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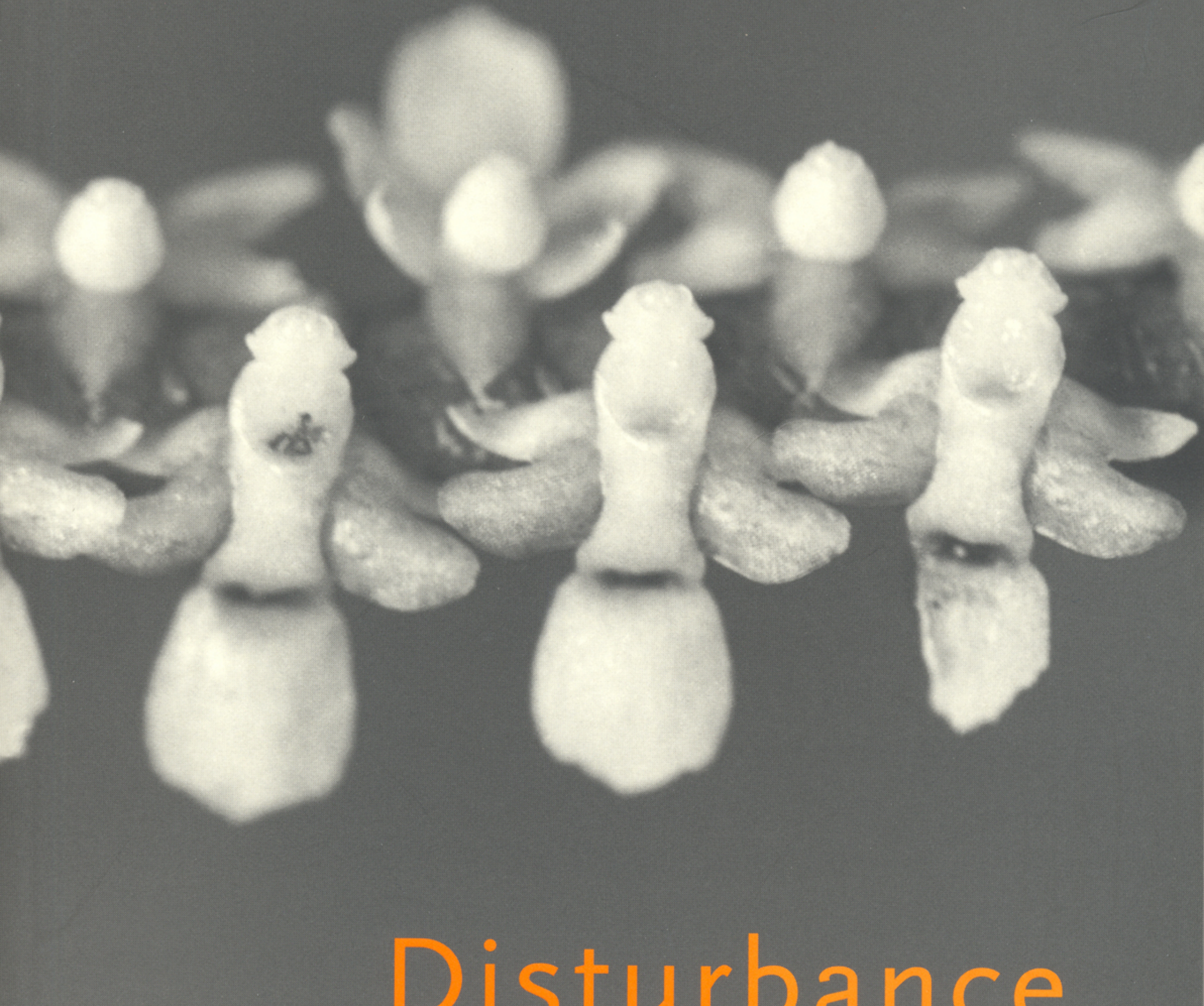

Disturbance, diversity and distributions

in Central African rain forest

Chapter 1

General introduction

Barend S. van Gemerden

African rain forests

Tropical rain forests are among the most complex and species-rich ecosystems on Earth (Wilson 1995). The main rain forest area in Africa is the Guineo-Congolian region that extends from Senegal to western Kenya and northern Angola (White 1979; *Figure 1a*). Although the rain forests in this region are generally less diverse than those in the Neotropics and Indo-Malaysia (Huston 1994), they are estimated to house more than half of Africa's species (Sayer *et al.* 1992). For example, the region holds some 84% of the primate species, 68% of the passerine bird species and 66% of the butterfly species found in Africa (Crowe & Crowe 1982; Carcasson 1964; Sayer *et al.* 1992). In addition, an estimated 8000 plant species are found in the Guineo-Congolian region (Sayer et al. 1992)

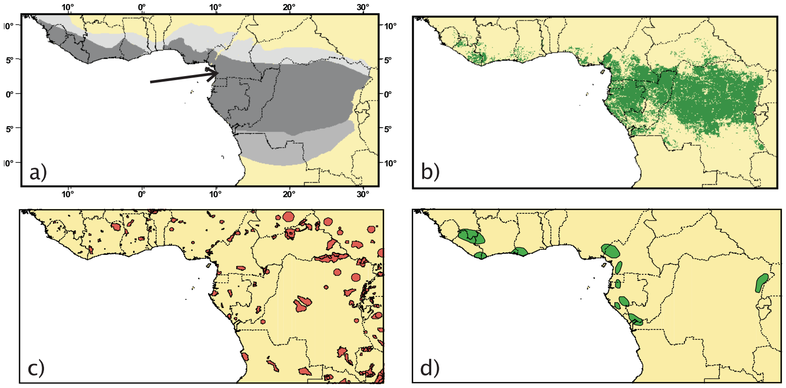

Figure 1. Distribution of rain forests in West and Central Africa; a) phytochoria of White (1979) indicating maximum rainforest extent in the Guineo-Congolian centre of endemism (dark grey); b) rain forest cover in 1990 (Iremonger et al 1997); c) protected areas (Iremonger et al. 1997); d) postulated Pleistocene rain forest refugia, i.e. centres of local endemism (Sosef 1994). Arrow in a) indicates location of research site in southern Cameroon (3°N, 10°E).

While the characteristics and functioning of the African rain forests are still poorly understood, they are increasingly subject to large-scale degradation, fragmentation and deforestation (Sayer *et al.* 1992; Archard *et al.* 2002). In West and Central Africa, an estimated 0.43% of the rain forests are deforested annually, mainly for agricultural purposes (Archard *et al.* 2002) while logging operations are estimated to affect another 0.7% (Laurance 1999). In absolute terms the conversion of African forests amounts to five million hectares per year (Laurance 1999;

Figure 1b). With the steady decline in forest cover in the region, secondary forests are be-coming increasingly important landscape elements. West and Central African forests play a prominent role in conservation schemes aimed at the protection of global biodiversity (Myers *et al.* 2000). However, less than 14% of the rain forests in the area are presently protected by law (UNEP & WCMC 2003; *Figure 1c*). Outside protected areas, human land use activities affect the rain forest species by modifying and degrading their habitat. To design effective conservation strategies and sustainable forms of land use, insight is required in the impact of human interventions on rain forest species (Lammerts van Bueren & Duivenvoorden 1996). In this thesis, I will focus on human impact on plant diversity in Central African rain forest.

Forest disturbance

A common element in current theories on the maintenance of plant diversity in tropical rain forests is the role of disturbances (Huston 1994; Rosenzweig 1995; Hubbell 2001). Huston (1994, p. 215) defines disturbance as 'any process or condition external to the natural physiology of living organisms that results in the sudden mortality of biomass on a time scale significantly shorter than that of the accumulation of the biomass'. Examples of disturbances are landslides, earthquakes, large-scale river dynamics, fires, droughts, but also falling branches and insect attacks. Human land use can also be considered as a type of forest disturbance. A disturbance creates opportunities for species to claim previously utilised space and resources. Individuals and species may differ in their ability to secure these resources and as a result disturbance may lead to a shift in species composition. The species composition at a given site is the result of its cumulative biogeographical history, including past disturbances.

For the present distribution and composition of African rain forests, the most important historical large-scale disturbances were arguably the periods of severe aridity and low temperatures during the last 40 000 years (Hamilton 1982; Bonnefille *et al.* 1990; Sosef 1994). These periods, coinciding more or less with the glacial periods, resulted in strong temporary reductions of the rain forest cover. At the height of the last glacial maximum some 18,000 years ago, it has been hypothesised that only a few isolated rain forest fragments ('refugia') remained, surrounded by savannah vegetation (Haffer 1969). During the interglacials, the climatic conditions for rain forest species was generally more favourable and resulted in the expansion of the rain forest cover. The repeated expansion and retraction of the rain forest cover has been hypothesised to explain the current distribution patterns of slow dispersers and endemic species (Haffer 1969; Sosef 1994). Areas with large numbers of endemics (i.e. species with small geographic distributions) are found in Sierra Leone -Liberia, Côte d'Ivoire - Ghana, Cameroon – Gabon and the eastern part of the Democratic Republic of Congo (former Zaire) (*Figure 1d*). While there is general agreement on their approximate location, the processes that lead to high species accumulation in these areas are much debated (e.g. Aubréville 1962; Maley 1991; Sosef 1994; Fjeldså & Lovett 1997). These large-scale patterns of biodiversity are the basis upon which more contemporary ecological processes involved in the maintenance of diversity work (Hill & Hill 2001)

At present large-scale disturbances such as hurricanes, landslides, volcanic activity and large river dynamics, are very rare in large parts of the African rain forest biome (Olivry 1986; Jans et al. 1993). The main natural disturbance in most African forests are canopy opening by tree and branch falls. Such natural gaps are generally relatively small (< ca. 100 m^2; Jans *et al.* 1993). The two most widespread land uses in Central Africa are selective logging and shifting cultivation (Sayer *et al.* 1992). Selective logging entails the felling and extraction of a small number of large individuals of a few commercial tree species. The proportion of the area that is physically affected by the logging operations depends on the logging intensity. In Cameroon, on average 0.7 trees were exploited per hectare, which caused damage to 5% of the area (Jonkers & van Leersum 2000). Logging gaps are generally larger than natural gaps, i.e. ca. 550 m^2 (Parren & Bongers 2001). Shifting cultivation is a traditional form of agriculture in which forest patches (generally 0.5 – 1.5 ha) are cleared, burned and interplanted with a variety of crops (Nounamou & Yemefack 2002). Depending on soil productivity, the tending and harvesting gradually stop after 2-3 years and the land is generally left fallow for more than 10 years. With adequate recovery periods, shifting cultivation is generally a sustainable form of land use (Nounamou & Yemefack 2002).

Forest microclimate and therefore recruitment conditions change after disturbance. In general, removal of the forest canopy results in more direct solar radiation, higher temperatures, and lower humidity (Whitmore 1989; Clark 1990). Disturbances caused by human land use tend to be more severe than natural gap phase dynamics. Individual logging gaps are generally larger than natural gaps as exploited trees are typically dominant trees with fully developed crowns while natural gaps are often the result of the collapse of medium-sized trees. Extraction of logs is done with heavy machinery and results in soil compaction and changed run-off patterns that does not compare to any natural disturbance

(Brujnzeel & Critchley 1994). In both natural gaps and logging gaps, the soil seed bank, soil organic matter, advanced regeneration and surrounding forest canopy remains largely intact (Vitousek & Denslow 1986; Uhl *et al.* 1988; van der Meer & Bongers 1996). Shifting cultivation fields are much larger than gaps and because fields are often clustered around human settlements, propagule sources of forest species tend to be remote. Burning and weeding of the fields effectively destroys the seed bank, advanced regeneration and soil organic matter (Uhl *et al.* 1981; Nepstad *et al.* 1996; Wijdeven & Kuzee 2000). Moreover, large open areas are rare phenomena in rain forests and may negatively affect the abundance of specific pollinators and dispersers of rain forest species (Guevara *et al.* 1986; Chapman & Chapman 1999).

Vegetation recovery and plant diversity

Disturbed sites in tropical rain forests tend to be colonised quickly. Size and intensity of the disturbance affects the extent and speed of this secondary succession. Advanced regeneration, sprouting and seed bank are relatively important in filling small canopy gaps while immigrants constitute the majority of plants filling large gaps (Bazzaz 1991; Whitmore 1991). Long-range dispersers are important for the vegetation recovery following severe anthropogenic disturbances like shifting cultivation (Uhl *et al.* 1981; Nepstad *et al.* 1996; Wijdeven & Kuzee 2000).

During secondary succession, the vegetation increases in height and becomes structurally more complex. With time, gaps in the forest canopy are gradually restored and light, humidity and temperature regimes become comparable to those of a mature forest (Saldarriaga *et al.* 1988; Brown & Lugo 1990). Secondary vegetation is typically dominated in its early stages by fast growing light demanding species. These so-called *pioneer* species are generally relatively short-lived and are gradually replaced by slower growing shade-tolerant species. Once established, especially woody species tend to be remarkably resilient to environmental change (Hubbell & Foster 1986).

While the role of forest disturbance in maintaining plant diversity is generally accepted (Huston 1994; Rosenzweig 1995; Hubbell 2001), the detailed processes that govern community composition following disturbance are much debated. More classical studies emphasise the role of interspecific competition in structuring plant communities (Ricklefs 1977; Denslow 1980; Ewel 1980; Brakow 1985; Whitmore 1989). Evolutionary trade-offs and constraints cause that each species is expected to be a superior competitor in a specific environment (its 'niche') and be a superior competitor in a specific environment (its 'niche') and therefore long-term coexistence of species is only assured if species occupy different niches. During secondary succession, environmental conditions change (especially light) and therefore is expected to result in shifts in species composition. In natural forests, gap-phase dynamics increase the spatial heterogeneity and so provide conditions favourable for the co-existence of large number of species in tropical rain forests (Hill & hill 2001). So far many studies have shown that species are indeed functionally different, especially with respect to light requirements (e.g. Denslow 1987; Grime 1988; Poorter & Arets 2003). However, other studies emphasise that these functional differences fail to explain the distribution of species over the forest mosaic, i.e. individuals show no apparent preference for specific ranges of the light gradient (Hubbell & Foster 1986; Hubbell *et al.* 1999). These studies argue that rain forest plant communities are dispersal assemblies in which species composition is mainly controlled by the balance between the availability of new recruitment sites and the composition of the species pool at larger scales. They argue that recruitment limitation, i.e. the failure of a species to recruit in all sites favourable for its growth and survival, and stochastic disturbance events can explain the overrepresentation of rare species in tropical rain forest communities (Hubbell *et al.* 1999). Indeed, model studies have shown that assemblages of functionally equivalent species governed solely by stochastic extinction and dispersal can result in diversity patterns observed in tropical rain forests (Bell 2001; Hubbell 2001).

The dualism in current ecological literature of tropical rain forest plant communities being either 'niche' or 'dispersal' assemblies is probably too simplistic. Most likely, both interspecific competition and dispersal limitation are important determinants for community structure (Etienne & Olff in press). However, the relative importance of these processes is likely to vary between regions and between different species groups. Identification of effective conservation measures requires insight in the relative importance of these processes as they both affect species survival in communities differently. For instance, if species survival in a community depends on the availability of suitable niches, habitat quality should be the main focus of conservation management. However, if dispersal limitation is the main structuring mechanism, habitat fragmentation is likely to be a greater threat to conservation of biodiversity.

Biodiversity assessments

The identification of priorities for biodiversity conservation requires insight in patterns of species richness and endemism. A major obstacle for setting balanced conservation priorities is the incompleteness of information on biodiversity. At present only few rain forest areas have been systematically surveyed for even a limited number of taxonomic groups (e.g. Howard *et al.* 1998, 2000). Moreover, complete biodiversity assessments of rain forest areas are extremely expensive and time consuming (Lawton *et al.* 1998). Therefore, conservation planners are challenged to set priorities on the basis of presently available, yet incomplete, information on biodiversity patterns in rain forests (Gaston & Rodrigues 2003).

Despite the lack of systematic large-scale biodiversity assessments in most tropical rain forest regions, data from small-scale inventories are generally available. Examples are collections made for taxonomic studies, tree surveys for forest exploitation, and vegetation sampling for mapping exercises. Pressed for quick conservation priorities, it is necessary to fully exploit the information potential of these different assessments. However, direct comparison of survey results is hindered by large differences in sampling method. To optimise the use of existing sources of biodiversity information for conservation planning, insight is required in the methodological differences between surveys and their consequences for the measurement of diversity.

Aim of this study

Human activities have influenced and continue to influence the rain forests of Central Africa. Although secondary forests are now dominant features in the African landscape, little information is currently available on the processes and extent of vegetation recovery in disturbed sites, especially for non-tree species.

The aim of this thesis is to increase our knowledge of the long-term impact of human land use on plant community composition, diversity and levels of endemism of Central African rain forest. Such insights are important elements for the identification of effective conservation measures and sustainable forms of forest use (Lammerts van Bueren & Duivenvoorden 1996).

Site description

The studies described in this thesis were carried out in the main research area of the Tropenbos – Cameroon Programme (TCP) in the South province of Cameroon (Mvila and Ebolowa divisions). The area is located at some 80 km East of Kribi, between 2° 47' – 3° 14' N and 10° 24' – 10° 51' E. The most important villages around the area are Bipindi, Akom II and Lolodorf. The climate in the area is humid tropical and the average annual rainfall is 2000 mm (Waterloo et al. 2000). Although rainfall occurs throughout the year there are two distinct wet seasons, i.e. March – May and August – November. Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry 1986). Landforms, soils and vegetation have been studied in some detail and a landscape ecological map at scale 1:100 000 has been compiled (van Gemerden & Hazeu 1999). Landforms range from low dissected plains in the northwest to relatively high mountains in the southeast. The altitude ranges from 40 – 1000 m. The parent matierial consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). Soils range from well-drained very clayey tot moderately well drained sandy loam and classify as Haplic Acrisols and Plinthic and Xanthic Ferrasols. In valleys, soils are generally very poorly drained.

Southern Cameroon forms part of the Guineo-Congolian region and the research area is situated in the Biafran Atlantic district, characterised by evergreen rainforest rich in Caesalpinioideae (Letouzey 1968, 1985). The area is rich in plant species. At present a total of 1264 plant species from the area have been fully identified and approximately 400 were classified as morphospecies. These species include at least fifty-one species that are restricted to the rain forests of Cameroon. Within the area, vegetation composition changes with increasing altitude and decreasing rainfall from west to east, and with recent land use history (van Gemerden & Hazeu 1999). Old growth lowland forests (altitude < 700 m) on well-drained soils are floristically quite similar throughout the area. Characteristic species are *Greenwayodendron suaveolens*, *Scaphopetalum blackii*, *Dialium* spp. and *Diospyros bipindensis*. These forests generally have a few emergents that surpass 50-55 m in height, while the closed forest canopy is at 40 m. At altitudes above 700 m, old growth forests resemble submontane vegetation with species such as *Anisophyllea purpurascens*, *Maranthes glabra*, *Scorodophloeus zenkeri*, *Garcinia lucida* and *Diospyros hoyleana*. These forests have an irregular canopy at heights of 15-20 m, occasionally 35 m. The canopy is generally infested with climbers and the presence of epiphytic mosses is characteristic. Poorly drained valleys are covered with a swamp forest characterised by *Hallea stipulosa*, *Diospyros preussii* and *Cyathea* cf. *cameroo-*

niana. Swamp forests have an open canopy at 35-40 m and lianas are abundant. Many trees have stilt roots. An estimated 30% of the land cover in the area is disturbed by shifting cultivation, mainly near villages and along the main access roads. In these areas a mosaic of forest patches in different stages or regrowth is found. Generally, recently abandoned agricultural field (< 5 years) are covered by a thicket of *Chromolaena odorata* while characteristic species of older secondary forest (5 – 20 years) are *Musanga cecropioides*, *Xylopia aethiopica*, *Zanthoxylum gilletii*, *Palisota ambigua* and *Megaphrynium secundiflorum*. The canopy of these secondary forests is open and only 15-20 m high. Floristically, secondary vegetation is remarkably uniform throughout the area (van Gemerden & Hazeu 1999).

The area is at present sparsely populated (8.6 persons km^{-2}) and population increase is marginal (Lescuyer *et al.* 1999). The population is mainly found in villages along the main access roads. The majority of the population are Bantus from the Bulu, Fang, Ngumba and Bassa tribes. All Bantu groups practice traditional shifting cultivation for subsistence and rely on cacao plantations for cash revenues. Major food crops include peanut, cassava, plantain and macabo. In addition, Bantus collect a large variety of non-timber forest products (van Dijk 1999). Some 2-4% of the population are Bagyeli (Bakola) pygmies (Lescuyer *et al.* 1999). The Bagyeli largely live in isolated villages at some distance from the main roads. Their mainstay is hunting and gathering.

The main industrial activity in the area is timber exploitation. Most of the forests in the area have been logged, and some parts twice, by international logging companies (Hazeu *et al.* 2000). However, these logging operations have been highly selective with only three main species of interest (*Lophira alata* (trade name Azobe, 60% of extracted volume), *Erythrophleum ivorense* (Tali) and *Pterocarpus soyauxii* (Padouk)). Logging intensity is low (10 m^3 ha^{-1} or 0.7 tree ha^{-1}; Jonkers & van Leersum 2000). The felling and extraction of logs causes physical damage to five percent of the area but locally much higher (25%) disturbance rates have been observed (Jonkers & van Leersum 2000).

Outline of this thesis

Chapter 2 analyses the disturbance history of species-rich and structurally complex old growth lowland rain forest and addresses the intriguing issue that the dominant tree species in present-day forests recruit poorly in a disturbance regime comparable to natural gap-phase dynamics. Chapter 3 examines long-term vegetation recovery following the disturbances caused by shifting cultivation and logging. The analysis focuses on the recovery of community characteristics of special interest to conservation planning, such as species diversity and levels of endemism and rarity. Chapter 4 investigates the relative importance of local and regional processes in structuring plant community structure during secondary succession. Chapter 5 examines methodological aspects of botanical diversity assessments and its effects on the recorded levels of diversity. As a case study, we attempt to reconcile four methodologically different assessments applied to the same area of lowland rain forest. In chapter 6, I synthesise the impact of human disturbance on plant diversity in Central African forests.

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Chapter 2

The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity

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Journal of Biogeography 30: 1381-1390 (2003)

Abstract

Aim Tropical rain forests are often regarded as pristine and undisturbed by humans. In Central Africa, community-wide disturbances by natural causes are rare and therefore current theory predicts that natural gap phase dynamics structure tree species composition and diversity. However, the dominant tree species in many African forests recruit poorly, despite the presence of gaps. To explain this, we studied the disturbance history of a species-rich and structurally complex rain forest.

Location Lowland rain forest in Southern Cameroon

Methods We identified the recruitment conditions of trees in different diameter classes in 16 ha of species-rich and structurally complex 'old growth' rain forest. For the identification of recruitment preference we used independent data on the species composition along a disturbance gradient, ranging from shifting cultivation fields (representing large-scale disturbance), to canopy gaps and old growth forest.

Results In nine out of 16 1-ha forest plots the older trees preferred shifting cultivation fields for recruitment while younger trees preferred gaps and closed forest conditions. This indicates that these nine sites once experienced large-scale disturbances. Three lines of evidence suggest that historical agricultural use is the most likely disturbance factor: (1) size of disturbed and undisturbed patches, (2) distribution of charcoal, and (3) historical accounts of human population densities.

Main conclusions Present-day tree species composition of a structurally complex and species-rich Central African rain forest still echoes historical disturbances, most probably caused by human land use between three to four centuries ago. Human impact on African rain forest is therefore, contrary to common belief, not only an issue of the last decades. Insights in historical use will help to get a more balanced view of the 'pristine rain forest', acknowledging that the dualism between 'old growth' and 'secondary' forest may be less clear than previously thought.

Introduction

Tropical rain forests are among the most complex and species-rich ecosystems of the world (Wilson 1995). However, the processes that structure this high diversity remain yet unclear. A common element in current theories on the maintenance of tree diversity is the role of disturbances, which create opportunities for species to claim previously utilised space and resources (Huston 1994; Hubbell 2001). Therefore, insight in the history, magnitude and impact of disturbances is critical in understanding rain forest tree diversity.

In large parts of the African rain forest biome, large disturbances such as hurricanes, river dynamics and volcanic activity are rare (Olivry 1986; Jans *et al.* 1993). Small-scale gap phase dynamics are therefore considered to be the main disturbance regime to provide colonisation sites for especially the light-demanding tree species. Intriguingly, many of the large tree species that currently dominate these forests are found to recruit poorly within the forest despite the presence of canopy gaps (Aubréville 1938; Richards 1952; Letouzey 1968; Poorter *et al.* 1996; Newberry & Gartlan 1996). Thus, the conditions needed for recruitment of the canopy species seem not to correspond with those occurring in natural gap phase dynamics. A number of rain forest studies have therefore questioned the view that only small-scale gap phase dynamics determine the present-day forest composition (Denevan 1992; Hart *et al.* 1996; Whitmore & Burslem 1998; Brown & Jennings 1998). Instead, the current species composition of African rain forests may still reflect large-scale historical disturbances, such as human impact (Jones 1955, 1956; Letouzey 1968, 1985; White & Oates 1999), or periods of sudden, extensive droughts (Reynaud & Maley 1994; Newberry *et al.* 1998).

The human use of African rain forest areas during the last millennia may have been more widespread than previously thought. Evidence of human activities up to three thousand years ago was found as charcoal, pottery and banana phytoliths in forest soils in Nigeria, Zaire and Cameroon (Hart *et al.* 1996; White & Oates 1999; Mindzie *et al.* 2001; Oslisly *et al.* 2001). These past human activities may have had a large impact on what we presently appreciate as 'pristine' and undisturbed rain forests. However, most biodiversity conservation strategies are implicitly based on the assumption that humans have never disturbed old growth rain forests. As a result, biogeographical setting and recent land use history are considered as the main determents of conservation value in rain forest areas (Myers *et al.* 2000). At present, the long-term impact of past human activities on current forest characteristics important to conservation, e.g. species composition and levels of biodiversity, is poorly understood.

The role of past human activities in shaping current community composition in African rain forests has generally been analysed on the basis of charcoal, pollen and distribution patterns of a limited number of well-known species (Letouzey 1968, 1985; Reynaud & Maley 1994; Hart *et al.* 1996). These studies give insight in historical land use patterns but fail to assess the full effects of past human disturbances on current community composition. An alternative method to assess both disturbance history and quantify its effects on species composition and diversity may be the interpretation of current tree species composition in terms of life history strategies. Most rain forest trees species have considerable life spans and therefore current tree species composition will, to a large extent, reflect historical disturbance regimes.

To test whether old growth forest in southern Cameroon still reflects historical large-scale disturbance, we developed a new approach that allows characterisation of the disturbance history that shaped the forest's species composition and diversity. We characterised the species in different diameter classes in 16 ha of old growth forest with respect to their preferred recruitment conditions. For the identification of recruitment preference we used independent data on the species composition along a disturbance gradient, ranging from shifting cultivation fields (representing large-scale disturbance), to canopy gaps and old growth forest. We expect that canopy trees belong to species that recruit in canopy gaps or closed forest if gap phase dynamics were important in structuring the present-day species assemblage. If historical large-scale disturbances were important, we expect that recruits of canopy trees will be found mainly in large forest clearings, comparable in size to shifting cultivation fields. If a forest stand was subject to a large disturbance event a long time ago and has not been disturbed since, this means that older trees established under conditions similar to shifting cultivation, while younger trees established in closed forest (or its gaps). Therefore, an increase in preference for large-scale disturbance with diameter was interpreted as evidence that historical large-scale disturbances structured present community composition, while a decrease supports the hypothesis of small-scale gap phase dynamics.

Material and methods

Study site

The study was conducted in the Bipindi – Akom II – Lolodorf region, south Cameroon (3° N, 10° E). The climate is humid tropical with two distinct wet seasons (March – May, August – November) and two relative drier periods. The average annual rainfall is 2000 mm (Waterloo *et al.* 2000). Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry 1986). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). Topography varies from flat erosional plains to rolling uplands with isolated hills, and mountains. Altitude varies from 50 – 1000 m above sea level. Soils range from moderately acid sandy clay loam to highly clayey and strongly acid and classify as Haplic Acrisols, and Plinthic and Xanthic Ferrasols (van Gemerden & Hazeu 1999). Evergreen forests of the Atlantic Biafrian type largely cover the area (Letouzey 1968, 1985). These forests are characteristically rich in Leguminosae-Caesalpinioideae and have a closed canopy at 30 – 40 m with emergents often surpassing 55 m. The area is rich in plant species. At present a total of 1264 species have been recorded, including 261 species that are endemic to the Lower Guinea forest region (Nigeria – Gabon) of which 51 species are restricted to the rain forests of Cameroon (B.S. van Gemerden, unpublished data).

During the last centuries, human populations in the Central African rain forest region were highly mobile as group semi-nomadism was the principal way of life (Diaw 1997). Between the 16th and 19th century, drought and slave trade evoked mass migration from savannah to forest regions on several occasions. Rivalry between immigrants and already settled populations resulted in further shifts in population composition and pressure (Laburthe-Tolra 1981). The last exponent of these mass migrations is the arrival in the research area of the Bulu around 1870 who now form the majority of the population. More recently, the German colonial rulers forced the population to abandon the villages that were scattered in the forests to settle along the main roads (van den Berg & Biesbrouck 2000). As a result of these mass migrations, population pressure and related land use patterns varied strongly during the last centuries.

The area is at present sparsely populated by humans (8.6 persons km^{-2}) and population increase is marginal (Lescuyer *et al.* 1999). Most people practice shifting cultivation, a form of agriculture in which forest patches of 0.5 – 1.5 ha are cleared, burned and interplanted with a variety of crops. A few large or valuable trees are often maintained in field preparation. Depending on soil productivity, the tending and harvesting gradually stops after two to three years and the land is left fallow for at least 7 – 15 years (Nounamo & Yemefack 2002). Shifting cultivation is confined to the direct surrounding of villages and along the main access roads (van Gemerden & Hazeu 1999). In addition, hunting and gathering of non-timber forest products is widespread and relatively intense throughout the area (van Dijk 1999).

The main current economic activity in the area is timber exploitation. International companies have selectively logged most of the area, and some parts twice. The logging involves the use of heavy machinery for road construction and log extraction. Present logging activities focus on *Lophira alata* (Azobe, 60% of the extracted volume), *Erythrophleum ivorense* (Tali), and *Pterocarpus soyauxii* (Padouk). The logging intensity is low (10 m^3 ha^{-1} or 0.7 tree ha^{-1}). The felling and extraction of logs causes physical damage to 5% of the area but locally much higher (25%) disturbance rates have been observed (Jonkers & van Leersum 2000). Individual crown fall gaps caused by commercial logging are between 300 and 900 m^2 (Parren & Bongers 2001) but simultaneous felling of clumps of commercially interesting trees often create much larger gaps (B.S. van Gemerden, unpublished data).

Vegetation sampling

We used two independent data sets to analyse the disturbance history of old growth forest in south Cameroon. Species' recruitment preference was based on a survey of 65 plots of 625 m^2 (25 x 25 m), hereafter referred to as the *recruitment plots*. Present-day tree species composition of old growth forest was based on a survey of 16 1-ha plots (100 x 100 m), hereafter referred to as the *forest plots*.

In the 65 recruitment plots, we enumerated all woody plants with height ≥50 cm and dbh < 10 cm. The majority of individuals in this size range have recruited relatively recently and therefore the present conditions were assumed to reflect the conditions in which they recruited. Plots were located in sites with different disturbance histories. The three disturbance histories studied were old growth forest (no signs of disturbance), logging gaps, and shifting cultivation fields (*Table 1*). Successional age since disturbance ranged in logging sites from 5 – 14 years and in shifting cultivation sites from 10 – 40 years. Land use history was determined with the help of local informants, often the proprietors of the sites. Information on logging activities in the area was also provided by the state forestry service ONADEF (Hazeu *et al.* 2000). Recruitment plots in old growth forest were distributed over five sample areas that represent the most important variation in vegetation, soil, landform and altitude in the Bipindi – Akom II – Lolodorf region (van Gemerden & Hazeu 1999). Recruitment plots in logged forest and shifting cultivation fields were located in respectively four and one of these sample areas. In general, secondary vegetation and especially regrowth in old agricultural fields was found to be very similar throughout the region (van Gemerden & Hazeu 1999). Plots in logging gaps were positioned in the estimated centre of the tree crown fall. Plots in fallow vegetation were positioned well away from sudden changes in vegetation structure or other anomalies. Within plot variation in topography, vegetation and drainage characteristics was minimal. Alongside the recruitment survey, we inspected soil profiles of 104 sites for charcoal. Soil observations were distributed over old growth forest, logging gaps and shifting cultivation fields (*Table 1*). Soils in each of the inspected sites were augered up to a maximum depth of 120 cm. In general, three samples were taken in the approximate centre of each plot while minimum distance to the nearest tree (dbh ≥10 cm), and between samples, was at least 1 m. The depth of observable charcoal fragments in the deepest profile was used for the analyses of charcoal distribution.

Table 1 Distribution of recruitment plots (individuals with height ≥ 50 cm and dbh < 10 cm) and soil charcoal observations (auguring to maximally 120 cm) over disturbance types

land use type	*old growth forest*	*logging gaps*	*shift. cult. fields*	*total*
vegetation age (yrs)	≥200	5 – 14	10-40	
# recruitment plots (625 m²)	36	17	12	65
survey area (ha)	2.25	1.06	0.75	4.06
# charcoal observations	39	43	22	104

In the 16 forest plots, species identity and diameter at breast height (dbh) of all trees with dbh ≥ 10 cm were determined. Plots were located in the Minwo catchment (3°05’N, 10°45’E) in the central part of the Bipindi – Akom II – Lolodorf region. Forest plots were clustered in an area of 300 ha. Altitude varied little between plots (520 ±40 m) and soils were remarkably uniform throughout the area. Floristically, the vegetation was homogeneous with *Greenwayodendron suaveolens* (Annonaceae), *Podococcus barteri* (Palmae) and *Crotonogyne preussii* (Euphorbiaceae) as characteristic species (van Gemerden & Hazeu 1999). The area had never been logged at the time of our survey and no signs were found of recent shifting cultivation activities Plots were positioned in fully developed old growth forest and plots did not include aberrant sites, e.g. steep slopes, boulders, large gaps and imperfectly drained soils.

In both surveys, the most common and readily identifiable species were directly named in the field and plant material was collected of all other species. Voucher material was processed at the Kribi Herbarium (Tropenbos-Cameroon Herbarium) and sent to the National Herbarium of Cameroon (IRAD Yaoundé) and the Nationaal Herbarium Nederland-Wageningen University branch for identification by specialists. Material that could not be identified to species level was categorised as morpho species. Nomenclature follows Lebrun *et al.* (1991 - 1997).

We classified species according to maximum stature in two classes, large trees (≥ 15 m tall) and understorey trees (3 – 15 m tall) on the basis of taxonomic literature, mainly Cable & Cheek (1998), Aubréville & Leroy (1963-2001, 1961-1992) and Keay & Hepper (1954-1972), and own field observations. In literature, information about the general ecology of African rain forest tree species is scarce. However, Hawthorne (1996) and Cable & Cheek (1998) classified a subset of the species occurring in the forest plots into three categories on the basis of shade tolerance. The inferred ecological guilds are: *shade-bearers* (both young and older plants frequent in shaded environments), *non-pioneer light demanders* (young plants frequent in shade but need higher light levels to fully develop), and *pioneers* (both young and older plants in high light levels). Of species not occurring in these references we attributed an ecological guild only if information in available taxonomic literature was sufficiently detailed.

Data analysis

We identified species' recruitment preference on the basis of the distribution of species along the disturbance gradient from low disturbance (old growth forest) via intermediate disturbance (logging gaps) to high disturbance (shifting cultivation fields). Three methods were used: occurrence preference, abundance preference and weighted average index (WAI). Occurrence preference was calculated on the basis of species presence/absence data per recruitment plot. Significance of preference was tested with a chi-square. Species with a significant ($P < 0.05$) preference were attributed to the disturbance type with the highest percentage of occurrence. Abundance preference was calculated on the basis of the number of individuals per recruitment plot. Number of individuals was log transformed to homogenise variance among groups. Analysis of variance was used to test significance of preference. Species with a significant ($P < 0.05$) preference were attributed to the disturbance type with the highest abundance. As many species were likely to have intermediate preferences, we calculated the optimal conditions for recruitment of each species along a disturbance gradient. For this, we used species composition data from recruitment plots in old growth forest (disturbance index = 1), logging gaps in old growth forest (index = 2) and shifting cultivation fields (index = 3). Next, we calculated for each species the mean value of the disturbance index, weighing for the mean log abundance (number of individuals) in each stage. This weighted average index (WAI) was then used as a species trait, indicating the relative recruitment preference of a species ranging from undisturbed forest (WAI = 1) to recent large-scale disturbance (WAI = 3).

Basal areas were based on measured dbh. For all other analyses, the trees were assigned to diameter classes (10-20, 20-30, ... ≥100 cm). Species diversity was expressed as Shannon diversity (see Magurran 1988). For all species together and for large tree species separately, we regressed average WAI per tree on diameter class and tested significance of regression using an F-test ($P < 0.05$). In the regression, the largest diameter class (dbh ≥100 cm) was excluded because this class had a much larger range of diameters than the other classes. Furthermore, as large trees are often left standing in field preparation in current shifting cultivation practices, individuals in this diameter class may have recruited under a different disturbance history than smaller trees.

Results

Tree species composition

We recorded a total of 8349 trees (dbh ≥ 10 cm) in the 16 1-ha forest plots in the Minwo catchment. More than 96% of the individuals were identified to species level and the rest was categorised as morphospecies. A total of 400 species from 53 families and 230 genera were recorded. Predominant families were the Euphorbiaceae (47 species), Leguminosae – Caesalpinioideae (31), Rubiaceae (28), Annonaceae (26) and Sterculiaceae (21). Only 28 species represented more than half of the individuals and the ten most abundant species accounted for 31% of the individuals. Maximum stature was identified for 241 species. Species with the potential to reach the forest canopy ('large tree species') accounted for 64% of the individuals recorded. Number of tree species per ha ranged from 105 – 149 (average 127). Shannon diversity index ranged from 3.97 – 4.42 (average 4.22) and basal area ranged from 29.7

– 42.6 m^2 per ha (average 35.6 m^2ha^{-1}). The ten most dominant species represented 38% of the basal area. Diameter distribution was typically skewed towards the smaller size classes, with on average 523 trees ≥ 10 cm, 105 ≥ 30 cm and 38 ≥ 50 cm per ha. Average dbh of the 5 largest trees per plot ranged from 103 – 143 cm (average 122 cm).

Recruitment preference

We identified recruitment preference for the 142 tree species that occurred in both the recruitment and in the forest plots. These species represent 36% of the species, 67% of the individuals and 76% of the basal area recorded in the forest plots. Abundance preference was significant for 49 species while occurrence preference was significant for 44 species. Preference for shifting cultivation fields was high among the species with a significant preference (*Table 2*). The remaining species did not show a significant preference for old growth, logging gaps or shifting cultivation fields. WAI was calculated for all 142 species (*Appendix A*). Species were normally distributed over WAI with most species having intermediate values. WAI values did not differ significantly between large and small tree species ($F_{1,137} = 2.67$, $P = 0.105$). Ecological guild was identified for 73 species. In general, the ecological guild classification corroborated well with preference based on WAI. Average WAI increased from shade-bearers to non-pioneer light-demanders and pioneers ($F_{2,70} = 10.28$, $P < 0.001$). Tukey tests ($P < 0.05$) indicated that shade-bearers and light demanding non-pioneers had significantly lower average WAI compared to pioneers.

Table 2. Identified recruitment preference of 142 tree species based on occurrence (presence /absence) and abundance (log transformed number of individuals) in old growth forest, logging gaps and shifting cultivation fields

recruitment preference for:	*occurrence preference # species (% species)*	*abundance preference # species (% species)*
old growth forest	12 (8.6)	13 (9.2)
logging gaps	13 (9.2)	13 (9.2)
shifting cultivation fields	19 (13.4)	23 (16.2)
no preference	98 (69.0)	93 (65.5)

The proportion of trees in the forest plots for which the recruitment pattern was identified varied with diameter class ($F_{9,144} = 3.50$, $P < 0.001$). Tukey tests ($P < 0.05$) indicated that only diameter classes 1 and 2 differed significantly from diameter classes 9 and 10. The rest of the classes were intermediate. Average proportion of trees with identified recruitment preference was 69% in classes 1 and 2, and 88% in classes 9 and 10. As large trees are less abundant, we do not expect that these small differences will influence the general outcome of the analyses.

Patterns of recruitment preference

Recruitment preference composition of forest plots changed with diameter. Both occurrence preference and abundance preference showed a general trend of decreasing old growth preference and increasing field and gap preference (*Figure 1*). Of the trees with a significant preference for one of the disturbance types, the majority belonged to species that prefer shifting cultivation fields for recruitment. Trees with dbh ≥ 100 cm were dominated by species that recruit in gaps. The relation between average WAI per tree and diameter class varied between plots (*Figure 2*). WAI increased significantly with diameter in nine plots and showed no increase in seven plots. When all plots were included, regression of average WAI on diameter class was still significant ($R^2 = 0.251$, $P < 0.001$). Analysis based on only the large tree species gave similar results. Plots with and without a significant increase in WAI with diameter were evenly distributed over the area. Plots with and without increase in average WAI with diameter did not differ significantly in species richness, Shannon diversity and basal area. However, the species – area curves (*Figure 3*) showed that the set of plots without a significant increase in WAI accumulate species much more rapidly (ANCOVA, log-area * trend type interaction, $F_{1,15} = 21.24$, $P < 0.001$).

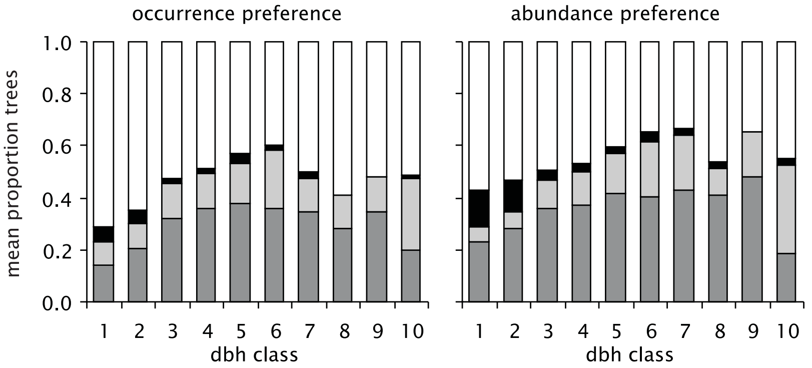

Figure 1 *Recruitment preference of trees in different diameter classes in 16 ha of lowland rain forest in southern Cameroon. Recruitment preference is based on species presence (occurrence preference) and log-transformed number of individuals (abundance preference) along a disturbance gradient (individuals height ≥ 50 cm and dbh < 10 cm). Preference classes are shifting cultivation fields (dark grey), logging gaps (light grey), old growth forest (black) and no preference (white)*

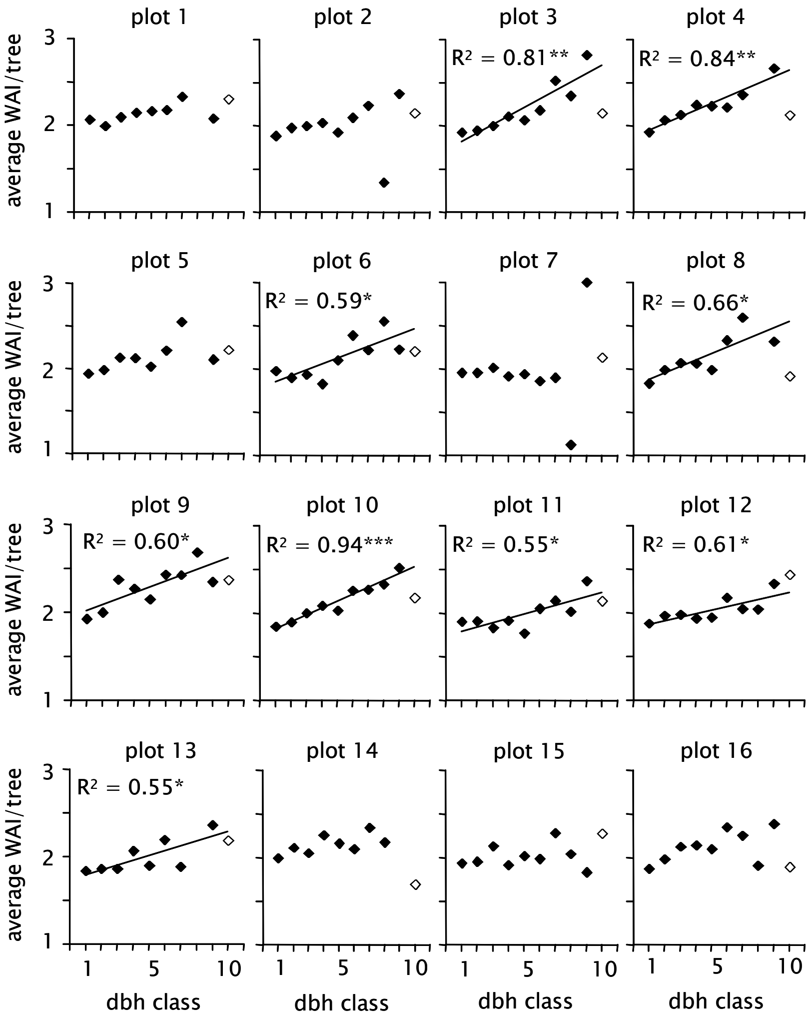

Figure 2 Average Weighted Average Index (WAI) of trees in relation to diameter class in 16 1-ha plots of lowland rain forest in southern Cameroon. WAI indicates the relative recruitment preference of species and ranges from undisturbed forest (WAI = 1) to shifting cultivation fields (WAI = 3). Significant (P < 0.05) regressions of average WAI on diameter class are indicated.

Charcoal

Charcoal was present in 29% of the sample points of the soil survey (n = 104). Charcoal depth varied from 4 – 120 cm. Of the sample points with charcoal, 20% had charcoal between 0 – 30 cm, 47% between 30 – 60 cm, 33% between 60 – 90 cm, and 23% deeper than 90 cm. Total charcoal frequency did not differ significantly between disturbance types (Kruskal-Wallis test: $x^2_2 = 3.77$, $P = 0.152$). Charcoal frequency per soil depth was also not significantly different between disturbance types (*Figure 4*; 0-30 cm: $x^2_2 = 0.42$, $P = 0.81$; 30-60 cm: $x^2_2 = 2.62$, $P = 0.27$; 60-90 cm: $x^2_2 = 5.55$, $P = 0.06$; and > 90 cm: $x^2_2 = 4.61$, $P = 0.10$).

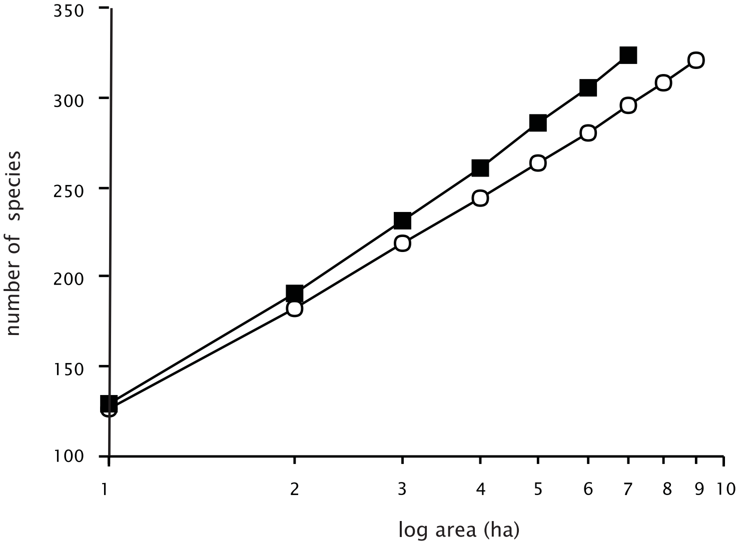

Figure 3 *Cumulative species - area curves for forest plots with (open circles) and without (solid squares) significant increase of average WAI with diameter. Significant increase of average WAI with diameter indicates historical large-scale disturbance. Data shown are mean values after 50 random permutations of plot order.*

Discussion

In this study, we found that the larger (older) trees in 9 out of 16 old growth forest plots preferred shifting cultivation fields for recruitment. In contrast, the forest understorey of these plots was largely made up of species that prefer smaller-scale disturbances like logging gaps. This shift in recruitment preference with diameter indicates that these nine sites once experienced a large-scale disturbance after which the forest was left to recover. The remaining seven plots did not show a significant shift in recruitment preference between size cohorts, suggesting that present community composition of these plots was mainly influenced by smaller gap-phase dynamics. Plots affected by large-scale events were evenly distributed spatially indicating the patchy nature of the large-scale historical disturbances.

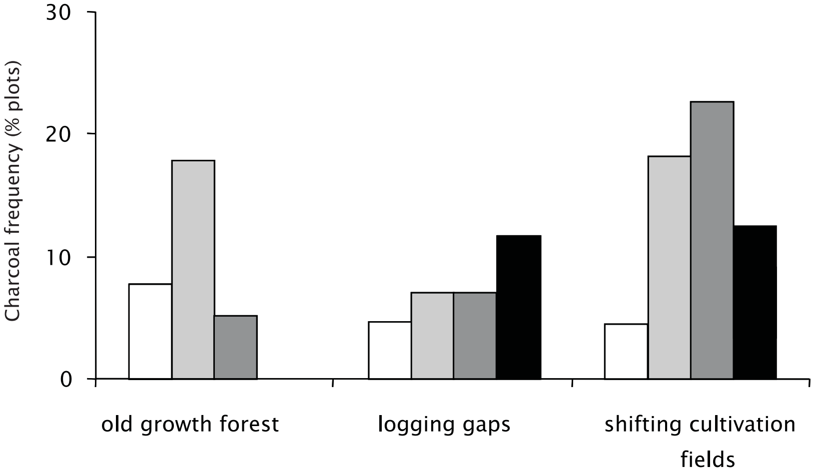

Figure 4 Soil charcoal frequency in sites differing in recent disturbance history. Charcoal frequency is expressed as percentage of the sample points with charcoal (old growth forest: n = 39, logging gaps: n = 43, and shifting cultivation fields: n = 22). Soil depth classes are 0 - 30 cm (white), 30 - 60 cm (light grey), 60 - 90 cm (dark grey) and 90 - 120 cm (black). Charcoal frequency per soil depth class did not differ significantly between disturbance types (Kruskal-Wallis test, P < 0.05).

The likely date of these suggested large-scale historical disturbances may be inferred from the diameter distribution of the trees. In the majority of the disturbed plots, the diameter class 90 –100 cm has the highest average WAI (*Figure 2*) and is likely to contain the trees that have recruited directly after the disturbance. Worbes & Junk (1999) found a strong general relationship between dbh and age of Central American rain forest species. Application of their formula (dbh = 0.33 * age) suggests that the trees of 90 – 100 cm in our survey, recruited between 273 – 303 years ago. Jones (1956) suggested that the average annual diameter increment of Nigerian forest trees is 0.25 cm and therefor trees of 90 – 100 cm are estimated to be 360 – 400 years old. However, it should be noted that these are only crude estimates, because of the potentially large variability in the general size and age relationships.

Three lines of evidence suggest that shifting cultivation is the most likely historical disturbance factor: (1) the size of disturbed and undisturbed patches, (2) distribution of charcoal, and (3) historical accounts of human population densities. The variation between plots in history of disturbance (*Figure 2*) suggests that historical shifting cultivation has created a mosaic of more and less disturbed forest patches at the scale of our plots (1 ha). The current size of fields in shifting cultivation varies between 0.5 – 1.5 ha (Nounamo & Yemefack 2002) and is likely to have been in this range during the last centuries as the solar energy need of cultivated crops cannot be assured in smaller fields (pers. comm. M. Yemefack). About 56% (9 out of 16) of the plots appear to have been disturbed in the past. This corresponds to current land use in shifting cultivation areas, where between 40 – 60 % of the area consists of young secondary forests, actual and recently abandoned fields (van Gemerden & Hazeu 1999). Furthermore, the widespread and frequent occurrence of charcoal supports the hypothesis of historical shifting cultivation. High charcoal occurrence in the soil is generally associated with human activities as naturally occurring forest fires are rare in the African rain forest region (Schwartz 1993; Hart *et al.* 1996). We found that 29% of the studied soil profiles in this area contained charcoal fragments, which is much higher than the 6% reported by Newberry *et al.* (1998) for a likely undisturbed site in Korup in west Cameroon. The soils in the study area are not subject to sedimentation or erosion, and therefore charcoal in especially the topsoil was expected to reflect recent land use. In the present survey no clear relation was found between recent land use, charcoal frequency and depth. Possibly fire also carbonises root material, which may at least partly explain the apparent random distribution of charcoal in the soil. Finally, Letouzey (1968, 1985) provides anthropological evidence that during the 18th century, population densities were high in the littoral forests of Cameroon. Large areas appear to have been cultivated and may explain the predominance of the pioneer species *Lophira alata* in the canopy but the virtual lack of regeneration in the forest understorey. Letouzey (1968, 1985) also found charcoal and artefacts in many places, which indicate the high population density in these regions a few hundred years ago. As also suggested by other studies (White & Oates 1999; Oslisly *et al.* 2001), these different lines of evidence suggest that large-scale, community-wide disturbances in this rain forest area are likely caused by widespread historical human impact.

Alternatively, historical widespread droughts may be responsible for the 'signature' of large-scale disturbance in the current forest composition. Especially relevant for the present study are the droughts that occurred in the 1765 – 1799 El Niño Southern Oscillations epoch (Quinn 1992; Newberry *et al.* 1998). Reynaud & Maley (1994) and Newberry *et al.* (1998) speculate that a drought or a series of droughts strongly increased mortality of the most drought-sensitive species, which lead to more and larger canopy gaps in which species with a competitive advantage regenerated massively. However, the assumption that many large trees will die as a result of a relatively short dry period may not be valid. The dry season in the African rain forest region is generally overcast and misty and therefore the water stress plants are exposed to is not as severe as for example in Amazonia (Maley & Brenac 1998; Charles-

Dominique *et al.* 2001). Moreover, mortality due to short dry periods is likely to be a largely non-specific random process (Hubbell 2001). Therefore, a sudden drought in this region is likely to affect forest dynamics and the regional species pool only to a limited extent and does not explain the current dominance of species that prefer large disturbances for recruitment. A non-selective perturbation, like forest clearing for agriculture, followed by a long period of recovery appears to be a much more robust explanation for this pattern. However, droughts may have enabled escaped human fires to spread short distances into the marginally inflammable forest, increasing the size of the disturbed site (Hart *et al.* 1996). We thus think that historical droughts are unlikely to be a separate, alternative explanation to historical human impact for the current forest composition. However, they may have contributed to the extent of the disturbances.

It has been argued that the absence of large-scale disturbances in tropical rain forests may lead to low tree diversity (Hart *et al.* 1989; Huston 1994) as species adapted to low disturbance will ultimately competitively displace species adapted to higher levels of disturbance. Contrary to the patterns of tree diversity in Guyana, where the least species-rich sites were those that are believed to have been the least used by pre-Colombian Amerindians (Ter Steege & Hammond 2000), we found that areas without historical human impact accumulated species more quickly (*Figure 3*). Our results suggest that historical large-scale disturbances have a significant negative effect on tree species diversity at larger scales and do not support the idea that large-scale disturbances promote diversity. Moreover, these findings question the validity of the common assumption of many current biodiversity conservation strategies that all old growth forests are equally important. Expanding the analysis to include sites from other Central African rain forests is likely to provide more insights in the long-terms effects of human disturbance on conservation values.

Our descriptive approach to analyse old growth forest in south Cameroon in terms of the recruitment preference of its species, enables the identification of the disturbance history that shaped species composition and diversity of this forest. The described method enables to distinguish between areas with and without historical human impact and is therefore potentially interesting for conservation planning, especially if existing survey data can be used. Ideally all tree species occurring in old growth forest are included in the analysis of disturbance history. However, the ecology of many rain forest species is poorly studied and systematic characterisation of their preferred recruitment conditions are scarce (e.g. Hawthorne 1996; Cable & Cheek 1998). In the present study, the ecological guild of only 18% of the old growth forest species was found in literature. Therefore, time-consuming and generally little cost-efficient recruitment surveys are still required to maximise the number of species included in the analyses. Quality and speed of the analyses would improve if patterns of recruitment in different disturbance regimes, preferably in different parts of a species biogeographical distribution range, were well documented. Including important functional traits such as fruit type, seed size, dispersal mode and wood density can further refine the classification of recruitment preference (Gitay *et al.* 1999; Weiher *et al.* 1999).

We conclude that present-day tree species composition of a structurally complex and species-rich Central African rain forest still echoes historical large-scale disturbances, most probably caused by human land use. Human impact on African rain forests is, contrary to common belief, not only an issue of the last decades, which is relevant for biodiversity conservation planning. Most likely, gaining more insights in historical use will help to get a more balanced view of the 'pristine rain forest', acknowledging that the dualism between 'old growth' and 'secondary' forest may be less clear than previously thought.

Acknowledgements

This study was carried out in the framework of the Tropenbos-Cameroon Programme (TCP). For assistance with plant identification, we like to thank G. Achoundong, J.P. Ghogue, A. Koufany, P. Mezili and J-M. Onana at the National Herbarium of Cameroon, and F.J. Breteler, J.J. Bos, C. Jongkind, A.J.M. Leeuwenberg, R.H.M.J. Lemmens, L.J.G. van der Maesen, J.J. Wieringa , J.J.F.E. de Wilde, and M.S.M. Sosef at the Nationaal Herbarium Nederland – Wageningen University branch *(Herbarium Vadense)*. All TCP staff is thanked for their logistic support, especially G. Shu Neba and M. Elad Epah. Comments by two anonymous reviewers were much appreciated. The European Union, Tropenbos International, and the Moabi Foundation supported this work.

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Appendix A Annotated list of 142 tree species included in the analysis of disturbance history of 16 ha of lowland rain forest in southern Cameroon

Family	Species	Habit*	Recruitment plots†				Recruitment‡			Guild§	Forest plots¶	
			N	individuals/plot			preference				trees	BA
				OG	L	SC	oc	ab	WAI		n ha^{-1}	m^2 ha^{-1}
Anacardiaceae	***Antrocaryon klaineanum*** Pierre	TL	13	0.19	0.12	0.33	3	4	2.37		0.81	0.25
	Pseudospondias microcarpa (A.Rich.) Engl.	TL	13	0.17	0.29	0.17	4	4	2.04		3.13	0.17
	Sorindeia grandifolia Engl.	TS	68	1.58	0.41	0.33	4	4	1.54		4.63	0.12
	Trichoscypha acuminata Engl.	TL	8	0.22	0.00	0.00	1	1	1.00		1.38	0.06
Anisophylleaceae	***Anisophyllea purpurascens*** Hutch. & Dalziel	TS	52	1.37	0.18	0.08	4	1	1.35		1.19	0.04
Annonaceae	***Annickia chlorantha*** (Oliv.) Setten & P.J.Maas	TL	58	0.61	1.12	1.42	4	4	2.19		6.50	0.31
	Anonidium mannii (Oliv.) Engl. & Diels	TL	128	1.11	2.41	3.92	3	3	2.35	Sb	0.31	0.04
	Greenwayodendron suaveolens (Engl. & Diels) Verdc.	TL	224	2.94	3.41	5.00	4	4	2.12		**8.88**	0.24
	Meiocarpidium lepidotum	TS	46	0.89	0.76	0.08	4	4	1.56	Sb	5.19	0.11
	Monodora myristica (Gaertn.) Dunal	TL	14	0.08	0.65	0.00	4	4	1.79	Sb	1.81	0.12
	Xylopia aethiopica (Dunal) A.Rich.	TL	106	1.11	2.24	2.42	2	2	2.22		5.06	0.28
Apocynaceae	***Alstonia boonei*** De Wild.	TL	26	0.03	1.18	0.42	3	2	2.34	Pr	2.19	**0.79**
	Funtumia africana (Benth.) Stapf	TL	3	0.08	0.00	0.00	4	4	1.00	Ld	0.56	0.03
	Funtumia elastica (Preuss) Stapf	TL	102	0.17	0.53	7.25	3	3	2.73	Ld	0.50	0.03
	Picralima nitida (Stapf) T.Durand & H.Durand	TL	1	0.00	0.06	0.00	4	4	2.00	Sb	2.13	0.07
	Rauvolfia caffra Sond.	TL	14	0.00	0.41	0.58	3	3	2.62		0.38	0.03
	Rauvolfia vomitoria Afzel.	TL	47	0.03	0.76	2.75	3	3	2.75	Pr	0.38	0.01
	Tabernaemontana crassa Benth.	TS	214	2.50	3.59	5.25	4	3	2.18	Sb	3.56	0.09
Bombacaceae	***Bombax buonopozense*** P.Beauv.	TL	2	0.00	0.00	0.17	4	4	3.00	Pr	0.06	0.01
	Ceiba pentandra (L.) Gaertn.	TL	2	0.00	0.12	0.00	4	4	2.00	Pr	0.13	0.10
Burseraceae	***Canarium schweinfurthii*** Engl.	TL	61	0.17	1.88	1.92	2	3	2.44	Ld	0.63	0.15
	Dacryodes edulis (G.Don) H.J.Lam	TL	269	7.22	0.47	0.08	1	1	1.20		2.81	0.18
	Dacryodes macrophylla (Oliv.) H.J.Lam	TL	73	1.53	0.82	0.33	1	1	1.60		3.81	0.17
	Santiria balsamifera Oliv.	TL	125	2.54	1.59	0.75	4	4	1.73		3.69	0.22
Cecropiaceae	***Musanga cecropioides*** R.Br. ex Tedlie	TL	122	0.00	7.06	0.17	2	2	2.06	Pr	5.63	**0.89**
	Myrianthus arboreus P.Beauv.	TL	7	0.08	0.06	0.25	4	4	2.49	Sb	0.56	0.02
Chrysobalanaceae	***Maranthes chrysophylla*** (Oliv.) Prance	TL	19	0.25	0.53	0.08	4	4	1.81	Sb	0.06	0.00
Combretaceae	***Terminalia superba*** Engl. & Diels	TL	6	0.03	0.00	0.42	4	3	2.82	Pr	2.44	**0.85**
Connaraceae	***Jollydora duparquetiana*** (Baill.) Pierre	TS	97	2.33	0.53	0.33	1	1	1.52		0.25	0.00
Ebenaceae	***Diospyros bipindensis*** Gürke	TS	35	0.81	0.24	0.17	1	1	1.53	Sb	3.44	0.08
	Diospyros conocarpa Gürke & K.Schum.	TS	90	2.19	0.53	0.17	1	1	1.44	Sb	0.38	0.01
	Diospyros crassiflora Hiern	TL	88	1.89	1.18	0.00	2	1	1.45	Sb	1.00	0.10
	Diospyros hoyleana F.White	TS	59	1.64	0.00	0.00	1	1	1.00		0.06	0.00
	Diospyros suaveolens Gürke	TL	76	1.14	2.00	0.08	4	4	1.68		2.81	0.08
	Diospyros zenkeri (Gürke) F.White	TL	12	0.19	0.24	0.08	4	4	1.79		0.81	0.02
Euphorbiaceae	***Alchornea floribunda*** Müll.Arg.	TS	143	2.83	2.06	0.75	4	4	1.72		4.06	0.19
	Antidesma laciniatum Müll.Arg.	TS	2	0.06	0.00	0.00	4	4	1.00	Sb	2.50	0.06
	Antidesma vogelianum Müll.Arg.	TS	15	0.22	0.24	0.25	4	4	1.99		0.19	0.01
	Bridelia micrantha (Hochst.) Baill.	TL	29	0.00	1.53	0.25	2	2	2.21	Pr	0.56	0.06
	Dichostemma glaucescens Pierre	TS	144	1.50	3.53	2.50	4	4	2.21		6.75	0.24
	Discoglypremna caloneura (Pax) Prain	TL	13	0.03	0.59	0.17	4	2	2.24	Pr	0.38	0.04
	Drypetes preussii (Pax) Hutch.	TL	26	0.53	0.29	0.17	4	4	1.66		1.13	0.04
	Maesobotrya barteri (Baill.) Hutch.	TS	10	0.28	0.00	0.00	4	4	1.00	Sb	0.06	0.00

Family	Species	Habit*	Recruitment plots†				Recruitment‡			Guild§	Forest plots¶	
			N	individuals/plot			preference				trees	BA
				OG	L	SC	oc	ab	WAI		$n\ ha^{-1}$	$m^2\ ha^{-1}$
	Maprounea membranacea Pax & K.Hoffm.	TS	26	0.00	1.47	0.08	2	2	2.10		0.63	0.02
	Margaritaria discoidea (Baill.) Webster	TL	7	0.00	0.12	0.42	4	4	2.70	Pr	2.06	0.19
	Ricinodendron heudelotii (Baill.) Heckel	TL	10	0.00	0.47	0.17	2	2	2.32	Pr	1.13	0.16
	Tetrorchidium didymostemon (Baill.) Pax & K.Hoffm.	TS	46	0.03	1.47	1.67	3	3	2.56	Pr	0.69	0.02
	Uapaca guineensis Müll.Arg.	TL	7	0.06	0.29	0.00	4	4	1.79	Ld	**11.00**	**0.64**
	Uapaca heudelotii Baill.	TL	3	0.06	0.06	0.00	4	4	1.57		0.25	0.02
	Uapaca staudtii Pax	TL	1	0.00	0.06	0.00	4	4	2.00		2.69	0.12
	Uapaca vanhouttei De Wild.	TS	45	0.42	1.12	0.92	4	2	2.13		0.56	0.04
Flacourtiaceae	***Casearia barteri*** Mast.	TL	76	1.47	0.94	0.58	4	4	1.74	Pr	0.69	0.02
	Scottellia klaineana Pierre	TL	29	0.69	0.12	0.17	4	4	1.50	Sb	2.94	0.07
Guttiferae	***Allanblackia floribunda*** Oliv.	TL	90	1.56	0.65	1.92	4	4	2.01	Sb	0.06	0.01
	Endodesmia calophylloides Benth.	TS	35	0.72	0.47	0.08	4	4	1.62		0.44	0.03
	Garcinia kola Heckel	TL	2	0.03	0.06	0.00	4	4	1.68	Sb	0.31	0.00
	Garcinia lucida Vesque	TS	224	6.22	0.00	0.00	1	1	1.00		0.31	0.02
	Garcinia mannii Oliv.	TL	57	0.75	0.59	1.67	4	4	2.03		**7.75**	0.15
	Mammea africana Sabine	TL	53	1.11	0.59	0.25	4	4	1.71	Sb	0.13	0.00
	Pentadesma butyracea Sabine	TL	45	1.25	0.00	0.00	1	4	1.00	Sb	2.63	0.14
Huaceae	***Afrostyrax kamerunensis*** Perkins & Gilg	TS	229	6.36	0.00	0.00	1	1	1.00		0.06	0.02
Hypericaceae	***Harungana madagascariensis*** Lam. ex Poir.	TS	2	0.00	0.06	0.08	4	4	2.59		0.06	0.00
Irvingiaceae	***Desbordesia glaucescens*** (Engl.) Tiegh.	TL	17	0.06	0.65	0.33	2	2	2.32		5.56	**0.64**
	Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill.	TL	77	0.78	2.35	0.75	4	4	2.06	Ld	4.00	0.35
	Irvingia grandifolia (Engl.) Engl.	TL	2	0.03	0.06	0.00	4	4	1.68		0.50	0.03
	Klainedoxa gabonensis Pierre ex Engl.	TL	14	0.31	0.06	0.17	4	4	1.68	Ld	1.56	0.28
Lecythidaceae	***Petersianthus macrocarpus*** (P.Beauv.) Liben	TL	13	0.00	0.12	0.92	3	3	2.83	Pr	0.94	0.08
Leguminosae-Caes.	***Afzelia bella*** Harms / ***A. pachyloba*** Harms	TL	14	0.14	0.53	0.00	4	4	1.79		0.50	0.04
	Anthonotha lamprophylla / ***A. fragrans*** (Baker f.) Exell & Hillc.	TL	2	0.06	0.00	0.00	4	4	1.00		0.38	0.01
	Anthonotha macrophylla P.Beauv.	TS	278	1.31	3.71	14.00	3	3	2.45	Sb	7.63	0.15
	Berlinia bracteosa Benth.	TL	33	0.36	0.88	0.42	4	4	2.07		1.63	0.56
	Brachystegia eurycoma Harms ***/ B. laurentii*** (De Wild.) Louis ex Hoyle	TL	61	0.29	2.53	0.67	4	4	2.18		0.13	0.01
	Dialium pachyphyllum Harms	TL	131	2.03	1.35	3.08	4	4	2.00		**7.69**	**0.83**
	Distemonanthus benthamianus Baill.	TL	71	0.17	0.41	4.83	3	3	2.66	Ld	1.31	0.08
	Erythrophleum ivorense A.Chev.	TL	29	0.33	0.71	0.42	4	4	2.09	Ld	1.19	**0.79**
	Hylodendron gabunense Taub.	TL	10	0.08	0.35	0.08	4	4	2.00		3.06	0.19
	Hymenostegia afzelii (Oliv.) Harms	TS	124	1.78	2.47	1.50	2	4	2.26	Sb	4.44	0.17
	Julbernardia pellegriniana Troupin	TL	83	1.44	1.82	0.00	4	4	1.55		0.13	0.01
	Tetraberlinia bifoliolata (Harms) Hauman	TL	257	3.94	6.65	0.50	4	4	1.71		1.44	0.08
Leguminosae-Mim.	***Albizia adianthifolia*** (Schum.) W.F.Wight	TL	53	0.08	1.06	2.67	3	3	2.68	Ld	0.81	0.11
	Calpocalyx dinklagei Harms / ***C. heitzii*** Pellegr.	TS	215	3.17	4.53	2.25	2	2	1.94		2.00	0.04
	Cylicodiscus gabunensis Harms	TL	2	0.06	0.00	0.00	4	4	1.00	Sb	0.38	0.08
	Parkia bicolor A.Chev.	TL	19	0.39	0.29	0.00	4	4	1.45	Ld	1.31	0.20
	Pentaclethra macrophylla Benth.	TL	139	1.86	1.76	3.50	4	4	2.15	Ld	2.94	0.32
	Piptadeniastrum africanum (Hook.f.) Brenan	TL	22	0.25	0.53	0.33	4	4	2.11	Ld	1.50	0.42

Family	Species	Habit*	Recruitment plots†				Recruitment‡			Guild§	Forest plots¶	
			N	individuals/plot			preference				trees	BA
				OG	L	SC	oc	ab	WAI		n ha^{-1}	$m^2\ ha^{-1}$
Leguminosae-Mim.	***Albizia adianthifolia*** (Schum.) W.F.Wight	TL	53	0.08	1.06	2.67	3	3	2.68	Ld	0.81	0.11
	Calpocalyx dinklagei Harms / ***C. heitzii*** Pellegr.	TS	215	3.17	4.53	2.25	2	2	1.94		2.00	0.04
	Cylicodiscus gabunensis Harms	TL	2	0.06	0.00	0.00	4	4	1.00	Sb	0.38	0.08
	Parkia bicolor A.Chev.	TL	19	0.39	0.29	0.00	4	4	1.45	Ld	1.31	0.20
	Pentaclethra macrophylla Benth.	TL	139	1.86	1.76	3.50	4	4	2.15	Ld	2.94	0.32
	Piptadeniastrum africanum (Hook.f.) Brenan	TL	22	0.25	0.53	0.33	4	4	2.11	Ld	1.50	0.42
Leguminosae-Pap.	***Amphimas ferrugineus***	TL	5	0.06	0.18	0.00	4	4	1.78		0.06	0.00
	Baphia laurifolia Baill.	TS	9	0.03	0.35	0.17	4	2	2.28		0.19	0.00
	Pterocarpus soyauxii Taub.	TL	17	0.11	0.35	0.58	4	3	2.40		1.50	0.38
Lepidobotryaceae	***Lepidobotrys staudtii*** Engl.	TS	1	0.00	0.00	0.08	4	4	3.00		0.81	0.07
Medusandraceae	***Soyauxia talbotii*** Oliv.	TS	2	0.06	0.00	0.00	4	4	1.00		5.13	0.14
Meliaceae	***Carapa procera*** DC.	TL	106	1.61	1.94	1.25	4	4	1.95	Sb	3.19	0.12
	Entandrophragma angolense (Welw.) C.DC.	TL	2	0.00	0.12	0.00	4	4	2.00	Ld	0.25	0.02
	Entandrophragma utile (Dawe & Sprague) Sprague	TL	1	0.03	0.00	0.00	4	4	1.00	Ld	0.56	0.38
	Guarea cedrata (A.Chev.) Pellegr.	TL	21	0.17	0.24	0.92	4	3	2.47	Sb	0.38	0.04
	Heckeldora staudtii (Harms) Staner	TS	10	0.22	0.12	0.00	4	4	1.43		0.06	0.00
	Lovoa trichilioides Harms	TL	87	1.17	1.65	1.42	4	4	1.99	Ld	1.56	0.14
	Trichilia gilgiana Harms	TL	2	0.03	0.06	0.00	4	4	1.68		0.19	0.00
	Trichilia rubescens Oliv.	TL	81	0.11	0.12	6.25	3	3	2.87		0.88	0.02
	Trichilia welwitschii C.DC.	TL	2	0.03	0.06	0.00	4	4	1.68		**8.63**	0.15
Moraceae	***Ficus mucuso*** Welw. ex Ficalho	TL	6	0.00	0.12	0.33	4	3	2.69	Pr	0.06	0.01
	Milicia excelsa (Welw.) C.C.Berg	TL	17	0.00	0.53	0.67	3	3	2.53	Pr	0.13	0.01
	Treculia africana Decne.	TL	14	0.14	0.41	0.17	4	4	2.04	Ld	1.00	0.03
	Treculia obovoidea N.E.Br.	TL	465	11.06	2.53	2.00	4	1	1.71		**14.31**	0.34
Myristicaceae	***Coelocaryon preussii*** Warb.	TL	191	1.92	3.00	5.92	3	3	2.28		**31.25**	**2.37**
	Pycnanthus angolensis (Welw.) Warb.	TL	108	0.83	1.76	4.00	3	3	2.36	Ld	**19.50**	**3.24**
	Staudtia kamerunensis Warb.	TL	247	2.39	2.94	9.25	4	3	2.26		**21.56**	**0.84**
Ochnaceae	***Lophira alata*** Banks ex Gaertn.f.	TL	125	0.17	5.65	1.92	2	2	2.37	Pr	1.69	**1.69**
Olacaceae	***Coula edulis*** Baill.	TL	16	0.28	0.18	0.25	4	4	1.83	Sb	7.38	**1.04**
100	***Olax subscorpioidea*** Oliv.	TS	1	0.00	0.00	0.08	4	4	3.00	Sb	0.44	0.01
	Ptychopetalum petiolatum Oliv.	TS	7	0.19	0.00	0.00	4	4	1.00		1.94	0.03
	Strombosia grandifolia Hook.f. ex Benth.	TS	80	1.64	0.59	0.92	4	1	1.72		**11.19**	0.36
	Strombosia pustulata Oliv.	TL	141	2.44	2.41	1.00	2	4	1.80		6.88	0.35
	Strombosiopsis tetrandra Engl.	TL	3	0.08	0.00	0.00	4	4	1.00		3.81	0.22
Palmae	***Elaeis guineensis*** Jacq.	TS	26	0.00	0.12	2.00	3	3	2.90	Pr	0.06	0.01
Pandaceae	***Panda oleosa*** Pierre	TS	12	0.08	0.35	0.25	4	4	2.26	Sb	1.69	0.21
Passifloraceae	***Barteria fistulosa*** Mast.	TS	24	0.00	0.24	1.67	3	3	2.81		0.94	0.02
Rhizophoraceae	***Poga oleosa*** Pierre	TL	7	0.03	0.24	0.17	4	4	2.31		0.31	0.11
Rubiaceae	***Aulacocalyx caudata*** (Hiern) Keay	TS	12	0.17	0.24	0.17	4	4	2.06		0.06	0.00
	Aulacocalyx jasminiflora Hook.f.	TS	17	0.39	0.18	0.00	4	4	1.32	Sb	1.06	0.02
	Aulacocalyx talbotii (Wernham) Keay	TS	1	0.00	0.06	0.00	4	4	2.00		1.25	0.02
	Hallea stipulosa (DC.) Leroy	TL	1	0.00	0.06	0.00	4	4	2.00		0.13	0.01
	Massularia acuminata (G.Don) Bullock ex Hoyle	TS	276	3.44	4.47	6.33	4	4	2.13	Sb	0.25	0.00
	Nauclea diderrichii (De Wild. & T.Durand) Merrill	TL	4	0.06	0.00	0.17	4	4	1.55	Pr	0.69	0.10
	Pausinystalia johimbe (K.Schum.) Pierre ex Beille	TL	55	0.36	0.18	3.25	4	4	2.20		3.38	0.17

Chapter 3

Recovery of conservation values in Central African rain forest after logging and shifting cultivation

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Biodiversity and Conservation 12: 1553-1570 (2003)

Abstract

Secondary forests in Central Africa are increasing in importance for biodiversity conservation as old growth forests outside the few protected areas are disappearing rapidly. We examined vegetation recovery in a lowland rain forest area in Cameroon based on a detailed botanical survey of old growth forest and different-aged logging gaps (5–27 years) and shifting cultivation fields (10–60 years). Our analysis focuses on the long-term recovery of botanical conservation values by analysing trends in vegetation structure, species composition, species diversity and levels of endemism and rarity. In the total survey (4.25 ha), we recorded 834 species of which 23% were endemic to the Lower Guinea forest region. The proportion of endemic species was high in shrubs and low in herbs. Geographic range and (local) rarity were not significantly associated. The proportion of rare species (relative frequency <10%) was high in woody climbers and low in trees. In logging gaps, recovery of all vegetation characteristics was relatively quick (5–14 years). Recovery in shifting cultivation sites took longer (30–60 years). Endemic species were found to be highly sensitive to shifting cultivation practices and even after 50–60 years the level of endemism was still significantly lower compared to old growth forest. The proportion of rare species was not significantly different between disturbed sites and old growth forest. We conclude that secondary forests can contribute to biodiversity conservation, e.g. as buffer zones around protected areas. However, this contribution should be assessed differently between land use types and widespread versus endemic species.

Introduction

Central and West African rain forests are estimated to hold 8000 plant species, of which 80% are endemic to the region (Sayer *et al.* 1992). Combined with substantial recent habitat loss, this has led to the classification of this forest region as one of the top 25 conservation priority areas of the world (Myers *et al.* 2000). Despite this importance, Central and West African rain forests are poorly protected. In West Africa some 20% of the remaining forest cover is protected, in Central Africa only 7% (Sayer *et al.* 1992). Outside protected areas, forest use such as logging, plantation agriculture and shifting cultivation has intensified during the last decades, leading to large-scale forest degradation (Sayer *et al.*1992). At present, research and conservation management tend to focus on undisturbed tropical forests while little attention is given to disturbed ecosystems. However, as relatively undisturbed ('old growth') forests are becoming scarce and fragmented in many tropical regions, secondary forests may become critical for future biodiversity conservation (Brown & Lugo 1990; Aide *et al.* 1995). To evaluate the role of secondary forests for biodiversity conservation, more insight is needed on the effects of human land use activities on forest composition, and especially conservation values.

Species diversity, levels of endemism and rarity, naturalness and exposure to threats are generally accepted as a robust set of criteria for setting conservation priorities (de Groot 1992; Hawthorne 1996). However, current evaluations of conservation values in tropical rain forests only use present-day characteristics of forest communities, while overlooking future potentials of recovery through secondary succession. Examples are the 'silver bullet' strategy for global conservation priorities proposed by Myers *et al.* (2000) and the identification of an optimal reserve network for biodiversity conservation in Uganda proposed by Howard *et al.* (2000).These static approaches may work for relatively stable old growth forests, but are unsuitable for highly dynamic secondary forests. On the other hand, existing studies of tropical forest succession characterise forest dynamics but often do not evaluate characteristics important to conservation (e.g. de Rouw 1991; Aide *et al.* 2000; Peña-Claros 2001).

Conservation values should ideally be assessed using different trophic and functional groups of organisms (Howard *et al.* 1998; Lawton *et al.* 1998). However, logistic problems and insufficient taxonomic knowledge make relatively rapid surveys of especially small-sized animal groups impossible in most tropical regions. Being taxonomically relatively well studied, plants are therefore often used as a proxy variable for conserva tion evaluations (Zonneveld 1995). Most plant regeneration studies of tropical forests focus on trees (e.g. Swaine & Hall 1983; Saldarriaga *et al.* 1988; Peña-Claros 2001; Slik *et al.* 2002). This may, however, underestimate the conservation value of an area. For instance, some 67% of the endangered and rare forest plant species of West Africa are non-trees (J.J. Wieringa, personal communication). Conservation evaluations using plants should therefore be based on as many growth forms, functional types and taxonomic groups as possible (Lawton *et al.* 1998).

The recovery potential of secondary forests is strongly influenced by the size and intensity of disturbances. In natural forests, advanced regeneration, sprouting and the seed bank are relatively important in filling small canopy gaps, while light demanding immigrants constitute the majority of plants filling large gaps (Bazaz 1991; Whitmore 1991). Anthropogenic disturbances like logging and forest clearing for agriculture are generally more severe than natural gap phase dynamics and therefore regeneration will be determined by long-range dispersers (Uhl *et al.* 1981; Nepstad *et al.* 1996; Wijdeven & Kuzee 2000). Many of these pioneer species are of limited concern to conservation, as they generally have large distribution ranges and are little site-specific (Ewel 1980). Therefore, studies that address the conservation value of secondary forest should extend beyond the pioneer stages of succession. However, current regeneration studies in West and Central Africa are restricted to the first 5–10 years (e.g. Aweto 1981; Swaine & Hall 1983).

In this study we analyse the recovery of lowland rain forest in south Cameroon following the two most widespread land uses in the region: logging and shifting cultivation. We conducted a detailed botanical survey, including all major terrestrial growth forms, of logging gaps of 5–27 years old and shifting cultivation fields of 10–60 years old. We evaluate the long-term recovery of vegetation characteristics and conservation values by analysing trends in vegetation structure, species composition, species diversity, and levels of endemism and rarity.

Methods

Research area

The study was conducted in the Bipindi–Akom II–Lolodorf region, south Cameroon (3°N, 10°E). The climate is humid tropical with two distinct wet seasons (March–May and August–November) and two relatively dry periods. The average annual rainfall is 2000 mm (Waterloo *et al.* 2000). Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry

1986). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). Topography varies from flat erosional plains to rolling uplands with isolated hills. Altitude varies from 50 to 600 m above sea level. Soils range from moderately acid sandy clay loam to highly clayey and strongly acid and classify as Haplic Acrisols, and Plinthic and Xanthic Ferrasols (van Gemerden & Hazeu 1999). Evergreen forests of the Atlantic Biafrian type largely cover the area (Letouzey 1968, 1985). These forests are characteristically rich in Leguminosae–Caesalpinioideae and have a closed canopy at 30–40 m with emergents often surpassing 55 m.

The area is sparsely populated (8.6 persons km^{-2}) and population increase is marginal (+0.4%; Lescuyer et al. 1999). Most people practice shifting cultivation, a form of agriculture in which forest patches of 0.5–1.5 ha are cleared, burned and interplanted with a variety of crops. Depending on soil productivity, the tending and harvesting gradually stops after 2–3 years and the land is left fallow for at least 7–15 years (Nounamo & Yemefack 2002). Shifting cultivation is confined to the direct surrounding of villages and along the main access roads (van Gemerden & Hazeu 1999). The main economic activity in the area is timber exploitation. Most of the area has been selectively logged, and some parts twice, by international logging companies. The logging involves the use of heavy machinery for road construction and log extraction. Present logging activities focus on *Lophira alata* Banks ex Gaertn. f. (Ochnaceae; commercial name Azobe; 60% of the extracted volume), *Erythrophleum ivorense* A. Chev. (Leg.-Caesalpinioideae; Tali), and *Pterocarpus soyauxii* Taub. (Leg.-Papilionideae; Padouk). The logging intensity is low (10 m^3 ha^{-1} or 0.7 tree ha^{-1}). The felling and extraction of logs causes physical damage to 5% of the area but locally much higher (25%) disturbance rates have been observed (Jonkers & van Leersum 2000). Individual crown fall gaps caused by commercial logging are between 300 and 900 m (Parren & Bongers 2001), but simultaneous felling of clumps of commercially interesting trees often creates much larger gaps (B.S. van Gemerden, personal observation).

Survey plots

Vegetation in gaps of 5, 14 and 27 years after logging, and in shifting cultivation fields of 10–20, 30–40, and 50–60 years since tending of fields has stopped, was sampled by plots of 25 x 25 m (625 m^2). A total of 68 plots were sampled, i.e. 4.25 ha. Plots were selected in homogenous and representative vegetation following a reconnaissance scale vegetation survey of the area (van Gemerden and Hazeu 1999). Secondary vegetation was found to be very similar throughout the area and therefore

shifting cultivation plots were clustered in one research site where reliable information on historical agricultural use was available. Logging plots were located in four research sites to increase the span of the studied chronosequence (*Table 1*). The maximum distance between sites was less than 40 km and land use practices were
comparable. In all four localities old growth forest was sampled.

Table 1 Vegetation characteristics and distribution of 25 x 25 m plots by land use and age classes.

landuse	*old growth forest*	*logging gaps*			*shifting cultivation fields*		
vegetation age (yrs)	≥200	5	14	27	10-20	30-40	50-60
canopy height (m)[a]	26	20	28	27	22	21	25
tree density ha^{-1} [a]							
- dbh ≥ 10 cm	639	435	384	379	365	435	400
- dbh ≥ 30 cm	117	80	96	77	93	67	85
# plots (625 m^2)	20	10	7	8	7	5	11
surveyed area (ha)	1.25	0.63	0.44	0.50	0.44	0.31	0.69
research sites[b]	ABCD	CD	AB	AB	C	C	C

[a] Means based on a random set of three plots extended to 25 x 50 m (1250 m^2) per land use / age category, except for old growth (6 plots) and Logging 14 years (2 plots). [b] A = Bibindi area (30°00'N, 10°24'E, altitude 120 - 300 m), B = Ebimimbang area (3°02'N, 10°26'E, 50 - 180 m), C = Ebom area (3°03'N, 10°43'E, 400 - 450 m), D = Minwo area (3°05'N, 10°45'E, 480 - 600 m).

Land use history was determined with the help of local informants, often the proprietors of the sites. Information on logging activities in the area was also provided by the state forestry service ONADEF (Hazeu *et al.* 2000). Plots in logging gaps were positioned in the estimated centre of the tree crown fall. Most exploited trees are *Lophira alata*, a species with extremely hard wood, and branches and bole were, even after 27 years, clearly visible. Plots in fallow vegetation were positioned well away from sudden changes in vegetation structure or other anomalies. Within-plot variation in topography, vegetation and drainage characteristics was minimal.

Survey methods

All individuals of terrestrial higher plants (all growth forms) were recorded per plot. Only woody plants with heights less than 50 cm were not sampled because of foreseen identification problems. Species and size class of each individual was recorded. Within each growth form category, individuals were assigned to the following size classes: total height (*h*) < 50 cm (non-woody species only), *h* ≥ 50 cm and diameter at breast height (dbh) < 2 cm, dbh 2–4.9, 5–9.9, 10–19.9, etc. We considered all apparent solitary ramets as individuals. Each tussock of herbs was counted as an individual. Diameters of stems of multi-stemmed shrubs were summed.

Plant species identification

In the field, the most common and readily identifiable species were directly named and plant material was collected of all other species. A total of nearly 11,000 vouchers were collected in the survey. The vouchers were processed at the Kribi Herbarium (Tropenbos Cameroon Herbarium) and sent to the National Herbarium of Cameroon in Yaounde and the Nationaal Herbarium Nederland (Wageningen University Branch) for identification by specialists. Unidentified species were categorised as morphospecies. Ferns and fern allies were collected but have not been identified. Nomenclature follows Lebrun *et al.* (1991 – 1997). Species' growth form and geographical distribution were identified on the basis of taxonomic literature, mainly Cable & Cheek (1998), Aubreville & Leroy (1961–1992, 1963–2001), Keay & Hepper (1954 – 1972), and own field observations. Growth form classification largely followed Cable & Cheek (1998), and species were classified as trees (single-stemmed, maximum height at least 3 m; generally much taller), shrubs (multi-stemmed or < 3 m tall), woody climbers (including rattans), non-woody climbers, herbs (terrestrial), hemi-epiphytes, palms or stranglers. Categories used to classify species' geographical distribution range reflect general patterns of biogeography. However, as large parts of West and Central Africa have only been poorly explored botanically, available information was generally too imprecise to assess species distribution patterns at smaller than regional scales. Therefore, species were classified as Lower Guinea endemics (species restricted to the forest region of Nigeria, Cameroon, Equatorial Guinea and Gabon), Guineo – Congolian species (species restricted to the Senegal–Gabon– Zaire forest region), and Paleo and pan tropical species (species widely distributed in Africa). Each species was assigned to the geographic range category that included the complete distribution range.

Data analysis

Analysis of variance (ANOVA) was used to compare plant density, basal area, species richness, and species diversity between vegetation ages and land use types. We compared disturbed sites with old growth forests using a Tukey test ($P < 0.05$). Species diversity was expressed as the Shannon diversity index (see Magurran 1988). Plant density and basal area were calculated using all individuals encountered in the plots.

Species richness and species diversity were calculated using individuals that were at least morphocategorised. As a result, our richness and diversity estimates are likely to be conservative.

Table 2 Mean relative abundance and relative frequency of the most abundant species per growth form in old growth forest, logging gaps and shifting cultivation fields.

family	*species*^{a,b}	*mean relative abundance*^{c,d}			*relative frequency* ^{c,e}		
		OG	L	SC	OG	L	SC
trees (345 species)							
Sterculiaceae	***Scaphopetalum blackii*** Mast.	7.1	2.9	3.1	IV	III	V
Moraceae	***Treculia obovoidea*** N.E.Br.	6.3	1.7	0.8	V	IV	V
Icacinaceae	***Lasianthera africana*** P.Beauv.	3.5	6.0	3.0	V	V	V
shrubs (151 species)							
Euphorbiaceae	*Manniophyton africanum* Müll.Arg.	22.9	9.5	0.2	III	III	I
Sterculiaceae	***Scaphopetalum thonneri*** Willd.	18.1	19.1	18.7	III	IV	III
Euphorbiaceae	***Alchornea floribunda*** Müll.Arg.	4.1	4.1	12.9	IV	IV	V
Monimiaceae	***Glossocalyx brevipes*** Benth.	3.5	6.1	3.4	III	II	IV
Rubiaceae	***Chazaliella sciadephora*** (Hiern) Petit & Verdc.	2.7	1.4	10.4	II	II	IV
Dracaenaceae	***Dracaena bicolor*** Hook.	1.8	10.2	0.1	I	III	+
Rubiaceae	***Chazaliella domatiicola*** (De Wild.) Petit & Verdc.	0.1	0.1	8.2	+	r	IV
woody climbers (150 species)							
Marantaceae	***Haumania danckelmaniana*** (J.Braun & K.Schum.) Milne-Redh.	49.2	54.4	57.5	V	V	V
Palmae	***Eremospatha cf. wendlandiana*** Dammer ex Becc.	8.7	7.1	4.9	V	V	V
Connaraceae	***Agelaea pentagyna*** (Lam.) Baill.	6.9	4.8	6.1	V	IV	IV
Icacinaceae	***Lavigeria macrocarpa*** (Oliv.) Pierre	4.2	6.4	4.3	IV	IV	V
Palmae	***Laccosperma secundiflorum*** (P.Beauv.) Kuntze	0.8	2.8	8.1	II	II	IV
non-woody climbers (37 species)							
Araceae	***Cercestis congensis*** Engl.	48.4	34.6	55.2	V	V	V
Araceae	***Cercestis mirabilis*** (N.E.Br.) Bogner	29.9	50.3	38.5	V	V	V
Araceae	***Culcasia obliquifolia*** Engl.	13.7	2.5	0.0	II	I	-
Vitaceae	***Cissus barteri*** (Baker) Planch.	0.5	5.1	0.7	I	II	II
herbs (72 species)							
Gramineae	***Leptaspis zeylanica*** Nees	27.6	9.7	1.0	V	V	III
Gramineae	***Microcalamus barbinodis*** Franch.	14.8	4.1	6.8	II	II	II
Marantaceae	***Trachyphrynium braunianum*** (K.Schum.) Baker	5.0	13.1	4.8	III	V	V
Araceae	***Stylochaeton zenkeri*** Engl.	3.0	3.5	15.4	III	III	V
Marantaceae	***Sarcophrynium cf. prionogonium*** (K.Schum.) K.Schum.	2.6	8.8	4.5	II	IV	III
Commelinaceae	***Palisota ambigua*** (P.Beauv.) C.B.Clarke	1.7	11.6	4.0	III	V	V
Marantaceae	***Megaphrynium macr ostachyum*** (Benth.) Milne-Redh.	1.1	9.3	20.2	I	V	V
Marantaceae	***Thaumatococcus daniellii*** (Benn.) Benth.	0.5	4.9	15.6	+	I	IV

[a] *Growth form was identified of 765 species (92% all species, 95% all individuals).* [b] *Species with mean relative abundance ≥ 5% in at least one land use category.* [c] *Land use categories: OG = old growth forest (n = 20); L = logging gaps (n = 25), SC = shifting cultivation fields (n = 23).* [d] *Mean relative abundance is average proportion of individuals per growth form per plot.* [e] *Species relative frequency is the proportion of plots per land use category in which the species was present. Frequency classes: - = not present; r = < 5% plots; + = 5-10%; I = 10-20%; II = 20-40%; III = 40-60%; IV = 60-80%; V = 80-100%*

To assess recovery in terms of species composition, we calculated the similarity of disturbed sites with each of the old growth sites ($n = 20$). Average similarity with old growth plots was used to compare recovery of species composition between disturbed sites (ANOVA followed by Tukey tests, $P < 0.05$). Both qualitative and quantitative similarity was calculated using the Sörenson index, expressing for two samples which proportion of all observed species they have in common (see Magurran 1988). Qualitative similarity was based on presence /absence data of species per plot. Quantitative similarity was based on the log transformed relative species abundance. Only individuals that are at least morphocategorised were included in the analyses.

Species rarity is a measure for the local distribution of species. Rare species have a higher risk of (local) extinction under unfavourable conditions (Rosenzweig 1995). Species rarity was calculated as the relative frequency of occurrence in 68 plots. Species were classified as rare (occurring in less than 10% of the plots), intermediate (10–60% plots) and common (≥ 60% plots). Association of rarity and geographic range was analysed with a Kruskal–Wallis test ($P < 0.05$), based on species' actual relative frequency. Association of rarity classes and growth form and of geographic range and growth form was tested with a chi-square test ($P < 0.05$).

Results

Floristic characteristics

We recorded a total of 63 384 individual plants (including ferns and fern allies) in 4.25 ha. Of all individual plants, 74% were identified to species level, and 10% were categorised as morphospecies. Only 3 and 4% remained undetermined at the genus level and family level, respectively. Finally, 9% of the plants were assigned to a field identification that turned out to represent a small number of morphologically similar (botanical) species. Such clusters were treated in the analyses as a single species. In total, 59 529 individual plants representing 94% of all individuals were at least morphocategorised and used in the analyses. The proportion of unidentified plants varied among the different land use/age categories ($F_{6,61} = 2.76$, $P = 0.019$, no Tukey subsets). The mean proportion of unidentified plants ranged from 2.2% in shifting cultivation fields of 30–40 years to 5.8% in old growth forest. We do not expect that these small differences will affect the overall outcome of the analyses. In the survey, we found a total of 834 species belonging to 359 genera and 90 families. Predominant families encountered were Rubiaceae (140 species), Euphorbiaceae (53), Apocynaceae (39), Leguminosae-Caesalpinioideae (34), Annonaceae (31)and Ebenaceae (27).

Rare species (species occurring in less than 10% of the plots) accounted for 63% of all species but represented only 6% of the individuals. Less than 7% of the species occurred in more than 60% of the plots. These 'common' species accounted for 53% of all individuals. Only one species, *Haumania danckelmaniana* (J. Braun and K. Schum.) Milne-Redh. (Marantaceae), was found in all plots. Woody climbers, non-woody climbers and herbs were dominated by a small number of species, while only three tree species had average relative abundance larger than 5% (*Table 2*).

We assigned 765 species (92% of species, 95% of individuals) to growth forms. The most species-rich growth forms were trees, woody climbers and shrubs (*Table 2*). Together they represent nearly 85% of the species and 54% of the individuals. The geographical distribution range was identified for 447 species (54% of species, 73% of individuals). Of these species, 22% had Paleo or Pan-tropical ranges. At the other extreme, more than 23% of the species were endemic to the Lower Guinea forest region (South Nigeria–Gabon). This category included 4% of the species that, according to available taxonomic literature, were strictly confined to Cameroon. Geographic distribution range and growth form were significantly associated ($x^2_8 = 25.13$, $P = 0.01$). The proportion of endemics was highest in shrubs (41%) and lowest in herbs (11%). Species rarity did not differ significantly among distribution ranges (Kruskal–Wallis tests, $P < 0.05$; *Table 3*). Growth form and rarity classes were significantly associated ($x^2_8 = 41.45$, $P < 0.001$). The proportion of rare species was high in woody climbers (73%) and shrubs (70%), and low in trees (49%).

Herbs were significantly more abundant in shifting cultivation sites of 10–20 years compared to old growth forest ($F_{6,61} = 14.53$, $P < 0.001$). The large number of herbs found in these sites accounted largely for the differences in total plant densities (*Figure 1a*; $F_{6,61} = 12.36$, $P < 0.001$). Furthermore, shifting cultivation sites of 10–20 and 30–40 years had a much larger number of individuals with $h \geq 50$ and dbh < 2 cm ($F_{6,61} = 10.52$, $P < 0.001$). Other size classes showed no significant trend among land use/age categories. Climbers, both woody and non-woody, reacted differently to logging and shifting cultivation practices. With vegetation age, densities of non-woody climbers ($F_{6,61} = 4.33$, $P < 0.001$) and woody climbers ($F_{6,61} = 5.26$, $P < 0.001$) increased in shifting cultivation sites and remained constant in logging sites. Both growth forms were significantly more abundant in 30–40 year old shifting cultivation sites compared to old growth forest. Densities of trees and shrubs were not affected by disturbance (*Table 4*).Both growth forms were significantly more abundant in 30–40 year old shifting cultivation sites compared to old growth forest. Densities of trees and shrubs were not affected by disturbance (*Table 4*).

Table 3 Distribution of species and rarity by geographic range of the most important growth forms.

growth form	*trees*			*shrubs*			*woody climbers*		
geographic range[a,b]	# spp	% spp	rarity[c]	# spp	% spp	rarity[c]	# spp	% spp	rarity[c]
Lower Guinea	53	22.3	7.7	27	40.9	4.6	17	20.2	14.9
Guinea – Congolia	125	52.5	15.4	28	42.4	6.2	57	67.9	10.4
Paleo and pan tropical	60	25.2	13.1	11	16.7	7.7	10	11.9	14.0
growth form	*non-woody climbers*			*herbs*			*all growth forms*		
geographic range[a,b]	# spp	% spp	rarity[c]	# spp	% spp	rarity[c]	# spp	% spp	rarity[c]
Lower Guinea	2	12.5	10.0	4	10.8	3.1	104	23.3	6.2
Guinea – Congolia	10	62.5	7.0	21	56.8	12.3	245	54.8	9.2
Paleo and pan tropical	4	25.0	10.0	12	32.4	10.0	98	21.9	11.6

[a] Geographic range and growth form was identified for 447 species (54% of all species). [b] Lower Guinea = species endemic to Nigeria, Cameroon, Equatorial Guinea and Gabon; Guinea - Congolia = species restricted to the Senegal - Gabon - Zaire forest region (Lower Guinea endemics not included); Paleo and pan tropical = species occurring throughout Africa (excluding Lower Guinean and Guinea - Congolian species). [c] Rarity is expressed as median of relative frequencies of species over 68 plots. Rarity per growth form did not differ significantly between geographic ranges (Kruskal-Wallis tests, trees: $x^2_2 = 5.05$, $P = 0.08$; shrubs: $x^2_2 = 0.65$, $P = 0.723$; woody climbers: $x^2_2 = 0.71$, $P = 0.707$; non-woody climbers: $x^2_2 = 0.03$, $P = 0.987$; herbs: $x^2_2 = 1.93$, $P = 0.382$; all growth forms: $x^2_2 = 4.41$, $P = 0.110$).

Table 4 Species rarity, geographic range composition and species and plant density of the most important growth forms in old growth forest, logging gaps and shifting cultivation fields.

growth form	*trees*			*shrubs*			*woody climbers*		
land use^{1}	OG	L	SC	OG	L	SC	OG	L	SC
species rarity^{2,3,4}									
rare species (<10% plots)	**2.5**	**2.8**	**3.6**	**12.8**	**13.4**	**18.0**	**13.3**	**14.3**	**10.0**
	1.0	*1.9*	*1.4*	*4.8*	*7.4*	*8.3*	*3.8*^{b}	*2.8*^{ab}	*1.5*^{a}
common species (≥60% plots)	**33.4**	**33.0**	**33.4**	**14.7**	**16.0**	**14.6**	**31.9**	**25.9**	**27.7**
	47.5	*46.6*	*51.5*	*28.0*	*29.2*	*34.7*	*73.9*	*75.6*	*75.7*
species geographic range^{2,4,5,6}									
Lower Guinea (endemics)	**21.6**^{b}	**14.8**^{a}	**13.1**^{a}	**38.8**^{a}	**48.9**^{b}	**30.4**^{a}	**38.1**^{b}	**24.9**^{a}	**24.3**^{a}
	18.6^{b}	*13.8*^{ab}	*11.2*^{a}	*23.4*^{a}	*40.8*^{b}	*15.7*^{b}	*74.1*	*70.2*	*69.4*
Guinea – Congolia	**63.9**^{ab}	**64.7**^{b}	**60.0**^{a}	**30.5**^{b}	**19.6**^{a}	**49.0**^{c}	**47.4**^{a}	**59.6**^{b}	**61.4**^{b}
	62.6^{a}	*71.9*^{b}	*64.8*^{ab}	*15.3*^{a}	*11.3*^{a}	*53.6*^{b}	*14.8*	*22.2*	*21.9*
Paleo and pan-tropical	**14.6**^{a}	**20.1**^{b}	**26.9**^{c}	**30.7**^{b}	**31.4**^{b}	**20.6**^{a}	**14.4**	**15.5**	**14.3**
	18.4^{ab}	*14.7*^{a}	*24.0*^{b}	*61.2*^{c}	*47.9*^{ab}	*30.7*^{a}	*11.2*	*7.6*	*8.7*
species and plant density^{2,5}									
mean # species per 625 m^2	68.2	69.3	70.1	17.2	17.3	17.9	14.2	16.3	16.0
mean # individuals per ha	4626	3934	4131	1803	1442	1906	1286^{a}	1317^{a}	2453^{b}

growth form	*non-woody climbers*			*herbs*			*all growth forms*		
land use^{1}	OG	L	SC	OG	L	SC	OG	L	SC
species rarity^{2,3,4}									
rare species (<10% plots)	**8.6**	**17.0**	**18.0**	**8.5**	**7.5**	**7.0**	**14.8**	**15.2**	**13.3**
	4.6	*2.2*	*2.8*	*4.6*	*1.1*	*2.5*	*7.8*	*4.8*	*5.1*
common species (≥60% plots)	**51.7**	**49.9**	**54.1**	**46.3**	**44.9**	**44.3**	**30.3**	**30.0**	**30.1**
	78.4	*84.9*	*93.6*	*46.2*	*53.2*	*53.8*	*49.3*	*53.8*	*56.4*
species geographic range^{2,4,5,6}									
Lower Guinea (endemics)	**15.1**^{b}	**7.6**^{a}	**0**^{a}	**0.6**	**2.1**	**1.8**	**23.7**^{c}	**18.9**^{b}	**14.5**^{a}
	14.8^{b}	*2.5*^{a}	*0*^{a}	*0.3*	*0.4*	*0.2*	*22.9*^{b}	*19.4*^{ab}	*14.4*^{a}
Guinea – Congolia	**82.8**	**81.0**	**89.4**	**81.1**^{b}	**63.3**^{a}	**59.6**^{a}	**60.0**	**59.2**	**59.9**
	85.7^{a}	*96.2*^{ab}	*98.2*^{b}	*87.0*^{b}	*62.5*^{a}	*62.4*^{a}	*53.5*	*57.4*	*58.4*
Paleo and pan-tropical	**3.1**	**11.4**	**11.1**	**18.3**^{a}	**34.6**^{b}	**38.7**^{b}	**16.3**^{a}	**21.9**^{b}	**25.6**^{c}
	0.3	*1.3*	*1.9*	*12.7*^{a}	*37.1*^{b}	*37.4*^{b}	*23.6*	*23.2*	*27.2*
species and plant density^{2,5}									
mean # species per 625 m^2	4.0	4.4	4.0	8.0^{a}	12.1^{b}	14.4^{b}	116.7	123.5	128.5
mean # individuals per ha	787^{a}	923^{a}	1626^{b}	2661^{a}	3747^{a}	8634^{b}	12004^{a}	12234^{a}	20152^{b}

[1] OG = old growth forest (n = 20); L = logging gaps (n = 25); SC = Shifting cultivation fields (n = 23). Plot size is 625 m2. [2] Species rarity and species and plant density are based on 834 species (growth form of 765 species was identified). Geographic range composition is based on 447 species (53.6% total species and 77.4% total individuals). [3] Species rarity is expressed as relative frequency of species over 68 plots. Rare species are species with relative frequency < 10%. Common species are species with relative frequency ≥ 60%. [4] Mean proportions of species (bold) and individuals (italics) per growth form and land use category. [5] Values with same letter are not significantly different between land use categories (Tukey test after analysis of variance, p < 0.05). [6] Lower Guinea = species endemic to Nigeria, Cameroon, Equatorial Guinea and Gabon; Guinea - Congolia = species restricted to the Senegal - Gabon - Zaire forest region (Lower Guinea endemics not included); Paleo and pan tropical = species occurring throughout Africa (excluding Lower Guinean and Guinea - Congolian species).

Basal areas ranged from 0.64–5.89 m^2 per plot (dbh ≥ 2 cm, average 2.13 m^2, i.e. 35.76 m^2 ha^{-1}). The general trend in both logging and shifting cultivation sites was that the basal area was lower at intermediate age compared to younger and older stands (*Figure 1b*). Variation within land use/age categories was, however, considerable; only shifting cultivation sites of 30–40 years had a significant lower basal area than old growth forest ($F_{6,61} = 3.40$, $P < 0.006$).

Recovery of species richness, diversity and composition

Species richness (# species per plot) ranged from 75 to 173 (average 123) and varied with growth form and land use (*Table 4*). The most species rich growth forms were trees (mean 69 species per plot), followed by shrubs (17), woody climbers (16), and herbs (13). With vegetation age, overall species richness decreased in logging sites and increased in shifting cultivation sites ($F_{6,61} = 2.72$, $P < 0.021$, *Figure 1c*). Trees, on average the most species rich growth form per plot, were largely responsible for the general trend ($F_{6,61} = 2.77$, $P < 0.019$). Herb species richness was, compared to old growth forest, higher in 5-year old logging sites and shifting cultivation sites of 30–40 years ($F_{6,61} = 6.73$, $P < 0.001$). Species richness of the other growth forms showed no clear trend. The Shannon diversity of the vegetation ranged from 2.3 to 4.3 (average 3.7). Five-year old logging sites already had Shannon diversity values comparable to those of old growth forest, while shifting cultivation sites of 10–20 years still had significantly lower values ($F_{6,61} = 7.35$, $P < 0.001$, *Figure 1d*).

The average qualitative (presence /absence) similarity between old growth plots varied from 40 to 47%. The mean qualitative similarity of disturbed sites to old growth vegetation increased with vegetation age ($F_{6,61} = 12.35$, $P < 0.001$; *Figure 1e*). Logging sites reached qualitative similarity values comparable to old growth forests after 14 years, whereas such values were only reached in shifting cultivation sites after 50–60 years. Mean quantitative similarity (log transformed relative abundance) of disturbed plots and old growth forest was generally lower than qualitative similarity and ranged from 16 to 34%. However, variation was high and no significant relation between quantitative similarity, land use and vegetation age was found. Quantitative similarity based only on woody species did not show a significant relation either.

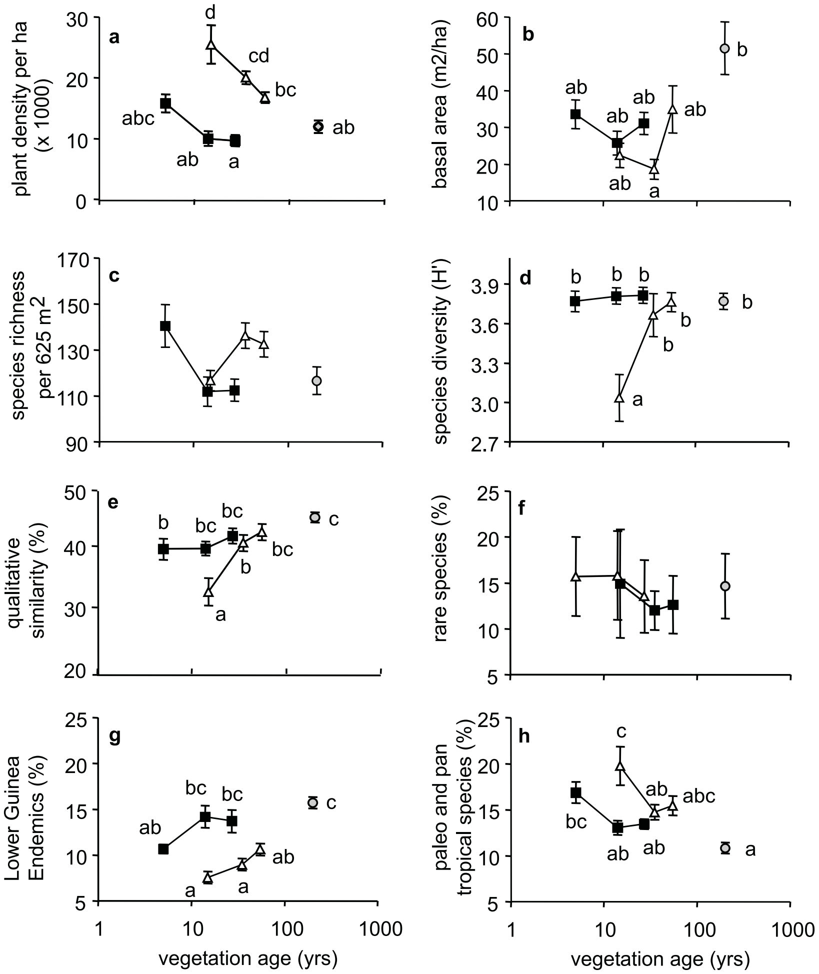

Figure 1 Recovery of different vegetation characteristics after selective logging (filled squares) and shifting cultivation (open triangles) as compared to old growth forest (shaded circles). Values represent means ± standard errors. Means with the same letter are not significantly different (Tukey test after ANOVA, $P < 0.05$).

Recovery of rare and endemic species

The proportion rare species (<10% plots) ranged from 6 to 14% and showed high variation within land use categories. Per growth form and for all species, the proportion of rare and common species (≥ 60% plots) did not differ significantly between old growth forest and disturbed sites (*Figure 1f; Table 4*). The level of endemism was strongly influenced by land use (*Table 4*).

The proportion of species endemic to Lower Guinea (Nigeria–Gabon) increased with vegetation age ($F_{6,61} = 13.81$, $P < 0.001$; *Figure 1g*). The proportion of species with large ranges decreased with vegetation age (Paleo and pan tropical; $F_{6,61} = 9.01$, $P < 0.001$; *Figure 1h*). The geographic range composition of logging sites was not significantly different from old growth forests, except for Paleo–pan tropical species and Lower Guinea endemics in 5-year old sites. Shifting cultivation sites recovered much slower and attained old growth values in 30–40 years for the Paleo–pan tropical species. Even after 50–60 years, the proportion of Lower Guinea endemics was still significantly lower in shifting cultivation sites compared to old growth forest.

Discussion

Vegetation recovery

The results show that most forest characteristics of rain forest in Cameroon recovered from selective logging and shifting cultivation. After 27 years logged sites strongly resembled old growth forest sites. In shifting cultivation sites, recovery was generally slower but after 50–60 years sites attained old growth values for most forest characteristics. However, even after 50–60 years the proportion of endemic species was still significantly lower in shifting cultivation sites compared to old growth forests. Changes in species composition, species richness and species diversity suggest that the mechanism of vegetation recovery is different in logging gaps and shifting cultivation areas (*Figure 1*). Species richness in logging gaps was initially high, but decreased with vegetation age and was similar to old growth forests after 14 years. Logging sites were also floristically similar to old growth forests after 14 years. This indicates that regeneration in logging sites was largely made up of species of the surrounding forest pool and the observed early reduction in species number appears to be at the cost of invading pioneer species. In shifting cultivation areas, pioneer species appear to dominate succession much longer. Species richness in these sites was initially similar to that of old growth forests, but floristically they were very different. With time, species diversity and floristic similarity increased and old growth values were attained after 30–40 and 50–60 years, respectively.

Logging and shifting cultivation practices probably influence regeneration differently as a result of differences in use intensity, rate of recurrence and species selectivity of the disturbance (e.g. removal of few large individuals of selected tree species or removal of all plants; Brown & Lugo 1990). In logging gaps, mass destruction of dominant vegetation cover occurs but generally many seedlings and saplings survive the crown fall (Whitmore 1991). Furthermore, resprouting is common among forest species and contributes considerably to the filling of canopy gaps (Uhl *et al.* 1981; Bazaz 1991; Parren & Bongers 2001). As a consequence, regeneration in most logging sites was formed by individuals that were already present before disturbance. In shifting cultivation sites, vegetation removal, burning, soil disturbance and weeding effectively eliminate possibilities for advance regeneration and resprouting and cause a depletion of the original forest seed bank (Uhl *et al.* 1981, 1988; Wijdeven & Kuzee 2000). Wijdeven & Kuzee (2000) found forest recovery in pastures to be strongly limited by the availability of seeds. The species that are successful in reaching open pasture sites and capable of avoiding seed and seedling predation were generally pioneer species. Although pastures are generally more intensively disturbed, the same mechanism seems to apply to shifting cultivation sites.

Compared to other tropical forests, recovery of basal area, plant densities and species composition was relatively fast in Cameroon. Basal area and plant density recovered in 5 years in logged areas and in 50–60 years in shifting cultivation sites. In Uganda, structural recovery following selective logging took more than 50 years (Plumptre 1996), while areas used for shifting cultivation in the Amazon region were estimated to need 200 years (Saldarriaga *et al.* 1988). We found that floristic recovery took 14 years in logged sites and 50–60 years in shifting cultivation sites. Floristic recovery in other regions ranged from 40 to 200 years (Kappelle *et al.* 1995; Kurpick *et al.* 1997; Aide *et al.* 2000) and is likely to be strongly influenced by the landscape context (Liu & Ashton 1999). Fast recovery of especially floristic composition after disturbance indicates that the old growth forests in this study contain a large set of species capable of colonising disturbed sites. As shifting cultivation sites are larger and much more intensively used than natural gaps, the species capable of colonising such sites are likely to be out competed in relatively stable forests with gap-phase dynamics as the main disturbance regime. Therefore, our results suggest that the history of the current old growth forests may have included large-scale disturbances. To explain the poor regeneration in canopy gaps of the currently dominating species *Lophira alata* and *Sacoglottis gabonensis* (Baill.) Urb. (Humeriaceae), Letouzey (1968) suggested that forests in large parts of the coastal zone of Cameroon have been cleared in the past for agriculture. An analysis of the complete old growth forest tree species composition in relation to recruitment preference also concludes that the forests in our study area were once subject to large-scale disturbances (*chapter 2*). Long-term higher dynamics therefore appear to increase the speed and rate of recovery after disturbance.

Recovery of conservation values

The main focus of this study was the long-term effect of land use on botanical conservation values of tropical forests. Species diversity, rarity and endemism, naturalness and exposure to threats are generally accepted criteria for the assessment of conservation values (de Groot 1992; Hawthorne 1996; Howard *et al.* 2000; Myers *et al.* 2000). It should be noted that a clear preference for undisturbed ecosystems is embedded in these criteria. However, the future of tropical biodiversity conservation may largely depend on the management of disturbed areas (Brown & Lugo 1990). Too much focus on present-day values of species diversity, rarity and endemism of highly dynamic disturbed forests may overlook the potential of restoration through secondary succession.

In our survey, species diversity recovered quickly after disturbance. We found that after 5 years species diversity was restored in logged sites and after 30–40 years in shifting cultivation sites. This is comparable to the results for logged sites in Borneo (Cannon *et al.* 1998) and shifting cultivation sites in Bolivia (Peña-Claros 2001). Species richness tended to increase following disturbance, most likely due to an influx of secondary species. For interpretation of the conservation value of secondary forests, species diversity appears to be a more robust characteristic than species richness.

We found that many species in our survey occurred infrequently in the plots; 63% of the species occurred in less than 10% of the plots (rare species). Woody climbers and herbs had relatively many of such rare species, while trees had few. The proportion of rare species was highly variable between land use/age categories and no general pattern was found. Decreasing the cut-off level for rare species to 5% or increasing it to 20% of the plots did not influence this outcome. Individual rare species have a higher risk of local extinction under unfavorable conditions, as source populations are few and generally far apart (Rosenzweig 1995). Therefore, the level of rarity is of interest to biodiversity conservation. However, in the present survey, disturbed and undisturbed sites harbored sets of rare species and the conditions that would eventually lead to their extinction seem to vary. Thus, we conclude that the rarity criterion is difficult to interpret in terms of recovery of conservation values for the tropical secondary forest we studied.

Species endemic to Lower Guinea recovered relatively quickly in logging sites. After only 14 years the proportion of endemic species was comparable to that in old growth forest. Endemics did not recover in shifting cultivation areas in the 60 year covered in our study (*Figure 1g*). The proportion of species with large distribution ranges was initially higher in disturbed sites and recovery took respectively 14 and 30–40 years for logging and shifting cultivation sites (*Figure 1h*). This matches the observation of Aide *et al.* (2000) that dominant species colonising abandoned pastures in Puerto Rico were species with large geographical and altitude ranges.

Possible explanations for the slow recovery of endemics on shifting cultivation fields are (1) poor intrinsic dispersal ability, (2) low abundance of propagule sources, and (3) decline of pollination and dispersal vectors. No comprehensive studies are available on dispersal ability and pollination and dispersal vectors of African rain forest species. Poorter *et al.* (2001) examined growth form, shade tolerance, and morphological traits, such as fruit type, seed length and dispersal syndrome, of the rare and endemic species of West Africa. They found that epiphytes and shrubs had smaller distribution ranges than herbs, trees and lianas. Likewise, our results show that the proportion of endemic species was highest in shrubs and lowest in herbs and non-woody climbers (*Table 3*). Poorter *et al.* (2001) found no clear relations between distribution range and morphological traits. This suggests that wide-ranging species and narrow endemics have in general similar functional responses to the environment. The spatial distribution and local abundance of propagule sources could alternatively explain the poor recovery of endemic species in shifting cultivation sites. However, we found that local rarity (expressed as relative frequency) was not significantly associated with geographic distribution range. As endemic and non-endemic species have similar relative frequencies, the availability of propagule sources does not appear to explain their poor recovery in shifting cultivation fields. Finally, pollination and dispersal vectors may be negatively influenced by disturbance. The main seed vectors for open areas are birds and bats (Uhl *et al.* 1981). These animals are capable of dispersing the small, lightweight seeds of pioneer species but not the generally larger, heavier seeds of mature forest species (Nepstad *et al.* 1996; Wijdeven & Kuzee 2000). Moreover, most seeds are dispersed close to the forest edge (Wijdeven & Kuzee 2000) and under remnant forest trees (Guevara *et al.* 1986). Most Lower Guinea endemics are mature forest species that probably rely on larger mammals for long-range seed dispersal. In southern Cameroon, hunting is widespread and especially intensive in shifting cultivation areas (van Dijk 1999). By suppressing populations of larger vertebrates, timber exploitation, forest clearance and hunting affect dispersal of large seeded mature forest plant species (Dirzo & Miranda 1991; Maury-Lechon 1991; Bennett & Robinson 2000; Putz *et al.* 2000). Whether this explains the prolonged recovery of endemic species in shifting cultivation sites is, however, yet unclear.

Conclusions

We found that level of endemism, species composition and plant density are most sensitive to shifting cultivation and selective logging. The best indicator for recovery of conservation value in our study was the level of endemism. From a biodiversity conservation standpoint, selective logging seems a better land use option than shifting cultivation. We do, however, acknowledge that sustainable forest use has socio-economic as well as biological components. Secondary forests still foster a wide range of forest plant and animal species (e.g. Lawton *et al*. 1998; Bennett & Robinson 2000; Putz *et al*. 2000). Despite the low level of endemism in especially young shifting cultivation sites, recovery of all other old growth forest characteristics was relatively fast. Therefore, secondary forests in Central Africa can contribute to biodiversity conservation, e.g. as buffer zones around forest reserves.

Acknowledgements

This study was carried out in the framework of the Tropenbos-Cameroon Programme (TCP). All TCP staff is thanked for their logistic support, especially Dieudonne Ndoum, Benjamin Mva, Jacques Ntolo, Etikeke Mbamba, Catherine Dikao and Olivier Mimbila. For assistance with plant identification, we like to thank G. Achoundong, J.P. Ghogue, A. Koufany, P. Mezili and J.M. Onana at the National Herbarium of Cameroon (IRAD), and F.J. Breteler, J.J. Bos, C. Jongkind, A.J.M. Leeuwenberg, R.H.M.J. Lemmens, L.J.G. van der Maesen, J.J. Wieringa, J.J.F.E. de Wilde, and M.S.M. Sosef at the Nationaal Herbarium Nederland – Wageningen University Branch. We thank Fulco Ludwig, Fred de Boer and two anonymous reviewers for critical comments on the manuscript. This study was partly funded by the European Commission (DG VIII).

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Chapter 4

Effects of local and regional processes on plant community structure of Central African rain forest

Barend S. van Gemerden & Han Olff

Abstract

The role of local (competition, predation, disease) and regional processes (dispersal, colonisation) in the maintenance of the typical high plant diversity in tropical rain forests is much debated. The aim of this study is to identify the effects of local and regional processes on community structure of lowland rain forest in Cameroon on the basis of a new set of community-level diagnostic criteria. We examined vegetation development in selective logging gaps (5-27 years), shifting cultivation fields (10-60 years) and old growth forest. Plots were distributed over two distinctly different landscapes (one dominated by forests and one dominated by agricultural fields), which enabled discrimination between local and regional effects. We found that overall species composition mainly reflected geographical locality and recent land use history while gap size, soil chemical properties and texture were not important. Species turnover during succession in logging gaps was most pronounced during the first 14 years of succession for large trees, small trees and shrubs, and to lesser extent climbers. Species composition of herbs took at least 27 years to stabilize. In same-aged gaps, the largest differences between within-mosaic and between-mosaic similarity was found in large trees, and to a lesser extent in small trees and shrubs. Climbers and terrestrial herbs were much less affected by regional setting. Landscape setting, land use history, and successional age influenced growth form composition. Herbs were especially abundant early in succession while abundance of trees increased with age. Similarity in species composition of tree recruits and nearby adults increased with vegetation age and was much higher in logging gaps compared to agricultural fields. We conclude that the relative importance of local and regional processes varied with vegetation age and between growth forms. Local processes were especially important early in succession. Regional processes governed species composition of large trees, climbers and to a lesser extent small trees and shrubs. Local processes structured community composition of herbs. Because of the differences between species groups, successful conservation and restoration management requires insight in the relative importance of local and regional processes for species of special concern (e.g. endemics). The method described in this paper can contribute to gaining such insights.

Introduction

Tropical rain forests are among the most species-rich ecosystems in the World (Wilson 1995) and the processes accounting for their high diversity is a much-debated issue in ecological literature (Ricklefs 1977; Hubbell & Foster 1986; Ricklefs & Schluter 1993; Huston 1994; Rosenzweig 1995; Chesson 2000; Hubbell 2001; Sheil & Burslem 2003). Classical studies typically interpret the observed patterns of plant diversity as the result of highly adapted species distributed over heterogeneous landscapes (Ricklefs 1977; Denslow 1980; Ewel 1980; Brakow 1985; Whitmore 1989). Evolutionary trade-offs and constraints cause that each species is expected to be a superior competitor in a specific environment. Therefore, the long-term coexistence of species is only assured if species occupy different niches (Tilman 1982). Gap-phase dynamics are hypothesized to increase landscape heterogeneity (especially light environments) and so provide conditions favorable for the coexistence of large numbers of species in tropical rain forests (Orians 1982; Denslow 1987; Sheil 1999; Sheil & Burslem 2003). Likewise, it has been proposed that at high local densities species' survival is negatively affected as the result of intensified predation and pathogen attack (Janzen 1970; Wright 2002; Lambers *et al.* 2002). Increased mortality in locally successful species leaves space for rare species and therefore density dependent mortality augments local diversity. These more classical views all emphasize the role of local processes, like competition, predation and pathogen attack, in structuring community composition of tropical rain forest plant communities.

Many studies have shown that plant species display functional differences (e.g. Denslow 1987; Grime et al. 1988; Sollins 1998, Brokaw & Busing 2000; Poorter & Arets 2003). However, others have questioned the central role of these local processes in structuring communities, especially for tropical forests (Hubbell & Foster 1986; Hubbell *et al.* 1999). Evidence is accumulating that in some cases regional processes govern local communities, and not vice versa (Ricklefs 1987; Ricklefs & Schluter 1993; Caley & Schluter 1997; Duncan *et al.* 1998; Loreau 2000). Hubbell *et al.* (1999) suggest that gap dynamics do not explain patterns of tree species diversity in Panama and argue that dispersal limitation from a regional species pool to local communities is the driving force for species coexistence. Indeed, model studies have shown that assemblages of functionally equivalent species governed solely by stochastic extinction and dispersal can result in diversity patterns observed in tropical rain forests (Bell 2001; Hubbell 2001). At least for tree species, chance processes in reaching recruitment sites (i.e. gaps) may overrule the effects of niche differentiation. The majority of tropical rain forest tree species tend to have similar life history strategies and local processes may be more important for other groups of plants (Schnitzer & Carson 2000, 2001). For instance, Schnitzer & Carson (2001) found that gaps promote liana richness, both on a per area and per stem basis, in a rain forest in Panama. At present, few studies have examined the effects of local and regional processes on plant community composition for a wider range of species groups than just trees.

It seems likely that both local processes (i.e. competition, predation, disease) and regional processes (i.e. dispersal, colonization) interact in structuring plant community composition of tropical rain forests (Ashton 1998; Brokaw & Busing 2000). However, the relative role of these processes may vary strongly between different regions, and between different species groups. Insight in the relative importance of local and regional processes is important for conservation management as the processes affect the likelihood of species extinction differently. If local processes structure local communities, conservation management should focus on habitat quality. However, if neutral processes and colonization are the main structuring mechanisms, habitat fragmentation is likely to be a greater threat to biodiversity conservation.

An elegant but expensive and time-consuming approach to study the relative importance of local and regional processes is to set up field experiments and monitor recruitment in relation to environment and species composition at larger scales. At present, few studies at scales (area and time) relevant to community composition have been conducted (Laurance *et al.* 1997, 2002; Hubbell *et al.* 1999; Condit *et al.* 2000). Moreover, existing studies focused on tree species, and none of them were located in the African rain forest biome. A different approach to study local and regional effects on community composition is to analyse structurally intact rain forest communities. Hubbell (2001) analysed dominance-diversity distributions of an old growth rain forest in Panama and interprets the overrepresentation of rare species in the community as an indication that regional processes dominate local structuring processes. However, presently no analytical tools are available to unambiguously distinguish communities governed by local processes from communities governed by regional processes.

Finally, examination of succession following forest perturbations can potentially aid at identifying the relative role of local and regional processes in structuring rain forest plant communities. Light, moisture and nutrients are the main limiting factors for plant growth in tropical rain forest environments. The availability of these resources changes abruptly after forest disturbance and is gradually restored in forest regeneration. Sampling a community in different successional stages and in different landscape mosaics (each differing in the composition of the regional species pool) may be a relatively easy method to study local and regional effects on community composition. If regional processes govern local communities, community composition is expected to reflect species composition in the surrounding landscape. However if local processes are more important, specific sets of highly adapted species are expected to dominate successional stages regardless of the landscape setting. Characterization of successional plots in terms of controlling mechanisms requires the identification of community-level diagnostic criteria for local and regional processes.

Table 1 *Diagnostic criteria of dominance of adaptive (local) and neutral (regional) processes in secondary succession*

perspective	*local / adaptive*	*regional / neutral*
key processes	*competition, predation and pathogen attack*	*dispersal and colonisation*
community characteristics		
1. community composition during succession	disturbance history-related; single and clear pathway to (constant) old growth forest composition	landscape mosaic-related; different (and diffuse) pathways to (variable) old growth forest composition
2. species similarity between sub samples of same age	high; few species sensitive to landscape mosaic	low; many species sensitive to landscape mosaic
3. species rank – abundance distributions	many common and few rare species (steep curve); small effect landscape mosaic	few common and many rare species (flat curve); large effect landscape mosaic
4. functional diversity during succession	low evenness functional types; small effect mosaic; rank functional types shifts during succession	high evenness functional types; large effect mosaic; rank functional types constant during succession
5. similarity between recruits and nearby adults	low; increasing with succession (long-term)	high; constant with succession

In *table 1* we present a list of suggested community-level diagnostic criteria to evaluate the role of local and regional process in structuring community composition. If local processes like competition for limited resources, predation and pathogen attack, govern local communities, each successional stage will be dominated by a specific set of highly adapted species. Therefore, sub samples with the same disturbance history will be floristically very similar, regardless of the landscape in which the sites are located. As each successional stage has its own set of characteristic species, succession will be highly predictable and leading to a more or less constant old growth forest composition. Moreover, recruits will be of different species than adults as recruitment conditions change during succession. Likewise, adaptation to local conditions will result in a shift of life-history traits during succession with pioneers gradually giving way to shade-bearers. If regional processes like dispersal limitation and colonization structure community composition, species composition during succession will largely reflect that of the surrounding area and will not necessarily be similar between sub samples with the same land use history. Moreover, because of high relative density of propagules, locally established adults will likely dominate recruitment. Regional processes have little influence on distribution of functional types, as both mortality and recruitment are neutral processes. As a result functional type distribution will show no trend with succession in communities governed by regional processes.

In this study we examined successional vegetation, including data on all terrestrial vascular plants, of old growth forest, 5-27 year old logging gaps, and 10-60 year old agricultural fields in a lowland rain forest area in Cameroon. Plots were distributed over two distinctly different landscape mosaics (forest mosaic and shifting cultivation mosaic) that differ in the relative abundance at larger scales of forest and secondary species. Vegetation composition during succession and in different landscape mosaics was analysed using the criteria described in *Table 1* to evaluate the relative importance of local and regional processes in structuring community composition in this Central African rain forest area. We expect that local processes are especially important if recruitment conditions are very dissimilar to those in a closed forest, i.e. the first stages of succession following high intensity disturbances. For the majority of plants older successional stages are expected to be less demanding and therefore recruitment limitation is likely to be more important for community composition. Moreover, we expect that the generally shorter-lived non-woody species are more sensitive to local conditions, while trees species composition is likely to be more related to the landscape mosaic.

Methods

Research area

The study was conducted in the Bipindi - Akom II – Lolodorf region, south Cameroon (3° N, 10° E). The climate is humid tropical with two distinct wet seasons (March – May, August – November) and two relatively dry periods. The average annual rainfall is 2000 mm (Waterloo *et al.* 2000). Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry 1986). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). Topography varies from flat erosional plains to rolling uplands with isolated hills. Altitude varies from 50 – 600 m above sea level. Soils range from moderately acid sandy clay loam to highly clayey and strongly acid and classify as Haplic Acrisols, and Plinthic and Xanthic Ferrasols (van Gemerden & Hazeu 1999). Evergreen forests of the Atlantic Biafrian type largely cover the area (Letouzey 1985). These forests are characteristically rich in Leguminosae – Caesalpinioideae and have a closed canopy at 30 – 40 m with emergents often surpassing 55 m.

The area is sparsely populated (8.6 persons km^{-2}) and population increase is marginal (+0.4%; Lescuyer *et al.* 1999). Most people practice shifting cultivation, a form of agriculture in which forest patches of 0.5 – 1.5 ha are cleared, burned and interplanted with a variety of crops. Depending on soil productivity, the tending and harvesting gradually stops after two to three years and the land is left fallow for at least 7 – 15 years (Nounamo & Yemefack 2002). Shifting cultivation is confined to the direct surrounding of villages and along the main access roads. The vegetation mosaic in shifting cultivation areas comprises generally 20 – 40% actual and recently abandoned fields and 20% secondary forest (van Gemerden & Hazeu 1999). Large parts of the remaining forests in these areas are also subject to selective use by the local population and logging companies.

The main economic activity in the area is timber exploitation. Most of the area has been selectively logged, and some parts twice, by international logging companies. The logging involves the use of heavy machinery for road construction and log extraction. Present logging activities focus on *Lophira alata* Banks ex Gaertn.f. (Ochnaceae; commercial name Azobé; 60% of the extracted volume), *Erythrophleum ivorense* A.Chev. (Leg.-Caesalpinioideae; Tali), and *Pterocarpus soyauxii* Taub. (Leg.-Papilionideae; Padouk). The logging intensity is low (10 m^3 ha^{-1} or 0.7 tree ha^{-1}). The felling and extraction of logs causes physical damage to 5% of the area but locally much higher (25%) disturbance rates have been observed (Jonkers & van Leersum 2000). Individual crown fall gaps caused by commercial logging are between 300 and 900 m2 (Parren & Bongers 2001) but simultaneous felling of clumps of commercially interesting trees often create much larger gaps (B.S. van Gemerden, personal observation).

Survey plots

We sampled vegetation in areas that differed in recent land use history and landscape mosaic (*Table 2*). Vegetation was sampled by plots of 25 x 25 m in old growth forest and in agricultural fields (10-20, 30-40 and 50-60 years since tending of fields had stopped). In logging gaps (5, 14, and 27 years since logging), most plots were 625 m^2 and a few slightly smaller. The total number of plots was 86 (i.e. 5.1 ha). Plots were distributed over four research sites located in two distinctly different landscape mosaics; *forest mosaic* and *shifting cultivation mosaic*. On landscape level, the vegetation in the forest mosaic was dominated by undisturbed and logged forest while actual fields covered less than five percent of the area. In the shifting cultivation mosaic, actual and recently abandoned fields, and young secondary forest covered respectively 40 and 20% of the area, while fragments of (logged) forests covered less than 40%. Being distinctly poorer in old growth forest, we expect that the total pool of forest species was smaller in the shifting cultivation mosaic compared to the forest mosaic, while the pool of secondary species was much larger. Old growth forest plots were distributed over the four research sites while agricultural fields were sampled in one site. Five-year old logging plots were sampled in two research sites and 14 and 27-year old logging plots were located in two different research sites. All different logging age categories were sampled in both the forest mosaic and the shifting cultivation mosaic. The maximum distance between the four research sites was less than 40 km. However, research sites with the same logging history were only 5-6 km apart.

Table 2 Distribution of vegetation plots by land use history and landscape mosaic

land use	*logging gaps*			*agricultural fields*			*forest*
vegetation age (yrs)	5	14	27	10-20	30-40	50-60	≥200
# plots[a]							
- shift. cult. mosaic	6	4	9	7	5	11	7
- forest mosaic	4	9	11	-	-	-	13
total survey area (ha)	0.63	0.72	1.08	0.44	0.31	0.69	1.25

[a] *Plots were distributed over four research sites. Shifting cultivation mosaic: Ebom area (3°03'N, 10°43'E, 400 - 450 m) and Ebimimbang area (3°02'N, 10°26'E, 50 - 180 m), forest mosaic: Minwo area (3°05'N, 10°45'E, 480 - 600 m) and Bibindi area (3°00'N, 10°24'E, altitude 120 - 300 m). Logging plots of five years were located in Ebom and Minwo areas, logging plots of 14 and 27 years were located in Ebimimbang and Bibindi areas. Shifting cultivation fields were located in Ebom area. Old growth forest was sampled in all research sites.*

Land use history was determined with the help of local informants, often the proprietors of the sites. Information on logging activities in the area was also provided by the state forestry service ONADEF (Hazeu *et al.* 2000). Plots in logging gaps were positioned in the estimated centre of the tree crown fall. Most exploited trees are *Lophira alata*, a species with extremely hard wood, and branches and bole were, even after 27 years, clearly visible. Plots in fallow vegetation were positioned well away from sudden changes in vegetation structure or other anomalies. Within plot variation in topography, vegetation and drainage characteristics was minimal.

Survey methods

All individuals of terrestrial vascular plants (all growth forms, including herbaceous species, but excluding ferns and fern-allies) were recorded per plot. Only woody plants with heights less than 50 cm were not sampled because of foreseen identification problems. Species and size class of each individual was recorded. Within each growth form category, individuals were assigned to the following size classes: total height (h) < 50 cm (non-woody species only), h ≥ 50 cm and diameter at breast height (dbh) < 2 cm, dbh 2 – 4.9, 5 – 9.9, 10 – 19.9, etc. We considered all apparent solitary ramets as individuals. Each tussock of herbs was counted as an individual. Diameters of stems of multi-stemmed shrubs were summed.

In the field, the most common and readily identifiable species were directly named and plant material was collected of all other species. A total of nearly 11,000 vouchers were collected in the survey. The vouchers were processed at the Kribi Herbarium (Tropenbos-Cameroon Herbarium) and sent to the National Herbarium of Cameroon in Yaounde and the Nationaal Herbarium Nederland (Wageningen University Branch) for identification by specialists. Unidentified species were categorised as morphospecies. Nomenclature follows Lebrun *et al.* (1991-1997).

Species' growth form was identified on the basis of taxonomic literature, mainly Cable & Cheek (1998), Aubréville & Leroy (1963-2001, 1961-1992), and Keay & Hepper (1954-1972), and own field observations. Species were classified as large trees (single-stemmed, maximum height ≥ 15 m), small trees (single-stemmed, maximum height 3 – 15 m), shrubs (multi-stemmed or <3 m tall), woody climbers (including rattans), non-woody climbers, herbs (terrestrial), hemi-epiphytes, palms or stranglers.

In each plot we collected data on a variety of environmental variables. Soils in each of the plots were augered up to a maximum depth of 120 cm. In general, three samples were taken in the approximate centre of each plot while the minimum distance to the nearest tree (dbh ≥ 10 cm), and between samples, was at least 1 m. We described the horizons of deepest profile and collected material of the topsoil (0 – 10 cm, mineral soil) for chemical analyses. Chemical analyses included total N, total P, CEC Mg, Na, Ca, K, ph KCl, and organic matter (Houba *et al.* 1995). All analyses were conducted at the laboratory of the Sub-department of Nature Conservation of the Wageningen University. We estimated the size of the original logging gap by measuring the distance from gap edge to gap edge perpendicular to the axis from stump to crown fall at 10 m intervals. The gap edge was defined by the boundary of trees (dbh ≥ 30 cm) that showed signs of damage that could be attributed to the logging event.

Data analysis

To identify the relative position of each of the 86 plots in terms of species composition along major underlying gradients, we performed an indirect gradient analysis (detrended correspondence analysis, DCA; Jongman *et al.* 1987), using the log transformed relative abundance per species per plot. In this type of analysis, the position of each sample point in the ordination is based on its species composition, while environmental variables are used to interpret the nature of the underlying gradients. Environmental variables included in the analyses were land use type, slope, exposition, altitude, successional age of vegetation, gap size, soil depth, depth A-horizon, characteristics topsoil (texture and chemical properties). As plot sizes in logging plots were not constant, plot size was also included as one of the variables in the analysis. To achieve normal distributions we log transformed the values of gap size, slope, total N, Mg, and Ca. Following the DCA we performed a direct gradient analysis (CCA) and tested the significance of the environmental variables using a Monte Carlo permutation analysis (n = 999). All analyses were performed with CANOCO 4 (Ter Braak & Smilaur 1998).

Per growth form, we examined the relative changes in species composition during succession by comparing the composition of different-aged plots to five-year old logging gaps. We used the Sörenson index to calculate the qualitative similarity in species composition based on species presence/absence per plot. This index expresses the proportion of all observed species two plots have in common (Magurran 1988). Five-year old logging plots were individually compared to all other logging and old growth forest plots in the same landscape mosaic. Mean plot similarities per vegetation age class were used in the analyses.

To analyse the effects of regional setting on species composition, we calculated the qualitative Sörenson similarity of same-aged plots in different landscapes. Of each plot, similarity in species composition was calculated for same-aged plots in (1) the same landscape mosaic (i.e. plots in forest mosaic compared to plots in forest mosaic, and plots in shifting cultivation mosaic compared to plots in shifting cultivation mosaic), and (2) the contrasting landscape mosaics (i.e. plots in forest mosaic and shifting cultivation mosaic compared). Mean similarity of each plot with the other plots per landscape contrast was used in the analyses. In addition, we also performed a direct gradient analysis (CCA, down weighing of rare species) followed by Monte-Carlo permutations (n = 999) to examine the distribution of species within same-aged gaps over the mosaic gradient. Similarly, we examined the preference of species within sets of same-aged gaps for either forest or landscape mosaics by calculating a modified chi-square (de Lyon & Roelofs 1986).

Species rank - abundance curves were constructed by pooling the individuals of all plots with the same land use history and landscape mosaic. As woody species are generally slower to react to changes than non-woody species, rank-abundance curves were drawn separately for woody species (i.e. large and small trees, shrubs, woody climbers, stranglers and palms) and non-woody species (i.e. terrestrial herbs, herbaceous climbers, hemi-epiphytes). The rank – abundance curves of logging gaps and old growth forests in forest and shifting cultivation mosaics were compared using a Wald-Wolfowitz (Runs) test. This test examines whether two data samples are compatible with being random samples of the same, unknown distribution.

Growth forms were used as proxy variables for functional types as species' ecology of most plant species occurring in African rain forests are poorly documented at present. Pielou's evenness index, expressing the distribution of individuals in a plot over the growth forms (Magurran 1988), was calculated per plot using relative abundance values. Analysis of variance (ANOVA) and Tukey tests ($P < 0.05$) were used to compare evenness and relative abundances of individual growth forms by land use histories and landscape mosaics.

To identify the similarity between recruits and nearby adults of tree species, we calculated the Morista-Horn quantitative similarity (Magurran 1988) between trees with dbh < 5 cm ('recruits') and trees dbh ≥ 5 cm ('adults') per plot. Morista-Horn similarity was based on species' relative abundance per size cohort per plot and was computed using EstimateS (Colwell 1997). Analyses of variance (ANOVA) and Tukey tests ($P < 0.05$) were used to compare cohort similarity between land use categories and landscape mosaics.

Results

Floristic characteristics

We recorded a total of nearly 75 000 plants in 5.1 ha. Of all individuals, 76% were identified to species levels, and 11% were categorised as morphospecies. Only 1 and 4% remained unidentified at the genus and family level, respectively. Finally, 9 % of the plants were assigned to a field identification that turned out to represent a small number of morphologically similar (botanical) species. Such clusters were treated in the analyses as a single species. In total, 71 203 individuals plants, representing 95% of all individuals were at least morphocategorised and were used in the analyses. The proportion of unidentified plants did not vary significantly among the different land use history categories ($F_{6,79} = 2.18$, $P = 0.054$). In the survey, we found a total of 909 species, belonging to 91 families. Predominant families encountered were Rubiaceae (138 species), Euphorbiaceae (59), Leguminosae-Caesalpinioideae (44), Apocynaceae (41), Annonaceae (40), and Ebenaceae (31). Only two percent of the species (representing 26.5% of the individuals) occurred in more than 75% of the plots. As much as 52.8% of the species occurred in less than 5% of the plots. These species accounted for only 3.4% of the individuals. We identified the growth form of 860 species, representing 94.6% of the species and 99.1% of the individuals. With 408 species trees were by far the most species rich growth from. Of these 149 were categorized as large tree species and 133 small tree species. Not sufficient information was available to classify the remaining 126 trees as either large or small. Trees accounted for 35.4% of the individuals recorded. A total of 162 shrub species and 160 woody climber species were recorded, representing respectively, 17.8 and 11.8% of the individuals. Herbs accounted for 32.8% of the individuals but only for 8.7% of the species.

The number of individuals per plot varied between land use history categories ($F_{6,79} = 20.22$, $P < 0.001$). High plant densities were found in 10 – 40 years old agricultural fields, while plant densities were low in old growth forest and 5 – 14 year old logging gaps. Average species richness per plot varied from 99 in 27-year old logging gaps to 142 in 5-year old logging gaps ($F_{6,79} = 6.40$, $P < 0.001$). Because plant density and plot sizes varied among land use categories, we normalized species richness per plot by dividing by number of plants (Hubbell *et al.* 1999). Normalized species richness per stem also varied between land use categories and was highest in old growth forest and 5 – 27-year old logging plots, and lowest in 10-20 year old agricultural fields ($F_{6,79} = 12.59$, $P < 0.001$).

Community composition during succession

Based on the relative abundance of species, the indirect gradient analysis (DCA) grouped the plots by research site. One plot in a 27-year old logging gap was considered an outlier on the basis of aberrant species composition and extreme soil characteristics and was omitted from the analyses. The variable research site accounted for 10.7% of the variation in species composition (CCA, Monte Carlo permutation, $P < 0.01$). After removing the site effect (research sites used as covariables), the plots were grouped by land use history categories. The first axis represented old growth to 10-20 year old shifting cultivation, and the second axis five-year-old logging gaps to old growth forest. The variation in species composition between plots was significantly correlated with land use history (monte carlo permutation, $P < 0.01$). Together, research site and land use history account for 19.9% of the variation in species composition. In addition, topographical position and slope have a small but significant effect. Soil chemical properties and texture, gap size and plots size were not important in explaining the found variation.

Changes in species composition in logging plots were most rapid during the initial stages of succession (*Figure 1*). However, rate of change differed strongly between growth forms and landscape mosaics. For all growth forms together, only species composition in five-year logging plots was significantly different from the other age classes ($F_{7,32} = 17.41$, $P < 0.001$). Small trees ($F_{7,32} = 33.31$, $P < 0.001$) followed this trend, as well as large trees ($F_{7,32} = 3.82$, $P < 0.001$), shrubs in ($F_{7,32} = 19.08$, $P < 0.001$), and climbers ($F_{7,32} = 5.33$, $P < 0.001$) in forest mosaics. In forest mosaics, herb species composition continued to change up to at least 27 after gap creation while in shifting cultivation mosaics it stabilized after 14 years ($F_{7,32} = 23.84$, $P < 0.001$). Species composition of climbers and large trees in a shifting cultivation mosaic showed no trend with vegetation age.

Species similarity between sub samples

Landscape mosaic influenced species composition in same-aged logging gaps (*Figure 2*). As was expected, plots had higher similarity in species composition with plots in its own landscape mosaic compared to plots in the other landscape mosaic. For all growth forms together, within-mosaic species similarity was fairly constant in the different age classes with the largest difference observed between 14-year old logging gaps and old growth forest ($F_{7,118} = 27.25$, $P < 0.001$). However, trends differed between growth forms. Within-mosaic similarity of large trees ($F_{7,118} = 26.17$, $P < 0.001$) and climbers ($F_{7,118} = 11.06$, $P < 0.001$) was significantly higher in old growth forest compared to all logging ages.

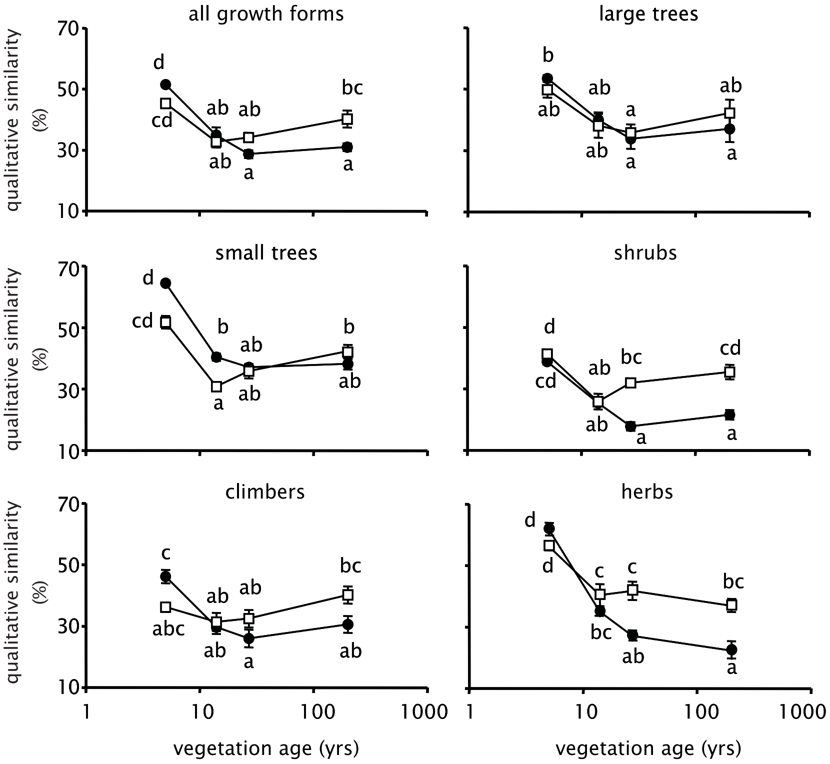

Figure 1 Relative change in species composition during succession in logging plots in forest mosaics (black circles) and shifting cultivation mosaics (open squares). Species composition of different-aged logging gaps as compared to five-year-old logging gaps within same mosaic. Symbols represent mean Sörenson qualitative similarity based on species presence/absence per plot ± standard errors. Means with the same letter are not significantly different (Tukey test after ANOVA, P < 0.05).

Within-mosaic similarity of shrubs ($F_{7,118} = 13.90$, $P < 0.001$) and herbs ($F_{7,118} = 3.70$, $P < 0.001$) showed no trend with vegetation age while small trees had significant lower similarity in 14-year old logging gaps compared to the other age classes. Between-mosaic similarity in species composition for all growth forms combined was relatively high in five-year old logging gaps, decreased at intermediate ages and increased again in old growth. Large trees, small trees and shrubs largely followed this trend. Between-mosaic similarity of shrubs was relatively low in logging gaps and increased in old growth forest. Between-mosaic similarity in herbs showed no trend with vegetation age. As a result, the largest discrepancy between within-mosaic and between-mosaic similarity was observed in large trees. Also species composition of shrubs and small trees were significantly different in different landscape mosaics in respectively intermediate and old successional stages. In contrast, within-mosaic and between-mosaic similarity was not significantly in any of the age classes for climbers and herbs.

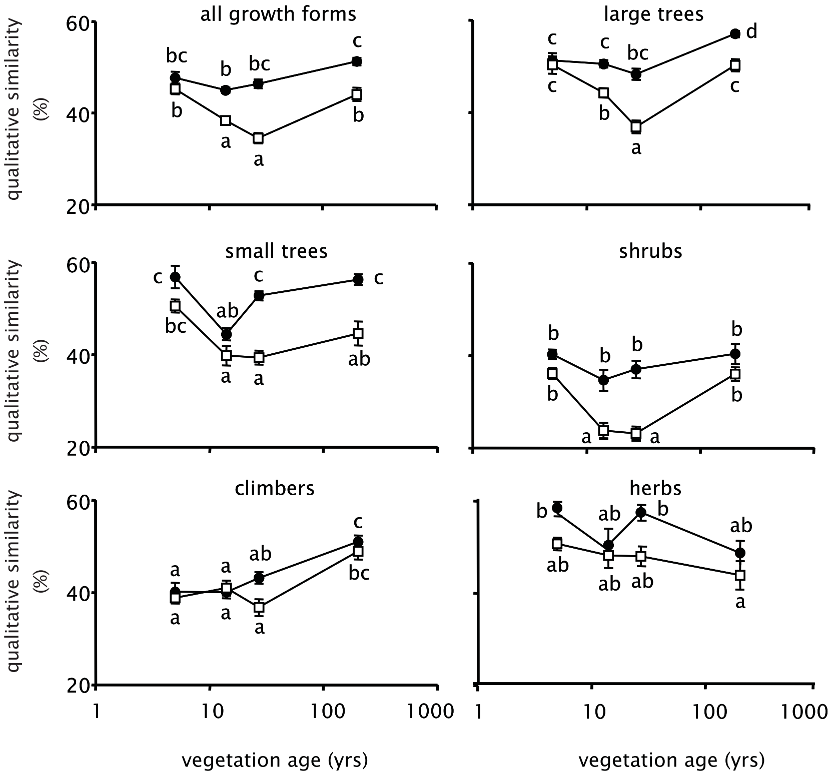

Figure 2 Effects of regional setting on species composition per growth form. Pair-wise comparison of same-aged logging gaps in (1) similar landscape mosaics (black circles), and (2) contrasting landscape mosaics (open squares). See text for details. Symbols represent mean Sörenson qualitative similarity based on species presence/absence per plot ± standard errors. Means with the same letter are not significantly different (Tukey test after ANOVA, $P < 0.05$).

The eigenvalue of the first axis of the CCA of subsets of same-aged gaps (landscape gradient as single explanatory variable), increased with vegetation age from five year old gaps (0.210) to 27 year old logging gaps (0.347) and was again lower in old growth forest plots (0.143; research sites as covariables). The larger eigenvalue of the first axis indicated that older logging gaps needed a longer gradient to accommodate the species-mosaic variation and suggested that more species were sensitive to landscape setting. Landscape mosaic was in all subsets of logging gaps and old growth forest the most important explanatory variable. It was significant for all groups but F-values increased from five-year-old logging plots (1.332, $P < 0.01$), to 14-year-old logging plots (1.951, $P < 0.001$), to 27-year old logging plots (3.553, $P < 0.001$). In old growth forest, landscape mosaic had an intermediate F-value (1.582, $p < 0.001$). The F-values indicated that landscape mosaic is even more important in old logging plots, but not so in old growth forest.

The number of indicative species followed the same general trend. In five-year old gaps 27 species (10.0% of all species in this subset) had a preference for either forest or shifting cultivation mosaic, while 14 and 27 year old gaps had respectively 51 (20.2%) and 76 (27.0%). Old growth forest had 47 indicative species, but as the total number of species encountered in this subset was higher, these represented only 14.2% of the species. Most of the indicative species per subset had a preference for forest-dominated landscapes.

Species rank – abundance distributions

The shape of the species rank - abundance curves of different aged logging gaps, agricultural fields and old growth forest plots were remarkably similar (*Figure 3*). Number of woody species was high compared to non-woody species and overall dominance was lower. The five most abundant woody species accounted for 22.6 – 36.4% of the individuals in the different land use history and landscape categories, while the five most abundant non-woody species accounted for 47.1 – 74.1%.

The rank distributions of both woody and non-woody species between forest mosaics and shifting cultivation mosaics were significantly different for all logging ages (Wald-Wolfowitz test, $P < 0.001$ for all comparisons except non-woody species in 27-year old logging gaps; $P = 0.003$). The curve of woody species in the shifting cultivation mosaics tended to lie above the one of forest mosaics. Differences between the distributions in the two landscape mosaics appeared to be larger for non-woody species, but no trend could be detected.

Growth form composition

The composition of vegetation in terms of growth forms varied between land use and landscape mosaic (*Figure 4*). Evenness of growth form distribution (Pielou's evenness) showed a significant trend with succession in logging plots located in shifting cultivation mosaics ($F_{3,22} = 3.51$, $P < 0.05$); evenness was highest in old growth forest plots and lowest in 5-year old logging gaps. In landscapes dominated by forests (forest mosaics), evenness was not significantly different between age categories. In agricultural fields, evenness of growth form distribution was lowest in relatively young (10-20 year old fields) vegetation and increased with age ($F_{3,26} = 11.66$, $P < 0.001$).

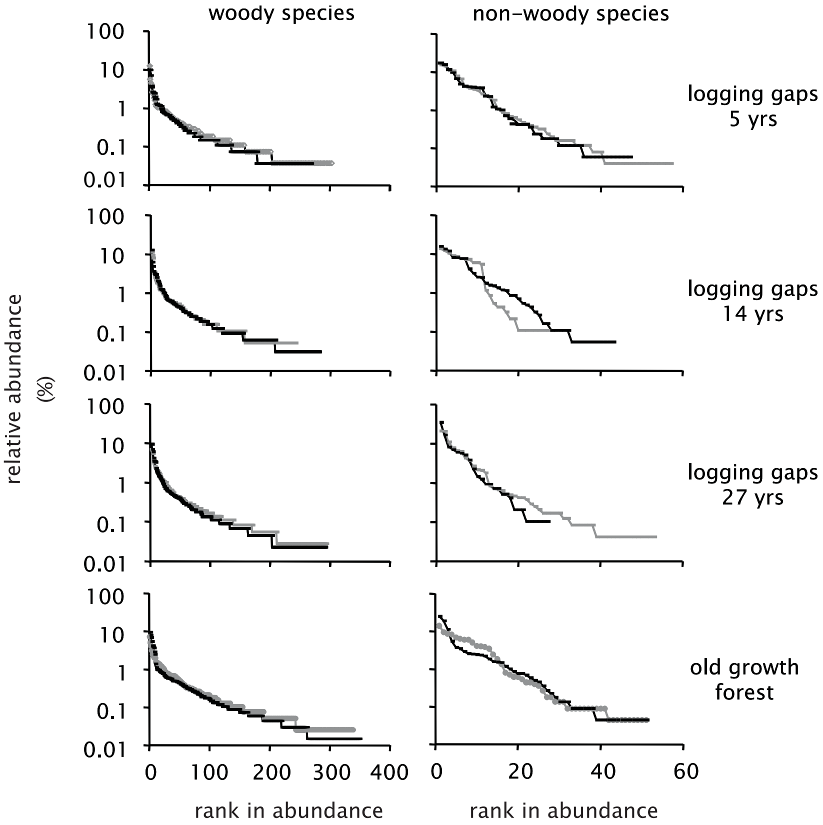

Figure 3 *Species rank in abundance curves for woody and non-woody species for logging gaps and old growth forest in forest mosaics (black) and in shifting cultivation mosaics (grey). Curves are based on plots pooled by land use history and landscape mosaic and are scaled to the maximum number of individuals observed per combination. All curves represent significantly different distributions between landscape mosaics (Wald-Wolfowitz runs test, p << 0.01).*

In each of the given landscape mosaics, relative abundance of most growth forms changed with vegetation age (*Figure 4*). The relative abundance of herbs decreased with succession in logging plots in forest mosaics ($F_{3,33} = 4.78$, $P < 0.01$), in logging plots in shifting cultivation mosaics ($F_{3,22} = 5.47$, $P = 0.01$), and in agricultural fields ($F_{3,26} = 11.58$, *P* < 0.001). The relative abundance of trees (all species) increased with vegetation age in forest mosaics ($F_{3,33}$ = 6.36, *P* = 0.01) and in agricultural fields ($F_{3,26}$ = 15.84, *P* < 0.001). The relative abundance of subset of large trees species increased with vegetation age followed the same trend ($F_{3,33}$ = 3.12, *P* < 0.05, and $F_{3,26}$ = 3.08, *P* < 0.05, respectively). Relative abundance of small trees was constant during succession in logging gaps located in forest mosaics but increased with time in the logging plots in shifting cultivation mosaics ($F_{3,22}$ = 4.55, *P* < 0.05) and in agricultural fields ($F_{3,26}$ = 6.52, *P* < 0.01). In forest mosaics, relative abundance of shrubs was higher in young logging plots and old growth forest ($F_{3,33}$ = 3.20, *P* < 0.05) compared to logging plots of intermediate ages. In agricultural fields, herbaceous climbers were more abundant in older vegetation ($F_{3,26}$ = 4.29, *P* < 0.05).

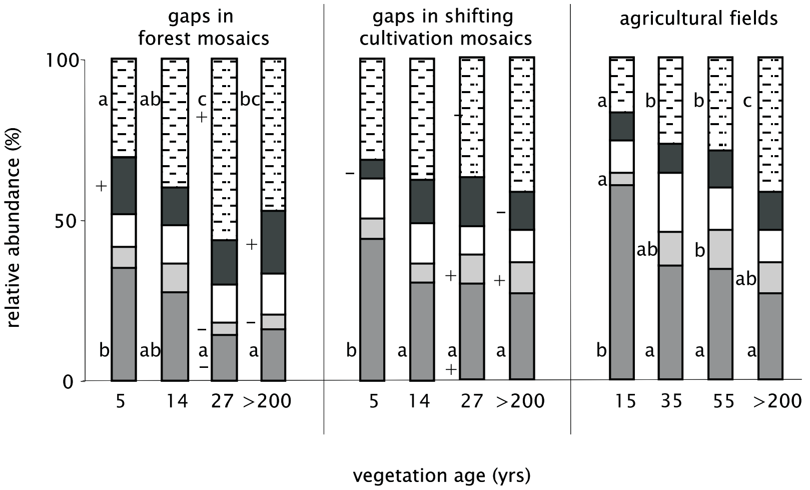

Figure 4 *Relative abundance per growth form during succession in logging gaps in forest mosaics and shifting cultivation mosaics, and in agricultural fields. Growth from classes are terrestrial herbs (dark grey), herbaceous climbers (light grey), woody climbers (white), shrubs (black) and trees (large trees, small trees and trees with unknown maximum height combined; dashed). Means with the same letter are not significantly different between age classes in the same mosaic. Significant higher (+) and lower (-) relative abundance of growth forms between same-aged logging gaps in different mosaics are indicated (Tukey test after ANOVA, P < 0.05).*

Landscape mosaic influenced growth form distribution in logging plots (*Figure 4*). Five-year old logging plots in forest mosaics had significant more shrubs than five-year old logging plots in shifting cultivation mosaics ($F_{1,18}$ = 9.61, *P* < 0.05). In 27-year old gaps, both large trees ($F_{1,18}$ = 16.21, *P* < 0.001) and small trees ($F_{1,18}$ = 8.18, *P* < 0.01) were more abundant in forest mosaics than in shifting cultivation mosaics, while herbs showed the opposite pattern ($F_{1,18} = 26.68$, $P < 0.001$). Interestingly, growth form distribution of old growth forest plots also varied between landscape mosaics for herbaceous climbers ($F_{1,18} = 12.01$, $P < 0.01$) and shrubs ($F_{1,18} = 7.07$, $P < 0.05$). Herbaceous climbers were more abundant in old growth forests that were part of forest mosaics, while shrubs were less abundant.

Species similarity between size cohorts

Quantitative similarity of species composition between size cohorts of trees varied with land use, vegetation age and landscape mosaic ($F_{10,75} = 3.87$, $P < 0.001$; *Figure 5*). Similarity increased strongly with vegetation age in agricultural fields. With vegetation age, between-cohort similarity increased in logging gaps in both forest mosaics and shifting cultivation mosaics to level of at intermediate ages. Old growth forests in landscapes dominated by forests had significantly higher between-cohort similarity than old growth forests found in shifting cultivation mosaics.

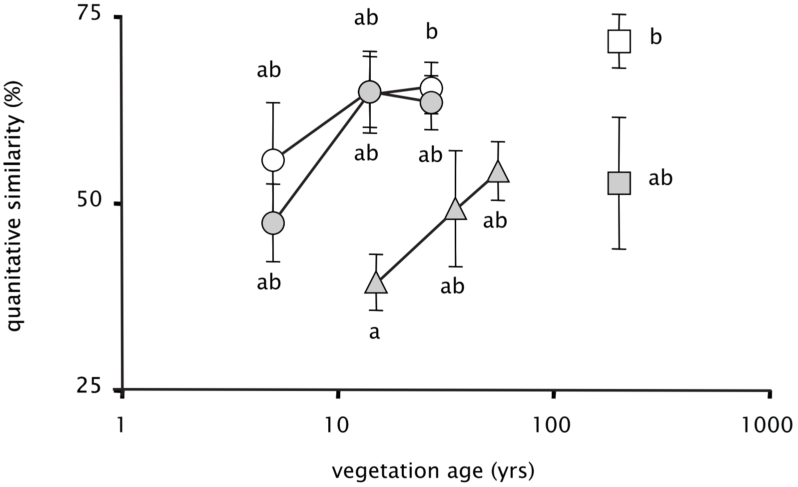

Figure 5 *Quantitative similarity in species composition between size cohorts of trees (dbh < 5 cm and dbh ≥ 5 cm) by land use history and landscape mosaic. Categories used are logging gaps (circles), agricultural fields (triangles), old growth forest (squares), forest mosaics (white symbols) and shifting cultivation mosaics (grey symbols). Symbols represent mean Morista-Horn quantitative similarity based on species relative abundance per plot ± standard errors. Means with the same letter are not significantly different (Tukey test after ANOVA, P < 0.05).*

Discussion

By analyzing the development of secondary vegetation in sites disturbed by selective logging and shifting cultivation, we identified the relative importance of local (i.e. competition, predation, disease) and regional processes (i.e. dispersal, colonization) in a Central African rain forest. The set of community-level diagnostic criteria (*Table 1*) largely enabled the separation of local and regional effects on community composition.

We found that the relative importance of local and regional processes changed during secondary succession. Regional processes were important in all stages of succession but less so in its early stages. The indirect gradient analysis (DCA) showed that overall community composition primarily reflected locality and recent land use history. Soil properties, gap size and other environmental variables were not important in explaining the variation in species composition. The direct gradient analysis (CCA) of species distributions in same-aged logging gaps over the landscape gradient, indicated in the later stages of succession more species were sensitive to regional setting. Likewise, the number of species with a clear preference (i.e. indicative species) for gaps in either forest mosaics or shifting cultivation mosaics increased with vegetation age. In sites with similar disturbance history, species similarity based on relative abundance showed marked differences between landscape mosaics in old logging gaps but only small differences in young gaps (*Figure 1*). The similarity in tree species composition of recruits and adults was initially low in old shifting cultivation fields but increased rapidly with successional age (*Figure 4*). We found much higher overlap in species composition between recruits and adults in logging gaps. Moreover, this overlap was more or less constant during succession. Combined, these results indicate that vegetation in the early successional stages were to a large extent dominated by the same limited set of species irrespective of landscape setting. Older secondary vegetation was much more variable in species composition and showed a larger relatedness to the regional setting. Moreover, higher intensity of land use appeared to prolong the period in which local processes were important. The relative importance of local processes early in succession indicated that in the extreme conditions of recent canopy gaps and shifting cultivation fields a different set of species occurred than in older stages of succession. Despite the abundance of recruitments sites in such disturbed localities, only a relatively small set of species were capable of successful colonization. This result concurs with many of the more classical succession studies in which specific sets of highly adapted species colonized disturbed sites (e.g. Denslow 1980; Whitmore 1989). However, later in succession functional differences between species were less important for community composition. In these stages, local species composition largely reflected the ability of species in the regional pool to reach the recruitment sites (e.g. Hubbell & Foster 1986; Hubbell *et al.* 1999).

Our results also indicated that the relative importance of local and regional processes differed strongly between growth forms. The relative abundance of large trees, shrubs and climbers during succession followed different trends in logging gaps situated in forest mosaics compared to logging gaps that were part of shifting cultivation mosaics (*Figure 3*). In forest mosaics, 27-year old logging gaps had more trees and less terrestrial herbs compared to similar sites in shifting cultivation mosaics. Likewise, shrubs were more abundant in 5-year old logging gaps in forest mosaics. Species composition in similar habitats also differed greatly between landscape mosaics for large trees, and to a lesser extent for small trees and shrubs (*Figure 2*). Differences in species composition between landscape mosaics were much less pronounced for climbers, and terrestrial herbs. Because recruitment conditions change during succession, species turnover with vegetation age was used as an indicator of the degree of niche differentiation. We found that species turnover during succession differed strongly between growth forms (*Figure 1*). After the first stage of succession, species composition changed relatively little in large trees, small trees and shrubs. Herb composition changed strongly during succession but climber composition was remarkably stable. Combined these results indicate that species composition of large trees, and to a lesser extent small trees and shrubs, was mainly governed by regional processes. Local processes largely structured species composition of herbs. Regional processes also governed species composition of climbers but as the majority of the occurring species had wide distributions only small differences were observed between landscape mosaics.

We observed a general functional equivalence of species within the groups of large trees and small trees for all except the initial stages of secondary succession. The species in these groups broadly share a similar life-history strategy aimed at gaining stature and occupying space in respectively the canopy and the sub canopy of the forest (Brown & Jennings 1998). Light is most important limiting resource for these plants (Poorter & Arets 2003) and competitive interactions for this resource are limited once a place in the canopy is assured. As a result of this preemptive space filling, there appears to be little opportunity for niche differentiation in trees except in the youngest stages of plant development.

After the initial stages of succession, the shrub species were also relatively insensitive to local conditions. Many of shrub species found are highly tolerant to shading (Cable & Cheek 1998) which may explain their persistence in many different light conditions. Turnover of shrub species in succession was higher for logging gaps in forest mosaics than for gaps in shifting cultivation mosaics. The vegetation in older logging gaps and even old growth forest in shifting cultivation mosaics contained many species characteristic for the early stages of succession. Moreover, the relative abundance of shrubs in old growth forest in the shifting cultivation mosaics was low compared to forest mosaics. As many of the Lower Guinea endemics in this forest region are shrub species (van Gemerden *et al.* 2003), the stagnant recovery of shrub species composition in shifting cultivation areas is of concern to conservation management. A possible explanation for the poor recovery of forest-type shrub species in such landscapes is that their intrinsic dispersal capacity is lower than that of the secondary species abundant in young secondary vegetation. In addition, pollination and dispersal vectors may have declined in landscapes altered by humans (Guevara *et al.* 1986; Poulsen *et al.* 2001). To test these hypotheses more insight is required in the pollination and dispersal syndromes of the shrub species.

Climbers were also relatively insensitive to successional age of the vegetation. Following forest disturbance, woody climbers are likely to establish quickly and grow rapidly thereafter (Schnitzer & Bongers 2002). Climbers are therefore typically found in the vegetation canopy, regardless of its height. Therefore, growing conditions may not change drastically during succession from the perspective of climbers. Dewalt *et al.* (2000) found that ordination of plots based on the presence-absence of woody climber species did not enable the separation of different-aged forest stands in a chronosequence of secondary forest in Panama. However, they did find a significant separation by stand age if relative abundance data were used. This suggests that the majority of woody climber species were capable of reaching the majority of the recruitment sites but their relative success in these sites depended on successional age and other environmental factors. These findings were not confirmed by our study. We found that 75% of the individual climbers per plot belonged to only 4 – 6 species. Moreover, species turnover between different-aged plots of these most abundant species was very low, e.g. all age-classes had 3 – 4 of these species in common. These result indicate that the same set of species were highly successful in all sites, regardless of vegetation age and landscape setting.

Herb species composition was strongly influenced by local conditions, especially in forest mosaics. Strong niche differentiation may result from the fact that herb species have competitive interactions during their complete life cycle for a multitude of resources (e.g. light, water, nutrients). High adaptation for specific conditions results in high species turnover during succession as forest conditions gradually change. As most herbs are short-lived, unsuitable recruitment conditions are quickly reflected in community composition. Colonisation of once heavily disturbed sites may be problematic for forest-type herb species. We found that herb species composition in shifting cultivation mosaics was much less differentiated along the succession gradient. This may be caused by differences in intrinsic dispersal ability between forest-type herbs and those found early in succession. For instance, quite some Begonia species are extreme short-range dispersers and therefore colonisation in fragmented landscapes will be very improbable (Sosef 1994). This implies that while herbs tended to be niche differentiated, regional processes were also important for herb species composition.

The maintenance of the typical high plant diversity of tropical rain forests receives much scientific attention (e.g. Huston 1994; Rosenzweig 1995; Hubbell 2001; Sheil & Burslem 2003). Although generalisations are often easily made, most studies of rain forest plant diversity are restricted to trees (Laurence *et al.* 1997, 2002; Hubbell *et al.* 1999; Condit *et al.* 2000). The results of our botanical survey, including all terrestrial vascular plants, indicated that patterns observed in trees might not be representative for the plant community as a whole. In accordance with Hubbell *et al.* (1999), we found that regional processes largely govern tree community composition, i.e. functional differences between species were not important for community structure. Similarly, we found that regional processes mainly govern shrub species composition. However, the statement that gap phase dynamics are trivial for the maintainance of species diversity in rain forest communities (Hubbell *et al.* 1999) may overlook the importance of local processes in other species groups (Schnitzer & Carson 2000, 2001). In our study we found that local processes (e.g. niche differentiation) were important for species composition of terrestrial herbs. Moreover, local processes were important in the initial stages of succession of all studied growth forms. This supports the observations made by Schnitzer & Carson (2001) that gap dynamics promoted diversity of pioneer tree species in a rain forest in Panama. Their claim that this holds also for woody climbers was not supported by our analysis. In general, a more detailed classification of species on the basis of life history traits, especially those related to competition and dispersal (Gitay *et al.* 1999; Weiher *et al.* 1999; Köhler *et al.* 2000), will likely identify more species groups sensitive to local processes. Nonetheless, a general claim for the dominance of either local or regional processes in structuring community composition of tropical rain forests is not supported by our findings.

We conclude that both local and regional processes influence community composition during succession. The relative importance of these processes varies with succession and between species groups. This implies that effective conservation management, especially in areas affected by human land use, requires insight in the relative importance of local and regional processes for the recruitment of target species, e.g. endemic or threatened species (Myers *et al.* 2000). A blanket conservation treatment for all species is unlikely to address adequately the specific sensitivity to habitat quality and habitat fragmentation of species with high conservation value.

Acknowledgements

This study was carried out in the framework of the Tropenbos-Cameroon Programme (TCP). All TCP staff is thanked for their logistic support, especially Gideon Shu Neba, Dieudonné Ndoum, Benjamin Mva, Jacques Ntolo, Etikeke Mbamba, Catherine Dikao and Olivier Mimbila. For assistance with plant identification, we like to thank G. Achoundong, J.P. Ghogue, A. Koufany, P. Mezili and J.M. Onana at the National Herbarium of Cameroon (IRAD), and F.J. Breteler, J.J. Bos, C. Jongkind, A.J.M. Leeuwenberg, R.H.M.J. Lemmens, L.J.G. van der Maesen, J.J. Wieringa, J.J.F.E. de Wilde, and M.S.M. Sosef at the Nationaal Herbarium Nederland – Wageningen University Branch. Tjakkie van der Laan, Jan van Walsem, Gerard Hazeu and Arie van Kekem assisted in the analyses of the soil samples. Constructive comments by Rampal Etienne and Andre Schaffers were much appreciated. This study was partly funded by the European Commission (DG VIII).

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Chapter 5

Reconciling methodologically different biodiversity assessments of species-rich tropical rain forests

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Abstract

Ongoing large-scale habitat destruction in tropical rain forest regions requires quick identification of conservation priorities such as sites rich in species and/or endemics. As biodiversity assessments of rain forests are time-consuming and expensive, surveys often rely on partial sampling. Therefore, optimal use should be made of all currently available sources of information. However, methodological differences between surveys hamper direct comparison of results. As diversity is scale-dependent, diversity characteristics of different sites are best compared on the basis of species – area relations. As a result of the incompleteness of sampling, the observed species – area relation deviates from the 'true' species-area relation. The key factors affecting the general shape and position of the species – area relation based on incomplete sampling are: (1) the total extent in which observations are made, (2) the spatial distribution of the observations, (3) the proportion of the total extent sampled, (4) the proportion of the individuals of the sampled area included in the survey, and (5) the proportion of the included individuals that was successfully identified. We analysed four botanical surveys in the same area of old growth lowland rain forest in South Cameroon with the aim of reconciling the methodologically different surveys. The studied methods were (1) reconnaissance scale vegetation mapping, (2) detailed botanical assessment (all individuals), (3) incomplete botanical assessment (10% individuals), and (4) herbarium collections. We found that recorded number of species and endemics was most sensitive to partial sampling of extent, partial sampling of individuals and partial identification of individuals. Correcting for partial sampling and scaling to extent, greatly increased comparability between the results of the four different biodiversity surveys. Our findings suggest that reconciliation of biodiversity assessments is possible if the differences between methods can be accounted for. This study provides an outline on how methodologically different surveys can be combined to optimise the use of existing data in the evaluation of conservation needs in tropical rain forest areas. Reliable documentation of survey methods, especially with respect to the mentioned key factors, greatly enhances the potential of methodologically different surveys for comparative biodiversity analyses.

Introduction

Biodiversity conservation in the tropics is an issue of increasing importance as ongoing large-scale habitat destruction poses a major threat to the survival of many species (Vitousek *et al.* 1997). Conservation planners are challenged to balance conservation efforts with societal demands for natural resources and conservation funds. Therefore, not all threatened species and ecosystems can be protected and priorities for biodiversity conservation need to be set (Myers *et al.* 2000) . There is a growing literature on reserve site selection theory (Margules *et al.* 1988, Csuti *et al.* 1997, Ando *et al.* 1998, Margules & Pressey 2000; Olff *et al.* 2002) and spatial optimisation for ecological management (Hof & Bevers 1998; van Langevelde *et al.* 2000). These studies present approaches to select sites that represent the highest possible number of species. Moreover, so-called gap analyses are conducted to identify gaps in representation of biodiversity in reserve sites (Scott *et al.* 1993). Here, critical is again what sites are selected to be included in the network of reserve sites.

Species richness, level of endemism and exposure to threats are generally accepted as a robust set of criteria for setting conservation priorities (Hawthorne 1996; de Groot 1992; Myers *et al.* 2000; ter Steege 2000). However, a major obstacle for setting balanced conservation priorities is the incompleteness of such biodiversity information (Howard *et al.* 1998; Faith & Walker 1996). For example, Lombard *et al.* (1997) proposed a reserve selection in the species-rich Agulhas Plain in South Africa and used, in absence of better data, herbarium records combined with fragmented observations on species distributions. Often, surrogate data are used in conservation planning to identify areas deserving high priority for protection such as key species, indicator species or umbrella species (Faith & Walker 1996, Simberloff 1998). In contrast to temperate regions, only little ecological knowledge is currently available for the majority of tropical species. Best studied are larger mammals and birds, and species conservation plans for these groups can be based on their distribution patterns and ecological requirements (e.g Mickleburgh *et al.* 1992; Oates 1996). For the majority of tropical plant and invertebrate species, neither species ecology nor distribution patterns are sufficiently known for such analyses. At present, only few rain forest areas have been systematically surveyed for even a limited number of taxonomic groups (e.g. Howard *et al.* 1998, 2000). Moreover, complete biodiversity assessments of tropical rain forests are extremely expensive and time-consuming, and arguably beyond the capacity of the global research community (Lawton *et al.* 1998; Howard *et al.* 1998). The ongoing rapid habitat destruction in many tropical regions now implies that conservation priorities need to be identified quickly. Therefore, conservation planners are urgently challenged to set priorities on the basis of presently available, yet incomplete, information on biodiversity patterns in tropical rain forests (Gaston & Rodrigues 2003).

The main sources of information in setting conservation priorities for tropical plants are species distribution maps based on collection localities of herbarium specimens (Lovett *et al*. 2000; Linder 2001; Poorter *et al.* 2003). The advantage of herbarium collections for biodiversity assessments is their state-of-the-art taxonomic identification. Moreover, collections are stored and can be re-examined if necessary. However, problematic for biodiversity assessments is that collections are generally clustered in areas with high collecting effort, often chosen for other reasons (historical, practical) than their high or characteristic diversity (Nelson *et al.* 1990; Funk *et al.* 1999; ter Steege *et al.* 2000; Poorter *et al.* 2003). In addition, herbarium collectors tend to focus on (flowering) material of relevance to their research (e.g. taxonomic revisions). As a result, collections are a poor representation of the whole plant community composition. Moreover, the number of collections stored in herbaria is generally too small to allow for biodiversity analyses at smaller than regional scales (ter Steege *et al.* 2000)

Fortunately, herbarium collections by taxonomists are not the only source of information on plant diversity of tropical forests. Most tropical rain forests have had their share of ecologists, vegetation surveyors, foresters, etc., who in a more or less systematic way collected data on forest composition. These surveys are generally less precise in a taxonomic sense but have the advantage that they include a larger proportion of the individuals present in the forest, e.g. through plot-based sampling. Moreover, survey effort is generally more equally distributed over the area. Although not always designed for conservation purposes, these surveys contain valuable information on biodiversity. However, so far few conservation analyses have been based on such surveys (ter Steege 1998). Pressed for quick conservation priorities, it is necessary to fully exploit the information potential of these alternative sources, possibly in conjunction with each other and the more traditional herbarium collection approach. This requires a formal comparative approach that captures the essential differences between sampling methods, and their consequences for the measurement of diversity.

In the present study, we will first identify the general critical differences between commonly used sampling methods. Then, we propose a method for reconciling assessments. Finally, we will try to reconcile the results of four methodologically different botanical diversity assessments in the same rain forest area in southern Cameroon.

Methods

Main methodological differences between diversity assessments

Botanical diversity assessments aim to identify the kind and number of plant species that inhabit a specific locality. Species – area relations describe the accumulation of new species with area. Such relations are nested and diversity at smaller scales is embedded in diversity at larger scales. Species – area relations are generally not linear or log-linear; species accumulate most rapidly in small areas, then more slowly in intermediate areas, and again more rapidly in larger areas (Arrhenius 1921; Gleason 1922; Hubbell 2001; *Figure 1*). The species – area relationship reflects the spatial variation in the density of individuals at small scales, and the spatial distribution of individuals of different species. In a given tropical rain forest environment, mean plant densities (i.e. # individuals per unit area) are generally very constant (Hubbell 2001) and species-area relations of such environments thus mainly reflect the more interesting spatial arrangement of individuals of different species. At uniform densities, the slope of the species – area relationship is steeper in areas where neighbouring individuals are less likely to be of the same species, i.e. where species are less clustered. As diversity is scale dependent (Rosenzweig 1995), diversity characteristics of different tropical rain forest sites are best compared on the basis of species-area relations. Comparing species accumulation over different scales is important as species – area curves of different sites can intersect.

The 'true' species – area relation should be based on the complete assessment of all individuals. However, such complete biodiversity assessments are impossible to conduct at sufficiently large scales in species-rich and taxonomically poorly studied ecosystems like tropical rain forests. Survey methods try to overcome these practical limitations by incomplete sampling. The incompleteness of the sampling causes an information shortage on the spatial distribution of species and therefore leads to deviations from the true species – area relation (*Figure 1*). Different assessment methods take different decisions on which individuals to include in the survey. We suggest that five main factors explain why different methods produce different information on diversity when applied in the same area. These causes for information shortage are: (1) the total extent (E) in which observations are made, (2) the spatial distribution (C) of the observations, (3) the proportion of the total extent sampled (p_e), (4) the proportion of the individuals of the sampled area included in the survey (p_i), and (5) the proportion of the included individuals that was successfully identified (p_d) (*Figure 2*).

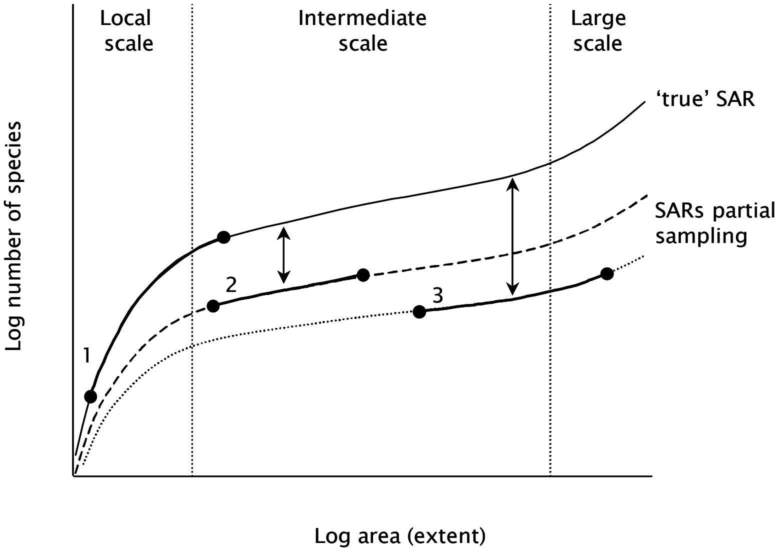

Figure 1. General shape of species - area relations (SAR). Solid line represents the 'true' SAR resulting from complete sampling. Partial sampling results in information shortage (indicated with arrows). Surveys (examples 1 - 3) generally only cover a limited range of the SAR.

EXTENT (E)

Because it is not possible for practical reasons to taxonomically identify all the individuals in any tropical rain forest region, most methods assess the diversity in selected sample areas, e.g. plots, transects. These sample areas are distributed in the much larger area that they are meant to represent (*Figure 2*). This larger area, hereafter referred to as extent (E), is the appropriate scale to analyse diversity characteristics. Simply constructing species – area relationships by collating the sampled areas underestimates the actual position on the species – area relationship. An often-suggested alternative to species – area relationships based on sampled area are species accumulation curves, i.e. the rate of species accumulation over individuals (e.g. Gotelli & Colwell 2001). However, such species accumulation curves still overlook the individuals that are in between the sampled areas (they have no true area anymore). Therefore, to compare the results of different methods it is necessary to distinguish between sampled area and extent.

SPATIAL DISTRIBUTION OF SAMPLE POINTS (C)

Within the extent, the spatial distribution of sample points (C) is likely to influence the observed species richness. Samples closer together are generally more related in species composition. Especially in areas with high beta diversity, clustering of sample points may therefore lead to underestimation of species richness. Spatial distribution of sample points may vary strongly between different methods (*Table 1*).

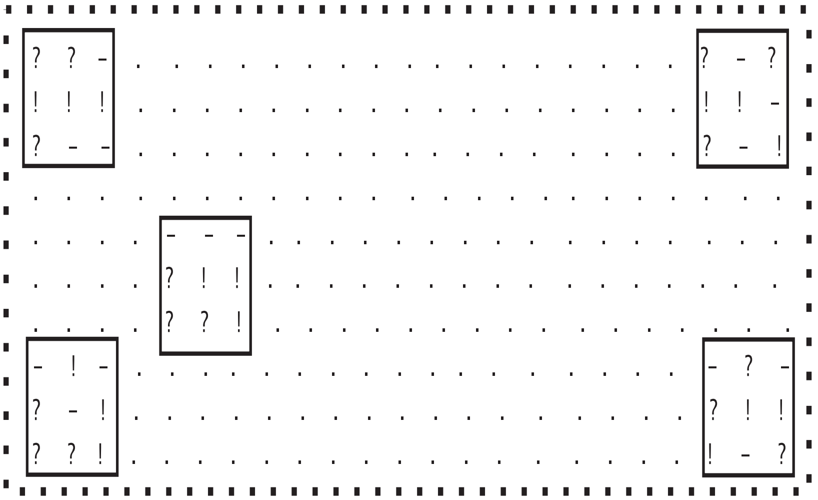

Figure 2 *Example of field layout of assessment based on partial sampling. Symbols represent individuals. Extent (dashed line) envelopes the areas actually sampled (solid lines). Individuals within sample area are either not sampled (-), sampled but not identified (?) or sampled and identified (!). In this example* $p_e \approx 0.02$, $p_i = 0.66$, and $p_d = 0.5$.

Proportion of total extent sampled (p_E)

Partial sampling of extent implies that observations are only made in selected sites and that no information was collected on the individuals in the area in between these sites (Figure 2). The proportion of the total extent (p_e) that is actually sampled reflects the size of the sample in relation to the area that was not sampled. P_e is likely to have a strong effect on observed species richness.

Proportion of individuals in sampled area included (p_I)

Sampling methods also vary with respect to the proportion of individuals (p_i) in the sampled areas that are included in the survey. Especially in plot-less sampling methods often not all individuals are included. But also in other methods cut-off levels are often applied for practical reasons (e.g. not all size-classes or taxonomic groups included). Differences between methods may result in different information shortages on the spatial distribution of species and may hamper comparison of the results (*Table 1*).

Table 1 Classification of common botanical assessment methods applied in tropical rain forests with respect to key factors affecting the observed species richness

key factors assessment methods	total extent survey (E)	proportion of total extent sampled (p_e)	proportion of individuals in sampled area included (p_i)	proportion of included individuals identified (p_d)
herbarium collections	large	large	very small	very large
vegetation mapping	large	small	medium	small
line intersect methods	medium	small	large	medium
rapid botanical assessment	medium	medium	medium	medium
parataxonomic sampling	medium	medium	large	very small
plot-based sampling	small	small	large	medium

PROPORTION OF INCLUDED INDIVIDUALS SUCCESSFULLY IDENTIFIED (p_D)

Finally, methods may vary in the proportion of individuals that is successfully identified (p_d). Species identification in highly diverse but taxonomically incompletely studied tropical rain forests requires much expertise. For the majority of surveys in tropical regions only limited botanical expertise, reference collections and identification keys are available. Moreover, some surveys rely on non-specialists or use a parataxonomic classification of species (Oliver & Beattie 1996a,b; Hellier *et al.* 1999; Danielsen *et al.* 2000; Kerr *et al.* 2000). An additional problem is that in tropical rain forests at any time only a fraction of the individual plants are flowering or fruiting. As classic identification keys are mainly based on reproductive organs, the absence of flowers and fruits complicates identification. Methods differ greatly in the efforts made to identify the individuals surveyed (*Table 1*).

Reconstruction of species – area relationship from incomplete data

The true species richness (S_{true}) in the total extent is based on a complete survey of individuals and their complete identification. The true species – area relationship gives the accumulation of species with area (extent) when all individuals are sampled in a nested design, and diversity is just a function of extent (*Figure 1*),

$$S_{true} = f(E) \qquad (Eq.\ 1)$$

Assessment methods based on partial sampling of individuals yield an observed diversity ($S_{observed}$). Reconciling methods implies reconstructing S_{true} from $S_{observed}$ values while correcting for the different components of information shortage, i.e. C, p_e, p_i, and p_d. The observed number of species will be some proportion r of the real number of species:

$$S_{observed} = r\, S_{true} \qquad (Eq.\ 2)$$

If we would know the exact value of r we can also calculate the real number of species from the observed number of species:

$$S_{true} = S_{observed} / r \qquad (Eq.\ 3)$$

A first approximation of r is the product of four reduction factors, representing the effects of respectively not sampling all the area in the total extent (r_e), spatial clustering of sample points (r_c), not sampling all individuals in the sampled area (r_i), and not successfully identifying all sampled individuals (r_d), therefore

$$r = r_c\, r_e\, r_i\, r_d \qquad (Eq.\ 4)$$

Finally, we need to find specific formulations for calculating these reduction factors from the components of information shortage,

$$r_c = f(k_c, C) \qquad (Eq.\ 5a)$$

$$r_e = f(k_e, p_e) \qquad (Eq.\ 5b)$$

$$r_i = f(k_i, p_i) \qquad (Eq.\ 5c)$$

$$r_d = f(k_d, p_d) \qquad (Eq.\ 5d)$$

In these functions k_c, k_e, k_i, and k_d are constants that represent the consequences for observed species richness of, respectively, the distribution of observations (C), incomplete sampling of area (p_e) and individuals (p_i) and partial determination (p_d). The values of k_c k_e, k_i, and k_d may vary between regions and need to be fitted to experimental data. Clustering of sample points has theoretically a negative effect on observed species richness. Therefore, r_c can be approximated as a linear

decline to fit maximum species richness on highest observed uniformity of data points. All other reduction factors can theoretically be described as power functions in which all species will be observed at complete sampling. Combining the equations 3, 4 and 5 yields the predicted species richness, corrected for the information shortage of the specific method, as:

$$S_{\text{predicted}} = S_{\text{observed}} / (r_c \, r_e \, r_i \, r_d) \qquad (\textit{Eq. 6})$$

Case study: diversity assessment with different methods

Study site

The study was conducted in the Bibindi – Akom II – Lolodorf region, south Cameroon (3° N, 10° E; 1700 km^2). The climate is humid tropical with two distinct wet seasons (March–May, August–November) and two relatively drier periods. The average annual rainfall is 2000 mm (Waterloo *et al.* 2000). Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry 1986). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). Topography varies from flat erosional plains to rolling uplands with isolated hills, and mountains. Altitude varies from 50 – 1000 m above sea level. Soils range from moderately acid sandy clay loam to highly clayey and strongly acid and classify as Haplic Acrisols, and Plinthic and Xanthic Ferrasols (van Gemerden & Hazeu 1999). Evergreen forests of the Atlantic Biafrian type largely cover the area (Letouzey 1968, 1985). These forests are characteristically rich in Leguminosae– Caesalpinioideae and have a closed canopy at 30 – 40 m with emergents often surpassing 55 m. The area is rich in plant species. So far approximately 1600 species have been recorded in the area of which 1264 species have been identified to species level (B.S. van Gemerden, unpublished data). The recorded species include 261 species that are endemic to the lower Guinea forest region (Nigeria – Gabon) of which 51 species are restricted to the rain forests of Cameroon.

Data sets

The vegetation in the area has been surveyed by different methods by a number of projects (Letouzey, 1968, 1985; van Gemerden & Hazeu 1999; Guedje *et al.* 2003; van Gemerden *et al.* 2003a,b; Parren 2003). The present study examines four surveys that vary in extent (E), spatial distribution of observations (C), proportion of the extent sampled (p_e), proportion of individuals sampled (p_i), and proportion of sampled individuals identified (p_d). The selected methods represent often-used approaches of vegetation survey in tropical rain forest regions. In order to minimize the effect of spatial heterogeneity, we focussed on undisturbed rain forests between 50 – 700 m altitude. According to a reconnaissance landscape ecological survey these forests are quite similar in terms of general floristic composition, soil properties and landforms (van Gemerden & Hazeu 1999). We will first present the characteristics of the four datasets needed to calculate C, p_e, p_i, and p_d (*Table 2*).

Table 2 Characteristics of the four studied botanical surveys of old growth lowland rain forest in south Cameroon

dataset	1 vegetation mapping[a]	2 diversity assessment (100%)[b]	3 diversity assessment (10%)[b]	4 herbarium collections[c,d]
total # plots	83	44	20	55
plot size (m2)	100	625	625	740
total sample area (ha)	0.83	2.75	1.25	3.75
maximum extent (km2)	1 235	219	180	896
# species recorded	320	767	207	378
% morphospecies	14.4	29.9	26.0	0
% endemic species	16.3	16.6	15.6	14.8
key factors:				
spatial distribution of samples				
Fisher's I	0.287	0.813	0.837	0.689
C standardised	0	0.526	0.550	0.402
prop. extent sampled (p_e x $1*10^{-5}$)[e]	0.25	6.86	5.78	2.11
prop. individuals included (p_i)	0.9	1.0	0.1	0.0175
prop. individuals identified (p_d)	0.54	0.76	0.76	0.72

[a] van Gemerden & Hazeu 1999. [b] van Gemerden, unpublished data. [c] Extract databases of Wageningen (Herbarium Vadense) and Kribi (Tropenbos/ IRAD) in 2000. [d] Herbarium data set included 640 fully identified collections. These collections form 72% of the collections actually made in the area. The remaining 28% were not identified yet or were not stored at the Kribi or Wageningen herbaria. Area surveyed was estimated as 800 m^2 per 17,5 collections (see text). [e] Proportion extent sampled at extent ≈100 km^2 (see Figure 2).

The first data set is an area-wide vegetation survey made for mapping the most important aspects of vegetation at scale 1:100 000 (van Gemerden & Hazeu 1999). Relatively homogenous tracts of land were identified on aerial photographs and joint descriptions of vegetation, soil and landform of the most important units were made in the field. In 83 localities, external foliage cover was estimated of the most important plant species in 10 x 10 m plots (100 m^2, total sample area 0.83 ha).

Plots were more or less evenly distributed over the area (*Figure 3*). Mosses, ferns, epiphytes and seedlings were not included in the survey. Plant identification was done in the field with the help of a field botanist and a local tree spotter. Plant material was collected of unknown species. Identification at the National Herbarium of Cameroon (Yaoundé) and Limbé Botanic Garden focussed on material of the most abundant species.

Abundant or characteristic species that could not be identified were categorised as morphospecies. In the total survey of 0.83 ha, 320 plant species were recorded.

The second data set used is a detailed botanical assessment of the area (van Gemerden, unpublished data). Vegetation was sampled in 44 plots of 25 x 25 m (625 m^2) representing a total sample area of 2.75 ha. Plots were grouped in four sample areas that represented the most important variation in vegetation, soils and landforms (*Figure 3*). In the plots all plants (except individuals of woody species less than 50 cm tall) have been identified. In the field, the most common and readily identifiable species were directly named and plant material was collected of all other species. Voucher material was processed at the Kribi Herbarium (Tropenbos – Cameroon Herbarium) and sent to the National Herbarium of Cameroon (IRAD Yaoundé) and the National Herbarium of the Netherlands-Wageningen University branch for identification by specialists. Collections that could not be identified to species level were systematically categorised as morphospecies. In the total survey of 2.75 ha, 767 species were recorded.

The third data set is a subset of the previous survey and includes the 20 plots (625 m^2, total sample area 1.25 ha) in which all individuals were enumerated. Plots were clustered in four localities (*Figure 3*). Ten percent of the individuals per plot were randomly selected and thus a plot-based dataset with low sampling intensity was constructed. Field methods and plant identification followed the procedures of set 2. In the total survey of 1.25 ha, 207 species were recorded.

The fourth data set consists of all botanical specimens that were collected in the area and stored in the National Herbarium of the Netherlands-Wageningen University branch, or the field herbarium of the Tropenbos-Cameroon Programme. The herbarium collections were made by a variety of collectors from 1885 – 2001. Only collections that were, according to the collection notes, made in undisturbed forest sites and that were accurately georeferenced were included. In addition, collections that were made as part of a more or less systematic vegetation survey were omitted. This set includes a total of 640 collections, made in 55 different localities that were grouped in a few disjoint clusters (Figure 3). The herbarium database only includes completely and confidently identified specimens, i.e. mostly fertile material that has been checked by specialists. The total number of species in this dataset is 378.

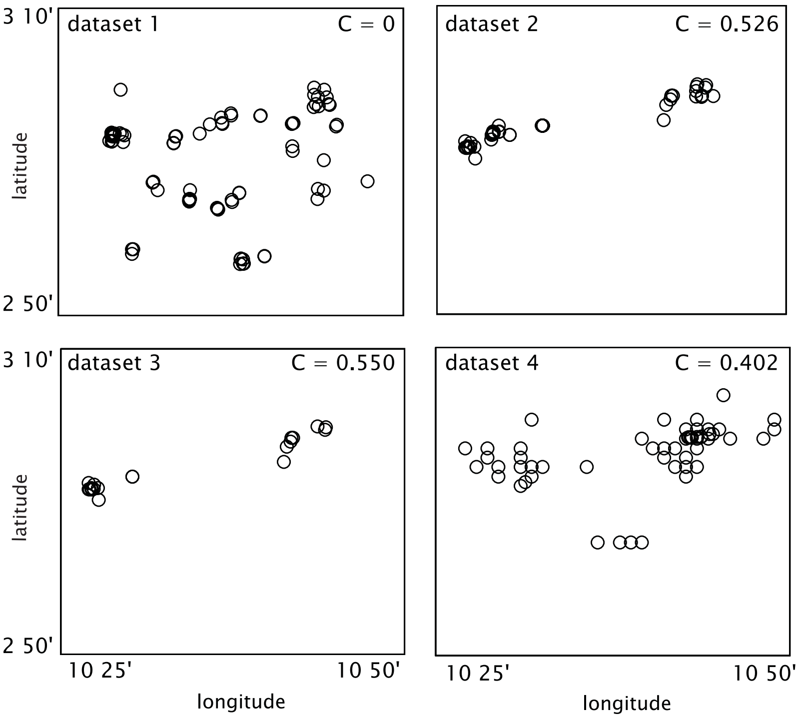

Figure 3 Spatial distribution of observations in the four datasets included in this case study.

Data analysis

Only species that, within a set, were uniquely named (i.e. were comparable between plots) were included in the analyses of species richness. This implied that fully identified species and morphospecies were included and other less precise identifications were omitted, such as field names that were found or were likely to refer to small clusters of morphologically similar species. Species richness was defined as the total number of species (including morphospecies). Of special concern to biodiversity conservation are endemic species, i.e. species with a restricted geographical distribution range. In the present study, we defined endemic species as species restricted to the Lower Guinean forest region (Nigeria, Cameroon, Equatorial Guinea and Gabon). A further refinement of endemic status is at present problematic as this part of Africa is generally poorly explored botanically.

We calculated per survey sample area, extent (E), species and endemic species richness, and the spatial distribution of the plots (C). The sample area is the area that was actually included in the survey. For set 1, 2, and 3 it is simply the total area covered by plots. For set 4 (herbarium collections) we calculated the sample area on the basis of the number of collections made. On an average collecting day a herbarium botanist collects 15 – 20 herbarium specimens while 'scanning' an area of approximately 7,5 ha (B.S. van Gemerden, personal observations; P. Tchouto, personal communication; F.J. Breteler, personal communication). However, not all individuals in this area will be thoroughly examined, as the herbarium collector's primary interest are flowering and fruiting plants. Based on a small trial, we estimated that 1000 plants are scrutinized during an average day collecting, representing an effective sample area of 800 m^2. However, as not all collectors will have spent equal time collecting, the area they covered will also vary. We grouped the collections by locality and estimated the sample area per locality on the basis of the above estimates. A further refinement of these estimates was necessary as not all collections made by a specific collector on a specific date were stored in the herbarium database. This was the result of the fact that herbaria generally do not incorporate unidentified material. In addition, a given herbarium may not have duplicates of all collections made in the area by (especially) collectors affiliated to other herbaria. As collections are generally uniquely and consecutively numbered, we identified the total number of collections per collector in a specific locality by assuming that missing intermediate numbers were also collected in the same locality. We calculated that some 28% of the collections made were not stored in the herbarium database. The total number of collections per locality was corrected for the proportion of missing material to get a more accurate estimate of the sampled area for dataset 4.

We defined the extent (E) as the surface of the polygon that included a given number of plots plus a buffer of 50 m. The size of the buffer reflects common practice in vegetation sampling that plots are not located too close to sudden changes in vegetation or environment. Calculations were performed with the GIS Arcinfo.

For each dataset we calculated species richness, and endemic species richness. To construct species - extent curves for each dataset, we plotted species richness and endemic species richness against the extent of increasing number of plots. Therefore, we made series of randomly selected plots to obtain series of randomised plot orders, and calculated for series the extent. We used average values over the total number of runs per dataset. The number of series of randomised plot orders varied per dataset due to computational limitations, i.e. 325 series for set 1, 795 series for set 2, 2123 series for set 3, and 331 series for set 4. In dataset 3, many repetitions were chosen because in this set also a random subset of 10% of the individuals was selected per series. Standard deviation of extent and species richness were very small for all datasets indicating that the numbers of runs used were amply sufficient.

We characterised the spatial distribution of the plots (C) by calculating Fisher's I index, i.e. the ratio of the standard deviation of all point-to-point distances to the average point-to-point distance (Cressie 1993). This index produces high values for clustered point distributions and low values for uniform distributions. We scaled the index values to the observed minimum in the datasets to obtain a range relevant to the present analyses, as $C = I_i - I_{minimum}$.

To analyse the effects of partial sampling on species richness, we constructed a simulation dataset. By varying one parameter and keeping all other parameters constant, we identified the separate effects of partial sampling of respectively C, p_e, p_i, and p_d. The simulation dataset is based on the 20 enumerated plots of dataset 3. All plots contained 267 randomly selected and fully identified individuals. We isolated the effect of spatial distribution of sample points on species richness by calculating C for all combinations of two plots together with four fixed plots forming the outer perimeter of the extent. As a result the spatial distribution C varied while p_e, p_i and p_d remained constant. Likewise, the effect of the proportion of the total extent sampled (p_e) on species richness was analysed by selecting the plots forming the outer perimeter of the extent and randomly adding plots to increase p_e while keeping extent E, p_i, and p_d constant. Average species richness values over 100 randomised runs were used in the analyses to average out variation in C.

We analysed per plot the effect of the proportion of individuals included in the sampled area (p_i) on species richness. Per plot, individuals were randomly chosen and average species richness values over 1000 runs at fixed proportions were used in the analyses. We analysed the effect of partial identification of included individuals (p_d) on species richness by randomly classifying different numbers of species per plot as either identified or unidentified. In field situations, individuals are generally quite accurately grouped by botanical species and therefore individuals within a group were assumed to have the same identification status. In the analyses, the average numbers of individuals representing 5, 10, 20, 40 and 55 identified species per plot over 5 random selections were used.

Results

Method characteristics

Although all datasets represented botanical surveys done in the same area of old growth rain forest at low altitudes, the observed number of species varied considerably between datasets (*Table 2*). Most species were recorded in dataset 2 (767 species), while dataset 3 had only 207 species. Despite these differences, the proportion of endemic species was surprisingly constant between sets, i.e. between 14.8 – 16.6%.

The sampled area per dataset varied from 0.83 ha (set 1) to 3.75 ha (set 4), while the maximum extent (E) varied from 180 km^2 (set 3) to 1236 km^2 (set 1) (*Table 2*). Distribution of sample points was most evenly spread in dataset 1 (Fisher's I = 0.287, C = 0), while dataset 3 was highly clustered (C = 0.402) (*Figure 3; Table 2*). The proportion of the extent covered by sampling (p_e) varied with extent and between datasets (*figure 4*). In general, p_e decreased in all sets with increasing extent until a critical value was reached after which p_e increased again. Dataset 3 did not show an increase in p_e at larger extents but did level off. The critical value varied between sets and was lowest in set 2 (≈100 km^2) and highest in set 1 (≈ 650 km^2).

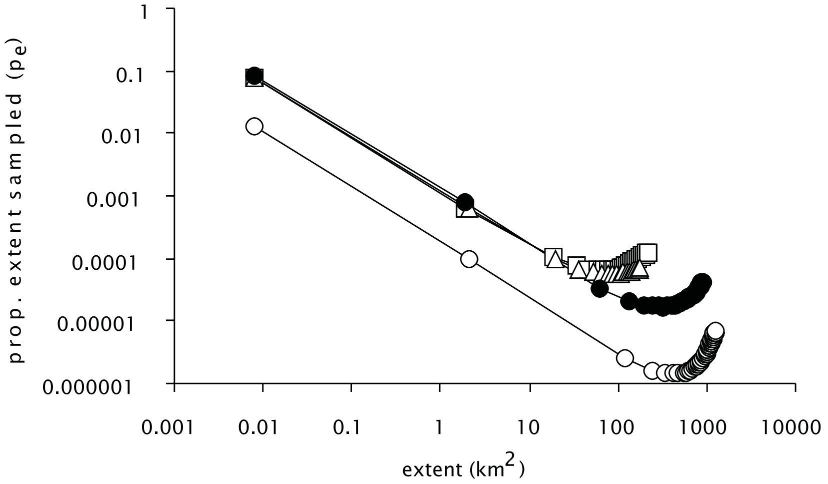

Figure 4 Relation between extent and proportion of the extent sampled for the different survey methods studied. Dataset 1 (open circles), dataset 2 (squares), dataset 3 (triangles), and dataset 4 (black circles).

The proportion of individuals included in the surveyed sites (p_i) varied between datasets. Set 2 included all individuals in the sampled area, while set 3 included, by definition, only 10% of the individuals. The prescribed methodology for the vegetation mapping survey (set 1) was to focus on the most characteristic features of the vegetation in the plot (i.e. dominant species per vegetation stratum). However, in the field an estimated 90% of the individuals were actually screened (B.S. van Gemerden, pers. observations). In set 4, material was collected of 17.5 individuals out of the 1000 individuals that were examined and therefore the estimated proportion of individuals included in the herbarium set is 0.0175.

The proportion of surveyed individuals that were successfully identified (p_d) was generally high. In set 2 and 3 more than 70% of the individuals were identified to species level and additionally 6% were morphocategorised. In set 4 all individuals were identified to species level. However, some 28% of the collection numbers that were assumed to be collected in the area were not stored in the databases of the Kribi and Wageningen herbaria and therefore p_d was effectively 0.72. In the vegetation survey on which set 1 was based, no information was recorded on the number of individuals. Therefore p_d was estimated using general individuals – area ($y = 1.2548*\text{area}\ (m^2)^{0.9963}$; $R^2 = 1.0$; all individuals dataset 3) and species – individuals relations ($y = 4.3927*\text{individuals}^{0.5037}$, $R^2 = 0.99$; all identified individuals dataset 3). The estimated total number of individuals per 100 m^2 was 123.4. In set 1, 90% of the individuals were included in sampling, i.e. 111.0 individuals were sampled per 100-m^2 plot. The species – individuals relation predicted that 111.0 individuals represent 47.1 species. However, in set 1 only 34.5 species were found on average per plot, i.e. only 60.0 individuals were identified in this survey. According to these estimations, the proportion of individuals identified in set 1 was only 54%.

Consequences of incomplete sampling

The simulation dataset permitted to assess the individual effects of partial sampling of each of the components C, p_e, p_i, and p_d. In order to estimate the area specific constants k_c, k_e, k_i, and k_d it was necessary to express the effects as a proportion of the maximum number of species. Effects of p_i and p_d were assessed per plot. With non-linear regression we fitted the data of simulation dataset to the model $r_x = p_x^{Kx}$ for each of the variables to obtain the constants k_i and k_d. The fitted values of k_i and k_d were respectively 0.582 ($R^2 = 1$) and 0.949 ($R^2 = 0.98$) (*Figure 5c, d*).

The plots in the simulation dataset were highly clustered and therefore standardised C values ranged only from 0.33 – 0.55. This range did not cover the degree of clustering of the different datasets (0 – 0.55). We estimated maximum species richness at the most uniform distribution (dataset 1, C = 0) by regressing the species richness data of the simulation set over C. Although regression fit was poor (y = -66.2 C + 244.2, R^2 = 0.14), this result agreed with the maximum cumulative species richness found in six plots in the simulation dataset and is supported by the general appreciation of low beta diversity in the area. For the present study we, therefore, used 244 species as the estimated upper limit of species richness for the range of C values. The value of the site-specific reduction factor k_c in the model $r_c = k_c C + 1$, was –0.271 (linear regression, $R^2 = 0.14$).

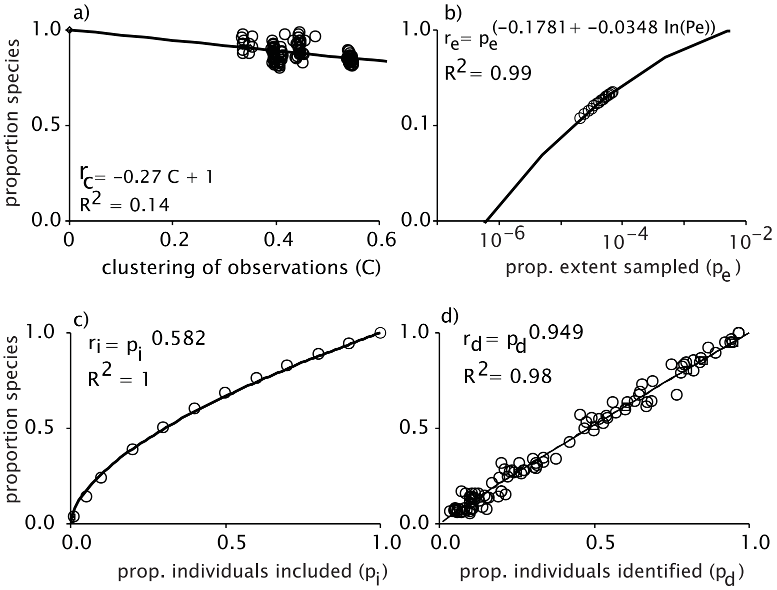

Figure 5 *Effects of partial sampling on observed species richness in simulations with a fully standardised dataset. Individual effects of a) spatial distribution of observations (C), b) partial sampling of extent (p_e), c) partial sampling of individuals (p_i), and d) partial identification of individuals (p_d).*

In the simulation dataset, p_e values ranged only from 2.1 10^{-5} – 6.9 10^{-5} and did not cover the range of p_e values observed in the different surveys, i.e. 0.2 10^{-5} – 0.08. Therefore, maximum number of species was estimated on the basis of a preliminary checklist of the area and available taxonomic literature (mainly Aubréville & Leroy 1961-1992, 1963-2001; Keay & Hepper 1954 – 1972; Cable & Cheek 1998). Based on these sources we estimated the total number of plant species occurring in old growth lowland rain forest in the Bipindi – Akom II – Lolodorf region to be 3000. However, plots in the simulation dataset contained only 267 individuals instead of the average number of 758 individuals in dataset 3. Therefore the total number of species expected in the simulations at $p_e = 1$ was estimated using the newly established relation between p_i and proportion species as: maximum species richness = $(p_i \text{ simulation set})^{Ki} * 3000 = 1634$ species. The model $r_e = p_e^{Ke}$ fitted the simulation data relatively well (non-linear regression: $k_e = 0.185$, $R^2 = 0.67$) but showed relatively large deviations in the range of p_e relevant for the present study. A much better fit was obtained by the model $r_e = p_e^{(b + a \ln Pe)}$, and therefore the site-specific reduction factor k_e was estimated as $-0.178 -0.0348 \ln p_e$ ($R^2 = 1$; *Figure 5b*).

The fitted values of the site-specific constants indicated that partial sampling of extent had the largest effect on observed species richness. Partial identification and partial sampling of individuals also affect survey results, while the effect of spatial distribution of sample points (C) had a much smaller effect. Our empirical model for *eq. 6* becomes:

$$S_{\text{predicted}} =$$

$$S_{\text{observed}} / ((-0.271\ C + 1)\ p_e^{(-0.178 + -0.0348 \ln Pe)}\ p_i^{0.582}\ p_d^{0.949}) \qquad (Eq.\ 7)$$

Reconciling methods

The rate of species accumulation with sampled area was variable between the surveys (*Figure 6a*). Scaling to extent made the slopes of the different datasets more similar but the absolute number of species recorded hindered comparison of the results (*Figure 6b*). Accumulation of endemic species with sample area and extent were very similar to the pattern found in all species (*Figure 6c,d*). Therefore, we focused in the remainder of the analyses on total species richness.

The results of the different surveys could be made more comparable by calculating the expected number of species while taking into account the methodological differences in sampling (*Eq. 7*). Spatial distribution of sample points varied little between datasets and because of the low beta diversity in the study region, correcting for C had little effect on the general shape and relative position of the species-extent curves (*Figure 7b*). Correcting for partial sampling of extent (p_e) resulted in an overall increase in the rate of species accumulation (*Figure 7c*). Despite the correction for p_e the curve of dataset 1, and to lesser extent that of dataset 2, decreased slightly at very large scales. Correcting for partial sampling of individuals (p_i) merged the curves of datasets 2, 3 and 4, while the curve of dataset 1 was considerably lower over all scales of extent (*Figure 7d*). Correction for p_i resulted in dataset 4 in a slight overestimation in absolute species richness at very large scales. Correcting for partial identification of individuals (p_d) slightly increased species richness in all sets but had no effect on the relative position of the different datasets (*Figure 7e*).

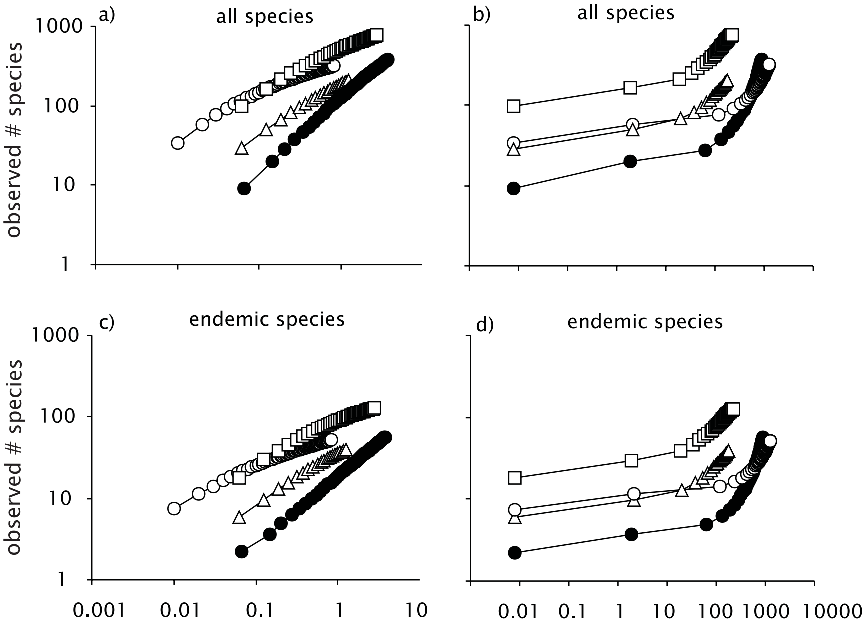

Figure 6 Observed species richness (a,b) and endemic species richness (c, d) scaled to sample area (a, c) and extent (b, d) of the four surveys studied. Dataset 1 (open circles), dataset 2 (squares), dataset 3 (triangles), and dataset 4 (black circles).

Correcting for all four factors of information shortage, i.e. C, p_e, p_i and p_d, greatly improved the comparability of the results of the four surveys over all scales of extent. Combined the corrections largely merged the curves of the different datasets (*Figure 7f*). The curve of dataset 1 was slightly lower than those of the other datasets while at very large scales a decrease in species numbers was predicted. Predicted species richness in extents between 120 – 130 km^2 varied between datasets (*Table 3*). Highest values were predicted in dataset 1 while lowest values were found for dataset 2. However, the predicted species richness of dataset 2 was still 67% of that of the dataset 1. Uncorrected species richness figures showed a much larger variation with dataset 4 having only 7% of the species richness observed in dataset 2. Nonetheless, predicted species richness tended to overestimate the actual species richness estimated on the basis of literature and a preliminary checklist of the area. Some 3000 species were expected to occur within the old growth lowland forests in the region at large scales (> 100 km^2). Predicted species richness at extents from 120 –130 km^2 were 107% (set 2) to 160% (set 1) of this figure (*Table 3*).

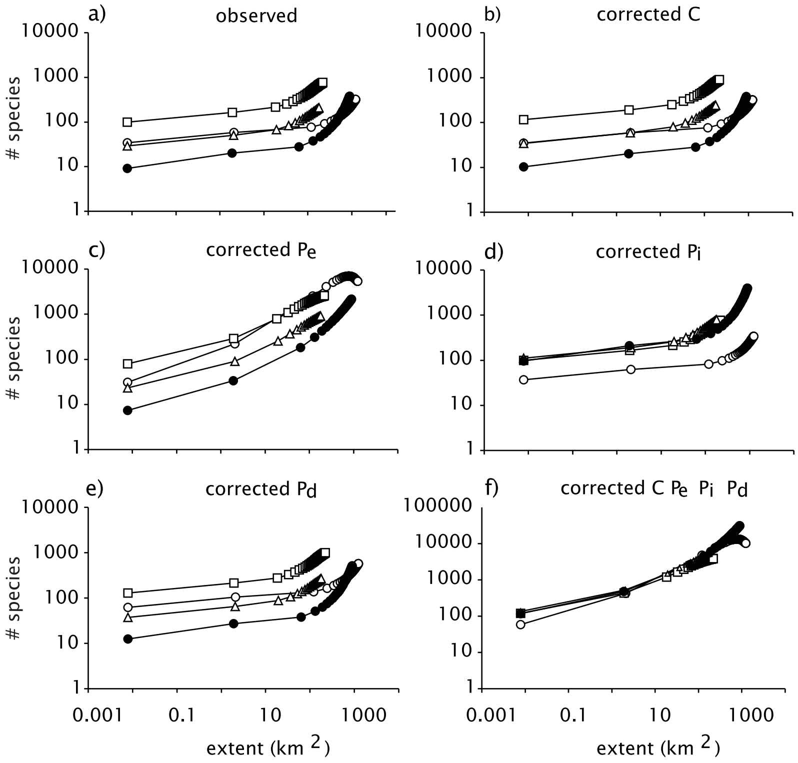

Figure 7 *Predicted species richness of surveys corrected for partial sampling, a) observed species richness (all species), b) predicted species richness corrected for spatial distribution of observations (C), c) predicted species richness corrected for partial sampling of extent (p_e), d) predicted species richness corrected for partial sampling of individuals (p_i), e) predicted species richness corrected for partial identification of individuals (p_d), f) predicted species richness corrected for all key factors. Note different scale y-axis. Dataset 1 (open circles), dataset 2 (squares), dataset 3 (triangles), and dataset 4 (black circles).*

Table 3 *Observed and predicted number of species at extents from 120 -130 km² for different survey methods in the same area of old growth lowland rain forest in south Cameroon*

dataset	observed # species	% of max.	predicted # species	% of max.	overestimation (%)[a]
1	77	15	4798	100	160
2	504	100	3213	67	107
3	160	32	4402	92	147
4	37	7	4483	93	149

[a] *Based on taxonomic literature and a preliminary checklist, actual species richness in the area was estimated at 3000 species.*

Discussion

Our analysis of four botanical surveys in the same area of old growth lowland rain forest in southern Cameroon showed that information relevant to conservation planning like species richness and endemic species richness were strongly influenced by survey method (*Table 2*; *Figure 6*). The main difference between sampling methods was the selection of the individuals that were included in the survey. We found that important components affecting the general shape of the species – extent relation were spatial distribution of samples (C), proportion extent sampled (p_e), proportion of individuals included in sampled area (p_i), and proportion of the sampled individuals identified (p_d). In simulations, these factors affected the number of species recorded differently (*Figure 5*). Recorded number of species was most sensitive to partial sampling of extent and individuals, and partial identification. Fitting of site-specific constants to data obtained by simulation enabled the correction of survey findings while taking into account the survey-specific methodological shortcomings. Despite the large variety in sampling methods and their generally poorly described methodology, predicted species numbers were surprisingly similar for all surveys over all scales of extent (*Figure 7*). However, correction for the effect of partial sampling resulted in an overestimation of species richness compared to estimations based on current biogeographical insights (*Table 3*). Nonetheless, the results suggest that the method we propose adequately copes with the essential differences between sampling methods and their consequences for the measurement of diversity. With the proposed framework we advocate a more efficient use of existing sources of botanical information for comparing conservation values of tropical forests.

The present analyses clearly showed the importance of scaling survey results to extent (E) instead of the sum of actually sampled areas (*Figure*

6). As stated earlier simply collating samples and suggesting that they formed a continuous area decouples the species from the actual area and therefore the interpretation of the species – area relation becomes troublesome at best. Especially for comparing different methods it is of paramount importance that the scale reflects the true area in which the species were recorded. Of course, species – sample area curves can also be corrected for partial sampling. However, as extent and spatial distribution of sample points are not explicit in such curves, they can only be corrected for proportion individuals included (p_i) and proportion individuals identified (p_d). Correcting for p_i and p_d did not improve comparability of results of the four surveys studied (data not shown) which stresses the importance of scaling the survey results to extent values.

We reconstructed the species-area relation from surveys with different types of information shortage (*Figure 1, 2*). Some of these surveys indeed focussed on biodiversity assessment while data collection in others was aimed at vegetation mapping or as baseline data for taxonomic revisions. As a result not all key characteristics important for reconciling assessments were readily available and a series of assumptions were required. It is likely that to some extent the observed variation is due to inaccurate estimations of sample areas, p_e, p_i, and p_d. Likewise, only one survey included fully enumerated plots (all individuals surveyed) and permitted to construct a standardised simulation dataset. However, this set of plots was a-typical with respect to extent and clustering (*Table 2; Figure 3*). Despite these shortcomings in the datasets, the results indicated that the majority of the assumptions made reflect general trends. For example, correcting for p_i merged the curves of datasets 2, 3, and 4 and suggests that the assumptions underlying the estimate of p_i for dataset 4 were accurate.

The identification of reduction factors was straightforward for p_i and p_d as these were based on plots and therefore the effect of partial sampling could be simulated over its full range. The effect of spatial distribution of sample points (C) on observed species richness required the extrapolation on the basis of a limited range of data points while variation in the data was high (*Figure 5*). By excluding samples from submontane forest, swamp forest and secondary vegetation in the present analyses, beta diversity in the area was kept low. As a result clustering of sample points will only have had a small effect on observed species richness. A more accurate assessment of the effect of spatial distribution of observation is especially important in areas with a high species turnover. The proportion of the extent sampled had the largest impact on observed species richness (*Figure 6*). However, its reduction factor was difficult to estimate, as the range of p_e values in the simulation dataset was very small and did not cover the range observed in the datasets. While the model $r_e = p_e^{(-0.178 + -0.0348 \ln Pe)}$ fitted the simulation data perfectly (*Figure 5*), the overestimation of predicted species richness in all surveys most likely originates from inaccuracies in the estimation of r_e especially at lower values of p_e. However, we expect that the described effects of partial sampling on observed species richness reflect the general trends for the rain forests in the study site, although the specific formulation of the reduction factors could likely be improved with additional data.

Tabel 4 Estimated scientist effort per hectare required for surveying, collecting and identifying (ID) plants in the different survey methods

method	1 vegetation mapping	2 diversity assessment (100%)	3 diversity assessment (10%)	4 herbarium collections
time needed to survey one sample (h)	1:04	5:05	1:36	8:00
area per sample (ha)	0.01	0.06	0.06	0.08
time needed to sample one hectare (h)	**106:40**	**81:32**	**25:36**	**100:00**
number of sterile collections made per ha	1000	1190	119	0
number of fertile collections made per ha	10	63	6.3	218:8
time needed to process one collection (h)	0:03	0:03	0:03	0:03
time needed to process one hectare (h)	**50:30**	**62:38**	**6:16**	**10:56**
time needed to ID one sterile collection (h)	0:05	0:05	0:05	0:05
time needed to ID one fertile collection (h)	0:48	0:48	0:48	0:48
time needed to ID one hectare (h)	**80**	**146**	**14:34**	**175**
time needed to survey, process and ID one hectare (h)	**245**	**290**	**46**	**286**

Ongoing large-scale habitat destruction in tropical forest regions, in combination with limited conservation funds and generally weak law enforcement, urges conservation planners to identify areas of high biological value (Frumhoff & Losos 1998; Myers *et al.* 2000). A wide range of criteria has been proposed to identify the value of forests for biodiversity conservation, including species diversity and level of endemism (de Groot 1992; Hawthorne 1996; Myers *et al.* 2000; Frumhoff & Losos 1998). However, assessment of these criteria in rain forest environments is expensive and time consuming and so far few regions are sufficiently explored to make accurate estimations for even a limited number of species groups (Howard *et al.* 1998, 2000; Lawton *et al.* 1998). In this study, we found that for terrestrial vascular plants total species richness and endemic species richness were highly correlated in all surveys. Despite the large methodological differences between surveys, the proportion of endemic plant species detected was surprisingly constant (i.e. 14.8 – 16.6%) in the old growth forests of the study area. Our findings support the analyses of Myers *et al.*(2000) that, at least for plants, level of endemism is an accurate indication of total species richness. In addition, recovery of endemic species was much faster in moderately disturbed logging gaps compared to highly disturbed shifting cultivation fields (van Gemerden *et al.* 2003a). Therefore, focus on endemic species in conservation assessments of tropical rain forests may be a cost-effective alternative to full species surveys (cf. Lawton *et al.* 1998).

The survey methods we studied differed in the selection of individuals included in the assessment. As a result, they also varied considerably in sampling effort. We estimated the average required sampling effort to conduct the described surveys on the basis of field experience. As involvement of scientists is generally the most expensive element in this kind of surveys, we focused on the required scientist input to survey, collect and identify individuals (*Table 4*). On a per area basis, sampling effort was highest in detailed botanical assessment (method 2) and the collection of herbarium specimens (method 4). The lowest effort was required for incomplete botanical assessment (method 3, 10% of the individuals surveyed). Most labour intensive were field sampling and plant identification. Proportion of specimens that was successfully identified (e.g. to species level) is likely to increase with identification effort. Datasets 1, 2 and 3 showed a similar response to increased sampling effort, while the recorded number of species in dataset 4 was significantly lower (*Figure 8*). However, the rate of increase was high in dataset 4 compared to the other sets. Moreover, the curves of the plot based surveys tended to level of at higher values of sampling effort, while rate of increase remained constant in the herbarium set. This effect was especially strong in dataset 1, and even more so for observed endemic species richness. Apparently, the capacity to continue to detect new species declines much more rapidly for surveys that relied partially on the classification of species by non-specialists, i.e. field identifications and morphocategorisation based to some extent on parataxonomy. The framework we propose for reconciliation of botanical assessments implicitly assumes that detection capacity is similar between datasets. Especially surveys based entirely on classifications by non-specialists, such as those promoted for surveys of invertebrates by Oliver & Beatie (1996a,b), and Kerr *et al.* (2000), are likely to show different detection trends compared to classifications by specialists. To cope with such methodological differences the present framework for reconciliation requires further expansion.

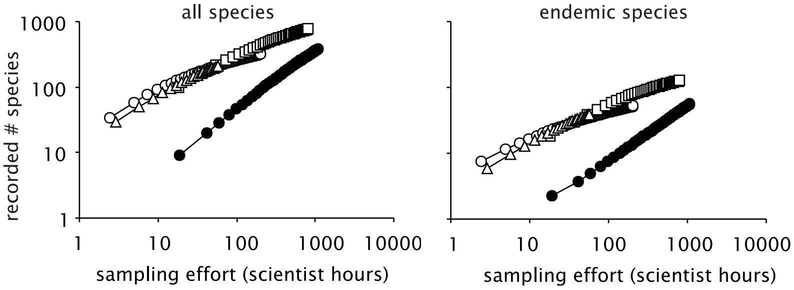

Figure 8 Observed species richness in relation to scientific effort made for surveying, processing and identifying plants in the four surveys in the same area of lowland rain forest. Dataset 1 (open circles), dataset 2 (squares), dataset 3 (triangles), and dataset 4 (black circles).

Conclusions

The main focus of the present study were the effects of partial sampling on observed species richness, and how methodologically different surveys of plant diversity in especially tropical rainforests can be compared. The reconciliation of methodologically different assessments of plant diversity can contribute to our understanding of patterns of diversity and endemism in tropical rain forest regions that are currently poorly explored. As biodiversity assessments in floristically diverse rain forests are generally time-consuming and little cost-effective, making optimal use of all currently available sources of biodiversity information could contribute to both quick and accurate assessment of conservation needs. The suggested method largely contributes to reserve site selection studies where the distribution and richness of species and endemics are crucial prerequisites (e.g. Margules *et al.* 1988; Freitag & van Jaarsveld 1997, 1998). For such studies, incomplete and fragmented data collected by different methods, are often available. This first attempt to reconcile four methodologically different surveys in old growth lowland rain forest in southern Cameroon suggests that species – area relations can be reconstructed from incomplete sample data if the key characteristics of the methods and the site can be statistically described. With these species – area relations local biodiversity can be estimated and the expected effect of increasing size and amount of reserve sites on the protected biodiversity can be calculated. Reliable documentation of these components of surveys would greatly enhance their use for comparative biodiversity analyses.

Acknowledgements

This study was carried out in the framework of the Tropenbos-Cameroon Programme (TCP). We like to thank the staff of TCP, Nationaal Herbarium Nederland – Wageningen University branch, National Herbarium of Cameroon (IRAD) and Tropical Nature Conservation and Vertebrate Ecology group of Wageningen University for their support. This study was partly funded by the European Commission (DG VIII) and Tropenbos International.

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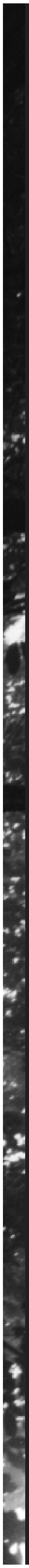

Chapter 6

Synthesis: Disturbance, diversity and distributions in Central African rain forest

Barend S. van Gemerden

Introduction

Plant diversity of tropical rain forests, among them those of Central Africa, is typically high. While tropical rain forests cover only 7% of the Earth, they are estimated to harbour more than 50% of all terrestrial and freshwater species (Wilson 1995). Moreover, these forests generally have many species with low abundances as well as many species with restricted geographical distributions. Despite their widely appreciated contribution to global biodiversity and the notion that large-scale forest degradation is taking place, less than 14% of the tropical rain forests worldwide are presently protected by law (UNEP & WCMC 2003). The present conservation effort is far too low to protect all rain forest species from present and future threats. To counter the loss of biodiversity as much as possible, conservationists are challenged to balance conservation need with societal demands for rain forest goods and services (Bowles *et al.* 1998; Myers *et al.* 2000; Balmford *et al.* 2001; Beattie & Ehrlich 2001). However, our understanding of the functioning of these complex ecosystems is still limited and therefore it is difficult to assess the compatibility of different forms of land use and biodiversity conservation. Essential elements for the identification of effective conservation measures and sustainable forms of land use are insights in the coexistence of rain forest species and the maintenance of high and characteristic diversity.

The stature of tropical rain forests is impressive. The tree canopy is often at heights of more than 40 meters with emergent trees reaching 55, and occasionally even 70 meters high. As a result of this impressive physiognomy, a long held perception was that tropical rain forest were extremely stable environments and high diversity resulted from long periods of speciation and coevolution (Hill & Hill 2001). Detailed paleoecological, biogeographical and climatological research has now shown that tropical rain forests were severely affected by climatic changes during the Pleistocene and the Holocene (Goldammer 1992; Jolly *et al.* 1997; Moore 1998). Similarly, small disturbance events have been shown to influence composition and diversity of tropical rain forests (Whitmore & Burslem 1998). It is now commonly accepted that frequent small and occasional intermediate-sized disturbances are common features in most tropical rain forests and are important elements in current theories on the origin and maintenance of high species diversity (e.g. Huston 1994; Rosenzweig 1995; Hubbell 2001).

Disturbances are relatively discrete events in time that cause high mortality of biomass and change the structure of a population, community or ecosystem (Pickett & White 1985; Huston 1994). Natural disturbances occur over a wide range of spatial and temporal scales and include global climate change, hurricanes, earthquakes, volcanic activity, large-scale river dynamics, as well as the passage of forest elephants, insect attacks and individual tree falls. The biotic and abiotic processes that influence species diversity vary with the scale of organisation of biological and ecological systems (i.e. community, ecosystem, landscape, region; *Figure 1*). At community level, local climate, community dynamics, competition, niche specialisation and space filling are among the most important processes and factors determining diversity. In ecosystems, species diversity is mainly influenced by environmental heterogeneity, and recruitment limitation. Regional climate and landscape heterogeneity are important factors at landscape scales, while global climate, productivity, geological processes, evolution, and extinction affects species diversity at regional and global scales. In a given area, present-day processes act upon the basis of species resulting from its cumulative biogeographical history (Hill & Hill 2001; Ek 1997; Putz *et al.* 2001). Especially important in this respect are the intensity, frequency and predictability of past disturbance regimes.

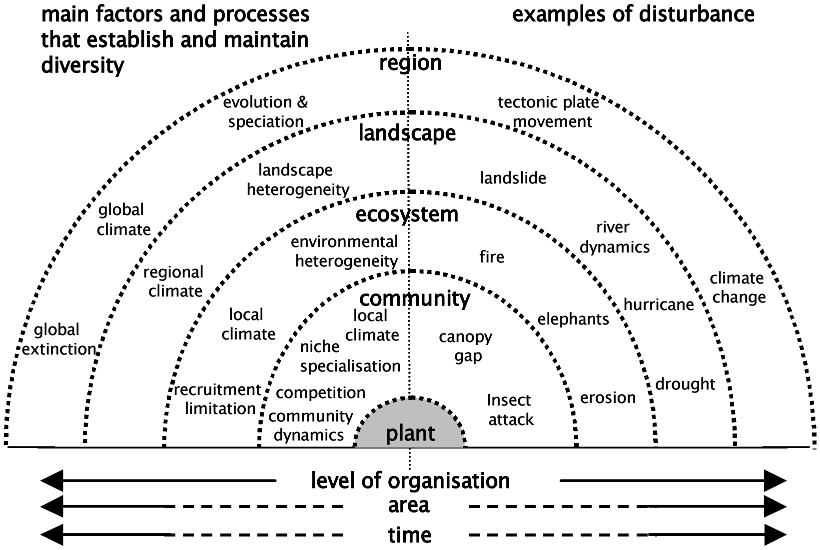

Figure 1 Main factors and processes that establish and maintain diversity and in relation to the organisation of biological and ecological systems, and some examples of (natural) disturbances.

While the natural dynamics of tropical rain forests has resulted in high levels of biotic diversity, many of the disturbances presently caused by humans pose a threat to this diversity (Sayer & Whitmore 1991; McKinney & Lockwood 1999). Human impact on tropical rain forests has increased over the last decades. In West and Central Africa, an estimated

0.43% of the rain forests are deforested annually, mainly for agricultural purposes (Archard *et al.* 2002) while logging operations are estimated to affect another 0.7% (Laurance 1999). In absolute terms, the conversion of African forests amounts to five million hectares per year (Laurance 1999). Triggered by the growth of the world population, especially in tropical countries, the scale of the disturbances is increasing. While historical human impact was mainly restricted to hunting and gathering and some small-scale agriculture, present human impacts include large-scale logging, plantations and (at least partly) global climate change. The present-day human induced disturbances are generally more frequent and more intense than the natural disturbance regimes during the last few millennia. As a result, a shift in species composition and diversity is likely to occur (Noss 2001). The growing pressure on tropical rain forest diversity requires the design (and implementation) of effective conservation strategies and sustainable forms of forest use. In-sight in the impact of human disturbances on rain forest diversity is therefore needed. In this synthesis, I will give an overview of the main effects of human land use on plant diversity in Central African rain forests.

Community level disturbance and diversity

Natural disturbances

The most common disturbance affecting rain forest plant communities are natural tree fall gaps (Aubréville 1938; Whitmore 1975). A disturbance in a plant community typically opens space (above and below-ground) and is usually associated with changes in temperature, and the availability of light, nutrients and moisture to plants (Denslow 1985, 1998; Ostertag 1998; Schnitzer *et al.* in prep.). Although its accurate measurement is difficult at best (van der Meer *et al.* 1994), gap size correlates positively with the relative change in microclimate directly after gap formation (Denslow *et al.* 1998; Brokaw & Busing 2000; but see Sheil & Burslem 2003). According to Jans *et al.* (1993), the average size of natural tree fall gaps varies in West Africa from 44 – 61 m^2, which is relatively small compared to other tropical rain forest regions, e.g. 75-93 m^2 in Central America and 91-104 m^2 in South America.

Natural gaps play a prominent role in theories on rain forest plant diversity (Huston 1994; Rosenzweig 1995; Hubbell 2001). By creating recruitment sites, gaps can contribute to high species diversity simply by harbouring large numbers of (young) plants, i.e. the density effect (Hubbell *et al.* 1999). Moreover, gaps can promote species coexistence if species differ in their ability to colonise the vacant space and resources (especially light). Many studies have shown that species may differ in their performance along the light gradient from gap centre to gap edge (Dirzo *et al.* 1992; Valladares *et al.* 1997; Svenning 2000; Schnitzer & Carson 2001; Pearson *et al.* 2003; Poorter & Arets 2003) and this suggests that gap partitioning may explain species coexistence (Brokaw & Busing 2000). However, most small to medium-sized gaps are filled through advanced regeneration, resprouting and recruitment from the seed bank (Bazaz 1991; Whitmore 1991). Therefore, presence prior to gap formation may be conclusive for species performance in gaps rather than gap size (Brown & Jenning 1998; Uhl *et al.* 1988: Ashton 1998), indicating a process of asymmetric competition (priority effects). Alternatively, the light gradient may be partitioned outside gaps by shade-tolerant species (Montgomery & Chazdon 2002). Once established in the shade, these species would increase their chances for growth in the event of gap creation.

Selective logging

So far commercial logging in Central Africa mostly entails the exploitation of a small number of large individuals of a small number of high graded species (Sayer *et al.* 1992; Bikié *et al.* 2000). Such forms of selective logging cause community level disturbances by felling trees, and the subsequent extraction of the log from the forest with heavy machinery. The felling of a tree generally creates two more or less clear openings in the canopy, i.e. one above the stump of the tree and one where the crown falls (Brokaw 1985). As crown fall gaps have the largest impact on vegetation structure and diversity, this zone is the main subject of this thesis.

Individual logging gaps are generally larger than natural gaps because exploited trees tend to be fully grown individuals with well-developed crowns. In contrast, natural gaps are often the result of the fall of medium-sized trees. In Cameroon individual logging gaps were generally 300-600 m^2 (Parren & Bongers 2001). However, many of the exploited species in the coastal zone of Cameroon have clumped distributions, e.g. *Lophira alata* (tradename Azobe). When simultaneously felled such trees created much larger gaps, occasionally up to 0.3 ha (B.S van Gemerden, personal observation). The change in microclimate associated with larger logging gaps is more extreme than in natural gaps. However, the logging gaps have in common with natural gaps that the stock of seeds, seedlings and saplings remains largely intact.

In the lowland rain forest of Cameroon, the vegetation in logging gaps recovered quickly through secondary succession (*chapter 3*). Plant density and basal area of logging plots were comparable to old growth forest after only five years. Species composition and species richness took only 14 years to recover. During the first 14 years of succession, logging gaps had higher species richness compared to the surrounding forest due to an influx of secondary species. However, the results suggest that most species of the later stages of succession were present soon after gap creation. Forest disturbance may increase insect damage to plants, especially herbivory on young leaves (Coley & Barone 1996). In logged forests in Cameroon, saplings of timber species suffered more insect attacks compared to old growth forests although most of these were not lethal to the plants (Foahom 2002). In Cameroon, recovery was quick compared to other tropical forests. For instance in Uganda, recovery of forest structure following selective logging took more than 50 years (Plumptre 1996).

Assessment of the effects of logging gaps on species diversity compared to natural gap dynamics is difficult as many studies (including the present) use logging gaps as a proxy for natural gaps. Gap size mainly affects microclimate and subsequently larger gaps through logging could affect niche availability and interspecific competition. However, in Cameroon we found that local recruitment conditions were important early in succession but less so in later stages (*chapter 4*). These findings suggest that the long-term impact of the logging gaps on species diversity may be very similar to those of natural gaps, although succession may be slower in extremely large gaps.

Shifting cultivation

Shifting cultivation in large parts of Central Africa entails the clearing and burning of forest patches of 0.5 – 1.5 ha which are subsequently interplanted with a variety of crops. A few large or valuable trees are often maintained in field preparation. Depending on soil productivity, the tending and harvesting gradually stops after 2-3 years and the land is generally left fallow for more than 10 years (Nounamou & Yemefack 2002). Field preparation and tending effectively eliminates advanced regeneration and stumps, and causes a depletion of the original forest seed bank (Uhl *et al.* 1981, 1988; Wijdeven & Kuzee 2000). Compared to natural gaps, temperatures and solar radiation are higher in shifting cultivation fields while soil moisture is lower.

Despite the abundance of recruitment sites, the initial stages of succession following shifting cultivation are generally dominated by a relatively small group of 'pioneer' species (Letouzey 1968; 1985; Swaine & Hall 1983; Uhl *et al.* 1988; Saldarriaga *et al.* 1988; Aide *et al.* 2000). In Cameroon, we found that vegetation recovery following shifting cultivation was much slower compared to recovery following selective logging (*chapter 3*). After 30-40 years, old fields in Cameroon were comparable to old growth forest in terms of species diversity, and in floristic composition after 50-60 years. However, species endemic to Lower Guinea (Nigeria – Gabon) did not recover from shifting cultivation in the 60 years of succession covered by the study. Floristic recovery from shifting cultivation ranged in other tropical regions from 40 to 200 years (Kappelle *et al.* 1995; Kurpick *et al.* 1997; Aide *et al.* 2000) and is likely to be also influenced by the landscape context (Liu & Ashton 1999).

Disturbance associated with shifting cultivation affects rain forest diversity by changing patterns in interspecific competition and niche availability compared to natural gaps. A small group of early colonisers can successfully dominate the vegetation for many years and delay the process of secondary succession (Schnitzer *et al.* 2000). Moreover, forest clearance and especially weeding involve a selection pressure for early reproduction. In addition, cultivators use parts of many plant species for food, traditional medicine, or construction and therefore maintain some of these species in their fields (van Dijk 1999; Nouna-mou & Yemefack 2002). As a result, shifting cultivation may cause a shift in long-term species composition after fields are abandoned.

Ecosystem level disturbance and diversity

Natural disturbances

Resulting from the high frequency of small-scale disturbances, tropical rain forests are mosaics of patches in different stages of succession (Aubréville 1938; Whitmore 1975). The turnover rate of rain forests varies by region and soil conditions. In a rain forest in Côte d'Ivoire, Jans *et al.* (1993) found that annually 0.8% of the area was directly affected by tree fall gaps and estimated that forest turnover was 244 years.

The spatial heterogeneity resulting from these gap-phase dynamics has been postulated to allow the coexistence of species. Locally, species composition may change with succession, e.g. pioneer species gradually giving way to shade-bearers (e.g. Swaine & Whitmore 1988). However, as new gaps are created continuously niche diversity is maintained at larger spatial scales (Hill & Hill 2001). Spatial heterogeneity is further increased by gap dynamics as gaps vary in size and orientation and can be formed at various stages in succession. Gap phase dynamics can also increase opportunities to coexist for more or less functionally equivalent species. As spatial distributions of individuals within an ecosystem may vary between species, species may have unequal chances in reaching newly formed gaps (Hubbell 2001). For instance, Condit *et al.* (2000) found that infrequently occurring species were more aggregated spatially than common species. This recruitment limitation is further enforced by differences in the timing of seed production in relation to mainly stochastic gap events and differences in dispersal capacity of species.

Selective logging

Within an area, logging operations are generally carried out within a short time-span, e.g. less than a year. As a result, logging creates more or less same-aged gaps and thus affects the relative proportion of the succession stages in the forest mosaic. In addition, clumped distributions of timber species will result in a change in the spatial distribution of successional stages.

Logging intensities in Central African rain forests are generally low compared to other tropical regions (Bikié *et al.* 2000). In a logging study in south Cameroon, Jonkers & van Leersum (2000) found that on average 0.7 trees or 10 m^3 were extracted per hectare. The associated logging operations caused physical damage to 5-25% of the area. Damage caused by logging was positively correlated to logging intensity. Log extraction with heavy machinery caused local soil compaction and, especially on steeper slopes, lead to changed run-off patterns and increased soil erosion (Waterloo *et al.* 2000).

Species distribution patterns at larger spatial scales had a large influence on plant recruitment in the later stages of succession for most growth forms (*chapter 4*). Species composition of especially large trees was strongly influenced by the vegetation mosaic. A similar but smaller effect was found in shrubs and small trees. These results indicate that shifts in spatial and temporal distribution of succession stages, and hence the relative abundance of species at larger scales, will affect recruitment patterns after logging operations. For instance for shrub species, floristic similarity of old and young logging gaps was high in landscapes dominated by secondary vegetation and much lower in landscapes dominated by forest vegetation (*chapter 4*). As the majority of the species endemic to Lower Guinea are shrubs (*chapter 3*), this poor recovery in fragmented landscapes is of concern to biodiversity conservation. The importance of vegetation composition at larger spatial scales was also shown for rain forest trees in Panama (Hubbell & Foster 1986; Hubbell *et al.* 1999). Therefore, logging intensities higher than natural gap-phase dynamics are likely to cause a shift in species composition and diversity of rain forests in Central Africa (cf. Chapman & Fimbel 2001).

In Central Africa, and in many other tropical regions, logging operations focus on a few species only. In most parts of Cameroon, logging companies are currently only exploiting five tree species (Bikié *et al.* 2000). In south Cameroon, 60% of the extracted volume was accounted for by a single species, i.e. *Lophira alata*. In general, only individuals with large sizes (e.g. dbh ≥ 80 cm) and good quality boles are selected. However, nearly all individuals within an area that meet these criteria are generally exploited. Only trees that are difficult to reach by loggers, e.g. in wamps or on steep slopes, or are located in areas with overall low timber density may escape exploitation. This selection for high-grade individuals may affect the genetic variability of the targeted species as only low quality and small individuals remain after exploitation. The effects of this selection pressure may be especially strong if areas are repeatedly logged.

Shifting cultivation

Fields in shifting cultivation systems are gradually abandoned after two to three years and left fallow for more than ten years. For socio-economic reasons, new fields created by farmers often lie in close proximity to the old fields. Generally, this confinement to the same area results in a shifting mosaic of vegetation patches differing in age.

Compared to natural gap-phase dynamics (i.e. a forest mosaic of gaps in different stages of succession), shifting cultivation mosaics have a high abundance of light- demanding and often fast-growing species. Repeated cultivation in the same area will favour those species that reproduce quickly and are good dispersers. Generally, such species are generalists with large geographic distributions and therefore of little interest to biodiversity conservation. In Cameroon, we found that species with large geographic ranges were relatively abundant in old shifting cultivation fields (*chapter 3*).

In heavily disturbed sites, forest recovery is mainly limited by the availability of seeds. The species that are successful in reaching open sites and are capable of avoiding seed and seedling predation are generally pioneer species (Wijdeven & Kuzee 2000). In abandoned agricultural fields in Uganda, Chapman & Chapman (1999) found that visitation by frugivores facilitated recruitment of tree seedlings. They also observed that seed dispersal by frugivores was mainly limited to birds and that larger mammals very rarely entered the old fields. Therefore, wind, birds and possibly bats appear to be the main dispersal vectors in shifting cultivation mosaics. These vectors are only capable of dispersing small seeds, and therefore large-seeded species will be less successful in colonizing old shifting cultivation fields (McClanahan & Wolfe 1993).

Landscape level disturbance and diversity

Natural disturbances

Disturbances at landscape-scale are rare phenomena in large parts of Central Africa (Olivry 1986; Jans *et al.* 1993). Recent volcanic activity is restricted to the Mount Cameroon region in southwest Cameroon (latest eruption in 1999) and near Goma in the eastern part of the Democratic Republic of Congo (2002). In the rain forest region of Cameroon, the climate is characterised by two distinct wet seasons (August – November, March – May) and total rainfall decreases from West to East (Olivry 1986). The winds are generally Southwest and gentle (Waterloo *et al.* 2000). However, at the beginning of the wet seasons the opening frontal storms can be quite violent and most natural tree falls occur in this season (Cable & Cheek 1998). Within our study area no signs of large-scale river dynamics were found. The strongly weathered acid clayey soils are remarkably uniform throughout the area (van Gemerden & Hazeu 1999).

Selective logging

Logging operations include the creation of a network of roads, bridges, timber landings, skid trails and logging gaps. Network intensity is likely to be positively correlated to logging intensity, although poor planning of forest operations has also been shown to affect the density of the network (Jonkers & van Leersum 2000). Such networks may effectively fragment the landscape and may change the flow of species between forest patches (Hamilton 1999; Putz *et al.* 2001). Edge effects negatively affect the persistence of forest patches in fragmented landscapes (Laurance *et al.* 1997; Gascon *et al.* 1999, 2000; Laurance 1999; Mesquita *et al.* 1999; Putz *et al.* 2001). However, the logging operations by itself may not have the largest effect on plant species composition. By removing physical barriers, logging roads greatly improve access to forests by local populations. In Central Africa, hunting pressure on larger vertebrates increased drastically as a result of logging (Wilkie *et al.* 1992). Similarly, in areas with high population pressure and land shortage an influx of shifting cultivators can be expected (Laurance 1999). In general, these associated land uses will greatly determine whether forest species composition and diversity recuperates from logging disturbance (Frumhoff & Losos 1998; Laurance 1999, 2001).

In our study site in south Cameroon, human population pressure was relatively low (8.6 person km^{-1}) and population increase marginal (+0.4% yr^{-1}; Lescuyer *et al.* 1999). Little evidence was found that populations actively followed logging operations, except for the commercial collection of non-timber forest products (e.g. bark of *Garcinia lucida*, seeds of *Strophantus* spp., rattans) and hunting (van Dijk 1999). The density and variety of large mammals in the area has sharply declined during the last decades, mainly as the result of excessive hunting (Bekhuis 1997; Mbelli 2002). Many rain forest plant species have been shown to rely on frugivores for dispersal and germination (Gautier-Hion *et al.* 1985; Chapman & Chapman 1995; Whitney *et al.* 1998; Poulsen *et al.* 2001; Mbelli 2002). However, the full effect of faunistic depletion on future plant species composition and diversity in logged landscapes is still poorly understood.

Shifting cultivation

Shifting cultivation may also lead to forest fragmentation. In our study site, and most likely in other parts of Central Africa as well, fields were confined to areas around villages and along the main access roads (van Gemerden & Hazeu 1999). The proportion of actual fields and recently abandoned fields in shifting cultivation mosaics varied between 20-40% while young secondary vegetation accounted for 20%. The remainder of the area was covered by old secondary forest and isolated patches of old growth forest. Cacao plantations cover only a small portion of the landscape mosaic. At present, most newly created fields are made in secondary forests.

In addition, hunting pressure is dramatically high close to the villages and in shifting cultivation areas. Only few people have access to rifles but trapping with snares is widespread. On average a household collects 5.6 kg of game per week (van Dijk 1999). Most frequently captured species are Giant Gambian rat (*Cricetomys gambianus*), Cane rat (*Protoxerus stangeri*) and Brush-tailed porcupine (*Atherurus africanus*). Although detailed studies are lacking, available data suggest that larger mammals are extremely rare close to villages (Bekhuis 1997; Mbelli 2002). High hunting pressures will further limit the possibilities for dispersal by animals and increases the proportion of seeds dispersed by wind, birds and bats. Therefore, the long-term chances of recruitment by large-seeded species are negatively affected by hunting.

Tropical rain forests are often regarded as pristine and undisturbed by humans. However, evidence is accumulating that the human use of these forests during the last millennia may have been much more widespread than previously thought. In Africa, evidence of human activities up to 3000 years ago was found in rain forest areas in Nigeria, Democratic Republic of Congo (former Zaïre) and Cameroon (Hart *et al.* 1996; Jolly *et al.* 1997; White & Oates 1999; Mindzie *et al.* 2001; Oslisly *et al.* in press). Likewise, large parts of the Amazon basin have likely sustained large populations during parts of the last 4000 years (Heckenberger *et al.* 2003).

These historical disturbances are likely to have influenced present-day species composition, especially of long-lived organisms like trees. In Cameroon, we analysed current tree species composition in relation to their recruitment preference and found that these structurally complex and species-rich rain forests still show signs of past large-scale disturbance events (*chapter 2*). These disturbances are most likely caused by shifting cultivation practices some three to four hundred years ago. Comparison of disturbed and undisturbed sites suggests that historical large-scale disturbances have a significant negative effect on tree species diversity at larger scales. This is contrary to the suggestion that in the absence of large-scale disturbances superior competitors successfully exclude inferior competitors and leads to low tree diversity (Connell 1978; Hart *et al.* 1989; Huston 1994). For instance, tree diversity in Guyana was found to be lowest in those sites that were least used by pre-Colombian Amerindians (ter Steege & Hammond 2000). The mechanisms that enable species long-term coexistence in disturbance regimes of frequent small-scale events, requires further study. Our findings do indicate that land use history may result in variation in species richness and therefore should be taken into consideration in conservation planning.

Global and regional level disturbance and diversity

Natural disturbances

The most important historical large-scale disturbances for present-day patterns of biodiversity were the periods of severe aridity and lower temperatures occurring in the past 40 000 years (Hamilton 1982; Bonnefille *et al.* 1990; Sosef 1994; Flenley 1998). These periods, more or less coinciding with world glacials, resulted in strong temporary reductions of the rain forest cover. At the maximum of the last glacial 18 000 years ago, the rain forests are hypothesised to have been reduced to a small number of 'forest refugia' surrounded by savannah vegetation (Haffer 1969). During interglacials the climatic conditions for rain forest species was generally more favourable and the rain forest cover extended again. The repeated retraction and expansion of the rain forest cover has had a profound impact on the distribution of species (Kingdon 1980; Sosef 1994; Maley & Brenac 1998). Haffer (1969) hypothesised that these climatic-vegetational fluctuations may have worked as a species pump by accelerating speciation in geographically isolated populations. However, Fjeldså & Lovett (1997) found that postulated Pleistocene refugia in lowland Africa are dominated by bird and plant species that represent lineages of pre-Pleistocene age. Moreover, patterns of recent species radiations within the lowland rain forests reflected present-day environmental variables. Highest rates of speciation were found in mountain areas and may reflect long-term stable precipitation regimes despite local and global climate changes (Fjeldså & Lovett 1997). Evidence is accumulating that the cyclic climatic-vegetational fluctuations during the Quaternary may have been as great a force for speciation as for extinction (Hewitt 2000). Current regions with high levels of endemism and species diversity are roughly located in Sierra Leone – Liberia, Côte d'Ivoire – Ghana, Cameroon – Gabon, and the Eastern part of the Democratic Republic of Congo (Kingdon 1980; Hamilton 1988; Sosef 1994). At smaller scales, the exact location of the highly biodiverse areas is less clear and may vary between species groups (Grubb 1982; Sosef 1994). Moreover, it has been suggested that riparian habitats along rivers may also have functioned as refugias (Colyn *et al.* 1991; Colinveaux *et al.* 1996; Leal 2001). In addition, many regions in Central Africa have been poorly studied and therefore diversity patterns may partly reflect sampling intensity (cf. Nelson *et al.* 1990).

Since the ending of the last glacial period, some 12 000 – 12 500 years ago, the climate in Africa became warmer and moister and climatic variability was since then less pronounced. Nonetheless, the El Niño Southern Oscillations (ENSO) also caused considerable variability in regional climates worldwide. Based on water-level records of the River Nile, Quinn (1992) reconstructed the occurrence of ENSO events during the last 1500 years. Apparently, there were two intense epochs of ENSO droughts in (East) Africa: 1765-1799 and 1692-1701. Most pronounced were the droughts associated with the ENSOs in the 1765-1799 period. Reynaud & Malley (1994) and Newberry *et al.* (1998) speculate that in Central Africa such droughts may have strongly increased mortality of the most drought-sensitive rain forest species. Higher forest dynamics would then result in a shift in species composition in favour of more light-demanding species. Such changes have been observed in Panama and make Condit (1998) predict that a structural four-week extension of the dry season could locally eliminate 25% of the species. However, in the African rain forest region the dry season is generally overcast and misty, and therefore the water stress that plants are exposed to may not be as severe as for example in Amazonia and Central America (Maley & Brenac 1998; Charles-Dominique *et al.* 2001). Moreover, Bigot *et al.* (2000) found that present-day ENSO periods appeared to have little effect on the variability of rainfall patterns in Central Africa. However, more data are needed to assess the long-term effects of relatively short droughts on rain forest species composition at larger scales.

Selective logging

Selective logging for a small number of high graded timber species may have evolutionary impact. Logging reduces the genetic variability of locally adapted populations and therefore reduces the capacity of timber species to adapt (Ledig 1992; Putz *et al.* 2001). Moreover, if large-sized individuals are repeatedly removed from a population, this will lead to a strong selection pressure for early reproduction and may affect life history traits of the species (Ashley *et al.* 2003; Stockwell *et al.* 2003). Recent studies in invertebrates, plants, fish, birds and mammals indicate that these changes can occur very rapidly, i.e. within a few generations (Ashley *et al.* 2003; Zimmer 2003). At present, little is known about the genetic variability of tropical (timber) species and how it is affected by human-disturbances. Meanwhile, efforts should be made to protect genetic diversity by reducing selection pressures and limiting forest fragmentation (Moritz 2002; Stockwell *et al.* 2003)

Shifting cultivation

Some survival strategies of plants are less successful in areas dominated by shifting cultivation. With a frequent disturbance regime, especially poor dispersers, niche specialists and species with a slow rate of reproduction have a disadvantage and populations of such species are likely to decline (McKinney & Lockwood 1999). The shift in species composition towards fast reproducing, well-dispersed species with broad ecological niches, will cause a regional decline in biodiversity as species composition of secondary vegetation following shifting cultivation is surprisingly similar over large areas (van Gemerden & Hazeu 1999).

Global climate change

Ozone depletion, and increase of airborne particulates and greenhouse gases, is currently invoking the largest human disturbance: global climate change. While the fundamental causes (both natural and anthropogenic) are generally appreciated, the full extent of global climate change is issue of much debate (Heywood & Watson 1995). Climate change is expected to invoke major changes in global vegetation cover as the result of changing temperature and precipitation (Gates 1990). However, the effects of climate change will differ profoundly between regions. For the tropical regions, Hulme & Viner (1998) constructed a climate change scenario based on the results of different models. The climate of this scenario can be expected before mid 21st century or as soon as 2030. For Central Africa, the scenario predicts a rise in temperature of less than 2°C. Although no change in total rainfall is foreseen, an increase in seasonality and interannual variability is expected. Global warming will also lead to a higher frequency of extreme rainfall events, and possibly an increase in storm intensity (Walsh & Pittock 1998).

For species composition and diversity in Central African rain forest, the most important changes are greater seasonality, larger interannual differences and lower soil moisture (Whitmore 1998). So far, information to assess the effects of climate change on biodiversity is largely lacking (Markham 1998). However, most vulnerable to climate changes are arguably populations found at the edge of a species' distribution range, species with restricted geographic ranges (endemics), and species only occurring in small isolated populations (Peters & Lovejoy 1992). It has been suggested that because tropical species tend to have more narrow niches than temperate species, shifts in species composition due to climate change are more likely to result in local extinction (Bazzaz 1998). Moreover, species are expected to react differently to climate change and this may jeopardise the highly specialised relations between coevolved species. Similarly, outbreaks of pests in a community may be the result of the (temporary) absence of its natural enemies (Markham 1998).

Although climate change is likely to have a large impact on species composition and diversity in the long term, current human land use in tropical regions is a much more acute threat to biodiversity. However, present land use practices also alter the resilience of species to adapt to climate change. The ability of species to adapt to new conditions is largely correlated to their genetic variability (Davies & Zabinski 1992). Forest fragmentation in general and particularly the selection of high graded timber species by logging, reduces population size and thereby most likely the genetic variability and the ability to adapt to climate change (McNeely *et al.* 1995; Stockwell *et al.* 2002). In landscapes altered by humans, species are also less likely to successfully avoid unfavourable conditions by retreating in successive generations to areas with more favourable conditions for survival. In fragmented landscapes and especially for short-range dispersers, the possibilities for such gradual shifts in distribution patterns are much reduced as human land use impedes successful colonisation (Quinn & Karr 1993; Whitmore 1998). Moreover, recent studies have shown that the forest fragments themselves are highly vulnerable for climate change, especially if dry periods are prolonged (Malcolm 1998). Human land use may also increase the frequency and extent of wildfires. In most rain forests of Central Africa, large fires are currently rare phenomena (Schwartz 1993; Hart *et al.* 1996; Newberry *et al.* 1998) but canopy opening by logging operations combined with higher seasonality are likely to make forests much more fire prone.

As a result of climate change and the limits posed by human activities it is likely that species composition of Central African rain forest will change in the near future. Species are likely to react individually to different aspects of climate change. Therefore, the result of climate change will not be a mere shift in the distribution of entire ecosystems, e.g. change in altitudinal range (cf. Flenney 1998). More likely, climate change will result in a major reorganisation of species and their interrelations. Species sensitive to prolonged dry periods and species with narrow distribution ranges are most vulnerable to local, and even global extinction, while species with high dispersal capacity and broad ecological niches are likely to extent their ranges. Based on contemporary population trends of a few species in human-altered landscapes and patterns in previous mass extinctions, McKinney & Lockwood (1999) estimate that between 5-29% of the species will be favoured by human-induced disturbances and will extent their ranges. In contrast, they predict that populations of more than 50% of the species will decline.

General conclusions

Central African rain forests are highly dynamic on all spatial and temporal scales. Present-day species composition and diversity of these forests reflects their cumulative biogeographical history. Therefore both present-day and historical disturbance regimes of forests should be considered to understand its current patterns of diversity and to predict its responses to future disturbances.

Disturbances resulting from human land use differ from naturally occurring disturbances by their intensity, frequency and spatial scale. Recovery of species composition and diversity relies on both the ability of species to reach recruitment sites as on their ability to successfully compete with other species and maintain themselves in these sites. Local recruitment conditions are especially important early in succession, while species composition at larger spatial scales is especially important in the later stages of succession. However, differences were found between growthforms with herbs being very sensitive to local recruitment conditions and large trees being sensitive to composition of the species pool at larger scales.

In many ways, selective logging mimics natural forest dynamics and short-term recovery in logging gaps is generally quick and complete. However, logging effectively removes large well-formed individuals of a very small group of high-graded species. This selection pressure may affect both the short-term viability of the population as well as invoke long-term changes in life-history traits. Logging operations contribute to fragmentation by creating a network of logging gaps, skid trails, timber landings, logging roads and bridges. In highly fragmented landscapes, the flow of species between areas may reduce as well as threaten the persistence of individual forest patches. Moreover, the infrastructure needed for logging operations may increase hunting pressure and shifting cultivation in previously poorly accessible areas.

Shifting cultivation strongly affects species composition and recovery is much slower and less complete than in logging gaps. Species with large distribution ranges are favoured by the repetitive disturbances at the cost of species with small distribution ranges. The species capable of surviving in landscapes dominated by shifting cultivation reproduce quickly, are wind or bird dispersed, and have broad ecological niches. Species composition in abandoned fields is remarkably similar over large areas and therefore this land use system reduces biodiversity at larger scales. Even after several centuries, areas that were most likely affected by historical shifting cultivation activities had fewer species than forest without traces of historical large-scale disturbances.

Biodiversity conservation in Central Africa

The rain forests in Central Africa are one of the last major ‘wilderness’ areas in the World (Mittermeier *et al.* 2003). At present, only some 7% of the region is protected by law (UNEP & WCMC 2003). In most parts of Central Africa, both deforestation rates and human population densities are relatively low compared to other tropical rain forest regions (Laurance 1999; Cincotta *et al.* 2000). Although these conditions may change in the near future, they provide a relatively favourable setting for biodiversity conservation.

Biodiversity conservation implies the protection of characteristic species and the ecological complexes of which they are part (e.g. Heywood & Watson 1995). For practical reasons and because they are important structural elements in tropical rain forests, this thesis focuses on vascular plants. While protecting species, it should be acknowledged that tropical rain forests are highly dynamic and that stochastic events, competition and predation cause constant shifts in its species composition and may even lead to (local) extinction. Moreover, it is unrealistic to think that any conservation scheme will effectively protect all species. What is required is a robust protection against harmful human interference in communities, landscapes and regions. Therefore, potential negative effects of human land use and global climate change must be accounted for in planning.

Conservation measures are especially important for species with restricted distribution ranges (endemics). For their survival, these species depend entirely on a specific region. Secondly, conservation measures should be directed at species that are sensitive to human-induced disturbances. Especially, species with slow dispersal rates, small population sizes, and high environmental selectivity should be targeted (McKinney & Lockwood 1999). Most likely, many of the endemic species also have these characteristics. These groups of species are likely the most extinction prone and therefore merit special attention in conservation (e.g. Mittermeier *et al.* 1998).

The distribution of endemic species in Africa has received considerable attention (Kingdon 1980; Hamilton 1988; Sosef 1994; Fjeldså & Lovett 1997; Kier & Barthlott 2001; Linder 2001; Moore *et al.* 2003). These studies indicate areas with high levels of local endemism in the Atlantic regions of Nigeria, Cameroon, Gabon, Republic of Congo and most likely also in Equatorial Guinea. In addition, the eastern part of the Democratic Republic of Congo is also rich in local endemics. In Cameroon, a countrywide vegetation map (scale 1:500 000) is available which permits a further stratification of areas (Letouzey 1968; 1985) although the degree of forest degradation needs updating. For the assessment of species richness at smaller scales (regions, landscapes) more detailed analysis are necessary. As biodiversity assessments are generally little cost-effective, we developed a method to compare the results of methodologically different biodiversity assessments (*chapter 5*). Although further testing is required, the results suggest that the method could greatly enhance the use of different existing sources of information (e.g. herbarium collections, mapping surveys and biodiversity assessments) for the quick identification of patterns in species richness. Unfortunately, virtually nothing is known at present about the ecology of most rain forest species and their vulnerability to human impact. Moreover, different species groups have been shown to react differently to disturbance (Lawton *et al.* 1998). However, in Uganda representative areas for most taxa resulted in a reserve network that covered other groups quite well (Howard *et al.* 1998). Plants appear to be a good proxy for a first evaluation of conservation need as they are taxonomically well-studied, relatively easy to record and their distribution is related to environmental conditions (van Rompaey 1993; Duivenvoorden & Lips 1995).

The expected climate changes at regional scales are still largely unclear. Meanwhile, a safe strategy would be to select conservation areas across environmental gradients (van Rompaey 1993). Current climate change predictions indicate larger seasonality and greater interannual variability in rainfall (Hulme & Viner 1998). As there are indications that along rivers and in swamps many rain forest species survived historical droughts (Colyn *et al.* 1991; Colinveaux *et al.* 1996; Leal 2001), such elements should feature prominently in regional reserve networks. Conservation areas should have robust linkages between them to allow species to disperse to areas where climate conditions allow survival (Noss 2001; Hannah *et al.* 2002). Moreover, such corridors allow species to maintain genetic variability, which increases their chances for adaptation in new environments. Fragmentation of forest areas has a severe negative impact on the persistence of forest patches because canopy opening destabilises the microclimate along the edges and causes higher dynamics (Laurance *et al.* 1997; Gascon *et al.* 1999; 2000; da Silva & Tabarelli 2000; Noss 2001). These edge effects are likely to become even more detrimental in a climate with longer dry seasons (Hulme & Viner 1998).

A regional network of large and interlinked landscape reserves is probably the best strategy to conserve most of the biodiversity during periods of rapid climate change (da Silva & Tabarelli 2000; Noss 2001). However, other actors also have legitimate claims on land and resources and setting aside land for strict conservation may not always be feasible (Cincotta *et al.* 2000; Balmford *et al.* 2001). Therefore, alliances must be sought with other stakeholders. Sustainable forest management has been widely promoted as viable combination of timber production and biodiversity conservation (Bowles *et al.* 1998; Fredericksen & Putz 2003).

In Cameroon, we found that vegetation recovery following logging was relatively quick (*chapter 3*). Especially large trees appeared to be recruitment limited (*chapter 4*), which suggests that as long as there are propagule sources nearby, species persistence in the forest is probably assured. In areas with smaller regional pools of forest species, we found that overall recovery was slower. Repeated logging in the same area is likely to affect both recruitment conditions and the availability of propgule sources. For sustainable forest management to be economically viable, polycyclic rotation cycles of approximately 30 years are suggested (Eba'a Atyi 2000; Fines *et al.* 2001). Moreover, sustainable forest management often includes silvicultural treatments, such as liberation of potential crop trees and liana cutting (Fines *et al.* 2001; Parren 2003). The combination of repeated logging and silvicultural treatments, will increase forest canopy openness as well as forest fragmentation. Kauffman & Uhl (1990) found that canopy opening of 50% in an Amazon forest had the potential to increase the average temperature inside the forest with 10°C and to decrease its relative humidity with 35%. It is unlikely, that the set of species of primary concern to conservation (forest specialists and endemics) will be favoured under such conditions. On the contrary, it is much more likely that pioneer species of little conservation value will be become dominant elements inside the logged forest.

Canopy opening in combination with prolonged dry seasons, is also likely to increase the frequency and extent of forest wildfires (Noss 2001). At present, fires are rare in large parts of the African rain forest biome (Schwartz 1993; Hart *et al.* 1996) and therefore rain forest species will not be adapted to even light surface fires (Uhl & Kauffman 1990). Moreover, Cochrane *et al.* (1999) found that forest fires increase the susceptibility for more intense fires in the future. Such a positive feedback will have serious repercussions for biodiversity conservation, timber production and efforts aimed at reduction of CO_2 emissions alike.

The arguments presented in this overview strongly suggest that the combination of biodiversity conservation and timber production in the same area will generally not be beneficial to the conservation goals unless logging damage and associated human land use can be minimised. However, forests used for sustainable timber production likely foster a wide range of forest plant and animal species (Bennet & Robinson 2000; Putz *et al.* 2001) and can be of value for conservation by linking protected areas.

An alternative alliance for biodiversity conservation can possibly found in the capitalisation of the environmental services of natural forest areas (Chichilnisky & Heal 1998; Beattie & Ehrlich 2001; Bonnie & Schwartzman 2003). For example carbon sequestration by tropical forests could provide a means for industrialised countries to meet the standards set by the Kyoto protocol. Unfortunately, this protocol emphasises reforestation above maintaining forest cover and is therefore not a direct incentive for forest protection (Stier & Fiebert 2002; Bonnie & Schwartzman 2003). However, in its wake a number of other initiatives have been developed. An example is the concept of 'conservation concessions' developed by Conservation International that aims at paying national governments and local communities to forego destructive forms of resource exploitation (Rice 2002). Similar initiatives are being developed and implemented by the International Union for the Conservation of Nature (Blom 2002). The elegance of these constructions is that biodiversity conservation is the primary objective in protected areas. In a recent survey, Brunner *et al.* (2001) have shown that parks and strictly protected areas in the tropics were largely effective in preventing habitat conversion and therefore in conserving biodiversity. Moreover, effectiveness of protection correlated with basic management activities such as enforcement, boundary demarcation and direct and sufficiently high benefit sharing with local populations (Prins *et al.* 2000; Brunner *et al.* 2001). This suggests that protected areas are a viable option for biodiversity conservation provided that sufficient funds are available. According to Rice (2002), there is a large and growing international willingness to fund biodiversity conservation programs. In addition to long-term funding, it is crucial for the success of concepts like conservation concessions that local actors are willing to execute management activities. Programmes along these lines may be an interesting alternative funding option for biodiversity conservation in tropical regions. However, field trials are urgently needed to test their practicality.

Local populations in tropical rain forest regions derive many goods and services from the forests in which they live. These populations have legitimate customary rights to natural resources although these are not always acknowledged by local and national governments and other user groups (Child 2000; van den Berg & Biesbrouck 2000). Management for biodiversity conservation may result in decreased access to natural resources. For the success of management it is crucial that all stakeholders concerned, participate in the process of decision-making (Lescuyer *et al.* 2001) and that the conservation programme results in tangible benefits for the local communities.

While it is imperative from an ecological viewpoint that a reasonable proportion of a protected area is old growth forest (e.g. to assure proximity of propagule sources of forest species), active restoration management of degraded areas could be part of a conservation strategy. In Cameroon, we found that recovery in logged forest and in shifting cultivation fields was relatively quick (*chapter 3*). Except for endemic species richness in old agricultural fields, all vegetation characteristics relevant to conservation recovered from the disturbance (e.g. species richness, species diversity, floristic composition). Moreover, it is likely that disturbed sites can recover more quickly and perhaps more completely if appropriate restoration measures can be identified. To increase the effectiveness of conservation management, insight is required in the mechanisms that make species and forest systems vulnerable to human induced disturbances, including global climate change.

Acknowledgments

I like to thank Han Olff, Marc Sosef, Antoine Cleef, Herbert Prins, Harm Duiker, Renaat van Rompaey, Wyb Jonkers, and especially Geerten Hengeveld for constructive discussions.

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Résumé

La présente étude à pour objectif de mieux appréhender l'impact des activités anthropiques sur la composition, la diversité et les niveaux d'endémisme des phytocénoses dans les forêts denses sempervirentes d'Afrique Centrale. Les perturbations dues aux hommes ont entraîné une dégradation des habitats de la région. La coupe sélective de bois d'œuvre et l'agriculture itinérante sur brûlis sont les deux formes d'activités humaines les plus répandues. L'évaluation des impacts à long terme des ces activités sur la composition floristique fournira les éléments d'importance pour la formulation des mesures de conservation et d'utilisation durable des ressources forestières.

Les perturbations sont des événements relativement discrets dans le temps et qui réduisent notablement la biomasse et causent des changements dans la structure des populations, communautés ou écosystèmes. Chaque individu ou espèce possède des aptitudes particulières à recouvrer l'équilibre suite à une perturbation ou concernant l'utilisation des ressources et de l'espace. Ainsi les perturbations engendrent des modifications (temporaires) des compositions floristiques et la diversité des phytocénoses. Dans la majeure partie des forêts denses sempervirentes africaines les petites ouvertures de la canopée, résultant des chutes de branches ou d'arbres, constituent la perturbation naturelle d'importance. Les perturbations de grande envergure, qui incluent les glissements de terrains, l'activité volcanique et le dynamisme des systèmes riverains aux cours d'eaux, apparaissent marginaux durant le millénaire passé. Dès lors il est fort probable que les espèces actuelles sont bien adaptées aux fréquentes perturbations de faible amplitude. De façon analogue à la dynamique des phases de cicatrisation suite aux chablis, les activités anthropiques peuvent être considérées comme des perturbations. Cependant, elles sont généralement beaucoup plus grandes, plus fréquentes, et plus intenses que les chablis naturels. Il en résulte souvent des effets plus pervers à long terme sur la composition floristique et la diversité des phytocénoses.

Le site principal du programme de recherche Tropenbos - Camerounnous a servi de zone d'étude. Il couvre une superficie de 2000 km^2 de forêts au sud Cameroun (3°N, 10°E). La végétation a été échantillonnée dans des forêts primaires, d'anciennes trouées résultant d'exploitation du bois d'œuvre et âgées de 5, 14 et 27 ans, et d'anciennes zones de culture d'âge variant entre 10-20, 30-40 et 50-60 ans. Toutes les plantes vasculaires (y compris tous les types biologiques) ont été collectées dans chaque placeau. L'analyse détaillée de l'impact humain sur la composition floristique s'est faite dans 10,1 ha. Beaucoup d'effort a été consacré à la collecte et l'identification des 11 000 échantillons de plantes. La détermination des plantes a été faite par des spécialistes. Les échantillons ont été envoyés aux herbiers de Wageningen (WAG) et IRAD/Tropenbos à Kribi. 75% des spécimens ont été identifiés au niveau espèce et 20% comme *morphospecies*. Au total 1264 espèces ont été formellement identifiées. On y dénombre 261 espèces qui se retrouvent uniquement dans la Basse Guinée (i.e. sud Nigéria - Gabon). Parmi ces espèces 51 espèces ne se retrouvent que dans les forêts denses sempervirentes du Cameroun.

Les forêts denses sempervirentes sont souvent considérées comme des forêts vierges. Dans le *chapitre 2* nous avons analysé l'historique de la perturbation de 16 ha de forêts dense sempervirentes considérée comme 'vieilles', structurellement complexes et riches en espèces (les données proviennent du projet de recherche en silviculture du programme Tropenbos – Cameroun). Le recrutement des espèces suivant un gradient de perturbation, allant des parcelles de culture itinérante sur brûlis, aux trouées de canopées, et aux vieilles forêts denses, a été comparé à la composition floristique actuelle. Dans neuf sur seize placeaux, les vieux (grands) arbres montrent une préférence de recrutement au niveau des parcelles jadis mises en culture alors que les jeunes arbres se retrouvent plus au niveau des petites trouées ou sous couvert dense. Ces résultats indiquent que ces placeaux ont déjà connu un régime de perturbation, notamment des perturbations de grande envergure spatiale. La datation de ces perturbations remonte à 300 – 400 années. La grande fréquence de charbon sur les sols de la forêt, et les données anthropologiques corroborent les types de distributions de perturbations d'origine anthropique au niveau des différents placeaux. Curieusement la richesse spécifique à large échelle s'est avérée plus faible au niveau des sites perturbés historiquement que dans ceux qui n'ont subit aucune perturbation. Ainsi les impacts des activités humaines passées sur la composition floristique et la diversité des forêts se ressentent encore de nos jours.

En dehors des aires protégées, les forêts sont l'objet d'exploitation forestière et de mise en culture. Les forêts secondaires deviennent de nos jours un élément important des paysages en Afrique Centrale. Le *chapitre 3* examine le potentiel et la contribution des forêts secondaires dans la conservation de la biodiversité. Les résultats montrent une reconstitution assez rapide et à plusieurs égards complète de la végétation dans les zones préalablement exploitées à des fins agricoles ou de bois d'œuvre. Cependant la reconstitution des espèces endémiques est assez lente dans les jachères. Nous avons remarqué que même après 60 ans après les cultures, la proportion d'espèces endémiques était toujours très faible comparativement aux vieilles forêts. La reconstitution assez rapide de toutes les caractéristiques de la végétation (y compris la richesse spécifique et la composition floristique) suggère que les forêts secondaires contribuent à la conservation de la biodiversité, en servant par exemple de zone tampon autour des aires protégées.

L'importance relative des processus locaux et régionaux de structuration de la composition floristique au cours de la succession forestière est analysée dans le *chapitre 4*. Les processus locaux sont relatifs à la capacité de compétition des espèces tout en évitant la prédation et les attaques d'agents pathogènes. Les processus régionaux font référence quant à eux à la dispersion et colonisation. Ces deux types de processus sont accrédités de favoriser une grande richesse spécifique dans les forêts tropicales primaires. Nos résultats indiquent que les processus locaux sont particulièrement important durant les premières phases de la succession forestière, alors que les processus régionaux sont prédominants pendant les phases tardives. Cependant les groupes de plantes ont montré différentes aptitudes face à ces processus. Les processus régionaux se remarquent plus au niveau de la composition floristique des espèces de grands arbres (hauteur maximale ≥ 15 m). Un effet similaire, mais moins marqué, a été observé au niveau des espèces de petits arbres (hauteur maximale entre 3 et 15 m) et des arbustes. Au contraire, les processus locaux structurent la composition floristique des herbacées. En général, les lianes ligneuses et non ligneuses se sont apparues comme des généralistes avec une composition floristique assez similaire dans tous les paysages mosaïques et tous les stades de succession. La variation entre groupe de plantes montre l'importance des processus locaux et régionaux pour une gestion et conservation effectives des espèces ciblées (e.g. espèces endémiques). Ainsi un traitement uniforme pour toutes les espèces apparaît incompatible aux sensitivités des espèces à fort potentiel de conservation face à la qualité et fragmentation des habitats.

L'absence quasi généralisée d'information sur la biodiversité est un problème sérieux pour la planification de la conservation dans la plupart des régions de forêts tropicales humides. Face aux destructions accélérées des habitats, les priorités en matière de conservation devraient être vite identifiées. Ainsi les sources d'informations disponibles devraient être utilisées de façon optimale. Cependant face à la multiplicité des méthodes d'évaluation une comparaison des résultats parait problématique. Dans le *chapitre 5*, nous avons tenté une réconciliation de différentes méthodes d'évaluation sur la base de leurs différences. A partir d'un échantillonnage partiel, les facteurs clés qui influencent la forme et position des courbes aires-espèces sont (1) la surface totale échantillonnée, (2) la distribution spatiale des observations, (3) la proportion de la surface totale échantillonnée, (4) la proportion des individus dans la surface échantillonnée qui sont inclus dans l'investigation, et (5) la proportion des individus inclus qui ont été adéquatement identifiés. Les simulations ont permis d'identifier les effets de l'échantillonnage partiel de ces facteurs sur les richesses spécifiques. En vue de tester la méthode nous avons comparé quatre investigations botaniques dans la même région au niveau des forêts primaires. Les investigations prises en compte sont (1) une inventaire pour la cartographie de végétation à l'échelle 1:100 000, (2) une évaluation botanique détaillée (100% des individus), 3) une évaluation botanique incomplète (10% des individus), et 4) des collections d'herbier. Une meilleure comparabilité des résultats a été obtenue suite à la correction spatiale de l'échantillonnage et au réajustement des résultats. Cette première tentative de combinaison de différentes méthodes d'investigation suggère que les relations aires – espèces peuvent être reconstruites à partir d'échantillons incomplets si les caractéristiques majeures des méthodes sont décrites statistiquement. Cette étude montre comment optimiser l'utilisation des données existantes pour évaluation des besoins en conservation des zones de forêts tropicales humides.

Dans le *chapitre 6*, une vue globale des principaux effets des activités humaines sur la diversité floristique des forêts primaires d'Afrique Centrale est présentée. Ces forêts primaires sont très dynamiques sur les plans spatiaux et temporels, et leur composition et diversité floristique actuelles ne sont que le reflet de leur histoire biogéographique. Dès lors les régimes de perturbations actuels et historiques devraient être pris en compte pour mieux comprendre les types de diversité actuels et prédire les implications de futures perturbations. Les processus biotiques et abiotiques qui influencent la diversité floristique sont non seulement différents mais aussi variables suivant l'échelle d'organisation des systèmes biologiques et écologiques (i.e. communauté, écosystème, paysage, région). L'influence humaine se caractérise non seulement par la dislocation des communautés végétales au niveau local, mais aussi par des effets pervers à une échelle plus large. A cette dernière échelle, suite aux dégradations et fragmentation des forêts, et aux changements climatiques mondiaux, la composition floristique des forêts primaires est susceptible de changer dans un avenir proche. Ainsi la gestion de la conservation devrait s'atteler à accroître les chances de survie des espèces endémiques et celles à faible distribution spatiale. Face aux tendances écologiques actuelles et incertitudes des changements climatiques futurs, il paraît plus judicieux d'investir dans de vastes réseaux d'aires protégées. De plus, il paraît peu probable que les zones d'exploitation forestière contribuent à la conservation de la diversité floris-

Samenvatting

Het doel van deze studie is inzicht te verkrijgen in de effecten van menselijk landgebruik op de soortensamenstelling en patronen van diversiteit en endemisme van plantengemeenschappen in Centraal Afrikaanse regenbossen. Menselijk landgebruik leidt in deze regio tot grootschalige habitatdegradatie. De meest wijdverspreide vormen van landgebruik zijn selectieve houtkap en zwerflandbouw. Inzicht in de lange termijn effecten van deze landgebruiken op plantengemeenschappen zal bijdragen aan de vaststelling van effectieve beschermingsmaatregelen en duurzame vormen van landgebruik.

Verstoringen zijn doorgaans relatief kortstondige gebeurtenissen die een hoge afname van biomassa tot gevolg hebben en veranderingen veroorzaken in de samenstelling van populaties, gemeenschappen en ecosystemen. Individuele planten en soorten verschillen in hun capaciteit om vrijgekomen ruimte en hulpbronnen te benutten. Dientengevolge kunnen verstoringen leiden tot al dan niet tijdelijke veranderingen in soortensamenstelling en diversiteit. Het meest voorkomende verstoringsregime in grote delen van het Afrikaanse regenbos is kleinschalige opening van het kronendak door vallende takken en bomen (*gap-phase dynamics*). Grootschalige verstoringen zoals landverschuivingen, vulkanische activiteit en veranderingen in de loop van rivieren zijn zeer zeldzaam geweest gedurende de laatste paar duizend jaar. Daarom zijn de nu aanwezige soorten waarschijnlijk in hoge mate aangepast aan een verstoringsklimaat dat gekenmerkt wordt door frequente kleinschalige verstoringen. Analoog aan de natuurlijke dynamiek van bossen kunnen menselijke ingrepen gezien worden als verstoringen. Door mensen in gang gezette verstoringen zijn echter in het algemeen grootschaliger, frequenter en intensiever dan natuurlijke verstoringen. Daardoor kan menselijk landgebruik leiden tot langdurige veranderingen in soortensamenstelling en diversiteit van plantengemeenschappen.

Het veldwerk voor de studies beschreven in dit proefschrift is uitgevoerd in het onderzoeksgebied van het Tropenbos-Cameroon Programma (TCP), een laagland regenbosgebied van 2000 km^2 in het zuiden van Kameroen (3°N, 10°E). Voor dit onderzoek is vegetatie geïnventariseerd in proefvlakken van 625 m^2 (25 x 25 m) .Deze proefvlakken bevonden zich in ongestoord bos, onder openingen in het kronendak (*gaps*) veroorzaakt door selective houtkap van respectievelijk 5, 14 and 27 jaar geleden, en in verlaten akkers van 10-20, 30-40 and 50-60 jaar oud. In de proefvlaken zijn alle groeivormen van terrestrische vaatplanten geïnventariseerd. Het totale geïnventariseerde oppervlak was 10.1 ha. Aan de identificatie van planten is hoge prioriteit gegeven en in totaal zijn bijna

11 000 planten verzameld en ter idenficatie voorgelegd aan specialisten. Het verzamelde plant materiaal is opgeslagen in de herbaria van Wageningen (onderdeel van Nationaal Herbarium Nederland) en Kribi (IRAD/Tropenbos). Ongeveer 75% van de planten zijn tot soortsniveau gedetermineerd terwijl daarnaast ongeveer 20% systematisch is gecategoriseerd als morpho species. In totaal zijn nu 1264 (botanische) soorten bekend van het gebied, waaronder 261 soorten met een verspreiding beperkt tot het laagland regenbos van Lower Guinea (Nigeria - Gabon), waarvan 51 soorten alleen voorkomen in het regenbos van Kameroen.

Tropische regenbossen worden vaak beschouwd als onaangetast door mensen. In *hoofdstuk 2* wordt de verstoringsgeschiedenis geanalyseerd van 16 ha structureel complex, soortenrijk en ogenschijnlijk ongestoord bos (data afkomsting van TCP bosbouw project). De voorkeur van soor-ten voor specifieke milieus voor verjonging langs een verstoringsgradiënt (van grootschalige verstoring in verlaten akkers, naar gaps en in gesloten bos), is vergeleken met de huidige soortensamenstelling van het bos (bomen met diameter op borsthoogte ≥ 10 cm). In negen van de 16 hectare percelen hadden oudere (grotere) bomen een voorkeur voor verjonging in verlaten akkers, terwijl de jongere bomen een preferentie hadden voor verjonging onder een volledig gesloten kronendak of onder bescheiden gaten in het kronendak. Deze resultaten geven aan dat deze negen proefvlakken eens zijn blootgesteld aan grootschalige verstoringen. Geschat is dat de verstoring 300-400 jaar geleden heeft plaatsgevonden. Het patroon van gestoorde en ongestoorde gebieden, de hoge frequentie van houtskool in de bosbodem en anthropologische data suggereren dat mensen verantwoordelijk zijn geweest voor deze verstoringen. Gebieden met een signatuur van grootschalige verstoring in het verleden waren op grotere schaal soortenarmer dan historisch ongestoorde gebieden. De resultaten geven aan dat de huidige bossamenstelling en diversiteit nog steeds historisch landgebruik weerspiegelt.

Buiten beschermde gebieden worden de bossen in Centraal Afrika in steeds grotere mate blootgesteld aan houtexploitatie en conversie naar landbouwgronden. Als gevolg van deze activiteiten worden secondaire bossen steeds belangrijkere elementen in het Centraal Afrikaanse landschap. In *hoofdstuk 3* wordt verslag gedaan van de mate van bosherstel na deze vormen van landgebruik, speciaal met betrekking tot het herstel van de natuurwaarden van plantengemeenschappen. De resultaten geven aan dat bosherstel in exploitatie gaps en verlaten akkers redelijk snel is en in veel opzichten ook verbazend compleet. Een opvallende uitzondering was echter het herstel van soorten met een beperkte geografische verspreiding in oude akkers. We vonden dat zelfs na zestig jaar de proportie Lower Guinea endemen (verspreiding beperkt tot laagland regenbos van Nigeria - Gabon) in oude akkers nog steeds lager was dan in ongestoorde bossen. Gezien het snelle herstel van alle andere vegetatiekenmerken (onder andere soortenrijkdom en floristische compositie), concluderen we dat desondanks secondaire bossen kunnen bijdragen aan het behoud van biodiversiteit bijvoorbeeld als bufferzones rond beschermde bosgebieden.

In *hoofdstuk 4* wordt het onderzoek naar het relatieve belang van lokale en regionale processen voor soortensamenstelling tijdens successie nader beschreven. Lokale processen hebben betrekking op het vermogen van soorten om succesvol te concurreren met andere soorten, en om predatie en ziekte te voorkomen. Regionale processen hebben betrekking op dispersie en kolonisatie. Processen uit beide categorieën worden aangedragen als verklaringen voor de typisch hoge soortenrijkdom in tropische regenbossen. Om inzicht te krijgen in het relatieve belang van lokale en regionale processen zijn de vegetaties met een vergelijkbare verstoringsgeschiedenis maar in verschillende landschapsmozaieken met elkaar vergeleken. Het ene landschapsmozaiek bestond voornamelijk uit bos (ten dele verstoord door selectieve hout-kap), terwijl het andere werd gedomineerd door secondaire vegetatie als gevolg van intensief gebruik voor landbouw. De resultaten geven aan dat lokale processen vooral belangrijk zijn in de jonge stadia van successie, terwijl regionale processen met name belangrijk worden in de latere successie stadia. Er zijn echter grote verschillen tussen verschillende groeivormen. Regionale processen bepalen in hoge mate de bossamenstelling voor wat betreft de grote boomsoorten (maximale hoogte ≥ 15 m). Een vergelijkbaar maar kleiner regionaal effect werd waargenomen bij kleine boomsoorten (maximale hoogte 3-15 m) en struiksoorten. Lokale processen waren daarentegen verantwoordelijk voor de samenstelling van terrestrische kruiden. Lianen en niet-houtige klimmende soorten waren in het algemeen wijdverspreide generalistenen een klein aantal soorten werd aangetroffen in alle landschappen en in alle successiestadia. Door de verschillen tussen de groepen soorten is het voor het vaststellen van effectieve beschermingsmaatregelen nodig om inzicht te hebben in de processen die bepalend zijn voor de verjonging van soorten met een hoge natuurwaarde (e.g. endemische soorten). Met een eenvormige gebiedsgerichte aanpak zal hoogstwaarschijnlijk onvoldoende rekening kunnen worden gehouden met de de specifieke kwetsbaarheid van deze soorten voor de gevolgen van habitatdegradatie en habitatfragmentatie.

Het algemene gebrek aan gedetailleerde informatie over patronen van biodiversiteit in tropische regenbossen bemoeilijkt een strategische planning van natuurbescherming in ernstige mate. De voortgaande degradatie van bossen in tropische gebieden maakt dat beschermingsprioriteiten snel vastgesteld moeten worden en dat daarom optimaal gebruik moet worden gemaakt van alle bronnen van informatie. De directe vergelijking van gegevens met betrekking tot biodiversiteit is echter problematisch als gebieden op verschillende manieren zijn geïnventariseerd. In *hoofdstuk 5* wordt een aanzet gegeven om methodologisch verschillende biodiversiteit assessments met elkaar in overeenstemming te brengen. De meest belangrijke factoren die de vorm en positie van de soort - oppervlak curve bepalen bij inventarisaties gebaseerd op steekproeven zijn: (1) grootte van het totale gebied waarin de observaties zijn gemaakt, (2) de ruimtelijke spreiding van de observaties, (3) de proportie van het totale gebied dat daadwerkelijk is geïnventariseerd, e.g. door middel van proefvlakken, (4) de proportie van het totale aantal individuen in het geinventariseerde gebied waaraan observaties zijn gedaan, en (5) de proportie van de bemonsterde individuen dat succesvol op naam kon worden gebracht. Door middel van computersimulaties hebben we een inschatting kunnen maken over de gevolgen van de inventarisatie 'incompleetheid' op het aantal waargenomen soorten en het aantal endemische soorten. Daarvan afgeleid zijn gebiedsspecifieke reductiefactoren bepaald welke tot doel hebben de soort - oppervlak relatie te reconstrueren uit incomplete datasets. Om deze methode te testen zijn de datasets van vier inventarisaties van hetzelfde laagland regenbosgebied met elkaar vergeleken. De gebruikte inventarisaties waren (1) een vegetatiekartering op schaal 1:100 000, (2) een gedetailleerde botanische assessment (alle individuen), (3) een incomplete botanische assessment (10% individuen), en (4) herbarium collecties. Door te corrigeren voor de beperking(en) van de verschillende inventarisaties voor de vijf boven genoemde methodische aspectenwerden de uitkomsten van de vier methoden zeer vergelijkbaar. De eerste resultaten suggereren dat het mogelijk is om soort - oppervlak relaties te reconstrueren uit incomplete datasets als de belangrijkste factoren van de methoden statistisch beschreven kunnen worden. Deze studie geeft een opzet hoe het gebruik van verschillende bronnen van informatie geoptimaliseerd kan worden voor het vaststellen van natuurbeschermingsprioriteiten in tropische regenwoudgebieden.

In *hoofdstuk 6* wordt een overzicht gegeven van de belangrijkste gevolgen van menselijk landgebruik op plantendiversiteit in Centraal Afrikaanse regenbossen. Regenbossen zijn zeer dynamisch op alle schalen van ruimte en tijd. De huidige soortensamenstelling en diversiteit is een afspiegeling van de cumulatieve biogeografische geschiedenis. Om inzicht te krijgen in de huidige patronen van diversiteit en om voorspellingen te doen over de gevolgen van menselijk ingrijpen moeten de karakteristieken van zowel de huidige als de historische verstoringen worden beschouwd. De biotische en abiotische processen die de diversiteit bepalen variëren met de schaal van organisatie van biologische en ecologische systemen (d.w.z. gemeenschap, ecosysteem, landschap, regio). Menselijk handelen heeft invloed op al deze niveaus van organisatie. Als gevolg van grootschalige bosdegradatie, bosfragmentatie en de voorspelde klimaatsveranderingen zal de soortensamenstelling van Centraal Afrikaanse regenbossen in de nabije toekomst zeer waarschijnlijk veranderingen ondergaan. Natuurbescherming moet zich met name inzetten om de overlevingskansen van endemische soorten en soorten met beperkte verspreiding te vergroten. In het licht van de huidige ecologische inzichten en de onzekerheid betreffende de te verwachten klimaatsveranderingen lijken investeringen in grote netwerken van beschermde gebieden op hun plaats. Bovenal is het onwaarschijnlijk dat beheer gericht op de duurzame productie van hout ook voldoende zal zijn voor de instandhouding van de karakteristieke plantendiversiteit, tenzij verstoringen tot een absoluut minimum kunnen worden beperkt. De verwachte vergroting van seizoensverschillen in combinatie met bosfragmentatie en minder dichte kronendaken door bosbouwkundige ingrepen zal waarschijnlijk leiden tot een sterke toename van pioniersoorten, terwijl soorten met hoge natuurwaarde waarschijnlijk zullen afnemen. Om de effectiviteit van beschermingsmaatregelen te vergroten is inzicht nodig in de mechanismen die soorten en bos-systemen kwetsbaar maken voor menselijke verstoringen, inclusief klimaats-veranderingen.

Summary

Résumé

Samenvatting

Summary

The aim of this study is to gain insight in the impact of human land use on plant community composition, diversity and levels of endemism in Central African rain forest. Human disturbance in this region is causing large-scale habitat degradation. The two most widespread forms of land use are selective logging and shifting cultivation. Assessment of the long-term effects of these land uses on plant species composition will provide elements for the identification of effective conservation measures and sustainable forms of forest use.

Disturbances are relatively discrete events in time that cause high mortality of biomass and change the structure of populations, communities or ecosystems. Individual plants and species differ in their ability to claim the previously utilised space and resources, and therefore disturbance events may cause (temporary) shifts in species composition and diversity. In large parts of the African rain forest biome, the most important natural disturbance regime is gap-phase dynamics in which relatively small canopy openings (gaps) are made by falling branches or trees. Larger-scale disturbances such as landslides, volcanic activity and large-scale river dynamics, have been extremely rare during the last millennia. Therefore, the present set of species is likely to be adapted to disturbance regimes characterised by frequent small-scale disturbances. Analogous to gap-phase dynamics, human land use can be considered as a disturbance. However, human induced disturbances are generally larger, more frequent and more severe. As a result, human land use may have long-term impacts on plant species composition and diversity.

The fieldwork for this thesis was conducted in the main research site of the Tropenbos-Cameroon Programme (TCP); an area of 2000 km^2 of forestland in South Cameroon (3°N, 10°E). Vegetation was sampled in old growth forest, logging gaps of 5, 14 and 27 years old, and in abandoned shifting cultivation fields of 10-20, 30-40 and 50-60 years old. Within plots, all terrestrial vascular plants (including all growth forms) were recorded. In total 10.1 ha was surveyed allowing the detailed analysis of human impact on full plant species composition. Much effort was devoted to plant identification and in total some 11 000 herbarium vouchers were collected, processed and sent to specialists for identification. Voucher material was stored in the Nationaal Herbarium Nederland – Wageningen University branch and in the IRAD/Tropenbos Field Herbarium in Kribi. Some 75% of the plants in the survey identified to species level and an additional 20% was systematically categorised as morphospecies. In total 1264 (botanical) species are now known from the area. These include 261 species with ranges restricted to Lower

Guinea (South Nigeria – Gabon) of which 51 are confined to the rain forest region of Cameroon.

Tropical rain forests are often regarded as being undisturbed by humans. In *Chapter 2*, we analyse the disturbance history of 16 ha of structurally complex and species-rich 'old growth' rain forest (data collected by TCP forestry research project). The recruitment preference of tree species along a disturbance gradient, ranging from shifting cultivation fields, to canopy gaps and old growth forest, was compared to present-day tree species composition. In nine plots out of 16, older (larger) trees preferred shifting cultivation fields for recruitment while younger trees recruited in small canopy gaps and under closed canopy. These results indicate that these plots once experienced a disturbance regime that included larger-scale disturbances. The estimated date of these disturbances is 300-400 years ago. Combined, the pattern of disturbed and undisturbed plots, the high frequency of charcoal in the forest soil and anthropological data strongly suggest that humans caused these disturbances. Surprisingly, species richness at larger scales was found to be lower in historically disturbed sites compared to undisturbed sites. Therefore, present-day species composition and diversity of old growth forests still reflects historical human impacts.

Outside protected areas, forests are subject to logging and shifting cultivation and secondary forests are therefore becoming important in many Central African landscapes. *Chapter 3* examines the potential of secondary vegetation to contribute to biodiversity conservation. The results indicate that vegetation recovery in logging plots and abandoned shifting cultivation fields is relatively quick, and in most aspects surprisingly complete. A notable exception is the poor recovery of endemics in shifting cultivation fields. We found that even after 60 years the proportion of endemic species was still significantly lower than in old growth forest. In light of the fast recovery of all other vegetation characteristics (including species richness and floristic composition), we conclude that secondary vegetation can contribute biodiversity conservation e.g. as buffer zones around protected areas.

In *Chapter 4* the relative importance of local and regional processes for structuring species composition during succession is analysed. Local processes refer to the ability of species to compete successfully with other species and avoid predation and pathogen attack. Regional processes refer to dispersal and colonisation. Both processes have been suggested to explain the typically high species richness in tropical rain forests. Our results indicate that local processes are especially important during the early stages of succession, whereas regional processes are especially important during the later stages. However, large differences were observed between different species groups. Regional processes mainly governed composition of large tree species (maximum height ≥ 15 m). A similar but smaller effect was observed in small tree species (3-15 m) and shrub species. Local processes structured composition of terrestrial herb species. In general, woody and non-woody climbers were widely distributed generalists with a very similar set of species occurring in all landscape mosaics and in all succession stages. The differences between species groups implies that effective conservation management requires insight in the importance of local and regional processes for the recruitment of target species (e.g. endemic species). A blanket conservation treatment for all species is unlikely to address adequately the specific sensitivity of species with high conservation value to habitat quality and habitat fragmentation.

The general lack of information on biodiversity patterns is a serious problem for conservation planning in most tropical rain forest regions. With ongoing habitat destruction, conservation priorities must be identified quickly. Therefore optimal use should be made of all currently available sources of information. However, direct comparison of results is problematic if assessment methods differ. In *Chapter 5*, we make a first attempt to reconcile different assessments by taking into account their methodological differences. The general shape and position of the species – area curve found by partial sampling is affected by five key factors. These are (1) the total extent in which observations are made, (2) the spatial distribution of the observations, (3) the proportion of the total extent sampled, (4) the proportion of the individuals in the sampled area that was included in the survey, and (5) the proportion of the included individuals that was successfully identified. Through simulations, the effects of partial sampling of these factors on observed species richness was identified. To test the method, we compared four botanical surveys conducted in the same area of lowland old growth rain forest. The surveys included were (1) a reconnaissance scale vegetation survey, (2) a detailed botanical assessment (100% individuals), (3) an incomplete botanical assessment (10% individuals), and (4) herbarium collections. Correcting for partial sampling and scaling the results to extent greatly increased the comparability between assessments. This first attempt to reconcile methodologically different surveys suggests that species – area relations can be reconstructed from incomplete sample data if the key characteristics of the methods can be statistically described. The study provides an outline for optimising the use of existing datasets in the evaluation of conservation needs in tropical rain forest areas.

In *Chapter 6*, I present an overview of the main effects of human land use on plant diversity in Central African forest. Rain forests are highly dynamic on all spatial and temporal scales. Present-day species composition and diversity reflects their cumulative biogeographical history. Therefore both present-day and historical disturbance regimes should be considered to understand current patterns of diversity and to predict its responses to future disturbances. The biotic and abiotic processes that influence diversity vary with the scale of organisation of biological and ecological systems (i.e. community, ecosystem, landscape, region). While human land use obviously disrupts local communities, the impact of humans is also evident on much larger scales. As a result of large-scale forest degradation, fragmentation and global climate change, species composition of most Central African rain forests is likely to undergo changes in the near future. Conservation management should aim at increasing the survival chances of endemic species and species with poor dispersal capacity. In light of the present ecological insights and the uncertainty of the upcoming climate changes, it seems wise to invest in large networks of protected areas. Moreover, it is unlikely that areas managed for timber production will be beneficial for the conservation of characteristic plant diversity unless damage control is rigid. The expected increase in seasonality in large parts of Central Africa, combined with forest fragmentation and canopy opening by silvicultural treatments and exploitation, is likely to increase the abundance of pioneer species while species of concern to conservation are likely to decline. To increase the effectiveness of conservation management, insight is required in the mechanisms that make species and forest systems vulnerable to human induced disturbances, including global climate change.