1100-9233(2005)016[0191:CVSEOS]2.0.CO;2

Götmark F, Paltto H, Norden B, Götmark E (2005) Evaluating partial cutting in broadleaved temperate forest under strong experimental control: short-term effects on herbaceous plants. For Ecol Manag 214:124–141

Halpern CA, Spies TA (1995) Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol Appl 5:913–934. doi:10.2307/2269343

Härdtle W, von Oheimb G, Wesphal C (2003) The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forest in northern Germany (Schleswig-Holstein). For Ecol Manag 182:327–338

Hughes JW, Fahey TJ (1991) Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. J Ecol 79:605–616. doi:10.2307/2260656

Hummel SS (2003) Managing structural and compositional diversity with silviculture. In: Monserud RA, Haynes RW, Johnson AC (eds) Compatible forest management. Kluwer Academic Publishers, the Netherlands, pp 85–120

Intergovernmental Panel on Climate Change (IPCC) (2007) The physical science basis. Cambridge University Press, New York

Jobidon R (1990) Short-term effect of three mechanical site preparation methods on species diversity. Tree Plant Notes 41:39–42

Junta de Castilla y León (1988) Análisis del medio físico de Segovia. EPYPSA, Valladolid

Kimmins JP (2004) Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry. Prentice Hall, NJ

Krebs CJ (1999) Ecological methodology. Addison-Welsey Educational Publishers, Menlo Park, CA

Krzic M, Newman RF, Broersma K (2003) Plant species diversity and soil quality in harvested and grazed boreal aspen stands of northeastern British Columbia. For Ecol Manag 182:315–325

Luis-Calabuig E, Torres O, Valbuena L, Calvo L, Marcos E (2002) Impact of large fires on a community of *Pinus pinaster*. In: Trabaud L, Prodon R (eds) Fire and biological processes. Backhuys Publishers, Leiden, pp 1–12

Madon O, Médail F (1997) The ecological significance of annuals on a Mediterranean grassland. Plant Ecol 129:189–199. doi:10.1023/A:1009759730000

Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford

M.A.P.A (1987) Caracterización agroclimática de la provincia de Segovia. Ministerio de Agricultura Pesca y Alimentación, Madrid

Margalef R (1972) Homage to Evelyn Hutchinson, or why is there an upper limit to diversity. Trans Conn Acad Arts Sci 44:211–235

Nagai M, Yoshida T (2006) Variation in understory structure and plant species diversity influenced by silvicultural treatments among 21- to 26-year old *Picea glehnii* plantations. J For Res 11:1–10. doi:10.1007/s10310-005-0176-5

Newmaster SG, Parker WC, Bell FW, Paterson JM (2007) Effects of forest floor disturbances by mechanical site preparation on floristic diversity in a central Ontario clearcut. For Ecol Manag 246:196–207

North M, Chen J, Smith G, Krakowiak L, Franklin J (1996) Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Sci 70:24–35

Oria de Rueda JA (2003) Guía de los árboles y arbustos de Castilla y León. Calamo, Palencia

Pausas JG, Bladé C, Valdecantos A, Seva JP, Fuentes D, Alloza JA et al (2004) Pines and oaks in the restoration of Mediterranean landscapes of Spain: new perspectives for an old practice-a review. Plant Ecol 171:209–220. doi:10.1023/B:VEGE.0000029381.63336.20

Peet RK (1978) Forest vegetation of the Colorado Front Range: pattern of species diversity. Vegetatio 37:65–78. doi:10.1007/BF00126830

Peltzer DA, Bast ML, Wilson SD, Gerry AK (2000) Plant diversity and tree responses following contrasting disturbances in boreal forest. For Ecol Manag 127:191–203

Pérez B, Moreno JM (1998) Fire-type and forestry management effects on the early postfire vegetation dynamics of a *Pinus pinaster* woodland. Plant Ecol 134:27–41. doi:10.1023/A:1009733818670

Pielou EC (1969) An introduction to mathematical ecology. Wiley, New York

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org

Ramovs BV, Roberts MR (2003) Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. Ecol Appl 13:1682–1700. doi:10.1890/02-5237

Roberts MR, Gilliam FS (1995) Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol Appl 5:969–977. doi:10.2307/2269348

Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000) Forests of the Mediterranean region: gaps in knowledge and research needs. For Ecol Manag 132:97–109

Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana

Small JC, McCarthy BC (2002) Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. Plant Ecol 164:37–48. doi:10.1023/A:1021209528643

Sternberg M, Danin A, Noy-Meir I (2001) Effects of clearing and herbicide treatments on coniferous seedling establishment and growth in newly planted Mediterranean forests. For Ecol Manag 148:179–184

Swindel BF, Conde LF, Smith JE (1983) Plant cover and biomass response to clear-cutting, site preparation, and planting in *Pinus elliottii* flatwoods. Science 219:1421–1422. doi:10.1126/science.219.4591.1421

Tárrega R, Calvo L, Marcos E, Taboada A (2006) Forest structure and understory diversity in *Quercus pyrenaica* communities with different human uses and disturbances. For Ecol Manag 227:50–58

Westman EW (1990) Managing for biodiversity: unresolved science and policy questions. Bioscience 40:26–33. doi:10.2307/1311236

Zar JH (1996) Biostatistical analysis. Prentice Hall, London

Zenner EK, Kabrick JM, Jensen RG, Peck JE, Grabner JK (2006) Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. For Ecol Manag 222:326–334

Land-use history affects understorey plant species distributions in a large temperate-forest complex, Denmark

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Abstract In Europe, forests have been strongly influenced by human land-use for millennia. Here, we studied the importance of anthropogenic historical factors as determinants of understorey species distributions in a 967 ha Danish forest complex using 156 randomly placed 100-m^2 plots, 15 environmental, 9 spatial, and 5 historical variables, and principal components analysis (PCA), redundancy analysis (RDA) as well as indicator species analysis. The historical variables were status as ancient (1805 AD) high forest, reclaimed bogs, $\leq$100 m from Bronze Age burial mounds, or former conifer plantation, and stand age. The PCA results showed that the main gradients in species composition were strongly related to the explanatory variables. Forward variable selection and variation partitioning using RDA showed that although modern environment was the dominant driver of species composition, anthropogenic historical factors were also important. The pure historical variation fraction constituted 13% of the variation explained. The RDA results showed that ancient-forest status and, secondarily, reclaimed bog status were the only significant historical variables. Many typical forest interior species, with poor dispersal and a strong literature record as ancient-forest species, were still concentrated in areas that were high forest in 1805. Among the younger forests, there were clear floristic differences between those on reclaimed bogs and those not. Apparently remnant populations of wet-soil plants were still present in the reclaimed bog areas. Our results emphasize the importance of historical factors for understanding modern vegetation patterns in forested landscapes.

Keywords Ancient-forest indicator species · Ancient woodland · Dispersal limitation · Forest history · Forest management · Historical factors

Introduction

An important goal in ecology is to establish the determinants of species distributions and community composition. Plant species distributions in temperate forest ecosystems are well-known to partly reflect natural heterogeneity in the environment, notably edaphic gradients and forest canopy structure (Ellenberg 1988; Motzkin et al. 1999; Svenning and Skov 2002; Dupré and Ehrlén 2002). However, natural and anthropogenic historical factors will often also be important. Historical factors may act not only via persistent environmental changes, but also via purely population dynamic legacies, notably dispersal limitation and the occurrence of remnant populations (Gilliam 2007; Eriksson 1996). Natural historical

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factors include the legacies of past natural disturbances such as hurricanes or fires (Motzkin et al. 1999) as well as postglacial migration (Popiela 2004; Van der Veken et al. 2007; Svenning et al. 2008) and other dispersal processes (Svenning and Skov 2002; Miller et al. 2002). Human land-use have pervasively affected temperate forest ecosystems for several thousands years (Ellenberg 1988; Peterken 1996; Björse and Bradshaw 1998; Bradshaw and Holmqvist 1999). A significant proportion of forests in Europe and North America are secondary forests that have developed on previously cleared lands (Peterken 1996; Gilliam 2007). Plant diversity in ancient forests often exceeds that of secondary forests and may continue to do so for hundreds of years (Peterken and Game 1984; Matlack 1994). The persistent differences in large part reflect the limited dispersal capabilities of many forest herbs (e.g. Matlack 1994; Hermy et al. 1999; Honnay et al. 2002; Hermy and Verheyen 2007). However, past deforestation and agricultural land-use can cause persistent soil changes (Kristiansen 2001; Dupouey et al. 2002; Dambrine et al. 2007), which may also contribute to the diversity and floristic differences between ancient and secondary forests (Honnay et al. 1999; Dupouey et al. 2002; Dambrine et al. 2007; but cf. Graae et al. 2004). Agricultural after-effects, legacy effects sensu Gilliam (2007), on plant species distributions may last >1,700 years (Dupouey et al. 2002; Dambrine et al. 2007). Although less studied, other aspects of past land-use than deforestation, notably past grazing practices, establishment of conifer plantations within broadleaved deciduous forests, artificial drainage and clear-felling of large stands, may also be important controls of understorey plant species distributions. For example, past grazing may have persistent effects due to slow recolonization by grazing-sensitive species (Brunet 1992).

The understorey is the most species-rich vegetation layer and an important ecological component of forest ecosystems (Gilliam 2007). The present study investigates the factors determining understorey species distributions, using a large Danish forest complex as a case study. In Denmark, forests have been strongly influenced by human land-use during the last 5,500 years (Nørrevang and Lundø 1980; Fritzbøger 1994; Bradshaw and Holmqvist 1999). In 1805 AD, unsustainable use had caused forest cover in Denmark to dwindle to 4%, but this has since increased to c. 11% due to protection and afforestation (Nørrevang and Lundø 1980; Fritzbøger 1994). During the last 200 years, most Danish forests have been subject to intense management by clear-felling, drainage and frequent conversion of broadleaved forest to plantations of introduced conifers (Nørrevang and Lundø 1980). Here, we use constrained ordinations, variation partitioning and indicator species analyses to evaluate the importance of anthropogenic historical factors as determinants of understorey species distributions in the broadleaved stands of a 967 ha forest complex in Denmark. We investigated five historical factors: (1) prehistoric forest clearance, as indicated by the occurrence of Bronze Age burial mounds with ancient forest; (2) historical forest continuity, as indicated by the contrast between ancient (1805 AD) high forest and younger forest; forest management, as represented by (3) the contrast between drained and afforested bogs and other forest; (4) the contrast between broadleaf-converted conifer plantations and other forest and (5) stand age. We asked the following specific questions: (1) what is the relative importance of the anthropogenic historical factors, modern environment and broadscale spatial factors, potentially reflecting unmeasured environmental variation or unknown historical effects, e.g. due to natural dispersal processes? (2) which of the anthropogenic historical factors affect modern distributions of understorey species in the forest complex?

Methods

Study area

The study area is the 967 ha Engestofte–Søholt forest complex (UTM coordinates: 663,100–667,800 E, 6,066,600–6,070,800 N) in south-eastern Denmark (Fig. 1). Annual precipitation is 600 mm and average January and July temperatures are −0.1 and 16.5°C, respectively (Laursen et al. 1999). The landscape is rather flat (maximum 30 m above sea-level), and soils are a mosaic of late-glacial moraine clay and moraine sand and 19th century alluvial sediments (Rasmussen 1966; Høy and Dahl 2000). The forest complex consists of nine more or less contiguous forests and is a mosaic of managed *Fagus sylvatica*- or, less commonly, *Quercus robur*-dominated forest, *Alnus glutinosa*-dominated swamps, mixed forests, part of which are left relatively unmanaged, conifer

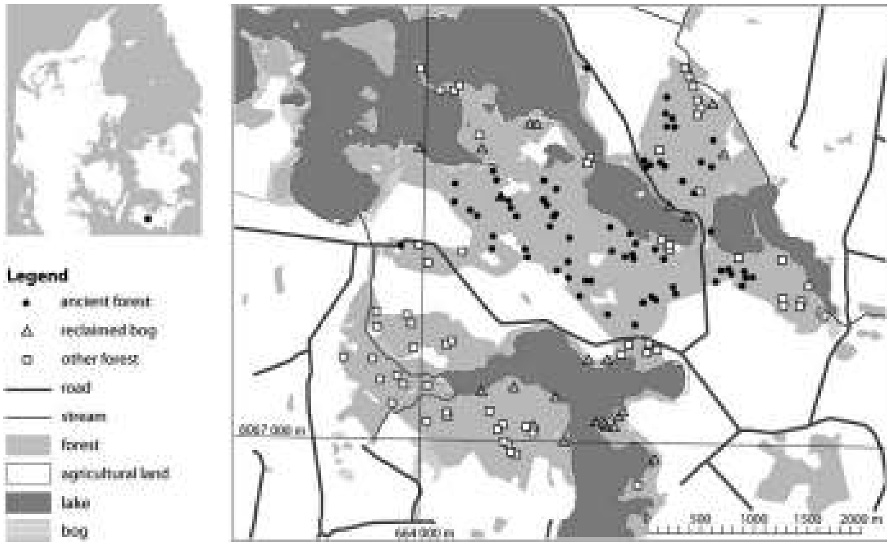

Fig. 1 Map of Denmark showing the study area in the south-eastern parts of the country. The larger map shows the forest complex of Engestofte–Søholt. The locations of the 156 study plots are shown, with symbols indicating whether they were located in ancient forest, on reclaimed bog, or elsewhere. The black triangle indicates one plot categorized both as reclaimed bog and ancient forest, probably reflecting the coarser resolution of the older maps used for the latter classification (see Methods)

plantations and open bogs. Large areas of the forest complex have been drained, and bogs and meadows have been afforested, partly with conifer plantations, during the last 200 years (cf. the historical maps discussed under *Methods: Explanatory variables*). The central-northern part contains 62 Bronze Age burial mounds dated to 1,500–800 BC (Henrik Schilling, Lolland-Falsters Stiftsmuseum, pers. comm., 2002). About half of the currently forested area was given status as protected high forest by the Forest Conservation Act in 1805 (Fritzbøger 1994). Much of the remaining area also had some degree of tree cover, but was not protected by law in 1805 mainly due to the degraded, patchy and scrubby nature of any forest vegetation present (Nørrevang and Lundø 1980; Fritzbøger 1994).

Understorey vegetation sampling

During July–October 2002, we inventoried vegetation and environmental descriptors in 156 sq. 10 × 10 m^2 macroplots placed throughout the study area using random coordinates, located using a Garmin eTrex Venture GPS (Garmin International, Kansas, USA). Sites on trails, below conifers, or in open areas (canopy openness >30%, see below) were not considered. During July–August 2002, all understorey species, i.e. species with potential height below 4 m, were recorded for each macroplot. Species frequencies were determined based on a 1 × 1 m^2 mesoplot placed at the centre of each macroplot; avoiding fallen trunks, stumps, large stones or large trees by moving the mesoplot to the northeast, if necessary. We used an Økland frame (Økland 1990), dividing the mesoplot into 16 microplots and recording the frequency of each species as the number of microplots in which it was rooted. In addition, understorey species present in the macroplot, but only outside the mesoplot, were given the frequency 0.1. Changing the value to 0.01 produced similar ordinations (results not shown). Plant nomenclature follows Hansen (1984). The species pairs, *Viola reichenbachiana* and *Viola riviniana*; and *Rubus fruticosus* agg. and *Rubus corylifolius* agg, were lumped as *Viola* sp. and *Rubus fruticosus*, respectively.

Explanatory variables

Five descriptors of past anthropogenic disturbance were derived for each macroplot based on historical maps. (1) Ancient forest: it was scored whether (1) or not (0), a macroplot was located in forest that was protected by the 1805 Forest Conservation Act, which protected contemporary high forest (Nørrevang and Lundø 1980; Fritzbøger 1994), according to the 1802–1815 Royal Danish Academy of Sciences and Letters maps (resolution slightly coarser than 1:20,000) available at the National Survey and Cadastre, Copenhagen, Denmark. The small Staverholm area was not covered by these maps, but since it is known as a traditional grazing area it was not scored as ancient forest. We note that the large majority of the younger forest areas were already afforested by the mid-1800s according to the 1842–1899 1:20,000 resolution General Staff's Topographic Department ordnance maps available at the National Survey and Cadastre. (2) Burial mounds: it was scored whether (1) or not (0), a macroplot was ≤100 m from a burial mound, as shown on the ordnance maps. Danish Bronze age burial mounds were located near settlements (Laursen 1994); hence, the surrounding area was most likely deforested at that time (1800–500 BC). (3) Reclaimed bog: it was scored whether (1) or not (0), a given macroplot was located in areas consisting largely of open bog according to the 1842–1899 ordnance maps, but now drained and forested. (4) Converted conifer plantation: we also assessed whether (1) or not (0), a macroplot was located in a conifer plantation according to the 1842–1899 ordnance maps, albeit it now has a broadleaved overstorey. (5) Stand age, computed from the year of establishment of the present tree stand according to stand-scale forestry maps made by Hedeselskabet, Viborg, Denmark in 1996.

Fifteen descriptors of the modern environment were also recorded for each macroplot. (1) Slope: the slope inclination measured by clinometer along the steepest diagonal of each macroplot. (2) Heat index: calculated as $\tan(\alpha_1) \times \cos(\alpha_2)$, where α_1 is the slope inclination and α_2 is the compass deviation from south-west (202.5°), the most favourable aspect for plant growth due to high incoming radiation at times of day with high temperatures (Lawesson et al. 2000). Based on one sample per mesoplot of the topmost 20 cm of soil taken using a 3-cm diameter auger, the soil type was described using indicator variables (McCune and Grace 2002) as (3) sandy, not possible to press the soil into a roll; (4) sandy–clay, the soil can be pressed together into a roll, but the roll disintegrates when rolled between ones palms; (5) clay, the soil can be made into a coherent roll or (6) organic, i.e. soils, which appear to be purely composed of organic material. The sandy–clay variable was chosen as the omitted category (McCune and Grace 2002). (8) Litter cover: scored as present (1) or absent (0) in each mesoplot in July–August. (7) Soil moisture: volumetric water content (%) was measured in each mesoplot at five random plots using a Theta probe type HH1 instrument (Thermo VG Scientific, East Grinstead, England) during September 27–30 after 1 month largely without rain. Values $> 60\%$ were truncated to 60% due to an apparent non-linearity in the measurements. The mean soil moisture per mesoplot was used in analyses after log transformation to reduce skewness. (9) Soil pH: measured in distilled water following Schierup and Jensen (1979) for one soil sample per mesoplot. Samples were collected September 27–30. (10) Canopy openness: estimated using a canopy-scope (Brown et al. 2000) 1.30 m above the centre of each mesoplot. Canopy openness was square-root transformed to reduce skewness. (11) Tree shade: based on the proportional tree species dominance in the canopy above each macroplot, a weighted shade score was computed based on Ellenberg's (1988) species-specific 'ability to produce shade' categories (very low = 1, low = 2, medium = 3, high = 4, and very high = 5). (12) Basal area: computed based on the diameter at 1.30 m above-ground (dbh) of all woody stems with dbh ≥ 1.0 cm rooted in the macroplot. (13) Stem density: the number of woody stems with dbh ≥ 1.0 cm rooted in the macroplot. Stem density was square-root transformed to reduce skewness. (14) Tree diversity: the number of tree species with stems with dbh ≥ 1.0 cm rooted in the macroplot. (15) Forest heterogeneity: estimated using the score system developed by Aude and Lawesson (1998): +1 for uprooted trees or left broken trees; +1 for branches on the forest floor; +1 for each number of woody stem diameter classes represented (0–5, 6–10, 11–20, 21–40, 41–60 and >60 cm); +2 for single trees >75 cm in diameter; +1 for big stones; −1 for trees in rows and −1 for being adjacent to conifer stands (our addition to emphasize natural structural heterogeneity). Understorey species were not considered.

To account for broad-scale spatial trends not accounted for by the historical and environmental descriptors, the nine terms of a cubic trend surface polynomial expansion (X, Y, X^2, Y^2, XY, X^3, Y^3, X^2Y and XY^2), where X and Y are the centred UTM coordinates, were used to derive as a set of spatial explanatory variables (Borcard et al. 1992).

Data analyses

We used unconstrained ordination to describe the main gradients in understory species composition across the 156 macroplots. The method employed was principal components analysis (PCA) on the Hellinger distance-transformed species data (Legendre and Gallagher

2001). This transformation allows species distribution data with many zeroes and non-linear species response curves to be analyzed by Euclidean-based ordination methods like PCA, which thereby offer an often preferable alternative to the chi-square distance-based correspondence analysis and its derivatives (Legendre and Gallagher 2001); notably, the Hellinger distance does not give rare species differential weighting. We used Wilcoxon rank sum chi-square approximation and Spearman rank correlation tests to test for relationships between the PCA axes and the explanatory variables. To directly assess the importance of the historical, environmental and spatial variables as controls of understorey species composition, linear redundancy analysis (RDA) was used, which can be viewed as the canonical extension of PCA with the ordination vectors being constrained by multiple regression to be linear combinations of the original explanatory variables (Legendre and Legendre 1998). By using the Hellinger distance transformation, RDA has the same advantages as described for PCA above. Furthermore, in contrast to the more frequently used canonical correspondence analysis RDA does not give sites with many species and individuals' higher weighting (Legendre and Gallagher 2001). Significance of the canonical models was tested using 9,999 unrestricted reduced-model permutations (ter Braak and Smilauer 2002). To provide an estimate of the best set of non-redundant variables for predicting species composition and to provide a ranking of the relative importance of the individual explanatory variable, we used forward selection of the explanatory variables in order of additional variance explained and tested by a permutation test (using 999 permutations) using *P*-to enter <0.05. We used RDA and partial RDA to partition the variation in the understory species distribution data into independent variation components (Borcard et al. 1992; Økland and Eilertsen 1994; Økland 1999) using all 28 explanatory variables. Following Økland (1999), the explained variation was expressed as fractions of the total variation explained (TVE) by the complete set of descriptors. The TVE was divided into seven non-overlapping fractions, viz. pure environmental, pure historical, pure spatial, mixed environmental–historical, mixed environmental–spatial, mixed historical–spatial and mixed environmental–historical–spatial. The pure fractions were computed using partial RDA, e.g. the pure historical fraction was computed from a partial RDA with the historical variables as explanatory variables and the environmental and spatial variables as co-variables. The mixed fractions were computed by subtraction and addition of the variation fractions produced by RDA and partial RDA of particular sets of explanatory and co-variables following Cushman and Wallin (2002). The unique importance of each single explanatory variable was assessed using partial RDA with all the other 27 variables set as co-variables. In addition, to further elucidate the historical influence a partial RDA with the historical factors as explanatory variables and the environmental variables as co-variables was also computed using the forward selection procedure described above. Since historical effects mediated by dispersal limitation are expected to be present in large part as broad- rather than fine-scale relationships with the causal historical factors (e.g. presence of ancient forest), we did not use the spatial variables as co-variables in this analysis, since this would remove the broad-scale component (Diniz-Filho et al. 2003). The PCA and RDAs were computed after centring, but not standardizing the species data table, i.e. on the covariance matrix (Legendre and Legendre 1998; McCune and Grace 2002). Indicator species analysis (Dufrêne and Legendre 1997) was used to pinpoint characteristic species for the categories of the historical factors found to have significant effects on understorey species composition according to the RDA. In addition to the original categories, we also derived new sets of categories for the historical factors based on the sample scores from final partial RDA model, with the historical factors as explanatory variables and the environmental variables as co-variables, to find characteristic species for the non-environmental historical legacies. CANOCO 4.5 was used for computing RDA and PCA (ter Braak and Smilauer 2002), while indicator species analysis was computed using PC-ORD, version 4 (McCune and Mefford 1999). All other analyses were done in JMP 4.0.4 (SAS Institute Inc., Cary, North Carolina, USA, 2001).

Results

In the 156 macroplots in the Engestofte–Søholt forest complex, we found 166 species of understorey plants, whereof 52 species (31%) were listed as ancient-forest species in Hermy et al. (1999). Understorey species richness per macroplots ranged 4–44. The most frequent species were *Melica uniflora* (109 macroplots), *Deschampsia caespitosa* (99), *Galium odoratum* (94), *Milium effusum* (92) and *Rubus idaeus* (86). Of the 166 understorey species, 26 (16%) were found in just a single macroplot. Among the macroplots, 70 macroplots were scored as ancient forest, 25 as $\leq$100 m from a burial mound, 23 as reclaimed bog, and 8 as converted conifer stands. The mean and median stand age was 71 and 65 years, respectively (range 10–144 years). There was no difference in stand age between ancient forest or reclaimed bogs and other forest (Wilcoxon rank sum chi-square approximation tests), while converted conifer stands had higher median stand age (88 years) than other forest (65 years; Wilcoxon rank sum chi-square approximation test, $P = 0.05$).

The first four axes of the PCA had eigenvalues accounting for 13.4%, 8.6%, 6.7% and 5.3% of the total variation, respectively. Among the historical variables, stand age did not correlate with the sample scores for the first four PCA axes (Spearman rank correlations, $P > 0.05$). However, Wilcoxon rank sum chi-square approximation tests indicated differences in PCA sample scores among plots that were or were not ancient forest (axis 1, $P < 0.0001$; axis 3, $P < 0.05$; axis 4, $P < 0.001$), reclaimed bog (axis 1, $P < 0.0001$; axis 3, $P < 0.05$; axis 4, $P < 0.05$), and $\leq$100 m from a burial mound (axis 1, $P < 0.05$), while there were no significant differences between plots that were or were not converted conifer plantations. The environmental variables with the strongest correlations with PCA axis 1 were soil pH ($r_s = 0.58$, $P < 0.0001$), forest heterogeneity ($r_s = 0.52$, $P < 0.0001$), tree diversity ($r_s = 0.44$, $P < 0.0001$), and tree shade ($r_s = -0.44$, $P < 0.0001$); with axis 2, slope ($r_s = 0.32$, $P < 0.0001$) and tree shade ($r_s = 0.31$, $P < 0.0001$); with axis 3, soil pH ($r_s = -0.32$, $P < 0.0001$) and with axis 4, stem density ($r_s = -0.28$, $P < 0.001$) and forest heterogeneity ($r_s = -0.25$, $P < 0.01$). Wilcoxon rank sum chi-square approximation tests also indicated differences in PCA sample scores among plots that had or had not organic soil (axes 1 and 3, $P < 0.05$), litter cover (axis 1, $P < 0.0001$; axis 1, $P < 0.05$). The spatial variable with the strongest correlations with PCA axis 1 was Y^2 ($r_s = 0.36$, $P < 0.0001$), with axis 3, X^2 ($r_s = 0.33$, $P < 0.0001$) and with axis 4, Y^2 ($r_s = 0.27$, $P < 0.001$). No spatial variables had $r_s \geq 0.20$ with axis 2.

The RDA using all 28 explanatory variables explained 32.4% of the total variation in understory species composition across the 156 macroplots (first canonical eigenvalue = 0.090, $P < 0.0001$; sum of all canonical eigenvalues = 0.324, $P < 0.0001$). Note that the sum of the eigenvalues equal the proportion of the TVE, since CANOCO sets the total variance = 1 in PCA and RDA (ter Braak and Smilauer 2002). After forward variable selection 15 of the 28 explanatory variables were included in the final model, which explained 24.9% of the total variation (Table 1; Figs. 2, 3). The three most important explanatory variables were the environmental variables soil pH and tree shade and the historical variable ancient forest (Table 1). Among the historical variables, reclaimed bog was also included in the final model, while stand age, converted conifer and burial mound were not (Table 1). From the RDA axes 1–2 biplot, it can seen that understorey species typical of ancient forest (notably *Lamiastrum galeobdolon*, *Melica uniflora*, *Poa nemoralis*, *Anemone nemorosa*, *Viola* sp. and *Galium odoratum*) also tended to be associated with shady, simply structured forest and relatively dry, acid soils with a thick litter layer, while those typical of reclaimed bogs (notably *Rubus caesius*, *Brachypodium sylvaticum*, *Eupatorium cannabinum*, *Lythrum salicaria* and *Rosa canina*) had the opposite associations (Fig. 2).

The RDA-based variation partitioning showed that the historical, environmental and spatial explanatory variable groups to a large extent had independent effects on understorey species composition (Table 2). While the component purely driven by modern environment was by far the largest, both the purely spatial and the purely historical components were also highly significant and of non-negligible size (Table 2). In a partial RDA with the five historical variables as explanatory variables and the 14 environmental variables as co-variables, the forward selection included first ancient forest (F-ratio = 3.65, $P = 0.001$) and then second and finally reclaimed bog (F-ratio = 2.26, $P = 0.001$). The resulting RDA model (first canonical eigenvalue = 0.020, $P < 0.0001$; sum of all canonical eigenvalues = 0.033, $P < 0.0001$) accounted for 13.3% of the variation explained by final model produced by forward selection among all 28 explanatory variables (Table 1). The species most strongly purely associated with ancient forest were *Carex sylvatica*, *Viola* sp., *Lamiastrum galeobdolon* and

Table 1 Redundancy analysis of understorey species composition in 156 100 m^2 macroplots in the Engestofte–Søholt forest complex, Denmark (first canonical eigenvalue $= 0.085$; F ratio $= 12.94$; $P = 0.0001$; sum of all canonical eigenvalues $= 0.249$; F ratio $= 3.09$; $P = 0.0001$)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.085	0.037	0.028	0.022
Species-explanatory variable correlations	0.809	0.709	0.664	0.717
Cumulative variance of species data (%)	8.5	12.1	14.9	17.1
Cumulative variance of species-explanatory variable relation (%)	34.0	48.8	59.9	68.8

Forward selection of variables	Extra fit	F ratio	*P*-enter
Soil pH	0.05	8.61	0.001
Tree shade	0.03	5.64	0.001
Ancient forest	0.02	4.12	0.001
Soil moisture	0.02	3.05	0.001
Slope	0.01	2.52	0.001
XY	0.01	2.44	0.001
Forest heterogeneity	0.01	2.27	0.001
Litter cover	0.01	2.19	0.003
X^2	0.01	2.18	0.001
X^3	0.01	1.76	0.006
Y^3	0.01	1.90	0.004
Reclaimed bog	0.01	1.61	0.033
Organic soil	0.01	1.71	0.015
Canopy openness	0.01	0.01	0.022
Y	0.01	1.63	0.020

Note that the sum of the eigenvalues equal the proportion of the total variation explained (ter Braak and Smilauer 2002). The results refer to the final model produced by forward variable selection with P-to enter < 0.05. The explanatory variables are listed with the extra amount of variance in the species data explained, F ratio, and P-value and sorted according to their order of selection

Anemone nemorosa; while those most associated with reclaimed bog were *Rubus caesius*, *Iris pseudacorus*, *Galium palustre*, *Potentilla reptans*, *Peucedanum palustre*, *Bromus ramosus*, *Fragaria vesca* and *Lysimachia thyrsiflora* (Fig. 4).

Indicator species analysis showed that 10 species were strong indicators of ancient forest, while 4 species were so for reclaimed bogs and none for other forest (Table 3a). Eight of the ten ancient-forest, but none of the reclaimed bog indicator species have also frequently been noted as associated with ancient forest in the literature (Table 3a). Three of the reclaimed bog indicators have high Ellenberg light values and two have high Ellenberg moisture values (Table 3a). To assess which species are indicative of ancient forest, reclaimed bog and other forest, when environmental differences are controlled for, we reclassified the macroplots according to their sample scores in the partial RDA with ancient forest and reclaimed bog as explanatory variables and the 14 environmental variables set as co-variables (Table 3b). The list of ancient forest indicators changed little, while just two species, neither with high Ellenberg moisture values, continued to be strong indicators of reclaimed bog, and two indicators (*Mercurialis perennis* and *Urtica dioica*) were added for other forest (Table 3b). We note that the latter two species were also associated with other forest before the reclassification, according to the RDA biplot (Fig. 2).

Discussion

Relative importance of history, modern environment and spatial location

The PCA-based results showed that the main gradients in understorey species composition in the Engestofte–

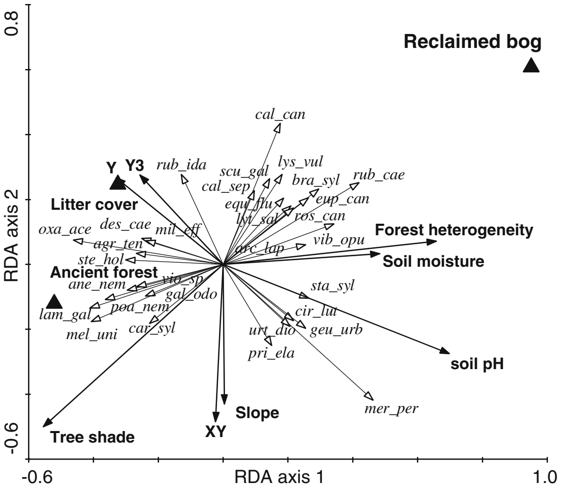

Fig. 2 Redundancy analysis of understorey species composition in 156 100-m^2 macroplots in the Engestofte–Søholt forest complex, Denmark: correlation biplot of the first and second axes. The final RDA model produced by forward variable selection is shown. Species with a fit range (% variation explained by the two ordination axes) between 0 and 5% were removed, as were explanatory variables with interset correlations between −0.2 and 0.2 (ter Braak and Smilauer 2002). Species acronyms are the first three letters of the genus followed by the first three letters of species epithet. Continuous explanatory variables are represented by arrows (indicating their direction of steepest increase), while binary variables are shown by symbols indicating their sample score centroid for samples with the value of 1 (ter Braak and Smilauer 2002)

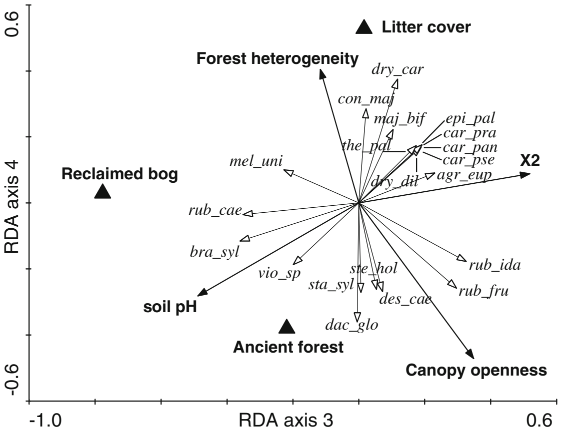

Fig. 3 Redundancy analysis of understorey species composition in 156 100-m^2 macroplots in the Engestofte–Søholt forest complex, Denmark: correlation biplot of the third and fourth axes. The final RDA model produced by forward variable selection is shown. See Fig. 2 for further details

Table 2 Partitioning of the variation in understorey species composition in 156 100-m^2 macroplots in the Engestofte–Søholt forest complex, Denmark into seven mutually exclusive fractions using RDA and partial RDA

Fractions	TVE (%)
Pure environment (E)	46.3****
Pure history (H)	13.0****
Pure space(S)	22.5****
Mixed E and H	2.2
Mixed E and S	6.8
Mixed H and S	3.1
Mixed E, H and S	6.5

**** $P \leq 0.0001$

All 14 environmental, 5 historical, and 9 spatial variables were used. The significance of the three pure fractions was assessed by partial RDA using 9,999 permutations. The total variation explained (TVE) is 32.4%

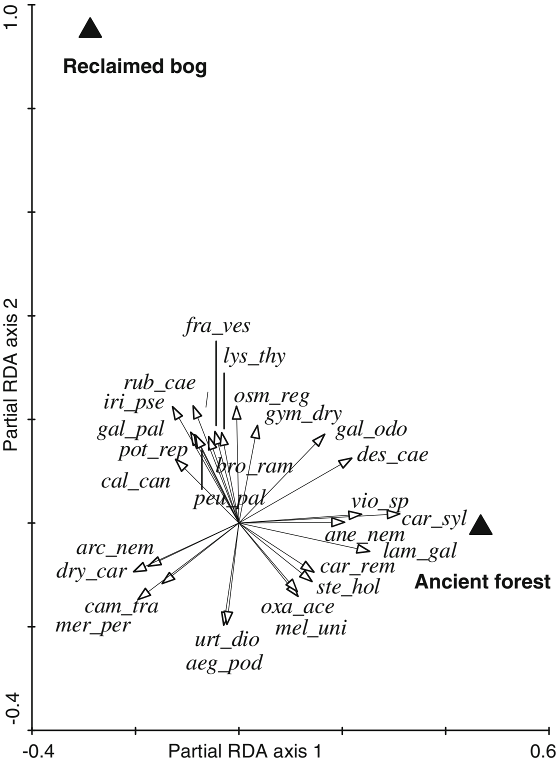

Fig. 4 Partial redundancy analysis of understorey species composition in 156 100-m^2 macroplots in the Engestofte–Søholt forest complex with ancient forest and reclaimed bog as explanatory variables and the 14 environmental set as covariables: correlation biplot of the first and second axes. Species with a fit range between 0% and 2% are not shown

Table 3 Indicator species analysis for (a) ancient forest (high forest in 1805 AD), reclaimed bog, and other forest, and (b) based on the sample scores from the partial RDA with ancient forest and reclaimed bog as explanatory variables and the 14 environmental variables set as covariables (Fig. 4)

(a) Ancient forest ($n = 69$)	Reclaimed bog ($n = 23$)	Other forest ($n = 64$)
Carex sylvatica (56.6****)[A]	*Rubus caesius* (43.0***)[L]	
Lamiastrum galeobdolon (53.6****)[A]	*Brachypodium sylvaticum* (42.7**)[a]	
Deschampsia caespitosa (47.0**)[L, M]	*Iris pseudacorus* (29.7***)[L, M]	
Melica uniflora (46.4**)[A]	*Calamagrostis canescens* (24.5*)[L, M]	
Oxalis acetosella (44.9**)[A]		
Stellaria holostea (44.0**)[A]		
Viola sp. (42.4**)[A]		
Anemone nemorosa (35.2**)[A]		
Poa nemoralis (29.4*)[a]		
Luzula pilosa (24.5*)[A]		

(b) “Pure” ancient forest ($n = 81$)	“Pure” reclaimed bog ($n = 35$)	Other forest ($n = 40$)
Lamiastrum galeobdolon (58.2****)[A]	*Rubus caesius* (38.1***)[L]	*Mercurialis perennis* (37.2****)[A]
Carex sylvatica (52.3****)[A]	*Brachypodium sylvaticum* (36.9**)[a]	*Urtica dioica* (34.1**)[M]
Melica uniflora (45.7**)[A]		
Galium odoratum (45.3**)[A]		
Oxalis acetosella (40.8**)[A]		
Deschampsia caespitosa (33.5*)[L, M]		
Stellaria holostea (43.2**)[A]		
Viola sp. (42.7***)[A]		
Anemone nemorosa (28.6*)[A]		

Following Fig. 4, “Pure” ancient forest are plots with positive axis 1 scores, while “Pure” reclaimed bog are plots with negative scores on axis 1 and positive scores on axis 2. Only species with indicator values ≥25% perfect indication at $P < 0.05$ (based on 9,999 Monte Carlo permutations) are shown

*$P < 0.05$

**$P < 0.01$

***$P < 0.001$

****$P \leq 0.0001$

[a] Listed as ancient-forest species in Hermy et al. (1999), but cited as such by <5 of the 22 publications considered by that study

[A] Listed as ancient-forest species by Hermy et al. (1999) and cited as such by ≥5 of the 22 publications considered

[L] Ellenberg light indicator value ≥6 (Ellenberg et al. 1992)

[M] Ellenberg moisture indicator value ≥6 (Ellenberg et al. 1992)

Søholt forest complex are strongly related to the environmental, historical, and spatial descriptors that were included in the study. The RDA forward selection results indicated that modern environment is most important, with four of the five first-selected variables being environmental (Table 1). The RDA-based variation partitioning further confirmed the dominant role played by modern environment as a driver of species distributions, with the pure environmental fraction, constituting nearly 50% of the TVE (Table 2). Hereby, our results agree with the many previous studies, which have shown modern environment to be a strong control of landscape- and local-scale understorey species distributions in temperate forests in Europe and North America (e.g. Motzkin et al. 1999; Svenning and Skov 2002; Gilbert and Lechowicz 2004; Graae et al. 2004; Borchsenius et al. 2004; Thomsen et al. 2005). Our results indicate that soil pH and tree shade, i.e. the extent to which the overstorey is dominated by heavily shade-producing trees, notably *Fagus sylvatica*, and soil moisture are the most important environmental drivers of understorey species distributions. The importance of soil pH and/or soil moisture is a frequent pattern at local and landscape scales in temperate forests (e.g. Motzkin et al. 1999; Richard et al. 2000; Verheyen and Hermy 2001a; Svenning and Skov 2002; Graae et al. 2004; Borchsenius et al. 2004; Windeballe et al. 2004; Thomsen et al. 2005). In the Engestofte–Søholt forest complex macroplots with a high tree shade value was generally dominated by *Fagus sylvatica*, which apart from producing heavy shade also produces acidic, nitrogen-poor litter (Ellenberg 1988; Neirynck et al. 2000; Hagen-Thorn et al. 2004). Previous studies have documented clear differences in understorey species composition between stands dominated by *Fagus sylvatica* and stands dominated by other tree species (e.g. Graae and Heskjær 1997; Svenning and Skov 2002; Graae et al. 2004). In temperate deciduous forests, overstorey tree species composition may be more important in managed forests, such as the Engestofte–Søholt complex, mainly composed of mono- and oligospecific stands (Svenning and Skov 2002) than in mixed-canopy natural forests (Thomsen et al. 2005).

While modern environment emerged as the dominant control of understorey species composition, two historical and five spatial variables were also included in the final RDA model produced by forward selection (Table 1). Notably, the historical variable ancient forest was the third explanatory selected by the forward selection procedure (Table 1). Furthermore, the RDA-based variation partitioning produced pure spatial and pure historical fractions that were also highly significant and non-negligible, constituting 23% and 13% of the TVE, respectively (Table 2). The spatial variables could reflect unmeasured broadscale variation in the modern environment or historical factors, e.g. natural dispersal-generated patterns reflecting internal landscape-scale dispersal dynamics (Svenning and Skov 2002; Miller et al. 2002) or regional-scale migration history (Popiela 2004; Van der Veken et al. 2007; Svenning et al. 2008).

Which historical factors are important?

The analyses of the PCA sample scores showed that ancient forest and reclaimed bog status were strongly associated with the main gradients in understorey species composition in the Engestofte–Søholt forest complex, while being near or far from burial mounds were of less importance, and neither stand age nor converted conifer plantation status were of any importance at all. These results were confirmed by the RDA (Table 1) and partial RDA analyses, in which only ancient forest and reclaimed bog were selected as significant, non-redundant predictors. Both analyses indicated ancient-forest status as more important than reclaimed bog status. In a similar vein, indicator species analysis showed that many more species were strong indicators of ancient forest than of reclaimed bog (Table 3).

The fact that eight of the ten ancient-forest indicators (Table 3) have frequently been reported as associated with ancient forest in earlier publications (Hermy et al. 1999) provide strong external support for the interpretation of the ancient-forest effect as a being to a large extent a historical legacy effect (Gilliam 2007). The variation partitioning shows that the historical effect on species compositions consists of a pure fraction of 13% TVE and three mixed fractions of totalling 12% TVE, hereof nearly 9% involving modern environment (Table 2). These mixed historical–environmental (–spatial) fractions may reflect persistent environmental changes induced by past history. A number of studies have shown that past land-use can cause edaphic changes that persist hundreds or even >1,000 years after reforestation has taken place (Kristiansen 2001; Dupouey et al. 2002; Dambrine et al. 2007; also cf. Brunet 2007). Furthermore, past land-use may cause long-term changes in overstorey tree species composition (Peterken 1996; Motzkin et al. 1999; Bellemare et al. 2002), which again may induce soil changes (Ellenberg 1988; Neirynck et al. 2000; Hagen-Thorn et al. 2004). However, the large pure historical fraction of the variation in species composition is suggestive of purely population dynamic legacies. The association of a number of well-known ancient-forest species with areas of ancient forest, i.e. 1,805 high forest, even when environmental factors are controlled for (Table 3b), is also suggestive of dispersal limitation. Dispersal limitation has been shown by many studies to pose a strong constraint on the rate at which understorey plants recolonize secondary forest (e.g. Peterken and Game 1984; Matlack 1994; Honnay et al. 2002; Bellemare et al. 2002; Gilliam 2007) and a recent review concluded that dispersal of diaspores appears to be the most critical step in the colonization of young forests by ancient-forest plant species (Hermy and Verheyen 2007). Furthermore, except for two species (*Galium odoratum*, *Poa nemoralis*) all the ancient-forest indicators in the present study have dispersal modes (myrmeco-, baro- or autochory) associated with slow recolonization rates of secondary forests (Matlack 1994; Brunet and von Oheimb 1998; Bossuyt et al. 1999; Bellemare et al. 2002; Brunet 2007) and particularly aggregated distributions within older forests (Svenning and Skov 2002; Miller et al. 2002).

The RDA and partial RDA results suggest that reclaimed bogs differ from other plots in understorey species composition beyond what can be explained by modern environment (Table 1; Figs. 2, 4). Overall, the species associated with the reclaimed bog plots after controlling for modern environment are a mixture of wet-soil and high-light species (Fig. 4). Considering the reclaimed bog indicator species, the wet-soil species *Iris pseudacorus* and *Calamagrostis canescens* could be interpreted as evidence that plots on reclaimed bog still somehow differ hydrologically from other plots (Table 3a). However, among the only two strong indicator species remaining after controlling for modern environment (Table 3b), *Rubus caesius* has no specific soil moisture preferences and *Brachypodium sylvaticum* prefers fresh, but not wet soils (Ellenberg moisture value = 5), just as most of the ancient-forest indicators in Table 3 (Ellenberg et al. 1992). Hence, it seems likely that at least part of the reclaimed bog effect reflect a non-environmental historical legacy. *Rubus caesius*, but not *Brachypodium sylvaticum* has relatively high-light requirements (Ellenberg et al. 1992). It is noteworthy that both species are likely to have relatively efficient dispersal, being endo- and epizoochorously dispersed by vertebrates, respectively (Hodgson et al. 1995; Hermy et al. 1999) and are therefore expected to be relatively fast colonizers of secondary forests (Brunet 2007). The abundance of *Brachypodium sylvaticum* is consistent with opportunistic expansion in the absence of more slowly dispersing competitors, while the abundance of *Rubus caesius* and other high-light species (Fig. 4) could reflect either opportunistically expanding populations or remnant populations, (Eriksson 1996) slowly declining after the initially open conditions. In a Swedish study, *Brachypodium sylvaticum* was similarly found to be more abundant in plantations adjacent to ancient forest than in the latter itself (Brunet 2007). The association of a number of wet-soil plants with reclaimed bog even after controlling for modern environment (Fig. 4) could also reflect their persistence in formerly wet areas as remnant populations (Eriksson 1996). Considering the two indicator species of the other young forests, i.e. forests that were neither bogs nor high forest in the early 1800s, *Urtica dioica* is well known to be favoured by anthropogenic disturbance (e.g. Bossuyt et al. 1999; Verheyen and Hermy 2001b), while *Mercurialis perennis* has often been found to be associated with ancient forest (Hermy et al. 1999). However, in England *Mercurialis perennis* has been shown to have rather efficiently recolonized 19th century secondary forests within 0.5 km of ancient-forest source populations (Peterken and Game 1981) and to be less constrained to ancient forests than many other ancient-forest species (Peterken and Game 1984). Notably, in the latter study *Mercurialis perennis* had only 54% of its localities in ancient woods, while the 10 ancient forest indicator species in Table 3 that are also listed as such in Hermy et al. (1999) had 58–97% (mean = 80%) of their localities in ancient woods. Furthermore, *Mercurialis perennis* may sometimes even occur in tall-herb and grassland vegetation (Jefferson 2008), so it may well have been present outside the high-forest areas in 1805. Although the abundance of *Urtica dioica* could reflect soil changes not captured by our environmental descriptors (notably phosphate enrichment: Pigott 1971; Verheyen and Hermy 2001b), the abundance of *Mercurialis perennis* is more suggestive of opportunistic expansion, as discussed for *Brachypodium sylvaticum*. Most of the other species associated with other forest according to the RDA biplots (Figs. 2, 4) are species with relatively good dispersal abilities, being epizoochorous (*Arctium nemorosum*, *Circaea lutetiana*, *Geum urbanum*, *Stachys sylvatica*) or having tiny wind-dispersed spores (*Dryopteris carthusiana*). Several previous studies have also found forest species with dispersal modes indicative of good dispersal abilities to be overrepresented in young forests (e.g. Matlack 1994, Brunet 2007).

While modern understorey plant species distributions have sometimes been linked to land-use >1,500 years back, no unique effect of being located in the vicinity of Bronze Age burial mounds was detected. This contrasts the evidence for persistent floristic effects on Roman agriculture on the understory vegetation in French forests, 1,700 years or more post-abandonment (Dupouey et al. 2002; Dambrine et al. 2007). Plausible explanations for these discrepancies include that later anthropogenic disturbances in the Danish study area erased all Bronze Age legacies, that the 2,500 years elapsed since the Bronze Age have been long enough to allow complete recolonization or, more generally, for any legacies to persist, or that the Bronze Age disturbances in Denmark were of much milder than the Roman agricultural impacts in France. While pre-1800 forest management clearly has strong impacts on the understorey species composition via its effects on modern environment (tree stand structure and composition, edaphic conditions), only artificial drainage, but neither stand age or the past presence of conifer plantations had any effect. Apparently these forestry-related disturbances have not been severe enough to produce persistent changes in the understorey species composition, as also found for stand age in another Danish forest area (Svenning and Skov 2002). Similarly, although some North American studies have suggested that there are long-term forestry-induced legacy effects, these results have been questioned and conflicting patterns have been found, causing a recent review to conclude that more research is needed to clarify this issue (Roberts and Gilliam 2003).

Concluding remarks

Our results emphasize the importance of historical factors and associated legacy effects for understanding modern vegetation patterns in forested landscapes. While modern environment is the main determinant of understorey species distributions in Engestofte–Søholt forest complex, past land-use also continues to exert important influence. Hereby, our study adds to the previous studies that have shown past land-use to be an important determinant of understorey plant species community composition and diversity in temperate forests of Europe and North America (reviewed in Hermy and Verheyen (2007) and Gilliam (2007)) and other forest ecosystems and regions, e.g. Central American tropical forest (Svenning et al. 2004). The Engestofte–Søholt forests have, as the large majority of Danish forests, been strongly affected by modern forestry. Nevertheless, the strong historical legacies found relate more to long-term forest continuity than to forest management. Many typical forest interior species were still concentrated in areas that were high forest in 1805 AD, probably in large part due to dispersal limitation, despite the fact that most of the areas studied were already afforested by the mid-1800s. Among the younger forests, there were clear floristic differences between those on artificially drained bogs and those not. Both included understorey species capable of relatively efficient recolonization, but apparently remnant populations of wet-soil plants were still present in the reclaimed bog areas, too. The observation that strong effects of past deforestation on the understorey vegetation can persist for several hundred years even within contiguous forests emphasises the conservation value of ancient forests.

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References

Aude E, Lawesson J (1998) Vegetation in Danish beech forests: the importance of soil, microclimate and management factors, evaluated by variance partitioning. Plant Ecol 134: 53–65. doi:10.1023/A:1009720206762

Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects in rich mesic forests. J Biogeogr 29:1401–1420. doi:10.1046/j.1365-2699.2002.00762.x

Björse G, Bradshaw R (1998) 2000 years of forest dynamics in southern Sweden: suggestions for forest management. For Ecol Manage 104:15–26

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecol 73:1045–1055. doi:10.2307/1940179

Borchsenius F, Nielsen PK, Lawesson JE (2004) Vegetation structure and diversity of an ancient temperate deciduous forest in SW Denmark. Plant Ecol 175:121–135. doi:10.1023/B:VEGE.0000048095.29961.c5

Bossuyt B, Hermy M, Deckers J (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. J Ecol 87:628–638. doi:10.1046/j.1365-2745.1999.00379.x

Bradshaw R, Holmqvist BH (1999) Danish forest development during the last 3000 years reconstructed from regional pollen data. Ecography 22:53–62. doi:10.1111/j.1600-0587.1999.tb00454.x

Brown N, Jennings S, Wheeler P, Nabe-Nielsen J (2000) An improved method for the rapid assessment of forest understorey light environments. J Appl Ecol 37:1044–1053. doi:10.1046/j.1365-2664.2000.00573.x

Brunet J (1992) Impact of grazing on the field layer vegetation in a mixed oak forest in south Sweden. Sven Bot Tidskr 86:347–353

Brunet J (2007) Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. J Appl Ecol 44:563–572. doi:10.1111/j.1365-2664.2007.01297.x

Brunet J, von Oheimb G (1998) Migration of vascular plants to secondary woodlands in southern Sweden. J Ecol 86:429–438. doi:10.1046/j.1365-2745.1998.00269.x

Cushman SA, Wallin DO (2002) Separating the effects of environmental, spatial and disturbance factors on forest community structure in the Russian Far East. For Ecol Manage 168:201–215

Dambrine E, Dupoey JL, Laüt L, Humbert L, Thinon M, Beaufils T, Richard H (2007) Present forest biodiversity patterns in France related to former Roman agriculture. Ecology 88:1430–1439. doi:10.1890/05-1314

Diniz-Filho JAF, Bini LM, Hawkins BA (2003) Spatial autocorrelation and red herrings in geographical ecology. Glob Ecol Biogeogr 12:53–64. doi:10.1046/j.1466-822X.2003.00322.x

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. Ecology 83:2978–2984

Dupré C, Ehrlén J (2002) Habitat configuration, species traits and plant distributions. J Ecol 90:796–805. doi:10.1046/j.1365-2745.2002.00717.x

Ellenberg H (1988) Vegetation ecology of Central Europe. Cambridge University Press, Cambridge

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18, 2nd edn. Verlag Eich Goltze KG, Göttingen

Eriksson O (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77:248–258. doi:10.2307/3546063

Fritzbøger B (1994) Kulturskoven: Dansk skovbrug fra oldtid til nutid. Gyldendal, Copenhagen

Gilbert B, Lechowicz MJ (2004) Neutrality, niches, and dispersal in a temperate forest understory. Proc Natl Acad Sci USA 101:7651–7656. doi:10.1073/pnas.0400814101

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845–858. doi:10.1641/B571007

Graae BJ, Heskjær VS (1997) A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark. For Ecol Manage 96:111–123

Graae BJ, Økland RH, Petersen PM, Jensen K, Fritzbøger B (2004) Influence of historical, geographical and environmental variables on understorey composition and richness in Danish forests. J Veg Sci 15:465–474. doi:10.1658/1100-9233(2004)015[0465:IOHGAE]2.0.CO;2

Hagen-Thorn A, Callesen I, Armolaitis K, Nihlgard B (2004) The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. For Ecol Manage 195:373–384

Hansen K (ed) (1984) Dansk Feltflora. Nordisk Forlag, Copenhagen

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson J (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol Conserv 91:9–22. doi:10.1016/S0006-3207(99)00045-2

Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecol Res 22:361–371. doi:10.1007/s11284-007-0354-3

Hodgson JG, Grime JP, Hunt R, Thompson K (1995) The electronic comparative plant ecology. Chapman & Hall, London

Honnay O, Hermy M, Coppin P (1999) Impact of habitat quality on forest plant species colonization. For Ecol Manage 115:157–170

Honnay O, Verheyen K, Butaye J, Jacquemyn H, Bossuyt B, Hermy M (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecol Lett 5:525–530. doi:10.1046/j.1461-0248.2002.00346.x

Høy T, Dahl J (2000) Danmarks søer—søerne i Storstrøms Amt og på Bornholm. Strandbergs Forlag, Birkerød

Jefferson RG (2008) Biological flora of the British Isles: *Mercurialis perennis* L. J Ecol 96:386–412. doi:10.1111/j.1365-2745.2007.01348.x

Kristiansen SM (2001) Present-day soil distribution explained by prehistoric land-use: Podzol–Arenosol variation in an ancient woodland in Denmark. Geoderma 103:273–289. doi:10.1016/S0016-7061(01)00044-1

Laursen J (1994) Historien i skoven—skove og fortidsminder i Århus Amt. Skippershoved, Århus Amtsmuseumsråd

Lawesson JE, Eilertsen O, Diekmann M, Reinikainen A, Gunnlaugsdóttir E, Fossa AM, Carøe I, Skov F, Groom G, Økland T, Økland R, Andersen PN, Bakkestuen V (2000) A concept for vegetation studies and monitoring in the Nordic countries. TemaNord 2000: 517. Nordic Council of Ministers, Copenhagen

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280. doi:10.1007/s004420100716

Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier, Amsterdam

Matlack GR (1994) Plant species migration in a mixed-history forest landscape in eastern North America. Ecol 75:1491–1502. doi:10.2307/1937472

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon

McCune B, Mefford MJ (1999) PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon

Miller TF, Mladenoff DJ, Clayton MK (2002) Old-growth northern hardwood forests: spatial autocorrelation and patterns of understory vegetation. Ecol Monogr 72:487–503

Motzkin G, Wilson P, Foster DR, Allen A (1999) Vegetation patterns in heterogenous landscapes: the importance of history and environment. J Veg Sci 10:903–920. doi: 10.2307/3237315

Neirynck J, Mirtcheva S, Sioen G, Lust N (2000) Impact of *Tilia platyphyllos* Scop., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Quercus robur* L. and *Fagus sylvatica* L. on earthworm biomass and physico-chemical properties of a loamy topsoil. For Ecol Manage 133:275–286

Nørrevang A, Lundø J (eds) (1980) Danmarks natur 6: Skovene. Politikens Forlag, Copenhagen

Økland RH (1990) Vegetation ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia Supplement 1:1–233

Økland RH (1999) On the variation explained by ordination and constrained ordination axes. J Veg Sci 10:131–136. doi:10.2307/3237168

Økland RH, Eilertsen O (1994) Canonical correspondence analysis with variation partitioning: some comments and an application. J Veg Sci 5:117–126. doi:10.2307/3235645

Peterken GF (1996) Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge

Peterken GF, Game M (1981) Historical factors affecting the distribution of *Mercurialis perennis* in Central Lincolnshire. J Ecol 69:781–796. doi:10.2307/2259636

Peterken GF, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. J Ecol 72:155–182. doi:10.2307/2260011

Pigott CD (1971) Analysis of the response of *Urtica dioica* to phosphate. New Phytol 70:953–966. doi:10.1111/j.1469-8137.1971.tb02597.x

Popiela A (2004) Phytogeographic aspects of the occurrence of forest vascular plant species in Pomerania (northwest Poland). Bot Jahrb Syst Pflanzengesch Pflanzengeogr 125:97–228. doi:10.1127/0006-8152/2004/0125-0097

Rasmussen HW (1966) Danmarks geologi. Gjellerup, Tønder

Richard M, Bernhardt T, Bell G (2000) Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest. Ecography 23:231–245. doi:10.1111/j.1600-0587.2000.tb00279.x

Roberts MR, Gilliam FS (2003) Response of the herbaceous layer to disturbance in eastern forests. In: Gilliam FS, Roberts MR (eds) The herbaceous layer in forests of eastern North America. Oxford University Press, Oxford, pp 302–320

Schierup H-H, Jensen A (1979) Vejledning i kemisk og fysisk analyse af jordprøver og plantemateriale. Botanical Institute, Aarhus University, Aarhus

Svenning J-C, Kinner DA, Stallard RF, Engelbrecht BMJ, Wright SJ (2004) Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85:2526–2538. doi:10.1890/03-0396

Svenning J-C, Normand S, Skov F (2008) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. Ecography 31:316–326. doi:10.1111/j.0906-7590.2008.05206.x

Svenning J-C, Skov F (2002) Mesoscale distribution of understorey plants in temperate forest (Kalø, Denmark): the importance of environment and dispersal. Plant Ecol 160:169–185. doi:10.1023/A:1015885321263

ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York

Thomsen RP, Svenning J-C, Balslev H (2005) Overstorey control of understorey species composition in a near-natural temperate broadleaved forest in Denmark. Plant Ecol 181:113–126. doi:10.1007/s11258-005-3996-7

Van der Veken S, Rogister J, Verheyen K, Hermy M, Nathan R (2007) Over the (range) edge: a 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. J Ecol 95:343–351. doi:10.1111/j.1365-2745.2006.01208.x

Verheyen K, Hermy M (2001a) The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. J Ecol 89:829–840. doi:10.1046/j.0022-0477.2001.00596.x

Verheyen K, Hermy M (2001b) An integrated analysis of the spatio-temporal colonization patterns of forest plant species. J Veg Sci 12:567–578. doi:10.2307/3237008

Windeballe BS, Svenning J-C, Balslev H (2004) The influence of past land-use on understory plant distributions in a near-natural deciduous forest in Denmark. Nord J Bot 23:69–81. doi:10.1111/j.1756-1051.2003.tb00370.x

Short-term responses of the understory to the removal of plant functional groups in the cold-temperate deciduous forest

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Abstract It is widely believed that functional diversity contributes to the stability of ecosystems. Indeed, greater redundancy among species within functional groups and greater complementarity among functional groups within communities should increase the resistance and resilience of ecosystems. In the present study, we tested for functional group complementarity by examining how the loss of specific functional groups may alter the role that other groups play in ecosystem functions. We removed different functional groups, one at a time, from the understory of three maple-dominated forests in southern Québec (Canada) and followed the understory response over a 2-year period. The experimental design included a control and five removal treatments. Five functional groups were defined: spring-flowering ephemeral species; spring-flowering persistent species; summer-flowering species; fern species; and seedlings and juveniles of woody species. Richness, cover, soil pH and organic matter content were determined after two years of removal. The results of our experiment revealed that richness was significantly lower than what we expected when spring-flowering persistent species or seedlings and juveniles of woody species were removed, suggesting not only *direct* but also *indirect* positive effects of both of these groups on understory richness (mostly through effects on summer-flowering species and fern species). Removal of the seedlings and juveniles of woody species and, to a lesser extent, of spring-flowering persistent species and of fern species lead to a decrease in the cover of summer-flowering species, implying a positive effect of the former groups on the latter. The cover–richness relationship in the control and in each one of the five removal treatments was positive and well fitted by a linear regression. Yet, the slope of the relationship differed *among* treatments, but not *between* the control and any one of the removal treatments (pair-wise comparisons). Our results suggest that the different functional groups are complementary and that positive interactions predominate over negative ones. Contrary to common belief, understory plants can respond quite rapidly to changes in community functional composition. Although we have not investigated the specific mechanisms responsible for the short-term responses reported here, we suggest that complex intergroup interactions may favour functional diversity and enhance ecosystem functions.

Keywords Cold-temperate deciduous forest · Complementarity · Cover-richness relationship · Experimental removal · Functional diversity · Functional group · Interdependence · Understory

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Introduction

Species that share physiological, morphological and/or phenological characteristics form distinct functional groups (Naeem et al. 1999) and, within such groups, species can be said to be functionally redundant. Indeed, the loss of one or a few species within a given group can be compensated for by other functionally similar species (Wardle et al. 1999); as a result, ecosystem functions can be maintained because of such functional redundancy (but see Balvanera et al. 2006).

Because of their distinct physiological, morphological and/or phenological characteristics, functional groups can partition resources among themselves (Fitter 1982; Hooper et al. 2002); such resource partitioning may contribute to reduce competitive exclusion (Cardinale et al. 2000) and increase overall ecosystem functions (Tilman 1997). However, the loss of a given functional group can have negative effects on an ecosystem and may even lead to a slowing down or a collapse in its functioning (Loreau et al. 2001). While trying to determine the consequences of the loss of groups of species on the functioning of ecosystems, several studies have shown two contrasted properties of functional groups: complementarity (i.e. positive intergroup interactions) and dominance (i.e. negative intergroup interactions; Naeem et al. 1999; Wardle et al. 1999; Cardinale et al. 2000; Díaz and Cabido 2001). These two properties are believed to be largely responsible for the specific form of the relationship between diversity and production (Grime 1973, 1977; Mittelbach et al. 2001; Tilman et al. 2002; Symstad et al. 2003). However, complementarity and dominance are not necessarily opposing properties: some functional groups may be complementary and particular subsets of complementary species may still be dominant over others (Loreau et al. 2001; Fox 2005).

Many papers, both empirical and theoretical, have reported that a decrease of diversity can alter ecosystem properties and functions (Naeem et al. 1995; Wardle et al. 1999; Loreau et al. 2001; Lepš 2004). Several empirical studies on this subject have been performed under controlled conditions, with synthetic, simplified assemblages (Tilman et al. 1997; Symstad et al. 1998; Hector et al. 1999; Naeem 2001; Hooper et al. 2002). In these, diversity was manipulated (independent variable) and ecosystem response was measured through changes in primary production. From their review of the literature on the subject, Loreau et al. (2001) concluded that the relationship between diversity and ecosystem functions could be shown under "natural" conditions using two types of approach: (1) an experimental approach, e.g. one in which species or groups of species are removed, and (2) a comparative approach, e.g. one in which variation in factors other than diversity is controlled for (Huston 1997; Wardle et al. 1999; Troumbis and Memtsas 2000; Buonopane et al. 2005).

In the present study, we use an experimental approach, based on the removal of groups of functionally similar species, to better understand the relationship between functional diversity and ecosystem functioning. Our objective is to determine how the loss of functionally similar species can affect the properties of the understory, in three deciduous forests of southern Québec (Canada). Our study is based on the premise that both positive and negative intergroup interactions may be present and that the loss of a given group may have significant effects on the other groups and on understory production.

Material and methods

Study site

The experiment was conducted in three forest fragments of the Bois-Francs region, two at Saint-Grégoire (46°17.820′ N, 72°30.740′ W; 46°17.525′ N, 72°31.076′ W) and one at Sainte-Françoise (46°29.341′ N, 71°56.156′ W), on the south shore of the St. Lawrence River, between Trois-Rivières and Quebec City (Québec, Canada). The dominant tree species is sugar maple (*Acer saccharum* Marsh.), along with American beech (*Fagus grandifolia* Ehrh.), American linden (*Tilia americana* L.), American hop-hornbeam [*Ostrya virginiana* (Mill.) K. Koch], yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* L.) and balsam fir (*Abies balsamea* L.). The region is part of the Great Lakes–St. Lawrence forest region of Rowe (1972), subsections Mid St. Lawrence (L-2) and High St. Lawrence (L-3).

At the nearby Trois-Rivières and Quebec City weather stations, annual precipitation totals 1100 mm (24% as snow) and 1230 mm (38% as snow), respectively, and annual mean daily temperature is 4.9°C and 4.0°C, respectively (URL: www.climate.weatheroffice.ec.gc.ca). The soils of the region are mostly brunisols except in low areas that are characterized by gleysols (Choinière and Laplante 1948).

All three forests have been lightly managed for sap over several years, although one of the sites at Saint-Grégoire is protected by the Québec government and has not been exploited since at least 1975. The size of the larger trees on the different sites suggest a minimum stand age of ~200 years (old, second-growth stands). Site selection was based on the following criteria: relatively uniform topographical features; easy road access; plant species richness representative of the region; different plant functional groups present; permission (from the owners or the Québec government) to carry out the experiment.

Sampling protocol and variables measured

In the spring of 2003, we established 30 2 m × 2 m quadrats at each one of the three study sites. Within sites, quadrats were positioned under homogeneous canopy composition and microtopography. Species richness was determined for each quadrat at three different times during the growing season (spring, summer and fall) and assigned to one of five functional groups, based on flowering period and growth form (Bratton 1976): spring-flowering ephemeral species, e.g. *Erythronium americanum* Ker-Gawl.; spring-flowering persistent species, e.g. *Trillium erectum* L.; summer-flowering species, e.g. *Epipactis helleborine* (L.) Crantz; ferns, e.g. *Dryopteris spinulosa* (O.F. Muell.) Watt; seedlings and juveniles of woody species, e.g. *Acer saccharum* Marsh. (nomenclature follows Marie-Victorin 2002).

We considered spring-flowering ephemeral species separately from spring-flowering persistent species because of the important role that they play in the nutrient dynamics of deciduous forests. Indeed, spring-flowering ephemeral species are believed to store in their tissues the nutrients flushed into the system during snowmelt and to release them progressively as they senesce (vernal dam hypothesis: Muller and Bormann 1976; Eickmeier and Schussler 1993; Tessier and Raynal 2003). The interest in considering fern species and seedlings and juveniles of woody species comes from the significant role that they play in primary production and in competition in the forest understory. Grasses and sedges were not abundant on the study sites and were included in the summer-flowering species.

For the experiment, we chose 18 quadrats per site, the most similar in terms of species richness and microtopography, among the 30 initially marked. Within sites, quadrats were grouped in three blocks on the basis of their spatial proximity. Treatments were assigned randomly to the quadrats within each block and were as follows: control; removal of spring-flowering ephemeral species; removal of spring-flowering persistent species; removal of summer-flowering species; removal of fern species; removal of seedlings and juveniles of woody species. Only aboveground parts were removed so as to avoid soil disturbance. Removals took place twice monthly, between May and August, in 2004 and again in 2005.

We are aware that the persistence of underground structures (bulbs, rhizomes or corms) and an increase in the decomposition of roots following the removal of aboveground parts may influence the responses to our treatments. However, the method we used is common in the literature and offers the advantage of avoiding the confounding effects of soil disturbance to species removals (Wardle et al. 1999; Buonopane et al. 2005; Wardle and Zackrisson 2005).

Biological variables

Floristic surveys (vascular plants <1 m in height) were done three times in 2005 on the experimental quadrats: in early May, in mid-July, and at the end of August. Each 4 m^2 quadrat was divided into two sections: a 20 cm buffer zone was established at the periphery of each quadrat to avoid trampling effects and no data were collected from this section; the central section of each quadrat (1.60 m × 1.60 m) was divided into 256 plots of 100 cm^2 each and the species present in each plot (there could be more than one species) were recorded.

Species-specific cover values for each quadrat were estimated as the frequency of 100 cm^2 plots, over 256, in which a given species was present. As three surveys were done in 2005, the maximum species-specific cover value was used to estimate the annual production of each species. Annual production per functional group was calculated as the sum of the maximum species-specific cover values for each

Table 1 F- and *P*-values (in parentheses) from the ANOVAs for the effects of site (df = 2), treatment (*df = 5; otherwise, df = 4) and their interaction (*df = 10; otherwise, df = 8) on the variables studied

Variables	Effects		
	Site	Treatment	Site × treatment
Richness (all functional groups)*	**189.16** (**<0.001**)	**5.92** (**<0.001**)	1.52 (0.181)
Richness of spring-flowering ephemeral species	4.27 (0.070)	0.28 (0.884)	1.35 (0.264)
Richness of spring-flowering persistent species	**62.60** (**<0.001**)	0.77 (0.556)	**3.20** (**0.013**)
Richness of summer-flowering species	**30.05** (**<0.001**)	2.64 (0.058)	2.26 (0.058)
Richness of fern species	**25.55** (**0.001**)	1.34 (0.286)	0.58 (0.779)
Richness of seedlings and juveniles of woody species	**10.55** (**0.011**)	0.53 (0.713)	0.99 (0.468)
Cover (all functional groups)*	**50.08** (**<0.001**)	**2.89** (**0.030**)	1.20 (0.327)
Cover of spring-flowering ephemeral species	**6.15** (**0.035**)	0.31 (0.864)	0.53 (0.823)
Cover of spring-flowering persistent species	**47.53** (**<0.001**)	0.48 (0.746)	0.40 (0.909)
Cover of summer-flowering species	4.05 (0.071)	**2.81** (**0.048**)	**2.42** (**0.045**)
Cover of fern species	**24.33** (**<0.001**)	1.37 (0.273)	2.02 (0.087)
Cover of seedlings and juveniles of woody species	**29.17** (**<0.001**)	0.82 (0.519)	0.74 (0.655)
Soil pH*	**5.92** (**0.038**)	1.53 (0.210)	1.00 (0.460)
Soil organic matter content*	5.11 (0.051)	1.30 (0.289)	0.44 (0.910)

Significant values are in boldface characters

quadrat. Species richness per functional group was also determined for each quadrat.

Environmental variables

In July 2005, four soil samples (each of 90.75 cm^3, to a depth of 10 cm) were collected in each quadrat. All samples were collected after a period of 2–3 days without rain. In the laboratory, each sample was passed through a 2-mm-mesh sieve to remove roots, twigs and stones, and then dried for 24 h at 75°C. Soil pH was measured in a 1:1 soil:water solution. Soil organic matter (a good surrogate of soil fertility in deciduous forests) was estimated as percent mass loss on ignition (10 ml of soil at 450°C for 5 h). For each one of these environmental variables, an average value was calculated for each quadrat and used for the statistical analyses.

Data analysis

The experimental design was made up of six treatments per block, three blocks per site, and three sites. The sources of variation of interest were sites (random, df = 2), blocks within sites (random, df = 6), treatments (fixed, df = 5 or df = 4), and the interaction between treatments and sites (fixed, df = 10 or df = 8; see Table 1).

The pre-experimental data set of 2003 (species richness only) and the experimental data set of 2005 (species richness of each functional group and of all five groups together, cover of each functional group and of all five groups together, soil organic matter content and pH) were analysed using SAS version 6.12 (SAS Institute, Inc., Cary, NC, USA). Differences between treatments were identified with LSD (least significant difference) tests when the ANOVAs revealed significant differences among treatments ($P \leq 0.05$).

The species richness and cover of a given removal treatment may be expected to be lower than that of the control treatment, simply because plants were removed. Thus, we calculated an expected value of richness and cover for each removal treatment by subtracting the richness or cover of a given functional group in the control from the overall richness or cover of the control. A paired *t*-test (df = 8, since we had a total of three blocks for each one of the three sites) was used to determine the significance of the differences between the observed and the expected richness and cover values, i.e. to determine if a removal treatment had a significant positive or negative effect on the variable of interest.

We determined the strength of the relationship between cover and richness (linear regression analysis, forced through the origin) for the control and for each one of the five removal treatments. We tested for differences among slopes, and since the test indicated that there were significant overall differences (see below), we compared the slopes two by two (Sokal and Rohlf 1995).

Results

Pre-experimental data (2003)

In 2003, species richness differed significantly among sites (F = 257.71; $P < 0.0001$), but not among treatments (F = 0.95, $P = 0.4635$). This latter result indicates that quadrats were initially similar within sites and it validates our randomization procedure within blocks.

Experimental data (2005)

Richness and cover

Species richness for all sites combined was dominated by herbaceous species (56 species, representing ~76 % of the total pool), whereas only 18 woody species were recorded. The mean number of species per site was 47.0 ± 11.3 (mean ± SE). The most important difference in species composition among sites was observed at Sainte-Françoise, which had 26 summer-flowering species (in comparison to 13 and 16 for Saint-Grégoire 1 and Saint-Grégoire 2, respectively). In the control quadrats, richness averaged 15.4 ± 1.9 species and cover amounted to 383.9 ± 48.1%.

As expected, the ANOVAs indicated that total richness differed significantly among treatments ($P < 0.001$; Table 1): the control had the highest and the seedlings and juveniles of woody species removal had the lowest richness (Fig. 1). Observed richness was significantly lower than expected richness for the spring-flowering persistent species removal and for the seedlings and juveniles of woody species removal ($P = 0.0304$ and $P = 0.0232$, respectively; Table 2). However, observed richness was somewhat higher (17.3%) than expected richness for the summer-flowering species removal ($P = 0.0907$).

There was a marginally significant effect of our treatments on summer-flowering species richness ($P = 0.058$; Table 1): indeed, summer-flowering species richness was low in the quadrats in which spring-flowering persistent species, fern species, or seedlings and juveniles of woody species had been removed (Fig. 1). There were no significant differences among treatments in the richness of spring-flowering ephemeral species, spring-flowering persistent species, fern species, or seedlings and juveniles of woody species (Table 1, Fig. 1).

As for richness, there were significant differences among treatments for the variable "cover" ($P = 0.030$, Table 1): indeed, cover was higher in the control, but lower in the spring-flowering persistent species removal, the summer-flowering species removal, the fern species removal and the seedlings and juveniles of woody species removal (Fig. 1). There were, however, no significant differences between the expected and the observed values of cover for any of the removal treatments, although observed cover was somewhat lower than expected in the spring-flowering persistent species removal ($P = 0.1015$; Table 2).

The cover of summer-flowering species differed significantly among treatments ($P = 0.048$; Table 1): there was a marked decrease of summer-flowering species cover when seedlings and juveniles of woody species were removed (Fig. 1). However, the significant treatment × site interaction indicated that the intensity of the treatment effect on summer-flowering species cover varied according to site ($P = 0.045$; Table 1). No significant differences were detected among treatments in the cover of the other functional groups (Table 1, Fig. 1).

All six cover-richness regressions were significant ($P < 0.0001$) with R^2 from 0.912 to 0.976 (Fig. 2). The slopes varied from 20.962 (fern species removal), to 28.692 (spring-flowering persistent species removal) and although there were significant differences *among* the six slopes ($P < 0.05$), none of the slopes of the removal treatments differed from that of the control (*pairwise comparison*). Log-transforming richness provided a poorer fit (lower R^2) for all the regressions (from 0.876 to 0.942).

Table 2 Observed and expected[a] richness and cover as a function of removal treatment. Mean ± SE ($n = 9$)

Treatments					
	Spring-flowering ephemeral species removal	Spring-flowering persistent species removal	Summer-flowering species removal	Fern species removal	Seedlings and juveniles of woody species removal
Richness					
Observed	12.9 ± 2.3	10.3 ± 1.4a	12.2 ± 1.7	11.8 ± 1.5	9.7 ± 1.5a
Expected	13.6 ± 1.7	12.6 ± 1.4b	10.4 ± 1.0	13.2 ± 1.6	12.0 ± 1.6b
Cover					
Observed	329.2 ± 49.6	291.6 ± 47.7	292.9 ± 51.2	250.9 ± 34.2	267.8 ± 42.7
Expected	308.8 ± 49.1	340.3 ± 42.9	246.3 ± 42.4	262.5 ± 41.5	298.6 ± 41.7

Different letters indicate significant differences between the observed and expected values for each treatment ($P \leq 0.05$; paired t-test, df = 8)

[a] We calculated an expected value of richness and of cover for each removal treatment by subtracting the richness or cover of a given functional group in the control from the overall richness or cover of the control (within each block)

Abiotic variables

The ANOVAs for the soil variables (pH and organic matter content) did not reveal any significant differences among treatments (Table 1). Soil pH values varied from 4.48 ± 0.07 to 4.68 ± 0.07 (mean ± SE). Soil organic matter content was relatively similar among treatments with means from 11.11 ± 0.38% to 14.24 ± 1.92%.

Inter-site differences

There were significant differences among sites for most of the variables studied: richness; cover; richness and cover of almost all of the functional groups; soil pH and organic matter content (Table 1).

Discussion

Richness

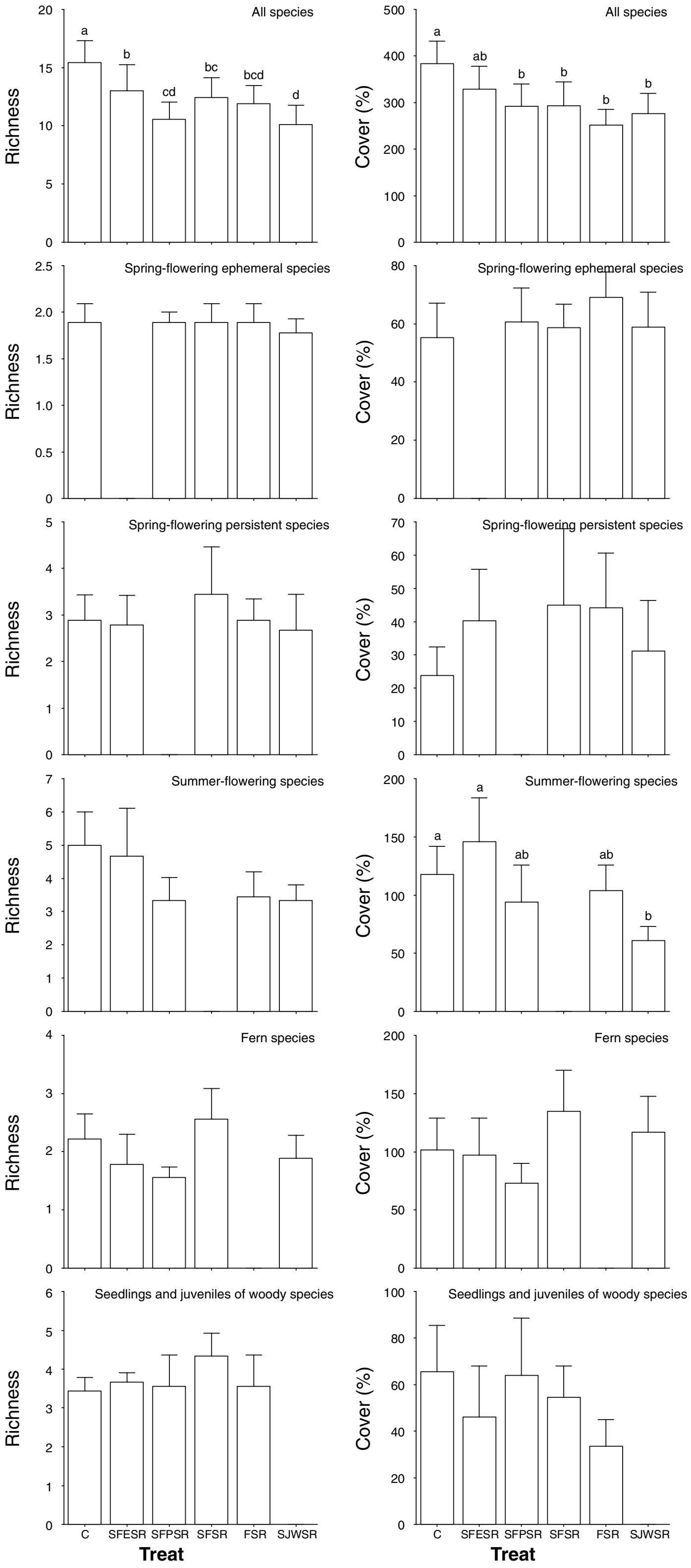
Richness decreased markedly when seedlings and juveniles of woody species or spring-flowering persistent species were removed (Fig. 1, Table 2): this was mostly through associated decreases in the richness of summer-flowering species and, to a lesser extent, of fern species. Spring-flowering persistent species and seedlings and juveniles of woody species complete their aboveground growth in the spring, mostly before tree canopy closure, but persist through the entire summer even under a thick overstory (Rothstein and Zak 2001). They often form a dense understory that protects the soil against erosion and contributes to reduce nutrient losses (Tessier and Raynal 2003); they also help maintain a lower soil and air temperature and a higher soil and air moisture (Scholes and Archer 1997). By doing so, they may contribute to create conditions favourable for the recruitment and/or maintenance of those species which complete their cycle in the summer (summer-flowering species and fern species), at a period when drought stress may be limiting. These mechanisms remain speculative, however, and need to be experimentally tested. Nevertheless, our results confirm those of George and Bazzaz (1999a, b) who demonstrated that interactions between functional groups could affect understory recruitment and, in the longer term, richness.

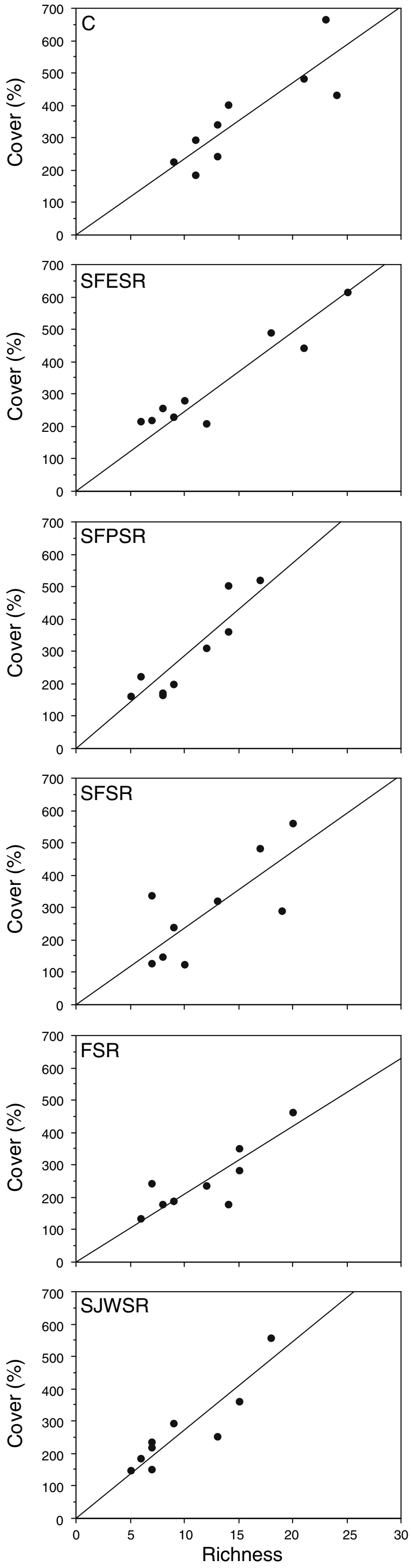
Our initial null hypotheses stipulated that the different functional groups had little or no interactions with each other, and that the loss of a group would not have any serious consequences on the functional properties of the system. Our results on richness do not support these hypotheses: some of the functional groups interacted positively with others and, thus, were not strictly independent. The loss of a given functional group had significant consequences on the understory richness, some groups having a greater proportional effect than others, however.

Cover

Cover decreased significantly following our removals and to a similar level regardless of which functional

Fig. 1 Richness (all functional groups together), individual functional group richness (left), cover (all functional groups together) and individual functional group cover (right) as a function of treatment. For each variable, different letters indicate significant differences among treatments ($P \leq 0.05$, protected LSD). Mean + SE. C, control; SFESR, spring-flowering ephemeral species removal; SFPSR, spring-flowering persistent species removal; SFSR, summer-flowering species removal; FSR, fern species removal; SJWSR, seedlings and juveniles of woody species removal. See Table 1 for details on the ANOVA results





◀ **Fig. 2** Cover-richness relationship for the control and the different removal treatments. Regression lines were forced through the origin: C, control: slope = 23.473, $P < 0.0001$, $R^2 = 0.963$; SFESR, spring-flowering ephemeral species removal: slope = 24.573, $P < 0.0001$, $R^2 = 0.976$; SFPSR, spring-flowering persistent species removal: slope = 28.692, $P < 0.0001$, $R^2 = 0.970$; SFSR, summer-flowering species removal: slope = 23.688, $P < 0.0001$, $R^2 = 0.912$; FSR, fern species removal: slope = 20.962, $P < 0.0001$, $R^2 = 0.959$; SJWSR, seedlings and juveniles of woody species removal: slope = 27.329, $P < 0.0001$, $R^2 = 0.969$

group was removed (except for the removal of spring-flowering ephemeral species, which did not differ significantly from the control; Fig. 1): this result would seem to suggest no short-term compensation in species production following the removal of a given functional group. Yet, differences in cover among functional groups were quite large in the control: [(summer-flowering species ~ fern species) > (spring-flowering ephemeral species ~ seedlings and juveniles of woody species) > spring-flowering persistent species]. In fact, cover decreased somewhat more than expected (14.3% more) when spring-flowering persistent species were removed (Table 2): this was mostly through a slight decrease in the cover of summer-flowering species and of fern species relative to the control. In contrast, cover was somewhat higher than expected (18.9% higher) when summer-flowering species were removed and this was mostly through a slight increase in the cover of fern species relative to the control.

The removal of seedlings and juveniles of woody species led to a significant decrease in the cover of summer-flowering species. As mentioned above, under the cover of seedlings and juveniles of woody species, soil and air temperature is reduced and soil and air moisture is higher, conditions that may favour the growth of summer-flowering species during a period when drought stress may otherwise limit growth (Schulz and Adams 1995; Scholes and Archer 1997). Herbivores may also respond to the spatial structure of the understory cover, some plant species benefiting from, and others being hindered by, the presence of some plant species (George and Bazzaz 1999b).

Our results for cover support those presented above with respect to the effect of the removal of a functional group on richness: significant interactions were present among some of the groups.

Cover-richness relationship

The linearity of the relationship between cover and richness, as described for the control, would seem to suggest strong complementarity among functional groups: indeed, according to Díaz and Cabido (2001, p. 651) "only when all species have equally complementary niches … the rate of ecosystem processes should be expected to increase linearly with species richness". However, assuming complementarity among groups, we could have expected the slope of the cover-richness regression to decrease significantly following our removals (Loreau et al. 2001); this was not the case (no significant differences between the slope of the control treatment and that of each one of our five removal treatments; pair-wise comparisons). Instead, these results suggest that there are no complementary effects among functional groups and that intergroup independence may be responsible for the linear cover-richness relationship reported for the control (see also Hooper and Dukes 2004).

Our results on cover-richness relationship also show that removing spring-flowering persistent species or fern species, two groups with comparable richness although very dissimilar cover, affects differently the cover-richness relationship (slopes significantly different between spring-flowering persistent species removal and fern species removal at $P < 0.01$): this suggests that the loss of a given number of species may have contrasting effects on ecosystem functioning depending on the characteristics of the species that are lost (e.g. their productivity), a conclusion already reached by Díaz and Cabido (2001). It also emphasizes the significance of functional composition and functional richness for ecosystem processes (Wardle et al. 2000; Loreau et al. 2001; Hooper and Dukes 2004).

Duration of the experiment

Overall, few significant effects were observed as a result of our removal treatments and a longer-term experiment may have revealed more complex intergroup interactions (some effects were marginally significant). Yet, the effects reported here after only two years of experiment indicate that even the understory can respond quite rapidly to removals, as has been shown by Stinson et al. (2007) only one year after having eradicated the invasive *Alliaria petiolata* from plots in the understory of a hardwood forest of New England. Not unexpectedly, considering the short duration of our experiment, none of the removal treatments had significant effects on the soil variables.

Conclusions

Both positive and negative interactions were detected between functional groups, although positive intergroup interactions prevailed. Spring-flowering persistent species and seedlings and juveniles of woody species appeared to be key groups, because of their positive effects on summer-flowering species and fern species, two groups having a particularly significant contribution to understory cover and richness. Such interactions may increase the stability of the forest understory and help maintain ecosystem functions (MacArthur 1955; Tilman and Downing 1994; Johnson et al. 1996): indeed, they may (1) lead to a higher collective capacity of the species to resist to minor disturbances and/or (2) allow the system to re-establish essential functions following more important disturbances (Walker et al. 1999; Upadhyay et al. 2000; Díaz and Cabido 2001).

Each one of the five functional groups contributed directly to richness and cover (Tilman et al. 1997), most likely because of the complementary morphological, physiological and/or phenological traits of their respective species (Loreau and Behera 1999; Reich et al. 2003). Yet, our results on the cover-richness relationship suggested a *relative* independence among functional groups. Further experimental work is needed to identify the specific mechanisms responsible for the interactions outlined here between the different functional groups of the understory and to confirm that short-term responses can be translated into still more significant responses with time.

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References

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156. doi:10.1111/j.1461-0248.2006.00963.x

Bratton SP (1976) Resource division in an understory herb community: responses to temporal and microtopographic gradients. Am Nat 110:679–693. doi:10.1086/283097

Buonopane M, Huenneke LF, Remmenga M (2005) Community response to removals of plant functional groups and species from a Chihuahuan Desert shrubland. Oikos 110:67–80. doi:10.1111/j.0030-1299.2005.13949.x

Cardinale BJ, Nelson K, Palmer M-A (2000) Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos 91:175–183. doi:10.1034/j.1600-0706.2000.910117.x

Choinière L, Laplante L (1948) Étude des sols du Comté de Nicolet. Ministère de l'Agriculture et Ministère de l'industrie et du Commerce, Québec

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655. doi:10.1016/S0169-5347(01)02283-2

Eickmeier WG, Schussler EE (1993) Responses of the spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the vernal-dam hypothesis. Bull Torrey Bot Club 120:157–168. doi:10.2307/2996945

Fitter AH (1982) Influence of soil heterogeneity on the coexistence of grassland species. J Ecol 70:139–148. doi:10.2307/2259869

Fox JW (2005) Interpreting the selection effect of biodiversity on ecosystem function. Ecol Lett 8:546–856. doi:10.1111/j.1461-0248.2005.00795.x

George LO, Bazzaz FA (1999a) The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology 80:833–845

George LO, Bazzaz FA (1999b) The fern understory as an ecological filter: growth and filter of canopy-tree seedlings. Ecology 80:846–856

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344–347. doi:10.1038/242344a0

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. doi:10.1086/283244

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze E-D, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127. doi:10.1126/science.286.5442.1123

Hooper DU, Dukes JS (2004) Overyielding among plant functional groups in a long-term experiment. Ecol Lett 7:95–105. doi:10.1046/j.1461-0248.2003.00555.x

Hooper DU, Solan M, Symstad A, Díaz S (2002) Species diversity, functional diversity, and ecosystem functioning. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, pp 195–281

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460. doi:10.1007/s004420050180

Johnson KH, Vogt KA, Clark HJ, Schmitz OJ, Vogt DJ (1996) Biodiversity and the productivity and stability of ecosystems. Trends Ecol Evol 11:372–377. doi:10.1016/0169-5347(96)10040-9

Lepš J (2004) What do the biodiversity experiments tell us about consequences of plant species loss in the real world? Basic Appl Ecol 5:529–534. doi:10.1016/j.baae.2004.06.003

Loreau M, Behera N (1999) Phenotypic diversity and stability of ecosystem processes. Theor Popul Biol 56:29–47. doi:10.1006/tpbi.1998.1408

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808. doi:10.1126/science.1064088

MacArthur R (1955) Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536. doi:10.2307/1929601

Marie-Victorin (2002) Flore Laurentienne, 3rd edn. Gaétan Morin Éditeur, Boucherville, Québec

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381–2396

Muller RN, Bormann FH (1976) Role of *Erythronium americanum* Ker. In energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science 193:1126–1128. doi:10.1126/science.193.4258.1126

Naeem S (2001) How changes in biodiversity may affect the provision of ecosystem services. In: Chichilnisky G, Daily GC, Ehrlich P, Heal G, Miller J (eds) Managing Human-dominated Ecosystems. Missouri Botanical Garden, St Louis, MO, pp 3–33

Naeem S, Chapin FSIII, Costanza R, Ehrlich PR, Golley FB, Hooper DU, Lawton JH, O'Neill RV, Mooney HA, Sala OE, Symstad AJ, Tilman D (1999) Biodiversity and ecosystem functioning: maintaining natural life support processes. Ecology 4:1–12

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philos Trans R Soc London [Biol] 347:249–262

Reich PB, Buschena C, Tjoelker MG, Wrage K, Knops J, Tilman D, Machado JL (2003) Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. New Phytol 157:617–631. doi:10.1046/j.1469-8137.2003.00703.x

Rothstein DE, Zak DR (2001) Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. Funct Ecol 15:722–732. doi:10.1046/j.0269-8463.2001.00584.x

Rowe JS (1972) Les régions forestières du Canada. Ministère de l'Environnement, publication N 1300F, Canada

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Annu Rev Ecol Syst 28:517–544. doi:10.1146/annurev.ecolsys.28.1.517

Schulz KE, Adams MS (1995) Effect of canopy gap light environment on evaporative load and stomatal conductance in the temperate forest understory herb *Aster macrophyllus* (Asteraceae). Am J Bot 82:630–637. doi:10.2307/2445421

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Stinson K, Kaufman S, Durbin L, Lowenstein F (2007) Impacts of garlic mustard invasion on a forest understory community. Northeastern Nat 14:73–88. doi:10.1656/1092-6194(2007)14[73:IOGMIO]2.0.CO;2

Symstad AJ, Chapin FSIII, Wall DH, Gross KL, Huenneke LF, Mittelbach GG, Peters DPC, Tilman D (2003) Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. Bioscience 53:89–98. doi:10.1641/0006-3568(2003)053[0089:LTALSP]2.0.CO;2

Symstad AJ, Tilman D, Willson J, Knops J-MH (1998) Species loss and ecosystem functioning: effects of species identity and community composition. Oikos 81:389–397. doi:10.2307/3547058

Tessier JT, Raynal DJ (2003) Vernal nitrogen and phosphorus retention by forest understory vegetation and soil microbes. Plant Soil 256:443–453. doi:10.1023/A:1026163313038

Tilman D (1997) Biodiversity and ecosystem functioning. In: Daily GC (ed) Nature's Services. Island Press, Washington, DC, pp 93–112

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367:363–365. doi:10.1038/367363a0

Tilman D, Knops J, Wedin D, Reich P (2002) Plant diversity and composition: effects on productivity and nutrient dynamics of experimental grasslands. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, pp 21–35

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302. doi:10.1126/science.277.5330.1300

Troumbis AY, Memtsas D (2000) Observational evidence that diversity may increase productivity in Mediterranean shrublands. Oecologia 125:101–108. doi:10.1007/PL00008880

Upadhyay RK, Rai V, Iyengar SRK (2000) How do ecosystems respond to external perturbations? Chaos Solitons Fractals 11:1963–1982. doi:10.1016/S0960-0779(99)00086-7

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems (NY, Print) 2:95–113. doi:10.1007/s100219900062

Wardle DA, Bonner KI, Barker GM (2000) Stability of ecosystem properties in response to above-ground functional group richness and composition. Oikos 89:11–23. doi:10.1034/j.1600-0706.2000.890102.x

Wardle DA, Bonner KI, Barker GM, Yeates GW, Nicholson KS, Bardgett RD, Watson RN, Ghani A (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecol Monogr 69:535–568

Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. Nature 435:806–810. doi:10.1038/nature03611

Host trait preferences and distribution of vascular epiphytes in a warm-temperate forest

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Abstract To illustrate the ecological factors and process leading to the observed diversity patterns of vascular epiphytes, we examined the effect and importance of host tree traits on epiphyte richness and spatial aggregation of epiphytes. The study was conducted in warm-temperate forest in Japan. The recorded host traits were diameter, height, species, habitat topography, and growth rate, and we analyzed the effects and importance of these traits on three species groups: total epiphytic species, epiphytic orchid species, and epiphytic pteridophyte species. Diameter and species of host trees had the greatest influence on epiphytes and their magnitudes were roughly similar in all species groups. Growth rate and topography were less important than host size and species. Growth rate had a negative effect on all three groups, and topography was important for pteridophytes. Epiphyte richness did not exhibit clear spatial aggregation. Our results suggest that size, stability, and quality of the host are equally important in determining epiphyte colonization.

Keywords Diversity · Evergreen broad-leaved forest · Orchid · Pteridophyte · Host specificity · Spatial pattern

Introduction

Vascular epiphytes are an essential component of the vegetation of forests, in terms of both species diversity and their role in forest ecosystem functions (Gentry and Dodson 1987; Benzing 1990; Burns and Dawson 2005; Flores-Palacios and García-Franco 2006). Their importance for forest diversity is based on their proportionally large contribution to the diversity of the local flora (Dawson and Sneddon 1969; Gentry and Dodson 1987; Benzing 1990; Burns and Dawson 2005). However, we still know little about the mechanisms that maintain epiphyte diversity.

In forests, the distribution pattern of vascular epiphyte diversity is affected by two major processes: dispersal and establishment. Host trees provide the substrate for epiphytes, so establishment seems to be affected by host tree traits, including area available for establishment, physical and chemical characteristics of bark, and architecture, e.g., canopy structure (Frei and Dodson 1972; Migenis and Ackerman 1993). Size and species of host trees are indicative traits of these factors, because an increase in size leads to an increase in habitat area and in the chance of epiphyte establishing. Host species determines traits, such as

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bark characteristics and canopy structure. Many previous studies have examined the influence of host size and species separately when examining the diversity and presence of epiphyte. Most studies have found a positive relation between host size and epiphyte diversity (Hietz and Hietz-Seifert 1995; Zotz and Vollrath 2003; Burns and Dawson 2005). In terms of the relationship between host species and epiphyte presence, there is little support for the notion of strict host-specificity in epiphytes (Benzing 1990). However, failure to find a one-to-one match between particular species of host trees and epiphytes dose not confirm 'neutrality' of host tree species identity with respect to the structuring of epiphyte communities (Laube and Zotz 2006). Some studies have shown that epiphyte diversity increases markedly with host tree size, and that the trend differs among host species (Callaway et al. 2002; Burns and Dawson 2005). Therefore, a combination of the host tree traits appears to be important in determining the epiphytes present and diversity, rather than simply host size or host species (Laube and Zotz 2006).

In addition, if the vascular epiphyte distribution shows an aggregative pattern, this suggests the possibility that another factor, such as dispersal limitation, affects epiphyte distribution in addition to habitat preference. In general, epiphytic plants are expected to be characterized by high seed numbers and long-distance dispersal, mainly wind-borne (Gentry and Dodson 1987; Nieder et al. 2000). As a result, a number of studies that have found a patchy, rather than random, distribution of epiphytes have concluded that aggregation was the result of the presence of preferred hosts with respect to size and substrate characteristics (Tremblay 1997; Nieder et al. 2000). However, some studies have shown that orchid seed dispersal, the most diverse group of epiphytes, occurs over relatively short distances (Tremblay 1997; Machon et al. 2003).

The ecological factors affecting epiphyte diversity may interact with one another. To understand these factors, it is necessary to examine the effects of host traits on vascular epiphyte diversity by analyzing all traits simultaneously. On the other hand, to understand the process causing the patterns of vascular epiphyte diversity, it is necessary to examine both the distribution pattern and habitat preference. For non-vascular epiphytes, i.e., bryophytes and lichens, Löbel et al. 2006 it was found that both environmental conditions and spatial aggregation can explain a substantial part of the variation in species richness. The relevant factors, however, have been studied rarely in a single system for vascular epiphytes.

The aims of this study were to assess the relative importance of host traits, such as size and quality, by analyzing them simultaneously, and to consider which habitat preference and dispersal limitation mechanisms affect the distribution of vascular epiphyte diversity. The host tree traits selected for examination were habitat topography and growth rate of the host tree, and host size and species, because we suspected that these host traits reflect the environment around host trees and the surface stability of the substrate, which may influence epiphyte colonization. The questions addressed in this article are:

(1) Which host tree traits affect epiphyte diversity?
(2) How are these traits important?
(3) Is epiphyte diversity patchy in its distribution?

Based on the answers to these questions, we discuss the mechanisms controlling the pattern of epiphyte diversity.

Materials and methods

Study area

The study area is in Kyushu Chuo Sanchi Semi-National Park, Southwestern Japan. The natural vegetation of this area is evergreen broad-leaved forest. An old-growth forest covering more than 300 ha is well preserved around the study area (Tanouchi and Yamamoto 1995). Most natural evergreen broad-leaved forests have been logged or greatly changed by human activity in Japan. The forest has a canopy that is more than 30 m tall. This is dominated by evergreen broad-leaved species, such as *Distylium racemosum* Sieb. et Zucc. and *Quercus acuta* Thunb. (Tanouchi and Yamamoto 1995; Saito 2002). A permanent 4-ha plot (200 m × 200 m) was set up on a north to northwest-facing slope on Mt. Omori (1,109 m asl; 32°04′ N, 131°09′ E) at an elevation ranging from 380 to 520 m in 1989 (Sato et al. 1999). This plot has been used for long-term ecological research since then; data of species name, diameter at breast height (DBH; 1.3 m), and location of all trees with a DBH greater than 5 cm, plus a microtopographical classification of the plot have been accumulated (Sato et al. 1999). During the period 1994 to 1998, the mean annual temperature in this plot at 495 m asl was 14.2°C. The mean annual precipitation from 1951 to 1997 was 3,070 mm at the nearest recording station, the Ayakita Prefectural Observatory, 294 m asl (Miyazaki Local Meteorological Observatory 1951–1997; Sato et al. 1999). Within the 4 ha permanent plot, we set up an 80 m × 120 m study plot for the epiphyte survey; this area contained most of the microtopographic types present in the surroundings (Fig. 1).

Host tree traits and epiphyte species richness

Within the study plot (80 m × 120 m), DBH, height, and species name of all the trees with a DBH greater than 20 cm (i.e., potential host trees) were recorded in 2007. The microtopography of the habitat in which the host trees were located was defined on the basis of data collected previously (Sato et al. 1999), namely: crestslope, upper sideslope, lower sideslope, headmost wall, head hollow, footslope, and bottomland (Tamura and Takeuchi 1980; Tamura 1987; Ohnuki et al. 1997; Fig. 1). The growth rate of each host tree was estimated by the ratio of 2007 DBH to the 2005.

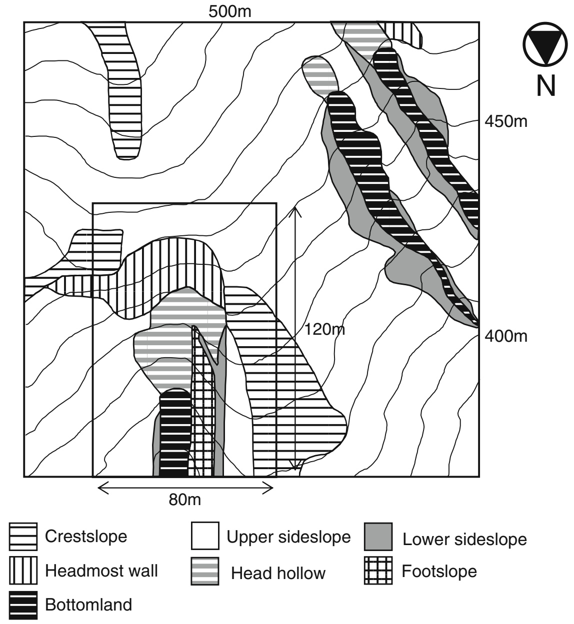


Fig. 1 Microtopography of the permanent 4-ha plot. An 80 m × 120 m quadrat shows our study plot

Within the study plot, we recorded the species name and growing site of all adult epiphytes on a total of 283 host trees. Growing sites were classified into five types following the revised zonation scheme presented by Johansson (1974): the basal part of the trunk (0–2 m), the trunk from 2 m up to the first ramification, the basal part of the canopy (1/3 of the total length of the branch), the middle part of the canopy (1/3 of the total length of the branch), and the outer part of the canopy (1/3 of the total length of the branch). We searched epiphytes from the ground using binoculars. The rope climbing technique was used when searching from the ground was not possible. With the exception of mistletoe and an accidental epiphyte (Benzing 1990), all species were used for the statistical analyses. In addition to the total epiphyte species, we examined two species groups: orchids and pteridophytes.

Statistical analysis

The effects of host traits on epiphyte species richness for the three species groups (total species, orchids, and pteridophytes) were analyzed using generalized linear models (GLM; McCullagh and Nelder 1989) with the log link function, assuming a negative-binomial error structure. Five host traits were used as predictor variables: species (Species), DBH (DBH), height (Height), growth rate (Growth), and habitat microtopography (Topography). The correlation between predictor variables was tested using the Pearson correlation coefficient or Cramer coefficient of association. Since all correlation coefficients between each of the predictor variables were lower than 0.3, all variables were used as predictors. To evaluate the importance of each predictor, Akaike information criterion (AIC) for all possible subsets of the predictor variables were calculated. The AIC minimizing model was considered to be the most suitable model, and predictor variables included in this model were considered to represent the factors that affected species richness. To evaluate the relative importance of each predictor variable, AIC values for the top five models and the variables included in these models, were compared for each functional group.

The spatial aggregation of epiphyte species richness was estimated using the semi-variance function. Semi-variance is a concept widely used to detect spatial and/or temporal patterns within datasets, e.g., in geostatistics (Bailey and Gatrell 1995), and describes how species richness covaries spatially among host trees (Löbel et al. 2006). It is defined by:

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{i=1}^{n} \left(z_i - z_j\right)^2,$$

where z_i and z_j represent the observed species richness on host trees i and j, respectively, h is a vector of distances between trees, and $n(h)$ is the number of pairs of host trees located at distance h from each other. The semi-variance is a measure of dissimilarity for species richness, and a plot of semi-variance against distance (i.e., a semi-variogram) can be used to explore whether the dissimilarity in species richness changes with distance between trees (Löbel et al. 2006). At short distance, the values of semi-variance are also small indicating that the spatial structure is at its strong intensity (Fortin and Dale 2005). As the distance increase, the semi-variance values also increase before leveling off to a plateau (Fortin and Dale 2005). We plotted the semi-variance values calculated for species richness against distance, and estimated whether dissimilarity of species richness changes with distance. In addition to species richness, semi-variance for the residual from the best model was calculated to examine the degree of spatial aggregation which could not be assigned to environmental variables.

All analysis was performed in the R environment for statistical computing (R Development Core Team 2006).

Results

Excluding species that are accidental epiphytes, 8 orchids, 13 pteridophytes, and 2 mistletoes were recorded (Table 1). Model selection using AIC resulted in the variables DBH, Species, and Growth being included in the best model for all species groups (Table 2). However, Height was not included in the best models for any of the three groups. DBH had a positive effect on epiphyte richness, and growth rate had a negative effect (Table 2). With respect to host species, the regression coefficient for *Persea japonica* (Sieb. et Zucc.) Kosterm. was the highest, and that for deciduous trees was the second highest when all epiphyte species were considered. For the orchids, *Camellia japonica* Linn. had the highest regression coefficient, and deciduous trees the second highest. For the pteridophytes, *P. japonica* had the highest regression coefficient, and *Persea thunbergii* (Sieb. et Zucc.) Kosterm. the second highest. On the other hand, the regression coefficients for *D. racemosum* were the lowest or second lowest for all groups (Table 2). Topography was included in the pteridophyte model, and the regression coefficient associated with crestslope was the lowest of all the topographic categories (Table 2).

Table 1 Epiphyte species at the study site

Epiphyte species	Family	Number
Neofinetia falcata	Orchidaceae	45
Bulbophyllum drymoglossum	Orchidaceae	43
Bulbophyllum inconspicuum	Orchidaceae	41
Sedirea japonica	Orchidaceae	28
Bulbophyllum japonicum	Orchidaceae	14
Eria reptans	Orchidaceae	13
Saccolabium japonicum	Orchidaceae	4
Dendrobium moniliforme	Orchidaceae	3
Lepisorus thunbergianus	Polypodiaceae	115
Lemmaphyllum microphyllum	Polypodiaceae	110
Davallia mariesii	Davalliaceae	32
Asplenium wilfordii	Aspleniaceae	24
Pyrrosia lingua	Polypodiaceae	23
Selaginella involvens	Selaginellaceae	20
Gonocormus minutus	Hymenophyllaceae	21
Loxogramme salicifolia	Polypodiaceae	17
Lepisorus onoei	Polypodiaceae	15
Lacosteopsis auriculata	Hymenophyllaceae	9
Lycopodium sieboldii	Lycopodiaceae	3
Vittaria flexuosa	Vittariaceae	3
Crepidomanes insigne	Hymenophyllaceae	2
Taxillus yadoriki	Loranthaceae	11
Korthalsella japonica	Loranthaceae	8

In Table 3, the top five models are ranked according to their AIC differences (delta AIC), from best to worst. DBH and Species were included in all the top five models for all groups. For the orchids and pteridophytes, AIC difference for model 3, which includes only the DBH and Species variables, was 2 units less, and these models had substantial support. In general Growth and Topography were not included in the top five models (Table 3).

The orchids were found most frequently at growing sites 3 and 4. The pteridophytes showed high frequency in growing site 1 to growing site 4 (Fig. 2).

Table 2 The regression coefficients of the generalized linear model (GLM), selected by AIC

Variable	Total		Orchid		Pteridophyte	
	β	SE	β	SE	β	SE
Intercept	0.113	0.229	−1.177**	0.378	0.451	0.390
DBH	0.635**	0.065	0.684**	0.103	0.453**	0.063
Species						
Quercus acuta	0.000		0.000		0.000	
Quercus gilva	0.567	0.347	0.751	0.554	0.334	0.347
Quercus salicina	0.238	0.277	0.627	0.440	−0.197	0.282
Castanopsis cuspidata var. *sieboldii*	0.015	0.339	−0.198	0.586	−0.233	0.331
Persea thunbergii	0.839**	0.233	0.975**	0.371	0.595**	0.220
Persea japonica	1.170**	0.270	1.224**	0.444	0.605*	0.282
Distylium racemosum	−0.932**	0.290	−1.136*	0.516	−1.094**	0.294
Actinodaphne longifolia	0.508	0.397	−0.146	0.856	0.016	0.421
Cleyera japonica	−0.354	0.479	0.393	0.685	−1.373*	0.637
Camellia japonica	0.719	0.432	1.328*	0.642	−0.111	0.500
Deciduous trees	1.164**	0.345	1.311*	0.545	0.561	0.341
Other evergreen trees	0.537	0.325	0.456	0.561	0.214	0.330
Growth	−0.157*	0.075	−0.271*	0.135	−0.102	0.075
Topography						
Crestslope	–	–	–	–	−0.764*	0.341
Upper sideslope	–	–	–	–	−0.314	0.308
Lower sideslope	–	–	–	–	−0.309	0.384
Headmost wall	–	–	–	–	−0.040	0.322
Head hollow	–	–	–	–	0.015	0.314
Footslope	–	–	–	–	−0.311	0.391
Bottomland	–	–	–	–	0.000	
Height	–	–	–	–	–	–
Residual deviance	271.25 (d.f. = 269)		204.45 (d.f. = 269)		256.74 (d.f. = 263)	

Bold text indicates a variable included in the best model for one or more species groups. β = coefficient, SE = Standard error, d.f. = degrees of freedom, * $P < 0.05$, ** $P < 0.01$

The semi-variance calculated using species richness and the residual from the best model exhibited no clear tendency to be small over short distance or to increase with distance between trees (Fig. 3). The plot of residuals from the best model exhibited a more consistent pattern than that of species richness.

Discussion

Factors that affect patterns of vascular epiphyte species richness

Size and species of host tree were the most important factors influencing vascular epiphyte richness (Tables 2, 3). The importance of these traits has been demonstrated individually (Zimmerman and Olmsted 1992; Hietz and Hietz-Seifert 1995; Callaway et al. 2002; Zotz and Vollrath 2003; Burns and Dawson 2005), but a quantitative comparison of these traits has not been previously conducted. Our results show, by analyzing host traits simultaneously, that they are equally influential. A quantitative comparison of host traits has been conducted for epiphytic bryophytes and lichens (Löbel et al. 2006), and it has been shown that host size and species are the crucial factors affecting richness of non-vascular epiphytes. However, size was only important for bryophytes, and species was only important for lichens. This result differed from present study, which found that these factors exert an equal influence.

Table 3 The variables included in the top five models, according to AIC, and the AIC value for each model

Number	Variables					AIC	Delta AIC
(a) Total							
1	D		S	G		888.14	0.00
2	D		S	G	T	889.67	1.53
3	D	H	S	G		890.13	1.99
4	D		S			890.78	2.64
5	D	H	S	G	T	891.32	3.17
(b) Orchid							
1	D		S	G		532.30	0.00
2	D	H	S	G		532.54	0.23
3	D		S			534.11	1.80
4	D	H	S			534.25	1.95
5	D	H	S	G	T	538.44	6.14
(c) Pteridophyte							
1	D		S	G	T	746.50	0.00
2	D		S		T	746.52	0.01
3	D		S			746.85	0.35
4	D		S	G		747.39	0.89
5	D	H	S			747.75	1.25

D: DBH; H: height; S: species; G: growth rate; T: topography

On the other hand, growth rate and topography were less important than host size and species (Table 3). Growth rate had a negative effect on all groups. High growth rate of the host tree may cause relatively rapid changes in the characteristics of the bark surface. Since vascular epiphytes attach to the bark surface of their host tree, they may be susceptible to changes to the surface. The influence of topography was important for pteridophytes (Table 2). The effect of topography may reflect a difference in drought survival strategy between pteridophytes and orchids. The pteridophyte richness was lowest in crestslope locations that were relatively dry at our study site. In general, it is known that vascular epiphytes use the CAM-pathway as a means of surviving in drought-prone habitats (Winter et al. 1983). However, previous studies have shown that few pteridophytes are CAM species, unlike the orchids, and the proportion of these species that are tolerant to drought increases from shaded trunk to exposed canopy habitats (Winter et al. 1983; Zotz and Ziegler 1997). Since orchids were mainly found in the canopy area in our study (Fig. 2), it is likely that many of them are highly drought-tolerant. However, pteridophytes are unlikely to be drought-tolerant, possibly explaining the importance of topography in determining their distribution.

Vascular epiphyte richness did not exhibit clear spatial aggregation (Fig. 3). This suggests that dispersal ability does not have a crucial effect on epiphyte richness patterns at the scale of our study. However, different trends may be exhibited at a larger scale, since diaspores of orchids and

Fig. 2 Frequency of appearance at each growing site. Growing site is indicated by numerals: 1, the basal part of the trunk; 2, the trunk from 2 m up to the first ramification; 3, the basal part of the canopy; 4, the middle part of the canopy; 5, the outer part of the canopy

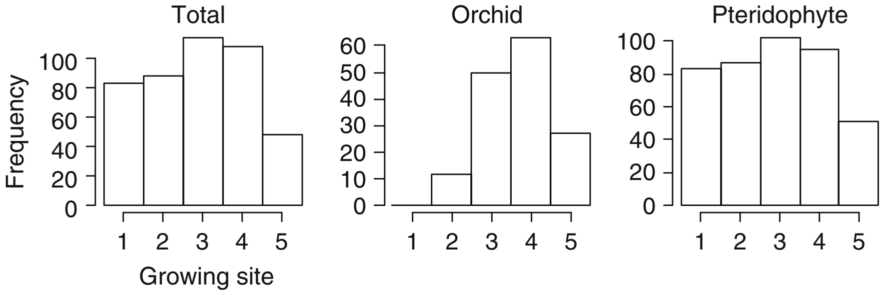
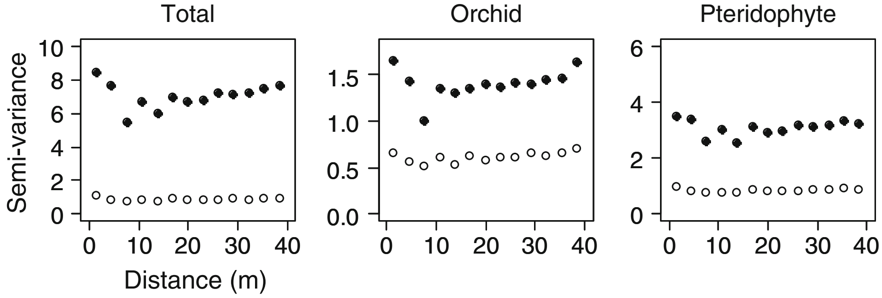


Fig. 3 Semi-variance values for arbitrary distance. Solid circle, species richness; open circle, residual from GLM



pteridophytes may disperse over a wider range than the distances examined in our study. On the other hand, the spatial trend suggested by the residual of the best model was more consistent than the pattern associated with species richness. Therefore, it is possible that habitat quality might have more influence than dispersal ability at our study site, although we did not compare the two factors directly.

Effect of host size and host species preference

The positive effect of host size seems to reflect habitat stability in the long-term in addition to habitat size. Because epiphyte growth and colonization are slow (Schmidt and Zotz 2002; Laube and Zotz 2003), it seems that habitat stability is one of the important factors for epiphyte establishment. It is known that the diversity of vascular epiphyte species is significantly higher in primary forest than in secondary forest (Barthlott et al. 2001; Ishida et al. 2005; Benavides et al. 2006). One possible reason is that forest structure developed over a long time, results in more complex, extensive, and stable habitats for epiphytes.

The host specificity of vascular epiphytes has been shown in previous studies, and it has been suggested that this can be explained by bark characteristics, such as water-holding capacity, nutrient status, and chemical composition (Frei and Dodson 1972; Callaway et al. 2002; Mehltreter et al. 2005). The results of our study also suggest that vascular epiphytes have preferred host species (Table 2). Most epiphyte groups preferred deciduous host trees. Not one group displayed a preference for *D. racemosum* (Table 2). Because deciduous trees have thin leaves than evergreen trees and lose their leaves in the winter, they provide a lighter habitat. Therefore, light conditions in the inner canopy may also be an important factor affecting host species preference. Although *D. racemosum* was the most common species in our study plot, it had the lowest associated epiphyte diversity. In contrast, there were relatively few deciduous trees in our study site, because most are pioneer species and are found on disturbed sites in temperate evergreen broad-leaved forest (Tanouchi and Yamamoto 1995). Nevertheless, deciduous trees provided an important epiphyte habitat. These results suggest that a diverse forest community helps to maintain epiphyte richness.

The water holding capacity of bark may also be an important factor affecting host preference by vascular epiphytes at our study site, since it is not cloud forest and experiences only moderate humidity. Callaway et al. (2002) have shown that water availability is a key factor in determining a good host; they argued that the host preference of vascular epiphytes may change with changing humidity. Among the most important factors for epiphyte richness, the positive effect of host size probably does not vary with environmental gradient or location. However, epiphyte host preference may vary along an environmental gradient.

Conclusion

Size and species of host tree were the most important factors influencing vascular epiphyte diversity, and it appears that both habitat suitability and quality are important for the establishment of vascular epiphytes. On the other hand, epiphyte diversity did not exhibit clear spatial aggregation, and it appears that dispersal limitation is not particularly influential at the scale of our study.

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References

Bailey TC, Gatrell AC (1995) Interactive spatial data analysis. Longman, Essex

Barthlott W, Schmit-Neuerburg V, Nieder J, Engwald S (2001) Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol 152:145–156. doi:10.1023/A:1011483901452

Benavides AM, Wolf JHD, Duivenvoorden JF (2006) Recovery and succession of epiphytes in upper Amazonian fallows. J Trop Ecol 22:705–717. doi:10.1017/S0266467406003580

Benzing DH (1990) Vascular epiphytes. Cambridge University Press, Cambridge

Burns KC, Dawson J (2005) Patterns in the diversity and distribution of epiphytes and vines in a New Zealand forest. Austral Ecol 30:883–891. doi:10.1111/j.1442-9993.2005.01532.x

Callaway RM, Reinhart KO, Moore GW, Moore DJ, Pennings SC (2002) Epiphyte host preferences and host traits: mechanisms for species-specific interactions. Oecologia 132:221–230. doi:10.1007/s00442-002-0943-3

Dawson JW, Sneddon BV (1969) The New Zealand rain forest: a comparison with tropical rain forest. Pac Sci 23:131–147

Flores-Palacios A, García-Franco JG (2006) The relationship between tree size and epiphyte species richness: testing four different hypotheses. J Biogeogr 33:323–330. doi:10.1111/j.1365-2699.2005.01382.x

Fortin M-J, Dale M (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

Frei JK, Dodson CH (1972) The chemical effect of certain bark substrates on the germination and early growth of epiphytic orchids. Bull Torrey Bot Club 99:301–307. doi:10.2307/2997072

Gentry AH, Dodson CH (1987) Diversity and biogeography of neotropical vascular epiphytes. Ann Mo Bot Gard 74:205–233. doi:10.2307/2399395

Hietz P, Hietz-Seifert U (1995) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. J Veg Sci 6:487–498. doi:10.2307/3236347

Ishida H, Hattori T, Hashimoto Y (2005) Comparison of species composition and richness among primeval, natural, and secondary lucidophyllous forests in southeastern Kyushu, Japan. Veg Sci 22:71–86

Johansson D (1974) Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr Suec 59:1–129

Laube S, Zotz G (2003) Which abiotic factors limit vegetative growth in a vascular epiphyte? Funct Ecol 17:598–604. doi:10.1046/j.1365-2435.2003.00760.x

Laube S, Zotz G (2006) Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. Ann Bot (Lond) 97:1103–1114. doi:10.1093/aob/mcl067

Löbel S, Snäll T, Rydin H (2006) Species richness patterns and metapopulation processes—evidence from epiphyte communities in boreo-nemoral forest. Ecography 29:169–182. doi:10.1111/j.2006.0906-7590.04348.x

Machon N, Bardin P, Mazer SJ, Moret J, Godelle B, Austerlitz F (2003) Relationship between genetic structure and seed and pollen dispersal in the endangered orchid *Spiranthes spiralis*. New Phytol 157:677–687. doi:10.1046/j.1469-8137.2003.00694.x

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman & Hall, London

Mehltreter K, Flores-Palacios A, García-Franco JG (2005) Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. J Trop Ecol 21:651–660. doi:10.1017/S0266467405002683

Migenis LE, Ackerman JD (1993) Orchid-phorophyte relationships in a forest watershed in Puerto Rico. J Trop Ecol 9:231–240

Miyazaki Local Meteorological Observatory (eds) (1951–1997) Monthly report of meteorology. Japan Weather Association Miyazaki Branch, Miyazaki (in Japanese)

Nieder J, Engwald S, Klawun M, Barthlott W (2000) Spatial distribution of vascular epiphytes (including Hemiepiphytes) in a lowland amazonian rain forest (Surumoni Crane Plot) of southern Venezuela. Biotropica 32:385–396

Ohnuki Y, Terazono R, Ikuzawa H, Hirata I, Kanna K, Utagawa H (1997) Distribution of colluvia and saprolites and their physical properties in a zero-order basin in Okinawa, southwestern Japan. Geoderma 80:75–93. doi:10.1016/S0016-7061(97)00076-1

R Development Core Team (2006) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna

Saito S (2002) Effects of a severe typhoon on forest dynamics in a warm-temperate evergreen broad-leaved forest in Southwestern Japan. J For Res 7:137–143. doi:10.1007/BF02762602

Sato T, Kominami Y, Saito S, Niiyama K, Manabe T, Tanouchi H, Noma N, Yamamoto S (1999) An introduction to the Aya Research Site, a long-term ecological research site, in a warm temperate evergreen broad-leaved forest ecosystem in southwestern Japan: research topics and design. Bull Kitakyushu Mus Nat Hist 18:157–180

Schmidt G, Zotz G (2002) Inherently slow growth in two Caribbean epiphytic species: a demographic approach. J Veg Sci 13:527–534. doi:10.1658/1100-9233(2002)013[0527:ISGITC]2.0.CO;2

Tamura T (1987) Landform-soil features of the humid temperate hills. Pedologist 31:135–146 in Japanese

Tamura T, Takeuchi K (1980) Land characteristics of the hills and their modification by man—with special reference to a few cases in the Tama hills, west of Tokyo. Geogr Rep Tokyo Metropol Univ 14/15:49–94

Tanouchi H, Yamamoto S (1995) Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. Vegetatio 117:51–60. doi:10.1007/BF00033258

Tremblay RL (1997) Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). Biotropica 29:38–45. doi:10.1111/j.1744-7429.1997.tb00004.x

Winter K, Wallace BJ, Stocker GC, Roksandic Z (1983) Crassulacean acid metabolism in Australian vascular epiphytes and some related species. Oecologia 57:129–141. doi:10.1007/BF00379570

Zimmerman JK, Olmsted IC (1992) Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. Biotropica 24:402–407. doi:10.2307/2388610

Zotz G, Vollrath B (2003) The epiphyte vegetation of the palm *Socratea exorrhiza*—correlations with tree size, tree age and bryophyte cover. J Trop Ecol 19:81–90. doi:10.1017/S0266467403003092

Zotz G, Ziegler H (1997) The occurrence of crassulacean acid metabolism among vascular epiphytes from Central Panama. New Phytol 137:223–229. doi:10.1046/j.1469-8137.1997.00800.x

Seed bank composition and above-ground vegetation in response to grazing in sub-Mediterranean oak forests (NW Greece)

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Abstract We investigate the persistent soil seed bank composition and its relation to the above-ground flora of grazed and non-grazed sub-Mediterranean deciduous oak forests of NW Greece. Twenty-eight taxa were recorded in the soil seed bank and 83 taxa (70 taxa in plots of seed bank sampling) in the above-ground vegetation. The dominant tree species and many woodland species found in the above-ground vegetation were absent from the soil seed bank. Similarity between the soil seed bank and the above-ground vegetation decreased with grazing, and grazing led to a decrease of species richness in above-ground vegetation and soil seed bank. Beta diversity of vegetation among grazed and among non-grazed plots did not differ, but was significantly higher between grazed and non-grazed areas. Beta diversity of the soil seed bank declined with grazing. When applying classification tree and logistic regression analyses, non-grazed forest sites are clearly differentiated by the presence of *Phillyrea latifolia*, *Euphorbia amygdaloides* and *Brachypodium sylvaticum*. PCA ordination of above-ground species composition reflected a gradient from sites grazed by ruminants to non-grazed sites, but no clear structure was detected in the seed bank.

Keywords Soil seed bank · Wood pasture · Grazing · Browsing · Deciduous oak forests · Greece · Wild boar · Ruminants

Introduction

The composition of a seed bank depends on present and former above-ground vegetation (Rice 1989) and seed rain from adjacent areas (Hutchings and Booth 1996). The historical composition of above-ground vegetation has often been identified as a key factor determining seed bank composition (Bekker et al. 1998). Soil seed bank composition is also influenced by the surrounding vegetation and former

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successional stages (Falinska 1999; Godefroid et al. 2006) and can undergo significant changes depending on the management applied (Wellstein et al. 2007). However, there is still considerable lack of knowledge on the seed bank characteristics of many species, including typical forest species (Bossuyt and Hermy 2001), and seed viability in forest soils (Grandström 1987; Thompson et al. 1997).

Mediterranean environments have undergone many changes due to human disturbances, such as sylvopastoralism (Le Houérou 1990). The effects of herbivory vary due to parameters such as intensity, plant taxa and soil properties. Species composition in European beech forests grazed by high densities of *Cervus elaphus*, *Cervus dama*, *Capreolus capreolus*, *Ovis musimon* and *Sus scrofa* has been significantly determined by two pathways: dispersal in time by a persistent seed bank, and dispersal in space using ungulates (Naaf and Wulf 2007). In the agricultural landscape of central Europe wild boars epizoochorously transport large amounts of seeds due to their fur characteristics, behaviour (wallowing and rubbing on trees), large local population size and general abundance (Heinken et al. 2006).

Ungulate species such as *Cervus elaphus*, *Capreolus capreolus* and *Sus scrofa* affect natural regeneration of forests throughout Europe. Selective browsing promotes changes in forest tree composition (Kuiters and Slim 2002). However, boars have different grazing behaviour from ruminants. Wild boars prefer acorns as a food source (Jedrzejewska et al. 1997), and forage on germinating oak seedlings, saplings and roots by digging, thus affecting both regeneration and soil properties (Groot Buinderink and Hazebroek 1996). Ruminants such as *Capreolus capreolus* and *Cervus elaphus* browse on seedlings, leading and lateral shoots causing structural changes (Pépin et al. 2006) and rub trunks resulting in tree damage (Ramos et al. 2006).

The role of browsing and grazing in woodland regeneration, and the long distance dispersal of seeds has been studied extensively. However, the impact of ruminant and boar grazing on soil seed bank composition, and its similarity to above-ground vegetation has received less attention. In different types of grasslands, grazing increases (Bakker and de Vries 1992; Ungar and Woodell 1996), decreases (Jutila 1998) or has no effect on (Peco et al. 1998) the similarity of seed banks and above-ground vegetation (Osem et al. 2006). For forests, discrepancies between above-ground vegetation and soil seed banks have been recorded (Thompson and Grime 1979; Bossuyt et al. 2002; Forrester and Leopold 2006; Roovers et al. 2006) and attributed to disturbance (Olano et al. 2002; Godefroid et al. 2006).

Earlier studies have investigated the seed bank composition of either undisturbed forests (Warr et al. 1994; Kjellsson 1992), or the relationship between seed bank composition and land use (Bossuyt and Hermy 2001; Brown and Oosterhuis 1981). Few studies on soil seed banks have investigated the impacts of differences and changes in management practices (Wellstein et al. 2007) and none, to our knowledge, have researched the impacts of overgrazing and different grazing regimes in sub-Mediterranean oak forests.

In the present study, we examine the hypothesis that long-term (more than 30 years) overgrazing affected not only the above-ground vegetation but also the seed bank of the seeds accumulated in the soil. A secondary goal of this study was to test the hypothesis that ruminant and non-ruminant grazers affect the soil seed bank and the above-ground vegetation in different ways. Above-ground vegetation and soil seed bank were analysed at the levels of species composition and richness (alpha diversity), and species turnover (beta diversity). The practical application of these findings is in the field of restoring heavily grazed woodlands in the Mediterranean region. Therefore, our results are discussed from the restoration point of view, to assess the potential role of soil seed banks in contributing to vegetation restoration after the cessation of overgrazing pressure.

Materials and methods

Study site

The research area is a deciduous mixed broad-leaved forest in north-western Greece (Bourazani area, municipality of Konitsa, Epirus), close to the Albanian border (40°02′ N, 20°38′ E). The forest was coppiced until a few decades ago. It consists of chiefly deciduous sub-Mediterranean thermophilous tree species with high proportions of *Quercus frainetto*, *Q. pubescens*, *Carpinus orientalis* and *Fraxinus ornus*, and scattered *Quercus cerris* and *Q. trojana*, while *Q. coccifera*, *Phillyrea latifolia*, *Cotinus coggygria* and *Juniperus oxycedrus* are common in the shrub layer (Tsaliki et al. 2005). The forests represent subtypes of the south-western Balkan association Verbasco glabrati-Quercetum frainetto (Quercion frainetto, Quercetalia pubescentis) (Bergmeier and Dimopoulos 2008).

The substrate is flysch locally substituted by limestone. The soils are shallow (15–30 cm) or of medium depth (30–60 cm). The topography of the study sites is hilly to mountainous (400–700 m a.s.l.). The climate is classified to sub-Mediterranean with a 4-month-long dry period (end of May to September) and about 700 mm average annual precipitation. Mean monthly temperatures range between 5°C in winter and 24°C in summer. Mean monthly rainfall ranges between 12 mm in July and 135 mm in December (Tsaliki et al. 2005).

The study site includes (A) a fenced, private wooded area (112 ha) grazed continuously since 1974 by ruminants and wild boar (*Sus scrofa*) in high but varying population densities, and (B) a non-fenced and non-grazed forest.

Site A, the fenced forest area (112 ha), was further subdivided into site A1 (26 ha) that was continuously grazed by wild boar and site A2 (86 ha) that was grazed by ruminants: *Dama dama*, *Cervus elaphus*, *Capreolus capreolus*, *Ovis musimon* and *Capra hircus cretica*. This subdivision and grazing practice precede our study by at least 30 years. As a result of over-grazing, the herb and litter layer of the oak woodland has almost completely vanished, soils are bare, compressed and eroded, and tree roots protrude from the ground.

Site B is adjacent to site A. During our study period, its vegetation cover and other ecological characteristics were similar to those of site A; however, the site was not systematically grazed. Therefore, samples from site B were used as controls (i.e. ungrazed sites) in the present study. This combination of overgrazed forests adjacent to undisturbed forests of identical climatic, geological and topographical conditions allows us to study the effect of grazing independently of other environmental parameters and is unique in the wider region.

Sampling

Above-ground vegetation was investigated in 42 permanent plots of 150 m^2. The plots were established in both grazed (22 plots, of which nine were grazed by wild boar and 13 by ruminants) and non-grazed (20 plots) forest sites.

In each plot, plant species composition (alpha diversity) was recorded twice: during spring-summer of 2004 and autumn of 2005. The data were combined into one data set so that the maximum number of species occurring in the above-ground vegetation of each plot is taken into account.

Of the 42 permanent vegetation plots, six plots were selected to sample the seed banks, and 20 sample soil cores were taken from each plot. The six plots were classified into the three types of grazing regime as follows:

Type 1: grazing by ruminants (R: ruminant regime sampled at two plots in site A2);
Type 2: grazing by wild boar (B: non-ruminant regime, sampled at one plot in site A1);
Type 3: no grazing by ruminants or boars (C: control, i.e. no grazing, sampled at three plots in site B).

As our research focused on the effects of grazing, our sampling scheme comprised three grazed plots (site A) and three ungrazed control plots (site B). In the grazed treatment there were two discrete sub-areas grazed by different species. In addition to the main research topic (grazed versus non-grazed), we regarded the two grazing treatments as well.

To assess the persistent seed bank composition, we collected soil samples at the end of May 2004, when germination had ended and before any new seeds were dispersed. Soil cores were sampled at two depths: 0–5 cm (upper layer) and 5–10 cm (deeper layer). In each plot we collected twenty soil samples, 10 for each depth (i.e. a total of 120 soil samples for the six plots studied). The quantitative and qualitative composition of the seed bank was investigated using the seedling emergence method (Thompson et al. 1997) and with the additional prior application of a 3-month period of artificial stratification, the soil samples were stored wet in a refrigerator, in the dark (3–5°C). The seedling emergence method, although laborious, is considered more reliable than elutriation for determining the species composition of the seed bank of a plant community (Gross 1990). Emerging seedlings were counted at regular intervals and, at a later developmental stage, identified to the closest taxonomic level possible (about 80% of the soil seed bank taxa were identified to the species level).

Data analysis

Similarity in species composition between seed bank and above-ground vegetation under different grazing regimes was assessed by Sørensen's qualitative similarity index (Kent and Coker 1994; Magurran 2004). We compared the values of the similarity index using the Mann–Whitney test. To measure the effect of grazing on the species richness of our samples, we used the Kruskall–Wallis test.

In order to descriptively display a structure of species composition possibly related to the grazing regimes, the indirect linear response model was used. Explorative ordinations (Principal Component Analysis, PCA) were carried out on the soil seed bank and above-ground vegetation species data, using CANOCO for Windows (ter Braak and Šmilauer 2002). All analyses were scaled on inter-species correlations and species-centred by dividing species scores by their standard deviation to obtain correlation matrices. Community parameters such as total cover were not taken into consideration, since our interest was focused on the presence of species with respect to possible grazing effects.

To test if the grazing regimes affect the species composition, we compared the samples from the different grazing regimes using two statistical methods: logistic regression and classification tree analysis. Classification trees have recently been applied to the analysis of ecological data (e.g. De'ath and Fabricius 2000; Kallimanis et al. 2005, 2007). They predict the value of a response variable (grazing regime in this study), from the values of a set of explanatory variables, which may be either numerical or categorical (Witten and Frank 2005). The basic assumption of this method is that the functional dependency among system variables is not uniform in the whole domain, but can be approximated as such on smaller sub-domains. Classification trees are induced by recursively dividing the data set to more homogeneous subsets. At each repetition, the most informative attribute is identified, and the data set is divided according to the values of that attribute. This process is repeated for each subset until pure datasets (i.e. datasets where all examples have the same value) or datasets that cannot be divided further are reached. Those datasets are the terminal "leaves" of our tree.

Species turnover (beta diversity) analysis

Beta diversity represents the spatial turnover of species and is a measure of changes in the species composition between two assemblages. There is a lack of agreement in the literature as to the feature of the pervasive spatial turnover in the identities of species that beta diversity is intended to capture, therefore there are several indices of beta diversity (see Koleff et al. (2003) for an extensive review on the subject). In this study, we estimated beta diversity according to the Colwell and Coddington (1994) index, which was calculated with the formula:

$$\beta = \frac{1}{n}\sum_{i=1}^{n}\left(1 - \frac{a_i}{b_i}\right)$$

where for every pairwise comparison i we estimated the number of species simultaneously present in both plots (a_i) and the total number of species recorded in the two plots (b_i), and n the total number of pairwise comparisons.

We analysed the species composition of six plots (three grazed and three ungrazed). To compare the patterns of beta diversity of seed bank and the patterns of beta diversity of vegetation, we used the same six plots for both analyses. Among those six plots there are a total of 15 possible pairwise comparisons. Three of these comparisons are among grazed plots and represent the beta diversity within grazed plots; three comparisons are among the ungrazed plots and represent the beta diversity within ungrazed plots. The nine remaining pairwise comparisons among grazed and ungrazed plots represent the beta diversity of the transition among grazed and ungrazed areas, i.e. between grazed and ungrazed treatments. Beta diversity was estimated for both above-ground vegetation and the soil seed bank.

Results

Effect of grazing on seed bank-vegetation similarity

The above-ground vegetation under different grazing regimes comprised 83 taxa, of which 70 taxa occurred in the above-ground flora of the six seed bank sampling plots; only 30% of these (21 taxa) were represented in the persistent soil seed bank, in which a total of 28 taxa were recorded (Table 1). Thus, 75% of the species found in the seed bank were also observed in the above-ground vegetation.

When comparing alpha diversity estimated as species richness of the samples (number of species per sample) from different grazing regimes, i.e. the species richness at the finest scale, we found that the difference was significant for both the above-ground vegetation (Kruskal Wallis $P < 0.0001$) and the soil seed bank ($P = 0.0003$). In the samples from control (non-grazed) plots more species were observed than in the samples from the grazed plots. Species richness in samples from the two grazing regimes did not differ significantly.

Next we analysed the extent of overlap between the species composition of the above-ground vegetation and the seed bank flora in each plot, i.e. how many of the species in the above-ground vegetation were present as seeds in the soil seed bank of each plot. Similarity of the above-ground vegetation with the seed bank flora varied considerably among the different plots (Table 2): it was higher in the non-grazed areas, and significantly lower in the grazed ones (Mann–Whitney $P = 0.046$ for the soil seed bank). In the grazed areas, similarity between above-ground vegetation and seed bank did not exceed 19%, and in the plots grazed by wild boar the similarity was 0%. In the non-grazed areas the similarity index reached 29%. Higher similarity was observed between ruminant and wild boar sites in above-ground vegetation (Table 2).

By applying logistic regression and classification tree analyses, we analysed the effect of grazing regimes on the species composition of the above-ground vegetation and the soil seed bank. Both approaches yielded similar results. Above-ground vegetation was clearly distinguished with small misclassification errors (12% for the tree model and 19% for the logistic regression) and high kappa statistic (0.8 and 0.7, respectively). The absence of *Phillyrea latifolia* indicates grazing by ruminants, while its presence in combination with the absence of *Euphorbia amygdaloides* and *Brachypodium sylvaticum* indicates grazing by wild boar (Fig. 1). The combined presence of *Phillyrea latifolia* and either *Euphorbia amygdaloides* or *Brachypodium sylvaticum* or both indicates non-grazed control plots. Contrary to the above-ground vegetation, seed bank

Table 1 Taxa found in three grazing regimes (R: ruminant, B: boar, C: control, i.e. non-grazed) for above-ground vegetation and soil seed banks in the six sampling plots

	Grazing regime		
	R	B	C
Taxa found only in the above-ground vegetation			
Acer campestre L.			×
Acer monspessulanum L.	×		×
Arbutus unedo L.			×
Aremonia agrimonoides (L.) DC.			×
Asparagus acutifolius L.		×	×
Bituminaria bituminosa (L.) C. H.Stirt.			×
Brachypodium sylvaticum (Hudson) Beauv.			×
Clematis vitalba L.			×
Clinopodium vulgare L.			×
Colutea arborescens L.			×
Cornus mas L.			×
Corylus colurna L.	×		×
Cotinus coggygria Scop.		×	×
Crocus chrysanthus (Herb.) Herb.			×
Cyclamen hederifolium Aiton			×
Echinops ritro L.			×
Epipactis microphylla (Ehrh.) Swartz			×
Galium lucidum All.			×
Geranium brutium Gasp.			×
Geranium purpureum Vill.			×
Hedera helix L.			×
Helleborus odorus subsp. *cyclophyllus* (A. Braun) Strid	×	×	
Juniperus oxycedrus L.			×
Lapsana communis L.			×
Lathyrus niger (L.) Bernh.			×
Lathyrus nissolia L.		×	
Melittis melissophyllum L.			×
Muscari neglectum Ten.	×		×
Osyris alba L.			×
Phillyrea latifolia L.		×	×
Poa trivialis L. subsp. *sylvicola* (Guss.) Lindb. fil.	×		
Potentilla micrantha DC.			×
Quercus cerris L.	×	×	×
Quercus coccifera L.			×
Quercus frainetto Ten.	×	×	×
Quercus pubescens Willd.	×	×	×
Quercus trojana Webb	×	×	×
Rosa gallica L.			×
Ruscus aculeatus L.			×

Table 1 continued

	Grazing regime		
	R	B	C
Sorbus domestica L.			×
Sorbus torminalis (L.) Crantz		×	×
Tamus communis L.			×
Tanacetum corymbosum (L.) Schultz Bip.			×
Thymus longicaulis C. Presl			×
Torilis arvensis (Hudson) Link			×
Trifolium ochroleucon Hudson			×
Trifolium pallidum Waldst. & Kit.			×
Trifolium tenuifolium Ten.			×
Vicia sativa L.			×
Number of taxa in each grazing regime	9	10	45
Total number of taxa in category: 49			
Taxa common to the above-ground vegetation and soil seed banks			
Campanula spec.	+		×
Carex flacca Schreb.	×	+	+/×
Carpinus orientalis Mill.		×	+/×
Cercis siliquastrum L.		×	+
Crataegus monogyna Jacq.		×	+/×
Dactylis glomerata L.	+		+/×
Dorycnium hirsutum (L.) Ser.			+/×
Euphorbia amygdaloides L.	+		+/×
Fraxinus ornus L.	×	×	+/×
Galium aparine L.			+/×
Gramineae			+/×
Inula salicina L.			+/×
Lathyrus laxiflorus (Desf.) O. Kuntze			+/×
Luzula forsteri (Sm.) DC.	+		+/×
Medicago lupulina L.			+/×
Silene italica (L.) Pers.	+		+/×
Trifolium arvense L.		+	+/×
Trifolium campestre Schreb.	+/×		×
Trifolium physodes Bieb.	+/×	×	+/×
Veronica chamaedrys L.	+/×	×	+/×
Viola alba Besser	+		+/×
Number of taxa in each grazing regime	11	8	21
Total number of taxa in category: 21			
Taxa found only in the soil seed banks			
Caryophyllaceae		+	
Parietaria judaica L.		+	
Petrorhagia cf. *saxifraga* (L.) Link	+		
Rubus sanctus Schreb.			+
Solanum nigrum L.			+
Sonchus asper (L.) Hill	+		+
Vicia cassubica L.			+
Number of taxa in each grazing regime	2	2	4
Total number of taxa in category: 7			
Total number of taxa in each grazing regime	21	19	70
Total number of taxa in Table: 77			

+ Indicates presence in the soil seed bank and × indicates presence in the above-ground vegetation

Table 2 Sørensen similarity index (%) between soil seed bank and above-ground vegetation in different grazing regimes

Type	Ruminant	Boar	Control
Ruminant	**19sv**	36v	23v
Boar	0s	**0sv**	24v
Control	32s	13s	**29sv**

v, Similarity among different types of above-ground vegetation; s, similarity among different soil seed banks; sv, similarity between soil seed bank and above-ground vegetation of the same type

Bold values represent the seed bank-vegetation similarity of the same type of grazing regime (i.e. between ruminants, between boar, between control plots)

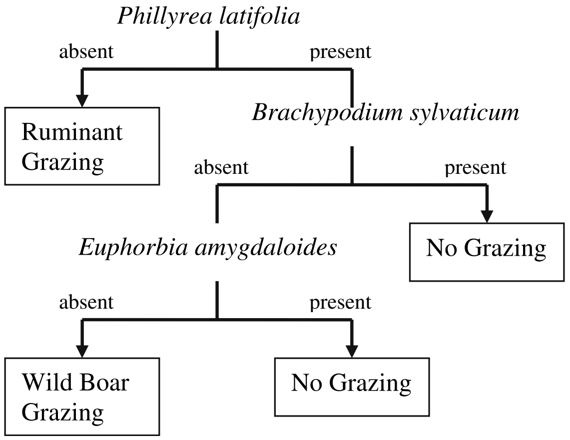

Fig. 1 Classification tree of the grazing regimes (ruminant, boar and no-grazing) on the basis of indicator plants. Each "leaf" is labelled according to presence-absence of the species *Phillyrea latifolia*, *Brachypodium sylvaticum* and *Euphorbia amygdaloides* in the above-ground vegetation. The misclassification error was minor (12%)

Table 3 PCA analysis on the above-ground vegetation; eigenvalues from ordination of plots for axes 1–4

Axes	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.249	0.107	0.083	0.066
Cumulative percentage variance of species data	24.9	35.6	43.9	50.5
Total inertia: 1.000				

species composition was not distinguishable by either logistic regression or classification tree analyses.

Examining the presence of particular species of the seed bank in more detail we find that frequent species like *Cotinus coggygria*, *Juniperus oxycedrus*, *Phillyrea latifolia*, *Quercus frainetto* and *Q. pubescens* are absent from the soil seed bank of the study area. Other less frequent species like *Hedera helix*, *Clematis vitalba* and *Lapsana communis* were also absent from the seed bank of the study area. On the other hand, some of the above-ground woody species *Carpinus orientalis*, *Cercis siliquastrum*, *Crataegus monogyna*, *Fraxinus ornus* and *Rubus sanctus* were found in the soil seed bank.

Ordinations of above-ground vegetation and soil seed banks

PCA ordinations were performed on the species presence data of the above-ground vegetation and soil seed bank separately. The first two PCA axes of the data set of the above-ground vegetation account for 36% of variance (see Table 3), a relatively low proportion that reflects a heterogeneous vegetation gradient structure. The first axis explains 25% of the variance reflecting a gradient of grazing intensity from the plots under heavy grazing conditions (left side of the diagram) to the non-grazed plots (right side of the diagram) (Fig. 2).

PCA on the soil seed bank composition did not reveal a clear structure of the identified species in relation to the differently grazed forest sites. In the ordination diagram of soil seed bank (not shown), species of grazed plots (left part along the first axis) were separated from species of non-grazed plots (right part along the first axis). The first two axes explained the bulk of the variance (31%) compared to the total variance of 49% explained by the first four axes (eigenvalues for the first four axes: 0.158, 0.150, 0.097 and 0.083, respectively).

Species turnover (beta diversity)

For the above-ground vegetation beta diversity among grazed plots did not differ significantly from beta diversity among non-grazed plots. However, the species turnover between grazed and non-grazed plots was significantly higher than the beta diversity within both grazing regimes (Kruskal–Wallis $P = 0.006$).

For the soil seed bank the differences in beta diversity were found to be statistically significant (Kruskal–Wallis $P = 0.005$). More precisely, beta diversity of grazed plots was significantly higher than that of non-grazed plots. Beta diversity between grazed and non-grazed plots was of intermediate value.

Discussion

Seed banks and above-ground vegetation compared

Approximately two-thirds of the taxa found in the vegetation did not occur in the soil seed bank of the study area; on the other hand, three-quarters of the soil seed bank taxa were found in the above-ground vegetation. This confirms the generally low similarity between above-ground vegetation and persistent soil seed bank floras in forest ecosystems, and that the above-ground vegetation does not necessarily reflect the soil seed bank composition (Olano et al. 2002). To our knowledge, this dissimilarity is reported for the first time in a sub-Mediterranean woodland. As expected, small-seeded species dominate the seed bank flora, while large-seeded species dominate the woody above-ground vegetation of the studied forest. Roovers et al. (2006) observed a similar pattern in a temperate mesophilous deciduous forest.

Looney and Gibson (1995) report that only few tree taxa of the above-ground vegetation were found in the soil seed bank, a fact attributed to animal predation and dormancy (Shen et al. 2007). Similarly, in our study some of the most frequent species like *Cotinus coggygria* (anemochorous), *Juniperus oxycedrus*, *Phillyrea latifolia* (both zoochorous), *Quercus frainetto* and *Q. pubescens* (both dispersed by gravity) are absent from the soil seed bank of the study area (not surprising of course for the latter two species, well known to bear recalcitrant seeds). Other species like *Hedera helix* are absent from the seed

Fig. 2 Ordination (PCA) species-samples diagram (species data set of 42 above-ground vegetation plots) along axes 1 and 2 (eigenvalues for the first two axes 0.249 and 0.107, respectively). The species are labelled by the first three letters of the generic name and the first three letters of the species epitheta (see Table 1 for full names). Plots are displayed as: ● boar-grazed plots; × ruminant-grazed plots; ■ control (i.e. non-grazed) plots

bank since they rarely produce seeds in shady habitats (Buckley et al. 1997). Another group of species with *Clematis vitalba* and *Lapsana communis* were absent from the seed bank of the study area, although they were found in seed banks of woody and disturbed habitats elsewhere (Roovers et al. 2006).

Some of the above-ground woody species were found in the soil seed bank: *Carpinus orientalis*, *Cercis siliquastrum*, *Crataegus monogyna*, *Fraxinus ornus* and *Rubus sanctus*. *Fraxinus ornus* and *Carpinus orientalis* are common tree species in the study area with noticeable regeneration in the sapling layer, thus contradicting Forrester and Leopold's (2006) observation that most of the dominant canopy species appearing in the soil seed bank are absent from the sapling and shrub layer of deciduous forests.

Effect of grazing on seed bank-vegetation similarity

In the studied sub-Mediterranean forest, grazing reduced the similarity between seed bank and above-ground vegetation. Especially in sites with wild boar, there were no common species between seed bank and vegetation. This finding is consistent with the general pattern of decreasing similarity between seed bank and vegetation under grazing (Marage et al. 2006; Haretche and Rodriguez 2006). In temperate forests, Heinken et al. (2006) found large numbers of seeds of chiefly non-forest species and others which occur both in forests and open habitats near trees rubbed by wild boar, and concluded that most plant species were dispersed epizoochorously by *Sus scrofa*. In our study, the wild boars were restricted inside the fenced area and it was therefore impossible for them to serve as long-distance vectors of diaspores (from outside the forest).

Effect of grazing on species richness

The impact of grazing on seed bank species richness and composition has been studied mainly in grasslands and to a lesser extent in forests, scrub and rangelands. In most studies species richness was found to decrease with grazing pressure (Marage et al. 2006; Miller 1999). However, two studies geographically close to our own (Heinken et al. (2006), temperate forest in Germany; and Malo et al. (2000), Mediterranean dehesas) showed the opposite, i.e. increase in the seed bank diversity under grazing. In our study, we found that species richness of the above-ground vegetation and the soil seed bank declined with grazing, thus confirming the general trend. We presume that contradictory statements in literature might be due to different grazing intensities and duration. Furthermore, our results indicate that long-term over-grazing as such is the determining factor and not the particular species of mammal, as the effects of ruminants and boars did not differ significantly.

Effects of grazing on beta diversity (species turnover)

The effect of grazing on beta diversity has recently attracted the interest of researchers, but presently no clear picture emerges from the literature. Although most studies found no effect (see Harrison 1999; Zhang 1998; Alrababah et al. 2007; Robson and Clay 2005), a few studies demonstrate increase (e.g. Bakker and Ruyter 1981) and others decrease (e.g. Chaneton et al. 2002) of beta diversity with grazing.

Our results show different effects of grazing on the beta diversity of the vegetation and the seed bank. Above-ground vegetation displayed no significant difference in the beta diversity among grazed and among non-grazed plots, but beta diversity was significantly higher between grazed and non-grazed plots. This finding and our community analysis results indicate that grazed and non-grazed plots are characterized by distinct species assemblages. Although the grazed plots had fewer species, these were not characterized by higher species turnover compared to the control plots. So our finding contradicts other studies that report increased beta diversity in areas with decreased alpha diversity (Kallimanis et al. 2008; Lennon et al. 2001).

Results for soil seed bank reflect a different picture, since species turnover was significantly higher in the grazed plots and our statistical analysis failed to identify distinct communities in the different grazing regimes, despite the existence of such communities in the above-ground vegetation. It is also indicative that the species turnover in the seed bank between grazed and non-grazed plots is lower than the respective one in the grazed plots. This discrepancy might indicate that the main seed dispersal mode is related to animals. This observation allows us to suggest that the zoochorous mode of dispersal and its role in shaping seed bank communities under grazing should be the focus of further study in the future.

Seed bank and restoration implications

Soil seed bank appeared consistent with the conclusion of Godefroid et al. (2006) that there is no close relationship between the species composition of the seed bank and that of the established vegetation. Thus, the seed bank is ‘capable’ of restoring the studied forests only to a limited extent. Studies on the restoration of forests through diaspores stored in the soil have also been carried out by Oke et al. (2006) and Warr et al. (1994), and the potential contribution of the soil seed bank to restoration of temperate deciduous forests has been recently investigated by Roovers et al. (2006).

Difficulties in the restoration of forests by soil seed banks are to be expected when the similarity between the above-ground species composition and that of the seed bank proves to be poor. Most of the dominant or frequent species of the herb layer rarely or never emerged from the soil samples of our forest, or from temperate forests with *Fagus sylvatica*, *Quercus robur* and *Pinus sylvestris* (Godefroid et al. 2006). Our study suggests that ruderal species in forest soil seed banks increase with grazing and typical non-weedy forest species decrease.

The potential of seed banks to restore communities is rather limited when many species of the community are either absent from the persistent seed bank or are not even able to create any seed bank at all (Handlova and Münzbergova 2006). The use of seed bank as a tool for restoration depends strongly on which taxa retain seeds able to recruit in degraded environments. The results presented in this study have implications on the restoration of heavily disturbed forests and are useful for the conservation management of overgrazed sub-Mediterranean forest types.

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References

Alrababah MA, Alhamad MA, Suwaileh A, Al-Gharaibeh M (2007) Biodiversity of semi-arid Mediterranean grasslands: impact of grazing and afforestation. Appl Veg Sci 10(2):257–264. doi:10.1658/1402-2001(2007)10[257:BOSMGI]2.0.CO;2

Bakker JP, de Vries Y (1992) Germination and early establishment of lower salt-marsh species in grazed and mown salt marsh. J Veg Sci 3:247–252. doi:10.2307/3235686

Bakker JP, Ruyter JC (1981) Effects of five years of grazing on a salt-marsh vegetation—a study with sequential mapping. Vegetatio 44(2):81–100. doi:10.1007/BF00133005

Bekker RM, Bakker JP, Kalamees R et al (1998) Seed size shape and vertical distribution in the soil: indicators of longevity. Funct Ecol 12:834–842. doi:10.1046/j.1365-2435.1998.00252.x

Bergmeier E, Dimopoulos P (2008) Identifying plant communities of thermophilous deciduous forest in Greece: species composition, distribution, ecology and syntaxonomy. Plant Biosyst 142(2):228–254. doi:10.1080/11263500802150357

Bossuyt B, Hermy M (2001) Influence of land use history on seed banks in European temperate forest ecosystems: a review. Ecography 24(2):225–238. doi:10.1034/j.1600-0587.2001.240213.x

Bossuyt B, Heyn M, Hermy M (2002) Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. Plant Ecol 162:33–48. doi:10.1023/A:1020391430072

Brown AHF, Oosterhuis L (1981) The role of buried seed in coppice woods. Biol Conserv 21:19–38. doi:10.1016/0006-3207(81)90066-5

Buckley GP, Howell R, Anderson MA (1997) Vegetation succession following ride edge management in lowland plantations and woods 2 The seed bank resource. Biol Conserv 82:305–316. doi:10.1016/S0006-3207(97)00025-6

Chaneton EJ, Perelman SB, Omacini M, Leon RJC (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. Biol Invasions 4(1–2):7–24. doi:10.1023/A:1020536728448

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc 345:101–118. doi:10.1098/rstb.1994.0091

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81(11):3178–3192

Falinska K (1999) Seed bank dynamics in abandoned meadows during a 20-year period in Bialowieza National Park. J Ecol 87:461–475. doi:10.1046/j.1365-2745.1999.00364.x

Forrester JA, Leopold DJ (2006) Extant and potential vegetation of an old-growth maritime *Ilex opaca* forest. Plant Ecol 183:349–359. doi:10.1007/s11258-005-9045-8

Godefroid S, Phartyal SS, Koedam N (2006) Depth distribution and composition of seed banks under different tree layers in a managed temperate forest ecosystem. Acta Oecol 29(3):283–292. doi:10.1016/j.actao.2005.11.005

Grandström A (1987) Seed viability of fourteen species during five years of storage in a forest soil. J Ecol 75:321–331. doi:10.2307/2260421

Groot Buinderink GWTA, Hazebroek E (1996) Wild boar (*Sus scrofa scrofa* L.) rooting and forest regeneration of podzolic soils in the Netherlands. For Ecol Manag 88:71–80. doi:10.1016/S0378-1127(96)03811-X

Gross KL (1990) A comparison of methods for estimating seed numbers in the soil. J Ecol 78(4):1079–1093. doi:10.2307/2260953

Handlova V, Münzbergova Z (2006) Seed banks of managed and degraded grasslands in the Krkonose Mts., Czech Republic. Folia Geobot 41:275–288. doi:10.1007/BF02904942

Haretche F, Rodriguez C (2006) Soil seed bank of an Uruguayan grassland under different grazing practices. Ecol Austral 16(2):105–113

Harrison S (1999) Native and alien species diversity at the local and regional scales in a grazed Californian grassland. Oecologia 121:99–106. doi:10.1007/s004420050910

Heinken T, Schmidt M, von Oheimb G (2006) Soil seed banks near rubbing trees indicate dispersal of plant species into forests by wild boar. Basic Appl Ecol 7(1):31–44. doi:10.1016/j.baae.2005.04.006

Hutchings MJ, Booth KD (1996) Studies on the feasibility of re-creating chalk-grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. J Appl Ecol 33(5):1171–1181. doi:10.2307/2404696

Jedrzejewska B, Jedrzejewski W, Bunevich AN, Milkowski L, Krsinski ZA (1997) Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriol (Warsz) 42(4):399–451

Jutila H (1998) Seed banks of grazed and ungrazed Baltic seashore meadows. J Veg Sci 9:395–408. doi:10.2307/3237104

Kallimanis AS, Kunin WE, Halley JM, Sgardelis SP (2005) Metapopulation extinction risk under spatially autocorrelated disturbance. Conserv Biol 19(2):534–546. doi:10.1111/j.1523-1739.2005.00418.x

Kallimanis AS, Ragia V, Sgardelis SP, Pantis JD (2007) Using regression trees to predict alpha diversity based upon geographical and habitat characteristics. Biodivers Conserv 16:3863–3876. doi:10.1007/s10531-007-9186-2

Kallimanis AS, Halley JM, Vokou D, Sgardelis SP (2008) The scale of analysis determines the spatial pattern of woody species diversity in the Mediterranean environment. Plant Ecol 196:143–151. doi:10.1007/s11258-007-9341-6

Kent M, Coker P (1994) Vegetation description and analysis. A practical approach. Wiley, Chichester

Kjellsson G (1992) Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. Ecography 15:86–100. doi:10.1111/j.1600-0587.1992.tb00012.x

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J Anim Ecol 72:367–382. doi:10.1046/j.1365-2656.2003.00710.x

Kuiters AT, Slim PA (2002) Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biol Conserv 105:65–74. doi:10.1016/S0006-3207(01)00204-X

Le Houérou HN (1990) Agroforestry and sylvopastoralism to combat land degradation in the Mediterranean Basin: old approaches to new problems. Agric Ecosyst Environ 33:99–109. doi:10.1016/0167-8809(90)90236-7

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. J Anim Ecol 70:966–979. doi:10.1046/j.0021-8790.2001.00563.x

Looney PB, Gibson DJ (1995) The relationship between the soil seed bank and above-ground vegetation of a coastal barrier island. J Veg Sci 6:825–836. doi:10.2307/3236396

Magurran AE (2004) Measuring ecological diversity. Blackwell, Oxford

Malo JE, Jiménez B, Suarez F (2000) Herbivore dunging and endozoochorous seed deposition in a Mediterranean dehesa. J Range Manag 53(3):322–328. doi:10.2307/4003440

Marage D, Rameau JC, Garraud L (2006) Soil seed banks and vegetation succession in the Southern Alps: effects of historical and ecological factors. Can J Bot 84(1):99–111. doi:10.1139/b05-142

Miller PM (1999) Effects of deforestation on seed banks in a tropical deciduous forest of western Mexico. J Trop Ecol 15:179–188. doi:10.1017/S0266467499000747

Naaf T, Wulf M (2007) Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. For Ecol Manag 244:141–149. doi:10.1016/j.foreco.2007.04.020

Oke SO, Oladipo OT, Isichei AO (2006) Seed bank dynamics and regeneration in a secondary lowland rainforest in Nigeria. Int J Bot 2(4):363–371

Olano JM, Caballero I, Laskurain NA (2002) Seed bank spatial pattern in a temperate secondary forest. J Veg Sci 13(6):775–784. doi:10.1658/1100-9233(2002)013[0775:SBSPIA]2.0.CO;2

Osem Y, Perevolotsky A, Kigel J (2006) Similarity between seed bank and vegetation in a semi-arid annual community: the role of productivity and grazing. J Veg Sci 17:29–36. doi:10.1658/1100-9233(2006)017[0029:SBSBAV]2.0.CO;2

Peco B, Ortega M, Levassor C (1998) Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. J Veg Sci 9:815–821. doi:10.2307/3237047

Pépin D, Renaud P-C, Boscardin Y, Goulard M, Mallet C, Anglard F, Ballon P (2006) Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings—an exclosure-based experiment. For Ecol Manag 222:302–313. doi:10.1016/j.foreco.2005.10.034

Ramos JA, Bugalho MN, Cortez P, Iason GR (2006) Selection of trees for rubbing by red and roe deer in forest plantations. For Ecol Manag 222:39–45. doi:10.1016/j.foreco.2005.10.017

Rice KJ (1989) Impacts of seed banks on grassland community structure and population dynamics. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, pp 212–230

Robson BJ, Clay CJ (2005) Local and regional macroinvertebrate diversity in the wetlands of a cleared agricultural landscape in south-western Victoria, Australia. Aquat Conserv: Mar Freshw Ecosyst 15(4):403–414. doi:10.1002/aqc.675

Roovers P, Bossuyt B, Igodt B, Hermy M (2006) May seed banks contribute to vegetation restoration on paths in temperate deciduous forest? Plant Ecol 187:25–38. doi:10.1007/s11258-006-9130-7

Shen Y, Liu W, Cao M, Li Y (2007) Seasonal variation in density and species richness of soil seed banks in karst forests and degraded vegetation in central Yunnan, SW China. Seed Sci Res 17:99–107. doi:10.1017/S0960258507708139

ter Braak CJF, Šmilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca

Thompson K, Grime JP (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J Ecol 67:893–921. doi:10.2307/2259220

Thompson K, Bakker J, Bekker R (1997) The soil seed banks of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge

Tsaliki M, Bergmeier E, Dimopoulos P (2005) Vegetation patterns and plant diversity in mixed oak woodlands in the region of Bourazani, Epirus (NW Greece). Bot Chron 18:209–235

Ungar IA, Woodell SRJ (1996) Similarity of seed banks to aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower Peninsula, South Wales. Int J Plant Sci 157(6):746–749. doi:10.1086/297398

Warr SJ, Kent M, Thompson K (1994) Seed bank composition and variability in five woodlands in south-west England. J Biogeogr 21:151–168. doi:10.2307/2845469

Wellstein C, Otte A, Waldhardt R (2007) Seed bank diversity in mesic grasslands in relation to vegetation type management and site conditions. J Veg Sci 18:153–162. doi:10.1658/1100-9233(2007)18[153:SBDIMG]2.0.CO;2

Witten IH, Frank E (2005) Data mining. Practical machine learning tools and techniques, 2nd edn. Morgan Kaufmann, San Francisco

Zhang W (1998) Changes in species diversity and canopy cover in steppe vegetation in Inner Mongolia under protection from grazing. Biodivers Conserv 7(10):1365–1381. doi:10.1023/A:1008852017493

On the detection of dynamic responses in a drought-perturbed tropical rainforest in Borneo

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Abstract The dynamics of aseasonal lowland dipterocarp forest in Borneo is influenced by perturbation from droughts. These events might be increasing in frequency and intensity in the future. This paper describes drought-affected dynamics between 1986 and 2001 in Sabah, Malaysia, and considers how it is possible, reliably and accurately, to measure both coarse- and fine-scale responses of the forest. Some fundamental concerns about methodology and data analysis emerge. In two plots forming 8 ha, mortality, recruitment, and stem growth rates of trees $\geq$10 cm *gbh* (girth at breast height) were measured in a 'pre-drought' period (1986–1996), and in a period (1996–2001) including the 1997–1998 ENSO-drought. For 2.56 ha of subplots, mortality and growth rates of small trees (10–<50 cm *gbh*) were found also for two sub-periods (1996–1999, 1999–2001). A total of *c*. 19 K trees were recorded. Mortality rate increased by 25% while both recruitment and relative growth rates increased by 12% for all trees at the coarse scale. For small trees, at the fine scale, mortality increased by 6% and 9% from pre-drought to drought and on to 'post-drought' sub-periods. Relative growth rates correspondingly decreased by 38% and increased by 98%. Tree size and topography interacted in a complex manner with between-plot differences. The forest appears to have been sustained by off-setting elevated tree mortality by highly resilient stem growth. This last is seen as the key integrating tree variable which links the external driver (drought causing water stress) and population dynamics recorded as mortality and recruitment. Suitably sound measurements of stem girth, leading to valid growth rates, are needed to understand and model tree dynamic responses to perturbations. The proportion of sound data, however, is in part determined by the drought itself.

Keywords Dynamics · Perturbation · Drought · Stem growth · Tree mortality · Validity

Introduction

Stochastic fluctuations in the environment are thought to play an important role in driving the long-term dynamics of tropical rain forests and in determining their structure and species composition (Newbery and Lingenfelder 2004, 2009). Droughts, fires, floods and hurricanes are notably examples of such external climatic influences. In South-East Asia, under normally aseasonal climatic conditions, it is droughts that probably have the most sustained and repeated

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effects on the forests. These periods of reduced precipitation are often associated with the El Niño-Southern Oscillation (ENSO) cycle (Walsh 1996; Walsh and Newbery 1999), a global process with its origins in changes in sea-surface temperature and air pressure in the Pacific Ocean (Trenberth 1997; Trenberth and Hoar 1997).

The ENSO reaches back 130,000 years and events are known to have affected Borneo for at least 18,000 years (Walsh and Newbery 1999; Cane 2005). They result in occasional moderate droughts which are an integral component of the environment (Walsh and Newbery 1999). Away from the eastern coast of Borneo, at the inland site of Danum (in Sabah, Malaysia) for instance, the tree species of the lowland dipterocarp forests appear well adapted to the correspondingly moderate perturbations to the ecosystem that the droughts cause (Newbery et al. 1999; Gibbons and Newbery 2003; Newbery and Lingenfelder 2004, 2009).

Compared to the preceding century, the last 30 years have shown an increase in the frequency and intensity of ENSO events (Trenberth et al. 2007). The trend had been expected by the earlier analyses of Hulme and Viner (1998), Timmermann et al. (1999, 2004) and IPCC (2001). Other recent models, however, lend less support to an increase continuing in the near future (Cane 2005; McPhaden et al. 2006; Meehl et al. 2007), even though when ENSO events do occur they may lead to a higher risk of strong drought (Christensen et al. 2007). Given that the prognoses are weak it remains important to be prepared for either an increase in droughts or a stabilization of the earlier pattern because it certainly will have profound implications on how the forests should be best conserved and managed.

All tropical rain forests can be viewed as being continuously in various complex and overlapping states of recovery from past perturbations, whether these are singular or closely timed multiple events, happening recently or in the more distant past (Newbery et al. 1999; Newbery and Lingenfelder 2004). Measuring precisely how the forests respond to currently occurring perturbations may lead nearer to reliable models which can estimate how increases and decreases in frequency and/or intensity of perturbation might affect their persistence.

After the last strong ENSO-related drought in 1997/1998 several studies have been conducted on the ecological effects of such short, but significant periods of drought stress on trees in South-East Asia (Nakagawa et al. 2000; Harrison 2001; Potts 2003; Ichie et al. 2004; Newbery and Lingenfelder 2004; Slik 2004). They variously concluded that some forest's species were well adapted to a moderate drought regime whereas for those of other forests this was not so evident. The focus was also mainly on recording mortality—growth and recruitment receiving less attention—and drought was simply defined to take effect when the 30-day running total (*30-d-rt*) of rainfall fell <100 mm. Plots and tree sample sizes were sometimes quite small, and the area measured may not have been fully representative of local topographic variation.

Drought is a stochastic factor and frequency and intensity of its complex effects requires careful consideration. Soil water status before and during an event, as well as the replacement of depleted soil water after it, need to be taken in to account using a dynamic approach based, for example, on the idea of 'antecedent rainfall history' proposed by Newbery and Lingenfelder (2009). In addition, since climatic variation is occurring at the scale of decades, and not annually or per century, only long-term measurements over 20–30 years that capture forest dynamics before and after a drought for several years (at minimum close to the return time of the event) are likely to provide enough ecologically meaningful information. To have such records for repeated droughts at the same and other replicated locations would of course be ideal.

From previous work in Borneo, it was concluded that the forest at Danum is most likely still recovering from a very strong drought *c*. 130 years ago and that it is well adjusted to coping with repeated lesser droughts that have happened since then. Seen at the scale of many centuries, the forest is perhaps in a state of dynamics equilibrium, with variously large and small 'set backs' occurring at different points in time (Newbery et al. 1992, 1996, 1999). Behind this process lies the dynamics of the individual species and how they are adapted to the actual physiological effects of the drought perturbations (Newbery and Lingenfelder 2004, 2009). Their responses will collectively determine the resilience of the ecosystem, i.e., how fast and to what extent it can recover after perturbation. In this context the pressing question, for both natural and secondary managed forests, is whether species selected under the past environmental history are able to survive as well as before when droughts come more intensely and closer together in the future.

Species-specific tree responses to the moderate perturbation regime at Danum have been presented recently by Newbery and Lingenfelder (2009). The present paper describes the structure of the permanent research plots at Danum and analyses tree dynamics between 1986 and 2001 in detail at the plot and subplot levels. The focus here is on the response of the whole forest to drought, particularly to the 1997/1998 ENSO-related event, in terms of mortality, recruitment and growth rates. Several field methodological and data analytical problems are tackled. These have wider relevance to tropical forest dynamics in general, and highlight some important limitations to conclusions that can be drawn from recensussing studies. The aims of the present study were thus: (1) to quantify the effect of the 1997/1998 main drought on forest dynamics at Danum, (2) to investigate the interactions between tree size and topography on dynamics, (3) to refine the treatment of stem growth estimates for aims 1 and 2, and (4) to place the dynamics responses into the frame of the forest ecosystem.

Methods

Study site

Location

The study site lies within the 438-km^2 Danum Valley Conservation Area (DVCA), Sabah, Malaysia, 66 km inland of Lahad Datu on the N.-E. coast of Borneo. The DVCA is an uninhabited and unlogged part of the 9730-km^2 Yayasan Sabah Concession Area; human artefacts suggest that there might have been some earlier settlement or visitation (Marsh and Greer 1992). The vegetation around the site is primary lowland dipterocarp forest of the *Parashorea malaanonan* category (Fox 1972). The topography is gently undulating, and the soils are mainly orthic acrisols of the Bang association which developed on sandstone and mudstone of the geological Kuamut-Formation (Wright 1975). Further details of the site are given in Newbery et al. (1992, 1996, 1999).

Climate

The climate at Danum Valley Field Centre (DVFC, 4°57′48″ N, 117°48′10″ E, 152 m a.s.l.) is typical of equatorial rainforest locations (Walsh and Newbery 1999) with the mean daily range of temperature (8.6°C) being larger than the monthly mean range (1.8°C) about an annual mean temperature of 26.8°C, high relative humidity and high annual rainfall (mean *c*. 2800 mm). There is no clear dry season indicating that Danum has a generally aseasonal tropical climate. Further details can be found in Newbery and Lingenfelder (2009).

Between 1985 and 2003, Danum experienced 19 low precipitation events of which one was ecologically severe (event centred in 1998), two moderately strong (1987 and 1992) and five of weaker intensity, as shown by antecedent rainfall history analysis (Newbery and Lingenfelder 2009). Severe droughts across large parts of Borneo that were probably stronger than the one in 1997/1998 were recorded in 1877/1878, 1914/1915 and just before the setting up of the main plots at Danum in 1982/1983 (Beaman et al. 1985; Walsh 1996; Walsh and Newbery 1999) and most likely affected them. The events of 1877/1878, 1982/1983, and 1997/1998 were the three strongest El Niño-events in terms of sea-surface temperature anomalies in the 'ENSO 3'-region since 1876, where reliable reconstructions can be made (IPCC 2001). Since that time droughts of weak to moderate intensity have occurred frequently across Sabah (3.25 times per 20 years) and the frequency of strong droughts at Danum was 1.54 per 20 years on average (Walsh 1996; Walsh and Newbery 1999).

Design

In 1985–1986, two permanent plots were first set up and enumerated (Newbery et al. 1992, 1996). They are located *c*. 0.8 km NW of DVFC, just north of Main Trail West on gently undulating terrain with elevations of 208–254 m a.s.l. Plot 2 lies *c*. 280 m parallel to, and west of, plot 1. The plots are rectangular in shape (each 100 m × 400 m, area = 4 ha) with the longer sides oriented north-south. Each was divided into 100 units of 20 m × 20 m (small subplots) and their corners marked with belian (ironwood) posts.

Relative differences in elevation and slopes within the plots are very similar (39–43 m; Fig. 1). Plot 1 includes steep east-facing slopes in its northern half: in plot 2 an episodic small stream cuts two small ridges with steep slopes. Interpolating from 20-m × 20-m-grid elevational data, ridge areas ($\geq$25 m, relative to SW-plot corners of 0 m) covered 18% and 33%, and lower slope areas (<12 m) 32% and 36% of the planimetric surfaces of plots 1 and 2, respectively. Of plot 1, 31% is flat (<10° inclination) and 14% is steep ($\geq$20°; max. 33°). In plot 2, the corresponding values are 26% and 18% (max. 31°). More than half of the area of each plot lies on intermediate slopes (10–20°).

Enumerations

Previous to 2001: background

The first enumeration of the plots was between 24 August 1985 and 15 December 1986 (median 15 March 1986; Fig. 2). Within each subplot, every living tree with a minimum stem girth at breast height (*gbh*) of 10 cm ($\geq$3.2 cm *dbh*) was mapped, tagged, (and identified) and its *gbh* measured at a painted mark, usually 1.3 m above ground (see Newbery et al. 1992, for details). The second enumeration was between 8 November 1995 and 23 February 1997 (median 18 June 1996; Fig. 2), in which all trees were recorded for alive/dead status and the *gbh* of survivors remeasured. Surviving trees that had grown to $\geq$10 cm *gbh* (recruits) were mapped, tagged, identified, and measured (see Newbery et al. 1999). The first and second enumerations each lasted 1.3 years. The mean time interval for the two plots was 10.0 years.

Eight 40-m × 40-m (large) subplots in each main plot, half of them on lower slopes and the other half on ridges, had been measured between 20 December 1998 and 29 March 1999 (median 25 January 1999;

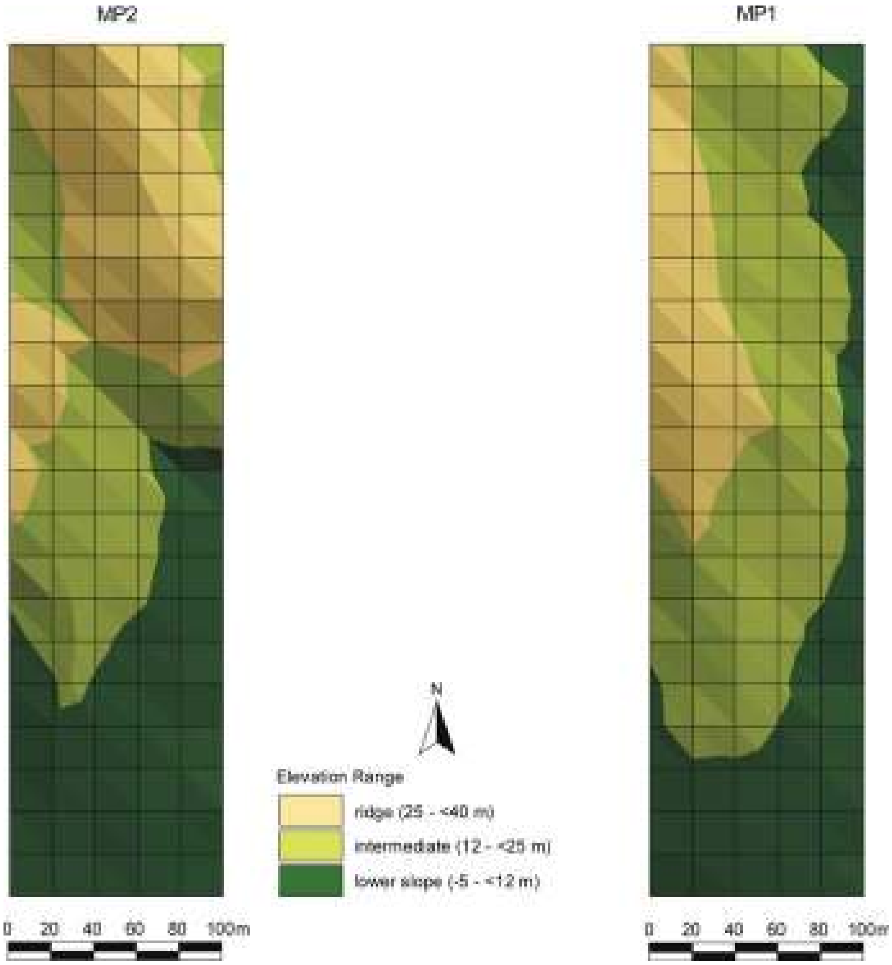


Fig. 1 Topographic variation within the two 4-ha permanent plots in the Danum Valley Conservation Area, Sabah, Borneo

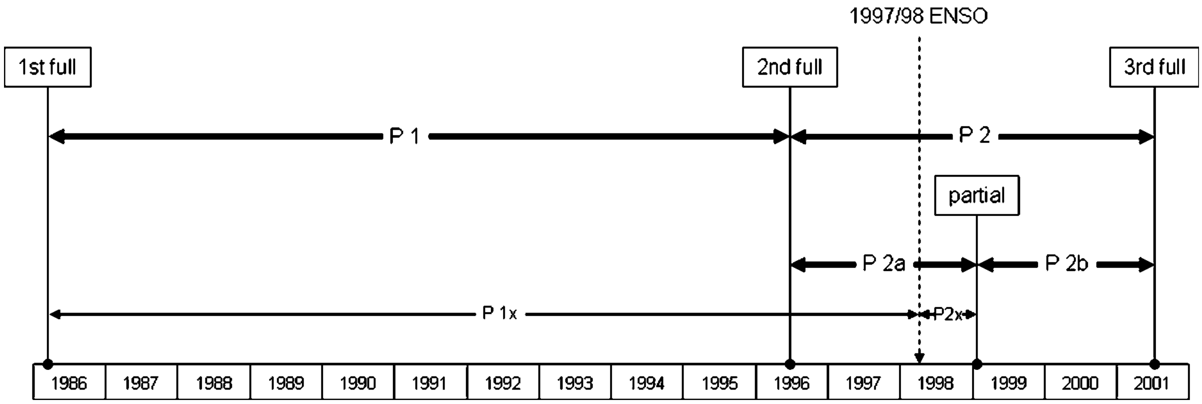


Fig. 2 The sampling scheme at Danum showing the dates of the three full and one partial enumeration, the timing of the 1998 ENSO drought and the corresponding periods (P1, P2) and subperiods (P2a, P2b), and the extension of P1 (P1x) and the estimated immediate post-drought sub-period (P2x)

Fig. 2). Each consisted of four small subplots in a square, as defined in Newbery and Lingenfelder (2004). Subplots were selected in a stratified random manner and represented 2.56 ha (32%) of the main plot area. In 1999, all 1996-recorded trees ≥10 cm *gbh* were scored for alive/dead status and surviving small trees (10 – <50 cm *gbh*) remeasured: recruits and regressors were not registered in 1999.

In 2001: advancements

The third full enumeration of the plots was conducted between 26 February 2001 and 4 February 2002 (median 29 June 2001, Fig. 2), taking nearly 1 year (109 field days). The mean time interval from the second enumeration was 5.0 years (Lingenfelder 2005). Dead trees were recorded in five status classes (e.g., dead standing or dead-broken: missing stems were assumed to be dead. Status of survivors was recorded in seven classes, e.g., undamaged or broken (see Supplementary materials—Appendix 1).

Stems of surviving trees were inspected at the paint-mark of the previous point of measurement (PoM). If the paint-mark was lost, a new one was established at 1.3 m on the uphill side of the tree or at the nearest suitable point on the stem avoiding stem deformations and obstructions. The same procedure was followed if a stem was broken below the old PoM and a new shoot had to be measured. Unless deformation was too great to allow remeasurement, *gbh* at the old PoM was measured and an alternative PoM was established at the nearest suitable point, and measured. An alternative PoM was also established if buttresses were already influencing stem growth, or was seen likely to do so in the next 5 years. In the latter case, the PoM was moved to at least 1 m above the buttress. This strategy of adding alternative PoMs was started in 1996 to ensure that at least in two consecutive enumerations the tree was measured at the same PoM. Alternative PoMs established in 1996 were utilized in 92 instances in 2001 (Lingenfelder 2005). PoM (original, new, etc.) and condition of the stem (CoS; e.g., stem normal or deformed) at that point were recorded in six and 16 classes, respectively (Supplementary materials—Appendix 1). Height of the PoM (if not at 1.3 m) was also noted.

Girth (*gbh*, to nearest mm) was measured with a thin 2-m steel tape, and for larger trees a wider 5-m one, after lightly cleaning the bark at the PoM. Trees with multiple stems ≥5 cm *gbh*, and of which one was ≥10 cm *gbh*, were included and a single hypothetical *gbh*-value found from their combined basal areas. When it was impossible to insert the tape under a constricting liana, callipers were used to measure tree diameter, taking two readings at 90° to one another. For trees where the PoM had to be moved upwards to > *c.* 2 m, a ladder was used. For trees with PoMs at *c.* >4 m ($n = 48$ trees), stem diameter was measured optically with a laser ranging instrument (Criterion 400, Laser Technology Inc., Centennial, USA), again with two readings taken at 90° apart. Method of measurement was recorded in five classes (Supplementary materials—Appendix 1). Recruits surviving the interval since the second enumeration, were mapped, tagged, painted, (identified) and measured.

To make use of the additional 1999 partial enumeration of the large subplots, trees of the same size class and subplots in the 1986, 1996 and now 2001—enumerations were selected. Because no recruits were recorded in 1999, n_{99} was lowered, and to have used this value mortality rates in sub-period 2b would have been overestimated. Accordingly, recruits in 1996 and 2001 were also excluded from the subplot data set. Individual trees were allocated to the three topographic classes as defined for the main plots; numbers of trees in the intermediate locations were *c.* half those on the ridges and lower slopes.

Calculations

The three sets of measurements are referred to as the '1986-', '1996-', '1999-' and '2001-enumerations'; the resulting time intervals as 'period 1' (1986–1996) and 'period 2' (1996–2001). Period 2 divided into two sub-periods: 2a (1996–1999, 2.6 years) and 2b (1999–2001, 2.4 years) when including the 1999-enumeration on the subplot level (Fig. 2). These periods and subperiods might be thought of as 'pre-drought', 'drought' and post-drought', except that period 1 was not free of any droughts (Newbery and Lingenfelder 2004), the length of the sub-period encompassing the 1997–1998 major event is arbitary, and post-drought effects did begin well before 1999. Analysis within different sizes was performed for trees with the following *gbh* limits: all, $\geq$10 cm *gbh* ($\geq$3.2 cm *dbh*); small, 10–<50 cm *gbh* (3.2–<15.9 cm *dbh*); medium, 50–<100 cm *gbh* (15.9–<31.8 cm *dbh*); and large, $\geq$100 cm *gbh* ($\geq$31.8 cm *dbh*). To allow comparison with some other studies, measures were also found for the population of trees with a *dbh* of $\geq$10.0 cm ($\geq$31.4 cm *gbh*).

Some trees above the minimum *gbh*-limit at first measurement were (due to natural shrinking, bark loss, slight measurement errors, or because multiple-stemmed trees lost one or more of their stems) too small at the second enumeration, and not being part of the population they were labelled 'regressors'. Between the second and third enumerations regressors either died, remained with *gbh* less that the minimum value, or regrew above that value. In the last case, a regressor was not viewed as a new recruit because it was a member of the population of trees $\geq$10 cm *gbh* at an earlier enumeration (original tag number used). This problem of trees regressing below the minimum size and potentially re-growing above that limit in a subsequent enumeration is addressed in Supplementary materials—Appendix 2 ('Losses and gains').

Basic dynamic rates

Periodic (m_p, r_p; %) and annualized (m_a, r_a; % year^{-1}) rates were found for mortality and recruitment, respectively, after Alder (1995) and Sheil et al. (1995), on the plot or subplot level for different size classes, using the mean time intervals of each individual group (see Supplementary materials—Appendix 3 for formulae). Confidence limits (95%) of m_a and r_a were estimated with an approximation based on the F-distribution. Correction of m_a for the differences in length of time interval (5-year basis) followed the method of Sheil and May (1996), as applied to the Danum data set in Newbery and Lingenfelder (2004). Absolute (*agr*; mm year^{-1}) and relative (*rgr*; mm m^{-1} year^{-1}) stem growth rates were similarly found (Supplementary materials—Appendix 3).

Growth rate calculations were based here on intervals of each individual tree. As frequency distributions of *rgr* values were always very strongly positively skewed, and no transformation could normalize, or a suitable probability density function be found as yet to model them, a bootstrapping procedure ($N = 2000$ runs) was used to find means and 95% confidence limits of these variables. Comparisons on this basis are to be made within each period separately. The database was handled in Microsoft Access and statistical analyses performed with GenStat versions 7 and 8 (Payne et al. 2007). Individual growth values were used for two reasons: (1) interest lay in topographic effects and differences between tree size classes, which were nested within plots; and (2) the limits would correspond to those derived for mortality rates which are de facto within-plot estimates also. Where confidence limits did not overlap means were judged to be significantly different ($\alpha = 0.05$). Growth rates were also found separately for trees that lived, and those that died, in a successive period.

Validity of growth rates

For each enumeration (except the one of 1986, when this information was not gathered) every tree was reviewed for suitability of its girth measurements with regard to calculating growth rates, and assigned a code accordingly: 1 = suitable, 0 = unsuitable. Growth rates were considered valid (i.e., sound) only if both start and end measurements were suitable. Measurements were unsuitable where (1) the status code showed that the tree was broken below, half-broken or dead at the PoM, or had lost one or more of multiple stems; (2) the CoS indicated major deformations due to buttress growth, cracked or split bark or stems, excrescence, fluted or hollow stems, termites or lianas (an irregular stem (CoS = DI) was not considered a major deformation unless additional notes in the remarks revealed this, e.g., 'heavy', 'extremely oval', or 'spiral growth'); (3) POMs were moved or newly established (except on recruits), or the laser ranging instrument was used. The use of callipers on liana-fused trees was only considered a reason for exclusion where it was not possible to take two measurements or the callipers were too small.

From the resulting valid rates, some trees had additionally to be excluded because they had negative growth rates below an operational threshold. To separate those values that resulted from faulty measurements or recording errors from those that would very likely be part of the population (e.g., due to slight shrinkage because of low stem water content, unapparent loss of bark), the approach developed by Newbery et al. (1999) was followed and applied to the 1996–2001 data set: relative frequencies, expressed as proportions, of all growth rates with *agr* ≤ 0 mm year^{-1} were logit-transformed and plotted in increasingly negative *agr*-classes. Both plots separately and combined showed an almost linear decline to -3.5 mm year^{-1}. Below that value (i.e., ≤ 4.0 mm) the distribution increased slightly, decreased again and then flattened, indicating that these values were probably not part of the 'natural' population (Lingenfelder 2005).

Spatial autocorrelation

As the growth of trees across an area might not be statistically independent from each other, the data set was explored for spatial autocorrelation (SAC). The analysis is based on mean valid relative growth rates of 10-m × 10-m subplots to account for the at-places rapidly changing topography within the main plots; a 20-m × 20-m subplot could be partly located on a flat ridge area but steeply sloping down into an intermediate elevation. Moran's test for SAC was calculated (Moran's I; using `moran.test` of the `spdep` package (Bivand 2007 in R 2.6.1, R Development Core Team 2007) and plotted at 5-m intervals across distances of 0–100 m across the whole plots as well as per hectare to investigate stationarity. Anisotropy was checked with a routine in S-Plus, Version 7.0 (Kalunsky et al. 1998). The effects of topography (elevation and slope) on *rgr* were investigated with a spatial conditional autoregression (CAR) model estimation by maximum likelihood (`spautolm` in `spdep`; Bivand 2007) and ordinary regression (R Development Core Team 2007). The models included linear, quadratic and cubic terms. Based on a likelihood ratio test (of the spatial coefficient; within `spautolm`) it was decided whether CAR spatial specification improved the model.

Results

Forest structure

Total numbers of trees in the main plots decreased by 299 and 679 in periods 1 and 2, respectively. Considering only trees with *gbh* $\geq$10 cm, the corresponding decreases were 677 and 642. The large difference for period 1 was due to regressors being excluded and gains included (Table 1). On an annual basis, tree numbers (*gbh* $\geq$10 cm) in period 2 declined almost twice as fast (128 stems year^{-1}) as in period 1 (68 stems year^{-1}). Results for the individual plots are given in Supplementary materials—Appendix 3.

With some slight variability between the plots, tree density decreased for all and for small trees in the two periods by 4% (Table 2 and Supplementary materials—Appendix 3). It increased for medium-sized and large trees in period 1 (by 5%), yet the density of medium-sized trees decreased in period 2 (by 2%) and did not change for large trees, the latter due to a 3% decrease in plot 1 but a 3% increase in plot 2. Recruits and dead trees had lower densities in period 2 than 1, largely due to the differing interval lengths. On an annual basis, the density of recruits increased by 7%, while the density of dead trees increased by 32%. The contribution of dead trees that had been regressors in 1996 was 1% of all trees (or 9% of all dead trees) in

Table 1 Numbers of trees at Danum for periods 1 (1986–1996) and 2 (1996–2001), two main plots combined, from those at the starts (n_{start}) to the ends (n_{end}), and showing the numbers that survived (n_s), died (n_d), recruited (n_r), were gained (n_{gains}) and lost (n_{losses})

	Period	
	1	2
n_{start}	17942	17643
$n_{start\_\geq 10}$	17942	17265
n_d	2655	1938
$n_{d\_reg\_p1}$		182
$n_{d\_\geq 10}$		1756
n_s	15287	15705
n_{reg}	378	341
n_{losses}	3033	1931
$n_{s\_\geq 10}$	14909	15364
n_r	2356	1259
$n_{reg\_p1\_\geq 10}$		30
n_{gains}	2356	1289
n_{end}	17643	16964
$n_{end\_\geq 10}$	17265	16623
$n_{diff\_\geq 10}$	−677	−642

The subscript ≥10 refers to numbers of trees with *gbh* ≥10 cm *gbh* (For details at the plot level, see Supplementary materials—Appendix 3)

$n_{d\_reg\_p1}$: number of regressors of period 1 that were found dead in period 2; n_{reg}: number of regressors in period 2: old(remaining) = 166, new = 175; $n_{reg\_p1\_\geq 10}$: number of regressors of previous period, *gbh* in 2001 ≥ 10 cm

Table 2 Densities of trees (n trees ha^{-1}) in the main plots at Danum in 1986, 1996 and 2001 for three size classes of tree

	1986	1996	2001
Size class			
All (≥ 10 cm *gbh*)	2243	2158	2078
Small (10 to <50 cm *gbh*)	2033	1939	1863
Medium (50 to <100 cm *gbh*)	146	153	150
Large (≥100 cm *gbh*)	63	66	66
≥31.4 (≥10 cm *dbh*)	432	452	435
Recruits		295	157
Dead (≥10 cm *gbh*)		332	220
Dead (regressors 1996)			23

For details at the plot level, see Supplementary materials—Appendix 3

2001 (Table 2). From 1986 to 2001, density decreased for all and small trees but increased for medium-sized and large trees. The ratio of densities in three size classes within each main plot was close to 90:7:3 for small, medium and large trees, respectively, over the three enumerations (Supplementary materials—Appendix 3).

The 16 subplots, with the restrictions applied, had 5190, 4239, 3885 and 3706 in 1986, 1996, 1999 and 2001, respectively. Small trees represented 91% of all trees in 1986 and 86% at the other three enumerations. During period 1 and sub-periods 2a and 2b, 741, 237 and 213 small trees, respectively, died, so that the original population in 1986 lost 23% of its trees by 2001 through mortality, 6% (293 trees) either regressing to <10 cm *gbh* or advancing to ≥50 cm *gbh*. Mean density (2027 ha^{-1}) in 1986 was similar to that of the main plots (cf. Table 2), but mainly as a consequence of the missing recruits, these values steadily declined to 1448 ha^{-1} by 2001. The mean number of small trees per subplot was 266 ($n = 16$, range, 169–386).

Coarse-scale dynamics

Basic rates

In period 1 (1986–1996) almost 15% of trees died across both plots and in period 2 (1996–2001) 11% died (Table 3). Differences between the two replicate plots were apparent in period 1: in plot 1 the periodic mortality rate was 4% above that in plot 2 (Supplementary materials—Appendix 3). In period 2 the difference between plots in m_p was much less (<1%). Annualized mortality was 45% higher in period 2 for both plots combined (Table 3a). The relative increase of m_a in plot 1 was almost twice that in plot 2 (33 vs. 61%) and m_a values in period 2 were correspondingly more similar than in period 1 (Supplementary materials—Appendix 3).

Based on a 5-year interval, the correction of m_{all} (the overall average mortality resulting from the taxa- and subplot-wise grouped mortalities) produced the expected result for period 1: shifting the annual mortality from 10 to 5 years using the correction factors (1.115 for plot 1 and 1.220 for plot 2) calculated from the data set where the rarest species were excluded ($n_{min} = 2$), increased mortality rates by 13% and 24% in plots 1 and 2, respectively. As the intervals of period 2 were similar for plot 1 (5.06 years) and plot 2 (4.94 years) and both of these were very close to an average of 5.0 years, m_{all} did

Table 3 Forest dynamics of the main plots at Danum for periods 1 (1986–1996) and 2 (1996–2001), trees ≥10 *gbh*: rates of mortality, recruitment and growth, and the estimated overall mortality based on species' rates

	Period	
	1	2
m_p (%)	14.80	10.98
m_a (% year^{-1})	1.59	2.30
r_p (%)	13.13	7.14
r_a (% year^{-1})	1.24	1.39
agr (mm year$^{-1)}$	3.05	3.12
rgr (mm m^{-1} year^{-1})	11.15	12.48
m_{all} (% year^{-1})	–	2.34[a]
m_{corr}	1.87[a]	–

For details at the plot level, see Supplementary materials—Appendix 3

m_p, m_a: periodic and annual mortality (all trees, including regressors: n_d/n_{start}); r_p, r_a: periodic and annual recruitment; agr, rgr: absolute, and relative, growth rate in stem girth; m_{all}: overall average mortality with species within subplots as groups; m_{corr}: m_{all} corrected to 5-year basis (no correction for period 2)

[a] Means of plot 1 and 2 values

not need an interval correction. On this basis of the foregoing considerations, mortality increased by 20% in plot 1 and by 31% in plot 2 between periods 1 and 2. The mortality rates for both plots combined were thus 1.87 and 2.34% year^{-1} in periods 1 and 2, respectively, implying an increase by 25% between the periods. Rates for trees ≥10 cm *dbh* are given in Supplementary materials—Appendix 3 also.

Periodic recruitment rate in period 2 was just over half of that in period 1, as expected from the differing time intervals (Table 3). Recruitment was lower than mortality in both periods and both plots. The annualized recruitment rate in period 2 was 12% chigher than that in period 1, for both plots combined. The changes in r_a between the periods were, however, smaller than for m_a and the two plots rather diverged than converged with time: plot 1 had a 16% higher recruitment rate in period 2 than 1 whereas in plot 2 it increased by just 7%. Thus plot 1 increased its prominence in regard to recruitment rate. Absolute (*agr*) and relative (*rgr*) growth rates were 9–17% higher in plot 1 than plot 2 (Supplementary materials—Appendix 3). Between periods 1 and 2 *agr* increased by 2.3% (from 3.05 to 3.12 mm year^{-1}) and *rgr* by 11.9% (from 11.2 to 12.5 mm m^{-1} year^{-1}; plots combined). The frequency distributions of *agr* and *rgr* were nevertheless strongly positively skewed.

Effects of tree size and topography

In periods 1 and 2 m_a was higher on intermediate positions and lower slopes than on ridges (Table 4), and did not differ greatly between size classes within topographic classes (Fig. 3). Considering the individual plots, however, the m_a of medium-sized trees in plot 1 was approximately double that in plot 2, a much larger difference than in the other size classes (Supplementary materials—Appendix 4). In period 2, m_a increased with size for all topographic classes combined (Fig. 3d), a reflection especially of the large (1.6-fold) difference between small and large trees in plot 1 (Supplementary materials—Appendix 4). This increasing trend with size was most clearly shown on the ridges (Fig. 3a), while on the lower slopes m_a was highest among the medium-sized trees (Fig. 3c), and intermediate positions had a complex pattern in between (Fig. 3b). In the small, medium and large size classes, m_a was overall 31, 42 and 94%, respectively, higher in period 2 than 1. The increase in m_a across periods was strongest for

Table 4 Comparison of annualized mortality (m_a, % year^{-1}), recruitment (r_a, % year^{-1}) and relative stem growth rates (rgr, mm m^{-1} year^{-1}) in plots 1 and 2 combined at Danum in three topographic classes for periods 1 (1986–1996) and 2 (1996–2001)

Topographic class	m_a		r_a		rgr	
Period:	1	2	1	2	1	2
Ridge	1.34 [1.25–1.43]	1.93 [1.78–2.09]	1.19 [1.12–1.26]	1.31 [1.19–1.43]	10.52 [10.10–11.00]	12.71 [12.22–13.30]
Intermediate	1.63 [1.55–1.71]	2.19 [2.06–2.33]	1.26 [1.20–1.32]	1.27 [1.17–1.36]	11.43 [11.04–11.83]	11.99 [11.59–12.49]
Lower slope	1.75 [1.66–1.85]	2.19 [2.05–2.34]	1.27 [1.20–1.33]	1.67 [1.56–1.78]	11.32 [10.90–11.78]	12.88 [12.36–13.42]

Numbers in square brackets are the 95% confidence limits (bootstrapped in case of *rgr*). Numbers of trees at the starts of the intervals (m_a) or numbers of valid trees (*rgr*) are found in Supplementary materials—Appendix 4 medium-sized trees in plot 2 with a 2.25-fold increase (Supplementary materials—Appendix 4). Again, it was the intermediate position (averages over size classes) that showed the largest differences between plots (plot 2 almost 40% higher than plot 1). Considering interactions between size class, topography and plot, the most marked changes were the increase in m_a of large trees on ridges plot 1 (period 2 > 5-fold period 1), and the amelioration for medium-sized trees in the intermediate position in plot 2. Small trees were in general much less affected. Between plot differences were important.

Recruitment was also lowest on ridges although differences between locations were smaller than for mortality (Table 4). Furthermore, r_a hardly changed on intermediate locations between periods, increased moderately (10%) on ridges but rather strongly (32%) on lower slopes (Table 4). Relative growth rates were higher in period 2 than 1 by 11, 21 and 18% in small, medium and large size classes, respectively (Table 4, Fig. 4d). Except for medium-sized trees in period 1, growth rates were higher in plot 1 than 2 in both periods, especially strongly for the small trees (Supplementary materials—Appendix 4). Relative growth rates generally decreased with increasing size class in both plots and both periods, more pronounced on ridges and intermediate positions (Fig. 4a, b) than on lower slopes in period 1 (Fig. 4c), while in period 2 the trend was broken by medium-sized trees on the intermediate positions performing marginally better

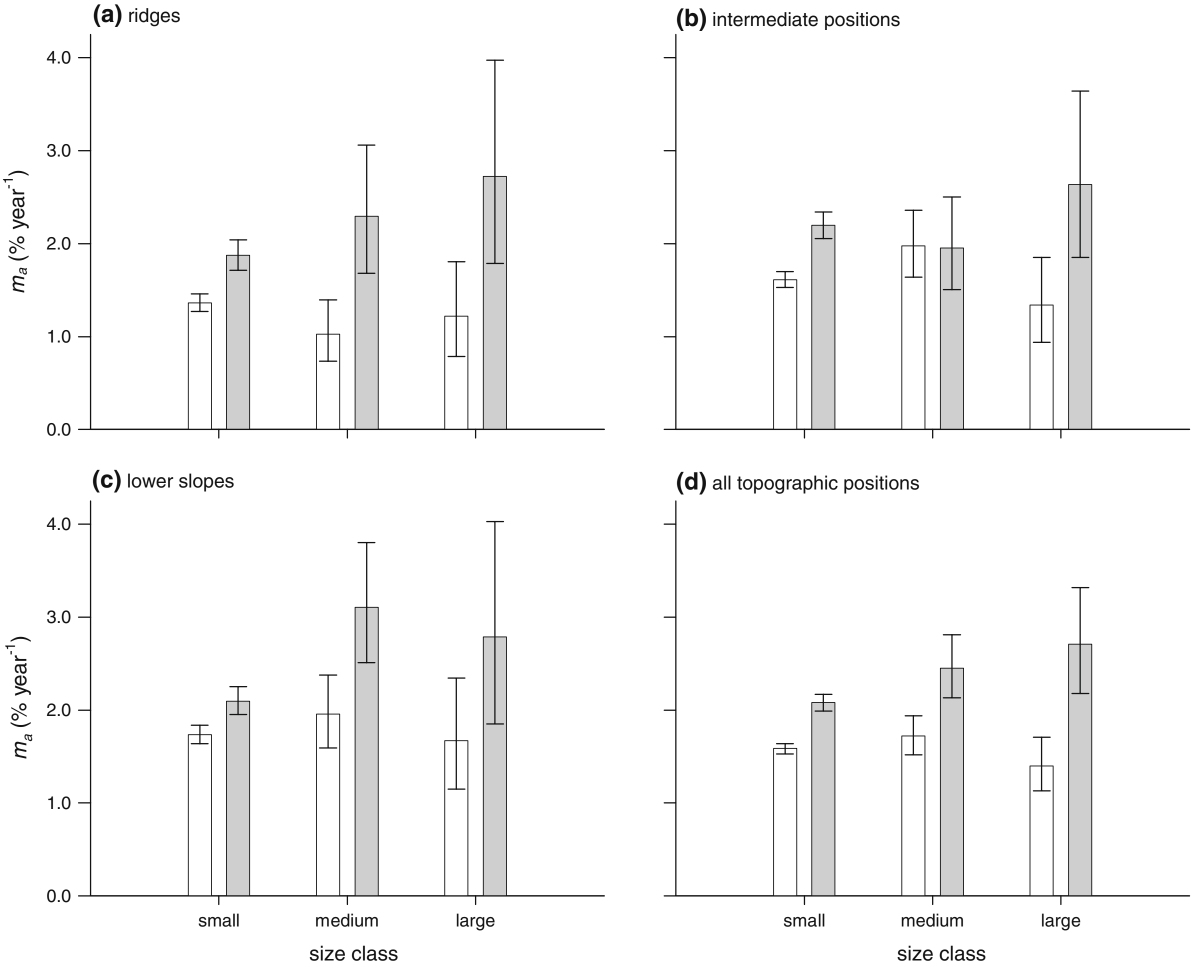


Fig. 3 Mortality rates within size and topographic classes in the main plots at Danum: m_a (% year^{-1}) for period 1 (*open bars*) and period 2 (*grey bars*) in the main classes of small, medium and large trees **a** on ridges, **b** at intermediate positions, **c** on lower slopes, and **d** for all topographic classes combined. Bars indicate 95% confidence limits

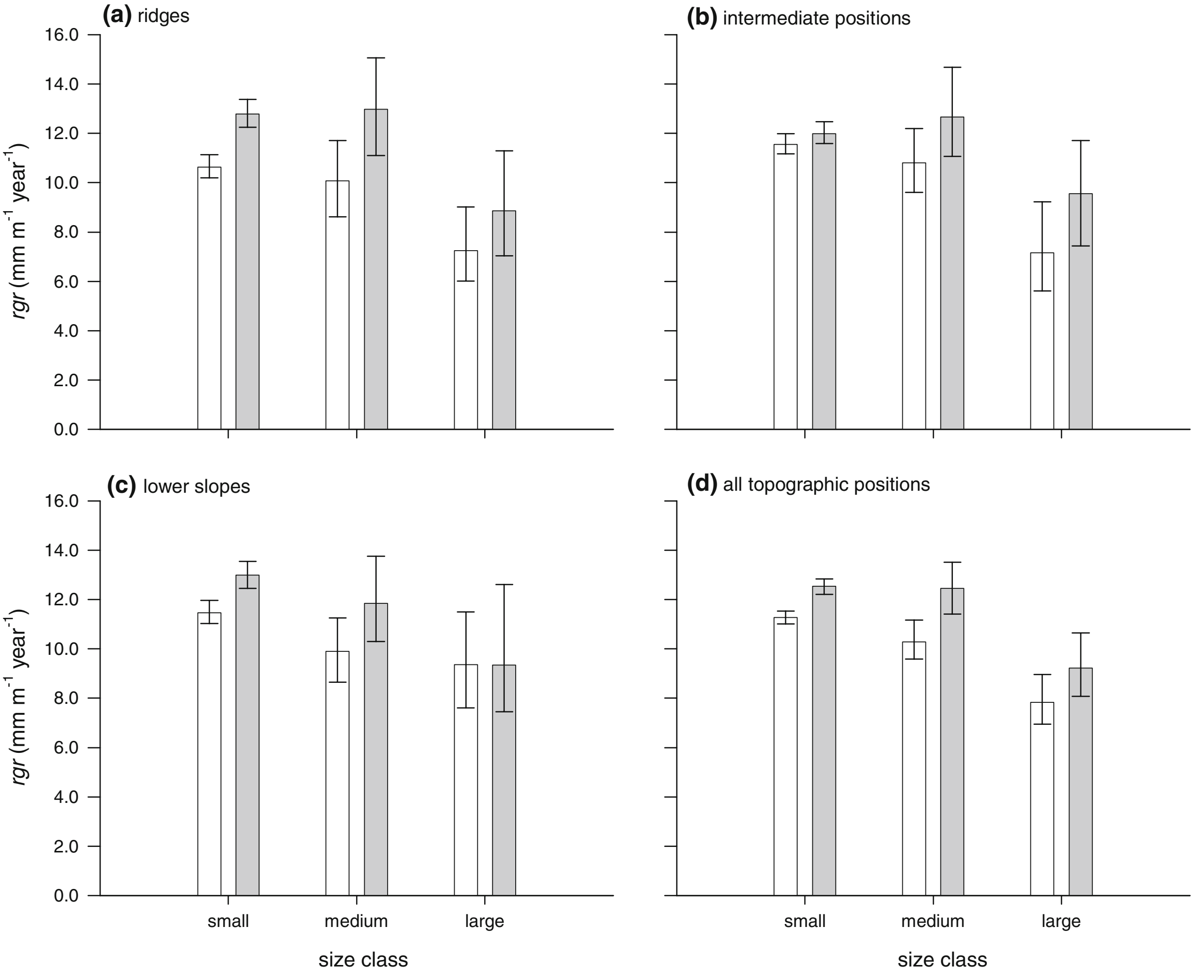


Fig. 4 Relative growth rates within size and topographic classes in the main plots at Danum: *rgr* (mm m^{-1} $year^{-1}$) for period 1 (*open bars*) and period 2 (*grey bars*) in the main classes of small, medium and large trees **a** on ridges, **b** at intermediate positions, **c** on lower slopes, and **d** for all topographic classes combined. Bars indicate 95% confidence limits

relative to the other size classes. Trees on intermediate positions had 22% and 39% higher mean *rgr* in plot 1 than 2 in periods 1 and 2, respectively (Supplementary materials—Appendix 4). Among the plot–plot differences (far fewer than for m_a) only one more is noteworthy: a >50% lower *rgr* in plot 2 than plot 1 for large trees in intermediate positions in period 1.

Growth, topography and spatial autocorrelation

Spatial autocorrelation (Moran's I) was detected for distances up to 25 m (period 1) in main plot 1 and up to 60 m (period 2, when neglecting the significant cases after some insignificant distances) in main plot 2 (Supplementary materials—Appendix 5). There was no sign of anisotropy but SAC showed non-stationarity, i.e., varying effect across both plots. Regular regression models showed very mixed results. There was a significant fit for main plot 1 of *rgr* on just elevation in period 1 ($P < 0.01$) and on slope in period 2 ($P < 0.01$), however, the variance accounted for in those cases was very small (2.5% and 1.7%, respectively). Likewise, for plot 2, the fit of *rgr* on elevation was significant in periods 1 and 2 ($P < 0.001$) but only for slope in period 2 ($P < 0.01$): r^2 lay between 3.2% and 9.2% in those cases. Spatial specification led to an improvement of the model in main plot 2: CAR of *rgr* on elevation and on slope had a significantly improved fit in periods 1 and 2 (LR probability <0.001 in three cases, <0.05 in one case). In plot 1, CAR led to no significantly improved fits. Interaction between the periods and elevation and slope was low.

Fine-scale dynamics

Basic rates

Annualized mortality rate (m_a) increased by 42% between period 1 and sub-period 2a, but by only 7% between sub-periods 2a and 2b (Table 5a). Correcting to the basis of $t = 5$ years and $n_{min} = 2$ (correction factors = 1.109, 0.834 and 0.849 for (sub-) periods 1, 2a and 2b, respectively; see Lingenfelder 2005), m_{corr} increased by just 6% between period 1 and sub-period 2a, and by 9% between sub-period 2a to 2b. Mean relative growth rates across subplots declined by 38% between period 1 to sub-period 2a but recovered substantially by 98% in sub-period 2b, 23% higher than in period 1 (Table 5b). All 16 subplots had lower *rgr* (−4 to −82%) in period 2a than in period 1, but only two decreased further in *rgr* (−8 to −16%) during period 2b. Of the 14 subplots with higher *rgr*, seven increased by >100% (up to 275%) compared to period 2a. Against period 1, seven subplots had lower *rgr* in period 2b, but in nine subplots growth was still elevated above the level of the pre-drought period (three subplots with >100%). Variability of growth rates was higher in sub-period 2b than before, pointing—after the more uniform reaction (reduced growth) immediately after the drought—to a strong positive, but spatially diverse response of trees starting *c.* 1 year after the drought.

Effects of tree size and topography

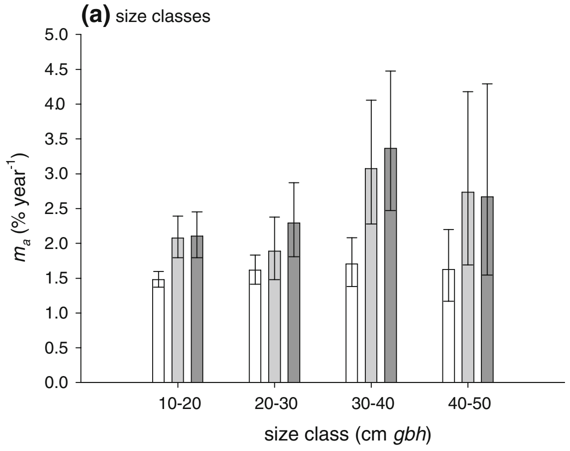
Small trees were divided into four 10-cm size classes, and in all of these mortality rates of sub-periods 2a and 2b were higher than in period 1 (Fig. 5a). The strongest increase in mortality of sub-period 2a over period 1 was in the 30–40 cm class (80%) with a smaller increase in sub-period 2b (10%), so that m_a in this size class almost doubled between period 1 and sub-period 2b. The 20–30 cm size class exhibited the strongest increase in m_a between sub-periods 2a and 2b (22%). All trees were affected immediately in sub-period 2a, most severely those 30 − <50 cm *gbh*. In sub-period 2b, trees 20–<40 cm still had increasing m_a but those 10–<20 and 40–<50 cm *gbh* appeared to be relatively less affected (Fig. 5a).

Small trees on lower slopes experienced higher m_a in period 1 than those on ridges and intermediate locations. In sub-period 2a, mortality in all topographic classes increased strongly by 25–65%, but the differences between classes were smaller than in period 1, trees on ridges showing a slightly higher mortality than those on lower slopes. Period 2b showed a further increase of mortality on the ridges (9%) and intermediate elevations (48%), but a decrease (16%) on lower slopes. Trees on intermediate elevations reached the highest mortality rates across the three topographic classes and periods (3.05% year^{-1}). Comparing m_a of sub-period 2b with that of period 1, the intermediate class more than

Table 5 Estimates of annualized mortality rate for small trees in subplots, and the rate corrected for differences in interval length for period 1 and sub-periods 2a and 2b at Danum, and the corresponding mean subplot (±SE) absolute (*agr*) and relative (*rgr*) stem growth rates

	Period / Subperiod		
	1	2a	2b
(a) Annualized mortality (% year^{-1}):			
Mean (m_a)[a]	1.53	2.17	2.32
Overall mean at $t = 5$ years (m_{all})	1.57	2.06	2.18
Corrected overall mean (m_{corr})	1.70 ± 0.11	1.81 ± 0.10	1.97 ± 0.23
(b) Growth rates:			
agr (mm year^{-1})	2.44 ± 0.18	1.60 ± 0.13	2.91 ± 0.33
rgr (mm m^{-1} year^{-1})	11.12 ± 0.79	6.90 ± 0.54	13.68 ± 1.56

[a] Weighted mean m_a values across subplots were almost identical



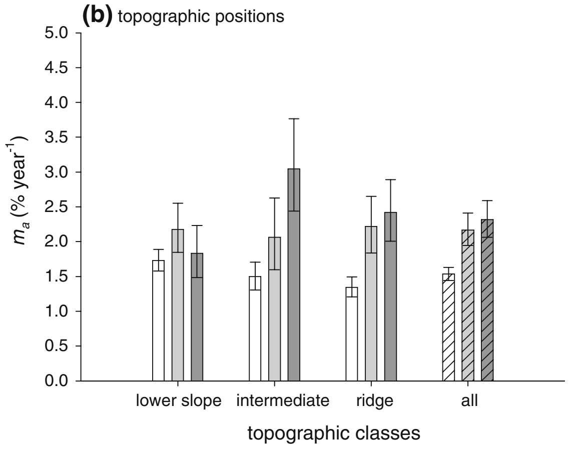
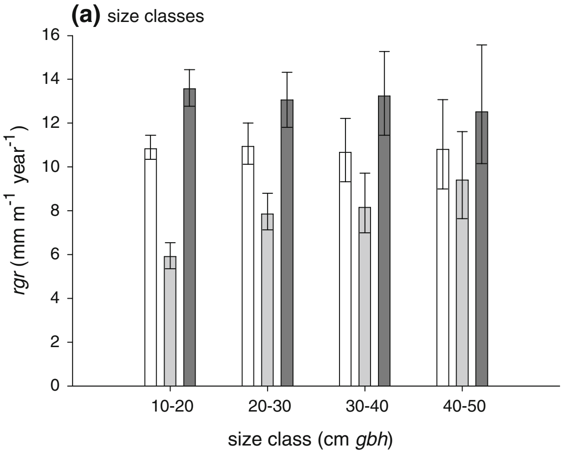


Fig. 5 Mortality rates of small trees in the subplots at Danum (m_a, % year^{-1}) for period 1 (*open bars*), and subperiods 2a (*light grey bars*) and 2b (*dark grey bars*): **a** in four 10-cm *gbh* classes, and **b** for three topographic classes. Bars indicate 95% confidence limits

doubled (increased by 104%) in mortality and ridges had 80% higher mortality but m_a for trees on lower slopes was elevated by only 6% (Fig. 5b).

The decline of *rgr* between period 1 and sub-period 2a, and subsequent recovery between sub-periods 2a and 2b was apparent across all size classes, this becoming less pronounced with increasing size (Fig. 6a). Mean growth rate of the smallest trees (10–<20 cm *gbh*) in sub-period 2a was 45% lower than in period 1 but increased by 129% between period 1 and sub-period 2b. All size classes had higher *rgr* in sub-period 2b compared to period 1 (by 16–25%). Differences in growth between size classes were small in period 1 and more variable in sub-periods 2a and 2b. During sub-period 2a, growth rates increased with size class: the smallest trees were most affected by the drought (Fig. 6a). Trees on intermediate topographic locations had the highest *rgr* in period 1, and also showed the greatest decline between period 1 and sub-period 2a (−45%) compared to trees on ridges and lower slopes (Fig. 6b). Trees on lower slopes grew slightly better than those on ridges in period 1 and sub-period 2a. Trees on ridges were more affected in sub-period 2a (40% less *rgr* than in period 1) but recovered better than those on lower slopes in sub-period 2b (135 vs. 65%, respectively, compared to period 2a) and then displayed the strongest gain in growth compared to period 1 (42%) and the highest rates of all topographic classes in all periods (Fig. 6b). Analysis for



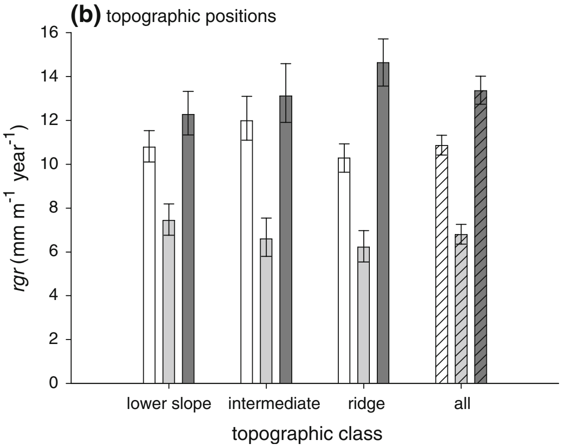


Fig. 6 Relative growth rates of small trees in the subplots at Danum (*rgr*, mm m^{-1} year^{-1}) for period 1 (*open bars*), and subperiods 2a (*light grey bars*) and 2b (*dark grey bars*): **a** in four 10-cm *gbh* classes, and **b** at three topographic classes. Bars indicate 95% confidence limits

SAC in subplots showed even fewer significant fits than on the whole plot level, again with little variance accounted for. Including the CAR model only proved to be useful in one case (main plot 1, sub-period 2b).

Growth and subsequent mortality

In period 1, the growth of trees that died between 1996 and 1999 was a little more than half of that of trees that were still alive in 1999 (Fig. 7a). This effect was again visible for trees that died between 1999 and 2001: their growth rates of period 1 lay still well below those of the alive-trees in 2001 (29% for *rgr*, less pronounced with 21% for *agr*). Growth in sub-period 2a of trees that died during sub-period 2b was even two-thirds lower than that of the trees that still lived in 2001 (Fig. 7b). Both Mann–Whitney *U*-test and Kolmogorov–Smirnov test showed highly significant ($P < 0.001$) differences between all combinations. Periodic mortality in period 2 fell nearly 3-fold between trees with <2 and those with $\geq$10 mm m^{-1} year^{-1} *rgr* in period 1 (from 17 to 6%; Fig. 7b).

Valid and invalid growth rates

Proportions invalid and sources of invalidity

The number of trees that were classified as having unsuitable *gbh* measurements decreased by 10% between 1996 and 2001 (Supplementary materials—Appendix 6; information was not available for the first enumeration of 1986). This was largely because of the much smaller (<50%) number of trees where a new PoM had to be established (or an existing PoM moved) in 2001 compared to 1996—understandable given the higher probability of losing a paint mark in the longer (10-year) interval. Conversely though, measurements were more affected by unsuitable stem conditions in 2001 than 1996 (Supplementary materials—Appendix 6).

During the part-enumeration of 1999 (where only ‘tree status’ and ‘condition of stem’ had been recorded), the status ‘standing’ (DS) was attributed to almost half of the dead trees, compared to much lower proportions in 1996 and 2001. Close to a third of dead stems were recorded as ‘damaged’ (DB, DA, DU) in 1999, but this status was attributed to around half of the trees in 1996 and 2001. Notably, the proportion of trees with lianas or liana damage increased steadily between 1996, 1999 and 2001 (Supplementary materials—Appendix 6).

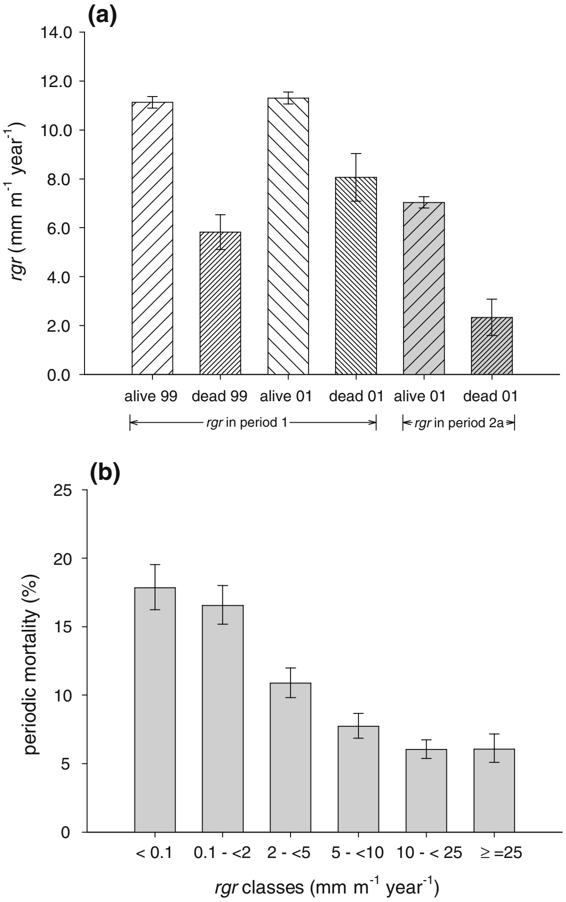


Fig. 7 Growth and subsequent mortality at Danum: **a** Relative growth rates of small trees in subplots for period 1 (*open bars*) and subperiod 2a (*grey bars*) categorized according to whether they lived (wide hatching) or died (narrow hatching) in subsequent subperiods; bars are SEs of subplot means. **b** Change in periodic mortality in period 2 of trees with increasing (valid) relative growth rate in period 1. Sample sizes of the six successive classes were 1508, 1950, 2336, 2483, 3447 and 1550. Bars indicate 95% confidence limits

The number of invalid growth rates increased by 40% (from 1754 to 2453), however, because mainly the newly unsuitable measurements in 2001 were not all for the same trees as in 1996—in 954 cases (Table 6). (The remaining difference in unsuitable measurements versus invalid rates in both periods/enumerations was due to (a) trees regressing <10 cm *gbh*, and (b) growth rates additionally excluded because *agr* ≤ -4 mm year^{-1}.) In periods 1 and 2, 12% and 16%, respectively, of the *rgr* values were invalid. Losing old PoMs and damage to stems were

Table 6 Relative contributions (%) of the causes of unsuitability that led to invalid growth rates

	Period	
	1	2
Damaged	26.4	25.1
Lianas	5.1	7.4
Moved PoM	7.8	1.2
New PoM	56.6	16.4
Relascope/laser/callipers	0.6	0.0
Buttresses	0.2	2.1
Irregular stem	2.5	5.8
Absolute growth rate ≤ -4 mm	1.0	1.3
Invalid at start of period		38.4
Other reasons (regressors, etc.)		2.4

See main text for numbers of invalid rates per period and Supplementary material—Appendix 6 for totals

the other main reasons why some growth values became invalid (although this ranking does depend on the importance given to the individual categories because the classifications concerned multiple aspects (CoS, PoM, MeM, etc.), a stem could have been damaged and been measured at a new PoM: the ranking chosen here is as shown in Table 6 (from top to bottom). Across size classes, the proportion of invalid growth rates increased with size, with a similar shape in both periods (Fig. 8a).

Comparison of valid with invalid growth rates

Being influenced by very negative values, the mean of the invalid rates lay well below (by 26–68%) the mean of the valid rates and in sub-period 2a the mean invalid *rgr* was negative (Fig. 8b). Both the increases in *rgr* between periods 1 and 2 and between sub-periods 2a and 2b, as well as the decrease between period 1 (subplots, small trees) and sub-period 2a, were much less pronounced for valid compared to invalid growth rates, indicating an underestimation of the changes between periods.

Setting those growth rates to zero where *agr* was >-4.0 and <0 mm year^{-1} and dropping the large negative values ≤ -4 mm year^{-1} (which yielded very similar results as when setting all *agr* values <0 mm year^{-1} to zero), resulted in elevated *rgr* compared to the preferred approach, only slightly (up to 1%) in periods 1 and 2, and in period 1 for small trees, but much more (20–43%) in sub-periods 2a and 2b. The consequence would have been a decrease in *rgr* between period 1 (small) and sub-period 2a by only 11% and an increase between sub-periods 2a and 2b by only 65%. Including the small negative rates (>-4 and <0 mm year^{-1}) but setting all invalid ones to zero growth, i.e., adding 304 to 2567 (depending on the period) *rgr* values of 0, growth rates would have been substantially lowered (by 8–17%) with the effect that the change in *rgr* would have been only 6% between periods 1 and 2 but similar between the sub-periods (P1 to P2a: +38%, P2a to P2b: +103%) when compared again to the preferred 'problem-free' approach.

Immediate effect of 1997/1998-drought

Mortality and growth rates of period 1 (1986–1996) were assumed to hold constant until the onset of the 1998-drought on 4 April 1998, the date on which the *30-d-rt* of precipitation had fallen <100 mm for 10 days. Period 1 was extended to t_{P1x}, by 1.84 years, leaving a drought sub-period 2x of 0.78 years (see Fig. 2). The number of trees present at the start of sub-period 2x (n_{98}) was estimated from: $n_{98} = n_{96}\,(1 - m_{a\_P1})^{tP1x-tP1}$. The number of trees dying in extension was: $n_{d1x} = n_{96}$–n_{98}, and consequently those dying in sub-period 2x: $n_{d2x} = n_{d99}$–n_{d1x}. The resulting m_a for sub-period 2x was 3.64% year^{-1} ($n_{96} = 4239$, $n_{98} = 4120$, $n_{d99} = 237$). Using m_a estimates uncorrected for interval length (1.53% year^{-1}), m_a more than doubled (increase of 138%) between period 1 (and sub-period 1x) and sub-period 2x. Applying the correction procedure developed for sub-periods 2a and 2b (above, and Lingenfelder 2005), and tentatively extrapolating the curve back from 1.0 to 0.78 years, an approximate correction factor which places m_{a_2x} on a 5-year interval basis is 0.90. This led to a corrected value of 3.28% year^{-1}, a slightly less-than-doubling in m_a (increase of 93% on 1.70% year^{-1} in Table 5). The absolute growth rates of period 1 were applied at the start of sub-period 1x to the *gbh* values of 1996. From the *gbh* values in 1998 so estimated, *rgr* for sub-period 2x could be found (trees 10 − <50 cm *gbh*). Mean growth rates in sub-period 2x were negative: $agr = -0.44$ mm year^{-1}, $rgr = -2.38$ mm m^{-1} year^{-1}. During sub-period 2x small trees on average therefore decreased by 0.34 mm *gbh* (or 0.11 mm *dbh*).

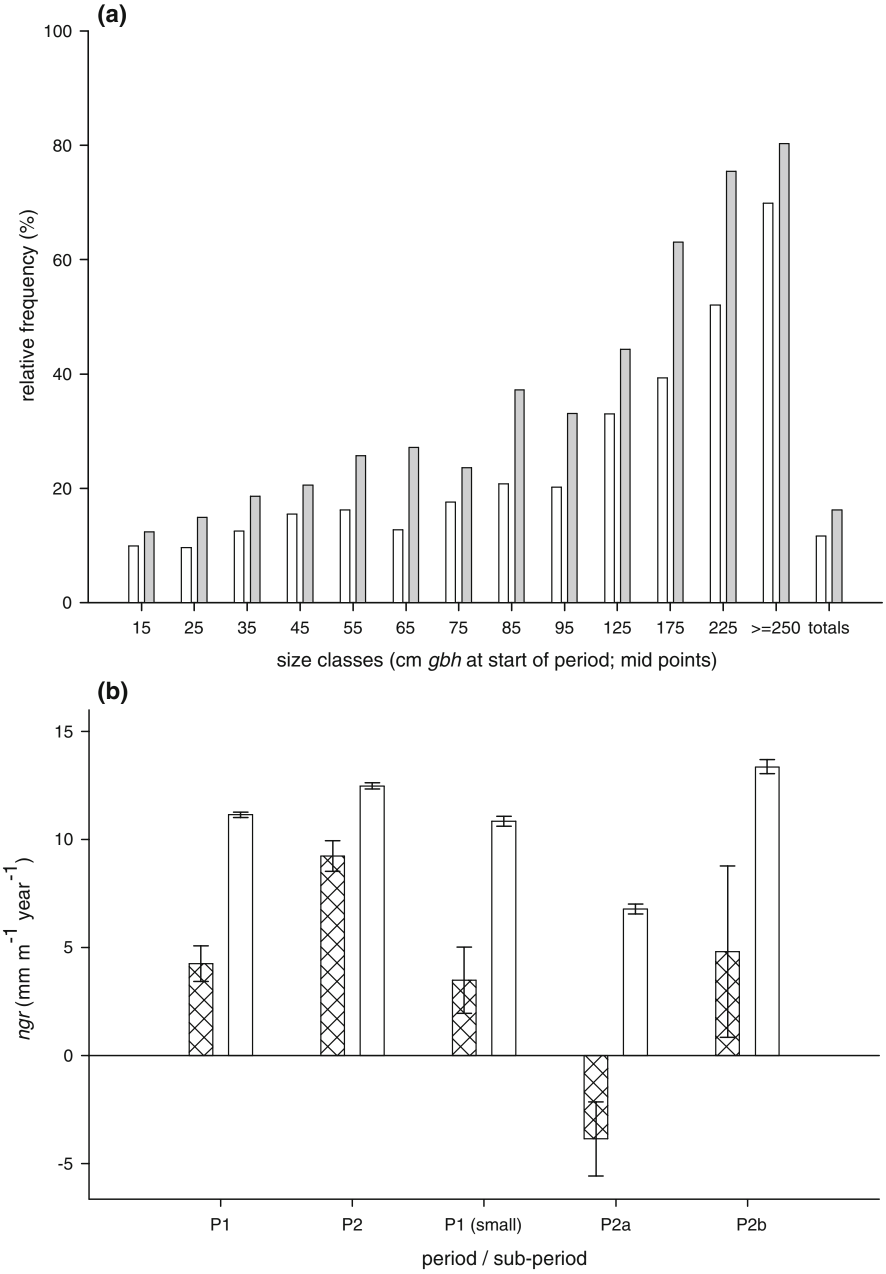


Fig. 8 Valid and invalid growth rates: **a** Relative distribution of invalid growth rates (trees ≥10 cm *gbh* at start of a period) in size classes, and for all trees in period 1 (*open bars*) and period 2 (*grey bars*). **b** Mean relative growth rates (±SE) of invalid (wide cross-hatching) versus valid (*open bars*) values for the main plots (all trees, periods 1 and 2) and the sub-plots (trees ≥10–50 cm *gbh* at start of period 1 and sub-periods 2a and 2b, respectively) at Danum

Discussion

Methodological and analytical considerations

Mortality and recruitment

The dynamics of the forest at Danum was based on measurements of two replicate 4-ha plots containing *c.* 19 K trees ≥10 cm *gbh* spanning 15 years. Taxonomic identification was almost 100% and done to a high level, with revisions at later enumerations reducing the proportion of singletons. Mortality, recruitment and stem growth rates of all trees from 1986 to 1996, and from 1996 to 2001 (periods 1 and 2) could be estimated at the plot level but only mortality and growth rates of small trees, from 1996 to 1999 and 1999 to 2001 (sub-periods 2a and 2b) were achievable at the subplot level (*c.* 1/3 of the plot area). Care was taken to confirm that trees recorded as having died really were dead (ideally for any enumeration this should be checked 3–6 months after), and that recruits corresponded precisely to the $\geq$10 cm lower *gbh* limit. At the plot level, rates in period 2 included trees that recruited at the end of period 1. By contrast, at the subplot level rates in sub-periods 2a and 2b were based on only the survivors of the previous period or sub-period. Accordingly, the results given here are slightly different from those of Newbery and Lingenfelder (2004) where the 1996-recruits for sub-period 2a were included. The important contribution of regressors in the dynamics calculations (leading to alternative calculations of gains and losses to the population, Supplementary materials—Appendix 2) was, accordingly, only possible at the plot level and for period 2.

Periodic mortality rates were slightly higher than recruitment rates in both periods, this being in part due to the underestimation of true recruitment rates. Without assuming unrealistic population equilibrium conditions, even for period 1, there is to date no fully satisfactory way of accounting for recruits which die within a period and go unrecorded at the next enumeration. The best corrected value for m_a increased by 25% between periods 1 and 2, while r_a (uncorrected) increased only 12%, giving the impression that recruitment lagged behind mortality. However, the lower r_a (than m_a) was probably due to a combination of the evident long-term succession (Newbery et al. 1992), the influence of the most recent drought (Newbery and Lingenfelder 2004) and the methodological underestimation. It means further that such a data set on tree dynamics—based on plots remeasured at intervals of several years—cannot be complete. It is not justified even to assume that m_a and r_a are constant with time, which on the one hand raises a problem for corrections of m_a for interval length (Sheil and May 1996; Newbery and Lingenfelder 2004), and on the other hand questions whether r_a can be similarly corrected (possibly in the way Lewis et al. 2004 have suggested), given that recruits of different species will also have their own different mortality rates.

Tree death is likely in part to be a consequence of reduced growth rate. Very low to zero, or negative growth rates, are often associated with trees in their last months or years before dying (Kobe 1996; Kobe and Coates 1997). Of particular interest for Danum is—apart from the time lag—that the difference in *rgr* of 2001 alive and dead trees was much larger for sub-period 2a than period 1, the former being directly associated with the 1998 drought perturbation. The larger difference for the 1999 than 2001 alive and dead trees' *rgr* in period 1 lends support in the same direction. A similar association of *rgr* with mortality has been shown by Chao et al. (2008).

Local-scale heterogeneity in forest dynamics was evident from the different responses of the two plots. Mortality rate (m_a) changed more in plot 2 than 1, but the converse was the case for r_a: plots differed less in m_a in period 2 than 1 (a convergence) but differed more in 2 than 1 for r_a (divergence). The plots differed in important details of topography especially the small stream running across plot 2, and the more exposed ridge in plot 1 (Fig. 1). It is interesting that often medium-sized trees in intermediate positions showed the largest plot–plot differences, suggesting that small (understorey species) and large (mostly canopy species) trees were adapted at the extremes of the gradient but between them drought caused the most reactivity.

Including regressors, and using a fixed population size threshold (to find alternatively losses and gains), had important consequences for these calculations. Of the two periods, evaluation of the dynamics was more complete for period 2 than 1 because information on regressors at the start of period 1 was lacking. A critical unknown concerns the dynamics of trees close to the minimum *gbh* used in the enumeration. This may perhaps be overcome in the future by closer study of subsamples of trees in the *c.* 7.5–25-cm *gbh* range over a series of shorter time intervals. More intensive sampling (with more persons involved), however, would mean more interference to the vegetation.

In the present analysis, data from the two replicate plots have been combined because overall plot differences were small compared with those over time (Newbery and Lingenfelder 2009). Confidence limits on means of m_a and *rgr* in tree-size and topographic classes approximately indicated the between-tree variability. Measurements of individuals will not be spatially or temporally independent from one another, though, and the true limits are likely to be slightly larger. Statistical comparisons between classes are inappropriate for another reason—the classes were arbitrarily defined on a continuous scale. Spatial auto-correlation was addressed in the analysis of growth in relation to topography with individual tree elevations and slopes rather than classes. The end result was that it had a relatively very small effect.

Stem growth

In the analysis reported in this paper attention was given to the determination of the validity of stem *gbh*, and hence *rgr*, and an extensive system of coding for invalid trees in the field (CoS, MeM, PoM). In the calculation of mean growth rates of trees per plot or subplot almost all other tropical studies have sought ways of correcting questionable *gbh* values (those appearing anomalous due to measurement or recording errors for plausible reasons) or unsuitable pairs of *gbh* (due to shift in PoM, poor CoS at start and/or end of the period) so that all surviving trees had an actual or estimated growth increment, and any finally omitted from the data set were those remaining unexplainable extreme negative and positive values. A major concern of many researchers has been how to deal properly with the small negative growth values, and no standard mathematical probability density function for tree *rgr* has been found which caters for the numerous small negative as well as the few highly positive growth rates encountered. These negative rates became important in evaluating drought effects in period 2 at Danum.

Condit et al. (1993) omitted trees whose *dbh* decreased by >5% or had an *agr* of >75 mm year^{-1}, and left the smaller decreases in the data set. Later though after excluding those decreasing >25% and the same class of extreme positives, negative increments in *dbh* were removed by resetting the second *dbh* of a pair to the first *dbh* + 0.5 mm (Condit et al. 2006). No mention was made of how increments where PoM, CoS, and MeM (equivalent to the terminology of this paper) were dealt with. Condit et al. (2004) excluded trees where the second *dbh* was ≥4 SDs (of a reference remeasurement) below the first one, which was equivalent to excluding only trees with growth rates ≤ -5 mm year^{-1} *dbh* (-15.7 mm year^{-1} *gbh*; positives >75 mm year^{-1} were also again excluded). Editing the data in this way will raise the mean growth increment unless the removal of the very few extreme positive values balances the many small negative ones. Clark and Clark (1999) moved the PoM when stem irregularities required it, but seemingly used the second *dbh* in finding the last period's growth increment even if the PoM was no longer suitable: the new PoM was applying to the next period. The data of Phillips et al. (1998) rest on a method of standardizing *dbh* measurements at old and new (shifted) PoMs using 'the ratio of diameters at both PoMs' (Peacock et al. 2007), but it is not explained how this was actually achieved. Feeley et al. (2007) simply changed the growth rate to zero for all trees where the PoM had changed, presumably replacing in this way both some negative and some positive values, and Nakagawa et al. (2000) excluded all growth rates ≤ -2 mm year^{-1} in diameter and set those > -2 and < 0 mm to zero growth.

Nevertheless, how frequent stem irregularities were in leading to new PoMs is not mentioned in any study we could find and it is not possible from any of them to ascertain what percentage of values were edited, rounded up, or omitted. Most authors simply write the problem off as being of 'negligible' consequence, and any details pertaining are sometimes hidden in appendices. Baker et al. (2004), finding plot basal area increments in Amazonian forests, also needed to deal with aberrant *dbh* values. Those with *agr* ≤ -2.0 mm year^{-1} or ≥ 40.0 mm year^{-1} were left out (following a recommendation of Sheil 1995, for one forest site in Africa), and those appearing unusual were replaced by either a value interpolated from *dbh* values before and after the datum in question or if at the end of a series by the median value of the other trees in its size class. Chave et al. (2008) applied a similar procedure but with class limits of -5.0 and 45.0 mm year^{-1}, and using means of *dbh* classes for substitution: PoMs were only painted when they deviated from the standard 1.3 m; a possible source of inaccuracy. In none of these studies is it explained objectively why the selected cut-off values were used or a justification of rounding negative values to zero or small positives was made. It gives the impression of practical convenience: Sheil (1995) referred to 'harmonizing' his data set on the grounds of 'common sense', and Phillips et al. (2002) call their procedure 'post measurement data checking' where so-called 'false' negatives are rounded up (to zero usually) but 'false' positives are not rounded down. In our analysis for Danum we have sought to avoid these arbitrary systems. We excluded only extreme negative values on the basis of an objective statistical technique (Newbery et al. 1999) and retained all other negative values as part of the sample of tree measurements. No extreme positive *rgr* values were omitted because the maximum *agr* was 75.5 mm year^{-1} *gbh* (24.0 mm year^{-1} *dbh*), for a dipterocarp in period 2. While this value is well within the limits used by Condit et al. (2004, 2006) and Sheil (1995), it is not unexpectedly large for these species and forests. In the present data set, modifications of negative or invalid growth rates would have led to different growth levels (elevated or lowered) and—in the case of setting slight negative values to zero—possibly an underestimation of the response of the forest to the 1997/1998 drought.

By excluding invalid trees, estimates of mean growth rates of valid ones were highly accurate, especially for the small trees (10 – <50 cm *gbh*). Possible biases as a result of unusual growth (e.g., buttresses moving upwards or development of reaction-wood on steep slopes), stem irregularities or measurement uncertainties through the use of optical instruments for large trees, were minimized. Nevertheless, trees that were labelled invalid because their stems were defect or unsuitable might have had relatively slow growth rates if these features were indicating damage or a stage prior to death. Conversely, large trees with buttresses, especially those emerging out of the main canopy, might have had relatively fast (valid) growth rates. Recording stem growth rates more accurately and completely could be achieved by a set of 3–5 (multiple) PoMs spaced along the bole, so that at least one (preferably more) gave a valid *rgr* for any period (Dawkins 1956). This would be prohibitively intensive in field work and as a trade-off limit the number of trees and area enumerated considerably.

Including growth rates down to -4 mm year^{-1}, and not excluding every rate <0 mm year^{-1} can be defended on grounds of (i) physiology and growth, since it has been shown in the present and other studies (e.g., Sheil 2003) that shrinkage of trees due to loss of stem water does occur to this extent; (ii) there are measurement errors, so that a tree of zero growth rate can be recorded with an error of ±1 or 2 mm; and (iii) the logit-plot technique of Newbery et al. (1999) highlighted a very different frequency distribution below -4 mm compared with above it where values formed part of an (unknown) exponential-type family function.

In the treatment of growth data there are two choices: to substitute unmeasured or erroneous rates by estimates (medians, means, interpolated values, ceven by zeros or small positives), or to leave them as unmeasured, and accept that where two *gbh* values do not meet acceptable accuracy then the *rgr* remains unknown. In the present paper, the second choice has been taken because the forest dynamics is clearly in a short-term non-equilibrium state and the response to a perturbation is being studied. Possibly in a steady-state equilibrium forest some replacement might be defended but even then it should not be necessary if 'errors' and unmeasured rates are at random and distributed proportionally across all size classes and species. To obtain *agr* and plot level basal area increments would simply require here a proportional multiplying up. Nevertheless, substitution must introduce bias and the more the system is away from a steady state the stronger the likely bias. This is an important issue given the increasing recognition that many forests are recovering from recent perturbations (Wright 2005; Chave et al. 2008).

Was the *rgr* in period 2 (12.5 mm m^{-1} year^{-1}) higher than in period 1 (11.6 mm m^{-1} year^{-1}) then because period 2 had a greater proportion of invalid trees than period 1, that is more trees (of largely low or negative *rgr*) were removed from the total sample in period 2 than 1? It cannot be known empirically what the valid rates of the invalid class would have been: they are undetermined. It is not even possible to reasonably assume, based on current knowledge, that they were proportional to the invalid rates with a common conversion equation applying to both periods, or that the invalid sample was a subsample of similar origins and frequency distribution in both periods. The same argument applies for the subperiods of period 2. The situation is not satisfactory but indicates the limits of what can be measured and how far the dynamics of the system can be reliably interpreted. We recommend that in future authors could report how many trees in their samples were edited and omitted, and for what reasons.

Assuming a dynamic equilibrium in order to substitute for missing values or make the analysis tractable has been repeatedly shown to be mistaken in ecology. It is clearly the case for the forest at Danum, where the continual readjustment in response to past perturbations means that the system never comes to a constant state, remaining in flux and unpredictable. A fundamental concern is how much the drought influenced the extent of the recording of valid growth, a problem further compounded by the need to use fine-scale time resolution to detect the dynamic response at all.

Dynamics and droughts at Danum and in relation to other tropical forests

Immediate and lagged mortality and growth

Mortality did increase after 1996 by 25% (interval corrected rates of all trees for both main plots combined). Taking the subset of small trees measured in 1999 into account, a rather moderate, continuous increase by 6% and 9% in sub-periods 2a and 2b, respectively, was indicated. However, in the calculation of these values, regressors, gains and recruits were excluded and thus they are probably overestimated. In a recent work at Danum (Newbery and Lingenfelder 2004), mortality was shown to have slightly decreased from 1996 to 1999 (the present sub-period 2a). If that is taken as the basis for the 'high drought intensity' period, then mortality started to take effect some time after the immediate perturbation—but still within the low precipitation-event—i.e., in the period between 9 months and 3 years after the drought. Also increases in growth rates did occur after 1999 (in period 2b), after a very strong decline in sub-period 2a. Even though during the partial enumeration from December 1998 to March 1999—9 months after the peak of the drought—rainfall was above average (mean *30-d-rt*: 275 mm), measurements were done within the drought event that lasted until mid-April 1999, with the antecedent rainfall history still indicating a deficit (Lingenfelder 2005; Newbery and Lingenfelder 2009). It seems reasonable that under these circumstances, water storage in the outer tree compartments was not refilled by then and growth was not substantial enough to result in positive rates. Sheil (2003) reviewed different studies and performed an exploratory study on tropical diurnal tree stem diameter variation. He found that fluctuations in girth (shrinkage and expansion) of 0.5 mm–2.0 mm day^{-1} were not exceptional. In Ghana, Baker et al. (2002) observed dry-season (*c.* 4 months) shrinkages as much as 2.8 mm in diameter (8.8 mm in girth). Although a theoretical calculation, the average shrinkage in tree girth of 0.34 mm in *c.* 9 months (during sub-period 2x) shown in the present study is therefore not surprising.

Two effects successively took place at Danum during and after the strong drought of 1997/1998: (a) an immediate response in growth (negative impact) while mortality did not increase or only slightly increased (resistance, but possibly weakening), followed by (b) lagged responses in mortality (negative impact) and increased growth (resilience). Harrison (2001) hypothesised that even though droughts are not the direct trigger for flowering, they have an influence on phenology with a general increase of leaf production and flowering after droughts (offering an advantage of not flowering during times of heavy rain which could possibly damage the flowers and disrupt pollination and possibly having increased light levels due to increased mortality). Leaf shedding and flushing within 2 months of experiencing a short dry spell was found for trees in Sarawak and the flushing seemed to have induced cambium growth: 2–4 months after the flushing or 3–6 months after a dry spell, growth rates peaked on two occasions in 1996 and 1997 (Ichie et al. 2004). At Danum, extensive defoliation occurred in March 1998 and growth rates were very low at least until early 1999 when the partial enumeration took place. As the 1997/1998-drought was more intense than the brief dry periods described in Sarawak, and it is not known when flushing recommenced at Danum, it is well possible that this process of shedding and flushing occurred in a similar but slowed-down manner. Severe water stress led to abscission of senescent leaves with reduced stomatal control (Walsh and Newbery 1999), bud break and flushing assumingly soon after rainfall increased again (perhaps when *30-d-rt* >100 mm), but hardly any (detectable) cambium growth until water storage in the trees was completely refilled in the first quarter of 1999 (possibly in April, when the antecedent rainfall history was turning positive again). Nutrient availability on the forest floor may have been increased by the defoliation and this additionally provided the basis for the boost in growth after April 1999.

The delayed increase in mortality after a severe drought is in contrast to results of other studies in Borneo. At two different sites within Lambir Hills National Park, Sarawak, Nakagawa et al. (2000) and Potts (2003) estimated mortality for pre-drought (1993–1997) and drought (1997–1998) periods. They found more than 3-fold higher mortality rates in the second interval that ended shortly (5–6 months) after the 1997/1998-event. This drought was possibly more severe in that region than at Danum, indicated by *30-d-rt* <100 mm for 89 days (at Danum the equivalent value was 58 days), although the preceding rainfall history at the Lambir site is not known. However, ‘true annualised mortality’ (Nakagawa et al. 2000) and ‘exponential mortality coefficient’ (Potts 2003) for two time intervals of quite different length were compared: *c.* 4 years versus *c.* 1 year. As the decline of mortality rate in heterogeneous populations due to dependence on the interval length is especially strong from $t = 1$ to $t = 2$ (Sheil and May 1996), the high rates of the short drought period in these two studies might have been substantially overestimated. Nakagawa et al. (2000) also did not find a large decline in relative growth rates in their drought period.

A similar pattern of mortality was found in East Kalimantan (Slik 2004). Although only ‘percentages of dead standing trees’ were given, these were much higher shortly (8–13 months) than 4 years after the drought (15.4% compared to 4.2% in the ‘undisturbed’ plots). Plots in logged areas of that study had an even higher percentage of dead trees, this also hinting at the possibly increased risk to disturbed ecosystems. Sites classified as ‘dry’ had more dead trees than those which were ‘wet’ (Slik 2004). By contrast, at Sungai Wain, a site close to that of Slik’s, lagged mortality was found by van Nieuwstadt and Sheil (2005): 8 months after the drought the proportion of dead trees was 18.5%, increasing to 26.3% at 21 months. In nearly all of these studies, there was no correction for interval length and the inferred drought effect was over-estimated.

Size-related effects

Across both main plots, mortality was highest for medium-sized and lowest for large trees in period 1. In the second period, mortality increased with increasing size, large trees being most affected by the drought, and this was most pronounced on ridges (although mortality was lower on ridges than on lower slopes in both periods). This pattern was not seen in Sarawak, where mortality decreased with increasing size; however, increase of mortality in the drought period was also greatest for large trees (Nakagawa et al. 2000; Potts 2003). On the other hand, in East Kalimantan, mortality increased with size (in the unburned plots) too, and the drought had its largest impact on large trees (van Nieuwstadt and Sheil 2005). The authors of that study ascribed this effect to the hydraulic limitation hypothesis, where water stress increases with the height of trees (all else staying constant) and imposes a greater risk of cavitation. During moderate droughts, large trees with deeper-reaching roots might be less affected, but if water stress is becoming more severe, cavitation would in addition to faster depletion of their root zones affect large trees more than smaller ones (van Nieuwstadt and Sheil 2005). This generally fits with the Danum data. Yet, the trend found at Danum that understorey species followed the general pattern (of increasing mortality with increasing size), but overstorey-species decreased in mortality with increasing size (Lingenfelder 2005), is contrary to the findings of van Nieuwstadt and Sheil (2005). Although small trees in general seemed to be less affected by the drought, the impact on large overstorey-trees possibly was not severe enough to increase their mortality.

Conversely to mortality, relative growth rate decreased with increasing size in both periods and growth was higher on lower slopes than on ridges in period 1. In period 2, however, the recovery (i.e., the increase in growth) was larger on ridges. Growth of trees on ridge locations reached similar levels as that of trees located on lower slopes, with medium-sized trees on ridges even exceeding those on lower slopes in growth. Although there was some variation between plots, topography also showed an influence on growth rates in the regression models. This seems to imply that the forest species are largely adapted to where they are on the gradient of elevation and that the perturbation (seen on the 5-year scale 1996–2001) did not have a large effect.

Results of the present work provide strong evidence that forest dynamics at Danum from 1986 to 2001 were influenced by the responses to several mild-to-moderate and one severe drought. However, the perturbations were not major disturbances in the sense that the forest was vitally damaged. Elsewhere we have demonstrated highly species-specific dynamics, operating in ways that increased some and decreased other species and so apparently balancing or compensating one another (Newbery and Lingenfelder 2009). If the forest was still recovering from catastrophic droughts *c.* 90–130 years ago (Newbery et al. 1999; Newbery and Lingenfelder 2004), then the event of 1997/1998 could be called a ‘set-back’, one that it seems the forest is capable of overcoming. Potentially threatening could be possible future increases in the intensity and frequency of droughts with shorter between-drought intervals for recovery that could lead to serious changes in the structure and the dynamics of lowland dipterocarp forests (Walsh 1996).

Conclusions

While recent moderate droughts affected the overall structure of the forest at Danum only slightly, showing that the forest can indeed accommodate such perturbations, the upper limits of drought frequency or intensity to which the forest is resilient remain uncertain. If, as a result of climatic change, drought events were to increase in the future, the forest might respond in either of two hypothetical ways: (1) an increase in faster growing, light-demanding species, because the canopy remains open for longer periods; or (2) an increase in drought-tolerant species, especially in the understorey, because the atmosphere and soil become drier also for longer periods. We prefer the second hypothesis because such a guild of drought-tolerant species has been demonstrated at the site, and increasing drought would presumably select them. Both outcomes would likely result in lower stature and biomass forest, with reduced densities of the dominant dipterocarp species that are largely drought-intolerant until they reach the sub-canopy. For the primary forest and its conservation, this would mean a substantially changed upper canopy, unless the understorey were to respond effectively enough to nurse the dipterocarps to the same degree as before, and in secondary logged forests it might lead to a tendency to replace pioneers by drought-tolerant understorey species, which could even increase (through nursing) dipterocarp restocking (Newbery et al. 1999). Clearly, it is essential to maintain long-term permanent plots like those at Danum which have the capability of following these changes, and use the data to model different drought scenarios.

The link variable between the external driving stress (e.g., drought perturbation) and forest dynamics is *rgr*. This rate is affected by numerous other factors, external and internal to the tree, but measured on stem size it is perhaps the best integrative measure of tree performance. Trees with very low, zero or even maintained negative rates tend to die, those with positive rates enable recruitment into the population and movement through the size classes. It is therefore critically important to measure *rgr* as accurately as possible and minimize the number of invalid trees because these introduce uncertainties and even biases in the final assessment. One way forward is to employ multiple PoMs, a second would be to use covariates of tree growth other than *gbh*. How the methodological and analytical problems highlighted in this paper are handled can clearly influence the conclusions drawn about how perturbations influence the dynamics of the ecosystem under study.

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References

Alder D (1995) Growth modelling for mixed tropical forest. Oxford Forestry Institute, Oxford

Baker TR, Affum-Baffoe K, Burslem D, Swaine MD (2002) Phenological differences in tree water use and the timing of tropical forest inventories: conclusions from patterns of dry season diameter change. For Ecol Manage 171:261–274

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A et al (2004) Increasing biomass in Amazonian forest plots. Philos Trans R Soc B 359:353–365

Beaman RS, Beaman JH, Marsh CW, Woods PV (1985) Drought and forest fires in Sabah in 1983. Sabah Soc J 8:10–30

Bivand R (2007) The spdep package. Spatial dependence: weighting schemes, statistics and models, version 04–13. http://cran.ch.r-project.org

Cane MA (2005) The evolution of El Niño, past and future. Earth Planet Sci Lett 230:227–240

Chao KJ, Phillips OL, Gloor E, Monteagudo A, Torres-Lezama A, Martinez RV (2008) Growth and wood density predict tree mortality in Amazon forests. J Ecol 96:281–292

Chave J, Condit R, Muller-Landau HC, Thomas SC, Ashton PS, Bunyavejchewin S et al (2008) Assessing evidence for a pervasive alteration in tropical tree communities. PLoS Biol 6:455–462

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I et al (2007) Regional climate projections. In: Solomon S et al (eds) Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK, pp 847–940

Clark DA, Clark DB (1999) Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. Ecol Appl 9:981–997

Condit R, Aguilar S, Hernadez A, Perez R, Lao S, Angehr G et al (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. J Trop Ecol 20:51–72

Condit R, Ashton P, Bunyavejchewin S, Dattaraja HS, Davies S, Esufali S et al (2006) The importance of demographic niches to tree diversity. Science 313:98–101

Condit R, Hubbell SP, Foster RB (1993) Mortality and growth of a commercial hardwood 'el-cativo', Prioria copaifera, in Panama. For Ecol Manage 62:107–122

Dawkins HC (1956) Rapid detection of aberrant girth increment of rain-forest trees. Emp For Rev 35:449–454

Feeley KJ, Wright SJ, Supardi MNN, Kassim AR, Davies SJ (2007) Decelerating growth in tropical forest trees. Ecol Lett 10:461–469

Fox JED (1972) The natural vegetation of Sabah and natural regeneration of dipterocarp forests. Ph.D. thesis, University of Wales

Gibbons JM, Newbery DM (2003) Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. Plant Ecol 164:1–18

Harrison RD (2001) Drought and the consequences of El Niño in Borneo: a case study of figs. Popul Ecol 43:63–75

Hulme M, Viner D (1998) A climate change scenario for the tropics. Clim Change 39:145–176

Ichie T, Hiromi T, Yoneda R, Kamiya K, Kohira M, Ninomiya I et al (2004) Short-term drought causes synchronous leaf shedding and flushing in a lowland mixed dipterocarp forest, Sarawak, Malaysia. J Trop Ecol 20: 697–700

IPCC (2001) Contribution of working group I to the third assessment report of the intergovernmental panel on climate change. In: Houghton JT et al (eds) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK

Kalunsky SP, Vega SC, Cardosa TP, Shelly AA (1998) S+ spatial stats: user's manual. Springer, Berlin

Kobe RK (1996) Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecol Monogr 66:181–201

Kobe RK, Coates KD (1997) Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can J For Res 27:227–236

Lewis SL, Phillips OL, Sheil D, Vinceti B, Baker TR, Brown S et al (2004) Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. J Ecol 92:929–944

Lingenfelder M (2005) Rain forest dynamics and response to drought in a Bornean primary lowland dipterocarp forest. PhD thesis. University of Bern, Switzerland. http://www.stub.unibe.ch/download/eldiss/05lingenfelder_m.pdf

Marsh CW, Greer AG (1992) Forest land-use in Sabah, Malaysia: an introduction to the Danum Valley. Philos Trans R Soc B 335:331–339

McPhaden MJ, Zebiak SE, Glantz MH (2006) ENSO as an integrating concept in Earth science. Science 314:1740–1745

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM (2007) Global climate projections. In: Solomon S et al (eds) Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK, pp 747–845

Nakagawa M, Tanaka K, Nakashizuka T, Ohkubo T, Kato T, Maeda T et al (2000) Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. J Trop Ecol 16:355–367

Newbery DM, Campbell EJF, Lee YF, Ridsdale CE, Still MJ (1992) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. Philos Trans R Soc B 335:341–356

Newbery DM, Campbell EJF, Proctor J, Still MJ (1996) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. Vegetatio 122:193–220

Newbery DM, Kennedy DN, Petol GH, Madani L, Ridsdale CE (1999) Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. Philos Trans Roy Soc B 354:1763–1782

Newbery DM, Lingenfelder M (2004) Resistance of a lowland rain forest to increasing drought intensity in Sabah, Borneo. J Trop Ecol 20:613–624

Newbery DM, Lingenfelder M (2009) Plurality of tree species responses to drought perturbation in Bornean tropical rain forest. Plant Ecol. doi:10.1007/s11258-008-9533-8

Payne RW, Harding SA, Murray DA, Soutar DM, Baird DB, Welham SJ et al (eds) (2007) GenStat Release 10 reference manual. VSN International, Hemel Hempstead, UK

Peacock J, Baker TR, Lewis SL, Lopez-Gonzalez G, Phillips OL (2007) The RAINFOR database: monitoring forest biomass and dynamics. J Veg Sci 18:535–542

Phillips OL, Malhi Y, Higuchi N, Laurance WF, Nunez PV, Vasquez RM et al (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282:439–442

Phillips OL, Malhi Y, Vinceti B, Baker T, Lewis SL, Higuchi N et al (2002) Changes in growth of tropical forests: Evaluating potential biases. Ecol Appl 12:576–587

Potts MD (2003) Drought in a Bornean everwet rain forest. J Ecol 91:467–474

R Development Core Team (2007) R: a language and environment for statistical computing, Version 2.6.1. http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria

Sheil D (1995) A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. For Ecol Manage 77:11–34

Sheil D (2003) Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by dendrometer bands. Can J For Res 33:2027–2035

Sheil D, Burslem DFRP, Alder D (1995) The interpretation and misinterpretation of mortality rate measures. J Ecol 83: 331–333

Sheil D, May RM (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. J Ecol 84:91–100

Slik JWF (2004) El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. Oecologia 141:114–120

Timmermann A, Jin FF, Collins M (2004) Intensification of the annual cycle in the tropical Pacific due to greenhouse warming. Geophys Res Lett 31:L12208

Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398:694–697

Trenberth KE (1997) The definition of El Niño. Bull Am Meteorol Soc 78:2771–2777

Trenberth KE, Hoar TJ (1997) El Niño and climate change. Geophys Res Lett 24:3057–3060

Trenberth KE, Jones PD, Ambenje P, Bojariu R, Easterling D, Klein TA (2007) Observations: surface and atmospheric climate change. In: Solomon S et al (eds) Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK, pp 235–336

Van Nieuwstadt MGL, Sheil D (2005) Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. J Ecol 93:191–201

Walsh RPD (1996) Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. J Trop Ecol 12:385–407

Walsh RPD, Newbery DM (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. Philos Trans Roy Soc B 354:1869–1883

Wright PS (1975) The soils of Sabah. Vol. 3: Western parts of Tawau and Lahad Datu. Ministry of Overseas Development, Surbiton, UK

Wright SJ (2005) Tropical forests in a changing environment. Trends Ecol Evol 20:553–560

Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil

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Abstract We investigated changes in species composition and structure of tree and liana communities along a successional gradient in a seasonally dry tropical forest. There was a progressive increase in tree richness and all tree structural traits from early to late stages, as well as marked changes in tree species composition and dominance. This pattern is probably related to pasture management practices such as ploughing, which remove tree roots and preclude regeneration by resprouting. On the other hand, liana density decreased from intermediate to late stages, showing a negative correlation with tree density. The higher liana abundance in intermediate stage is probably due to a balanced availability of support and light availability, since these variables may show opposite trends during forest growth. Predicted succession models may represent extremes in a continuum of possible successional pathways strongly influenced by land use history, climate, soil type, and by the outcomes of tree–liana interactions.

Keywords Forest structure · Floristic composition · Succession · Liana–tree interactions · Land use history

Introduction

Seasonally dry tropical forests (SDTFs) are considered as one of the most threatened tropical ecosystems (Janzen 1986) and, in Latin America, $\sim$60% of all SDTFs have already been destroyed (Miles et al. 2006). Current deforestation rates are still high and unknown for many regions. Between 1980 and 2000, approximately 11,000 km^2 (0.6%) of SDTFs disappeared yearly in the Americas (Miles et al. 2006) mainly due to slash-and-burn practices and conversion to agriculture (Murphy and Lugo 1986; Murphy 1995; Miles et al. 2006). Other

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potential threats include global climate changes, habitat fragmentation and increasing human population density (Arroyo Mora et al. 2005; Wright et al. 2007). Conservation efforts are concentrated in the creation of conservation units, which has a very limited impact. For example, only 1% of SDTFs in Central America (Janzen 1988; Sánchez-Azofeifa et al. 2003) and 3.9% in Brazil (Sevilha et al. 2004) are under some sort of protection.

During the past few decades, forest restoration after pasture abandonment has increased in importance to complement conservation strategies such as creation of conservation units (Janzen 1983), since it can also minimize global problems, such as climate change (Prentice et al. 1992). However, a fundamental preliminary requirement is to understand how successional processes operate in each forest type. Virtually all the current knowledge in tropical forest succession was obtained in rain forests and may not be applicable to STDFs (Vieira and Scariot 2006). For example, SDTF plant species are predominantly wind dispersed, compared to a high proportion of zoochory syndromes in tropical moist forests (Howe and Smallwood 1982; Gentry 1995; Justiniano and Fredericksen 2000; Morellato et al. 2000). Also, there is evidence that resprouting is relatively more important in SDTF than moist forest natural regeneration (Vieira and Scariot 2006; Vieira et al. 2006; Sampaio et al. 2007). Thus, information on changes in forest composition and structure, as well as the abiotic and biotic interactions driving successional changes is needed for developing successful restoration programs.

Recent studies in Brazilian SDTFs indicate that late successional forests are composed mainly by plant species already present in early succession, due to their high resprouting capacity (Vieira et al. 2006; Sampaio et al. 2007). Thus, succession in SDTFs may not follow the ‘relay floristic model’ (Egler 1954), which predicts a gradual substitution of pioneer by late species along forest recovery. Instead, these ecosystems may conform to the ‘initial floristic composition model’, with pioneer species remaining in advanced stages of succession (Egler 1954). However, it is well documented that previous land use history affects the speed and pathway of forest succession in a given area after agricultural land abandonment (Guariguata and Ostertag 2001; Kennard 2002; Chazdon 2003; Vieira et al. 2006; Sampaio et al. 2007). Thus, SDTFs under different land uses (i.e. agriculture vs. cattle ranching) and management practices (clear-cutting, ploughing and burning frequencies) may show contrasting regeneration patterns.

Studies on succession and efforts to promote natural regeneration of SDTFs also have to recognize the importance of lianas as a key component of forest structure. In tropical forests, lianas can account for up to 40% of leaf area and leaf productivity (Hegarty and Caballé 1991) and can contribute 10–25% of plant species richness (Gentry and Dodson 1987; Gentry 1995; Nabe-Nielsen 2001). Lianas greatly influence tropical forest dynamics, since they reduce tree growth and fecundity and increase tree mortality (Putz 1984; Clark and Clark 1990; Schnitzer and Bongers 2002), rapidly growing in canopy gaps and suppressing sapling growth (Putz 1984). Therefore, they can hinder gap-phase regeneration and impede forest structure recovery, altering patterns of forest succession (Putz 1984; Clark and Clark 1990; Schnitzer et al. 2000; Pérez-Salicrup 2001). Lianas are usually more common in young, secondary forests and fragment edges, where light availability is higher, decreasing in abundance with canopy closure in mature forests (Clark and Clark 1990; DeWalt et al. 2000; Laurance et al. 2001). In spite of that there is very little information on liana community changes with succession (but see DeWalt et al. 2000), specially in SDTFs.

In this study, we compared forest fragments in different successional stages to describe changes in tree and liana communities in a Brazilian SDTF. We used the same approach of Kalácska et al. (2004, 2005) and Arroyo Mora et al. (2005) instead of using age, and our definition of successional stages was based on the forest structural characteristics. One of the main concerns of using age since disturbance or abandonment to define successional stages is that the structure and composition of stands of the same age vary drastically depending on past land use, soil type, topography and propagule availability (Kellman 1970; Sader et al. 1989; Corlett 1994; Guariguata and Ostertag 2001; Chazdon 2003; Vieira et al. 2006; Sampaio et al. 2007). By using a structural approach to successional stages (i.e. vertical and horizontal forest structure), we eliminate potential confounding variables related to the land use history (Arroyo Mora et al. 2005; Kalácska et al. 2005).

We tested the following hypotheses about ecological succession in the studied SDTF: (i) successional dynamics is dominance controlled. In this case, tree diversity would be higher in intermediate stages of succession, due to the competitive exclusion of mid-successional species as the forest matures (Yodzis 1986; Begon et al. 2006). (ii) Succession pathways conform to the 'initial floristic composition model' (Egler 1954), as proposed by Vieira and Scariot (2006) and Sampaio et al. (2007). (iii) Lianas are more abundant in early and intermediate successional stages, decreasing in late forests due to a negative interaction with trees. For this purpose, we compared forest structure and composition among early, intermediate and late successional stages of a SDTF in south-eastern Brazil, simulating the regeneration process that would naturally occur in this ecosystem.

Methods

Study area

This study was conducted in the Parque Estadual da Mata Seca (hereafter PEMS), a conservation unit of integral protection created by merging of four farmlands in 2000, and managed by the Instituto Estadual de Florestas (IEF, State Forestry Institute). The PEMS has an area of 10281.44 ha and is located in the valley of the São Francisco River, Minas Gerais state, Brazil, between 14°48′36″–14°56′59″S and 43°55′12″–44°04′12″W. The original vegetation of the park is SDTFs, growing on flat and nutrient-rich soils (IEF 2000). These forests are dominated by deciduous trees, with almost 90–95% of loss in leaf area during the dry season (May–October). The climate of the region is considered as tropical semi-arid (Köppen's classification), characterized by the existence of a severe dry season during the winter. The average temperature of the study region is 24°C (Antunes 1994), and the average annual precipitation is 818 ± 242 mm (mean ± standard deviation; data from the meteorological station in the city of Manga, 10 km from the study area). The main economic activities in the area before protection were extensive cattle ranching, and bean and corn plantations inside two central pivots of 80 ha each. Approximately 1,525 ha of the PEMS is covered with abandoned pasture fields in early regeneration stages, while the remaining area supports dry forest fragments in secondary and primary stages (IEF 2000).

Sampling

In January 2006, 20 plots of 20 m × 50 m (0.1 ha each, 2.0 ha in total) were delimited in early, intermediate and late forest fragments. To determine the successional stage of a given forest fragment, we followed the structural approach of Kalácska et al. (2004, 2005) and Arroyo Mora et al. (2005). These authors used the forest vertical structure (i.e. the number of tree crown layers in a vertical profile of the forest) and horizontal structure (the horizontal distribution of tree crowns per area) to define stages, regardless of forest age. In this sense, our early successional stage is characterized by a forest area composed of sparse patches of woody vegetation, shrubs, herbs and grasses with a single stratum of tree crowns composing a very open canopy up to 4 m. This area was used as pasture for at least 20 years and abandoned in 2000, though cattle from adjacent pastures still use the areas occasionally. Intermediate successional stages have two vegetation layers: the first one is composed by deciduous trees with 10–12 m and some emergent trees up to 15 m. The second layer is formed by a dense understory with many young trees and abundant lianas. This area was used as pasture for an unknown period and was abandoned at the late 1980s. Pastures where both early and intermediate successional forests fragments now occur were managed similarly: after clear-cutting, the area was ploughed to plant exotic grasses and burned every 2 years right before the rainy season. The late successional stage is also characterized by two strata, but the first stratum was composed by taller deciduous trees which form a closed canopy 18–20 m high. The second stratum is formed by a sparse understory with reduced light penetration and low density of young trees and lianas. There are no records of clear-cutting in this area for the last 50 years.

Six plots were established in one early successional forest fragment, the same occurring for intermediate succession plots. For late succesional stages, eight plots were established in two forest fragments (~3 km from each other). All forest fragments were located under similar topographic, soil and microclimatic characteristics, thus reducing variation in physical conditions that could affect succession. The

20 plots were located along a 5 km transect encompassing these fragments, between 14°50′–14°51′S and 43°57′–44°00′W. All plots were situated inside the original area of a single farm, in which management practices were similar for all pasturelands in the last 30 years, when the property belonged to the same owner. Plots from the same successional stage were located ~0.2–1.0 km from each other.

We identified and measured the diameter at breast height (DBH) of all living trees with a DBH equal or greater than 5 cm inside all plots. We also visually estimated the height of these individuals in each plot, using a 2 m graduate stick as reference. Moreover, all independently growing liana stems with a DBH equal or greater than 2 cm had their DBH measured, and their height was estimated as the height of their host tree. Lianas were identified at the morpho-species level, due to difficulties to collect plant vegetative and reproductive parts. Voucher specimens were deposited at the herbarium of the Universidade Estadual de Montes Claros, in Montes Claros, Brazil.

Data analyses

We compared the forest structural characteristics (height, basal area and tree density) for both the tree and liana components among successional stages using general linear models (GLMs) for each characteristic. Then, all factor levels (stages) were compared using contrast analysis by aggregating level and comparing deviance change (Crawley 2002). If the level of aggregation did not significantly alter the deviance explained by the model, the levels were pooled together (amalgamation) simplifying the model. Rejected amalgamation implied that levels were indeed different and no further comparisons were made. Thus, the complete model was simplified by stepwise omission of non-significant terms. All models were submitted to residual analyses, so as to evaluate adequacy of error distribution (Crawley 2002).

We computed the Holdridge complexity index (HCI) (for the tree component only; Holdridge 1967; Holdridge et al. 1971) as a measure of community complexity. This index is calculated by the following equation: $C_{HCI} = (\text{Height} \times \text{Density of stems} \times \text{Basal area} \times \text{Number of species})/1{,}000$. The original HCI considers only trees with DBH > 10 cm. Thus, we used a modified version of the index since we sampled trees with DBH ≥ 5 cm (Lugo et al. 1978). The HCI was compared among successional stages using the same procedure used for the other structural variables.

To compare tree richness among successional stages, observed species richness was calculated for each plot. Estimated species richness was also calculated using a non-parametric estimator, the incidence-based coverage estimator (ICE) using species-by-sample data (Colwell and Coddington 1994; Chazdon et al. 1998), with the software EstimateS 8.0 (Colwell 2006). We used a GLM to compare the observed species richness among the three successional stages.

In order to assess the variation in species composition between different successional stages (β diversity), we calculated the Morisita–Horn index (quantitative). We also calculated Jaccard's similarity coefficient (C_j) (Magurran 2004) to examine the floristic similarity between all plots of the three successional stages. Then, we used GLMs to test the relationship between similarity in species composition (measured as Jaccard's similarity index between plots) and the distance between plots within and between successional stages in order to determine if plot selection had any influence on species composition within successional stages.

To test the relationship between liana density and tree structural attributes, we used a GLM. The complete model was then simplified following the same procedure used for the other structural variables.

Results

Tree community composition

We identified a total of 1,543 tree individuals, representing 59 tree species and 23 plant families in the 20 plots (2 ha) of the three successional stages (Appendix). In the early stage, we found 296 individuals from 24 species, representing 11 families. Three of these families (Fabaceae = 59.1%, Anacardiaceae = 23.3% and Bignoniaceae = 10.1%) corresponded to 92.6% of all individuals in this stage. From a total of 13 families and 457 individuals (33 species) in the intermediate stage, three families (Bignoniaceae = 31.3%, Combretaceae = 25.6% and Fabaceae = 21.0%) constituted 77.9% of the individuals. In the late stage, we identified a total of 790 individuals belonging to 42 species and 19 families. Again, three dominant families (Bignoniaceae = 35.8%, Fabaceae = 24.4% and Combretaceae = 19.5%) were responsible for 79.7% of all individuals from this stage.

Individual species dominance changed along the successional gradient, markedly from the early to the intermediate stages, but only slightly from the intermediate to late stages (Fig. 1). In the early stage, *Senna spectabilis* (Caesalpiniaceae) and *Myracrodruon urundeuva* (Anacardiaceae) had high relative abundances, 40.5% and 21.6%, respectively. While *S. spectabilis* was present only in the early stage, *M. urundeuva* appeared in all three successional stages and was also a dominant species in the late stage, although with varying abundance/importance (relative basal area) (Fig. 1). There was little change in species dominance from the intermediate to late stages: from the five species, dominant in both stages, four were dominant in the intermediate and late stages: *Anadenanthera colubrina* (Mimosaceae), *Combretum duarteanum* (Combretaceae), *Caesalpinia pyramidalis* (Caesalpiniaceae) and *Tabebuia roseo-alba* (Bignoniaceae) (Fig. 1). The only remarkable change in composition between the intermediate and late stages was the dominance of *Tabebuia ochracea* (28.1%) in the latter, whereas this species was rare (relative abundance of 1.3%) in the former.

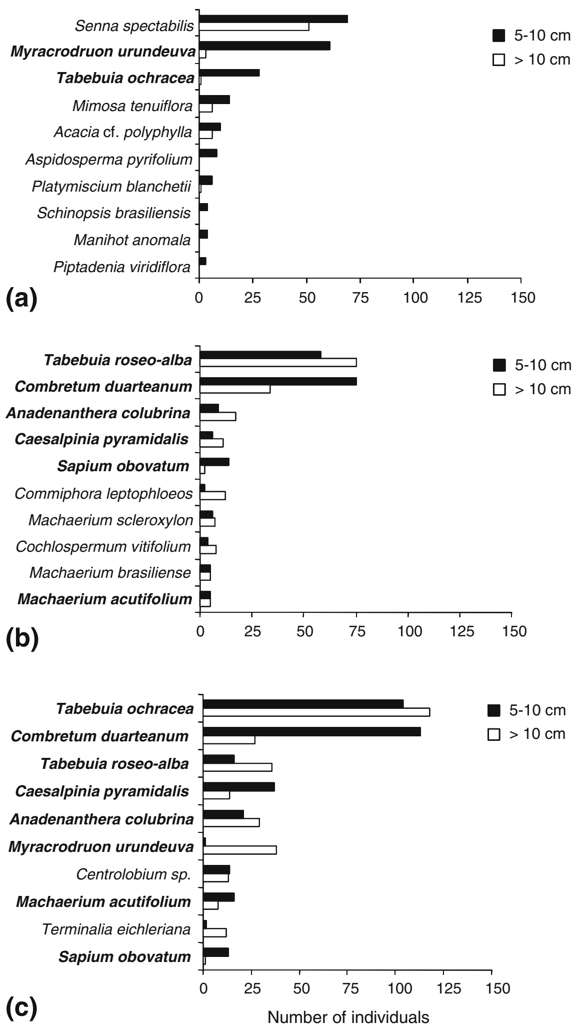

Fig. 1 Number of individuals for the 10 most abundant tree species in early (**a**), intermediate (**b**) and late (**c**) successional stages, by DBH classes of 5–10 and ≥10 cm. Species in bold were represented in more than one successional stage

The early stage presented a lower species richness than intermediate and late stages, but no significant difference was observed between intermediate and late stages (Tables 1, 2). Observed species accumulation curves and the species richness estimator (ICE) showed contrasting results between successional stages. No stabilization was observed for the early stage, and observed richness accumulation curve was below the estimated richness accumulation curve (Fig. 2a). Both curves indicated stabilization for the intermediate stage at 0.4 ha, although observed species richness showed a slight increase at 0.6 ha (Fig. 2b). For late stages, both curves tended to stabilized at 0.8 ha (Fig. 2c). In contrast with the early stage, the difference between the observed and estimated species richness was much lower for the intermediate and late stages (Fig. 2b, c).

The greatest similarity was observed between the intermediate and late stages, with a Morisita–Horn index of 0.55 (the probability to find an individual of the same species in a sample of the two stages). There was a very low similarity between the early and late stages (Morisita–Horn = 0.062) and, interestingly, an even lower similarity was observed between the early and intermediate stages (Morisita–Horn = 0.014), meaning a high turnover between successional stages. On the other hand, we observed a higher similarity in species composition between plots from the same successional stage than from different successional stages (Fig. 3). Besides, similarities in species composition were not influenced by the distance between plots from the same successional stage ($n = 58$, $F = 0.263$, $P = 0.61$), but decreased with distance between plots from different successional stages

Table 1 Mean values (mean ± standard deviation) of the tree and liana structural characteristics (height, basal area and density) and the Holdridge complexity index (C_{CHI}) in three successional stages in the Parque Estadual da Mata Seca, MG

Stage	Height	Basal area	Density	No. of species	C_{HCI}
Trees					
Early	3.4 ± 0.8^a	3.1 ± 0.8^a	49.3 ± 21.0^a	8.3 ± 2.4^a	0.6 ± 0.5^a
Intermediate	8.0 ± 4.1^b	15.2 ± 3.4^b	76.2 ± 10.0^b	16.3 ± 1.9^b	15.0 ± 8.3^b
Late	11.8 ± 5.6^c	22.0 ± 6.4^c	98.8 ± 17.2^c	17.3 ± 2.0^b	46.1 ± 25.7^c
Lianas					
Intermediate	8.2 ± 5.2^a	0.56 ± 0.1^a	32.0 ± 4.2^a	–	–
Late	13.3 ± 6.0^b	0.36 ± 0.2^b	15.5 ± 6.9^b	–	–

Height given is measured in metres, basal area in $m^2\ ha^{-1}$, and density in number of individuals $ha^{-0.1}$. Different letters indicate the statistical difference (refer to Table 2)

Table 2 Analysis of variance of the forest structural characteristics (height, basal area and density), number of tree species and of the Holdridge complexity index (C_{CHI}) between three successional stages and of the liana structural characteristics between the intermediate and late stages in the Parque Estadual da Mata Seca, MG

Response variable	Source	d.f.	Deviance	Residual d.f.	Residual deviance	*F*	*P*	Errors
Trees								
Height	Stage	1	241.629	17	41.257	49.782	<0.0001	Normal
Basal area	Stage	1	1227.86	17	342.07	30.511	<0.0001	Normal
Density	Stage	1	113.569	17	75.154	13.195	<0.0005	Poisson
Number of species	Stage	1	22.383	17	6.90	26.925	<0.0001	Poisson
Holdridge index	Stage	1	406.56	17	112.43	30.624	<0.0001	Poisson
Lianas								
Height	Stage	1	90.493	12	112.484	9.654	0.009	Normal
Basal area	Stage	1	0.176	12	0.394	5.359	0.039	Normal
Density	Stage	1	40.826	12	25.552	40.826	<0.0001	Poisson

No lianas were found in early plots

($n = 132$, $F = 23.161$, $P < 0.0001$, Fig. 3). Thus, there was no effect of spatial autocorrelation in species composition within successional stages.

Forest structure

All the tree structural variables evaluated in this study varied among the three successional stages (Table 1). For tree diameter, this pattern is clearly demonstrated by the higher frequency of large class diameters (>10 cm) in intermediate and late stages, whereas lower class diameters predominate in early stages (Fig. 1). Although changes in forest structure from intermediate to late stages were statistically significant (Table 2), more dramatic changes were observed from the early to intermediate stage for all structural variables (Table 1). Overall, the HCI increased 30 times from the early (0.5 ± 0.2, mean ± standard error) to intermediate (15.0 ± 2.1) stage and only 3.1 times between intermediate and late (46.1 ± 9.2) stages (Table 1).

In contrast, liana structure showed a reverse pattern along the successional gradient (Table 1). We sampled 192 liana individuals in 6 intermediate plots and 124 individuals in 8 late plots, representing a significant decrease in stem density along the successional gradient. No lianas were found in the early successional stage. Although the height where lianas were found increased from intermediate to late stages, basal area and liana density were significantly higher in the intermediate stages (Tables 1, 2). Liana density was negatively correlated with tree density, and the correlation was statistically significant for both the intermediate and late stages, indicating that liana density decreases as succession unfolds (Table 3, Fig. 4).

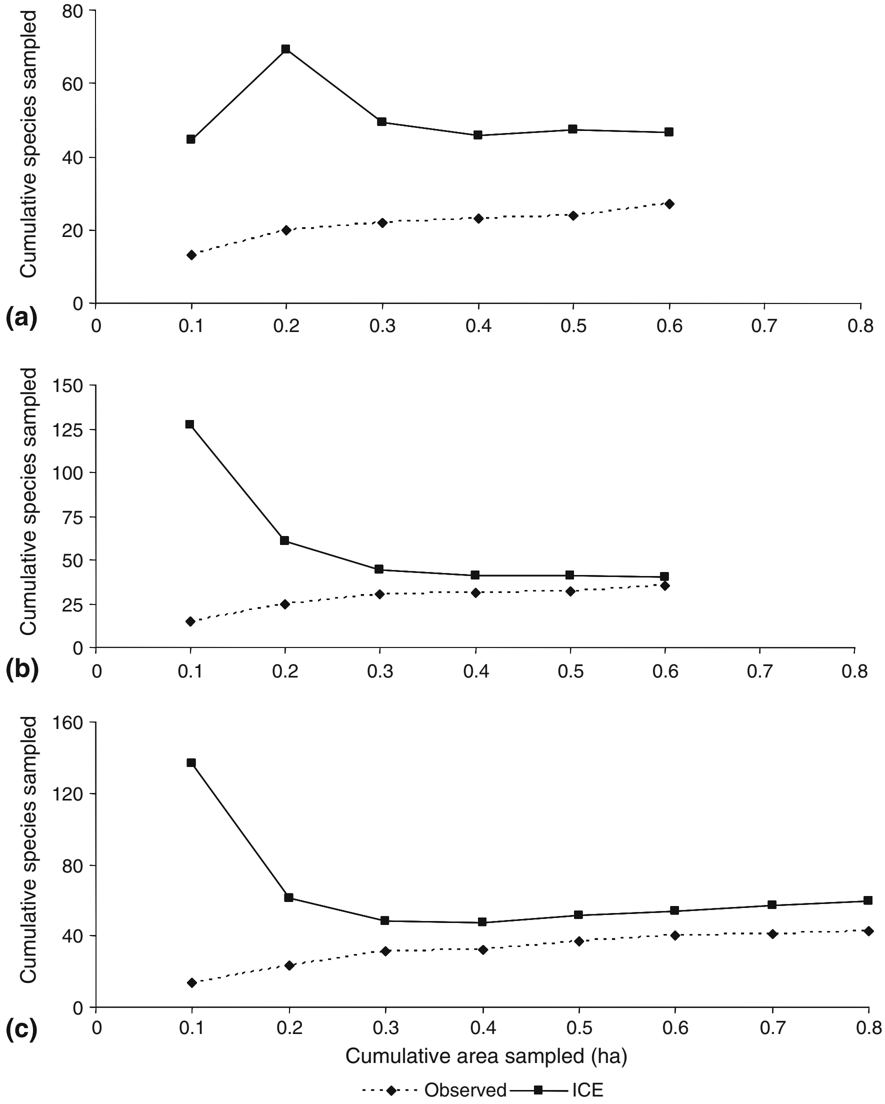

Fig. 2 Species accumulation curves of trees for the early (**a**), intermediate (**b**) and late (**c**) successional stages. ICE = incidence-based coverage estimator

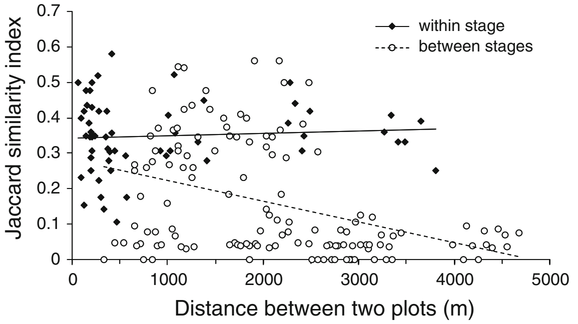

Fig. 3 Linear regression between Jaccard's similarity index (response variable) and distance between plots (explanatory variable) from the same (full line, closed points) and different (dashed line, open circles) successional stages

Discussion

Tree structure and diversity: successional changes

Forest structure changed along the successional gradient according to the general pattern of secondary succession described for tropical forests, with a gradual increase in height and basal area (Guariguata and Ostertag 2001; Kalácska et al. 2004; Ruiz et al. 2005). On the other hand, variation on stem density along successional stages observed here did not conform to general patterns observed for both wet and dry forests. Usually, there is a high density of stems with low DBH in early and intermediate stages,

Table 3 Analysis of variance of the complete and minimal adequate linear models of the density of lianas (response variable) and the forest structural characteristics (tree species richness, basal area of trees and density of trees) between the two sucessional stages in the Parque Estadual da Mata Seca, MG

Source	Errors	d.f.	Deviance	Residual d.f.	Residual deviance	F	P
Complete model							
Density of trees	Quasipoisson	1	26.687	12	39.691	12.16	0.00686
Tree species richness		1	0.447	11	39.243	0.204	0.662
Basal area of trees		1	5.884	10	33.359	2.681	0.136
Stage		1	11.778	9	21.581	5.367	0.0457
Minimal adequate model							
Density of trees	Quasipoisson	1	26.687	12	39.691	13.804	0.00341
Stage		1	16.246	11	23.445	8.403	0.0145

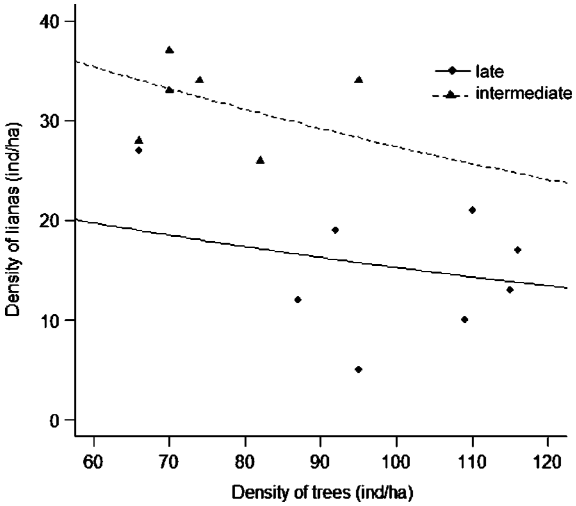

Fig. 4 Linear regression between the density of lianas (response variable) and the density of trees (explanatory variable) in intermediate and late successional stages

and as DBH increases with forest growth, stem density decreases (Mizrahi et al. 1997; Saldarriaga et al. 1988; Denslow and Guzman 2000; Kennard 2002; Kalácska et al. 2004; Ruiz et al. 2005). In spite of the gradual increase in average stem density observed here, the pattern described above is clearly illustrated for one species of the PEMS. *M. urundeuva*, a very common species in Brazilian STDFs (Oliveira-Filho et al. 1998; Pereira et al. 2003; Salis et al. 2004), is the second most abundant species in the early stages, with low DBH values. It was also encountered in the late stages, where this species was the sixth most abundant tree, but with much higher DBH values (see Fig. 1). Nevertheless, the successional changes in stem density observed at the PEMS were also detected for a STDF in Chamela, Mexico (Kalácska et al. 2005).

In spite of the high species dominance observed for all successional stages, the succession gradient observed here did not conform to the dominance-controlled community model, which predicts higher tree diversity in mid-successional forests (Yodzis 1986; Begon et al. 2006). According to this model, tree species diversity is low in early successional stages, which are colonized by a limited group of pioneers. As succession progresses, other species invade the area and intermediate regeneration stages are composed by a high number of mid- and late successional tree species. As the forest matures towards the climax, late, efficient competitor species oust mid-successional species, causing a decrease in tree community diversity, which is dominated by a lower number of late species (Yodzis 1986; Begon et al. 2006). However, a higher tree diversity in late compared to intermediate stages was described for other STDFs, such as Chamela, Palo Verde (Kalácska et al. 2005) and Providence Island (Ruiz et al. 2005), whereas the successional gradient observed in Santa Rosa conforms partially to the predicted for dominance-controlled tree communities (Kalácska et al. 2005). One likely alternative explanation is that the forest sites considered as late stages in these studies (including the present) are more similar in structure and diversity to secondary forests in an advanced stage of regeneration than to mature forests. In this case, we would expect a decrease in tree diversity in the late stages in the next decades. Indeed, some estimates indicate that the recovery time for lowland dry forest ecosystems is around 150 years (Opler et al. 1977). Nevertheless, the structure of the late stages in the above-mentioned forests is consistent with that described for mature STDFs (see Murphy and Lugo 1986; Ruiz et al. 2005). Thus, more long-term studies are necessary to test whether succession patterns in STDFs conform to the predicted for dominance-controlled communities.

The relative importance of seed colonization and resprouting in forest recovery is controversial, originating opposing succession models. In the 'relay floristics model', a gradual species substitution is expected across time, whereas the 'initial floristic composition model' predicts that pioneer species remain in advanced stages of succession (Egler 1954). The successional gradient analysed in the present study corroborates the former model, since there are striking changes in tree community composition from early to intermediate and late stages. On the contrary, some recent studies on Brazilian SDTFs found that a vast majority of the plant species are present in recently abandoned pastures and remain later in the succession (Vieira et al. 2006; Sampaio et al. 2007). These authors related this pattern to the great resprouting capacity of dry forest tree species, which can be affected by the intensity of pasture management practices such as fire, clear-cutting and tractor use. In our areas, ploughing probably removed the majority of plant roots after clear-cutting, preventing resprouting and reducing the presence of late species in early sites. In areas recovering from this type of pasture management, succession is more likely to conform to the 'relay floristic model'. When resprouting is intense, succession may resemble the predicted by the 'initial floristic composition model'. However, the presence of multi-stemmed trees in early plots and the occurrence of *M. urundeuva* in all three successional stages of the PEMS suggest that regeneration by resprouting is also occurring. Thus, succession models may represent extremes in a continuum of possible successional pathways strongly influenced by land use history.

The great tree species substitution from early to intermediate and late stages is probably related to changes in light penetration through the forest canopy along the successional gradient. Light quality and quantity may have a profound effect in determining the survivorship of shade-intolerant pioneer trees. For instance, *S. spectabilis*, the most abundant species in the early stage, can be considered a pioneer species according to the classification proposed by Swaine and Whitmore (1988). The plant is a short-lived heliophyte, with rapid growth in height, especially under direct sunlight (Lorenzi 1992). This can explain the absence of this species from the shaded understory of intermediate and late forest fragments. Also, light availability can affect seed germination and seedling growth in early successional stages. Though there is only scattered information on the ecophysiology of the majority of the tree species encountered in this study, some of the dominant species in early successional plots have either positive photoblastic or neutral seeds. For instance, although *M. urundeuva* is considered a climax, shade-tolerant species, it was the second most abundant species in early stage plots, and its seeds may be able to germinate both in gaps, exposed to direct sunlight and daily temperature fluctuations, and in the understory, where diffuse light and lower daily temperature variations predominate (Silva et al. 2002). Similarly, the germinative behaviour of *A. polyphylla*, fifth most abundant species in early stage plots, also indicates that it can germinate in different-sized gaps, exposed to diverse temperature and light conditions (Araújo Neto et al. 2003). Thus, it is likely that most species encountered in early plots are adapted to open canopy conditions, though some late, shade-tolerant species can also regenerate by sprouting in these areas.

Liana structure and liana–tree interactions

Lianas represented a very important structural component of the SDTFs in PEMS, with marked changes along the successional gradient considered in this study, probably related to changes in light and support availability. In the early stages light is not limiting, but there are few branches thick enough to support the growth of lianas with more than 2 cm. In fact, the dependence of large lianas on large trees has been reported in other studies (Clark and Clark 1990; Nabe-Nielsen 2001; Phillips et al. 2002). In the intermediate stages, light availability decreases, but the canopy is still open enough to allow successful liana establishment, due to the presence of adequate support (Sánchez-Azofeifa, unpubl. data). As succession progresses, the canopy increases in height (from 8.2 m in intermediate stages to 13.3 m in late stages, on average) and continuity, reducing the habitat suitability for lianas for two reasons: first, energetic costs associated with ascent may reduce liana capacity to climb a great distance to the canopy (DeWalt et al.

2000); second, lianas are light-demanding (Castellanos 1991; Teramura et al. 1991) and, in closed canopies of late forests, they are only able to establish and grow in tree gaps (Putz 1984; Schnitzer and Carson 2001). These factors may be responsible for the decline in abundance observed here from intermediate to late stages, as well as for the negative relationship verified between liana density and tree density, considering all the sampled plots from both stages.

Our results corroborate other studies, mostly from wet forests, which reported a higher density of lianas in younger forests (DeWalt et al. 2000; Schnitzer and Bongers 2002; Kuzee and Bongers 2005; Schnitzer 2005). We are not aware of any other study comparing liana structural characteristics along a succesional gradient of SDTFs. However, Kalácska et al. (2005) found indirect evidence that lianas are also more abundant in intermediate successional stages. They reported that the proportion of liana leaves collected on leaf traps along a successional gradient in a SDTF in Santa Rosa, Costa Rica, were higher in the intermediate than early and late stages. Thus, there is an urgent need for more studies concerning successional changes in the liana component of SDTFs, in order to understand the regeneration processes in these ecosystems and allow comparisons with the better studied wet forests.

Conclusions

Studies with successional gradients can be very useful to understand natural regeneration patterns in SDTFs, and to compare the consequences of different land use histories for forest recovery. Resprouting can be a very common mechanism of SDTF regeneration, but its intensity may depend on previous land management practices. Pasture colonization through seed germination is more likely in ploughed areas, which can lead to the classical succession pattern characterized by a gradual but marked change in community composition. However, a mixture of both processes is probably the rule for most SDTFs. Many others factors are thought to affect forest regeneration, such as climate, soil type and the abundance of lianas. To our knowledge, this was the first study that analysed changes in liana structure along a successional gradient in SDTFs, providing a possible explanation for their higher abundance at intermediate secondary forests based on trade-offs in support and light availability. Lianas certainly play an important role in SDTF recovery, and the strength of their influence on tree growth needs further attention, with long-term and experimental studies to allow comparisons with the better known wet forests.

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Appendix

Table 4 List of tree species (DBH ≥ 5 cm) identified in the 20 plots in three successional stages in the dry forest of the Parque Estadual da Mata Seca, MG

Family	Species	Stage		
		Early	Intermediate	Late
Anacardiaceae	*Astronium fraxinifolium* Schott	x		
	Myracrodruon urundeuva All.	x	x	x
	Schinopsis brasiliensis Engl.	x		
	Spondias tuberosa Arruda		x	x

Table 4 continued

Family	Species	Stage		
		Early	Intermediate	Late
Apocynaceae	*Aspidosperma pyrifolium* Mart.	x		x
	Aspidosperma polyneuron Mull.Arg.			x
	Aspidosperma subincanum Mart.		x	x
Araliaceae	*Aralia warmingiana* (Marchal) J. Wen		x	x
Arecaceae	*Syagrus oleracea* (Mart.) Becc.			x
Asclepiadaceae	*Calotropis procera* (Aiton) W.T. Aiton	x		
Asteraceae	*Vernonia* sp.	x		
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC.) Standl.		x	x
	Tabebuia ochracea (Cham.) Standl.	x	x	x
	Tabebuia roseo-alba (Ridl.) Sandwith		x	x
	Zeyheria tuberculosa Bureau ex Verlot	x		
Bombacaceae	*Cavanillesia arborea* K. Schum.		x	x
	Chorisia glaziovii (Kuntze) E. Santos		x	x
	Pseudobombax longiflorum (Mart. & Zucc.) A. Robyns.		x	x
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B. Gillett		x	x
Cactaceae	*Cereus jamacaru* DC.		x	x
Cactaceae	*Pereskia grandifolia* Haw.		x	x
Cochlospermaceae	*Cochlospermum vitifolium* Spreng.		x	x
Combretaceae	*Combretum duarteanum* Cambess.		x	x
	Terminalia eichleriana Alwan & Stace		x	x
Euphorbiaceae	*Cnidoscolus pubescens* Pax		x	
	Manihot anomala Pohl	x	x	
	Maprounea guianensis Aublet			x
	Sapium obovatum Klotzsch ex Mull. Arg.		x	x
Fabaceae	*Acacia* cf. *polyphylla* DC.	x	x	x
	Acacia sp. 1	x		
	Acacia sp. 2			x
	Anadenanthera colubrina (Vell.) Brenan		x	x
	Bauhinia sp.	x		
	Caesalpinia pyramidalis Tul.	x	x	x
	Cassia multijuja Rich.	x		
	Centrolobium sp. Mart. Ex Benth.		x	x
	Chloroleucon tortum (Mart.) Barneby & J.W. Grimes	x	x	x
	Enterolobium contortisiliquum Vell. (Morong.)		x	x
	Goniorrhachis marginata Taub.			x
	Machaerium acutifolium Vog.		x	x
	Machaerium brasiliense Vog.		x	x
	Machaerium cf. floridum (Mart.) Ducke		x	x
	Machaerium scleroxylon Tul.		x	
	Mimosa tenuiflora Benth.	x		
	Piptadenia viridiflora Kunth. (Benth.)	x	x	
	Plathymenia reticulata Benth.	x	x	
	Platymiscium blanchetii Benth.	x		x
	Pterocarpus rohrii Vahl			x
	Senna spectabilis (DC.) H·S. Irwin & Barneby	x		
Meliaceae	*Cedrela odorata* L.		x	x
Myrtaceae	Myrtaceae sp.			x
Nyctaginaceae	*Ramisia brasiliensis* Oliv.			x

Table 4 continued

Family	Species	Stage		
		Early	Intermediate	Late
Picramniaceae	*Picramnia sellowii* Planch.		x	x
Polygonaceae	*Coccoloba schwackeana* Lindau	x		x
Rhamnaceae	*Zizyphus joazeiro* Mart.	x		
Rubiaceae	*Randia armata* DC.	x		x
Sterculiaceae	*Sterculia striata* A. St.-Hil. & Naudin			x
Ulmaceae	*Celtis iguanaea* (Jaqc.) Sarg.	x		
Vochysiaceae	*Callisthene major* Mart.			x
Total		24	33	42

References

Antunes FZ (1994) Caracterização Climática—Caatinga do Estado de Minas Gerais. Informe Agropec 17:15–19

Araújo Neto JC, Aguiar IB, Ferreira VM (2003) Efeito da temperatura e da luz na germinação de sementes de *Acacia polyphylla* DC. Revta Bras Bot 26:249–256

Arroyo Mora JP, Sánchez-Azofeifa GA, Rivard B, Calvo J (2005) Quantifying successional stages of tropical dry forests using Landsat ETM+. Biotropica 37:497–507. doi: 10.1111/j.1744-7429.2005.00068.x

Begon M, Harper JL, Townsend CR (2006) Ecology: individuals, populations and communities. Blackwell, Oxford

Castellanos AE (1991) Photosynthesis and gas exchange of vines. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 181–202

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspect Plant Ecol 6:51–71. doi:10.1078/1433-8319-00042

Chazdon RL, Colwell RK, Denslow JS, Guariguata MR (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier F, Cominsky JA (eds) Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies. Parthenon Publishing, Paris, pp 285–309

Clark DB, Clark DA (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican wet forest. J Trop Ecol 6:321–331

Colwell RK (2006) EstimateS: statistical estimation of species richness and shared species from samples, version 8.0. Available via http://purl.oclc.org/estimates. Accessed 12 August 2008

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos T R Soc B 345:101–118. doi:10.1098/rstb.1994.0091

Corlett R (1994) What is secondary forest? J Trop Ecol 10: 445–447

Crawley MJ (2002) Statistical computing: an introduction to data analysis using S-Plus. Wiley, Chichester

Denslow JS, Guzman S (2000) Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. J Veg Sci 11:201–212. doi:10.2307/3236800

DeWalt SJ, Schnitzer SA, Denslow JS (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. J Trop Ecol 16:1–19. doi: 10.1017/S0266467400001231

Egler FE (1954) Vegetation science concepts I. Initial floristic composition: a factor in old field vegetation development. Vegetatio 4:412–417. doi:10.1007/BF00275587

Gentry AH (1995) Diversity and floristic composition of Neotropical dry forests. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp 146–194

Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19:149–156. doi:10.2307/2388737

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manage 148:185–206. doi:10.1016/S0378-1127(00)00535-1

Hegarty EE, Caballé G (1991) Distribution and abundance of vines in forest communities. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 313–336

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose

Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JA Jr (1971) Forest environments in tropical life zones: a pilot study. Pergamon Press, New York

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228. doi:10.1146/annurev.es.13.110182.001221

IEF—Instituto Estadual de Florestas (2000) Parecer técnico para a criação do Parque Estadual da Mata Seca. Instituto Estadual de Florestas, Belo Horizonte

Janzen DH (1983) No park is an island: increase in interference from outside as park size decreases. Oikos 41:402–410. doi:10.2307/3544100

Janzen DH (1986) Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, DC, pp 130–137

Janzen DH (1988) Management of habitat fragments in a tropical dry forest: growth. Ann Mo Bot Gard 75:105–116. doi: 10.2307/2399468

Justiniano MJ, Fredericksen TS (2000) Phenology of tree species in Bolivian dry forests. Biotropica 32:276–281

Kalácska M, Sánchez-Azofeifa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH (2004) Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. For Ecol Manag 200:227–247

Kalácska M, Sánchez-Azofeifa GA, Calvo-Alvarado JC, Rivard B, Quesada M (2005) Effects of season and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests. Biotropica 37:486–496. doi:10.1111/j.1744-7429.2005.00067.x

Kellman MC (1970) Secondary plant succession in tropical montane Mindanao. Australian National University, Department of Biogeography and Geomorphology, Canberra

Kennard DK (2002) Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. J Trop Ecol 18: 53–66. doi:10.1017/S0266467402002031

Kuzee ME, Bongers F (2005) Climber abundance, diversity and colonization in degraded forests of different ages in Côte d'Ivoire. In: Bongers F, Parren MPE, Traoré D (eds) Forest climbers of West Africa: diversity, ecology and management. CABI Publishing, Wallingford, pp 67–84

Laurance WF, Pérez-Salicrup D, Delamônica P, Fearnside PM, D'angelo S, Jerozolinski A, Pohl L, Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–116

Lorenzi H (1992) Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil, vol 2. Plantarum, São Paulo

Lugo AE, Gonzalez-Liboy JA, Cintron B, Dugger K (1978) Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10:278–291. doi: 10.2307/2387680

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Malden

Miles L, Newton AC, Fries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE (2006) A global overview of the conservation status of tropical dry forests. J Biogeogr 33:491–505. doi:10.1111/j.1365-2699.2005.01424.x

Mizrahi A, Ramos-Prado JM, Jimenez-Osorio J (1997) Composition, structure, and management potential of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan Mexico. For Ecol Manage 96:273–282. doi:10.1016/S0378-1127(97)00008-X

Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB (2000) Phenology of Atlantic rain forest trees: a comparative study. Biotropica 32:811–823. doi: 10.1111/j.1744-7429.2000.tb00620.x

Murphy PG (1995) Dry forests of Central America and the Caribbean. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp 9–34

Murphy PG, Lugo AE (1986) Ecology of tropical dry forests. Annu Rev Ecol Syst 17:67–88. doi:10.1146/annurev.es.17.110186.000435

Nabe-Nielsen J (2001) Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. J Trop Ecol 17:1–19. doi:10.1017/S0266467401001018

Oliveira-Filho AT, Curi N, Vilela EV (1998) Effects of canopy gaps, topography, and soils on the distribution of woody species in a central Brazilian deciduous dry forest. Biotropica 30:362–375. doi:10.1111/j.1744-7429.1998.tb00071.x

Opler PA, Baker HG, Frankie GF (1977) Recovery of tropical lowland forest ecosystems. In: Cairns J Jr, Dickson KL, Herricks EE (eds) Recovery and restoration of damaged ecosystems. University of Virginia Press, Charlottesville, pp 379–421

Pereira IM, Andrade LA, Sampaio EVSB, Barbosa MRV (2003) Use-history effects on structure and flora of caatinga. Biotropica 35:154–165

Pérez-Salicrup DR (2001) Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. Ecology 82:389–396

Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, Alexiades M, Cerón C, Di Fiore A, Erwin T, Jardim A, Palacios W, Saldias M, Vinceti B (2002) Increasing dominance of large lianas in Amazonian forests. Nature 418:770–774. doi:10.1038/nature00926

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) Special paper: a global biome model based on plant physiology and dominance, soil properties and climate. J Biogeogr 19:117–134. doi: 10.2307/2845499

Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724. doi:10.2307/1937767

Ruiz J, Fandino MC, Chazdon RL (2005) Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. Biotropica 37:520–530. doi:10.1111/j.1744-7429.2005.00070.x

Sader S, Waide RB, Lawrence WT, Joyce AT (1989) Tropical forest biomass and successional age class relationships to a vegetation index derived from Landsat TM data. Remote Sens Environ 28:143–156. doi:10.1016/0034-4257(89)90112-0

Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. J Ecol 76:938–958. doi:10.2307/2260625

Salis SM, Silva MP, Matos PP, Silva JSV, Potti VJ, Pott A (2004) Fitossociologia de remanescentes de florestas estacionais deciduais em Corumbá, Estado do Mato Grosso do Sul, Brasil. Rev Bras Bot 27:671–684. doi: 10.1590/S0100-84042004000400008

Sampaio AB, Holl KD, Scariot A (2007) Regeneration of seasonal deciduous forest tree species in long-used pastures in Central Brazil. Biotropica 39:655–659. doi: 10.1111/j.1744-7429.2007.00295.x

Sánchez-Azofeifa GA, Castro K, Rivard B, Kalascka M, Harriss RC (2003) Remote sensing research priorities in tropical dry forest environments. Biotropica 35:134–142

Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. Am Nat 166:262–276. doi:10.1086/431250

Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends Ecol Evol 17:223–230. doi:10.1016/S0169-5347(02)02491-6

Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913–919

Schnitzer SA, Dalling JW, Carson W (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J Ecol 88:655–666. doi:10.1046/j.1365-2745.2000.00489.x

Sevilha AC, Scariot A, Noronha SE (2004) Estado atual da representatividade de unidades de conservação em Florestas Estacionais Deciduais no Brasil. In: Sociedade Brasileira de Botânica (org) Biomas florestais. Editora da Universidade Federal de Viçosa, Viçosa, pp 1–63

Silva LM, Rodrigues TJD, Aguiar IB (2002) Efeito da luz e da temperatura na germinação de sementes de aroeira (*Myracrodruon urundeuva* Allemão). Rev Arvore 26:691–697

Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86. doi:10.1007/BF00044629

Teramura AH, Gold WG, Forseth IN (1991) Physiological ecology of mesic, temperate woody lianas. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 245–285

Vieira DLM, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. Restor Ecol 14:11–20. doi:10.1111/j.1526-100X.2006.00100.x

Vieira DLM, Sampaio AB, Scariot A, Holl K (2006) Tropical dry forest regeneration from root suckers in Central Brazil. J Trop Ecol 22:1–5. doi:10.1017/S0266467405003135

Wright JC, Sánchez-Azofeifa GA, Portillo C, Davies D (2007) Poverty and corruption compromises tropical forest reserves. Ecol Appl 17:1259–1266. doi:10.1890/06-1330.1

Yodzis P (1986) Competition, mortality and community structure. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 480–491

Woody plant composition of forest layers: the importance of environmental conditions and spatial configuration

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Abstract The species–environment relationships for woody species may vary according to the forest layers considered. In fragmented forest, spatial configuration may also influence forest layer composition. We investigated the relationships between four forest layer compositions and environmental conditions, and spatial variables accounting for forest fragmentation, in 59 forest stands. Field and shrub layer compositions were mainly linked to environmental conditions, particularly to soil pH and slope aspect, while the upper layer compositions were principally correlated to the spatial configuration. The distance from the forest edge was correlated with all the forest layer compositions. Our results suggest that woody species respond to factors acting at different spatial and temporal scales, depending on the forest layer they belong to. The species–environment relationship seems to weaken from the lower to upper layer, the upper layer being more closely linked to the spatial configuration and probably to the past management. This study underlines the importance of taking spatial configuration in addition to environmental conditions into account when studying woody plant diversity for different forest layers in stands located in deciduous fragmented forests. Moreover, stand history seems to have a lasting effect on woody plant composition, particularly for the tree layer.

Keywords Coppice-with-standards · Land-use history · Fragmented forest · Slope aspect · Soil pH · South-western France

Introduction

Woody plant species is a key biological group for forest ecosystems since it is responsible for their architecture (Stapanian et al. 1997), which subsequently determines many of the ecological conditions found within forest. The factors that explain the diversity of woody plants differ from those of non woody species because of their larger size, their stratification, and their longevity; the study of woody plant diversity needs to account for these specificities. Diversity is a scale-dependent concept (Magurran 1988); thus, the scale at which the factors are studied needs to be defined. We know that factors acting on plant diversity at fine scales are not the same as those acting at larger spatial scales (Whittaker et al. 2001; Decocq 2002; Weiher and Howe 2003). Besides, within the possible range of spatial scales at which we can study diversity and its determinants, it seems

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to be important to study the diversity patterns at the spatial scale at which biodiversity is usually managed (Bestelmeyer et al. 2003), with the perspective of preserving such diversity. Woody plant diversity and their driving factors are likely to be affected by forest logging interventions at the stand scale. Forest fragments in agricultural landscapes, particularly those owned by farmers, frequently pertain to several owners (Guyon et al. 1996), and, as a consequence, different management practices can be found in a given forest fragment (De Warnaffe et al. 2006).

According to the traditional niche-based approach, many authors have sought for species–environment relationships to understand the determinants of community composition (Svenning and Skov 2002). These studies commonly found a predominant effect of soil pH on plant diversity (i.e., richness and composition) (Brunet et al. 1997; Sagers and Lyon 1997; Diekmann et al. 1999; Augusto et al. 2003; Borchsenius et al. 2004; Schuster and Diekmann 2005; Lenière and Houle 2006), and also of slope aspect in forested landscapes with dissected topography (Cantlon 1953; Small and MacCarthy 2002; Gracia et al. 2007). These studies usually ignored the potential effect of spatial configuration on the observed patterns (but see de Blois et al. 2001). However, there is now a growing interest in taking spatial configuration into account when studying the drivers of forest stand diversity since recent studies in plant ecology have reported important effects of seed dispersal limitations in forest plant communities (Svenning and Skov 2002; McEuen and Curran 2004). For stands located in fragmented forests, spatial variables that account for forest fragmentation (i.e., forest fragment area, distance from the forest edge and isolation) may explain the residual variation of species–environment relationships (Schuster and Diekmann 2005). At the forest fragment scale, several studies have compared the effects of site conditions and spatial configuration on forest plant species richness and composition (Dzwonko and Loster 1988, Grashof-Bokdam 1997, Honnay et al. 1999; Butaye et al. 2001; Jacquemyn et al. 2003). At the stand scale (i.e., spatial units within forest fragments with uniform canopy composition, structure, age and management), the influence of the forest edge has been extensively studied (see Murcia 1995; Ries et al. 2004; Harper et al. 2005 for reviews on edge effect). Few studies, however, have investigated the relationships between forest fragment area, or isolation, and forest plant species diversity (but see Petersen 2002 and Guirado et al. 2007).

Woody plants, given their longevity and the important differences in size between individuals found in the different forest layers, have been shown to present different relationships with environmental variables (Bratton 1975; Burnett et al. 1998; Lyon and Gross 2005) and also spatial variable (distance from edge) (Ranney et al. 1981; Gehlhausen et al. 2000), depending on the forest layers considered. Moreover the composition and the amount of cover in the understory are also dependent on the identity of the trees present in the overstory (Augusto et al. 2003; Legare et al. 2002).

The purpose of our article is to examine the factors determining woody plant composition of stands located in forest fragments. We investigated both species–environment relationships and relationships between woody species composition and spatial variables in 59 stands located in fragmented forests for four forest layers. We also investigated the relationship between the compositions of the four forest layers.

Methods

Study area

Field research was conducted in a 632-km^2 area located in the “Coteaux de Gascogne,” in south-western France (43°13′N, 0°52′E). The climate is mild, with a mean annual temperature of 12.5°C and mean annual precipitation of 750 mm. This hilly area (200–400 m a.s.l.) has short and steep slopes along the river valleys descending from the Pyrenees Mountains. The forests have three types of soil: superficial calcareous soils (rendosols or calcosols), brown acid soils (brunisols), and brown washed soils (neoluvisols) (Duchaufour 1983). Forests cover 15% of the area with numerous small forested fragments ranging from <1 to 50 ha, and a few larger forests (max = 600 ha) (Balent and Courtiade 1992). The vegetation shows both Atlantic and Mediterranean influences on medio-European type flora, where oaks (*Quercus robur* L., *Quercus pubescens* Willd., *Quercus petraea* Liebl.) are the main tree species, often in combination with hornbeam (*Carpinus betulus* L.), cherry (*Prunus avium* L.), wild service tree (*Sorbus torminalis* (L.)

Crantz), chestnut (*Castanea sativa* Mill.), and field maple (*Acer campestre* L.). Most of these forest fragments are owned or managed by farmers who produce firewood, and to a lesser extent, timber. Stands are mostly coppice, with 30–50 oak standard trees per ha (Deconchat and Balent 2001) retained to produce timber. Coppice trees are cut every 30 years and standard trees are cut approximately every 60 years. They are regenerated by natural seeding while coppice is mainly regenerated by resprouting.

Vegetation sampling

We selected 39 forest fragments in the study area, i.e., woodlots of various sizes, ranging from 0.32 to 693 ha (median ± SD = 5.75 ± 136). We chose a total of 59 mature stands within these 39 forest fragments, after a thorough survey of the area, with mature stand selection based on two criteria: stands with percent of canopy openness <20% and a coppice layer close to harvest age (i.e., about 30 years). We thus avoided, recently, cut areas or young stands with thin canopies. We controlled the percentage of canopy openness for a subset of 43 stands, using hemispherical photographs taken at the center of the plot, at 1.0 m above ground, and analysed with 'Gap Light Analyser' software (Frazer et al. 1999) (median = 14.6%, SD = 1.57), thus confirming our visual selection of the target stands. Within a given forest fragment, the number of stands selected was determined according to the forest fragment heterogeneity (i.e., the number of different stands in terms of their composition and structure) observed during the survey of the entire forest fragment. The higher the heterogeneity of the forest fragment, the higher the number of stands inventoried in the forest fragment. Our sampling procedure was, in fact, designed so as to cover the maximum range of variation in composition in stands with closed canopies and a maximum range of distances from the forest fragment edge. These selection criteria led to the following sampling scheme: 26 forest fragments with one stand inventoried, 9 forest fragments with two stands inventoried, 2 forest fragments with three stands inventoried, 1 forest fragment with four stands inventoried, and 1 forest fragment with five stands inventoried.

For each stand, we inventoried all woody individuals in a 400-m^2 square plot (Harcombe et al. 2002), as this area corresponds to the optimal plot size established in these forests for woody species. The inventories were made for four forest layers: field layer (<1.30 m), shrub ($1.30 \leq$ height < 7 m), coppice ($7 \leq$ height < 15 m), and canopy ($\geq$15 m height). We added the coppice layer to the three strata (tree, shrub, and field layer) commonly used in forest studies since the type of sylvicultural management used in the forest studied (i.e., coppicing) produces a supplementary layer (Leroyer 2002). Each individual was identified to species level and assigned to one forest layer according to its height. We thus obtained the abundance of all the species found during the inventories in each layer. For species which were coppice, we counted the number of stumps. Nomenclature follows *Flora Europaea* (Tutin et al. 1983). Individuals were also classified according to their d.b.h. (diameter at breast height, i.e., 1.3 m), allowing for the calculation of stand basal area for each plot.

Explanatory variables

Environmental conditions

For each plot, we recorded the slope inclination (%) using an inclinometer and the slope aspect using a compass. The aspects were grouped into two categories as follows: "north-facing" (North, Northeast, Northwest, and one plot facing East; $n = 42$), corresponding to cool and wet climatic conditions and "south-facing" (South, Southeast and Southwest; $n = 15$), corresponding to warm and dry climatic conditions (Bratton 1975; Gonin 1993; Gracia et al. 2007). Two stands located in the valley had no aspect.

We collected one soil core sample at the centre of the square plot, in the A horizon, with an auger (8 cm in diameter) for a subset of 30 plots, selected so as to cover a wide range of different types of stands in terms of the composition of dominant species, structure, and overall species richness. These samples were analysed for pH-H_2O, total C and total N, C/N ratio and available phosphorus content (Duchaufour and Bonneau 1959).

Spatial configuration

For each stand, we measured the distance from the nearest forest edge from the centre of the square plot (in meters) using a tape measure. Hereafter, the distance from the nearest forest edge is referred to as "distance from the forest edge."

All the 39 forest fragments (containing the plots inventoried) were digitised in ArcView® v.3.2 (ESRI 1999) from aerial photographs (scale 1/25,000, year 2002, distributed by the French National Geographic Institute). Forest fragment area (in ha) was calculated using Patch Analyst® v.3 (Elkie et al. 1999) extension of ArcView® v.3.2 (ESRI 1999).

All other woodlots present within a radius of 1000 m around the perimeter of each of the 39 forest fragments (containing the plots) were also digitised based on the same aerial photographs. Using Patch Analyst® v.3 (Elkie et al. 1999) extension of ArcView® v.3.2 (ESRI 1999), the following four variables were calculated to describe landscape context: $D =$ distance to the nearest woodlot (in meters; measured from edge to edge) and Cov100, Cov500, Cov1000 = the percentage of wood cover within radii of 100, 500, and 1000 m, respectively, around the perimeter of the target forest fragment (containing the plots inventoried).

Data analysis

We first performed a Correspondence Analysis (CA) (Benzécri 1973) for each of the four forest layer matrices: plots × species. The plot scores on the two first axes were used as species composition variables (Okland et al. 2003; Bennie et al. 2006). We then analysed the relationship between the composition of each forest layer (plots scores on the two first principal axes of the CA) and environmental (canopy openness only for the two lowest forest layers, slope inclination, pH, C and N contents, C/N and phosphorus content) and spatial (distance from the forest edge, forest fragment area, distance to the nearest woodlot and the three wood covers) variables using Spearman rank correlation analyses. We tested the differences in forest layer composition (plots scores on the two first principal axes of the CA) between slope aspect categories using the Mann–Whitney *U* test. We then used GLM analysis, after transforming the variables (to achieve normality tested with a one-sample Kolmogorov–Smirnof test), to determine for each forest layer which variables (environmental and spatial) were the most important to explain species composition, using a stepwise forward selection procedure. We also investigated whether the composition of the forest layers was similar using Spearman rank correlation analysis between plots' scores of the CA performed for each forest layer.

Correspondence analyses were performed using the ade4 package developed by Thioulouse et al. (1997) in the R free software (Ihaka and Gentleman 1996). Spearman rank correlations analyses, Mann–Whitney *U* tests, and GLM analyses were carried out in SYSTAT® v 9.0 (SYSTAT 1999).

Results

Species richness and composition of the forest layers

We recorded a total of 34 woody species in this survey (Appendix): 30 species in the field layer, 31 species in the shrub layer, 16 species in the coppice layer, and 14 species in the canopy layer. The shrub and the field layers included saplings of tree species that occurred also in canopy and coppice layers, with a tendency of shade-tolerant tree species to be more abundant in the understory layers compared to more light-demanding species (Fig. 1).

The total variance in the species data explained by the two first axes of the CA performed on the four forest layer data matrices ranged from 12.24 (shrub layer) to 20.00% (canopy layer) for the first axis, and from 9.74 (field layer) to 16.38% (canopy layer) for the second axis. The first axes of the three lower forest layers (i.e., field, shrub, and coppice) presented the same pattern of species distribution (Fig. 2), with *Fagus sylvatica* L., *Ilex aquifolium* L., *C. betulus* L., and *Q. petraea* Liebl., at one end of the axis, and *Q. pubescens* Willd., *Q. robur* L., and *Fraxinus excelsior* L. and *S. torminalis* (L.) Crantz, at the opposite end of the axis. For the canopy layer, the first axis separated a group of six plots containing *Populus tremula* L. and *A. campestre* L. from the rest of the plots inventoried. The second axis presented some similarities with the first axis of the CA performed on the other forest layers regarding the location of *F. sylvatica* and *C. betulus* at one end, and of *Q. pubescens* and *F. excelsior* at the other end of the axis.

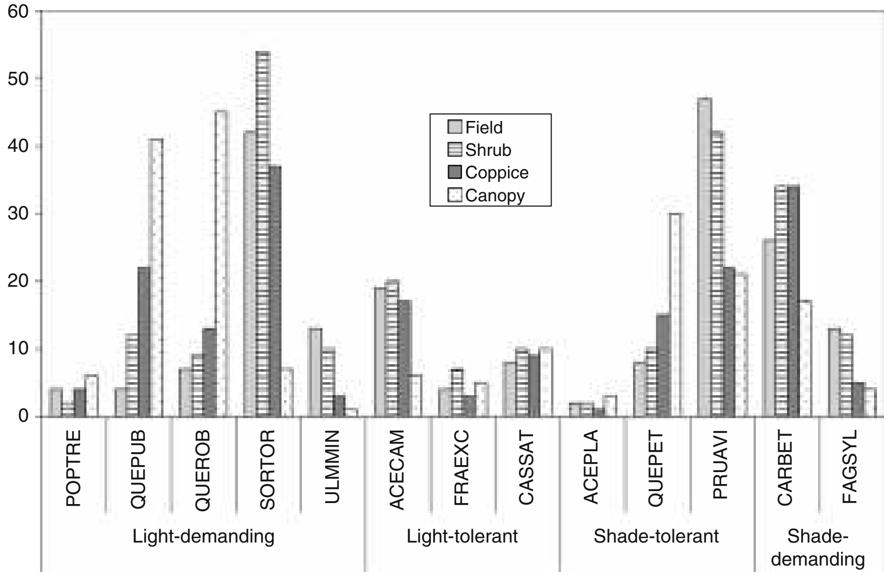

Fig. 1 Frequencies ($N = 59$) of the tree species (i.e., species able to be present in the canopy layer) in the four forest layers, from field to canopy layer. Species are grouped according to their shade tolerance (see Appendix for complete names of species and shade tolerance source)

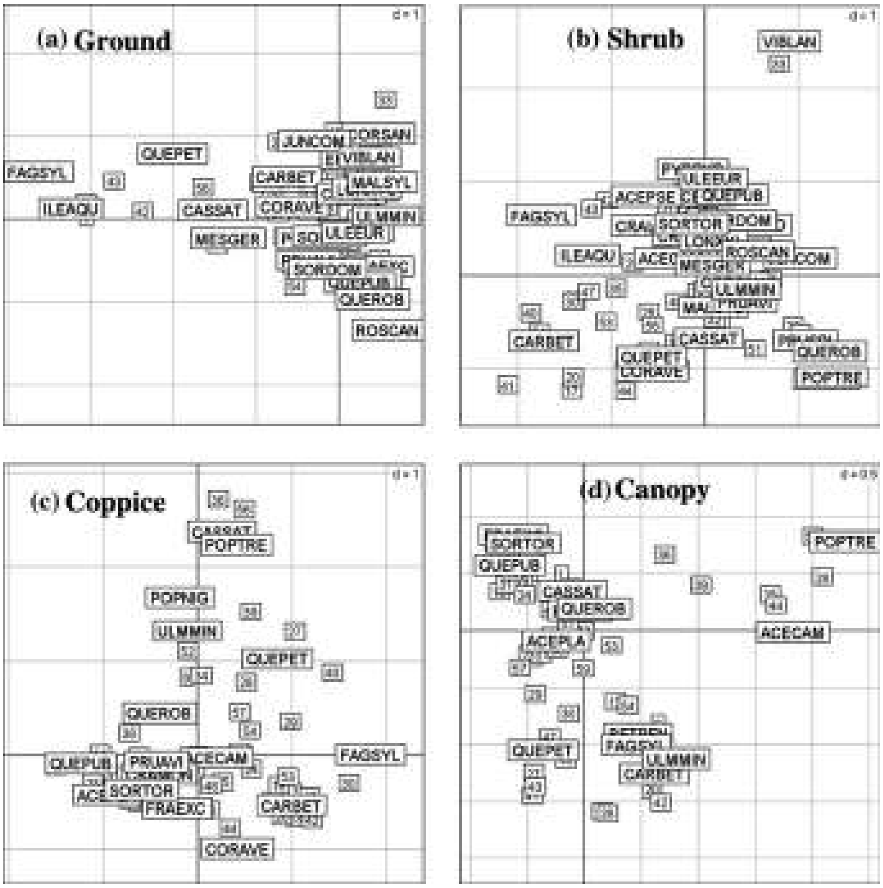

Fig. 2 Factorial maps (axes 1 and 2) of the Correspondence Analysis performed: **a** field layer matrix (59 plots × 30 species), inertia axis 1 = 12.84% and axis 2 = 9.74%; **b** shrub layer matrix (59 plots × 31 species), inertia axis 1 = 12.24% and axis 2 = 10.82%; **c** coppice layer matrix (59 plots × 16 species), inertia axis 1 = 14.26% and axis 2 = 12.83%; and **d** canopy layer matrix (59 plots × 14 species), inertia axis 1 = 20% and axis 2 = 16.38%. The species labels correspond to the first three letters of the genus plus the first three letters of the species name (for example, POPTRE refers to *P. tremula*) and are given in Appendix. The numbers correspond to the plots labels

Relationships with the environmental variables

The composition of the stands inventoried (plot scores in the first axis of the CA) was particularly different between the two categories of slope aspect (“north-facing” vs. “south-facing” slope) for the two lower forest layers studied (Table 1). The differences were less significant for the coppice layer (axis 1) and not significant for the canopy layer (axes 1 and 2: same results). Forest layer compositions were not significantly correlated to the slope inclination, and the two understory layers (field and shrub) were not significantly correlated to the canopy openness (Table 1). Plot scores on the first axis for the field layer and plot scores on the second axis for the shrub layer were significantly and positively correlated with soil pH, and plot scores on the first axis for the coppice layer was significantly and negatively correlated with soil pH (Table 2). Plot scores on the first of the coppice layer were significantly and negatively correlated to C and N contents and positively to soil C/N ratio. Plot scores on the second axis for the shrub layer were positively and significantly correlated to both C and N contents but not to C/N ratio. No relationships were found with phosphorus content for any of the four forest layers.

Relationships with the spatial variables

The spatial variable showing the strongest relationship with forest layer composition was the distance from the forest edge (Table 3). The correlation was significant for the four forest layers investigated. Concomitantly, forest layer compositions were correlated significantly with the forest fragment area. The distance from the forest edge was positively correlated with the forest fragment area in our sampling scheme ($R^2 = 0.670$; $P < 0.001$). For the canopy layer, plot scores on the first axis showed several significant relationships with the spatial

Table 1 Differences in composition (plots scores on the two first axes of the correspondence analysis) between the two types of aspects (“north-facing” and “south-facing” slopes) investigated for the four forest layers (field, shrub, coppice, and canopy layers) with the Mann–Whitney *U* test[a]; $N = 57$[b]. Spearman rank correlations between plots scores and slope inclination (in %; $N = 59$) and canopy openness[c] (in %; $N = 43$) are also given

	Field layer		Shrub layer		Coppice layer		Canopy layer	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Slope aspect	**10.289*** **	0.579	**10.878*** **	3.154	**5.256***	1.202	3.831	3.83
Slope inclination	−0.2	0.116	−0.05	0.107	−0.055	−0.088	0.023	0.048
Canopy openness	0.087	0.086	0.06	−0.104	–	–	–	–

[a] Chi-square approximation are given with 1 d.f., and level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[b] Two stands located in the valley with no aspect are not considered in this analysis

[c] For the canopy openness only relationships with field and shrub layers are investigated as they are the layers susceptible to be linked to this variable

Table 2 Spearman rank correlations between plot scores on the two first axes of the Correspondence Analysis performed on the matrices of the field, shrub, coppice, and canopy layers and the soil variables: pH-H_2O, Carbon (C) and Nitrogen (N) content, C/N ratio and phosphorus content for the A horizon ($N = 30$)

	Field layer		Shrub layer		Coppice layer		Canopy layer	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
pH	**0.529****	0.101	0.107	**0.345***	**−0.491****	−0.205	−0.117	0.251
C	0.166	0.202	−0.051	**0.552****	**−0.337***	0.126	−0.305	−0.035
N	0.175	0.218	−0.114	**0.560****	**−0.338***	−0.052	−0.285	0.012
C/N	−0.167	0.080	0.075	−0.189	**0.317***	**0.449****	0.076	−0.259
Phosphorus	0.016	0.023	−0.135	−0.151	0.247	−0.235	−0.034	−0.006

Bold type indicates significant relationships, with *: $P < 0.05$ and **: $P < 0.01$

Table 3 Spearman rank correlations between plot scores on the first two axes of the Correspondence Analysis performed for the field, shrub, coppice and canopy layers and the spatial variables: forest fragment area (FF area, in ha), distance to the nearest woodlot (*D*, in meters), percentage of wood cover within three radii: 100, 500, and 1000 m (Cov100, Cov500, and Cov1000, respectively) and distance from the forest edge (DFE, in meters) ($N = 59$)

	Field layer		Shrub layer		Coppice layer		Canopy layer	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
FF area	**−0.282***	**0.258***	**−0.301***	**−0.313****	**0.430****	0.045	0.146	**−0.357****
D	0.022	**−0.243***	0.008	**0.280***	**−0.234***	−0.184	**−0.230***	0.155
Cov100	0.079	0.269	−0.009	−0.118	0.177	0.153	**0.220***	−0.037
Cov500	−0.048	0.142	0.009	−0.142	0.030	0.078	**0.258***	0.061
Cov1000	−0.032	0.072	0.168	−0.122	0.009	**0.327****	**0.310****	0.003
DFE	**−0.292***	0.143	**−0.406****	**−0.294***	**0.442****	0.029	**0.228***	**−0.431****

Bold type indicates significant relationships, with * $P < 0.05$ and ** $P < 0.01$

variables accounting for landscape context (i.e., distance to the nearest woodlot and wood covers within the different radii) (Table 3).

Relative effects of environmental versus spatial variables on forest layer compositions

The composition of the field layer was principally linked to the soil pH (Fig. 3), while the shrub layer composition was more influenced by the distance from the forest edge and by slope aspect (Fig. 4 and Table 4). The coppice layer composition was both influenced by the soil pH and the distance from the forest edge (Fig. 5). Finally, the composition of the canopy layer was best explained by the percentage of wood cover in the radii of 1000 m around the forest fragment containing the stand (Fig. 6).

Relationships between the compositions of the four forest layers

All the scores of the stands on the first axis of the CA performed on the three dominated layers' matrix, i.e., the coppice, shrub, and field layers, had a significant

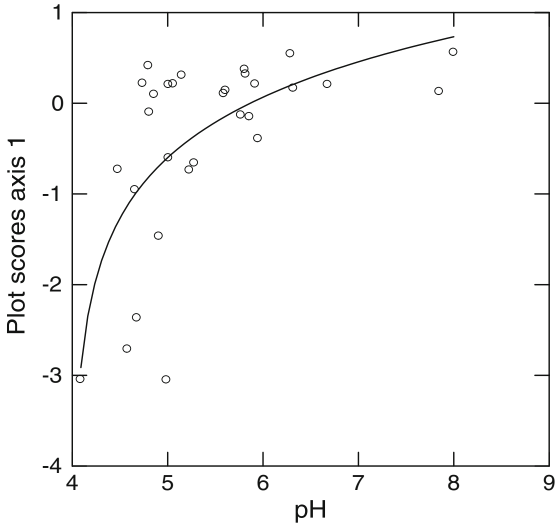

Fig. 3 Relationship between the plot scores on axis 1 of the CA performed on the *field layer* matrix (height < 1.30 m) and soil pH. The line was obtained with a logarithmic smoothing method

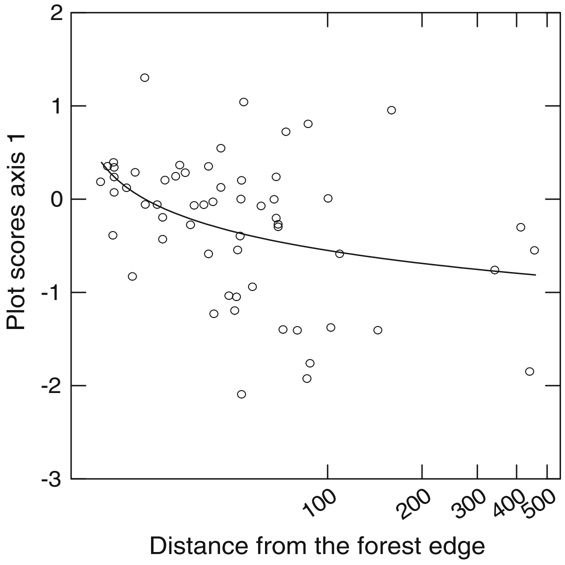

Fig. 4 Relationship between the plot scores on axis 1 of the CA performed on the *shrub layer* matrix (1.30 < height < 7 m) and distance from the forest edge (in meters, in a logarithmic scale). The line was obtained with a logarithmic smoothing method

Table 4 Final model of the GLM analysis obtained after a forward stepwise procedure performed for the four forest layers with plots scores on axis 1 of the CA used as the dependent variable

Forest layer	Effect	Std Coef	P(2Tail)	N
Field				
$F = 12.843$, adjusted $r^2 = 0.290$, $P = 0.001$	pH	0.561	0.001	30
Shrub				
$F = 12.923$, multiple $r^2 = 0.324$, $P = 0.0001$	DFE	−0.348	0.008	57
	Slope aspect	0.433	0.001	
Coppice				
$F = 11.319$, adjusted $r^2 = 0.416$, $P = 0.0001$	pH	−0.483	0.002	30
	DFE	0.489	0.002	
Canopy				
$F = 6.893$, adjusted $r^2 = 0.092$, $P = 0.011$	Cover1000	0.328	0.011	59

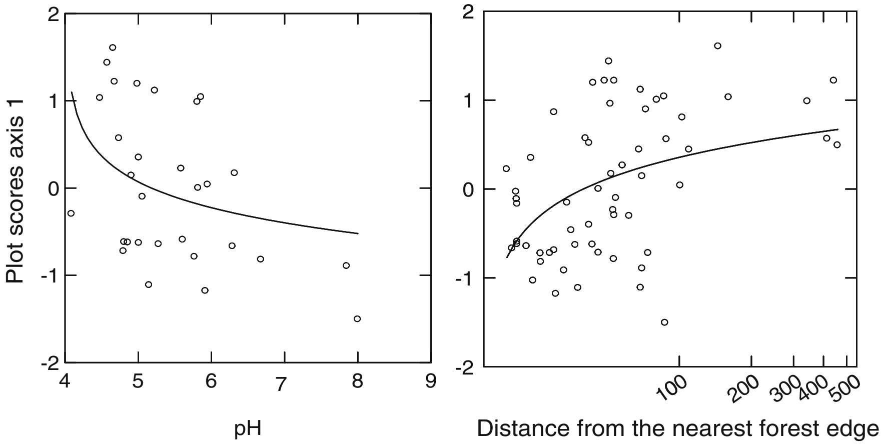

Fig. 5 Relationship between the plot scores on axis 1 of the CA performed on the *coppice layer* matrix (7 < height < 15 m); and *left*: the distance from the forest edge (in meters, in a logarithmic scale) and *right*: the soil pH. The lines were obtained with a logarithmic smoothing method

relationship with the scores of the stands on the second axis of the CA performed on the canopy layer (Table 5). The plot's scores on the first axis of the canopy layer were less correlated with the plot's scores of the different forest layers investigated.

Discussion

Environmental conditions

The composition of the forest layers was significantly correlated to the environmental variables, and particularly to soil pH and slope aspect. The prevailing effect of soil pH on vegetation composition found here is in accordance with other forest studies (Brunet et al. 1997; Sagers and Lyon 1997; Augusto et al. 2003; Borchsenius et al. 2004; Schuster and Diekmann 2005; Lenière and Houle 2006). As is the case in other hilly landscapes, we also found a significant relationship between slope aspect (Cantlon 1953; Burnett et al. 1998; Gracia et al. 2007) and stand composition. Stand composition differences between slopes aspects decreased as the height of the layer investigated increased, as previously reported by Cantlon (1953). The pattern for the relationship between species and soil pH across the different layers investigated was less clear. This environmental variable had a significant relationship with field, shrub, and coppice forest layer composition but not with the canopy layer composition. In an old forest, Borchsenius et al. (2004) found a relationship with soil pH for both the field and the tree layer floristic gradients.

These observed patterns of species–environment relationships are in accordance with previous works in which it was reported that the strength of the species–environment relationship decreased from field to canopy layer (Stohlgren et al. 1998; Collins and Carson 2004). The reduced height and less

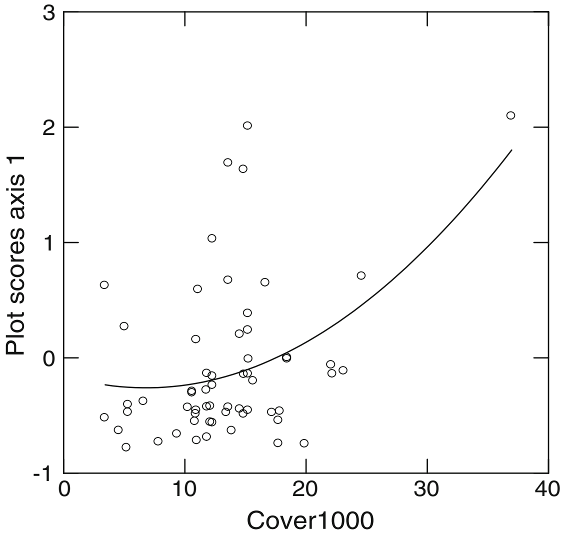

Fig. 6 Relationship between the plot scores on axis 1 of the CA performed on the *canopy layer* matrix ($7 < \text{height} < 15$ m) and the percentage of wood cover in a radii of 1000 m around the forest fragment containing the plot. The line was obtained with a quadratic smoothing method

extensive root systems of the field layer could make them more sensitive to local environmental differences (finer grain) that may not influence trees (Sagers and Lyon 1997; Burnett et al. 1998; de Blois et al. 2001). Moreover, such differences between forest layer responses to environmental conditions could be linked to the vertical changes of physical parameters from field to canopy level, such as humidity or temperature (Cantlon 1953).

However, given the importance of human activities in these forests (De Warnaffe et al. 2006), the canopy layer may also reflect the influence of past or current management practices that can disrupt the correspondence between canopy composition and environmental conditions (Decocq 2000; de Blois et al. 2001). For the canopy layer, the composition described by plot scores on axis 1 (CA of the canopy layer) differs from those found for the three understory layers. Two species, *A. campestre* and *P. tremula*, considerably contribute to the first axis. These two species are present in stands characterized by a low basal area (correlation between plot scores on axis 1 and stand basal area: $r_s = -0.413$, $P < 0.001$). The low basal area of these stands may indicate that they are young stands (from a successional point of view). By investigating their history, we effectively found that these stands were temporarily cleared for agriculture between 1860 and 1998 (Arrignon 2003). The trees (*Acer* and *Populus*) now present in the canopy had therefore established themselves in a previously unforested open area. These conditions no longer exist, which could explain why we did not find the same floristic gradient on axis 1 for the understory layers. Decocq (2000) also observed that pioneer species (such as *P. tremula*) were present in the arborescent layer but not in the understory, probably due to the young age of the forests he studied. He hypothesized that since the canopy was now closed, the shaded environment in the understory prevented the regeneration of these pioneer species. We observed the same pattern for pioneer light-demanding species like oaks in our stands with little regeneration and the contrary for shade-demanding species like *Carpinus* or *Fagus* more represented as young stages than as adults. Orwig and Abrams (1994) have shown that the majority of the adult oaks present in the stands they studied had established themselves from the mid of

Table 5 Spearman correlations between the plots scores on the two first axes obtained from the CA performed on the four forest layers matrix ($N = 59$)

		Canopy		Coppice layer		Shrub layer	
		Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Coppice layer	Axis 1	**0.482****	**−0.677****	1.000			
	Axis 2	0.127	0.113	−0.070	1.000		
Shrub layer	Axis 1	**−0.284***	**0.580****	**−0.679****	**0.419****	1.000	
	Axis 2	**−0.417****	0.206	**−0.426****	−0.099	0.204	1.000
Field layer	Axis 1	**−0.360****	**0.458****	**−0.520****	0.077	**0.506****	**0.278***
	Axis 2	0.181	**−0.231****	**0.276****	0.157	−0.190	0.013

Significant relationships are indicated in bold characters with * $P < 0.05$ and ** $P < 0.01$

the 1800 to the start of the 1900, during a period of repeated cutting. They also observed a low rate of regeneration of these oaks in the understory layers probably due to a reduction in the frequency of fires and of cuttings in their study area. Several works have shown that land-use history can have long-term effects on woody species composition (de Blois et al. 2001; Bellemare et al. 2002; Onaindia et al. 2004). In our study area, previous works (Guyon et al. 1996; De Warnaffe et al. 2006) have shown a lengthening of cutting regimes which could also explain the distribution of the tree species in the upper and understory layers according to their shade tolerance.

Spatial variables

Forest fragment area and distance from the forest edge were significantly correlated with stand composition for all the forest layers investigated. One limitation of our study is that the distance from the forest edge and the forest fragment area are correlated in our sampling scheme. The opposition in the factorial map of the localization of *C. betulus*, *F. sylvatica*, and *Q. petraea* corresponding to the plots located far from the forest edge, and the localisation of *Q. pubescens* and *F. excelsior* corresponding to the plots located near the forest edge, are consistent with the observations made by Ranney et al. (1981) and Matlack (1993), who found light-demanding species at the edges, as opposed to shade-demanding species in forest interiors. The relationships were stronger for the dominant layers since the composition of the field layer was less influenced by the distance from the forest edge than by environmental conditions (soil pH and slope aspect), as reported by McDonald and Urban (2006). De Blois et al. (2001) found that the edge had a significant effect on herbaceous and shrub compositions but not on tree composition. De Blois et al. (2001) hypothesized that the absence of relationship for the tree layer was linked to the past disturbances and that trees had a lower response rate to edge effect, leading more to changes in density than in composition for this forest layer (Murcia 1995). In our forest fragments, forest edges are more frequently logged than forest interiors (De Warnaffe et al. 2006). This may explain the discrepancies between our results and those of de Blois et al. (2001). It was shown in the study area that the repeated coppicing had an adverse effect on *F. sylvatica* and *Q. petraea*, to the advantage of more pioneer-type species such as *Q. pubescens* and *Q. robur*, for example (Gonin 1993). This has also been found in other forests (Orwig and Abrams 1994; Decocq et al. 2004; Onaindia et al. 2004). Thus, even if forest owners, mainly farmers, do not plant trees (De Warnaffe et al. 2006), they can still modify woody species composition through their management practices and particularly through cutting frequency and spatial distribution of cuttings relative to the distance from the edge. The variation of species composition according to the distance from the edge for the four layers in our stands may therefore be related to both a microclimatic (e.g., temperature and/or humidity) or a biotic gradient (e.g., seedling predation) linked to edge effect (Matlack 1993; Gehlhausen et al. 2000; Harper et al. 2005) and/or to the differences in disturbance frequency between edge and forest interior (Palik and Murphy 1990; Kupfer and Runkle 2003). Further work is needed to evaluate these non-exclusive hypotheses.

Landscape context (i.e., wood cover) accounted in large part for the composition of the dominant layers and particularly for the canopy layer (plot scores on axis 1). Petersen (2002) also found a correlation between tree composition and distance to the nearest forest source. In our study, the more significant correlation was found with the wood cover in a buffer zone with a radius of 1000 m. This distance corresponds to the limiting dispersal distance of 1000 m found by Greene and Johnson (1995) for *Acer negundo*, a wind-dispersed species, like *A. campestre* and *P. tremula*, the two main species contributing to the first axis of the canopy CA. The minor role played by landscape context for the understory layers is consistent with the results of Guirado et al. (2007), who found that woodlot size and connectivity played a minor role on forest species richness and composition for understory layers, compared to plot level factors.

Important relationships between the forest layer compositions

Overstory and understory compositions were strongly correlated when investigated by using plot scores in the CA, as also found by Sagers and Lyon (1997) for the plots scores of the first axis for the three strata they investigated (including the tree strata). However, in our study we found that the principal floristic gradient of the canopy layer diverged from the gradient of the other forest layers.

The relationships found between the floristic gradients obtained for each forest layer suggest that they are depending on some common underlying factors. For the canopy (axis 2), the coppice and the shrub and to a lesser extent for the field layer, they probably have, in common, their response to the distance from the forest edge. The field and coppice layers seem to respond also concomitantly to the soil pH gradient. And finally, field and shrub layers probably have in common their differences in composition between the two main slope aspects. However, these relationships do not mean that composition of the understory changes across environmental gradients at the same rate of the composition of overstory, as previously underlined by several authors (Bratton 1975; McCune and Antos 1981).

Woody species sub-communities corresponding to the different forest layers are different compartments of the total woody plant community that do not respond to the same ecological factors, or not to the same extent. The lower forest layers were more related to the environmental variables than overstory strata. For the canopy layer, besides the influence of spatial variables, which explained a little part of variation of the composition, we suspect a potential masking effect exerted by logging activities and forest history that could explain why the plots scores on the first axis of the CA do not relate to environmental variables. This work underline the interest of considering separately the different forest layers when studying woody species diversity and its driving factors in forests, as previously suggested by other authors (Bratton 1975; Lyon and Gross 2005). Further work with variables accounting for logging activities and forest history is needed to improve our understanding of the driving factors of forest layers composition in these managed fragmented forests.

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Appendix

Table 6 List of the species inventoried and their frequency in the four forest layers investigated: (field ($H < 1.30$ m), shrub ($1.30 < H < 7$ m), coppice ($7 < H < 15$ m) and canopy ($H > 15$ m)) ($N = 59$ plots)

Species	Acronym	Life history traits		Forest layer			
		Shade tolerance	Dispersal	Field	Shrub	Coppice	Canopy
Acer campestre L.	ACECAM	Light tolerant	Wind	19	20	17	6
Acer platanoides L.	ACEPLA	Shade tolerant	Wind	2	2	1	3
Acer pseudoplatanus L.	ACEPSE	Shade tolerant	Wind	0	1	0	0
Betula pendula Roth	BETPEN	Light demanding	Wind	0	0	0	1
Carpinus betulus L.	CARBET	Shade demanding	Wind	26	34	34	17
Castanea sativa Mill.	CASSAT	Light tolerant	Animals	8	10	9	10
Corylus avellana L.	CORAVE	Shade demanding	Animals	24	27	1	0
Cornus sanguinea L.	CORSAN	Light tolerant	Birds	40	34	0	0
Crataegus laevigata D.C.	CRALAE	Light tolerant	Birds	9	17	0	0
Crataegus monogyna Jacq.	CRAMON	Light tolerant	Birds	51	52	3	0
Cytisus scoparius L.	CYTSCO	Light demanding	Animals	4	4	0	0
Erica vagans L.	ERIVAG	Light tolerant	Wind	1	0	0	0
Fagus sylvatica L.	FAGSYL	Shade demanding	Animals	4	7	3	5

Table 6 continued

Species	Acronym	Life history traits		Forest layer			
		Shade tolerance	Dispersal	Field	Shrub	Coppice	Canopy
Frangula dodonei Ard.	FRADOD	Light tolerant	Birds	2	2	0	0
Fraxinus excelsior L.	FRAEXC	Light tolerant	Wind	13	12	5	4
Ilex aquifolium L.	ILEAQU	Shade demanding	Birds	7	7	0	0
Juniperus communis L.	JUNCOM	Light demanding	Birds	10	9	0	0
Lonicera xylosteum L.	LONXYL	Light tolerant	Birds	30	26	0	0
Malus sylvestris Mill.	MALSYL	Light tolerant	Animals	1	11	0	0
Mespilus germanica L.	MESGER	Light tolerant	Animals	4	4	0	0
Populus nigra L.	POPNIG	Light demanding	Wind	0	0	1	0
Populus tremula L.	POPTRE	Light demanding	Wind	4	2	4	6
Prunus avium L.	PRUAVI	Shade demanding	Animals	47	42	22	21
Prunus spinosa L.	PRUSPI	Light tolerant	Birds	37	27	0	0
Pyrus pyraster L.	PYRPYR	Light tolerant	Animals	0	1	0	0
Quercus petraea Liebl.	QUEPET	Shade tolerant	Animals	8	10	15	30
Quercus pubescens Willd.	QUEPUB	Light demanding	Animals	4	12	22	41
Quercus robur L.	QUEROB	Light demanding	Animals	7	9	13	45
Rosa canina L.	ROSCAN	Light demanding	Birds	1	7	0	0
Sorbus domestica L.	SORDOM	Light tolerant	Animals	1	1	0	0
Sorbus torminalis (L.) Crantz	SORTOR	Light demanding	Birds	42	54	37	7
Ulex europaeus L.	ULEEUR	Light demanding	Animals	1	1	0	0
Ulmus minor Mill.	ULMMIN	Light demanding	Wind	13	10	3	1
Viburnum lantana L.	VIBLAN	Light tolerant	Birds	15	6	0	0

After each species name, the acronym used in the factorial map and two life history traits, shade tolerance and dispersal mode, are given(according to Rameau et al. 1989)

References

Arrignon F (2003) Importance de l'histoire et de la topographie sur la répartition spatiale de la flore dans un bois fragmenté du Sud-Ouest de la France. Dissertation, University of Toulouse

Augusto L, Dupouey JL, Ranger J (2003) Effects of tree species on understory vegetation and environmental conditions in temperate forests. Ann Sci 60:823–831. doi:10.1051/forest:2003077

Balent G, Courtiade B (1992) Modelling bird communities/landscape patterns relationships in a rural area of south-western France. Landscape Ecol 6:195–211. doi:10.1007/BF00130031

Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. J Biogeogr 29:1401–1420. doi:10.1046/j.1365-2699.2002.00762.x

Bennie J, Hill MO, Baxter R et al (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. J Ecol 94:355–368. doi:10.1111/j.1365-2745.2006.01104.x

Benzécri JP (1973) L'analyse des données. II. L'analyse des Correspondances. Dunod, Paris

Bestelmeyer BT, Miller JR, Wiens JA (2003) Applying species diversity theory to land management. Ecol Appl 13:1750–1761. doi:10.1890/02-5089

Borchsenius F, Nielsen PK, Lawesson JE (2004) Vegetation structure and diversity of an ancient temperate deciduous forest in SW Denmark. Plant Ecol 175:121–135. doi:10.1023/B:VEGE.0000048095.29961.c5

Bratton SP (1975) A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. Bull Torrey Bot Club 102:55–60. doi:10.2307/2484413

Brunet J, Falkengren-Grerup U, Rühling A et al (1997) Regional differences in floristic change in south Swedish oak forests as related to soil chemistry and land use. J Veg Sci 8:329–336. doi:10.2307/3237321

Burnett MR, August PV, Brown JH et al (1998) The influence of geomorphological heterogeneity on biodiversity. I. A patch-scale perspective. Conserv Biol 12:363–370. doi:10.1046/j.1523-1739.1998.96238.x

Butaye J, Jacquemyn H, Honnay O et al (2001) The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. J Veg Sci 13:27–34. doi:10.1658/1100-9233(2002)013[0027:TSPCAT]2.0.CO;2

Cantlon JE (1953) Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. Ecol Monogr 23:241–270. doi:10.2307/1943593

Collins RJ, Carson WP (2004) The effects of environment and life stage on Quercus abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients? For Ecol Manage 201:241–258. doi:10.1016/j.foreco.2004.06.023

de Blois S, Domon G, Bouchard A (2001) Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. Landscape Ecol 16:421–436. doi:10.1023/A:1017548003345

De Warnaffe GD, Deconchat M, Ladet S et al (2006) Variability of cutting regimes in small private woodlots of south-western France. Ann Sci 63:915–927. doi:10.1051/forest:2006075

Decocq G (2000) The masking effect of silviculture on substrate-induced plant diversity in oak-hornbeam forests from northern France. Biodivers Conserv 9:1467–1491. doi:10.1023/A:1008919027221

Decocq G (2002) Patterns of plant species and community diversity at different organizational levels in a forested riparian landscape. J Veg Sci 13:91–106. doi:10.1658/1100-9233(2002)013[0091:POPSAC]2.0.CO;2

Decocq G, Aubert M, Dupont F et al (2004) Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. J Appl Ecol 41:1065–1079. doi:10.1111/j.0021-8901.2004.00960.x

Deconchat M, Balent G (2001) Effets des perturbations du sol et de la mise en lumière occasionnées par l'exploitation forestière sur la flore à une échelle fine. Ann Sci 58:315–328. doi:10.1051/forest:2001129

Diekmann M, Eilertsen O, Fremstad E et al (1999) Beech forest communities in the Nordic countries—a multivariate analysis. Plant Ecol 140:203–220. doi:10.1023/A:1009768225798

Duchaufour P (1983) Pédologie. Tome I: Pédogénèse et classification, 2nd edn. Masson, Paris

Duchaufour P, Bonneau M (1959) Une nouvelle méthode de dosage du phosphore assimilable dans les sols forestiers. Bull. Assoc. Fr. Etude Sol 4:193–198

Dzwonko Z, Loster S (1988) Species richness of small woodlands on the western Carpathian foothills. Vegetatio 76:15–27

Elkie P, Rempel R, Carr A (1999) Patch Analyst User's Manual. Ont. Min. Natur. Resour. Northwest Sci. & Technol. Thunder Bay, Ont. http://flash.lakeheadu.ca/~rrempel/patch/

ESRI (1999) Arcview GIS (version for Windows 3.2a). Environmental Systems Research Institute, Inc., Redlands, CA, USA http://www.esrifrance.fr/

Frazer GW, Canham CD, Lertzman KP (1999) Gap Light Analyser GLA Version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs: users manual and program documentation. Simon Frazer University and the Institute of Ecosystems Studies, Burnaby, British Columbia and Millbrook, New York

Gehlhausen SM, Schwartz MW, Augspurger CK (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecol 147:21–35. doi:10.1023/A:1009846507652

Gonin P (1993) Les stations à intérêt forestier sur les coteaux et vallées de Midi-Pyrénées situés à l'est de la Garonne. I-Catalogue; II- Méthodologie. CETEF Garonnais, Catalogue station, Toulouse, France

Gracia M, Montané F, Piqué J et al (2007) Overstory structure and topographic gradients determining diversity and abundance of understory shrub species in temperate forests in central Pyrenees (NE Spain). For Ecol Manage 242:391–397. doi:10.1016/j.foreco.2007.01.056

Grashof-Bokdam C (1997) Forest species in an agricultural landscape in The Netherlands: effects of habitat fragmentation. J Veg Sci 8:21–28. doi:10.2307/3237238

Greene DF, Johnson EA (1995) Long-distance wind dispersal of tree seeds. Can J For Res 73:1036–1045

Guirado M, Pino J, Roda F (2007) Comparing the role of site disturbance and landscape properties on understory species richness in fragmented periurban Mediterranean forests. Landscape Ecol 22:117–129. doi:10.1007/s10980-006-9009-y

Guyon JP, Bessières F, Faingnaert O (1996) Evolution des formations boisées sur le territoire de deux communes du canton d'Aurignac (Haute-Garonne) de 1942 à 1992. In: Balent G et al (eds) La forêt paysanne dans l'espace rural. Biodiversité, paysages, produits. INRA, Paris

Harcombe PA, Bill CJ, Fulton M et al (2002) Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. J Ecol 90:947–957. doi:10.1046/j.1365-2745.2002.00735.x

Harper KA, MacDonald SE, Burton PJ et al (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19:768–782. doi:10.1111/j.1523-1739.2005.00045.x

Honnay O, Hermy M, Coppin P (1999) Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. Biol Conserv 87:73–84. doi:10.1016/S0006-3207(98)00038-X

Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. J Comput Graph Statist 5:299–314. doi:10.2307/1390807

Jacquemyn H, Butaye J, Hermy M (2003) Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. Ecography 26:768–776. doi:10.1111/j.0906-7590.2003.03620.x

Kupfer JA, Runkle JR (2003) Edge-mediated effects on stand dynamic processes in forest interiors: a coupled field and simulation approach. Oikos 101:135–146. doi:10.1034/j.1600-0706.2003.12119.x

Legare S, Bergeron Y, Pare D (2002) Influence of forest composition on understory cover in boreal mixedwood forests of western Quebec. Silva Fenn 36:353–366

Lenière A, Houle G (2006) Response of herbaceous plant diversity to reduced structural diversity in maple-dominated (*Acer saccharum* Marsh.) forests managed for sap extraction. For Ecol Manage 231:94–104. doi:10.1016/j.foreco.2006.05.024

Leroyer C (2002) Structure spatiale de la végétation forestière à une échelle fine. Dissertation, National School of Agronomy of Toulouse

Lyon J, Gross NM (2005) Patterns of plant diversity and plant–environmental relationships across three riparian corridors. For Ecol Manage 204:267–278. doi:10.1016/j.foreco.2004.09.019

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton

Matlack GR (1993) Microenvironment variation within and among forest edge sites in the eastern United States. Biol Conserv 66:185–194. doi:10.1016/0006-3207(93)90004-K

McCune B, Antos JA (1981) Correlations between forest layers in the Swan Valley, Montana. Ecology 62:1196–1204. doi:10.2307/1937284

McDonald RI, Urban DL (2006) Edge effect on species composition and exotic species abundance in the North Carolina Piedmont. Biol Inv 8:1049–1060. doi:10.1007/s10530-005-5227-5

McEuen AB, Curran LM (2004) Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. Ecology 85:507–518. doi:10.1890/03-4006

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10:58–62. doi:10.1016/S0169-5347(00)88977-6

Okland T, Rydgren K, Okland RH et al (2003) Variation in environmental conditions, understorey species number, abundance and composition among natural and managed Picea-abies forest stands. For Ecol Manage 177:17–37. doi:10.1016/S0378-1127(02)00331-6

Onaindia M, Dominguez I, Albizu I et al (2004) Vegetation diversity and vertical structure as indicators of forest disturbance. For Ecol Manage 195:341–354. doi:10.1016/j.foreco.2004.02.059

Orwig DA, Abrams MD (1994) Land-use history (1720–1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. Can J For Res 24:1216–1225. doi:10.1139/x94-160

Palik BJ, Murphy PG (1990) Disturbance versus edge effects in Sugar-Mapple/Beech forests fragments. For Ecol Manage 32:187–202. doi:10.1016/0378-1127(90)90170-G

Petersen PM (2002) Importance of site conditions and time since abandonment for coppice vegetation on Langeland, Denmark. Nord J Bot 22:463–482. doi:10.1111/j.1756-1051.2002.tb01400.x

Rameau J-C, Mansion D, Dumé G (1989) Flore Forestière Française. Guide écologique illustré. Plaines et collines. Institut Développement Forestier, Dijon

Ranney JW, Bruner MC, Levenson JB (1981) The importance of edge in the structure and dynamics of forest islands. In: Burgess RL, Sharpe DM (eds) Forest Island dynamics in man-dominated landscapes. Springer, New York

Ries L, Fletcher RJJ, Battin J et al (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522. doi:10.1146/annurev.ecolsys.35.112202.130148

Sagers CL, Lyon J (1997) Gradient analysis in a riparian landscape: contrasts among forest layers. For Ecol Manage 96:13–26. doi:10.1016/S0378-1127(97)00050-9

Schuster B, Diekmann M (2005) Species richness and environmental correlates in deciduous forests of Northwest Germany. For Ecol Manage 206:197–205. doi:10.1016/j.foreco.2004.10.063

Small CJ, MacCarthy BC (2002) Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. Plant Ecol 164:37–48. doi:10.1023/A:1021209528643

Stapanian MA, Cassel DL, Cline SP (1997) Regional patterns of local diversity of trees: associations with anthropogenic disturbance. For Ecol Manage 93:33–44. doi:10.1016/S0378-1127(96)03944-8

Stohlgren TJ, Bachand RR, Onami Y et al (1998) Species–environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. Plant Ecol 135:215–228. doi:10.1023/A:1009788326991

Svenning JC, Skov F (2002) Mesoscale distribution of undersorey plants in temperate forest (Kalo, Denmark): the importance of environment and dispersal. Plant Ecol 160:169–185. doi:10.1023/A:1015885321263

SYSTAT (1999) Systat (R) 9.0 for Windows (R). Statistics I. SPSS, Chicago

Thioulouse J, Chessel D, Dolédec S et al (1997) ADE-4: a multivariate analysis and graphical display software. Stat Comput 7:75–83. doi:10.1023/A:1018513530268

Tutin TG, Heywood VH, Burges NA et al (1983) The Flora Europaea. Cambridge University Press, Cambridge

Weiher E, Howe A (2003) Scale-dependence of environmental effects on species richness in oak savannas. J Veg Sci 14:917–920. doi:10.1658/1100-9233(2003)014[0917:SOEEOS]2.0.CO;2

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. J Biogeogr 28:453–470. doi:10.1046/j.1365-2699.2001.00563.x

The importance of clonal growth to the recovery of *Gaultheria procumbens* L. (Ericaceae) after forest disturbance

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Abstract We investigated the importance of clonal growth to the recovery of a common eastern North American sub-shrub, *Gaultheria procumbens* L. (Ericacea), after clearcut logging. Changes in vegetative growth and development of *G. procumbens* clones and clonal populations were examined in a chronosequence of logged stands representing different stages of successional development after clearcutting (open habitat, young regenerating forest, closed regenerating forest) and in neighboring undisturbed late-successional forests representative of presettlement conditions. We specifically quantified seedling presence and above-ground ramet production, demographic condition (e.g., sexual vs. vegetative stems), belowground rhizome growth and spread, and assessed the degree of intraspecific variation in clonal morphology and biomass allocation in stands differing in their disturbance history and degree of successional development. Recovery in *G. procumbens* was largely driven by the "release growth" of pre-existing clonal bud-banks in response to canopy removal. Release growth was expressed as greater ramet initiation, rhizome branching and clonal spread. Conversely, we found no evidence of sexual establishment in the species, although production of reproductive biomass (e.g., inflorescence mass, number of flowering shoots) was significant. These findings support a deterministic model of vascular resistance and resilience to catastrophic disturbance, in which recovery of forest plant communities derives from the life-history characteristics of constituent species.

Keywords Clonal growth · Disturbance · Ericacea · Old growth · Phalanx · Resilience · Rhizome · Understory

Introduction

The understory flora of temperate forests exhibit a variety of life strategies, but many are functionally clonal (Eriksson 1989; Peterson and Jones 1997; Miller et al. 2002). Although recruitment from seeds is important for many species and may be favored under certain environmental conditions (Bierzychudek 1982; Kanno and Seiwa 2004), many forest plants are

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maintained in the understory by the asexual propagation of rhizomes, stolons, layers and other perennating structures (Klimes et al. 1997; Peterson and Jones 1997; Lezberg et al. 1999). For example, long-lived clonal perennials predominate the understories of coniferous forests of the Pacific Northwest (Halpern 1989; Lezberg et al. 1999) as well as mixed broadleaved forests in eastern Canada (Sobey and Barkhouse 1977; Roberts and Ramovs 2005) and western Europe (Peterken and Game 1984; Graae and Sunde 2000). Although, persistence in a vegetative form has been shown to be advantageous in all stages of forest succession (Hughes et al. 1988; O'Dea et al. 1995; Lezberg et al. 1999), it is particularly important immediately after forest disturbance, with the only exception being plant recovery after very severe disturbance events (e.g., landslides, erosion, land cultivation, Lee 2004; Roberts 2004). Such truly disruptive disturbances destroy all pre-existing plants and propagules due to the severity of damage they incur to the forest floor and soil (Hughes and Fahey 1991; Matlack 1994; Ramovs and Roberts 2003). Conversely, in less intensively disturbed habitats (e.g., areas impacted by wildfire, windthrow or logging), clonal growth can allow for the continuity of successful genotypes after forest disturbance (Matlack et al. 1993b; Lezberg et al. 2001; Roberts 2004). This is because vegetative reproduction allows most understory herbs and shrubs to re-establish quickly in situ through the vegetative re-growth of pre-existing clones as opposed to the recruitment of new individuals from buried or dispersed seed (Halpern 1989; Hughes and Fahey 1991; Cirne and Scarano 2001).

The above-ground stems (i.e., ramets) of clonal plants are often interconnected for long periods of time, and thus long-lived clonal forest flora are likely to experience heterogeneity in environmental and resource conditions as succession proceeds after disturbance (e.g., changes in light intensity and quality concomitant with canopy recovery, Antos and Zobel 1984; Marino et al. 1997; Cirne and Scarano 2001). Both experimental and field studies have shown that clonal plants may respond to such environmental and resource heterogeneity by changing their morphology (e.g., shortening spacer lengths under favorable conditions, de Kroon et al. 1994; de Kroon and Hutchings 1995), reducing expenditures (e.g., decreasing ramet production under unfavorable conditions, Lezberg et al. 2001) or shifting the allocation of biomass (e.g., between vegetative and sexual structures) under different conditions of resource supply (Pitelka et al. 1980; Messier et al. 1989; de Kroon and Hutchings 1995; Sun et al. 2002). However, few studies have investigated such intraspecific variation in clonal traits in relation to succession after large-scale anthropogenic disturbances, such as clearcut logging (but see Huffman et al. 1994; O'Dea et al. 1995; Moola and Mallik 1998). Greater autecological knowledge is necessary to determine the mechanisms by which clonal growth may confer species' resistance to logging and thereby facilitate the recovery and long-term persistence of understory flora in managed forests.

The objective of this study was to examine the importance of clonal growth as compared to sexual reproduction in the recovery of a common eastern North American sub-shrub, *Gaultheria procumbens* L. (eastern teaberry), after catastrophic forest disturbance (clearcut logging). Earlier work has documented the response of the species to other land use impacts and natural disturbance (Matlack et al. 1993a; Donohue et al. 2000), but detailed studies of long-term recovery with succession have not yet been made. In this study we report and discuss a large set of field data on the autecology of the species in a chronosequence of logged and undisturbed forest sites. We specifically quantified seedling presence and above-ground ramet production, demographic condition (e.g., sexual vs. vegetative stems), belowground rhizome growth and spread across the chronosequence. In addition, we present new information on the degree of intraspecific variation in clonal morphology and biomass allocation exhibited by the species during forest succession after disturbance.

Methods

Study species

Gaultheria procumbens L. (Ericaceae) is an evergreen sub-shrub (<20 cm in height) common to the understories of closed-canopy coniferous (*Pinus* spp., *Picea* spp., *Abies balamea* L. Mill), mixedwood (*Picea* spp.–*Acer rubrum* L.–*Abies balsamea* L. Mill) and tolerant hardwood (*Acer* spp.–*Quercus* spp.) forests in central and eastern North America (Donohue et al. 2000; Roberts and Zhu 2002; Moola and

Vasseur 2004). It is also found in the understories of open-canopy forested heathlands (e.g., New Jersey Pine Barrens, Matlack et al. 1993a), scrub forest (e.g., pitch pine (*Pinus rigida* Mill.), scrub oak (*Quercus ilicifolia*/*Q. prinoides*), Motzkin et al. 1999; Donohue et al. 2000), treeless barrens (Strang 1970, 1972), sphagnum bogs (Mirick and Quinn 1981) and cutover land (Roberts and Zhu 2002; Moola and Vasseur 2004). It has an affinity for acidic soil, and grows well on many soil types of low nutrient status, including peat, sand, and sandy loam.

The perennating clonal structures of *G. procumbens* are restricted to the upper sections of the Ao soil horizon (2–3 cm in depth, Coladonato 1994), thereby making the species vulnerable to severe disturbances that impact organic soil layers, such as hot forest fires, which can burn-up upper soil horizons, or tillage, which destroys buried rhizomes and roots from mechanical soil turnover (Matlack et al. 1993a; Donohue et al. 2000). Due to the vulnerability of its clonal structures to damage or destruction, some earlier studies have suggested that the species may be restricted to habitats that have remained continuously wooded or have otherwise escaped intensive landuse (Whitney and Foster 1988; Motzkin et al. 1999).

Vegetative reproduction is by additional branching on existing old aerial ramets (*re-growth*) or the initiation of new ramets from buds on belowground rhizomes (*new growth*) (Mirick and Quinn 1981). New ramets that are initiated as either *re-growth* or *new growth* can produce flowers and fruit in their year of formation and thus presumably contribute to sexual reproduction (sexual stems) (Donohue et al. 2000). Alternatively, they may remain as purely vegetative stems. Ramet life span is unknown, but is expected to be far less than the duration of belowground clonal components (Moola and Mallik 1998). This is because, unlike belowground components, aerial ramets are far more susceptible to processes that can result in stem mortality, such as self-thinning, herbivory, and disturbance (e.g., fire; Peterson and Jones 1997; Sun et al. 2002). Annual elongation of rhizomes through additional lateral growth (spacer length) moves the clone along the forest floor approximately 10–43 cm year^{-1} (Sobey and Barkhouse 1977; Donohue et al. 2000). Nodes (points of root initiation) are located at least several centimeters apart along the length of the spreading rhizomes (Matlack et al. 1993a).

Study area

We studied the clonal recovery and development of *G. procumbens* in a chronosequence of logged stands representing different stages of successional development after clearcutting and in neighboring undisturbed late-successional forests, which are representative of presettlement conditions in the Acadian Forest Region (AFR) of North America (Mosseler et al. 2003) (Table 1). The chronosequence was located in the vicinity of Liverpool, Nova Scotia (lat. 44°05′ N, long. 64°46′ W). This area has been classified by Rowe (1972) as belonging to the Atlantic Uplands Zone of the Acadian Forest Region. Historically, the area was dominated by late-successional stands of red spruce (*Picea rubens* (Sarg.)) in mixture with lesser amounts of eastern hemlock (*Tsuga canadensis* L. Carr.), white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* (Ait.)), balsam fir (*Abies balsamea* L. Mill), black spruce (*Picea mariana* (Mill) B.S.P.), red maple (*Acer rubrum* L.), and white birch (*Betula papyrifera* (Marsh.)) (Rowe 1972). However, a long history of forest clearance from agriculture and timber harvesting has had a significant impact on both the age structure and species composition of forests in the study area (Basquill et al. 2001). The climate of the study area is humid temperate maritime and is the mildest in Atlantic Canada. The mean annual temperature is 7.3°C. Mean annual precipitation is 1,601.0 mm, nearly 90% of which occurs as rainfall. The abundant precipitation is evenly distributed throughout the year (Canadian Climate Normals Atlantic Provinces (1961–1990) (1993). Moola and Vasseur (2004) provide a more comprehensive description of the study area.

Stand selection

To evaluate the variation in environmental conditions and patterns of clonal re-establishment, stands were replicated in a completely randomized design: 2-year clearcuts ($n = 3$); 8-year clearcuts ($n = 3$); 56-year clearcuts ($n = 2$); and late-successional forests ($n = 3$). The youngest stands (2-year-old clearcuts) correspond to the open and exposed conditions found immediately after clearcutting (*open habitat*); the 8-year-old stands correspond to the early stages of canopy re-establishment (*young regenerating forest*), the 56-year-old stands correspond to the dense

Table 1 Characteristics of chronosequence stands used for individual clone and clone population studies. Mean values with standard errors (in brackets) are presented

	Late-successional forest	2-Year clearcut	8-Year clearcut	56-Year clearcut
Number of stands (n)	3	3	3	2
Age (years)	128.22 (8.17)	1 (0)	5 (0)	55 (0)
Tree DBH (cm)[b]	17.36 (0.97)	–	–	13.55 (0.26)
Tree basal area (m^2/ha)[b]	42.63 (2.27)	–	–	47.68 (3.54)
Tree density (no./ha)[b]	1253.00 (124.00)	–	–	2336.00 (179.00)
Spring canopy cover (%)[a]	82.17 (0.60)	0 (0)	0.96 (0.40)	89.97 (0.70)
Summer canopy cover (%)[a]	95.40 (0.30)	0 (0)	5.09 (1.40)	95.94 (0.30)
% PPFD at 0.1 m height[c]	5.80 (0.85)	77.40 (21.66)	56.64 (2.20)	6.78 (1.37)
% PPFD at 0.5 m height[c]	6.34 (0.50)	100.00 (0)	74.36 (7.53)	7.11 (1.17)
% PPFD at 1.0 height[c]	6.71 (0.15)	100.00 (0)	85.62 (13.79)	7.83 (1.39)
Total number of clonal fragments sampled[d]	36	36	36	0[d]

[a] From Moola and Vasseur (2004)

[b] From Moola and Vasseur (2006)

[c] From Moola (2005)

[d] No clonal fragments were sampled from the 56-year-old clearcuts due to a prohibition on destructive sampling in Kejimkujik National Park (see Methods)

closed-canopy conditions of overstory recovery (*closed regenerating forest*), and the late-successional stands (age 100–165 years) are representative of pre-settlement conditions (*mature–old growth climax forest*) (Mosseler et al. 2003).

Replicate stands within each age-class were randomly chosen from a pool of candidate sites identified in GIS queries of available forest inventory databases maintained by Kejimikujik National Park, the Nova Scotia Department of Natural Resources, and Bowater Pulp and Paper Company (see Moola and Vasseur 2004). In addition, we ground-truthed all candidate stands prior to sampling, in an effort to ensure that they were similar in site type, slope, aspect, soil pH, and drainage. All of the sites were found on Danesville sandy loam, Halifax sandy loam, or Bridgewater sandy loam soils that are stony and shallow, with cobbles and boulders present in the parent material and on the surface. Soils are derived from olive colored sandy loam till with which quartzite is the dominant rock. The topography is undulating to knobby and soils are well-drained (Cann and Hilchey 1959). Company records provided information about the forest cover prior to logging and silvicultural history (P. Jones, personal communication). All of the post-clearcut stands had been mature mixed-coniferous stands dominated by red spruce, prior to being logged. Clearcuts were tree-length harvests in which only trunks of delimbed trees were removed. However, younger and older clearcuts did differ in the method of skidding. The pre-disturbance canopies of the oldest clearcuts (56 years) had been hand-felled, with trimmed logs horse-skidded to secondary roadways. Conversely, the younger post-clearcut stands (2–8 years) originated from mechanical harvests with logs moved from stumps to roadside using wheeled skidders. Because of the differences in harvesting system used to log young and old clearcuts, disturbance intensity and recovery time are the confounding effects in this study. None of the stands have received any post-harvest silvicultural treatment, such as planting, vegetation management (e.g., herbicide treatment) or pre-commercial thinning.

Sampling techniques

Individual clones

Morphological and biomass allocation measurements were made on excavated fragments of *G. procumbens* clones (polycormons). Polycormons consist of the portions of a clonal genet that are still attached through living tissue (Kull 1995). In *G. procumbens*, this includes interconnected aboveground (stems, leaves, flowers, fruits) and belowground (rhizomes, roots) biomass (Donohue et al. 2000). Representative polycormons were sampled in all stands, except for the oldest clearcut sites in the chronosequence (56-year clearcuts). This was because these sites occur on federally protected land in Kejimkujik National Park, where we were not given permission to destructively sample *G. procumbens* populations.

In sites where we had permission to destructively sample *G. procumbens* clones, we randomly located three 0.04 ha destructive sample plots (DSP) in each stand. We excavated four polycormons in each 0.04 ha DSP, for a total of 12 clonal fragment samples per replicate stand (108 clonal fragments in total). Sampling was done in mid October 1999. Each polycormon was excavated from a randomly chosen undamaged aerial ramet to include all attached rhizomes, roots, and associated aboveground biomass. Excavations began at the initially selected ramet and proceeded along the length of attached rhizomes until the decayed end or the distil tip of a new rhizome module was reached (Lezberg et al. 2001). On occasion, a selected polycormon extended beyond the perimeter of the 0.04 ha DSP. In such cases, we excavated the entire clonal fragment but excluded the proportion of plant biomass located outside the DSP from subsequent data analysis. Excavations were made by carefully removing the attached clonal components from organic soil layers with fingers and the assistance of a small trowel. Following excavation, several morphological parameters were measured on-site (see *Morphological measurements*). Afterwards, the clonal fragment was labeled, bagged, and then placed in a cooler for transport to the laboratory. In the laboratory, the clonal fragments were carefully washed of remaining dirt and debris, air-dried, and frozen for later biomass allocation analysis (Lezberg et al. 2001).

As part of the excavation of polycormons we also searched for any *G. procumbens* seedlings that may have been present among established clones.

Morphological measurements

The following morphological parameters were measured on each clonal fragment immediately following its excavation in the field: (a) the length of individual new rhizomes (spacer length, cm), measured from the distil growing tip to the proximal point of branching or linear extension from older rhizome modules (Huffman et al. 1994). Spacer length distance is equivalent to the annual extension of rhizomes, and determines the speed of vegetative mobility (Kull 1995); (b) the summed length of all new rhizome growth (total new rhizome length, cm); (c) the summed length of all older rhizome growth (total old rhizome length, cm); (d) the summed length of all rhizome growth combined (total rhizome length, cm); (e) the number of rhizome apices (new tips); (f) number of rhizome branches (branching intensity); (g) number of aerial ramets; and (h) the distance between consecutive aerial ramets (inter-ramet distance, cm). We also estimated, (i) the current relative growth rate in each excavated clonal fragment (annual growth percent, %) by dividing the total length of new rhizome growth by the total length of older rhizome growth (Huffman et al. 1994). New (i.e., current season) rhizomes could be distinguished from older rhizomes by the unsuberized, fleshy, and pink colored condition of their tissue. In contrast, older rhizomes were suberized, woody, and brown or reddish-brown in color (Donohue et al. 2000).

Biomass measurements

Frozen polycormons were thawed at room temperature and subsequently separated into four biomass components: (a) rhizomes and roots, (b) aerial stems, (c) leaves, and (d) sexual organs (flowers and fruit). All plant tissues were oven-dried to constant mass at 70°C for 48 h. and then weighed to 0.001 g. Proportions of component biomass (i.e., % of total) were calculated by dividing different component weights by the weight of the entire excavated polycormon (Sun et al. 2002). The ratio of above- to belowground biomass was calculated for each clonal fragment by dividing the dry weight of aboveground structures (stems, leaves, flowers, and fruit) by belowground structures (rhizomes and roots).

Clonal populations

Gaultheria procumbens populations were described in four 1 m^2 quadrats adjoining the area where the clonal fragments were excavated. Sampling was conducted during a 2-week period in early July when clones were flowering, but had not yet produced fruit. The population quadrats were located on the outside four corners of each 0.04 ha DSP plot, for a total of 12 quadrats per replicate stand (132 quadrats in total). Within each 1 m^2 quadrat we assessed total ramet production (standing stem density) and reproductive activity by unit area by counting the number of flowering (i.e., sexual) and non-flowering (i.e., vegetative) aerial stems as well as the overall number of flowers per m^2. A sub-sample of 15 randomly chosen stems in each quadrat was also measured for height, depth of origin, and the number of leaves and flowers (reproductive activity per stem) on each stem. On occasion, a quadrat contained less than 15 suitable stems that could be sampled in this way. In such cases, we sampled additional aerial stems immediately outside the 1 m^2 quadrat until a sample of 15 aerial stems was obtained. Atypical large or small stems were excluded from the sample (Lezberg et al. 1999). Each of the selected aerial stems in the sample was also classified according to its current demographic condition in four classes: (a) *old non-reproductive* (i.e., an old vegetative stem without current growth), (b) *old re-growth* (i.e., an old vegetative stem with additional clonal branching), (c) *new growth* (i.e., a new vegetative stem), and (d) *seedling* (i.e., an independent stem possessing intact primary roots) (Donohue et al. 2000). New clonal growth was easily distinguished, as new aerial stems and branches were unsuberized, fleshy, and white-green in color. Conversely, older aerial stems were brown to black in color and well suberized (Donohue et al. 2000). The relative proportion of ramets in each demographic class was determined at the stand scale (i.e., among 180 stems) and compared across the chronosequence ($n = 2$–3 replicate stands per chronosequence age-class). In total, 1,980 aerial stems were examined across the chronosequence. All were of vegetative origin as no seedlings were observed among any of the quadrats.

Statistical analysis

Individual clones: univariate analysis

One-way analysis of variances (ANOVA) was used to test whether the measured morphological and biomass parameters differed significantly across the chronosequence. Aggregated stand means of each parameter were tested (i.e., means of 12 clonal fragments per stand were tested). Where a significant effect was found, a Tukey HSD test was used to compare stand means among individual age-classes (Zar 1996). Log transformations were used on most variables in order to improve the homogeneity of variances and normality of data prior to statistical analysis. The distribution of spacer lengths and inter-ramet distances within harvested polycormons was also compared between age-classes with a Kolmogorov–Smirnov test (Zar 1996; Sun et al. 2002). Significance in means for all tests was determined at the $P = 0.05$ level. Analyses were conducted in SPSS ver. 6.1.3. (SPSS 1995).

Individual clones: multivariate analysis

In addition to comparing how individual morphological traits in *G. procumbens* differed across the chronosequence, we were also interested in whether polycormons harvested from different age classes could be discriminated on the basis of overall morphology (i.e., multiple morphological parameters tested together). For this purpose, we employed a multivariate linear discriminant analysis (LDA) (Jongman et al. 1995) on harvested clonal fragments, with measured morphological parameters employed as explanatory factors and chronosequence age-classes treated as *a priori* defined groups (Leps and Smilauer 2003). The LDA was initially run using all 14 morphological measurements taken from the clonal fragments harvested in the late-successional, 2-year, and 8-year clearcuts. Polycormons from the 56-year clearcut stands had to be excluded from this analysis, as we did not have a full suite of morphological data (see Methods—Sampling techniques). All the clonal measurements were log transformed prior to analysis, since most did not meet the criterion of homogeneity of variance (Leps and Smilauer 2003). The original morphological parameters employed in the LDA included: ramet number per clonal fragment, ramet number per centimeter of rhizome, mean inter-ramet distance (cm), branching intensity, number of rhizome tips, mean spacer length (cm), total new rhizome length (cm), total old rhizome length (cm), total rhizome extension (cm), relative clonal growth rate (%), absolute rhizome weight (g), absolute stem weight (g), absolute leaf weight (g), and the ratio of above- to belowground biomass. From this full set of morphological measurements, we subsequently excluded those parameters that were either highly correlated or of low explanatory power, since such measurements were more or less redundant or superfluous in the LDA (Norusis 1992). The total rhizome length, total old rhizome length, and stem weight variables were removed since they were all highly correlated with other measured morphological parameters (e.g., with rhizome weight and ramet number per clonal fragment, $r > 0.70$ in a pooled within-groups correlation matrix) (Norusis 1992). We employed a "Forward Selection" of remaining morphological parameters to determine the minimum number required to discriminate polycormons, approximately as well as the full suite of clonal measurements (Leps and Smilauer 2003). Based on this analysis, we decided to exclude the mean spacer length, total new rhizome length, and the ratio of above- to belowground biomass measurements from the final LDA, as they were insignificant in a non-parametric Monte Carlo permutation test ($P \geq 0.05$, 999 random runs). Thus, the final LDA model was based on eight morphological (explanatory) parameters, following the exclusion of 6 of the original 14 clonal measurements. This sub-set of morphological parameters explained 89.9% (1.172 of 1.303) of the variation that could be explained by all original 14 clonal characteristics together. Pooled within-group correlations between the selected morphological measurements and canonical discriminant functions were obtained from the LDA to assess the contribution of individual clonal traits to the discrimination of polycormons along multivariate axes (Norusis 1992). Forward Selection was conducted in CANOCO ver. 4.0.2 (ter Braak and Smilauer 1999) and the LDA was run in SPSS ver. 6.1.3. (SPSS 1995).

Clonal populations: univariate analysis

Differences in the standing-stem density and the relative proportion of vegetative and reproductive ramets summarized at the stand level were tested across the chronosequence in a one-way analysis of variance (ANOVA), followed by a Tukey HSD test to compare the means of individual age-classes ($n = 2$–3 replicate stands/age-class). The proportions of aerial ramets in each demographic condition class and the number of leaves, number of flowers, height, and sprouting depth of clonal ramets were treated statistically in the same way. Ramet proportion data was transformed (arcsine) to ensure normal distribution. The other variables were analyzed after log transformation in order to homogenize the variation. Significance in means summarized at the stand scale ($n = 2$–3 replicates) was determined at the $P = 0.05$ level. Analyses were conducted in SPSS ver. 6.1.3. (SPSS 1995).

Results

Clonal populations: general response to clearcutting

Gaultheria procumbens populations exhibited a delayed positive response to clearcutting. Total standing stem density did not significantly change immediately following canopy removal (Tukey HSD of late-successional versus 2-year clearcut sites; $P = 0.981$) but did so shortly thereafter (Table 2). In particular, the mean number of ramets per unit area (m^2) increased by five times in the eighth growing season after logging, relative to pre-disturbance conditions (Tukey HSD of late-successional versus 8-year clearcut sites; $P = 0.008$). This dramatic increase in population numbers after clearcutting was short-lived, as ramet density returned to pre-disturbance levels by the fifth decade of secondary succession after logging (Tukey HSD of late-successional versus 56-year clearcut sites; $P = 0.239$).

Changes in the reproductive composition of *G. procumbens* populations exhibited a similar successional response to logging. Both the absolute and relative number of vegetative and sexual stems changed several years after clearcutting, only to return to pre-disturbance conditions later on in secondary succession (ANOVA; $P \leq 0.05$) (Table 2). Populations were dominated by vegetative ramets in all chronosequence age-classes, although the proportion of vegetative stems was significantly greater in closed-canopy stands (late-successional and 56-year clearcuts, 94.8 and 98.1% of all stems, respectively), than in early seral open habitats (2-year and 8-year clearcuts, 76.2 and 69.8%, respectively) (Table 2; Tukey HSD; $P \leq 0.005$).

Sexual reproductive activity per unit area (m^2) and per stem increased significantly with clearcutting at

Table 2 Standing stem density and reproductive activity per unit area (m^2) and per stem in *G. procumbens* populations sampled in a chronosequence of late-successional and clearcut stands

Age class	Absolute density of aerial ramets (no./m^2)			Relative density of aerial ramets (%/m^2)		Flowers (no./m^2)	Flowers (no./per stem)
	Flowering	Non-flowering	Total	Flowering	Non-flowering		
Late-successional forest ($n = 3$)	1.39a (1.23)	27.7a (5.42)	29.06a (4.89)	5.24%a (4.27)	94.8%a (4.27)	2.22a (1.90)	0.08a (0.07)
2-Year clearcut ($n = 3$)	6.56a (1.33)	19.9a (5.9)	26.50a (6.01)	23.76%b (6.15)	76.2%b (6.15)	22.28b (8.29)	1.04b 0.36)
8-Year clearcut ($n = 3$)	41.72b (13.64)	101.4b (23.10)	143.11b (35.32)	30.23%b (5.79)	69.8%b (5.79)	105.28b (36.56)	1.44b (0.16)
56 Year Clearcut ($n = 2$)	0.42a (0.25)	12.8a (2.33)	13.25a (2.58)	1.85%a (0.93)	98.1%a (0.93)	0.33a (0.00)	0.001a (0.001)
P-value in ANOVA	0.002	0.003	0.001	0.022	0.024	0.001	0.01

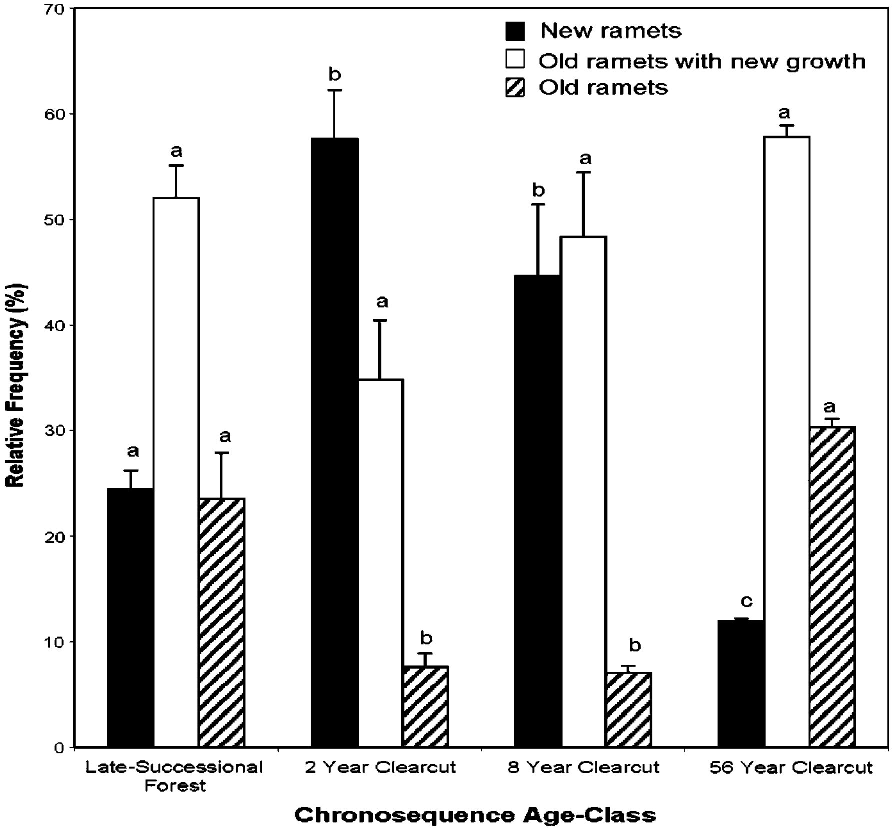
Mean values with standard errors (in brackets) are presented. Like letters within columns denote statistically similar means (Tukey HSD) at $P \leq 0.05$ following a significant 1-Way ANOVA

first (2–8 years after logging), but dropped to extremely low levels later on in secondary succession, concomitant with canopy closure (Table 2; ANOVA; $P \leq 0.05$). For example, a much higher proportion of aerial ramets consisted of flowering stems in open (2-year clearcut; 23.8%) and young regenerating forests (8-year clearcut; 30.2%), than in closed-canopy secondary (56-year clearcut; 1.9%) or late-successional stands (5.2%) (Tukey HSD; $P \leq 0.05$). Similarly, the number of flowers per unit area (m^2) and per stem was far greater in recently logged sites, than in older recovering forests or undisturbed late-successional stands (e.g., ANOVA on number of flowers per m^2; $F_{[3,7]} = 18.06$, $P = 0.001$).

Despite the major increase in sexual reproductive activity with clearcutting, we found no evidence of actual recent sexual establishment in *G. procumbens* populations. For example, of the 1,980 stems that we examined in detail in the chronosequence, all were of vegetative origin (Fig. 1). Furthermore, we failed to locate a single seedling in any of the population surveys (132 quadrats) or among the destructively harvested polycormons (108 clonal fragments) in the chronosequence, despite the wide range in resources (e.g., light), stand conditions (e.g., canopy cover), and substrates (e.g., decayed wood, exposed mineral soil) investigated (Table 1).

The demographic structure (i.e., ramet condition classes) of *G. procumbens* populations was affected by clearcutting (Fig. 1). Populations in the 2-year clearcuts were comprised primarily of new vegetative ramets (57.6% of all stems examined), that originated from buds on buried rhizomes (*new growth* ramets). The proportion of *new growth* ramets decreased with stand recovery after logging and was statistically lowest in the 56-year-old clearcut sites (11.9%) (ANOVA on proportion of new ramets, $F_{[3,7]} = 36.27$, $P = 0.0001$). The predominant form of ramet recruitment in older clearcuts (8–56 years) and late-successional forests was by additional branching of pre-existing stems (*old re-growth* ramets), the proportion of which remained constant across the chronosequence (ANOVA on proportion of re-growth ramets, $F_{[3,7]} = 3.74$, $P = 0.078$). Conversely, the proportion of old ramets with no growth (*old non-reproductive* ramets) varied significantly among chronosequence age-classes, indicating a significant effect of clearcutting (ANOVA on proportion of old ramets,

Fig. 1 Mean relative number of (a) new ramets, (b) old ramets with new growth, and (c) old ramets in *Gaultheria procumbens* populations in a chronosequence of late-successional and clearcut stands. Standard error bars are shown. Means sharing the same letter within a ramet stage class (i.e., above like bars) are not significantly different (Turkey HSD) at $P \leq 0.05$, following a significant ANOVA. Demographic stage structure was assessed from 180 randomly chosen ramets in each replicate stand of the chronosequence ($n = 2$–3 replicates per chronosequence age-class)



$F_{[3,7]} = 21.84$, $P = 0.001$). In particular, a higher proportion of ramets were non-reproductive in the understories of closed-canopy forests (56-year clearcut and late-successional sites, 23.5–30.3% respectively) than in early-seral open or regenerating habitats (2-year and 8-year cleracuts, 7.0–7.6% respectively) ($P \leq 0.005$ in Tukey HSD). None of the stems surveyed were of seedling origin.

Individual clones: above- and belowground morphology

Logging increased the growth and vigor of *G. procumbens* clones, although this positive response was not apparent in measured polycormons (i.e., clonal fragments) until the eighth growing season after disturbance (Table 3). For example, harvested polycormons in 8-year clearcuts supported a far greater number of aerial ramets (on the whole and per length of rhizome), had larger belowground rhizome systems (e.g., greater in current season and overall rhizome growth), and produced more new rhizomes (rhizome tips) and branches (branching intensity) per polycormon than in other age-classes (Tukey HSD; $P \leq 0.05$). Polycormons growing in open and regenerating clearcuts also produced more leaves per ramet (ANOVA on leaf number per ramet; $F_{[2,5]} = 14.39$, $P = 0.002$), but were significantly shorter in height (ANOVA on ramet height; $F_{[3,7]} = 8.42$, $P = 0.01$).

Although polycormons in 8-year clearcuts comprised significantly larger rhizome systems in absolute terms, the rhizome relative growth rate (annual growth percent) was greatest in the 2-year clearcuts. Polycormons in these sites expanded by 43.38% annually, compared to 13.64% in the 8-year clearcut sites and 8.08% in the late-successional stands (Table 3). Even though the difference in annual rhizome growth percent was large between clearcut age-classes, it was not statistically significant because of high variation among measured clonal fragments (Tukey HSD of 2-year clearcut versus 8-year clearcut sites; $P = 0.183$).

None of the harvested polycormons possessed intact primary roots, which would have indicated that they

Table 3 Morphological characteristics of above- and belowground plant components of sampled *G. procumbens* clonal fragments in a chronosequence of late-successional and clearcut stands

	Late-successional Forest ($n = 3$)		2-Year clearcut ($n = 3$)		8-Year clearcut ($n = 3$)		56-Year clearcut ($n = 2$)		
	Mean	S.E.	Mean	S.E.	Mean	SE	S.E.	Mean	*P*-value in ANOVA
Aboveground characteristics									
Ramet height (cm)[a]	5.08a	0.46	4.27b	0.22	4.75b	0.11	6.83a	0.42	0.01
Number of leaves per ramet[a]	4.11a	0.29	5.74b	0.26	5.89b	0.07	4.64a	0.02	0.01
Number of ramets per clonal fragment §	29.72a	11.02	16.58a	2.16	114.71b	42.29			0.02
Number of ramets per centimeter of rhizome §	0.08a	0.01	0.09ab	0.00	0.11b	0.00			0.03
Inter-ramet distance (cm) §	12.61a	0.38	6.32b	0.38	5.49b	0.40			0.00
Belowground characteristics									
Rhizome depth (cm)[a]	2.34a	0.24	3.18a	0.24	3.18a	0.19	2.92a	0.04	0.12
Number of rhizome branches per clonal fragment (branching intensity) §	5.56a	3.06	7.69a	0.43	52.75b	26.75			0.03
Number of rhizome tips per clonal fragment §	4.33a	1.92	5.78a	0.31	23.17b	12.67			0.05
Mean spacer length (cm) §	7.14a	0.77	8.98a	0.86	8.68a	0.81			0.26
Total new rhizome length (cm)	31.89a	16.39	51.48a	3.64	156.85b	83.40			0.05
Total old rhizome length (cm)	382.12ab	113.94	256.03b	24.46	1136.79a	434.47			0.03
Total rhizome extension (cm)	414.01ab	130.16	307.52b	130.16	1293.65a	517.87			0.04
Aboveground:belowground biomass	0.92a	0.03	1.43a	0.18	1.64a	0.49			0.14
Rhizome relative growth rate (%) §	8.08a	1.92	43.38b	1.92	13.64ab	3.86			0.04

Mean values with standard errors (S.E.) are presented in rows. Like letters within rows denote statistically similar means (Tukey HSD) at $P \leq 0.05$, following a significant 1-Way ANOVA. Data on most plant components were unavailable for clonal fragments in the 56-year-old clearcut stands due to a prohibition on destructive sampling (see Methods). Morphological parameters employed in the Linear Discriminant Analysis of clonal fragments (see Fig. 5) are identified with the symbol §

* Mean of 180 randomly selected ramets in each stand of the chronosequence (2–3 replicate stands per chronosequence age-class)

had started from seed somewhat recently (<10 years previously, Lezberg et al. 2001). Rather, the presence of well-suberized, thickened, and decaying older rhizome clumps from which newer rhizomes had clearly originated in the past suggests that most polycormons had been clonal for many years if not decades. However, we were unable to confirm this by aging the polycormons. This was due to the extent of decay among older rhizomes, which made counting annual rhizome growth rings impossible.

Clearcutting had no effect on the mean length of new rhizomes (spacer length) produced annually in *G. procumbens* clones (Table 3; ANOVA on spacer length; $F_{[5,7]} = 1.76$, $P = 0.264$). Nevertheless, the distribution of spacer lengths was significantly different in clones growing in late-successional stands compared to clearcut forests (e.g., Kolmogorov–Smirnov test on polycormons in late-successional versus 2-year clearcuts; $P = 0.002$) (Fig. 2). Spacer lengths in early-seral habitats tended to be greater than in late-successional habitats. For example, approximately 19% of spacer lengths produced by polycormons growing in open (2-year clearcuts) were longer than 10 cm. Conversely, only 4% of spacer lengths in late-successional habitats were >10 cm in length (Fig. 2).

As with spacer length, the distribution of clonal inter-ramet distances was significantly different in late-successional stands compared to clearcut forests (e.g., Kolmogorov–Smirnov test on polycormons in late-successional versus 2-year clearcuts; $P = 0.0001$) (Fig. 3). Generally, the distance between ramets was much shorter on polycormons growing in clearcut habitats than in late-successional stands (Table 3; ANOVA on inter-ramet distance; $F_{[5,7]} = 78.10$, $P = 0.0001$). This was because polycormons in clearcut habitats produced a greater density of ramets per length of rhizome (Table 3), thereby forming coalesced clumps of stems in the understory. For example, although inter-ramet distance ranged from 0.5 cm to as much as 48 cm in clearcut polycormons, consecutive ramets were most often produced less than 2 cm apart (Fig. 3). Conversely, ramets were more equitably initiated along the length of rhizomes growing in late-successional stands and in many cases were separated by considerable distances (>20 cm). The consequence of this, was that ramets in some late-successional polycormons were formed in significant isolation from one another on the forest floor.

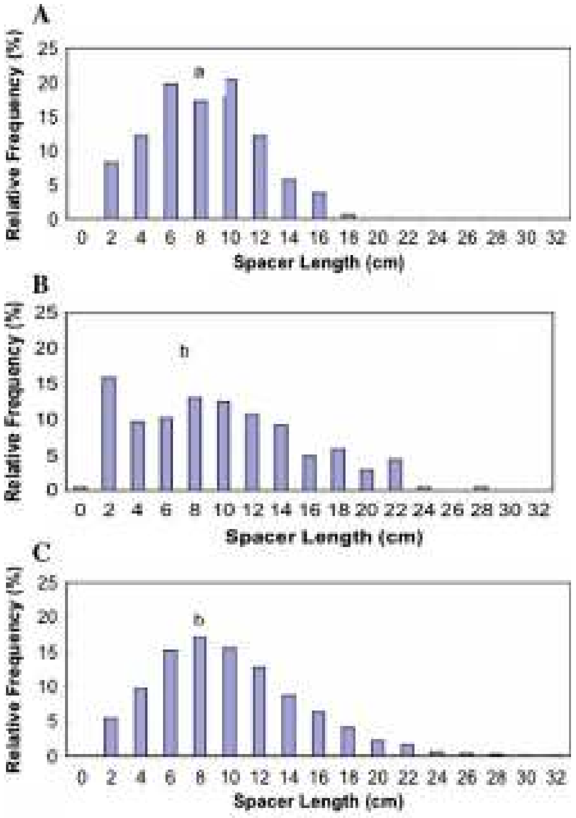


Fig. 2 Distribution of annual extension of rhizome (spacer length, cm) in *Gaultheria procumbens* polycormons harvested from (**A**) late-successional forest, (**B**) 2-year clearcut, and (**C**) 8-year clearcut stands of the chronosequence. Frequencies represent the average of 12 clonal fragments per stand and three replicate stands per chronosequence age-class. Spacer length data was unavailable for *Gaultheria* clonal fragments present in the 56-year clearcut stands of the chronosequence (see Methods). Different letters above the histograms indicate that the distribution of spacer lengths was significantly different among chronosequence age-class ($P \leq 0.05$, Kolmogorov–Smirnov test)

Individual clones: biomass allocation

Gaultheria procumbens did not allocate biomass differently to various vegetative components in response to disturbance (Fig. 4). Biomass allocation to leaves, stems, rhizomes, and roots remained constant across the chronosequence (ANOVA; $P \geq 0.05$). The exception to this was allocation to sexual components (inflorescences, fruit). A greater proportion of overall biomass consisted of sexual biomass in open and regenerating clearcuts than in late-successional forests in the chronosequence

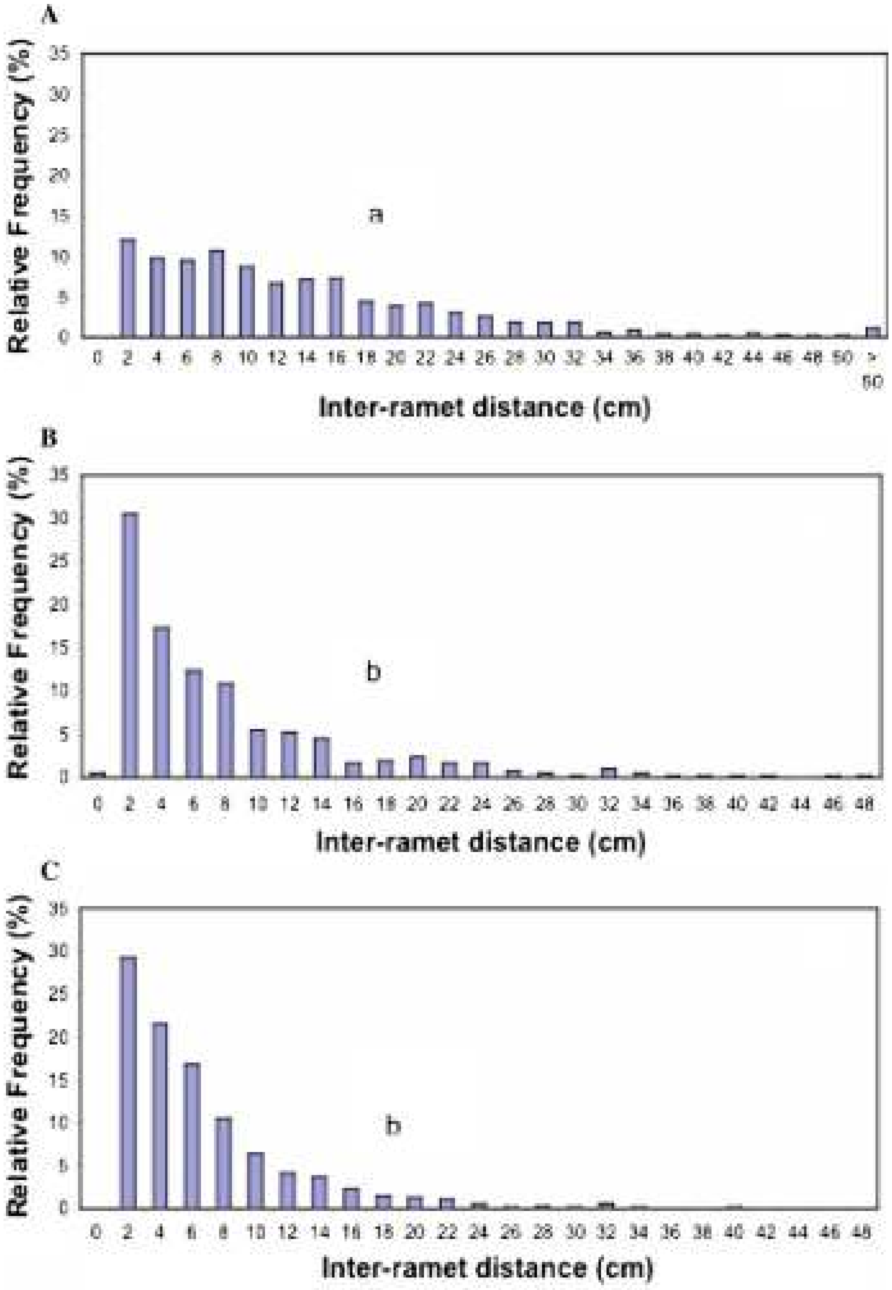


Fig. 3 Distribution of inter-ramet distances (cm) in *G. procumbens* polycormons harvested from (**A**) late-successional forest, (**B**) 2-year clearcut, and (**C**) 8-year clearcut stands of the chronosequence. Inter-ramet data was unavailable for *Gaultheria* clonal fragments present in the 56-year clearcut stands of the chronosequence (see Methods). Different letters above the histograms indicate that the distribution of inter-ramet distances was significantly different among chronosequence age-class ($P \leq 0.05$, Kolmogorov–Smirnov test)

(ANOVA on relative proportion of reproductive biomass; $F_{[5,7]} = 6.766$, $P = 0.038$).

Individual clones: intraspecific variation in overall morphology

Linear discriminant analysis confirmed the separation of the harvested polycormons according to seral origin (open habitat, young regenerating forest, late-successional forest) with 92.2% accuracy. The first discriminant function accounted for 71.6% of the variation among harvested clonal fragments (Table 4). Function 1 was most strongly correlated with inter-ramet distance, branching intensity, and the number of new rhizomes, indicating that these morphological parameters best

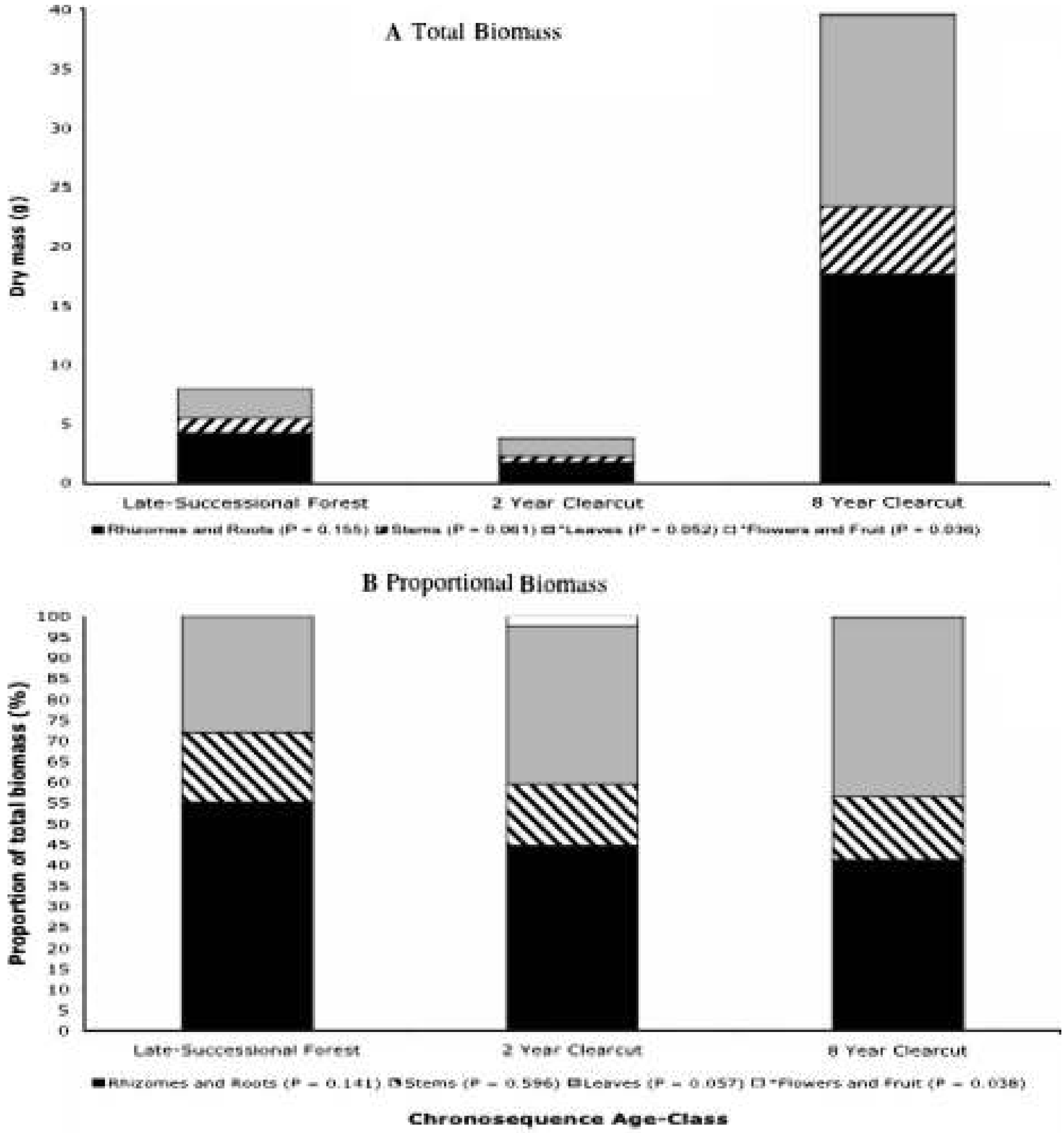


Fig. 4 Mean biomass and proportional biomass (i.e., % of total) of component plant parts of *Gaultheria procumbens* polycormons harvested from a chronosequence of late-successional and clearcut stands. (**A**) Mean dry mass (g) of rhizomes and roots, stems, leaves, and flowers and fruit. (**B**) Mean proportion of total dry biomass (%) for component plant parts. Component plant parts that are significantly different in either biomass or proportional biomass are identified in the figure with the symbol * (1-way ANOVA at $P \leq 0.05$). Standard errors and significant pair wise differences among age-classes are described in the text (see Results). Biomass data were unavailable for *Gaultheria procumbens* polycormons present in the 56-year clearcut stands of the chronosequence (see Methods)

distinguish polycormons along the first multivariate axis. This axis is indicative of a gradient in growth form that is associated with successional development. Function 2 accounted for 28.4% of the variance and was best correlated with ramet density, dry mass of rhizomes, and the relative

Table 4 Summary of a Linear Discriminant Analysis (LDA) of *G. procumbens* clonal fragments harvested from a chronosequence of late-successional and clearcut stands

Function	Eigenvalue	% of variance	Cumulative (%)	Canonical correlation	df	Significance
1	2.477	71.6	71.6	0.844	20	0.00
2	0.981	28.4	100.0	0.704	9	0.00

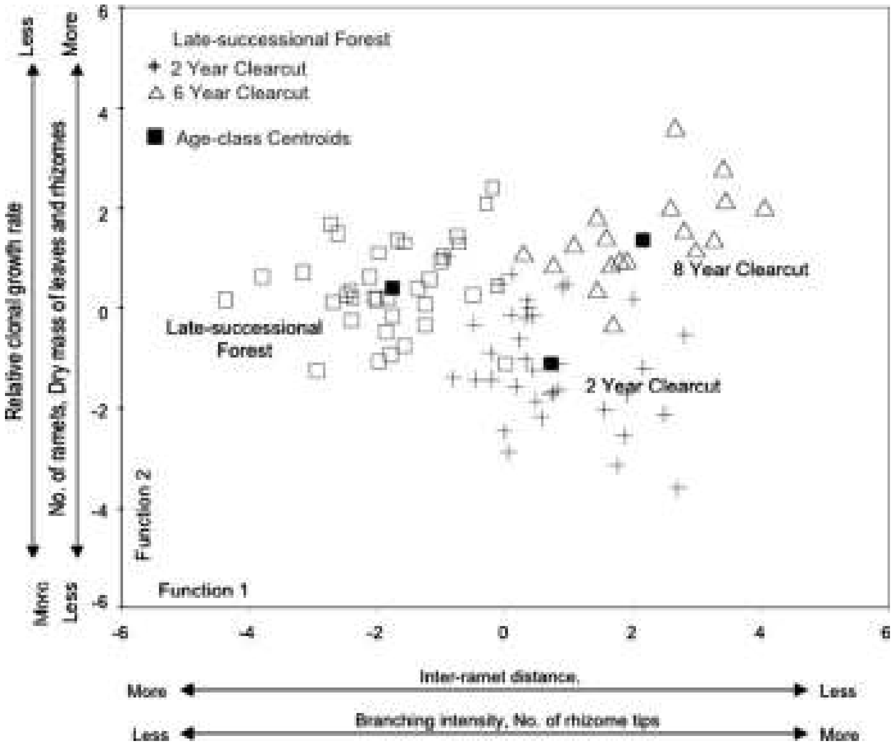


Fig. 5 Ordination plot of *Gaultheria procumbens* polycormons based of a Linear Discriminant Analysis (LDA) of eight significant morphological parameters. Symbols represent individual clonal fragments harvested from a chronosequence of late-successional and clearcut stands. Morphological data was unavailable for *G. procumbens* polycormons present in the 56-year clearcut stands (see Methods). Function axes 1 and 2 are shown

clonal growth rate. It distinguishes polycormons in open habitats from those in young regenerating forests.

As shown in the ordination diagram (Fig. 5), polycormons growing under late-successional conditions are distinct from polycormons in seral habitats in terms of overall morphology and architecture. Clones occur as large coalesced clumps of stems in open habitats (*phalanx growth form*) and spreading isolated chains of connected stems in late-successional stands (*guerrilla growth form*). The differences in these two archetype growth forms are largely related to the intensity of clonal branching, inter-ramet distance, the initiation of new rhizomes, and the overall biomass of clonal components (primarily leaves) (Table 5).

Discussion

Importance of clonal growth to recovery and persistence after disturbance

The results of this study show that *G. procumbens* is tolerant of clearcut logging due to its ability to respond positively to canopy removal with the recruitment of new stems aboveground and vigorous vegetative expansion belowground (e.g., increased relative rhizome growth rate). Ramet initiation in early-seral habitats (e.g., open and young regenerating forest) is dominated by the “release growth” of new vegetative stems initiated from persistent rhizome bud-banks, rather than additional branching of existing ramets (Matlack et al. 1993a). Conversely, populations

Table 5 Pooled within-groups correlations between morphological parameters and standardized canonical discriminant functions in a Linear Discriminant Analysis (LDA) of harvested *G. procumbens* clonal fragments

Morphological Parameters	Function 1	Function 2
Inter-ramet distance (cm)	−0.475*	0.284
Branching intensity	0.465*	0.367
Number of rhizome tips	0.349*	0.260
Number of ramets per centimeter of rhizome	−0.099*	0.048
Number of ramets	0.235	0.786*
Dry mass of leaves (g)	0.353	0.671*
Dry mass of rhizomes (g)	0.148	0.587*
Relative clonal growth rate (% year^{-1})	0.265	−0.487*

Morphological parameters are ordered by absolute size of correlation with each ordination axis. The largest absolute correlation between each variable and any discriminant function is denoted by a *. Only morphological parameters with significant explanatory value were included in the LDA (Forward Selection; $P \leq 0.05$ in a Monte Carlo Permutation test of the marginal effects of individual parameters; see Methods). Age-class means of morphological parameters are presented in Table 3

remain largely non-reproductive in closed-canopy stands, where light transmission to the understory is extremely low due to interference from taller shrub and tree strata. Dense canopy conditions have also been shown to reduce ramet recruitment and other aspects of clonal growth (e.g., rhizome branching) in other understory species (Tappeiner and Alaback 1989; Whitman et al. 1998; Lezberg et al. 2001). Decreased production of new biomass in favor of greater persistence of existing stems and foliage may be advantageous in stressful low resource environments such as deeply shaded forest understories as it reduces costly resource expenditures (Silva et al. 1982; Lezberg et al. 2001). For example, Lezberg et al. (2001) found that continual re-leafing of persistent non-reproductive stems in *Maianthemum dilatatum* L. was less costly than the vegetative initiation of new ramets when resources such as light are in short supply (e.g., after canopy closure, >20 years, de Kroon and Hutchings 1995; Lezberg et al. 2001). This survival strategy is in accordance with Grime's (1979) conceptual model of stress-tolerance during succession and may explain the long-term persistence in the understory of *G. procumbens* and other understory species in all stages of stand recovery after disturbance (Halpern 1988; Moola and Vasseur 2004). Indeed, the long-lived stems and evergreen habitat of *G. procumbens* reduces the costly turnover of plant parts such as its succulent leaves (Matlack et al. 1993a). Furthermore, its persistent foliage is photosynthetically active for much of the year, thereby allowing it to avoid competition with co-occurring deciduous shrubs and trees through phenological displacement, even though these strata overtop it year-round (Matlack et al. 1993a).

Advantages of clonal growth over sexual reproduction

Although a significant proportion of *G. procumbens* aerial ramets are potentially sexually reproductive in the first year of growth (e.g., high rates of flowering), establishment from seed appears to be insignificant as a means of recovery after logging disturbance. Indeed, though Reyes (2002) found seeds of *G. procumbens* to be abundant in the soil profile of the open habitat and young recovering forest sites of our chronosequence, we observed no seedlings in any of the population survey plots nor did we find any polycormons of recent sexual origin. Matlack and Good (1990) similarly failed to observe any evidence of seedling establishment in *G. procumbens*, despite a much greater sampling effort (2,040 quadrats 1 m^2) and surveys over a much larger range of soil types and disturbance conditions than represented in our chronosequence. These findings indicate that, similar to other understory species in northern temperate forests (e.g., *Vaccinium myrtilloides* Michx., *Rubus spectabilis* Pursh., Tappeiner et al. 1991; Moola and Mallik 1998), recovery of *G. procumbens* after disturbance is driven primarily by vegetative processes such as ramet initiation and persistence

(Hughes and Fahey 1991; Tappeiner et al. 1991; Cirne and Scarano 2001).

The dominance of vegetative propagation over sexual establishment has been described as paradoxical (Vander Kloet and Hill 1994), given the significant allocation of resources that understory species, like *G. procumbens*, invest in the development of reproductive biomass, with often limited benefits in terms of regeneration success. For example, though we found no change in biomass allocation among vegetative components (leaves, rhizomes, stems), allocation to sexual biomass increased immediately after logging in *G. procumbens*. Increased allocation to reproductive biomass after canopy removal may simply be due to the larger size of *G. procumbens* polycormons in younger clearcuts (Tappeiner et al. 1991; Cirne and Scarano 2001; Sun et al. 2002). Alternatively, it may be related to the greater density of stems in disturbed habitats relative to late-successional stands. For example, Sun et al. (2002) found that sexual reproduction is favored over clonal propagation in *Scirpus mariqueter* L. when the density of ramets becomes so high that inter-ramet interference occurs (e.g., self-thinning).

Vegetative growth confers a number of advantages that directly improve regeneration success in disturbed habitats, though these benefits have not yet been studied in detail in *G. procumbens*. For example, stored carbohydrate reserves in the biomass of pre-existing clonal structures (e.g., buried rhizomes) may subsidize the growth of vegetative offspring after disturbance (Peterson and Jones 1997; Price and Marshall 1999). These subsidies have been shown to increase growth and improve the survivorship of new clonal ramets, relative to seedlings, in other understory species (Frost 1984; de Steven 1989; Peterson and Jones 1997).

Environmental heterogeneity and intraspecific variation in clonal growth

Forest logging creates habitat heterogeneity and changes the availability of resources for understory plants, like *G. procumbens*. For instance, the complete removal of the overstory with clearcut logging immediately alters the microclimatic conditions affecting pre-existing understory plants (e.g., + in solar radiation and temperature maxima,—in relative soil moisture and humidity, Ramovs and Roberts 2003). In addition, the direct mechanical effects of logging and its associated practices (e.g., site preparation) can affect the spatial heterogeneity of the forest floor (microtopography), by fragmenting coarse woody debris, removing the litter layer, and creating mounds and deep ruts in the ground (Roberts and Zhu 2002; Ramovs and Roberts 2003; Moola and Vasseur 2004). These processes create an environmental and resource matrix that is spatially and temporally variable at a scale relevant to clonal plants during succession after disturbance (Matlack et al. 1993a; Price and Marshall 1999; Sun et al. 2002). Foraging hypotheses predict that clonal plants will respond to such heterogeneity by shifting their morphology and architecture so as to preferentially exploit higher resource patches (de Kroon and Hutchings 1995; Price and Marshall 1999). In many plants, this plasticity in growth form is mediated by greater branching of rhizomes, reduced spacer length, and reductions in inter-ramet distance (i.e., internode length) (Peterson and Jones 1997). In this study, we found that *G. procumbens* does show considerable variation in morphology in response to disturbance and subsequent stand recovery. The results of the multivariate Linear Discriminant Analysis show that *G. procumbens* clones exhibit archetypal growth forms in resource-rich disturbed habitats (e.g., open and regenerating young forests) versus late-successional forests, that are characterized by low light conditions. Clones exist as large coalesced clumps of stems in open habitats (*phalanx growth form*) and spreading isolated chains that cover large areas of the forest floor in late-successional stands (*guerrilla growth form*) (de Kroon and Hutchings 1995; Klimes et al. 1997). The morphological traits that drive this intraspecific variation in growth form are inter-ramet distance, branching intensity, rhizome density, and the biomass of vegetative components. Furthermore, the frequency distribution of spacer lengths and inter-ramet distances reveals that polycormons tend to concentrate growth under more favorable conditions through the "space-packing" of ramets, as opposed to reductions in overall spacer length. Such a strategy may be interpreted as an effort to consolidate growth in an effort to exploit newly created favorable patches or to rapidly re-establish aboveground photosynthetic biomass after local disturbance (Matlack et al. 1993a; Cirne and Scarano 2001).

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References

Antos JA, Zobel DB (1984) Ecological implications of belowground morphology of nine coniferous forest herbs. Bot Gaz 145(4):508–517. doi:10.1086/337486

Basquill SP, Woodley SJ, Pardy AB (2001) The history and ecology of fire in Kejimkujik National Park. Parks Canada, Halifaxa

Bierzychudek P (1982) Life histories and demography of shade—tolerant forest herbs: a review. New Phytol 90: 757–776. doi:10.1111/j.1469-8137.1982.tb03285.x

Canadian Climate Normals Atlantic Provinces (1961–1990) (1993) Ottawa, Environment Canada

Cann DB, Hilchey JD (1959) Soil survey of Queens County, Nova Scotia. Nova Scotia Soil Survey, Nova Scotia Department of Agriculture and Marketing, Truro, Nova Scotia

Cirne P, Scarano FR (2001) Resprouting and growth dynamics after fire of the clonal shrub *Andira legalis* (Leguminosae) in a sandy coastal plain in south-eastern Brazil. J Ecol 89:351–357. doi:10.1046/j.1365-2745.2001.00557.x

Coladonato M (1994) *Gaultheria procumbens* (L.). Fire Effects Information System [Online]. F. S. U.S. Department of Agriculture, Rocky Mountain Research Station, Fire Sciences Laboratory. **2005**

de Kroon H, Hutchings MJ (1995) Morphological plasticity in clonal plants: the foraging concept reconsidered. J Ecol 83:143–152. doi:10.2307/2261158

de Kroon H, Stuefer JE, Dong M et al (1994) On plastic and non-plastic variation in clonal plant morphology and its ecological significance. Folia Geobot Phytotax Praha 29:123–138. doi:10.1007/BF02803790

de Steven D (1989) Genet and ramet demography of *Oenocarpus mapora* ssp. mapora, a clonal palm of Panamanian tropical moist forest. J Ecol 77:579–596. doi:10.2307/2260771

Donohue K, Foster DR, Motzkin G (2000) Effects of the past and the present on species distribution: land-use history and demography of wintergreen. J Ecol 88:303–316. doi:10.1046/j.1365-2745.2000.00441.x

Eriksson O (1989) Seedling dynamics and life histories in clonal plants. Oikos 55:231–238. doi:10.2307/3565427

Frost PGH (1984) The responses and survival of organisms in fire-prone environments. In: Booysen P de V, Tainton NM (eds) Ecological effects of fires in South African ecosystems. Springer, New York, pp 273–310

Graae BJ, Sunde PB (2000) The impact of forest continuity and management on forest floor vegetation evaluated by species traits. Ecography 23:720–731. doi:10.1034/j.1600-0587.2000.t01-1-230509.x

Halpern CB (1988) Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703–1715. doi:10.2307/1941148

Halpern CB (1989) Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70:704–720. doi:10.2307/1940221

Huffman DW, Tappeiner JC, Zasada JC (1994) Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. Can J Bot 71:39–51. doi:10.1139/b94-006

Hughes J, Fahey TJ (1991) Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. J Ecol 79:605–616. doi:10.2307/2260656

Hughes J, Fahey TJ, Bormann FH (1988) Population persistence and reproductive ecology of a forest herb *Aster acuminatus*. Am J Bot 75:1057–1064. doi:10.2307/2443773

Jongman RHG, ter Braak CJF, van Tongeren OFR (eds) (1995) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK

Kanno H, Seiwa K (2004) Sexual vs. vegetative reproduction in relation to forest dynamics in the understory shrub, *Hydrangea paniculata* (Saxifragaceae). Plant Ecol 170: 43–53. doi:10.1023/B:VEGE.0000019027.88318.54

Klimes L, Klimesova J, Henriks R, et al. (1997) Clonal plant architecture: a comparative analysis of form and function. de Kroon H, van Groenendael J (eds) The ecology and evolution of clonal plants. Backhuys, Leiden, pp 1–29

Kull K (1995) Growth form parameters of clonal herbs. In: Aaviksoo K, Kull K, Paal J, Trass H (eds) Consortium Masingii: a Fetschrfit for Victor Masing, vol 9. Tartu university, Tartu, pp 106–115

Lee P (2004) The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forests. Can J Bot 82:1468–1480. doi:10.1139/b04-108

Leps J, Smilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Lezberg AL, Antos J, Halpern C (1999) Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. Can J Bot 77:936–943. doi:10.1139/cjb-77-7-936

Lezberg AL, Halpern C, Antos J (2001) Clonal development of *Maianthemum dilatatum* in forests of differing age and structure. Can J Bot 79:1028–1038. doi:10.1139/cjb-79-9-1028

Marino PC, Eisenberg RM, Cornell HV (1997) Influence of sunlight and soil nutrients on clonal growth and sexual reproduction of the understory perennial herb *Sanguinaria canadensis* L. J Torrey Bot Soc 124:219–227. doi:10.2307/2996609

Matlack G (1994) Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491–1502. doi:10.2307/1937472

Matlack G, Gibson DJ, Good RE (1993a) Clonal propagation, local disturbance, and the structure of vegetation: ericaceous shrubs in the pine barrens of New Jersey. Biol Conserv 63:1–8. doi:10.1016/0006-3207(93)90067-B

Matlack G, Gibson DJ, Good RE (1993b) Regeneration of the shrub *Gaylussacia baccata* and associated species after low-intensity fire in an Atlantic coastal plain forest. Am J Bot 80:119–126. doi:10.2307/2445029

Matlack G, Good RE (1990) Spatial heterogeneity on the soil seed bank of a mature coastal plain forest. Bull Torrey Bot Club 117:143–152. doi:10.2307/2997053

Messier C, Honer TW, Kimmins JP (1989) Photosynthetic photon flux density, red:far-red ratio, and minimum light requirement for survival of Gaultheria shallon in western red cedar-western hemlock stands in coastal British Columbia. Can J For Res 19:1470–1477. doi:10.1139/x89-223

Miller TF, Mladenhoff DJ, Clayton MK (2002) Old growth northern hardwood forests: spatial autocorrelation and patterns of understory vegetation. Ecol Monogr 72:487–503

Mirick S, Quinn JA (1981) Some observations on the reproductive biology of *Gaultheria procumbens* (Ericaceae). Am J Bot 68:1298–1305. doi:10.2307/2442728

Moola FM (2005) Recovery and persistence of late-successional vascular plants in managed coastal Acadian forests. Department of Biology. Dalhousie University, Halifax 195 pp

Moola FM, Mallik AU (1998) Morphological plasticity and regeneration strategies of velvet leaf blueberry following canopy disturbance in boreal mixed wood forests (*Vaccinium myrtilloides* Michx.). For Ecol Manage 111:35–50. doi:10.1016/S0378-1127(98)00306-5

Moola FM, Vasseur L (2004) Recovery of late-seral vascular plants in a chronosequence of post-clearcut forest stands in coastal Nova Scotia, Canada. Plant Ecol 172:183–197. doi:10.1023/B:VEGE.0000026326.09137.06

Moola FM, Vasseur L (2006) Compositional stability following catastrophic disturbance in coastal Acadian forests: recovery and relationships among woody strata and environmental factors (unpublished data)

Mosseler A, Lynds JA, Major JE (2003) Old-growth forests of the Acadian Forest Region. Environ Rev 11:47–77. doi:10.1139/a03-015

Motzkin G, Patterson WAIII, Foster DR (1999) A historical perspective on pitch pine—scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems (NY, Print) 2:255–273. doi:10.1007/s100219900073

Norusis MJ (1992) SPSS/PC + Professional statistics version 5.0. Chicago

O'Dea ME, Zasada J, Tappeiner JCII (1995) Vine maple clone growth and reproductive in managed and unmanaged coastal Oregon Douglas-fir forests. Ecol Appl 5:63–73. doi:10.2307/1942052

Peterken GF, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. J Ecol 72:155–182. doi:10.2307/2260011

Peterson CJ, Jones RH (1997) Clonality in woody plants: a review and comparison with clonal herbs. In: de Kroon H, van Groenendael J (eds) The ecology and evolution of clonal plants. Backhuys Press, Leiden, pp 263–289

Pitelka LF, Stanton DS, Peckenham MO (1980) Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). Am J Bot 67:942–948. doi:10.2307/2442435

Price EAC, Marshall C (1999) Clonal plants and environmental heterogeneity. Plant Ecol 141:3–7. doi:10.1023/A:1009838300691

Ramovs BV, Roberts MR (2003) Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. Ecol Appl 13:1682–1700. doi:10.1890/02-5237

Reyes G (2002) Factors affecting vegetation re-establishment patterns following clearcutting of coastal red spruce-balsam fir stands in southwestern Nova Scotia. Biology. Dalhousie University, Halifax

Roberts MR (2004) Response of the herbaceous layer to natural disturbance in North American forests. Can J Bot 82:1273–1283. doi:10.1139/b04-091

Roberts MR, Ramovs BV (2005) Response of plant functional groups within plantations and naturally regenerated forests in southern New Brunswick, Canada. Can J For Res 35:1261–1276. doi:10.1139/x05-049

Roberts MR, Zhu L (2002) Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. For Ecol Manage 5594:1–15

Rowe JS (1972) Forest regions of Canada. Department of the Environment, Canadian Forestry Service, Ottawa

Silva JF, Kana TM, Solbrig OT (1982) Shoot demography in New England populations of *Mainthemum canadense* Desf. Oecologia 52:181–186. doi:10.1007/BF00363834

Sobey DG, Barkhouse P (1977) The structure and rate of growth and rhizomes of some forest herbs and dwarf shrubs of the New Brunswick—Nova Scotia border region. Can Field Nat 91:377–383

SPSS (1995) Version 6.1.3. SPSS Inc, Chicago

Strang RM (1970) The ecology of the rocky heathlands of western Nova Scotia. Annual tall timbers fire ecology conference. Tall Timbers Research Station, Tallahassee

Strang RM (1972) Ecology and land use of the barrens of western Nova Scotia. Can J For Res 2:276–290. doi:10.1139/x72-045

Sun S, Cai Y, An S (2002) Differences in morphology and biomass allocation of *Scirpus mariqueter* between creekside and inland communities in the Changjiang estuary, China. Wetlands 22:786–793. doi:10.1672/0277-5212(2002)022[0786:DIMABA]2.0.CO;2

Tappeiner J, Zasada J, Ryan P et al (1991) Salmonberry clonal and population structure: the basis for a persistent cover. Ecology 72(2):609–618. doi:10.2307/2937201

Tappeiner JC, Alaback PB (1989) Early establishment and vegetative growth of understory species in the western hemlock–Sitka spruce forests of southeast Alaska. Can J Bot 67:318–326. doi:10.1139/b89-046

ter Braak CJF, Smilauer P (1999) Canoco for windows version 4.02. Centre for Biometry Wageningen, CPRO-DLO, Wageningen

Vander Kloet SP, Hill NM (1994) The paradox of berry production in temperate species of *Vaccinium*. Can J Bot 72:52–58. doi:10.1139/b94-007

Whitman AA, Hunter MLJ, Witham JW (1998) Age distribution of ramets of a forest herb, wild sarsaparilla, *Aralia nudicaulis* (Araliaceae). Can Field Nat 112:37–44

Whitney GG, Foster DR (1988) Overstorey composition and age as determinants of the understorey flota of woods of central New England. J Ecol 76:867–876. doi:10.2307/2260578

Zar JH (1996) Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ

Species richness and resilience of forest communities: combined effects of short-term disturbance and long-term pollution

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Abstract Recovery of the species richness of plant communities after experimental disturbances of various severities were studied in spruce forests polluted by atmospheric entry of SO_2 and heavy metals from a copper smelter. In the three toxic load zones (impact, buffer, and background), 60 experimental "pit-and-mound" complexes (sized 1 m × 2 m, 20 complexes in each zone) were created. Colonization of disturbed areas by vascular plants was observed during a 6-year period after the disturbance. The results showed that the recovery processes were affected by disturbance severity and that the recovery differed significantly among the communities. In all of the zones, species richness increased rapidly after mild disturbance. In degraded communities, levelling of differences in the rate of colonization after mild and severe disturbances was observed. The highest colonization rate was found in the communities of background zone, while the lowest was found in the heavily degraded communities of impact zone. The disturbances significantly increased the species diversity of communities in all zones and caused a certain reversion of degraded communities to previous stage of anthropogenic succession. Mild disturbance promoted the greatest increase in the diversity indices. The study results indicate that recovery rate of species richness of plant communities is determined by the duration of negative effect of disturbances. Recovery also depends significantly on the magnitude and endurance of positive effect of disturbances. The studied communities differed significantly in these parameters. The study results also suggest that short-term disturbances can significantly modify the process of transformation of plant communities by atmospheric pollution. On the other hand, long-term pollution can considerably modify the response of forest communities to disturbances. The results also conclude that the resilience of communities does not exclusively depend on their species richness.

Keywords Copper smelter · Spruce forests · Species diversity · Recovery · Succession · Vascular plants

Introduction

Short-term disturbances (windfalls, fires, eruptions, etc.) constitute an inalienable part of natural ecosystems and they play an important role in their structural organization and dynamics (Georgievsky 1992; Falinski 1978; Frelich and Reich 1999; Forest et al. 1998; Kuuluvainen 1994; Peterson and Pickett 1995; Skvortsova et al. 1983; Turner et al. 1998; Ulanova 2000). Currently, many ecosystems are

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subject to long-term anthropogenic stress exposure, which had led to significant decrease in biodiversity, and to changes in their composition and structure. Such changes can even modify ecosystem functions (Hooper et al. 2005; Peterson et al. 1998), e.g., their responses to natural disturbance. In this regard, questions concerning the functional after-effects of biodiversity decrease, and the changes in the composition and structure of the communities, are becoming issues of current importance.

An important component of the general stability of communities is resilience (recovery ability), in particular the time needed to return to the initial state after some perturbation. The majority of community resilience investigations have been carried out in grasslands (Lavorel 1999; McNaughton 1977; Tilman and Downing 1994; Whitford et al. 1999; see also review Hooper et al. 2005) or in forest ecosystems (Skvortsova et al. 1983; Cooper-Ellis et al. 1999; Hautala et al. 2001, 2008; Jonsson and Essen 1998; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004), which had not been affected by atmospheric pollution. Meanwhile, environmental pollution is one of the most wide-ranging types of long-term anthropogenic stresses. It has caused significant decreases in biodiversity and also changes in the composition and structure of the forest ecosystems (Vorobeichik et al. 1994; kompleksnaya ecologicheskaya 1992; lesnye ekosystemy 1990; Lukina and Nikonov 1993; Makhnev et al. 1990; Smith 1985; Trubina and Makhnev 1997; Chernenkova 2002; Bobbink et al. 1998; Freedman and Hutchinson 1980; Lee 1998; Salemaa et al. 2001).

Recovery rate of forest communities depends on their diversity, composition, and structure at the time of the disturbance (Forest et al. 1998; Jonsson and Essen 1998; Hooper et al. 2005; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004; Skvortsova et al. 1983; Turner et al. 1998). In a degraded forest ecosystems, one can expect certain changes in recovery, e.g., the decrease in colonization rate and recovery ability of species richness on the whole. On the other hand, under atmospheric pollution, short-term disturbances may also considerably modify processes of ecosystem transformation, e.g., they may accelerate or slow down the decreasing species richness.

These assumptions were examined experimentally in the vicinity of a functioning copper smelter. Spruce forests of the area have been affected by long-term emissions of heavy metals and sulfur dioxide since 1940. In 1999, 60 pit-and-mound complexes, partly imitating treefall disturbance, were created in the area. Recovery of vegetation on the plots was followed during 6 years. The objectives of this work were: (1) to describe the recovery of vascular plant species richness after different levels of disturbance severity, and (2) to evaluate the degree of modifying influences of the short-term disturbances on species richness of forest plant communities under long-term pollution.

Methods

The investigation was carried out in the vicinity of a copper smelter located near the town of Revda, 50 km west of Ekaterinburg in the Middle Urals. The area belongs to the southern taiga phytogeographical subzone with a forest cover of about 60% consisting mostly of secondary forests with mixed coniferous and deciduous trees as well as birch and aspen stands (Kolesnikov et al. 1973). The most common dominants of the overstorey include *Pinus sylvestris* L., *Picea obovata* (Ledeb.), *Betula pendula* (Roth.), *B. pubescens* (Ehrh.), *Abies sibirica* (Ledeb.), and *Populus tremula* L. Climate of the area is moderately continental, annual precipitation level is 400–600 mm on average, while depth of snow cover is 40–50 cm and more. Average annual temperature is +1°C, while during January and July temperatures are between −16°C to −17°C and +16°C to +18°C, respectively. The length of frost-free period is 90 days and the prevailing winds are westerly and southwesterly (Prokaev 1976).

The copper smelter has been operating since 1940, emitting a mass of particulate and gaseous pollutants (in a ratio of 1:8), of which sulfur dioxide makes up 98.7% of the gaseous pollutants, while copper, zinc, arsenic, and lead constitute 46.9%, 31.5%, 11.5%, and 10.1% of the particulate pollutants, respectively (Vorobeichik et al. 1994). The study sites were established in coniferous forest stands in three zones, which had been determined earlier according to the degree of forest community transformation in previous investigations (Vorobeichik et al. 1994): the impact—the zone of high load (distance from the source of emission 1 km), the buffer—the zone of intermediate load (6 km), and the background—the zone of low load (30 km). The soils of the sites are mountain forest brown soils. The tree layer has a multilayered canopy and an uneven age structure. The dominating tree species include Siberian spruce (*Picea obovata*) and Siberian fir (*Abies sibirica*), of which a few are up to 140 years old. In addition, some deciduous trees occur, of which silver birch (*Betula pendula*) is the most abundant. Detailed information on the contents of toxicants, soil characteristics, and changes in forest communities in these areas have been described earlier in the publications by Gol'dberg (1997), Kaigorodova and Vorobeichik (1996), Vorobeichik et al. (1994), and Vorobeichik and Hantemirova (1994).

Ground vegetation of the background zone consists of a mix of the following dominants and co-dominants: *Oxalis acetosella*, *Aegopodium podagraria*, *Gymnocarpium dryopteris*, *Dryopteris carthusiana*, *Asarum europaeum*, *Majanthemum bifolium*, *Cerastium pauciflorum*, and *Calamagrostis obtusata*. Ground vegetation of the buffer zone consists of *Oxalis acetosella*, *Cerastium pauciflorum*, *Majanthemum bifolium*, *Carex montana*, *Calamagrostis obtusata*, *Rubus saxatilis*, and *Rubus idaeus* and in the impact zone consists of *Equisetum sylvaticum*, *Agrostis tenuis*, *Calamagrostis arundinacea*, *Calamagrostis langsdorffii*, *Chamerion angustifolium*, and *Majanthemum bifolium*. The total cover (sum of the projective cover of all species, ± SE) of vascular plants on the undisturbed sites of the background, the buffer, and the impact zones was 152.4 ± 3.0%, 78.5 ± 5.6%, and 5.9 ± 0.8%, respectively, and the variation coefficient along the toxic gradient increased from 16% to 126%.

In the beginning of August 1999, altogether 20 complexes of disturbed plots (sized 1 m × 2 m) were created in each load zone. The distance between the complexes was 5–10 m. The experimental plots were designed to imitate the pit-and-mound complexes that tend to form after tree uprooting (Liechty et al. 1997; Peterson et al. 1990). The 1 m^2 pits were created by removing all vegetation and the topsoil from the depth of 20 cm. The disturbance was thought to represent a severe one, as it did not only destroy the vegetation, but also removed the diaspore bank and baring of the mineral soil horizons. The excavated topsoil was deposited near the pits in an area of 1 m^2. These plots imitated the mounds and represented mild disturbance (partial death of plants, preservation of soil diaspore bank, and favorable physical and chemical substrate properties).

The species richness (which was measured by counting the number of species) was recorded from 1 m × 1 m plots during the 6-year post-disturbance period (2000–2005). The species richness of the plots that had no visible signs of natural disturbances (the undisturbed plots) was measured twice, during 2000 and 2005. In the year 2000, species richness was estimated at 140 undisturbed plots (sized 1 m × 1 m). The plots were located within a radius of 500–700 m from the experimental complexes. In the year 2005, 60 similar undisturbed plots (20 plots per toxic load zone) were studied within a radius of 50 m from the experimental complexes. As species richness of the undisturbed plots was similar during the two years, their mean values were used in the further analysis.

One-way analysis of variance (ANOVA) was used to test the differences in species richness between disturbed and undisturbed plots in the each toxic load zone. Two-way mixed-effects ANOVA was used to test the importance of toxic load influence (random factor), disturbance severity (fixed factor), and their interactions during the different study years. Two-way repeated-measurements ANOVA was used to estimate the influence of toxic load zone, time, disturbance severity, and their interactions. The multiple comparisons method (Scheffe's test) was used to test the differences between means in the three toxic load zones. Before the variance analysis, square-root transformation was applied to the data.

Results

Species richness of vascular plants in the undisturbed plots of the background zone was 2 and 10 times higher compared with the buffer and the impact zones, respectively (Table 1). Besides, a significant increase in the space variation of indices along the toxic gradient was observed.

The colonization rate of disturbed plots differed between the toxic load zones ($F_{2,114} = 69.04$; $P < 0.001$). During the study period, complexes of the background zone had the highest average species richness (Fig. 1), while the lowest values were found in the impact zone. The colonization rate also significantly depended on the degree of disturbance severity ($F_{1,114} = 67.95$; $P < 0.001$). In all of the toxic load

Table 1 Mean number (±SE) of species and variation coefficient (CV) of index at the undisturbed forest floor patches in the different toxic load zones

Indices	Toxic load zone		
	Background	Buffer	Impact
Number of species per m^2	12.2 ± 0.4a	6.2 ± 0.5b	1.1 ± 0.1c
CV (%)	27.9a	58.9b	75.7c

Values followed by the same letter are not significantly different at an overall $P < 0.05$

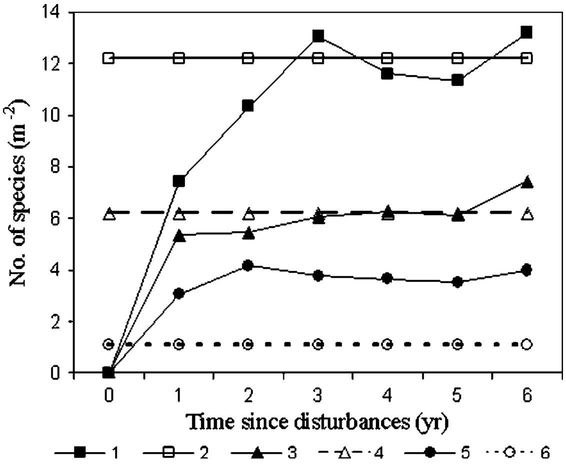

Fig. 1 Change in the number of species (mean values, m^{-2}) during the study period on the experimentally distributed complexes sited in different toxic load zones. Symbols: (1) disturbed and (2) undisturbed plots of background zone; (3) disturbed and (4) undisturbed plots of buffer zone; (5) disturbed and (6) undisturbed plots of impact zone

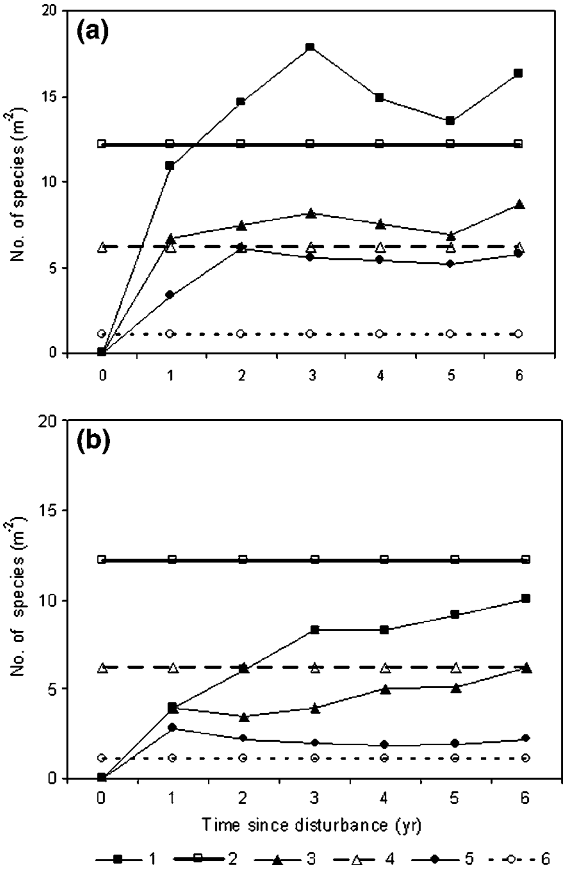

Fig. 2 Change in the number of species (mean values, m^{-2}) during the study period after **a** mild and **b** severe disturbances in the different toxic load zones. Symbols: (1) disturbed and (2) undisturbed plots of background zone; (3) disturbed and (4) undisturbed plots of buffer zone; (5) disturbed and (6) undisturbed plots of impact zone

zones, species richness increased more slowly after severe disturbance (Fig. 2b) than after mild disturbance (Fig. 2a). The successional colonization processes also differed significantly between the toxic load zones of (zone × time $F_{10,570} = 11.16$; $P < 0.001$). Maximum colonization rate was recorded in all toxic load zones within 1 year after the disturbance. In the background zone, high colonization rate was evident for three post-disturbance years, while in the buffer zone—for 1 year, and in the impact zone—for 2 years after mild disturbance and only 1 year after severe disturbance.

The toxic load zones modified significantly the colonization processes after severe and mild disturbance (zone × type of disturbances × time $F_{10,570} = 7.06$; $P < 0.001$). Levelling of the differences between the colonization rates after severe and mild disturbance was observed along the toxic gradient, especially during the first post-disturbance year. The mean (±SE) species richness after severe and mild disturbances was 3.95 ± 0.47 and 10.9 ± 0.74 in the background zone, 4.00 ± 0.54 and 6.7 ± 0.77 in the buffer zone, 2.80 ± 0.31, and 3.30 ± 0.33 species in the impact zone. Six years after the disturbance, the greatest differences between the indices of severely and mildly disturbed plots were observed in the background zone, and the lowest in the buffer zone.

One year after disturbance, species richness of the mildly disturbed plots in the background zone already did not differ from values of the undisturbed plots ($F_{1,83} = 2.12$; $P < 0.149$). In the subsequent years, the species richness of mildly disturbed plots was significantly higher than in the undisturbed ones ($P < 0.001$). Six years after the disturbance, species richness was significantly lower in severely disturbed plots than in undisturbed plots ($F_{1,83} = 6.52$; $P < 0.013$). On the whole, the species richness of the complexes in the background zone did not differ from the undisturbed areas by the third post-disturbance year ($F_{1,103} = 1.02$; $P < 0.314$).

One year after disturbance, species richness of the mildly disturbed plots in the buffer zone did not differ from the undisturbed areas ($F_{1,73} = 0.26$; $P < 0.610$). In the subsequent years, the indices were only slightly higher if compared with undisturbed plots. By the fourth post-disturbance year, the severely disturbed plots did not differ significantly in their species richness from the undisturbed ones ($F_{1,73} = 1{,}66$; $P < 0.202$). In the buffer zone, 1 year after disturbance, species richness of the complexes did not differ from that in the undisturbed areas ($F_{1,93} = 1.44$; $P < 0.233$).

One year after disturbance, the species richness of both mildly and severely disturbed plots in the impact zone was already higher than in the undisturbed ones ($F_{1,98} = 63.48$; $P < 0.001$ and $F_{1,98} = 47.92$; $P < 0.001$, respectively). The same trend continued through the subsequent years in spite of a certain decrease after the first (severe disturbances) and the second (mild disturbances) years of succession. Six years after the disturbance, complexes of the impact zone had significantly higher species richness than in the undisturbed areas ($F_{1,118} = 88.01$; $P < 0.001$).

The pattern of species richness dynamics in the total area of 20 m^2 (Fig. 3) was very similar to that in the area of 1 m^2 (Fig. 2). An important observation was that, from the second year after the disturbance onwards, species richness of the mildly disturbed buffer zone plots on the mesoscale (20 m^2) was close to the values of the undisturbed plots in the background zone (Fig. 3a). However, on the microscale (1 m^2), reversion to the previous succession state was not clearly pronounced (Fig. 2a). Species richness of the mildly disturbed impact zone plots was close to the values of the undisturbed plots in the buffer zone on both scales.

The total number of species found in the experimentally disturbed plots was considerably higher than in the undisturbed areas in all toxic load zones (Table 2). The highest number of species was registered in the mildly disturbed areas. After severe disturbance, the total number of species in the background, buffer, and impact zones increased by 13%, 45%, and 72%, respectively, and by 50%, 50%, and 85% after the mild one, respectively. The proportion of the species registered in the disturbed patches of the background, buffer, and impact zones made up 51.3%, 57.4%, and 85.3% of the total number of species in each zone, respectively. The total number of species that were found from the treated plots decreased along the toxic gradient and the species composition was different (Table 3). The disturbed plots in the background zone had mainly ruderal (e.g., *Plantago major*, *Taraxacum officinale*, *Tussilago farfara*, *Urtica dioica*), open (e.g., *Agrostis tenuis*, *Alchemilla* sp., *Coronaria flox-cuculi*, *Lathyrus*

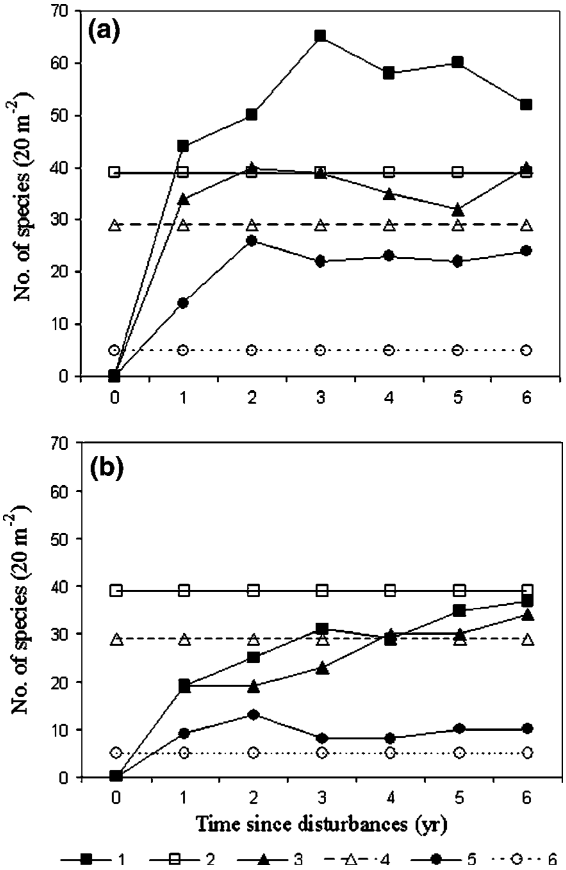

Fig. 3 Change in the total number of species on the area 20 cm^2 during the study period after **a** mild and **b** severe disturbances in the different toxic load zones. Symbols: (1) disturbed and (2) undisturbed plots of background zone: (3) disturbed and (4) undisturbed plots of buffer zone; (5) disturbed and (6) undisturbed plots of impact zone

Table 2 Total number of species observed in experimentally disturbed and undisturbed forest floor patches in the different zones of pollution

Type of site	Toxic load zone		
	Background	Buffer	Impact
Undisturbed (20 m^2)	39	29	5
Severe disturbances (20 m^2)	45	53	18
Mild disturbances (20 m^2)	78	58	33
Total (60 m^2)	80	68	34

pratensis, *Potentilla erecta*, *Prunella vulgaris*) or wet (e.g., *Calamagrostis langsdorfii*, *Crepis paludosa*, *Geum rivale*, *Filipendula ulmaria*, *Ranunculus repens*) habitat species, but also pioneer species of the initial stages of secondary succession (e.g., *Chamerion angustifolium*, *Chrysosplenium alternifolium*, *Phegopteris connectilis*) along with pine forest species (e.g., *Calamagrostis arundinaceae*, *Betonica officinalis*, *Vicia sylvatica*, *Viola canina*).

The disturbed plots of the degraded communities had species from the aforementioned groups, and also common spruce forest species, such as *Athyrium filix-femina*, *Cerastium pauciflorum*, *Dryopteris carthusiana*, *Gymnocarpium dryopteris*, *Galium odoratum*, *Luzula pilosa*, etc. The proportion of these species in the disturbed patches of buffer and impact zones made up 28% and 40% of the total number of new species in each toxic load zone, respectively.

Discussion

Peculiarities of species richness recovery after disturbance

The results of this study suggest that species richness of communities decreases under long-term atmospheric pollution by heavy metals and sulfur dioxide and that this is accompanied by a significant decrease in the colonization rate of the disturbed plots. The result is quite expectable, especially if we take into account the direct dependence of the colonization processes on the initial state of communities before disturbance (Forest et al. 1998; Hooper et al. 2005; Jonsson and Essen 1998; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004; Skvortsova et al. 1983; Turner et al. 1998).

The highest colonization rate in all of the toxic load zones was observed during the first post-disturbance year, but the investigated communities differed in the length of their intensive recovery periods. The colonization rate in the background zone decreased after 3 years of succession, which supports the view of other researches on the succession rate in unpolluted forests (Rydgren et al. 2004). The colonization rate in the degraded communities decreased already during the first (or the second) year of succession. The observed phenomenon cannot be related to the lack of colonization space, as the vegetation cover of the disturbed plots at the initial stages of succession was rather low (Trubina 2003). It is more likely caused by very fast exhaustion of the available diaspore bank in the degraded communities. The phenomenon is especially exhibited in the zone of heaviest contamination (impact zone) and under severe disturbance, i.e., when the diaspore bank (the additional resource for colonization) is absent.

Species richness increased significantly more slowly after severe disturbance than after mild disturbance. The observed data agree perfectly with results of other investigations concerning the influence of disturbance severity on colonization processes (Hautala et al. 2001, 2008; Jonsson and Essen 1998; Mayer et al. 2004; Peterson and Campbell 1993; Rydgren et al. 2004; Skvortsova et al. 1983). This phenomenon is most likely induced by the almost complete destruction of the soil bank of vegetative and generative diaspores of the soil bank after a severe disturbance, as the importance of soil bank in the processes of colonization is known to be very high (Jonsson and Essen 1998; Mayer et al. 2004; Putz 1983; Rydgren et al. 2004; Turner et al. 1998). It is also possible that the removal of upper layers of soil (deterioration of the physical and chemical properties of the substrate) might have reduced colonization and survival of plants, but the importance of the latter factor can hardly be assessed within this experiment.

Increasing levels of toxic loads and degree of ecosystem degradation led to levelling of differences in the colonization rate after severe and mild disturbance. Weakening of the disturbance severity effect along the toxic load gradient may be related to several reasons. Some investigations (Komulainen et al. 1994) have proved that, even if viable seeds are present in the degraded communities, colonization may be impeded by very high levels of soil toxicity. In

Table 3 List of species found on the disturbed plots in the three toxic load zones

Zone of pollution		
Background	Buffer	Impact
Agrostis tenuis	*Adenophora lilifolia*, M	*Adenophora lilifolia*, M
Alchemilla sp., M	*Adoxa moschatellina*, M	*Ajuga reptans*, M
Angelica sylvestris, M	*Agrostis tenuis*	*Athyrium filix-femina*, M
Betonica officinalis, M	*Alchemilla* sp.	*Carduus* sp., M
Calamagrostis arundinaceae, M	*Athyrium filix-femina*	*Carex* sp.
Calamagrostis langsdorfii, M	*Cacalia hastate*, M	*Cerastium pauciflorum*
Carex montana	*Cerastium* sp., S	*Deschampsia cespitosa*
Carex sp.	*Chrysosplenium alternifolium*	*Circaea alpina*
Chamerion angustifolium, M	*Coronaria flos-cuculi*	*Coronaria flos-cuculi*
Chrysosplenium alternifolium	*Dactylis glomerata*, S	*Dryopteris carthusiana*
Cirsium sp., M	*Dryopteris filix-max*	*Fragaria vesca*, M
Coronaria flos-cuculi	*Fragaria vesca*	*Galium* sp., M
Crepis paludosa, M	*Galeopsis bifida*	*Gymnocarpium dryopteris,* M
Dryopteris filix-max, M	*Galium odoratum*	*Impatiens noli-tangere*, M
Filipendula ulmaria, M	*Galium uliginosum*	*Lathyrus pratensis*
Galeopsis bifida	*Geranium sylvaticum*, M	*Lathyrus vernus*, M
Galium uliginosum	*Gymnocarpium dryopteris*	*Luzula pilosa*
Geranium sylvaticum, M	*Juncus* sp., M	*Majanthemum bifolium*
Geum rivale	*Lathyrus pratensis*	*Melica nutans*, M
Glechoma hederacea, S	*Phegopteris connectilis*	*Phegopteris connectilis*
Goodyera repens, M	*Poa* sp., M	*Poa* sp.
Hieracium sp., M	*Prunella vulgaris*	*Ranunculus repens*, M
Lathyrus pratensis	*Pulmonaria dacica*	*Rubus idaeus*
Luzula palescens, M	*Pyrola media*, M	*Stellaria nemorum*
Orthilia secunda, M	*Silene* sp.	*Taraxacum officinale*
Phegopteris connectilis	*Solidago virgaurea*	*Thalictrum minus*, M
Plantago major, M	*Stellaria* sp., S	*Tussilago farfara*
Poa nemoralis	*Stellaria nemorum*	*Urtica dioica*, M
Poa sp., M	*Taraxacum officinale*	*Veratrum lobelianum*, M
Potentilla erecta, M	*Thalictrum minus*	*Viola* sp.
Prunella vulgaris	*Trientalis europaea*	
Ranunculus borealis, M	*Tussilago farfara*	
Ranunculus cassubicus, M	*Urtica dioica,* M	
Ranunculus repens, M	*Valeriana wolgensis*	
Stachys sylvatica	*Veratrum lobelianum*, M	
Taraxacum officinale	*Veronica chamaedrys*	
Tussilago farfara	*Vicia sylvatica*	
Urtica dioica	*Viola canina*, S	
Veronica chamaedrys	*Viola selkirkii*	
Vicia sylvatica, M		
Viola canina, M		

Species occurring at mildly disturbed plots are marked with M; S marks species of severely disturbed plots; the rest of the species occurred at both types of disturbance high-toxicity areas, colonization of vacant areas may also be impeded by a very thick layer of forest litter (more than 5 cm), which is typical for the degraded forest ecosystems near this particular copper smelter (Vorobeichik 1995). The negative influence of litter on regeneration and survival of plants, composition, and species richness of communities has been shown in a range of studies (Peterson and Campbell 1993; Sydes and Grime 1981a, b; Xiong and Nilsson 1999; Weltzin et al. 2005; Sannikov 1992). Apparently, disturbance of the thick and highly toxic forest litter and exposure of the less contaminated soil lessens the negative effect of the disturbance severity and led to its weakening. The levelling of differences may also result from a significant decrease of soil seed bank diversity in the degraded communities, which often takes place under long-term pollution (Ginocchio 2000; Meerts and Grommesch 2001; Salemaa and Uotila 2001). The low number of post-disturbance species in the heavily degraded communities (Table 3) also confirms indirectly this supposition. Another reason for the observed phenomenon may be in the composition of these communities, e.g., the high proportion of eurytopic species that are quite indifferent to unfavorable conditions of the substrate, but these questions would require a special study.

In the course of the recovery period, species richness of the disturbed areas at certain stages was significantly higher than in the undisturbed area. This phenomenon is quite typical for post-disturbance successions after disturbances in most forest communities (Barik et al. 1992; Cooper-Ellis et al. 1999; Goldblum 1997; Mayer et al. 2004; Peterson and Campbell 1993; Skvortsova et al. 1983) and implies the presence of at least two time points during which disturbed and undisturbed areas of communities will not differ significantly in their species richness. The first of these time points characterizes the duration of the negative effects of the disturbances and is a very important component of the resilience of communities, in addition to the period of positive effects and the time of the final return (T_R) to the initial state. The negative-effect period, as a rule, seems to be shorter after mild disturbance than after severe disturbance, which is not unexpected, as severity of disturbance largely defines colonization rate. Differences in the duration of the negative effect after severe and mild disturbance were greatest in the background zone and were not observed in the impact zone. The possible reasons for levelling of the differences between the effects of severe and mild disturbances along the toxic load gradient have been discussed above. However, the following important points should be emphasized.

The duration of the negative effect of mild disturbance was equal in the investigated communities. After severe disturbance, this period was significantly longer in the background zone than in the intermediately and heavily degraded communities, despite the highest species richness and colonization rates in the background zone. The results prove that it is not only the species richness of communities that determines the duration of the negative effects. It is quite possible that the composition of communities or functional diversity (Hooper et al. 2005) also plays a decisive role in the rate of recovery. In the degraded communities, the prevalence of pioneer species and clonal plants (see above) with high colonization abilities could have promoted faster overcoming of the negative effects of disturbance.

Data from a few studies (e.g., Skvortsova et al. 1983) provide evidence that high species richness can be preserved in disturbed areas for several decades. Therefore, longer-term data is needed to determine the time of the final return to the initial state. Nevertheless, some suppositions about recovery of species richness after disturbance can be made from the given index rate of recovery changes and its degree of deviation from the indices measured from the undisturbed areas. After the 6 years of recovery from mild disturbance, the greatest positive deviation and the lowest rate of recovery were found in the communities of the impact zone. One can suppose that, after mild disturbance, communities of this zone will return to the initial state more slowly than communities of less contaminated habitats. However, on the basis of the present data, hardly any suppositions can be made for the communities in the buffer and background zones. However, if we consider the complexes of the disturbed areas in general, and suppose that the species richness of disturbed plots will not increase significantly in the course of further succession, we may conclude that the highest recovery rate of the initial species richness prevails in the buffer-zone communities ($T_R = 1$ year on observed time interval), a lower rate prevails in the background-zone communities ($T_R = 3$ years), and the lowest rate prevails in the communities in the impact zone ($T_R \gg 6$ years).

In general, the results suggest that the period of final return to the initial state depends on the duration of the negative effects of disturbance. It also depends on the magnitude and duration of the positive effects. The heavily degraded communities were characterized by the shortest period of negative effects of disturbance, the greatest magnitude and duration of positive effects, and as a result the greatest deviation of species richness from the indices of the undisturbed areas after 6 years of recovery. The intermediately degraded communities were characterized by an average duration of negative effect of disturbances, the lowest magnitude and duration of positive effects, and the highest recovery rate of species richness on the whole. Recovery of the least degraded communities occurred at an intermediate rate owing to the longest period of negative effects after severe disturbance. This fact once again confirms that resilience of communities is not determined merely by their species richness.

Influence of short-term disturbances of various severity levels on species richness of communities under long-term pollution

In this study experimental disturbance promoted a considerable increase in the total number of species in the investigated communities. The observed results coincide especially with the study results on the influence of windfall disturbances to diversity of forest communities (Barik et al. 1992; Cooper-Ellis et al. 1999; Goldblum 1997; Kuuluvainen 1994; Peterson and Campbell 1993; Skvortsova et al. 1983; Ulanova 2000). At the same time, the degree of modifying influence of disturbances depended on their severity, as well as on the community degradation level.

The increase in species richness in the background-zone communities derived from the emergence of open and wet habitat species, ruderals, pioneer species of initial stages of secondary successions or species of other forest communities. The composition of species growing in the disturbed sites of the background zone is in agreement with data cited for the initial stages of succession after treefalls in unpolluted areas (Skvortsova et al. 1983; Ulanova 2000). The positive effects of disturbance increased considerably along the gradient of toxic load. In the impact zone, the total number of species in the communities after the disturbances became seven times higher than in undisturbed areas. Moreover, species richness increases at the expense of both the characteristic species of disturbed patches in the unpolluted forest and of the most common unpolluted spruce forest species that disappear from the communities as a result of long-term pollution. Interestingly, a similar phenomenon was observed in the studied communities after treefalls (unpublished data).

Such a large increase in the diversity of degraded communities may be related to the preservation of sufficiently diverse and viable diaspore bank in the degraded communities, as well as to dispersal of diaspores from outside. However, the role of the latter factor may be small, as diversity and total cover of vegetation were extremely low in this load zone.

It has been proved earlier that diaspore bank can remain viable under long-term pollution by copper-smelter emissions (Ginocchio 2000; Huopalainen et al. 2001; Komulainen et al. 1994; Meerts and Grommesch 2001; Salemaa and Uotila 2001). Increased species richness after mild disturbances proves indirectly that the diaspore bank can preserve certain diversity in heavily polluted zone. The results also suggest that, after 60 years of copper smelter functioning, only partial recovery of species richness from the diaspore bank is possible in highly degraded communities.

Mild disturbances decreased diversity differences between the studied communities on both micro- and mesoscale, and caused a certain reversion of the degraded communities to the earlier state of anthropogenic succession. Particularly, after the second post-disturbance year, species richness of mildly disturbed plots in the impact zone was close to the level observed in undisturbed plots of the buffer zone on both scales. In the buffer zone, reversion to the indices of undisturbed plots of the background zone was observed only on the mesoscale. This is most likely due to the different species elimination rates from the communities on the micro- and mesoscale. Particularly, the number of species in undisturbed 1 m^2 plots (microscale) in the buffer zone was 2 times lower compared with the background zone, whereas in the area 20 m^2 (mesoscale) was lower only 1.3 times. It was remarkable that severe disturbance only slightly modified species richness of the communities on the micro- and mesoscale and increased only the total number of species. Moreover, the positive effect of severe disturbance on the total number of species was less pronounced than that of mild disturbance, which again emphasizes the importance of diaspore bank in the maintenance of high community diversity.

Thus, our results suggest that short-term small-scale disturbance promotes species richness in plant communities and that, under strong long-term pollution, it slows down the decline in species richness and may also lead to certain reversion of degraded communities to the previous state of succession. However, the following important points should be emphasized. Short-term disturbances, e.g., treefalls, at the initial pollution stages can promote elimination of typical forest species, because during the first years of succession disturbed plots are actively occupied by untypical species (Kuuluvainen 1994; Nakashizuka 1989; Rydgren et al. 2004; Skvortsova et al. 1983; Ulanova 2000). The duration of negative effects after severe disturbance in the background zone proves that severe disturbance of vegetation and soil, such as tree uprooting, could have led to the significant and long-term decrease in species richness of communities on both micro- and mesoscales. In other words, severe disturbance can accelerate the processes of diversity decline in communities during the initial stages of environmental contamination. The positive effect of disturbance that is currently observed in the degraded communities may subsequently decrease or disappear due to the continuing input of toxicants. In particular, germination of spores and seeds of species intolerant to contamination and their subsequent elimination because of persisting toxic influence will lead to the exhaustion of the diaspore bank and to the further decrease in diversity and recovery abilities of the degraded communities as a whole.

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References

Alexeyev VA (ed) (1990) Lesnye ekosystemy i atmosfernoe zagryaznenie. Nauka, Leningrad

Barik SK, Pandey HN, Tripathi RS, Rao P (1992) Microenvironmental variability and species-diversity in treefall gaps in a subtropical broadleaved forest. Vegetatio 103(1):31–40

Bobbink R, Hornung M, Roelofs JGM (1998) The effect of airborne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J Ecol 86:717–738. doi:10.1046/j.1365-2745.1998.8650717.x

Chernenkova TV (2002) Reaktsiya lesnoy rastitel'nosti na promyshlennoe zagryaznenie. Nauka, Moskow

Cooper-Ellis S, Foster DR, Carlton G, Lezberg A (1999) Forest response to catastrophic wind: results from an experimental hurricane. Ecology 80(8):2683–2696

Falinski JB (1978) Uprooted trees, their distribution and influence in primeval forest biotope. Vegetatio 38(3): 175–183. doi:10.1007/BF00123268

Forest DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems (NY, Print) 1:497–510. doi:10.1007/s100219900046

Freedman B, Hutchinson TC (1980) Long-term effects of smelter pollution on forest community composition. Can J Bot 55(19):2123–2140

Frelich LE, Reich PB (1999) Neighborhood effects, disturbance severity and community stability in forests. Ecosystems (NY, Print) 2:151–166. doi:10.1007/s100219900066

Georgievsky AB (1992) Faza okon v korennykh elovykh lesakh yuzhnoy taygi. Bot J 77(6):52–62

Ginocchio R (2000) Effects of a copper smelter on a grassland community in the Puchuncavi Valley, Chile. Chemosphere 41:15–23. doi:10.1016/S0045-6535(99)00385-9

Gol'dberg IL (1997) Changes in the moss layer of Southern taiga dark coniferous forests under conditions of technogenic pollution. Russ J Ecol 28(6):417–419

Goldblum D (1997) The effects of treefall gaps on understory vegetation in New York state. J Veg Sci 8(1):125–132. doi:10.2307/3237250

Hautala H, Tolvanen A, Nuortila C (2001) Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. J Veg Sci 12:503–510. doi:10.2307/3237002

Hautala H, Tolvanen A, Nuortila C (2008) Recovery of pristine boreal forest floor community after selective removal of understorey, ground and humus layers. Plant Ecol 194:273–282. doi:10.1007/s11258-007-9290-0

Hooper DU, Chapin FSIII, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DF (2005) Effects of biodiversity on ecosystems functioning: consensus of current knowledge. Ecol Monogr 75(1):3–35. doi:10.1890/04-0922

Huopalainen M, Tuittila E-S, Vanha-Majamaa I, Nousiainen H, Laine J, Vasander H (2001) Effects of long-term aerial pollution on soil seed banks in drained pine mires in Southern Finland. Water Air Soil Pollut 125:69–79. doi:10.1023/A:1005276201740

Jonsson BG, Essen P-A (1998) Plant colonization in small forest-floor patches: importance of plant group and disturbance traits. Ecography 21:518–526. doi:10.1111/j.1600-0587.1998.tb00443.x

Kaigorodova SY, Vorobeichik EL (1996) Changes in certain properties of grey forest soil polluted with emissions from a copper-smelting plant. Russ J Ecol 27(3):177–183

Kolesnikov BP, Zubareva RS, Smolonogov EP (1973) Lesorastitel'nye usloviya i lesnaya tipologiya Sverdlovskoy. UNC AN SSSR, Sverdlovsk

Komulainen M, Vieno M, Yarmishko VT, Daletskaja TD, Maznaja EA (1994) Seedling establishment from seeds and seed banks in forests under long-term pollution stress: a potential for vegetation recovery. Can J Bot 72:143–149. doi:10.1139/b94-019

Kuuluvainen T (1994) Gap disturbance, ground microtopography and the regeneration dynamics of boreal coniferous forests in Finland: a review. Ann Zool Fenn 31(1):35–51

Lavorel S (1999) Ecological diversity and resilience of Mediterranean vegetation to disturbance. Divers Distrib 5:3–13. doi:10.1046/j.1472-4642.1999.00033.x

Lee JA (1998) Unintentional experiments with terrestrial ecosystems: ecological effects of sulfur and nitrogen pollutants. J Ecol 86:1–12. doi:10.1046/j.1365-2745.1998.00257.x

Liechty HO, Jurgensen MF, Mroz GD, Gale MR (1997) Pit and mound topography and its influence on storage of carbon, nitrogen and organic matter within an old-growth forest. Can J Res 27(12):1992–1997. doi:10.1139/cjfr-27-12-1992

Lukina NV, Nikonov VV (1993) Sostoyanie elovykh biogeotzenozov Severa v uscloviyakh tekhnogennogo zagryazneniya. Kola Scientific Centre, Apatity

Makhnev AK, Trubina MR, Pryamonosova SA (1990) Lesnaya rastitel'nost' v okrestnostyakh predpriyatiy tsvetnoy metallurgii. In: Shiyatov SG, Shilova II (eds) Estestvennaya rastitel'nost' promyshlennykh i urbanizirovannykh territoriy Urala. UD AS USSR, Sverdlovsk

Mayer P, Abs C, Fischer A (2004) Colonization by vascular plants after soil disturbance in the Bavarian Forest—key factors and relevance for forest dynamics. For Ecol Manage 188:279–289

McNaughton SJ (1977) Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. Am Nat 111(979):515–525. doi:10.1086/283181

Meerts P, Grommesch C (2001) Soil seed banks in heavy-metal polluted grassland at Prayon (Belgium). Plant Ecol 155:35–45. doi:10.1023/A:1013234418314

Nakashizuka T (1989) Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70(5):1273–1278. doi:10.2307/1938186

Peterson CJ, Campbell JE (1993) Microsite differences and temporal change in plant-communities of treefall pit and mounds in an old-growth forest. Bull Torrey Bot Club 120(4):451–460. doi:10.2307/2996750

Peterson CJ, Pickett STA (1995) Forest reorganization—a case-study in old-growth forest catastrophic blowdown. Ecology 76(3):763–774. doi:10.2307/1939342

Peterson CJ, Carson WC, McCarthy BC, Pickett STA (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58(1):39–46. doi:10.2307/3565358

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. Ecosystems (NY, Print) 1:6–18. doi:10.1007/s100219900002

Prokaev VI (1976) Fiziko-geograficheskoe rayonirovanie Sverdlovskoy oblasti. Part 1. Sverdlovsk State Pedagogical Institute, Sverdlovsk

Putz FE (1983) Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64(5):1069–1074. doi:10.2307/1937815

Rydgren K, Økland RH, Hestmark G (2004) Disturbance severity and community resilience in a boreal forest. Ecology 85(7):1906–1915. doi:10.1890/03-0276

Salemaa M, Uotila T (2001) Seed bank composition and seedling survival in forest soil polluted with heavy metals. Basic Appl Ecol 2:251–263. doi:10.1078/1439-1791-00055

Salemaa M, Vanha-Majamaa I, Derome J (2001) Understory vegetation along a heavy-metal pollution gradient in SW Finland. Environ Pollut 112:339–350. doi:10.1016/S0269-7491(00)00150-0

Sannikov SN (1992) Ekologiya i geografiya estestvennogo vozobnovleniya sosny obyknovennoy. Nauka, Moscow

Skvortsova EB, Ulanova NG, Basevich BF (1983) Ekologichskaya rol' vetrovalov. Forestry Industry, Moscow

Smith YK (1985) Les i atmosfera. Progress, Moscow

Stepanov AM (ed) (1992) Kompleksnaya ekologicheskaya otsenka tekhnogennogo vozdeystviya na ekosistemy yuzhnoy taygi. TsEPL, Moskow

Sydes C, Grime TP (1981a) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. 1. Field investigations. J Ecol 69(1):237–248. doi:10.2307/2259828

Sydes C, Grime TP (1981b) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. 2. An experimental investigation. J Ecol 69(1):249–262. doi:10.2307/2259829

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367:363–365. doi:10.1038/367363a0

Trubina MR (2003) Kolichestvennye pokasateli iskusstvenno narushennykh uchastkov temnokhvoynykh lesov na nachal'nykh stadiyakh vosstanovitel'nykh mikrosuktzessiy v usloviyakh zagryazneniya. In: Mamaev SA, Makhnev AK, Chibrik TS (eds) Biologicheskaya rekul'tivatsiya narushennykh zemel'. Ural Division of Russian Academy of Science, Ekaterinburg

Trubina MR, Makhnev AK (1997) Dynamics of ground vegetation in forest phytocenoses under conditions of chronic pollution by fluorine. Russ J Ecol 28(2):73–77

Turner MG, Baker WL, Peterson CJ, Peet RK (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems (NY, Print) 1:511–523. doi:10.1007/s100219900047

Ulanova NG (2000) The effects of windthrow on forests at different spatial scales: a review. For Ecol Manage 135:155–167

Vorobeichik EL (1995) Change of thickness of forest litter under chemical pollution. Russ J Ecol 26(4):252–258

Vorobeichik EL, Hantemirova EV (1994) Reaction of forest phytocenoses to technogenic pollution: dose-effect dependencies. Russ J Ecol 25:171–180

Vorobeichik EL, Sadykov OF, Farafontov MG (1994) Ecologicheskoe normirovanie tekhnogennykh zagryaznenii nazemnykh ekosistem (lokal'nyi uroven'). Nauka, Ekaterinburg

Weltzin JF, Keller JK, Bridgham SD, Pastor J, Allen PB, Chen J (2005) Litter controls plant community composition in a northern fen. Oikos 110:537–546. doi:10.1111/j.0030-1299.2005.13718.x

Whitford WG, Rapport DJ, Soyza AG (1999) Using resistance and resilience measurements for 'fitness' tests in ecosystem health. J Environ Manage 57:21–29. doi:10.1006/jema.1999.0287

Xiong S, Nilsson C (1999) The effects of plant litter on vegetation: a meta-analysis. J Ecol 87:984–994. doi:10.1046/j.1365-2745.1999.00414.x

Hurricane disturbance in a temperate deciduous forest: patch dynamics, tree mortality, and coarse woody detritus

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Abstract Patch dynamics, tree injury and mortality, and coarse woody detritus were quantified to examine the ecological impacts of Hurricane Fran on an oak-hickory-pine forest near Chapel Hill, NC. Data from long-term vegetation plots (1990–1997) and aerial photographs (1998) indicated that this 1996 storm caused patchy disturbance of intermediate severity (10–50% tree mortality; Woods, J Ecol 92:464–476, 2004). The area in large disturbance patches (>0.1 ha) increased from <1% to approximately 4% of the forested landscape. Of the forty-two 0.1-ha plots that were studied, 23 were damaged by the storm and lost 1–66% of their original live basal area. Although the remaining 19 plots gained basal area (1–15% increase), across all 42 stands basal area decreased by 17% because of storm impacts. Overall mortality of trees >10 cm dbh was 18%. The basal area of standing dead trees after the storm was 0.9 m^2/ha, which was not substantially different from the original value of 0.7 m^2/ha. In contrast, the volume and mass of fallen dead trees after the storm (129 m^3/ha; 55 Mg/ha) were 6.1 and 7.9 times greater than the original levels (21 m^3/ha; 7 Mg/ha), respectively. Uprooting was the most frequent type of damage, and it increased with tree size. However, two other forms of injury, severe canopy breakage and toppling by other trees, decreased with increasing tree size. Two dominant oak species of intermediate shade-tolerance suffered the largest losses in basal area (30–41% lost). Before the storm they comprised almost half of the total basal area in a forest of 13% shade-tolerant, 69% intermediate, and 18% shade-intolerant trees. Recovery is expected to differ with respect to vegetation (e.g., species composition and diversity) and ecosystem properties (e.g., biomass, detritus mass, and carbon balance). Vegetation may not revert to its former composition; however, reversion of biomass, detritus mass, and carbon balance to pre-storm conditions is projected to occur within a few decades. For example, the net change in ecosystem carbon balance may initially be negative from losses to decomposition, but it is expected to be positive within a decade after the storm. Repeated intermediate-disturbance events of this nature would likely have cumulative effects, particularly on vegetation properties.

Keywords Canopy gap dynamics · Coarse woody debris · Forest ecosystem · Intermediate disturbance · Net ecosystem carbon balance · North Carolina Piedmont · Snag dynamics · Wind disturbance

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Introduction

Wind is a leading agent of disturbance in the temperate deciduous forests of eastern North America (White 1979; Lorimer 1980; Runkle 1985). Within the eastern deciduous forest (sensu Barbour et al. 1980) small patches (or canopy gaps) created by the death of one or a few trees are the most frequent form of disturbance (Runkle 1982, 1985; Lorimer 1989). Yet, hurricanes and other violent windstorms can create larger patch disturbances having strong ecological impacts that differ quantitatively and qualitatively from those of small-patch disturbances (Dunn et al. 1983; Canham and Loucks 1984; Foster 1988; Peart et al. 1992; Boose et al. 1994; Peterson and Pickett 1995; Greenberg and McNab 1997; Frelich 2002; Woods 2004). Hurricane disturbance in the eastern deciduous forest is not fully characterized with respect to immediate impacts and long-term impacts on vegetation and ecosystems. What types of forest damage occur over the landscape and within stands, and the implications for dynamics of vegetation and ecosystems require attention. Consideration of vegetation and ecosystem recovery processes and rates following hurricane disturbance contributes toward understanding of long-term dynamics of these forests.

In this article, we examine the impacts of Hurricane Fran, which passed through the North Carolina Piedmont in September 1996, on community and ecosystem attributes of an eastern deciduous forest. Windstorm impact is usually assessed through basal area loss, but one can include other measures such as estimates of the size, abundance and dynamics of disturbance patches (e.g., Platt et al. 2000) as well as the changes in canopy cover (e.g., Peart et al. 1992), coarse woody detritus (CWD) (e.g., Whigham et al. 1991), and ecosystem carbon dynamics to better quantify disturbance severity and impacts on the forest community and ecosystem (Everham and Brokaw 1996).

Relying primarily on a set of permanent vegetation plots established prior to Hurricane Fran in oak-hickory-pine forest, we consider changes in forest structure, composition, and ecosystem properties following the storm. Our general hypothesis is that the hurricane disturbance differs from small-gap disturbances in its impacts on vegetation and ecosystems. We ask the following questions: (1) How different is the size of disturbance patches created by the storm compared to other disturbances in this system? (2) Do the type and degree of damage differ by tree size, by tree species, and by ecological guild (e.g., shade-tolerance class)? (3) How are the forest composition and succession affected? (4) To what degree are detritus levels and forest ecosystem processes related to carbon dynamics altered? In addressing these objectives and questions, we assess both live and dead trees, allowing evaluation of vegetation and ecosystem impacts. Long-term impacts and the role of cumulative disturbance effects due to successive hurricanes are projected and discussed.

Study area

The North Carolina Botanical Garden is a 242-ha tract of oak-hickory-pine forest (Braun 1950; Greller 1988) in Chapel Hill, North Carolina (35°53′ N, 79°2′ W). The development, dynamics, and environment of the Piedmont hardwood forest of North Carolina are well studied (Oosting 1942; Peet and Christensen 1980). It is an area defined by undulating topography, soils of poor to good quality, and a temperate climate. Soils of the study area include Wedowee sandy loam and Goldston slaty silt loam (Dunn 1977). The climatic regime of the area fits Thornthwaite's (1948) humid mesothermal class, with a mean annual temperature of 16°C and a mean annual precipitation of 116 cm (NOAA 1974).

Human history of the study area is incompletely known. Some productive sites (e.g., floodplains and lower slopes) of the study area were farmed starting from the mid- to late 1700s and ending between the late 1800s and 1920. It is likely that some of the upland forests studied here survived as woodlots in the farm landscape, with occasional cutting of trees for firewood or lumber and with understory grazing; oaks were considered a valuable source of forage for livestock. Fire was used by Native Americans prior to 1700 and by farmers thereafter. Some lower slope forest patches are about 80 years old, whereas most forests are probably 120 years old, and the older woodlots have been continuously in the forest for hundreds of years and support occasional trees that are 200–250 years old.

Hurricane Fran, a category three storm, passed through the region on the morning of 6 September 1996. The eye passed about 7 km east of the study area. Wind data from the closest meteorological station at Raleigh-Durham International Airport

40 km east of Chapel Hill indicated sustained winds of 72 km/h and gusts of up to 128 km/h during the storm (NOAA, unpublished data).

Methods

Sampling prior to the hurricane

Forty two 0.1-ha (20 × 50 m) plots were established in upland forests of the North Carolina Botanical Garden from March 1990 to May 1991. A 100 × 100 m grid was surveyed across garden lands prior to the establishment of the plots. The grid of 1-ha cells covered a landscape ca. 50 ha in area. Plots were dispersed so that no more than one plot occurred in each 1-ha grid cell. Design of the permanently marked plots followed that of the North Carolina Vegetation Survey (Peet et al. 1998), featuring nested subplots for multiscale sampling of composition, structure, and diversity.

During the initial sampling, we laid out each 0.1-ha plot with ten contiguous10 × 10 m subplots. Within each subplot, all trees larger than 1 cm dbh (diameter at breast height) were identified according to species and measured for diameter. In addition, all live and dead trees over 10 cm dbh were mapped to allow subsequent data collectors to track individual stems. Each fallen dead stem of this size was mapped and assigned to a 10-cm diameter class. Vegetation type (pine, mixed, or hardwood), canopy height, elevation, aspect, slope, and soil characteristics such as nutrient content and density of soil were measured and documented for each plot during pre-hurricane sampling (White et al. 1991, 1992).

Sampling after the hurricane

In the summer of 1997, we re-sampled all of the 42 original upland plots. We re-measured every tree greater than 1 cm dbh and assigned one of the four damage-type codes to hurricane-damaged individuals: uproot (H1, if uprooted by wind), breakage (H2, if canopy was damaged by the wind), leaner angle (H3, if the tree was leaning), and leaner support (H4, if the tree was supporting another tree). A damage severity level (1–3 or 1–4) was assigned as well, depending on the damage-type code (e.g., H1 = 3 for a tree completely uprooted by wind) yielding a total of 15 classes of damage type and severity (H1 = 1–3, H2 = 1–4, H3 = 1–4, and H4 = 1–4). All trees greater than 10 cm dbh in the previous survey were incorporated into a dataset summarizing the fates of individual large stems (White 1999).

To quantify differences in damage among plots, the amount of basal area severely damaged by the hurricane was determined within each plot (Everham and Brokaw 1996). We considered severely damaged stems to be those that had been completely tipped up (H1 = 3), had lost >35% of canopy from breakage (H2 = 3 or 4), or had fallen with their bole lying on the ground (trees fallen, H3 = 4; or toppled and pinned by other trees, H4 = 4). If any of these categories applied to the individual tree in question, it was effectively eliminated from the canopy of the forest because it was no longer fully present as a live tree in the canopy. We excluded any tree considered severely damaged from our canopy live basal area estimates after the hurricane.

Fallen CWD (diameter >10 cm) and canopy disturbance were measured after the hurricane. In 1997, all fallen boles and branches were sampled using the planar transect method (Brown 1974; Harmon and Sexton 1996). Pieces intercepted by the 50-m centerline of each plot were measured for diameter at point of intercept. In addition, each piece was classified as input before or after the hurricane. The amount of decay was noted for each piece using the two-stage classification of Brown (1974). Total volume was calculated following VanWagner (1968):

$$V = \pi^2 \left(\Sigma D^2 \right) / 8L$$

where V is the volume in m^3/m^2, L is the transect length (50 m), and D is the diameter of individual pieces (m). Mass was calculated using the approximate density of fresh wood (0.46 Mg/m^3—averaged across all species) and decomposed wood (0.29 Mg/m^3—averaged across all species and decay classes). Density was determined by sawing out sections from recently fallen trees as well as those in various states of decomposition. Volume of the sections was calculated from surface measurements and mass was determined by weighing the entire section and then subsampling it to determine moisture content. Density was calculated as the dry mass (oven dried at 55°C) divided by the undried volume.

Changes in net ecosystem carbon balance (NECB, Chapin et al. 2006) after the 1996 hurricane were projected using net primary production (NPP) and mass decay of CWD:

$$\mathrm{NECB} = \mathrm{NPP_b} - D_{\mathrm{CWD}},$$

where $\mathrm{NPP_b}$ is bole NPP of the relatively undisturbed forest plots and D_{CWD} are the losses due to the decay of CWD. $\mathrm{NPP_b}$ was estimated using measurements of stem diameter growth and allometric equations for stem biomass of trees grouped by genus or species (Ter-Mikaelian and Korzukhin 1997). The losses from decomposition were calculated as:

$$D_{\mathrm{CWD}} = M_{\mathrm{CWD}t} - M_{\mathrm{CWD}t-1},$$

where $M_{\mathrm{CWD}t}$ is the mass of CWD at time t calculated with a negative exponential model (Olson 1963):

$$M_{\mathrm{CWD}t} = M_{\mathrm{CWD0}}\,\mathrm{e}^{-kt},$$

where k is the decomposition rate constant, assumed to range between 0.1 and 0.2/year (Onega and Eickmeier 1991).

Canopy disturbance after the hurricane was assessed at the plot level and at the landscape level. The amount of canopy loss in each plot was quantified with a canopy densitometer, taking measurements at 10-m intervals along the plot centerline. For landscape-level estimates, stereoscopic aerial photographs taken in April 1998 were examined for large canopy gaps ($\geq$0.1 ha) across a 45-ha area covering undeveloped garden lands. We only included openings with an unobstructed view of the ground surface. The length and width of all canopy gaps approximately 0.1 ha or larger were measured. Area of individual gaps was estimated using the formula for the area of an ellipse (Runkle 1982):

$$A = \pi L \times W/4,$$

where A is gap area (m^2), L is gap length (m), and W is gap width (m). Upper and lower estimates of the size of each gap were obtained using a tolerance of 6 m for gap length and width. The tolerance level represented the precision of gap length and width measurements from the photographs. Using these methods, upper, intermediate, and lower estimates of total land area in gaps $\geq$0.1 ha were generated.

Several plot-level variables such as basal area, dead tree density, CWD volume, and CWD mass, were compared before and after the hurricane. Statistical differences before and after were assessed with paired t-tests (SAS Institute Inc 1985) using plot-level values from before and after. Two-tailed probabilities were used to assess the significance of changes.

Results

Landscape disturbance

The initial, pre-hurricane survey of forested lands in the study area indicated that large, naturally created gaps ($\geq$0.1 ha) were either rare or absent. Circa 1990, prior to the hurricane, large gaps occupied less than 1% of the undeveloped land area. Two years after the hurricane, the estimated total land area in large gaps ($\geq$0.1 ha) was 4%. The lower and upper bounds for this estimate based on the measurement tolerances were 1 and 7%, respectively (see Methods).

Physical structure of stands

Basal area

Over the entire study area, live basal area declined significantly by 17% (Table 1). The coefficient of variation, indicating the variability among plots, increased from 19 to 33%. Of the 42 plots visited after the hurricane, 23 lost 1–66% of their original live basal area (Fig. 1). The mean amount of basal area lost in these damaged stands was 25%. In the 19 plots that were relatively undamaged by the hurricane, basal area increased on average by 8% over the sampling interval (ca. 1990–1997). Basal area gains ranged from 1 to 15% in these plots over this interval.

Canopy cover

Although canopy cover was not measured prior to the hurricane, comparison of cover between damaged and undamaged stands provided an indication of the amount of cover lost in the storm. Mean canopy cover was 92% in the 19 undamaged plots and 81% in the 23 damaged plots (see Appendix Table A1), respectively. Canopy cover ranged from 89 to 95% in the undamaged plots, and from 60 to 93% in the damaged plots.

Table 1 Live trees, standing dead trees, and fallen trees before and after the 1996 hurricane (ca. 1990 vs. 1997)

	Mean	Std. Dev.	Min.	Max.	Coeff. Var.	*N*
Basal area of live trees (m^2/ha)						
Before storm	27	5	19	43	19	42
After storm	22**	7	6	43	33	42
Basal area of standing dead trees (m^2/ha)						
Before storm	0.7	1	0	3.1	108	42
After storm	0.9	1	0	4.9	112	42
Added by storm	0.9	1	0	4.6	110	42
Density of standing dead trees >10 cm DBH (stems/ha)						
Before storm	22	18	0	70	83	42
After storm	30**	20	0	80	66	42
Added by storm	29	38	0	80	67	42
Density of standing dead trees >30 cm DBH (stems/ha)						
Before storm	2	4	0	10	226	42
After storm	4	9	0	40	225	42
Added by storm	4	8	0	30	213	42
Density of standing dead trees >50 cm DBH (stems/ha)						
Before storm	0.5	2	0	10	453	42
After storm	0.5	2	0	10	453	42
Added by storm	0.2	2	0	10	648	42
Volume of fallen trees >10 cm diameter (m^3/ha)						
Before storm	24	26	3	110	107	40
After storm	129**	126	6	532	97	40
Added by storm	105	126	0	522	120	40
Mass of fallen trees >10 cm diameter (Mg/ha)						
Before storm	7	7	1	32	106	40
After storm	55**	58	2	244	105	40
Added by storm	48	58	0	240	120	40

For several variables the amount added by the storm was measured directly; this amount did not necessarily equal the difference between 1990 and 1997 values. Significant differences between before and after values are noted (** significance at the $p < 0.01$ level)

Standing dead trees

Pre-hurricane basal area of standing dead trees (or snags) across the study area was low (0.7 m^2/ha) (Table 1). Density of standing dead trees (>10 cm dbh) averaged 24 stems/ha. Few of the dead trees exceeded 30 cm dbh (2 stems/ha). As a result of hurricane damage, across the study area an average of 0.9 m^2/ha of new dead basal area was added. An average of 29 stems/ha of new standing dead trees >10 cm dbh was added, and a significantly higher mean value of 30 m^2/ha was attained. The associated coefficient of variation declined from 80 to 66% indicating decreased variability among plots.

Fallen trees

Prior to the hurricane the volume and mass of downed CWD in the study forest averaged 24 m^3/ha and 7 Mg/ha, respectively (Table 1). Although the range of values was quite large, for example, volume ranged from 3 to 110 m^3/ha, the average value is quite typical for a warm temperate deciduous forest (Muller and Liu 1991). The hurricane increased CWD volume approximately sixfold to an average of 129 m^3/ha (Table 1). Mass increased to a greater degree, approximately eightfold to 55 Mg/ha, because of the higher density of fresh wood added by the disturbance.

The volume of CWD after the storm was much greater in the stands that lost live basal area (see Appendix Table A1). Nonetheless, the hurricane did not substantially alter the relative variability of downed CWD among plots as the coefficients of variation for pre- versus post-hurricane volume were 107 and 97, respectively (Table 1).

Tree damage

Of all stems greater than 10 cm dbh, 18% were severely damaged by the hurricane event (Table 2). Certain types of injury were dependent on tree size. For example, the occurrence of full uprooting increased with tree size (Fig. 2a). By contrast, the occurrence of severe canopy breakage (Fig. 2b) and of toppling by other trees (Fig. 2c) decreased with tree size. When all of these forms of damage were considered, the tendency was for small-sized trees to suffer the least damage (Fig. 2d).

Two moderately shade-tolerant species, red oak (*Quercus rubra*) and black oak (*Quercus velutina*), suffered the largest average basal area losses per plot (41% and 30%, respectively), as shown in Table 3. Conversely, shade-intolerant pine species lost only 7% of their basal area on average over all plots

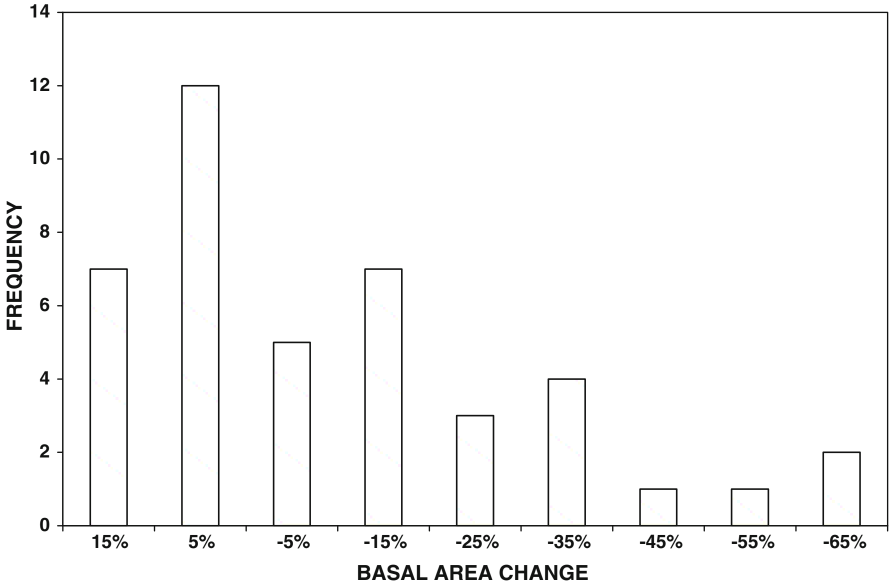

Fig. 1 Basal area change in the set of study plots before and after the 1996 hurricane (ca. 1990 to 1997)

Table 2 Comparison of all stems and larger-sized stems with respect to frequency snapped (H2 = 3 or 4), frequency uprooted (H1 = 3), and frequency severely damaged (H1 = 3, H2 = 3 or 4, H3 = 4, or H4 = 4)

Damage parameter	All stems >1 cm dbh (*n* = 10,547)	All stems >10 cm dbh (*n* = 1,899)
Frequency snapped	297 stems	117 stems
Percent snapped	2.8%	6.2%
Frequency uprooted	325 stems	210 stems
Percent uprooted	3.1%	11.2%
Frequency severely damaged	1014 stems	332 stems
Percent severely damaged	9.6%	17.7%

Values are for the entire 4.2-ha area sampled in summer 1997 after the September 1996 hurricane

(Table 3). Deciduous canopy species such as tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), beech (*Fagus grandifolia*), white oak (*Quercus alba*), and ash (*Fraxinus* sp.) suffered light to moderate damage (7–19%). Consequently, they showed large gains in importance (relative basal area) after the hurricane. Their shade-tolerance classifications range from intolerant to tolerant.

Despite the differences in damage among species, damage was not restricted to a particular shade-tolerance class (Table 4). However, in undamaged stands all but the shade-intolerant class increased in relative basal area. For shade-tolerant species the loss of basal area in damaged plots was partially offset by gains in undamaged plots. Overall, damage caused little change in the relative basal area of various shade-tolerance classes.

Projected changes in NECB

The NPP of boles in undamaged stands was 2.5 Mg/ha/year. Assuming that level of NPP is maintained despite hurricane damage, the losses of mass due to decomposition were projected to exceed forest inputs during 5–10 years (Fig. 3). After that point the forest should have a positive NECB.

Discussion

Disturbance patterns, patch dynamics, and succession

Hurricane disturbance on the upland landscape was patchy. About half of the study stands suffered basal area loss. Even in those stands, canopy disturbance was incomplete at the scale of 0.1 ha. Stands that were damaged lost, on average, one-quarter of their original live basal area and about one-tenth of their canopy cover. The lowest canopy cover estimate after the disturbance was 60% across a 0.1-ha area. Nonetheless, inputs of CWD in damaged stands were

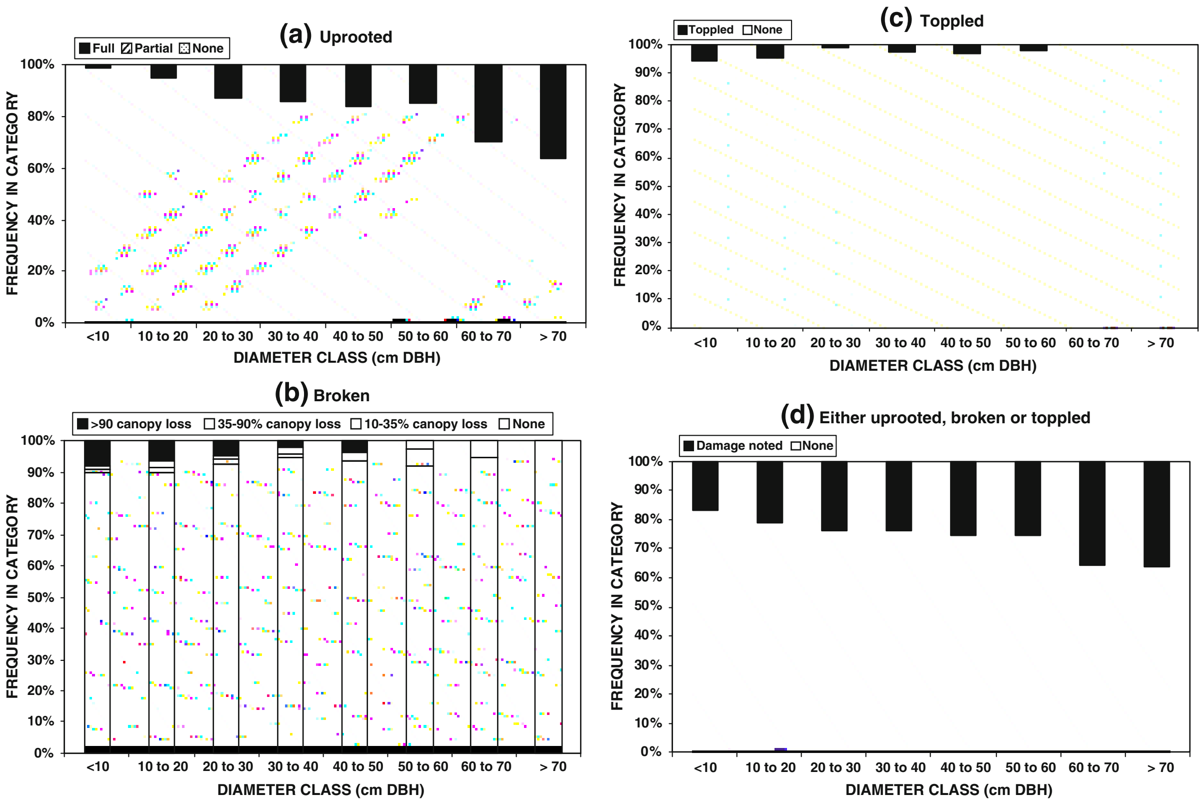

Fig. 2 Hurricane damage by type and tree size for **a** uprooted trees, **b** broken trees, **c** toppled trees, and **d** all damaged trees. Sample sizes vary by class (*left* to *right*, $n = 8648, 938, 371, 250, 203, 89, 37$ & 11)

substantial. Forest-wide, including both damaged and undamaged stands, live basal area and canopy cover declined only moderately, but necromass levels increased markedly.

Whereas long-term studies of tree mortality in the eastern deciduous forest give a mean rate of nearly 1% of the population dying per year (Parker et al. 1985; Runkle 2000; Busing 2005), the storm produced much higher levels of mortality. For stems >10 cm dbh, 18% were classified as severely damaged; most were uprooted (11%) or had broken boles (6%) (Table 2). Given that the mean return interval of hurricanes of category three or higher is at least 40 year in the Chapel Hill area (NOAA, unpublished data) and assuming a mean annual mortality rate of nearly 1%, hurricanes probably account for less than half of the total long-term mortality of forest trees.

Overall, larger trees suffered the greatest damage (cf. DeCoster 1996). The pattern of increasing injury and mortality with tree size did not fully conform to Everham and Brokaw's (1996) two generalized conceptual models of hurricane disturbance effects on forests. Neither the unimodal response model, wherein intermediate-sized trees suffer the most damage, nor the bimodal response model, wherein intermediate-sized trees suffer the least amount of damage, was followed. However, the commonly observed tendency of minimal damage to small stems (Everham and Brokaw 1996) was exhibited in this case. The observed pattern contrasted sharply with that of tree mortality between storm events, where mortality of small trees is relatively high (Peet and Christensen 1987).

Damage also varied by species and by patch composition prior to the storm. The broad-leaved deciduous species tended to suffer higher losses of basal area than the needle-leaved coniferous species. The fact that these deciduous species were in leaf at the time of the storm was important. Their relatively broad leaves and crowns made them susceptible to wind damage. By contrast, early successional patches of needle-leaved coniferous species (e.g., *Pinus*) were

Table 3 Frequency of trees in plots, basal area before and after the 1996 hurricane, basal area change, and percent of total basal area lost or gained between the two sampling periods (ca. 1990 vs. 1997)

	Frequency	Basal area before storm (m^2)	Basal area after storm (m^2)	Change in basal area (%)	Shade tolerance
Canopy species					
Acer barbatum	18	0.38	0.29	−24	Tolerant
Acer rubrum	42	8.50	7.39**	−13	Tolerant
Carya species	39	16.42	13.06**	−21	Intermediate
Fagus grandifolia	29	4.53	3.83	−16	Tolerant
Fraxinus species	30	1.29	1.20	−7	Intermediate
Liriodendron	34	8.79	7.12*	−19	Intolerant
Pinus species	23	18.43	17.11**	−7	Intolerant
Quercus alba	42	39.87	36.37*	−9	Intermediate
Quercus rubra	36	9.19	5.39**	−41	Intermediate
Quercus velutina	22	3.46	2.43	−30	Intermediate
Sub-canopy species					
Carpinus caroliniana	19	0.09	0.09	0	Tolerant
Cercis canadensis	16	0.06	0.06	0	Tolerant
Cornus florida	42	2.16	1.63**	−25	Tolerant
Crataegus species	11	0.01	0.02	50	Unknown
Ilex decidua	13	0.04	0.05*	25	Tolerant
Juniperus	36	0.72	0.82	14	Intolerant
Liquidambar	23	1.31	1.19	−9	Intolerant
Morus rubra	17	0.05	0.06	20	Tolerant
Nyssa sylvatica	40	1.69	1.41*	−17	Tolerant
Ostrya virginiana	30	0.68	0.62	−9	Tolerant
Oxydendron	39	4.98	4.86	−2	Tolerant
Ulmus species	17	0.11	0.13	18	Intermediate

Basal area is the total over the 4.2 ha area sampled. Significant differences are noted (** significance at the $p < 0.05$ level, * significance at the $p < 0.10$ level). Shade tolerance classifications (1 is the highest tolerance class) are according to Baker (1949) or Burns and Honkala (1990) (*Liriodendron = Liriodendron tulipifera*, *Liquidambar = Liquidambar styraciflua, Juniperus = Juniperus virginiana, Oxydendron = Oxydendron arboreum*)

less affected. The variation in susceptibility among species has implications for community dynamics. First, the initial impacts of the storm altered forest composition directly by reducing the abundance of certain dominant deciduous species. Second, resources (e.g., light and nutrients) made available by disturbance appear to have enhanced the growth of some species.

Overall, the forest continued to be dominated by intermediate and shade-tolerant species after the storm despite the newly created disturbance patches. Taken as a group, shade-tolerant species have increased in basal area in undamaged stands, whereas shade-intolerant species have not increased in these same stands. Thus, the trends in undamaged stands are consistent with patterns in mid-successional forests, as shade-intolerant species are giving way to shade-tolerant species. In damaged stands, the loss in basal area included species from all shade-tolerance classes. Yet, some intolerant species were unaffected by the storm, potentially stalling or setting succession back to an earlier stage, at least in the disturbance patches.

Ecosystem dynamics

The loss of tree basal area (and biomass) resulting from the storm is a disruption to ecosystem development in this otherwise aggrading forest. Large amounts of organic debris were transferred to the

Table 4 Basal area of major species before and after the 1996 hurricane by tolerance grouping and stand damage (ca. 1990 vs. 1997)

Shade tolerance class	Basal area before storm (m^2 ha^{-1})	Basal after storm (m^2 ha^{-1})	Change in basal area (%)
Damaged stands ($n = 23$)			
Tolerant	4.0	2.9**	−27
Intermediate	20.2	13.5**	−33
Intolerant	3.9	2.6**	−34
Undamaged stands ($n = 19$)			
Tolerant	3.0	3.2**	8
Intermediate	16.8	17.3**	3
Intolerant	6.4	6.3	−0.1
All stands ($n = 42$)			
Tolerant	3.5	3	−14
Intermediate	18.6	15.1**	−19
Intolerant	5.0	4.3**	−15

Damaged stands are defined as those with lower live basal area after the storm. Mean basal area values and percent change are provided. Significant differences are noted (** significance at the $p < .01$ level)

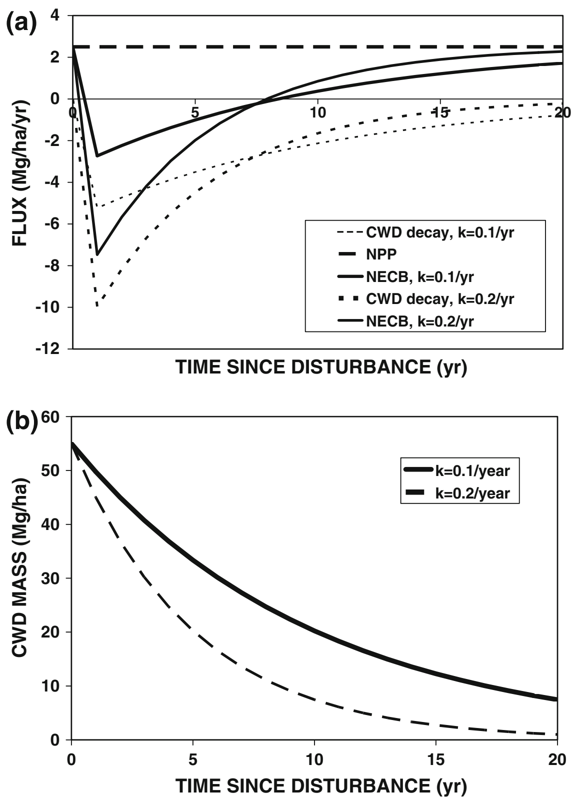

Fig. 3 Projected net ecosystem carbon balance (NECB) and major components after the 1996 hurricane showing **a** fluxes and **b** detritus mass decay

forest floor during the storm, particularly in heavily damaged stands with new CWD. The rate of decomposition of detritus can have important consequences for ecosystem energetics and nutrient dynamics (Harmon et al. 1986). Much of the detritus is wood, which decomposes slowly in temperate forests (<15% mass lost per year).

NECB, the overall change in organic matter, was likely negative immediately following the hurricane. Negative NECB would have been caused by the large input of newly decomposing wood with losses exceeding forest gains by net primary production (NPP) (Fig. 3). The duration of the period of negative NECB through losses to the atmosphere depends on the decomposition rate and the time required for NPP to recover to pre-hurricane levels. It is possible that NPP of boles was temporarily reduced by the hurricane and this may delay the switch from negative to positive NECB. However, alternative calculations with delays in NPP recovery did not alter our conclusions regarding the time required to go from negative to positive NECB as long as NPP reached pre-hurricane levels within a decade. In contrast, delaying the recovery of NPP promoted a negative NECB because the lower NPP failed to offset decomposition losses.

Long-term consequences

The changes in forest patch structure, composition, and coarse detritus brought about by this disturbance event are expected to last for decades. Reversion toward the pre-hurricane state is expected for at least some parameters, however. For ecosystem parameters such as live biomass and necromass, a direct but potentially slow, recovery toward pre-hurricane levels is anticipated. With the recovery of leaf area and the additional resources made available by disturbance, NPP will be maintained or increased during the recovery period (Beard et al. 2005). Based on published rates of CWD decomposition in similar ecosystems (Onega and Eickmeier 1991; Busing 2005), CWD added by the hurricane should be largely gone within 20–30 years (Fig. 3).

In contrast to biomass, forest composition and diversity may initially diverge further from pre-disturbance levels as a result of new colonization and recruitment. The direction and duration of community-level dynamics are potentially complex given that much of the pre-hurricane forest was in mid-succession. A simple projection, based on community resilience through positive feedback mechanisms, is that after initial divergence, composition and diversity will revert to their pre-hurricane states. For example, seeds, seedling banks, and sapling banks generated by existing adult trees would be expected to maintain recruitment of existing canopy species. If post-hurricane recruitment of shade-tolerant seedlings, presumably established before the storm, is relatively successful then succession may be accelerated (Abrams and Scott 1989); however, elevated recruitment of shade-tolerant tree seedlings was not detected shortly after the storm (White 1999). An increase in exotic plants was evident within the first 2 years after the storm (White 1999). If the hurricane disturbance facilitates invasion (Crawley 1987), novel composition and dynamics may result. For these reasons, full recovery of pre-hurricane composition and dynamics is unlikely.

Although hurricane disturbance is rarely catastrophic in Piedmont forests, episodic events of this nature may have important, lasting impacts on forests (Foster et al. 1998). Yet, the long-term effects of hurricane disturbances in the Piedmont are not well studied. It is increasingly clear that partial damage to stands, as observed in this study, is typical of the regional disturbance regime. The long-term response of ecological parameters to intermediate-disturbance events similar to the one described here is less clear. Responses are likely to vary among community and ecosystem parameters. It would be particularly useful to know which parameters exhibit delayed recovery or no recovery at all. If recovery times approach or exceed the return interval for disturbances of this severity, then the possibility of cumulative effects of multiple intermediate-disturbance events on forest dynamics must be considered.

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Appendix

Table A1 Forest stand parameters by 0.1 ha study plot in the North Carolina Botanical Garden before and after the 1996 hurricane

Plot number	Basal area before storm (m^2/ha)	Basal area after storm (m^2/ha)	Basal area change (%)	Densitometer reading after storm (Cover, %)	CWD before storm (m^3/ha)	CWD after storm (m^3/ha)
50	22.1	7.6	−65.6	ND	74.6	170.7
25	28.0	10.9	−61.1	60.3	20.5	363.6
72	28.2	12.9	−54.2	63.8	8.49	412.2
8	22.6	13.2	−41.5	82.3	40.8	105.3
51	33.2	20.2	−39.1	86.0	38.9	413.6
24	35.5	21.9	−38.2	87.0	75.4	207.6
36	32.5	22.2	−31.8	63.8	20.9	287.9
33	25.7	18.0	−30.1	81.0	6.3	101.6
47	26.7	20.1	−24.8	83.2	17.8	183.1
28	33.3	25.1	−24.5	80.5	15.3	209.5
65	30.0	23.1	−22.9	89.0	ND	ND
42	25.2	20.3	−19.6	71.0	11.9	211.2
67	34.9	28.3	−19.0	90.3	36.5	36.9

Table A1 continued

Plot number	Basal area before storm (m^2/ha)	Basal area after storm (m^2/ha)	Basal area change (%)	Densitometer reading after storm (Cover, %)	CWD before storm (m^3/ha)	CWD after storm (m^3/ha)
54	35.3	28.7	−18.6	81.7	4.8	160.4
40	28.1	22.9	−18.4	70.0	25.1	190.8
71	38.2	31.4	−17.8	88.3	6.5	21.8
34	27.0	23.1	−14.3	90.2	ND	ND
41	28.9	24.9	−13.7	92.8	11.9	84.3
4	32.1	28.9	−9.9	ND	18.1	233.3
32	29.2	27.2	−6.9	83.7	8.9	90.5
44	33.1	31.1	−6.0	86.2	12.0	90.4
70	22.5	21.4	−5.0	80.8	10.3	532.0
35	30.2	29.9	−1.1	ND	108.6	132.1
37	27.2	27.5	1.0	89.8	4.2	9.4
39	25.7	26.1	1.6	90.0	10.5	47.7
55	44.6	46.2	3.6	91.7	7.2	18.3
14	28.8	29.9	3.7	90.2	16.7	63.2
48	30.6	31.8	4.0	90.5	11.3	100.5
16	26.8	28.0	4.6	89.8	17.5	61.2
3	28.4	29.9	5.4	93.0	5.9	20.8
22	30.3	32.1	5.8	93.2	2.9	59.4
43	20.8	22.0	6.0	89.2	20.6	75.4
31	20.4	21.8	7.1	92.3	39.0	39.3
30	26.1	28.0	7.2	ND	6.3	8.3
46	21.6	23.7	9.7	88.7	22.7	26.3
2	27.1	29.9	10.2	93.7	26.7	99.5
49	28.9	31.9	10.3	94.8	4.4	5.7
52	37.7	41.7	10.6	90.7	20.5	83.0
1	29.9	33.2	11.0	90.5	11.4	13.1
68	21.2	23.9	12.7	92.3	33.8	51.4
9	26.0	29.7	14.4	95.3	17.8	17.8
17	28.8	33.1	14.9	92.2	109.8	124.1

Plots are ranked by change in basal area. Basal area change represents basal area losses from severe damage and gains due to growth between sampling periods (ca. 1990 and 1997). Densitometer readings consist of the average of six measurements along the centerline to determine cover of the canopy in each plot (ND = no data). Coarse woody detritus (CWD) is the amount of fallen wood bisecting the 50 m centerline plane (ND = no data)

References

Abrams MD, Scott ML (1989) Disturbance-mediated accelerated succession in two Michigan forest types. For Sci 35:42–49

Baker FS (1949) A revised tolerance table. J For 47:179–181

Barbour MG, Burk JH, Pitts WD (1980) Terrestrial plant ecology. Benjamin Cummings, New York

Beard KH, Vogt KA, Vogt DJ, Scatena FN, Covich AP, Sigurdardottir R, Siccama TG, Crowl TA (2005) Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecol Monogr 75:345–361. doi:10.1890/04-1114

Boose ER, Foster DR, Fluet M (1994) Hurricane impacts to tropical and temperate forest landscapes. Ecol Monogr 64:369–400. doi:10.2307/2937142

Braun EL (1950) Deciduous forests of eastern North America. Blakiston, Philadelphia

Brown JK (1974) Handbook for inventorying downed woody material. USDA Forest Service GTR INT-16, Ogden, Utah

Burns RM, Honkala BH (1990) Silvics of North America. USDA Forest Service, Washington

Busing RT (2005) Tree mortality, canopy turnover and woody detritus in old cove forests of the southern Appalachians. Ecology 86:73–84. doi:10.1890/04-0410

Canham CD, Loucks OL (1984) Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803–809. doi:10.2307/1938053

Chapin FS et al (2006) Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9:1041–1050. doi: 10.1007/s10021-005-0105-7

Crawley MJ (1987) What makes a community invasible? In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonization, succession and stability. Blackwell Scientific, Oxford, pp 429–453

DeCoster J (1996) Impacts of tornados and hurricanes on the community structure and dynamics of North and South Carolina forests. Ph.D. Dissertation, University of North Carolina, Chapel Hill, North Carolina, USA

Dunn J (1977) Soil survey of Orange County, North Carolina. Department of Agriculture, Soil Conservation Service, in cooperation with the North Carolina Agricultural Experiment Station and the Orange County Board of Commissioners

Dunn CP, Gutenspergen GR, Dorney JR (1983) Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. Can J Bot 61:211–217. doi:10.1139/b83-023

Everham EM, Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. Bot Rev 62:113–185. doi:10.1007/BF02857920

Foster DR (1988) Species and stand response to catastrophic wind in central New England, U.S.A. J Ecol 76:135–151

Foster DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1:497–510. doi:10.1007/s100219900046

Frelich LE (2002) Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge

Greenberg CH, McNab WH (1997) Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. For Ecol Manage 104:179–191. doi:10.1016/S0378-1127(97)00246-6

Greller AM (1988) Deciduous forest. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, New York, pp 287–316

Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. Publication no. 20. U.S. LTER Network Office. University of Washington, Seattle, Washington

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302. doi:10.1016/S0065-2504(08)60121-X

Lorimer CG (1980) Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169–1184. doi:10.2307/1936836

Lorimer CG (1989) Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology 70:565–567. doi:10.2307/1940207

Muller RN, Liu Y (1991) Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Can J For Res 21:1567–1572. doi: 10.1139/x91-218

NOAA (1974) Climates of the states: eastern states. Water Information Center, Port Washington

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331. doi:10.2307/1932179

Onega TL, Eickmeier WG (1991) Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull Torrey Bot Club 118:52–57. doi:10.2307/2996975

Oosting HJ (1942) An ecological analysis of the plant communities of the Piedmont, North Carolina. Am Midl Nat 28:1–126. doi:10.2307/2420696

Parker GR, Leopold DJ, Eichenberger JK (1985) Tree dynamics in an old-growth deciduous forest. For Ecol Manage 11:31–57. doi:10.1016/0378-1127(85)90057-X

Peart DR, Cogbill CV, Palmiotto PA (1992) Effects of logging history and hurricane damage on canopy structure in a northern hardwoods forest. Bull Torrey Bot Club 119:29–38. doi:10.2307/2996917

Peet RK, Christensen NL (1980) Hardwood vegetation of the North Carolina Piedmont. In: Leith H, Landolt E (eds) Contributions to the knowledge of flora and vegetation in the Carolinas. Veroff. Geobot. ETH, Zurich, pp 14–38

Peet RK, Christensen NL (1987) Competition and tree death. Bioscience 37:586–595. doi:10.2307/1310669

Peet RK, Wentworth TR, White PS (1998) A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274

Peterson CJ, Pickett STA (1995) Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76:763–774. doi:10.2307/1939342

Platt WJ, Doren RF, Armentano TV (2000) Effects of Hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the everglades region of south Florida (USA). Plant Ecol 146:43–60. doi:10.1023/A:1009829319862

Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests in eastern North America. Ecology 63:1533–1546. doi:10.2307/1938878

Runkle JR (1985) Disturbance regimes in temperate forests. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 17–33

Runkle JR (2000) Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology 81:554–567

SAS Institute Inc. (1985) SAS/STAT guide for personal computers. SAS Institute Inc., Cary

Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree species. For Ecol Manage 97:1–24. doi:10.1016/S0378-1127(97)00019-4

Thornthwaite CW (1948) An approach towards a rational classification of climate. Geogr Rev 38:55–94. doi:10.2307/210739

VanWagner CE (1968) The line intersect method in forest fuel sampling. For Sci 14:20–26

Whigham DF, Olmstead I, Harmon ME (1991) The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. Biotropica 23:434–441. doi:10.2307/2388263

White PS (1979) Pattern, process, and natural disturbance in vegetation. Bot Rev 45:229–299. doi:10.1007/BF02860857

White RD (1999) The impacts of Hurricane Fran on a North Carolina Piedmont woodland. M.A. Thesis, University of North Carolina, Chapel Hill

White PS, Busing RT, Larke JO (1991) Conservation project: the William Lanier Hunt Arboretum and Gray Bluff Garden. Technical Report, University of North Carolina, Chapel Hill

White PS, Busing RT, Larke JO (1992) Conservation project: Mason farm biological reserve. Technical Report, University of North Carolina, Chapel Hill

Woods KD (2004) Intermediate disturbance in a late-successional hemlock-northern hardwood forest. J Ecol 92:464–476. doi:10.1111/j.0022-0477.2004.00881.x