Plant communities in land-use systems of coastal Ecuador: diversity patterns, endemism, and species turnover at landscape scale

Dissertation
to obtain the Ph. D. degree
in the Faculty of Agricultural Sciences,
Georg-August-University Göttingen, Germany

presented by
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born in Ecuador

Göttingen, May 2006

D7

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Data of dissertation: 18-05-2006

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1

Diversity and conservation of plant communities in human-impacted landscapes

General introduction

Introduction

Biodiversity, or the variety of life forms, is in rapid decline as result of human alteration of the global environment (Dirzo and Raven 2003; Chapin et al. 2000). Deforestation, due to conversion of forest to agricultural land and logging for timber, is the leading cause of habitat destruction. In 2005, deforestation continued at an alarmingly high rate: about 13.1 million hectares per year (FAO 2005). Even when including afforestation and natural regrowth of forest in the analysis, the net global loss of forest area is estimated at 7.3 million hectares per year. South America, which accounts for 21% of global forest land, is the region which suffered the largest net loss with about 4.3 million hectares per year (FAO 2005).

Conservation of biodiversity is intimately linked to natural forest and has traditionally aimed at the establishment of protected areas. National reserves are the basis of most biodiversity conservation programs and their creation and management is a key measure of how well a country protects its biological resources. Unfortunately, the location and coverage of reserves has often been determined by their political value and low opportunity cost, rather than on their biological significance (Sierra et al. 2002). Globally, terrestrial protected areas cover a total of 18.8 million km^2, which represent 11.5% of the Earth's land surface (IUCN 2005). The remaining land is affected by human activities, predominantly agriculture and urbanization. Therefore, conservation efforts should not only focus on pristine forest within protected areas but complement these with a matrix of areas managed on the basis ecological principles (Moguel and Toledo 1999, Bawa et al. 2004). Some human-intervened ecosystems have been recognized for their high biodiversity value such as secondary forests, and managed and/or abandoned agroforestry systems (Bawa et al. 2004). At the sixth meeting of the Conference of the Parties to the Convention of Biological Diversity (COP6), the importance of conservation and sustainable use of forest biological diversity through the restoration of degraded forest landscape were emphasized (UICN and WWF 2002). Also, the international programme on biodiversity science Diversitas (www.diversitas-international.org), stresses the importance of research on biodiversity in managed ecosystems in order to make human activities more compatible with conservation (Jackson et al. 2005).

A possibility for sustainable management of tropical forest is based on the inherent dynamism and regeneration potential of species. It has been suggested that selective harvest of timber mimics natural forest disturbance, promoting regeneration of timber species and rare species that can benefit from removal of the dominant tree competitors. Cannon et al. (1998) showed that in the tropical forest of Borneo many tree species recovered from destructive commercial logging operation and that logged forest contained as many tree species as unlogged forest. Under the right conditions, forests regenerate and gradually recover after hurricanes, landslides as well as clear-cutting and conversion to pasture (Finegan 1996, Guariguata and Ostertag 2001). Therefore a high number of tree species and forest-dependent species can be found within some selectively logged forests and secondary forests (Chazdon 1998) although, depending on intensity, selective logging can also lead to forest degradation (Asner et al. 2005).

Land-use activities - whether practicing subsistence agriculture or intensive farmland production - have as ultimate outcome the acquisition of natural resources for immediate human needs (Foley et al. 2005). Modern agriculture, although successful in increasing food production, has also caused extensive environmental damage, for example, degradation of soil and water quality due to mechanized tillage and chemical inputs, and declines of non-target species due to inappropriate pesticide application (McLaughlin and Mineau 1995, Foley et al. 2005). In response, wildlife-friendly farming which increases densities of wild populations but may decrease agricultural yields has been promoted as a mechanism to reduce the impact of agriculture on biodiversity. Approaches include maintaining patches of natural habitats and extensively farmed seminatural habitats in the landscape, and minimizing the negative effect of fertilizers and pesticides (Green et al. 2005).

In tropical regions, agroforestry systems, which integrate trees and other tall woody plants on farms, have been recognized as management practices that diversify production for increased social and economic benefits and at the same time enhance conservation of tropical biodiversity (Perfecto et al. 1996, Schroth et al. 2003). Tropical agroforestry systems contribute to supporting many species and varieties of plants and animals that are not present in agricultural monocrops and pastures (Perfecto et al. 2003). Besides they could help conserve tropical biodiversity by creating a biodiversity-friendly matrix that facilitates movements among existing patches of natural habitats. For instance, in a study performed at Los Tuxtlas, Mexico, Estrada et al. (1997) showed that isolation resulting from forest fragmentation is diminished by small agroforestry patches that are used by birds as stepping stones.

Although the potential contribution of managed ecosystems to biodiversity at the landscape level has been recognized, their value for conservation has been studied much less than that of undisturbed ecosystems. We used a highly replicated field study to evaluate the importance of isolated patches of forest and managed land-use types in the conservation of plant diversity at a landscape scale.

Study area

Our study was carried out in coastal Ecuador in South America. Ecuador is the smallest of the Andean countries, with a surface area of approximately 283,000 km^2. Ecuador is traditionally divided into four natural regions: 1) the Pacific Coastal region, which includes the lower western slopes of the Andes below 1,000 m elevation; 2) the Andes Mountains above 1,000; 3) the Amazon which includes lowlands east of the Andes; and

4) the Galápagos Islands, a volcanic archipelago in the Pacific Ocean 1,000 km east of the mainland. Approximately 16,000 plant species are known to occur in Ecuador, of which more than 4,000 are recorded as endemic to the country (Valencia et al. 2000). The highest number of plant species is found in the Andes, about 64% of the total. In the coastal region, Amazon region and Galápagos 29%, 32% and 5% of the total species are found, respectively. A comparison of species composition reveals low similarity between the four different regions, which results in an exceptional high plant diversity (Jørgensen and León-Yánez, 1999).

Two biodiversity hotspots are found in Ecuador: the Tropical Andes and the Chocó-Darien-Western Ecuador (Myers et al. 2000). The Chocó region is globally recognized as one of the most biologically diverse; it supports large number of species and high levels of endemism. Our study was performed within the Chocó. Due to its relatively fertile soils and associated rapid expansion of agriculture and high human population density, the mayor part of the forest that once covered this region has been eliminated (INEC-MAG-SICA 2002).

The study was conducted on private farms spread across two agriculture-dominated landscapes. The first landscape (hereafter called high-impact landscape) is situated in the vicinity of the village of Jipijapa (UTM 17, 546800 S, 9849274 W) in Manabí Province, mid-west Ecuador, with an elevation range of 100-500 m. The climate is characterized by a mean annual precipitation of 1170 mm (excluding El Niño years), with a dry season from June to December (INAMHI, 2002). The original vegetation is semi-deciduous forest, which is an intermediate vegetation in the gradient from deciduous forest in southwestern Ecuador to rainforest in northwestern Ecuador. The canopy is composed of some species that shed their leaves during the dry season while others retain them. Among the most common species are *Centrolobium ochroxylum* Rose ex Rudd, *Castilla elastica* Sessé and the understorey palm *Phytelephas* *aequatorialis* Spruce (Jørgensen and León-Yánez, 1999; Sierra, 1999). In the high impact landscape agricultural practices were promoted by the land reform programs initiated in the early 1960s (Dodson and Gentry 1991). More than 60% of the total area is dominated by pasture, agroforestry systems with coffee, and the arable crops rice and maize, whereas natural vegetation, found mainly on steep slopes, accounts for less than 25% of the landscape (INEC-MAG-SICA 2002; Fig. 1a).

Figure 1. Two landscapes in coastal Ecuador: A. high-impact landscape where small patches of forest are embedded in a mosaic of agroforest systems, pasture, and arable land; B. low-impact landscape where large patches of forest are intact.

The second landscape (hereafter called low-impact landscape) is located to the north of the high-impact landscape, in the neighborhood of the village of Cabo San

Francisco (UTM 17, 72685 N, 604100 W), in Esmeraldas Province, with altitudes between 0 and 200 m. The climate is characterized by a mean annual rainfall exceeding 3000 mm (INAMHI 2002) and the absence of a distinct dry season. The natural vegetation, classified as lowland evergreen forest, is recognized as an extension of the wet Colombian Chocó region with a high proportion of endemic species. Common tree species include *Pseudolmedia rigida* subsp. *eggersii* (Standl.) C.C.Berg, *Exarata chocoensis* A.H. Gentry, *Virola dixonii* Little, and *Protium ecuadorense* Benoist (Burseraceae) (Jørgensen & León-Yánez 1999). In this region it is possible to find epiphytes in forest as well as on isolated trees within agroforestry systems. In the low-impact landscape, natural forest accounts for approximately 50% of the total surface (INEC-MAG-SICA 2002), as the expansion of the agricultural frontier has reached the surroundings of Cabo San Francisco much later than around Jipijapa (Fig. 1b).

We considered the five most predominant land-use types which represent a gradient of decreasing anthropogenic disturbance: open arable land with rice, pasture, managed agroforest, abandoned agroforest and forest. Rice and pasture have been established by manual sowing of *Oryza sativa* L. and *Panicum maximum* Jacq., respectively, and no mechanical soil tillage or chemical fertilizers are being used. Managed agroforest systems result from the replacement of understorey vegetation by coffee plants (in the high-impact landscape) or cacao plants (in the low-impact landscape) while maintaining a complex structured tree community with large old trees, a multi-layer canopy, and high tree species richness. In managed agroforest, sometimes original canopy trees have been replaced by species with economical value such as *Schizolobium parahyba* (Vell.) S.F. Blake or *Cordia alliodora* (Ruiz & Pav.) Oken. In abandoned agroforest no management has been practiced for about 15 years due to low market prices or commercialization problems. Abandoned agroforestry systems have a dense understorey. Finally, natural forests occur in the high impact landscape as small patches embedded in a matrix of agricultural land, with no visible present management, high heterogeneity in species richness and structure, but evidence of some selective logging in the past. In the low-impact landscape, forest fragments are the dominant habitat type in the landscape. Some selective logging of timber species has taken place but the disturbance level is relatively low.

Outline of chapters

In Chapter 2, species richness, floristic composition, and population structure in intervened forest, 12-15 yr-old abandoned coffee and actively managed coffee are investigated. The main question was whether natural regeneration in forest and abandoned coffee is mediated by bird dispersal and stimulated by the presence of agroforestry systems. We found similar structural characteristics among all land-use types. Besides, analyses of floristic similarity revealed similarities in species composition among seedlings of forest and abandoned agroforest. We conclude that isolated patches of intervened forest and abandoned coffee appear to have a similar pattern of forest recovery, providing a refuge for plant and bird species. Further, agroforestry systems offer stepping-stones to birds and thereby reduce isolation resulting from forest fragmentation.

In Chapter 3 plant diversity patterns at multiple spatial scales are analyzed through additive partitioning of species diversity. The main objective was to determine the critical spatial scales that explain overall plant diversity going from quadrants within plots to landscape scale. Plant diversity was mainly explained by the variability at large spatial scales, i.e., among landscapes and land-use types. The results demonstrated that human-intervened agroecosystems should not be disregarded when regional vegetation diversity is considered in tropical areas because they can contribute significantly to overall diversity.

Species with small latitudinal range sizes are often priority species in conservation programs. In Chapter 4 is analyzed how species with different latitudinal range sizes respond to anthropogenic disturbance. It was found that this response is influenced by traits that determine their range size. Although species with narrow range species are mainly preserved in forest, the other land-use type support many unique narrow range species and therefore makes an important contribution to their preservation at the landscape level.

In order to explain species coexistence in the different land-use types, the impact of anthropogenic activities on patterns of spatial aggregation at two spatial scales is investigated in Chapter 5. Patterns of human diversity in different land-use types and at different spatial scales could be explained by combining theories on intraspecific aggregation and the trade-off between colonization and competition.

At the end of this thesis, two appendices are included with the complete lists of tree and herb species sampled in both landscapes.

Chapter

2

Tree recovery and seed dispersal by birds, comparing forest, agroforestry and abandoned agroforestry in Coastal Ecuador

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Abstract

We used a highly replicated study to evaluate the contribution of patches of intervened forest, agroforestry with coffee, and abandoned agroforestry to tree diversity and recovery in a tropical landscape. In all habitats, plant structural characteristics, individual abundance, species richness and composition were recorded for the three plant size classes: adult trees, saplings, and seedlings. Furthermore, bird species richness and composition, and seeds dispersed by birds were recorded. Tree abundance was higher in forest habitats while saplings and seedlings were more abundant in abandoned coffee sites. Although species richness of adult trees was similar in the three habitats, species richness of saplings and seedlings was much higher in forest and abandoned coffee than in managed coffee sites. However, in spite of their relatively low species richness, managed coffee sites are an important refuge for tree species common to the almost disappeared mature forest in the area. Floristic similarity for adult trees was relatively low between land use types, but clearly higher for seedlings, indicating homogenizing processes at the landscape level. More than half of the saplings and seedling were not represented by adults in the canopy layer, confirming the importance of seed dispersal by birds between habitats. Our results show that each of the studied ecosystems plays a unique and complementary role as seed source and as habitat for tree recovery and tree diversity. This offers scope for conservation efforts in a highly impacted area, where isolation effects may be reduced by small patches of forests and agroforestry that are used by birds as stepping stones.

Keywords: forest structure; hotspot; species composition, seed dispersal, biodiversity, Ecuador.

Introduction

Tropical secondary forests, referred to as the woody vegetation that regrows after abandonment of agricultural activities or after selective logging, have been recognized for their value in conserving biological diversity in fragmented landscapes (Brown and Lugo 1990; Finegan 1992; Guariguata et al. 1997; Guariguata and Pinard 1998; Chazdon 2003). In general, secondary forest succession can be described in terms of a series of colonization stages during which forest structural characteristics (e.g., basal area, biomass, canopy height, stem density) and total number of species (i.e., species richness) can rapidly approach levels found in old-growth forest (sometimes in less than 30 years). However, recovery of floristic similarity, if any, may take centuries. (Uhl et al. 1988; Finegan 1996; Guariguata and Pinard 1998; Chazdon 2003; Hardwick et al. 2004).

Plant recolonization and species turnover are mainly determined by factors related to previous land-use type and intensity, such as soil conditions for germination or presence of soil-stored seed and seed arrival via off-site dispersal (Guariguata and Ostertag 2001). Wijdeven and Kuzee (2000) describe dramatic differences between abandoned pasture and nearby secondary forest with respect to both seed density and composition of the soil seed bank in Costa Rica. While grasses and herbs, and only few tree species dominated the seed bank of abandoned pasture, the forest bank consisted mainly of shrubs and trees. As intensity of previous land-use increases, the potential to regenerate from stored seed diminishes (Uhl et al. 1988; Guariguata and Ostertag 2001). Besides, seed bank floristic composition and density may also be influenced by the dominant type of land-use in the surroundings. For instance, Dupuy and Chazdon (1998) show that floristic composition of soil-stored seeds in secondary forest close to agricultural land contain large amounts of light-demanding shrub and herb species. In extensively deforested areas, seed dispersal is one of the critical factors for succession (Holl et al.

2000; Guariguata and Ostertag 2001; Marcano-Vega et al. 2002; Hardwick et al. 2004). Therefore, the lack of input of forest seeds is considered the overriding factor impeding reestablishment of forest in cleared or disturbed areas (Da Silva et al. 1996; Duncan and Chapman 1999; Holl et al. 2000; Ingle 2003). Frugivorous birds and bats are the most important seed dispersal vectors in fragmented landscapes as vegetation structure of grassland or early successional vegetation poses less of a barrier to them than to other vectors such as mammals (Ingle 2003). Most of the studies carried out in abandoned pasture found that seed input declined with the distance from source habitats since dispersal vectors (e.g. birds) do not cross open pasture unless attractive trees are in sight (Martínez-Garza and González-Montagut 2002; White et al. 2004). However, much remains unclear about dispersal when small patches of forested habitats are embedded in a matrix of agricultural land, especially about the role of birds as dispersal vectors in a mosaic landscape and about the importance of small forest fragments as refuge areas for birds.

We used a highly replicated field study to examine the processes of forest recovery as determined by land-use and seed dispersal in a fragmented landscape in western Ecuador. The area is part of the Chocó-Darién Western Ecuador biogeographical region, which is a global hotspot for biodiversity (Myers et al. 2000). We examined the variation in species richness, floristic composition and population structure between patches of logged forest, secondary forest (result of 12-15 yr of abandonment of agroforestry systems with coffee) and actively managed agroforestry systems with coffee. In addition to tree diversity, we analyzed the role of these land-use types for forest regeneration, assessing the diversity of saplings and seedlings. Since several studies have shown the importance of coffee agroforestry as refugia for birds and other organisms within an agricultural landscape (Perfecto et al. 1996; Moguel and Toledo

1999; Perfecto et al. 2003), we evaluated the role of managed coffee agroforestry as templates for forest recovery and as seed source.

We hypothesized that natural regeneration in logged forest and abandoned coffee in a high human-impacted landscape is mediated by bird dispersal and stimulated by the presence of agroforestry systems in use. Therefore, we evaluated the role of agroforestry systems in conserving biodiversity (i.e. woody plants and birds) and in reducing isolation between patches of forested areas.

Methods

Study area

We conducted this study on private farms in the vicinity of the villages Paján (UTM 17, 563969 S, 9828342 E) and Noboa (UTM 17, 567374 N, 9844106 E), in Manabí Province, western Ecuador, with an elevation range from 100 to 500 masl. Data recorded for the period 1990 to 2002 (excluding El Niño years) at Colimes Paján Metereological Station indicate a mean annual precipitation of 1170 mm (INAMHI 2002). The dry season, with a monthly precipitation of < 30 mm, lasts from June to December. Mean annual temperature is 25˚C. The original vegetation is semi-deciduous forest (i.e. intermediate in the moisture gradient between deciduous forest, which occurs in southwestern Ecuador, and rain forest in northwestern Ecuador (Jørgensen and León-Yánez 1999; Sierra 1999). A large part of this original vegetation has been converted to pasture, annual crops or agroforestry systems dominated by coffee. Only few patches of logged forest and secondary forest (developed after abandonment of agricultural activities) are embedded in a matrix of agricultural land. Coffee agroforestry plots are normally established by the replacement of the forest understorey vegetation with coffee plants. They consist of remnant old trees with a multi-layered canopy structure. Some coffee farms have been abandoned after the decline of international coffee prices.

Plant surveys and habitat structure

Six replicates were selected in each of three studied habitat types: selectively-logged neotropical forest (hereafter called “forest”), ca. 15 yr abandoned coffee agroforestry sites (hereafter called “abandoned coffee”) and coffee agroforestry sites in use (hereafter called “managed coffee”), see Fig. 1. At each site a series of nine quadrants (10 m x 10 m) were laid out in a 3 x 3 grid, within a 50 x 50 m quadrant. Within each quadrant, we characterized all free-standing woody vegetation (including palms) into the following size classes: (1) canopy trees (stems > 10 cm Diameter at Breast Height (DBH), (2) sapling (stems>1.4m tall and <10cm DBH), and (3) seedlings (stems between 0.20m and 1.4m tall). Trees, saplings, and seedlings were recorded in each 10 x 10 m quadrant (total area sampled per land-use type = 0.54 ha). Tree species with multiple stems were counted as single individuals. Saplings and seedlings were registered as separate individuals if no physical connection was observed near or just below the soil surface. We did not attempt to discern whether stems originated from stump sprouts or seeds.

Height (measured with Haglöf Laser Vertex Hypsometer), diameter (DBH), and canopy cover (calculated using the formula for a circle, since the shape of the canopy of these trees was more circular than elliptical) were recorded for every single tree individual. Diameter and height were not measured for saplings or seedlings. Light availability at ground level per study site was measured with a luxmeter (digital light gauge with four ranges from 0-1999 W m^{-2}), under standardized conditions (close to the ground, at local times between 11h00 and 13h00) and the mean of 45 observation points per site was calculated. Finally, basal area defined as the sum of the areas of a transverse section of all stems of all trees, taken at breast height was defined for each sampling site.

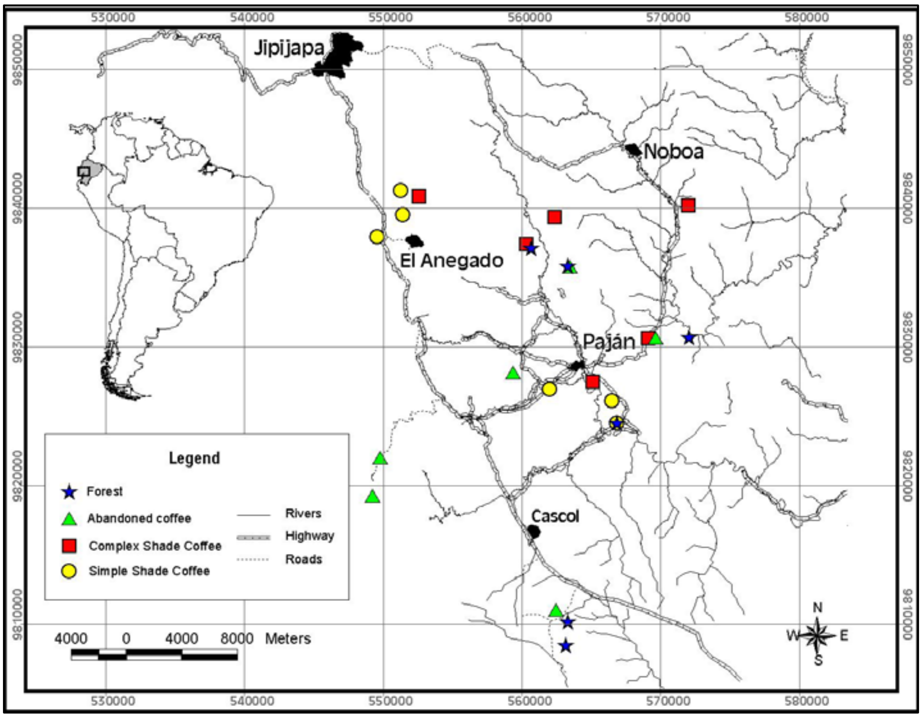


Figure 1. Map of the study region showing distribution of sites in relation to the major towns.

To evaluate competition between tree seedlings and herbaceous vegetation, nine smaller quadrants (2.5 m x 2.5 m) were laid out with the same center as the 10 m x 10 m quadrants. All herb individuals (including ferns) were counted and sampled. For species determination, fertile voucher specimens were collected for each plant species found in the quadrants and when not possible, sterile specimens were gathered. Since many of the plants found in the sites were lacking reproductive organs, several plants with flowers or fruits were additionally collected randomly to serve as reference material. Specimens were identified in the field by a local expert (Angel Choéz, Bio-Sys) and by experts at Quito (QCA) and Guayaquil (GUAY) herbaria in Ecuador. Voucher specimens were deposited at QCA and GUAY.

Bird community and seed dispersal

The overall bird community was recorded five times per plot during the dry season with the fixed-radius point count method. Bird species richness and abundance were registered within a 30 m fixed radius through visual observations and by sound recordings using a directional microphone (Marché et al. submitted 'Diversity of birds and their resources in tropical coffee landscapes R. Marché, A.M. Klein, L. Carrassco, T. Tscharntke). To evaluate seed dispersal and the relations between plant species richness and/or abundance with bird species richness and abundance, we sampled bird faeces from plant leaves and leaf litter. Two people spent ten minutes searching for faeces after each bird-sampling. After drying of the faeces, all seeds found were extracted, counted and classified into morphotypes. Each seed morphotype was assumed to be a single plant species.

Data analyses

The effects of land-use on plant structure (i.e., abundance, canopy height, canopy cover, basal area, light intensity, and herb presence), plant species richness, bird species richness and abundance, and seed dispersal were tested using one-way analyses of variance (ANOVA) and post-hoc Tukey's pairwise comparisons. When necessary, variables were log-transformed in order to meet assumptions of homogeneity of variance. All values of $P < 0.05$ are reported as significant throughout (Sokal and Rohlf 1995). To measure whether our samples were close to species saturation, we calculated the abundance-based coverage estimator (ACE) and Chao 1 estimates of species richness using ESTIMATES 7.5 (Colwell 2004). Then, for each size class, we tested correlation between sampled species richness and estimated species richness per site.

The degree of floristic similarity was assessed between land-use types. To avoid misleading results due to small sampling size or unseen shared species, we used the abundance-based Jaccard's Estimate, which is a derivation for the classic Jaccard Index

(Chao et al. 2005). These tests were done using ESTIMATES 7.5 (Colwell 2004). Similarity composition of bird community and dispersed seed composition were also studied with the Jaccard's index.

The regeneration potential of every adult tree was determined by direct comparison between species found as adults and species found regenerating as saplings or seedlings. To determine the plausible seed sources, we compared species found as saplings or seedlings with adult trees inside the same site and adult trees found outside. The effect of land-use on species turnover was tested using one-way ANOVA. By means of generalized linear model analyses, we tested the response of sapling and seedling species richness to two independent habitat variables: canopy cover and dispersed seed diversity. Land-use was included as a categorical variable: from low management intensity (i.e. forest sites) to high management intensity (i.e. managed coffee sites). Since our variables were over-dispersed we assumed a quasi-poisson distribution. Statistical analyses were performed with SPSS 10.0 for Windows and R (R Development Core Team 2004).

Results

Vegetation structure

The analyses of vegetation structure revealed considerable differences between land-use types (Trees: $F = 4.5$, $P = 0.030$; Saplings and seedlings: $F > 24$, $P<0.001$). Tree abundance was higher in forest sites in comparison to abandoned coffee or managed coffee sites (Fig. 2A). In turn, saplings and seedlings were significantly more abundant in abandoned coffee compared to forest and managed coffee sites (Fig. 2B and C). Despite differences in tree abundance (Fig. 2A), canopy cover, and basal area were not significantly different among land-use types ($F = 3.2$, $P > 0.05$ for both, Table 1). In contrast, canopy height varied among land-use types ($F = 4.7$, $P = 0.026$ for log transformed data): taller trees were found in managed coffee sites compared to abandoned coffee sites and even compared to forest sites.

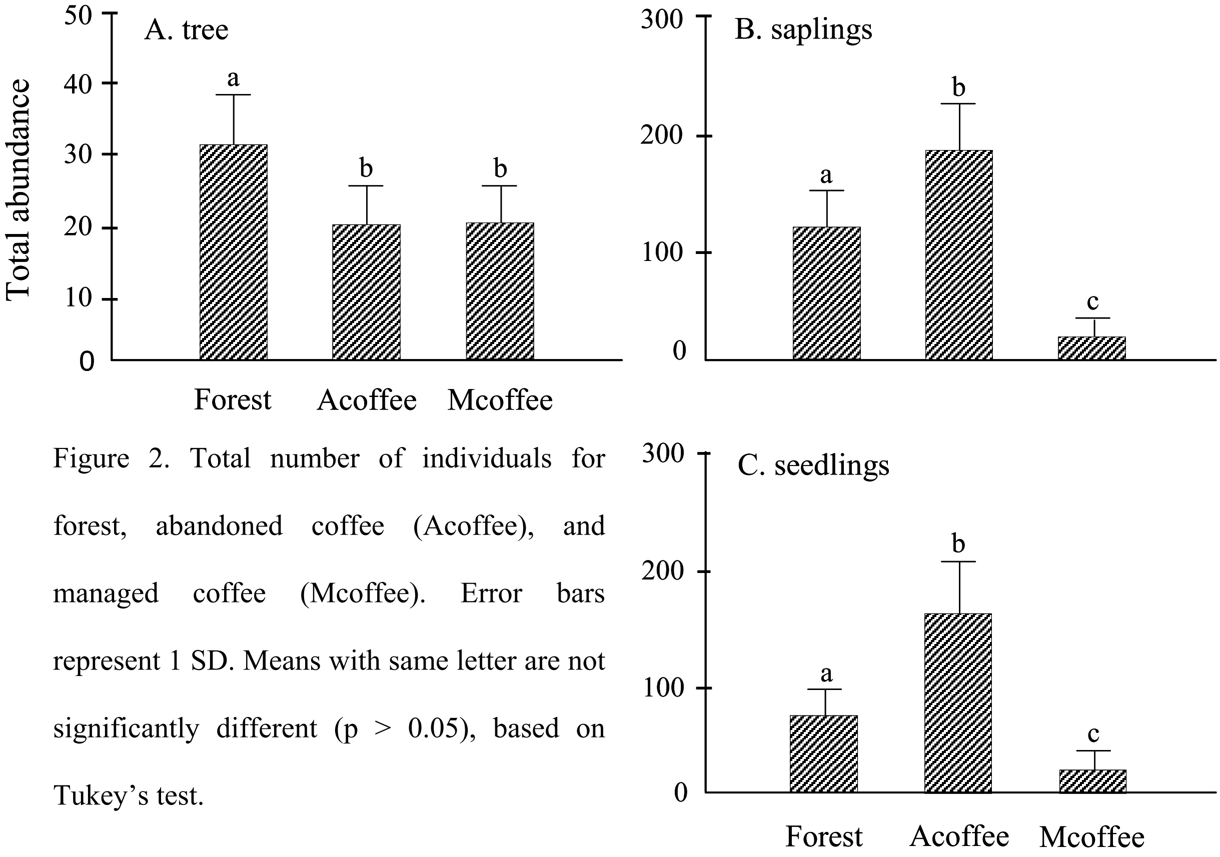


Figure 2. Total number of individuals for forest, abandoned coffee (Acoffee), and managed coffee (Mcoffee). Error bars represent 1 SD. Means with same letter are not significantly different ($p > 0.05$), based on Tukey's test.

This result clearly shows that many large trees were selectively extracted from abandoned coffee and forest sites as timber sources, while some original canopy tree species such as *Erythrina fusca* Lour. (Fabaceae) or *Pseudobombax millei* (Standl.) A.Robyns (Bombacaceae) persisted in managed coffee sites. Low levels of light intensity were found, and no significant differences existed between land-use types ($F = 0.139$, $P > 0.05$, Table 1). Weedy herbs, ferns, and grasses were abundant in all land-use types with no significant differences between land-use types ($F = 3.32$, $P = 0.062$; Table 1). The dominant species in forest and abandoned coffee was *Achyranthes aspera* L. (Amaranthaceae), while *Euphorbia graminea* Jacq. (Euphorbiaceae) was predominant in managed coffee sites.

Table 1. Mean (± 1SD) of structural variables sampled in forest, abandoned coffee (*Acoffee*), and managed coffee (*Mcoffee*) sites. Canopy height (in meters), canopy cover (as a percentage of sky area cover by the canopy layer), basal area (in m^2 per site) per land-use type. Light intensity measured in Wm^2 and herb density as the mean number of herbaceous individuals found in $56m^2$ per site. Probability values from one-way ANOVA. The letters indicates results of pairwise comparison with Tukey test

	Forest	Acoffee	Mcoffee	p
Canopy height	9.94 ± 1 *a*	11.9 ± 1 *ab*	12.1 ± 1 *b*	0.035
Canopy cover	50.6 ± 19	40.8 ± 17	71.7 ± 27	0.068
Basal Area	1.4 ± 0.4	0.8 ± 0.2	1.2 ± 0.6	0.070
Light intensity	19.8 ± 17	23.8 ± 17	17 ± 5	0.535
Herb density	246 ± 70	345 ± 50	292 ± 75	0.062

Species richness

A total of 128 woody plant species belonging to 43 families were encountered across all sites. Forest and abandoned coffee sites had a total of 91 and 74 tree species, respectively, while in managed coffee sites only 48 tree species were recorded. No correlation was found between observed species richness and estimated species richness for the tree size class. This result should not be related to sampling limitations but to a large fraction of rare species (i.e. species with a total abundance of one individual per site) arising from management practices. In contrast, the number of observed species and estimated species were highly correlated for the sapling and seedling size classes (Pearson $R > 0.900$, $P < 0.001$, $n = 18$; for both indices). Therefore, we decided to make comparisons with original species richness data of all size classes, rather than estimated values.

Overall species richness was significantly higher in abandoned coffee and forest sites in comparison to managed coffee sites (F = 21.21, P < 0.001). We found no consistent pattern of diversity reduction among land-use types. While canopy tree species richness was statistically similar (F = 3.3, P = 0.064, Fig. 3), species richness for the smaller size classes varied among land-use types (saplings: F = 33, P < 0.001; seedlings: F = 14.6, P < 0.001). Mean species richness for saplings was similar between forest and abandoned coffee and significantly lower in managed coffee sites (Fig. 3). When seedlings were analyzed, however, abandoned coffee had relatively higher species richness (Fig. 3) than managed coffee, while seedling richness in forest was not significantly different from the other land-use types.

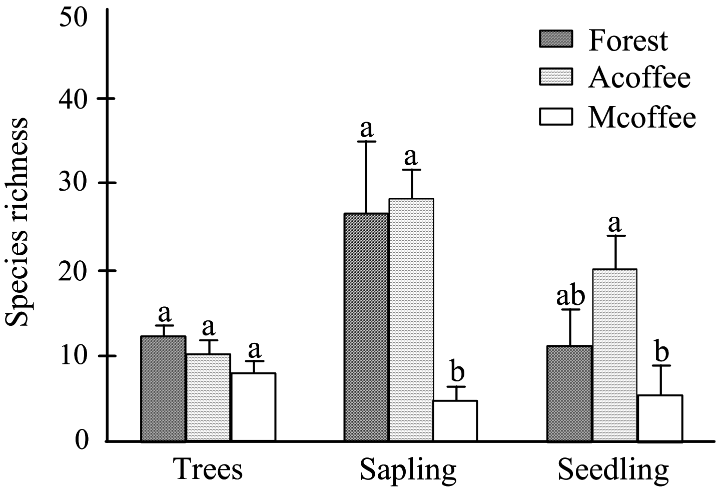


Figure 3. Species richness of tree, sapling, and seedling size class found in our three land-use types: forest, abandoned coffee (Acoffee), and managed coffee (Mcoffee). Error bars represent 1 SD. Means with same letter are not significantly different (P>0.05), based on Tukey’s test.

Species composition

The abundance-based Jaccard’s similarity index of all pairwise comparisons showed high similarity values for all life forms, including birds. Floristic similarities were found to be higher for all size classes between forest and abandoned coffee than between other combinations of land-use types (Table 2). For the forest with abandoned coffee comparison, similarity values increased with decreasing plant size classes, from 47% for canopy trees to 82.1% for seedlings. The lowest floristic similarity values were recorded for the managed coffee with forest comparison.

Table 2. Percent of similarity matrix (abundance-based Jaccard's index) for trees, saplings, and seedlings among land-use types: forest, abandoned coffee (Acoffee), and managed coffee (Mcoffee). Bird species composition and seed morphotype composition were also compared between land-use types.

	Forest + Acoffee	Forest + Mcoffee	Acoffee + Mcoffee
Floristic similarity			
Tree size class	47.3	21.7	44.9
Sapling size class	67.4	10.3	20.6
Seedling size class	82.1	56.7	73.6
Bird species	79.4	76	76
Dispersed seeds	63	50	58

The canopy layer in forest and abandoned coffee sites was dominated by *Cecropia maxima* Snethl. (Cecropiaceae), *Guazuma ulmifolia* Lam. (Sterculiaceae) and *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae). In most sites one or two individuals of common species in mature forest, such as *Ficus citrifolia* Mill. (Moraceae) or *Poulsenia armata* (Miq.) Standl. (Moraceae) were also recorded. The dominant species in the understorey of forest and abandoned coffee sites were *Triplaris cumingiana* Fisch. & CA Mey. ex CA Mey (Polygonaceae), *Nectandra reticulata* (Ruiz & Pav.) Mez (Lauraceae) and species from the genus *Pseudopiptadenia* (Mimosaceae) and *Brosimun* (Moraceae). The managed coffee canopy was dominated by shade and timber tree species, such as *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae) and *Pseudosamanea guachapele* (Kunth) Harms. (Mimosaceae), but also here species from mature forest such as *Pseudobombax millei* (Standl.) A.Robyns (Bombacaceae) or *Gliricidia brenningii* (Harms)Lavin (Fabaceae) were found. Finally, several individuals of endemic species *Phytelephas aequatorialis* Spruce. (Arecaceae) and *Erythrina smithiana* Krukoff. (Fabaceae) were frequently found in the understorey of managed coffee sites.

Birds and seed dispersal

A total of 46 frugivorous bird species were recorded in our study sites. Surprisingly, bird species richness and abundance did not differ between land-use types (F < 1, P > 0.05). Overall, similarity values for bird species composition among land-use types were higher than 70% (Table 2). Most of the observed bird species were woodland generalists, except for three species of forest specialists (R. Marché, *pers. comm.*).

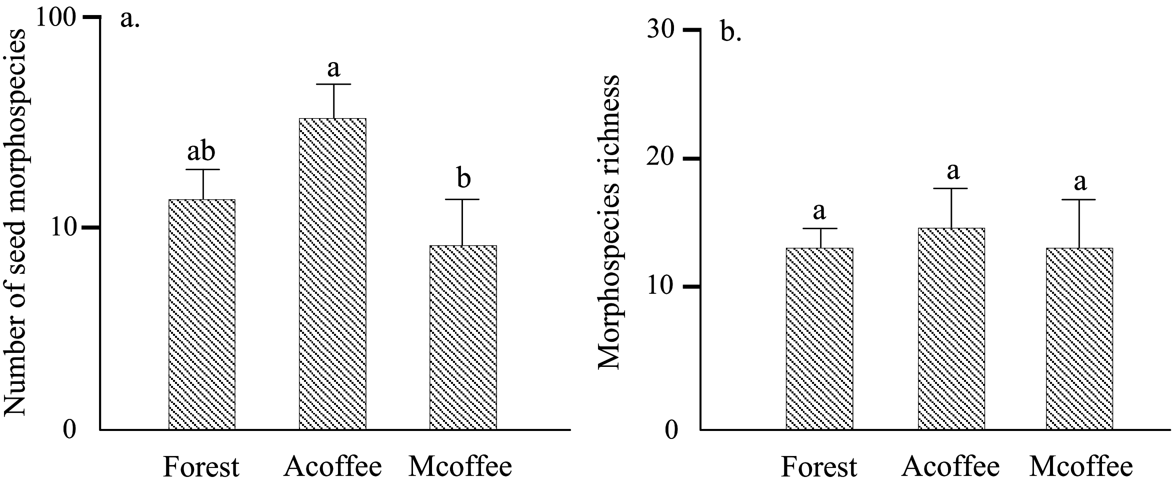


Figure 4. Seed dispersed by birds in forest, abandoned coffee (Acoffee), and managed coffee (Mcoffee): a) Number of seeds (x100) found, b) Morphotypes richness. Error bars represent 1 SD. Means with same letter are not significantly different (P>0.05), based on Tukey's test.

In the collected faeces, more than 39 000 seeds belonging to 57 morphotypes, were retrieved in all land-use types together. Land-use significantly affected seed abundance (*F*=5.12, *p*=0.02 for log-transformed data). More seeds were found in abandoned coffee compared to managed coffee sites (Fig. 4a), while seed species richness did not differ between land-use types (*F*<1, *p*>0.05, Fig. 4b). Overall, similarity values for dispersed seed composition among land-use types were lower than those for birds. Once again, higher values were recorded between forest and abandoned coffee sites than between other combinations of land-use types (Table 2).

Regeneration process

The regeneration potential of canopy trees depends on land-use type (F = 9.03, P = 0.003): significantly more tree species were found to be regenerating, either as saplings or seedlings, in abandoned coffee sites than in managed coffee (Fig. 5). Survival of saplings and seedlings originating from parent plants found in the same study site, did not differ between land-use types (F = 1.829, P > 0.05).

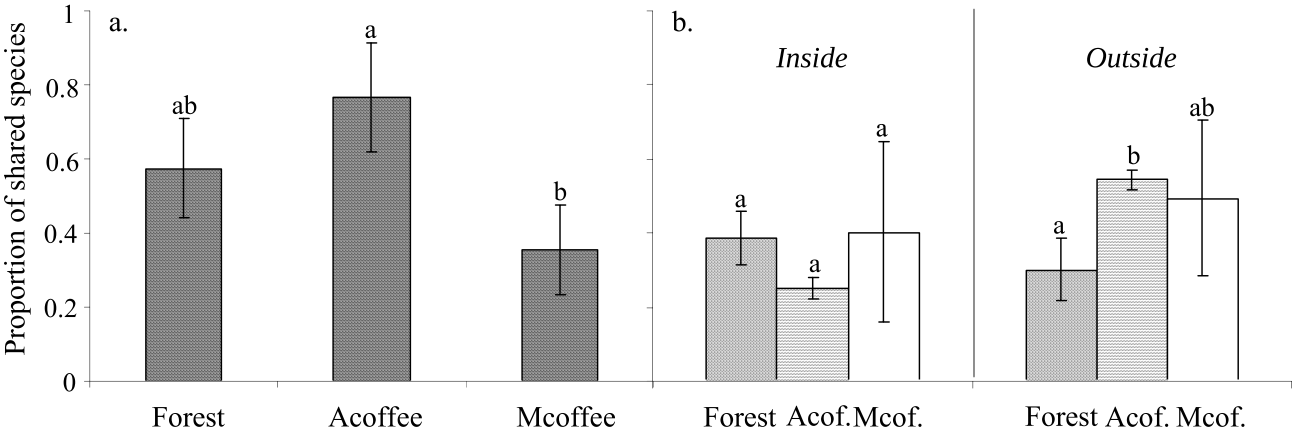


Figure 5. Proportion of species shared by canopy trees and saplings/seedlings in relation to land-use type. (a) Proportion of canopy trees found as saplings and/or seedlings. (b) Proportion of saplings and seedlings found as canopy trees within the same site (i.e., Inside), and within other sites (i.e., Outside). Means with same letter were not significantly different (p>0.050).

Less than 40% of species found as saplings or seedlings were also recorded as canopy species. However, land-use significantly affected the number of sapling and seedling species common to adult trees found outside the site (F = 13.688, P < 0.001). We considered as outside the site all the plots from the same and other land-use types together. More species common to outside the site were found in abandoned coffee and managed coffee compared to forest sites. Through a generalized linear model, we examined which of the independent habitat variables were more important for the diversity of saplings and seedlings. Sapling species richness could be explained best by the combination of canopy cover and land-use, with decreasing richness with increasing land-use intensity and canopy cover. In contrast, seedling species richness was only explained by dispersed seed diversity. Seedling diversity was not significantly related to land-use or canopy cover (Table 3).

Table 3. Results of generalized linear model analyses assuming *quasi*-Poisson distribution of the effects of dispersed seed diversity and canopy cover on species richness of sapling and seedling size classes. Only significant relationships are shown.

Dependent variables	Independent variables	*Z*	*p*
sapling species richness	canopy cover	-2.36	*
	land-use	-3.88	**
seedling species richness	seed morphotype diversity	2.17	*

Significant levels *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n=18

Discussion

Several studies of natural regeneration carried out in abandoned pasture and coffee sites have described differences in species composition, even after similar structural characteristics were attained (Zimmerman et al. 1995; Rivera and Aide 1998; Pascarella et al. 2000). In our study region, even though land-use management may have influenced the initial recovery process, our results appear to show a convergence of both structural characteristics and species composition between forest and abandoned coffee sites, while in managed coffee sites tree recovery through natural regeneration was impossible due to management practices. Since species composition depends largely on the arrival of seeds, the patterns of plant diversity found in forest and abandoned coffee is probably partially explained by bird dispersal. In all our land-use types, structural characteristics were closely related to previous management. The high levels of canopy cover and canopy height recorded in managed coffee sites result from the presence of some original shade trees, as described by Perfecto et al. (1996) for agroforestry systems in Mexico. The selective extraction of large individuals of commercial tree species in forest sites as well as in abandoned coffee sites produces locally high light intensity, stimulating vine population and creating a mosaic of microhabitats (T. Lozada *pers. obs.*). The comparable number of tree species in forest, abandoned coffee, and managed coffee in our study region is consistent with many studies conducted in coffee systems, which demonstrated that shade coffee contains high levels of biodiversity in fragmented landscapes (Moguel and Toledo 1999).

Between forest and abandoned coffee sites, floristic similarity is largely due to the presence of short-lived, light demanding "pioneer" tree species such as *Cecropia maxima* (Cecropiaceae) and the presence of some species common to old-growth forest. On the other hand, the high level of floristic similarity between abandoned coffee and managed coffee sites partly results from the presence of nitrogen-fixing legumes (i.e. *Inga sp., Erythrina smithiana*) and some fuel wood- and timber-producing trees such as *Cordia alliodora* (Boraginaceae) or *Cedrela odorata* L. (Meliaceae). Tree diversity in abandoned coffee arises as a sum of species frequently found in managed coffee and species common to logged forest. Thereby, due to their different tree species composition, the presence of the three land-use types in the studied landscape results in an increase in seed source and species diversity.

At an early stage, succession largely depends on seed source. If there are no seeds stored in the soil from original tree species and there is no input from off-site sources, we would expect to find the same composition among vegetation layers (Rivera and Aide 1998; Marcano-Vega et al. 2002) as all seedlings and saplings would be from seeds from the existing adult trees. In our study sites, less than 40% of species were found in regeneration and were also present as adult trees in the same site, even though the vast majority of adult tree species were also recorded either as saplings or as seedlings. This reflects the importance of other seed sources.

Seed bank contribution to development of secondary vegetation is more important when land-use intensity before abandonment has been low to moderate (Guariguata and Ostertag 2001). Even though logging or agroforestry practices are low impact activities in our study area, seed bank composition revealed a dominance of grasses, herbs, and light demanding shrubs (C. Enriquez, *pers.comm.*). Therefore, forest recovery in our land-use types seems to depend largely on “external” seed sources.

Wind seems to play some role in colonization, as demonstrated with several individuals of the wind dispersed *Triplaris cumingiana* present in the understorey layer of forest and abandoned coffee sites. Also some animal-dispersed species were found, such as from genus *Brosimun* and *Pseudopiptadenia*. Despite lacking information on the dispersal modes of the majority of our woody species, the high diversity of dispersed seed found in our study sites and the statistical relationship between seedling and dispersed seed diversity indicates the important role of birds as dispersers.

In a study carried out in a fragmented landscape in los Tuxtlas- Mexico, Estrada and Estrada et al. (1997) showed that the density of the vegetation as well as the presence of many fruiting tree species and the diverse fauna of insects found in regenerating forest (i.e., arboreal agricultural lands with cacao, coffee or citrus) attracted large numbers of birds. Several studies have described a decline in bird presence and seed dispersal with distance to natural habitats (Bleher and Böhning-Gaese 2001; Ingle 2003). However, bird species are capable to reach forested habitats outside the patch in which they reside if they can make use of forested agricultural sites as stepping stones (Estrada et al. 1997). In our study region, bird diversity was independent to land-use types: similar number of bird individuals was recorded in all sites and bird species composition was similar among land-use types. This result indicates that birds moved between forests, abandoned coffee and managed coffee sites, allowing for seed exchange between land-use types. This is supported by similarities in diversity and species composition of seedlings and dispersed seeds between land-use types (up to 82% of similarity was found for seedlings between forest and abandoned coffee sites).

However, seedling recruitment does not depend only on seed availability, other factors such as seed predation, low seed germination, soil conditions, and microhabitat heterogeneity are also important (Guariguata and Pinard 1998; Holl 1998; Hardwick et al. 2004). Saldariaga et al. (1988) suggest that the heterogeneous crown structure of old-growth forest was responsible for a higher number of establishment sites in comparison with the relative uniform canopy of young secondary forests. Even though microhabitats in abandoned coffee sites have been described as uniform due to a closer, well-established, canopy layer (Rivera and Aide 1998), we speculate that in our study region, microhabitat heterogeneity was high in forest and in abandoned coffee sites. Sapling species richness decreased with increasing canopy cover, confirming lower number of species under a uniform canopy layer.

Finally, forest recovery in our study sites is influenced by several habitat variables. While sapling species richness seems to be related to microhabitat heterogeneity, seedling species richness depends on seed arrival. Managed coffee sites play a major role in biodiversity conservation in our study region. In our agricultural landscape, abandoned and managed coffee sites are much more common than forest patches, and they provide a refuge for plant and bird species. In such a mosaic landscape, where the vast majority of natural forest has been replaced by agricultural land, agroforestry systems offer birds stepping-stones and thereby reduce isolation resulting from forest fragmentation.

Chapter

3

Scale-dependence of plant diversity assessment in tropical human-dominated landscapes

T. Lozada, G.H.J. de Koning, A.-M. Klein & T. Tscharntke

Abstract

Aim: We analyzed plant diversity patterns at multiple spatial scales in the mayor land-use types within two tropical landscapes with different levels of anthropogenic intervention. Our aim was to determine the critical spatial scales that explain overall plant diversity, going from quadrants within plots to landscape level. Additionally, we wanted to determine if there is a possible link between critical spatial scales and inherent abilities of plant species (herbs as well as woody species) to survive disturbance.

Location: The Chocó biogeographical region, western Ecuador.

Methods: We used a highly replicated study in two tropical landscapes with different degrees of disturbance. Within each landscape, plant diversity in six replicates of the five most dominant land-use types (rice, pasture, agroforestry systems, abandoned agroforestry and near-natural forest) was recorded. Through additive partitioning of biological diversity we quantified alpha, beta and gamma diversity at four hierarchical levels, corresponding to different spatial scales: landscape, land-use type, plot, and quadrant. To identify which spatial scale is important in explaining species diversity, we used randomization procedures to test the null hypothesis that the observed diversity across spatial scales is not different than expected diversity for a random distribution of plants. Finally, we tested the influence of management practices on beta diversity at plot level.

Results: Our results suggest that plant diversity is mainly explained by the variability at large spatial scales (i.e., landscape and land-use types). However, when considering each landscape independently, variability of management in different plot of the same land-use type is also important for explaining diversity patterns. At finer spatial scales, plant diversity is more determined by the link between plant characteristics and the degree of landscape disturbance which in turn affects seed dispersal. Although beta diversity decreased with disturbance; even intensively managed land use systems had rather high beta diversity indicating their heterogeneous conditions and contribution to diversity.

Main conclusions: We concluded that observed patterns of species diversity depend strongly on spatial scales and furthermore that land use types with different levels of anthropogenic intervention have specific contributions to overall plant diversity at the landscape level. This should be taken into account when implementing conservation measures like bio-corridors or payments for ecosystem services.

Keywords: Additive partitioning, land-use history, Ecuador, alpha diversity, beta diversity, gamma diversity, randomization tests.

Introduction

Fragmentation and destruction of once continuous natural vegetation are major threats to biodiversity (Harrison and Bruna 1999). In most parts of the world, habitat fragmentation results from selective human activities impact some vegetation types more than others. The resulting vegetation pattern reflects the dynamic adaptations of plants to changes in available resources (e.g. light, water, and nutrients), substrate availability, seed sources, plant-insect interactions, inter- and intraspecific interactions and biophysical conditions such as soil type, topography or climate. Moreover, the frequency and intensity of anthropogenic disturbance also strongly influence components of biodiversity loss such as decline of species richness, changes in community structure and modifications in ecosystem functioning (Harrison and Bruna 1999; Debinski and Holt 2000). Human intervention leads to a heterogeneous landscape formed by a number of distinct habitat types such as farmland with different management intensities, woodland and sometimes remnants of (semi-) natural forest (de Blois et al. 2002).

The concomitant loss of biological diversity, hence, calls for a shift from traditional conservation policies and scientific approaches to increased emphasis on how mosaic landscapes with patches of different habitats due to human disturbance affect and determine the existence and functioning of entire communities at multiple spatial scales (Luck et al. 2003; Bawa et al. 2004). Since different habitats of a landscape typically vary in their contribution to overall species richness and composition, it is essential to recognize that different factors govern patterns of species diversity and the scales at which they operate (Loreau 2000). For instance, at a small scale (e.g. plot scale) species diversity may depend on strong direct interactions among organisms, such as inter- or intraspecific interactions (Veech 2005). At a larger scale, species richness may be mainly affected by environmental heterogeneity or the species pool of the surrounding landscape (Tuomisto et al. 2003; Pyšek et al. 2005; Roschewitz et al. 2005). Several recent studies performed in natural (De Vries and Walla 2001; Gering et al. 2003) as well as agricultural landscapes have examined spatial scale effects on species diversity (Wagner et al. 2000; Fournier and Loreau 2001). They were all unanimous in concluding that spatial scale is critically important in determining species diversity and therefore, studies restricted to only one spatial scale (e.g. single habitat) may produce partial or even misleading results.

Agricultural ecosystems have long been viewed as homogeneous with low species diversity. However, their importance in biodiversity conservation on the regional and global scale is now being acknowledged (von Arx et al. 2002; Perfecto et al. 2003; Tscharntke et al. 2005). In many industrialized countries, where intensive management of agriculture has led to landscape simplification and overall ecological degradation, there are more and more national efforts to revitalize agricultural landscapes and to protect rare species as well as common and widespread species (Duelli 1997). In a number of these intensive agricultural landscapes, the role of distinct habitat types in the maintenance of diversity at different spatial scales have been assessed and defined for vascular plants (Wagner et al. 2000; Gabriel et al. 2005) as well as invertebrates (Fournier and Loreau 2001). In tropical areas, where the highest concentration of biodiversity exists, research on diversity patterns at different spatial scales has been limited and has primarily focused on predominantly undisturbed ecosystems while ignoring human-dominated ecosystems (De Vries and Walla 2001). Furthermore, most tropical studies examining the importance of human-dominated habitats for biodiversity deal with differing management intensities of a single habitat type and take only one single spatial scale into account (Klein et al. 2002; Perfecto et al. 2003). Henceforth, studies evaluating the contribution of different land-use types (including intensively managed land-use types) to overall diversity at different spatial scales are rare (but see Tylianakis et al. in press).

In western Ecuador, part of the Chocó biogeographical region, one of the world's hotspots of biodiversity (Myers et al. 2000), we used a highly replicated field study to address the question of how plant species diversity varies across a hierarchy of spatial scales in heterogeneous human-intervened tropical landscapes. Through the additive partitioning of diversity in alpha and beta components, we expected to determine which spatial scales, from quadrants within a plot up to the biogeographical region, most strongly influence plant diversity. Following Veech *et al.* (2002) alpha diversity is "the average within sample diversity" while beta diversity is "the average amount of diversity not found in a single randomly-chosen sample". We tested the null hypothesis that the observed diversity across hierarchical scales is not different than expected diversity from random distribution of plants in space. Specifically we asked the following questions: (1) Is variability between landscapes as important as differences between land-use types in explaining overall species richness (broad scale effects)? (2) Do differences between plots of the same land-use type (e.g. due to variability in management) have an influence in plant diversity (intermediate scale effects)? (3) Are fine scales effects (within plots), which might result from direct interactions among species, important for explaining overall species diversity? (4) What is the impact of management practices on within plot diversity? (5) Is there a possible link between critical spatial scales and inherent abilities of plant species (herbs and woody species) to survive the disturbance or recolonize after disturbance?

Methods

Study design

We used a nested design to study plant diversity in a heterogeneous mosaic of land-use types in western Ecuador. The study design comprised four hierarchical levels, corresponding to different spatial scales: landscape, land-use type, plot, and quadrant. The broadest spatial scale was represented by two landscapes, about 300 km apart, which differ in climatic conditions, vegetation formations, and degree and time of anthropogenic disturbances. The first landscape (hereafter called high impact landscape) is situated in the vicinity of the village Jipijapa (UTM 17, 546800 S, 9849274 W) in Manabí Province. The dominant natural vegetation is semi-deciduous forest. The climate is characterized by an average annual rainfall (excluding El Niño years) of 1170 mm and a rainless period of about six months (INAMHI 2002). Agricultural practices in the high-impact landscape were promoted by the land reform programs initiated in the early 1960s (Dodson and Gentry 1991) and therefore it is possible to frequently find in the area agroforestry systems or annual crops that have persisted for more than 20 years (farm owners pers. comm.). More than 60% of the total area is dominated by pasture, agroforestry systems with coffee and the arable crops rice and maize, while natural vegetation, found mainly on steep slopes, accounts for less than 25% of the landscape (INEC-MAG-SICA 2002).

The second landscape (hereafter called low impact landscape) is located in the neighborhood of the village Cabo San Francisco (UTM 17, 72685 N, 604100 W) in Esmeraldas Province (north of Manabí province). The dominant natural vegetation is lowland rain forest. The climate is characterized by an average annual rainfall exceeding 3000 mm and absence of a distinct dry season (INAMHI 2002). In this second landscape, natural forest accounts for approximately 50% of the total surface (INEC-MAG-SICA 2002) as the expansion of the agricultural frontier has reached the surroundings of Cabo San Francisco much later than around Jipijapa. Information provided by the farmers showed that some years ago the main agricultural activities in the region were agroforestry systems with cacao and banana plants. Nowadays, due to commercialization problems (mainly related to lack of roads) banana and cacao are no economically important for the region and most of the agroforestry systems were abandoned. Arable crops and pasture, on the other hand, have become more important in recent years (pers. comm.).

Within each landscape, we considered the five most predominant land-use types which represent a gradient of decreasing anthropogenic disturbance: rice, pasture, managed agroforestry systems (hereafter called *managed agroforest*), which result from the replacement of understory vegetation by coffee plants (in the high-impact landscape) or cacao plants (in the low-impact landscape), while maintaining a multilayer canopy cover; abandoned agroforestry systems (hereafter called *abandoned agroforest*) where no agricultural practices have been applied for at least 15 years; and near-natural, selectively logged forest (hereafter referred to *forest*). In each plot nine fixed points were positioned (in a regular 3 x 3 grid, 25 m between adjacent points) within a 50 x 50 m area. Herb species (including ferns) were collected in 2.5 x 2.5 m fixed quadrants positioned around each of the nine points. Woody species (including seedlings and adults of all forms of trees, shrubs and palms) were sampled in 10 x 10m fixed quadrants positioned around each of the nine points in the shaded land-use types with shade (i.e., managed agroforest, abandoned agroforest, and forest). To consider possible variation of herb diversity and abundance due to climatic conditions, two plant surveys were conducted: in April and October of 2003 for the high impact landscape and April and October 2004 for the low-impact landscape. Total species richness and abundance were calculated for the total of the two sampling dates for each quadrant, and the abundance was the mean value of individuals in these two quadrants. Specimens were identified up to the lowest possible taxonomic level (i.e., genus or species level) with the help of experts at Quito (QCA, QCNE) and Guayaquil (GUAY) herbaria in Ecuador.

Pre-analyses

In a pre-analysis we assessed the adequacy of our sampling effort by calculating the abundance-based coverage estimator (ACE) of species richness using EstimateS version 7.5 software, with 500 randomizations (Colwell 2004). The degree of species saturation, which is expressed by the percentage of observed species richness relative to the estimated species richness was 82% and 87% for herb species in the high and low-impact landscapes, respectively. Slightly higher percentages were found for woody species: 87% and 90% in the high- and low-impact landscapes, respectively, suggesting that sample size and sampling effort were sufficient.

Data analyses

The effects of land-use on herb and woody species richness were tested for each landscape separately using one-way analyses of variance (ANOVA) on data with normally distributed model residuals. All values of $P < 0.05$ are reported as significant throughout. When the effect was significant, we performed Tukey's pairwise comparisons to determine which land-use types differed significantly. All statistical analyses were performed using Statistica 6.1 (StatSoft, Tulsa, Oklahoma, USA).

Additive partitioning of diversity

To evaluate how species diversity is distributed over spatial scales, we partitioned the total diversity into the average diversity within-community (alpha-diversity) and among-community (beta-diversity or species turnover), so that gamma = alpha + beta (Veech et al. 2002). Within the context of our hierarchical design, alpha and beta diversity are defined relative to a given spatial scale. For instance, alpha_2 represents the mean diversity of plots, while beta_2 corresponds to the variability betweens plots of the same land-use type. Since alpha-diversity at a given spatial scale equals the sum of alpha and beta diversity at the next lower scale (e.g., alpha$_2$ (plots) = alpha$_1$ (quadrants) + beta$_1$ (quadrants)), the overall plant diversity in our study area (i.e., combining both landscapes) is the sum of alpha and beta diversity at the lowest scale (i.e., quadrant) plus beta-diversity at each of the higher scales (i.e., plots, land-use types and landscapes). Total diversity can be expressed as the sum of proportional contributions of diversity at each scale in the hierarchical sampling design (Fig. 1; Wagner et al. 2000; Gering et al. 2003).

	Within-community diversity		Between-community diversity
Quadrant	Alpha$_1$ *diversity of single quadrant*	→ +	Beta$_1$ *variability among quadrants of the same management unit* +
Plot	Alpha$_2$ *diversity of the management plot*		Beta$_2$ *variability between sites of the same land-use type* +
Land-use type	Alpha$_3$ *diversity of a land-use type*		Beta$_3$ *variability between different land-use types* +
Landscape	Alpha$_4$ *diversity of a mosaic landscape*		Beta$_4$ *Variability between different landscapes*
Biogeographical region	Alpha$_5$ *overall diversity of the two landscapes*	= ↙	

Figure 1. Hierarchical model of species diversity: additive partitioning between scale-specific components to describe the total diversity of the geographical area. In *italics* a description of each level based on Wagner et al. (2000).

We conducted additive partitioning on species richness and Shannon diversity index which is strictly concave (i.e., gamma-diversity equals or exceeds alpha-diversity) to account for effects of pure species richness and the combined effect of species richness and abundance. The Shannon index measures evenness, and it is calculated from the proportional abundance, *Pi*, of all species in the sample and it is equally weighted towards rare and common species. The Shannon index is $-[\Sigma Pi(\ln Pi)]$ for species $i = 1$ to n, where n equals the number of species in the sample.

Scale effects

Scale effects on overall plant biodiversity were tested through a randomization procedure. The statistical significance of observed diversity components is assessed by testing the null hypothesis that the observed partitioning of diversity could have been obtained by the random distribution of individuals among samples at all hierarchical scales. We used the computer program PARTITION to conduct individual-based randomization, where the numbers of individuals and species in samples are determined by the random allocation of all individuals into samples at the lowest scale (for further details see Crist et al. 2003). Each randomization test is then partitioned into alpha and beta components at each hierarchical scale for the two diversity measurements. To obtain a null distribution of alpha and beta, the randomization procedure is repeated 10 000 times. Finally PARTITION gives the probability p that a component greater than or equal to the observed component could have been obtained by chance alone. Therefore, the null hypothesis is accepted if $0.05 < P < 0.95$ and rejected if P exceeds theses bounds. Through this process, we were able to identify which scales contributed most significantly to the overall plant diversity. We conducted the randomization process for herb species and woody species separately, since plant species will react to disturbance according to inherent life-history traits.

Species turnover (single scale effect)

To test the effect of management practices on habitat homogeneity or heterogeneity (i.e. species turnover among quadrants within a single plot) we used one way analysis of variance (ANOVA) for each landscape separately. To avoid misleading results due to differences in species richness between land-use types, we calculated the proportion of total plot diversity explained by the variability among quadrants or species turnover (i.e., beta$_1$). Arcsine-square root transformation of the data was used to achieve normality of the residuals. If the effect of land-use type was significant, the five land-use types (for herb species) and three land-use types (for woody species) were compared pairwise with the Tukey's test to determine which land-use types differed significantly from each other.

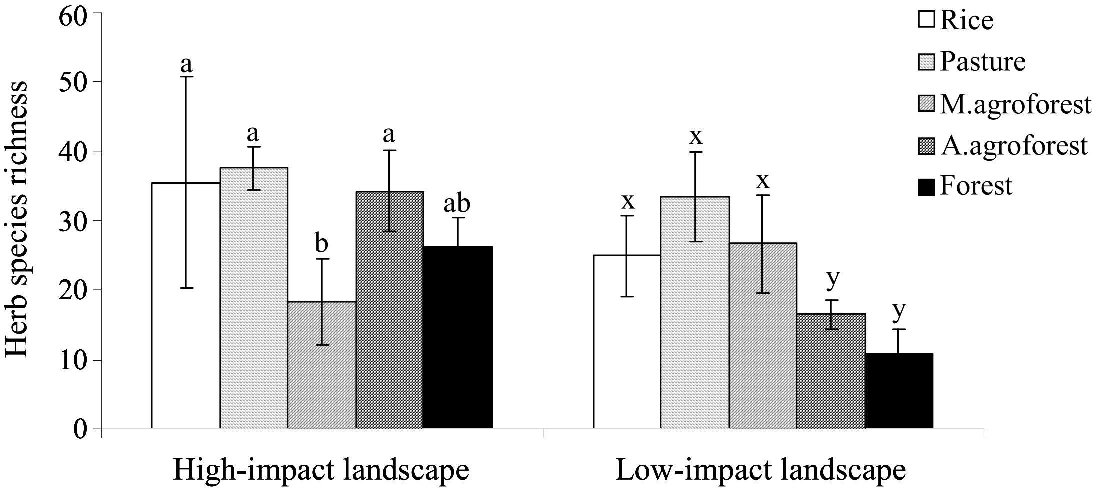
Results

Species richness

We sampled a total of 49 032 plants belonging to 591 species, of which 295 were herbaceous and 296 were woody species. Overall species richness was slightly higher in the high-impact (398 spp.) compared to the low-impact landscape (294 spp.). There was a considerable difference in the proportion of herb and woody species found within each landscape. In the high-impact landscape, herb diversity accounted for the 60% of the total species richness (i.e, 233 species out of 398) while in the low-impact this percentage was only 36% (i.e, 107 species out of 294). Herb diversity, in terms of Shannon index, was roughly equal among landscapes. In contrast, woody diversity (Shannon index) was lower in the high-impact (2.292) than in the low-impact landscape (4.189), suggesting that the high-impact landscape was dominated by a number of widespread woody species. For instance, the understorey of agroforest as well as forest plots in the high impact landscape were dominated by the wind-dispersed *Triplaris cumingiana* Fisch. & C.A. Mey. ex C.A. Mey. (Polygonaceae), which represented nearly 15% of the individuals sampled.

The effect of land-use type on species richness was assessed for each landscape separately. Although, land-use type had an effect on herb diversity in the high-impact landscape (F = 6.34, P = 0.001), we found no consistent decrease of herb species richness with land-use intensity (Fig. 2a). There were no significant differences of herb species richness between highly impacted land-use types such as rice and pasture and more “natural” land-use types such as abandoned agroforest or forest. In contrast, in the low-impact landscape management practices had stronger effect on herb diversity (*F* = 15.2, *P* < 0.001): species richness clearly decreased with decreasing land use intensity.

a. Herb species



b. Woody species

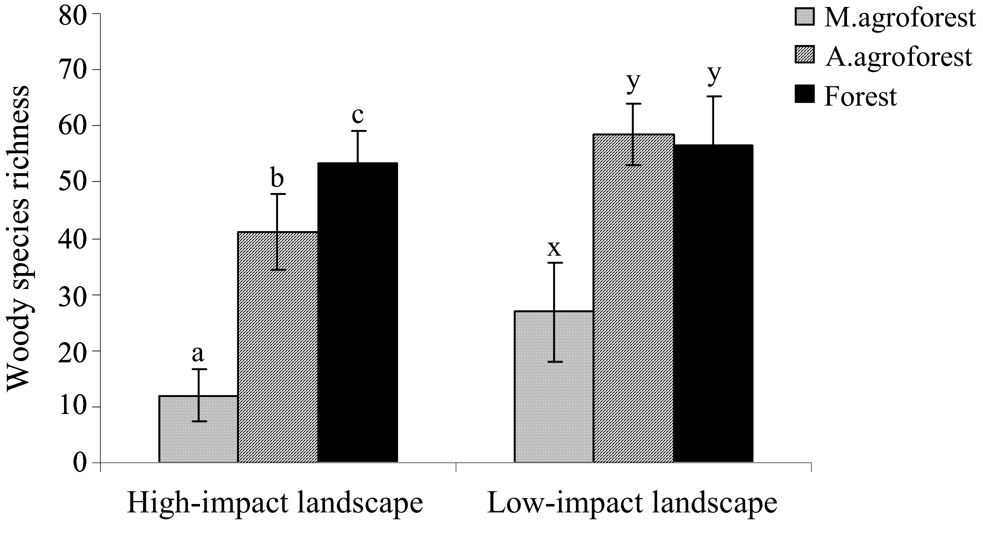


Figure 2. The effects of land-use type on mean species richness per plot (± SD). a: herb species and b: woody species.

Land-use management strongly affected woody species richness. As expected, woody species number increased with decreasing land-use intensity in the high-impact region (Fig. 2b). In the low-impact region, however, diversity in abandoned agroforest plots was not statistically different to forest plots suggesting a rapid increase of species richness through natural regeneration after abandonment of agricultural practices.

Additive partitioning of plant diversity

The partitioning of overall herb and woody diversity showed that alpha_1 (quadrants within plots) accounted for a strikingly small proportion of the total species richness observed (around 4% for herb species and 5% for woody species; Fig.3a). The proportions of between plots (beta2) and between land-use types (beta3) variations were roughly equal and comprised a relatively high proportion of the total species richness (47% for herb diversity and 45% for woody diversity). However, the highest proportions were found for the variability between landscapes (beta_4) which explained 42% of herb diversity and 40% of woody diversity (Fig. 3a).

Additive partitioning of the Shannon index showed that alpha_1 (diversity within quadrants) comprised 38% and 45% of the total herb and woody diversity, respectively (Fig. 3b). In contrast to species richness, between quadrants (beta_1), plots (beta_2), and landscape (beta_4) were roughly equal and comprised each around 15% of the total species diversity. Only the diversity between land-use types (beta_3) differed among herb and woody species, being more important for herb species (16%) than for woody species (8%). The differences in the two types of partitioning can be explained primarily by the influence of widespread dominant species occurring at the smallest scale.

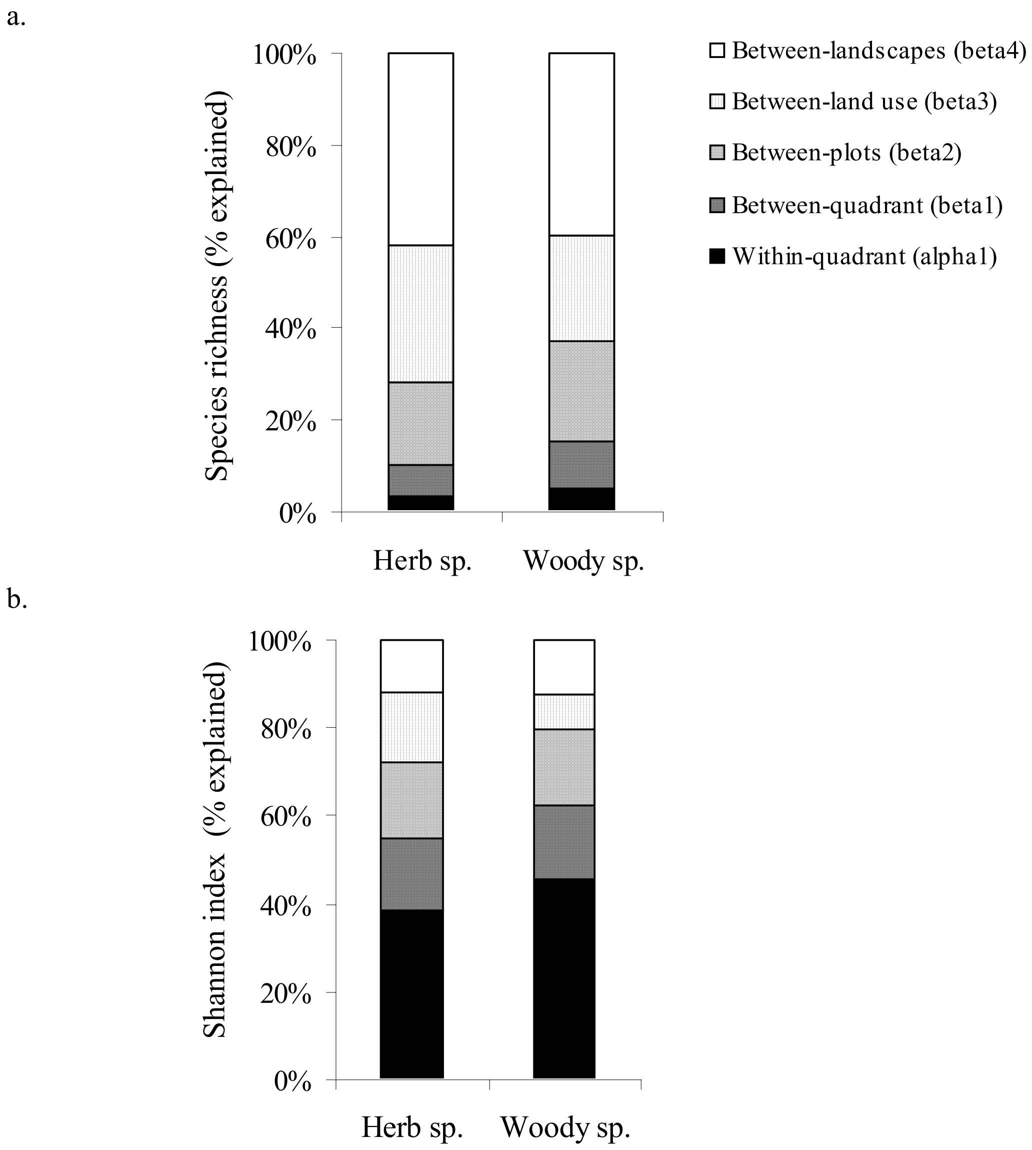


Figure 3. Additive partitioning of total species richness (a) and Shannon index (b) explained by alpha and beta components of diversity on four hierarchical levels: quadrant, plot, land-use type, and landscape.

Scale-specific contributions to diversity

Through a randomization procedure we identified the contribution of each of the different spatial scales to the overall species diversity. With a four hierarchical level model, the partitioning of species richness at the broader spatial scales (i.e., landscapes and land-use types) was always greater than expected by chance, whereas the species partitioning at the finest scales (i.e., plot and quadrant) was always lower than expected

(Table 1). This pattern was observed for both herb species and woody species, suggested that differences among landscapes and land-use types structure the richness and composition of species. Diversity in terms of Shannon index was only explained by differences among landscapes and land-use types (data not shown), despite the fact that alpha$_1$ accounted for a large proportion of diversity.

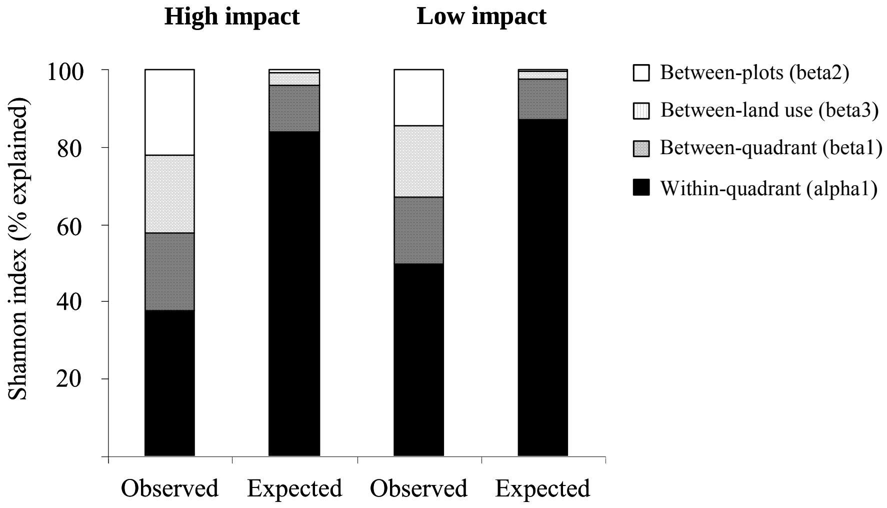
Table 1. The number of observed (obs) and expected (exp) species at different spatial scales. Additive partitioning of species richness in four and three hierarchical scales (i.e., for the low and high impact landscape separately). *P*-values obtained by comparing observed values against null estimates from the PARTITION program. All significant p-values determined at the 0.05 level. A plus (+) indicates that the observed values are significantly higher than expected, a minus (-) that they are significantly smaller than expected, n.s. that they are not significant.

	Herb species				**Woody species**			
Source	**samples**	**obs**	**exp**	**obs-exp**	**samples**	**obs**	**exp**	**obs-exp**
Four-hierarchical scales								
Between landscapes	2	124	24	+	2	117	30	+
Between land-use type	10	89	54	+	6	69	43	+
Between plot	60	52	79	-	36	64	91	-
Between quadrant	540	20	83	-	324	30	83	-
Within-quadrant		10	55	-		16	49	-
Three-hierarchical scales								
High-impact								
Between land-use type	5	132	48	+	3	60	22	+
Between plot	30	69	66	+	18	62	52	+
Between quadrant	270	23	71	-	162	27	49	-
Within-quadrant		9	48	-		16	42	-
Low-impact								
Between land-use type	5	43	11	+	3	75	33	+
Between plot	30	35	22	+	18	61	62	ns
Between quadrant	270	17	35	-	162	33	61	-
Within-quadrant		12	39	-		18	31	-

We also performed a detailed analysis of species richness within each landscape (i.e., three spatial scales). Again, species richness for herb and woody species in both landscapes was explained by the broadest scale in the model (i.e., land-use type). However, variability between plots of the same land-use type (beta$_2$) is also important in explaining overall species richness in the high and low-impact landscapes. Variability among plots of the same land-use type (beta$_2$) explained herb diversity in the high and low impact landscape (i.e., observed diversity between plots was greater than expected by chance; Table 1). Interestingly, the effect of plot in explaining woody diversity varied among landscapes. While in the high-impact landscape the observed variability between plots (i.e., beta$_2$) for woody diversity was significantly greater than expected by chance and therefore important in explaining overall woody species richness, in the low-impact landscape it did not differ from a random distribution of individuals (Table 1).

When for each of the landscapes independently the combined effect of diversity and abundance was analyzed (i.e., Shannon index) for herb diversity, the observed beta diversity for all hierarchical scales was always greater than expected, suggesting that diversity using the Shannon index was – in contrast to species richness–also explained by the variability between quadrants within a plot (Fig. 4a). This pattern was also found for woody species in the high impact landscape, however, in the low impact landscape differences between quadrants (beta$_1$) were not important in explaining total diversity as observed beta$_1$ was lower than expected (Fig. 4b).

a. Herb species



b. Woody species

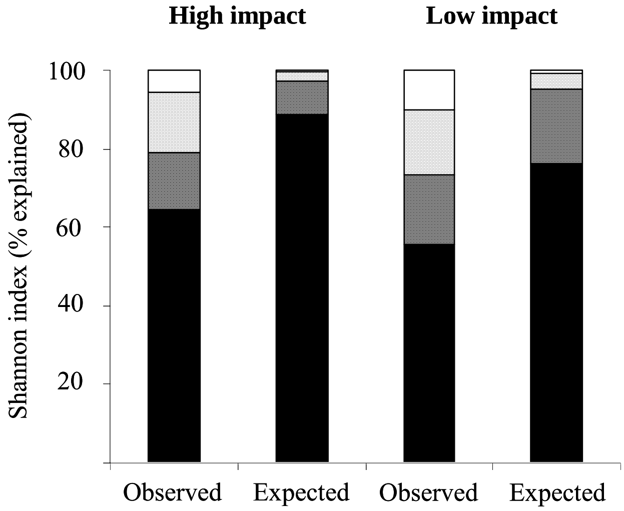
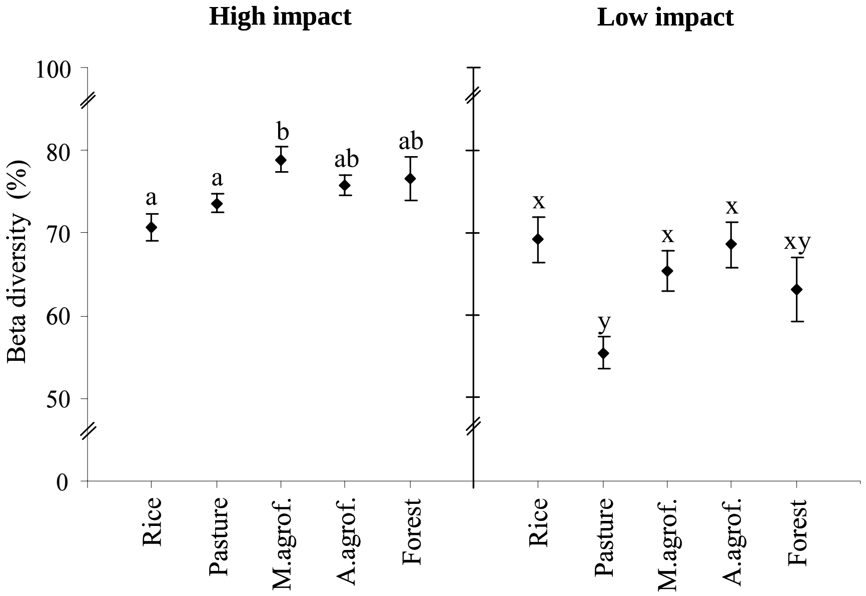


Figure 4. Additive partitioning of Shannon index across three hierarchical levels: quadrant, plot and land-use type for the high impact and low-impact landscapes, separately. The observed partitioning is compared to expected values from the null hypothesis: a. Herb species, b. Woody species. For statistics, see Table 1.

Beta diversity at the plot level

Beta diversity or species turnover at plot level explained more than 50% of overall diversity, for all land-use types and in both landscapes (Fig. 5). Land-use significantly affected beta diversity of herb species. In the high-impact landscape, beta diversity slightly increased with decreasing anthropogenic disturbance (*F* = 3.114, *P* = 0.033). As expected lower values were recorded for rice and pasture, however, these were not significantly different from values registered in abandoned agroforestry and forest plots (according to Tukey's test).

a. Herb species



b. Woody species

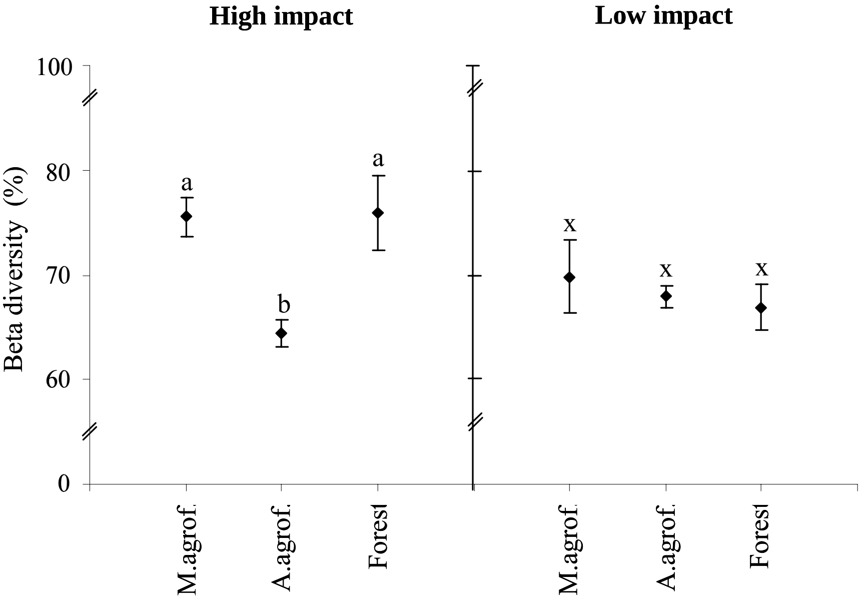


Figure 5. The effect of land-use on the percentage of total diversity explained by beta diversity (i.e. species turnover at the plot level) (± SE): a. herb species and b. woody species.

In contrast in the low-impact landscape ($F = 3.621$, $P = 0.018$), beta diversity did not increase with decreasing anthropogenic disturbance as could be expected. Surprisingly, statistically similar values were recorded for rice and all forested habitats (i.e., managed agroforest, abandoned agroforest and forest) but a significantly lower species turnover was recorded for pasture. Still, species turnover in this habitat explained more than 55% of overall species richness (Fig. 5a). The effect of land-use type on beta diversity at plot level for woody species was different among landscapes. While, woody species were affected by land-use type in the high-impact region ($F = 6.599$, $P = 0.008$), there was no significant effect in the low-impact region ($F = 0.389$, $P > 0.05$). In contrast to our expectations, beta diversity was significantly lower in abandoned agroforest compared to managed agroforest and forest (Fig. 5b).

Discussion

Large-scale effects

Our results suggest that overall species diversity was mainly determined by large spatial scales: variability between landscapes ($beta_4$) and variability between land-use types ($beta_3$). The observed beta diversity found among landscapes accounted for more than 40% of species diversity, with a large number of species unique to each landscape: 117 unique woody species and 123 unique herb species occurred in just one of the two landscapes, even though similar land-use types with similar dominant species (e.g. *Panicum maximum* Jacq. in all sampled pastures) were selected.

Broad scale components (e.g. ecoregions) have also been recognized in other studies as important factors in determining community composition and species richness of arboreal beetles and forest Lepidoptera in temperate forest. Among ecoregions, differences in glacial exposure, topography, soil types, dominant vegetation formation, and land-use history have been shown to play a major role in structuring insect communities (Gering et al. 2003; Summerville et al. 2003). For intensively managed agricultural landscapes in Europe it has been demonstrated how environmental heterogeneity (e.g. differences in soil types, water regime, floristic region) and/or complexity of the surrounding landscape influence local assemblages and community composition of arable weed communities and increased heterogeneity in plant communities at multiple spatial scales (Loreau 2000; Kneitel and Chase 2004; Gabriel et al. 2005; Pyšek et al. 2005; Roschewitz et al. 2005). Likewise, in tropical forest high beta diversity or species turnover of understorey plant species composition (i.e., pteridophytes and melastomataceae species) has been attributed to dispersal limitations and/or environmental heterogeneity, which in turn are directly affected by geographical distance (Tuomisto et al. 2003). However, analysis of tropical trees distribution has shown that distance and environmental heterogeneity together, explained only the 24% of the variation in species similarity (Duivenvoorden et al. 2002). Therefore, geographical distance might not be the only explanatory variable of the high beta diversity recorded between our landscapes.

Variability among land-use types ($beta_3$) also strongly affected plant community composition in our study. This result confirms the extremely different environmental conditions (e.g. rice vs. natural forest) of the selected land-use types, but it also suggests that even highly intervened land-use types contribute significantly to overall plant diversity in a heterogeneous landscape. Fédoroff et al. (2005) found that land-use intensification increased plant diversity by providing herbs with more light and nutrients. Our analysis of herb species richness revealed different diversity patterns depending on the landscape context. In the low impact landscape, highly intervened land-use types harbored on average more herb species than more natural land-use types such as forest plots. In contrast in the high impact landscape, species richness hardly varied among land-use types. The pattern observed in the high impact regions can be explained by the "intermediate disturbance hypothesis" (Connell 1978). Selective logging in forest and abandoned agroforest sites in the high impact region appeared to have created a heterogeneous environment where light demanding herb species were favored (Tannya Lozada, unpublished data). On the other hand, forest and abandoned agroforest plots in the low impact region did not suffer high disturbance which, in turn, explains low herb species richness. In both cases, the high beta diversity recorded among land-use types implies that many herb species present in the richer land-use type are not present in the species-poorer land-use type and vice versa. Therefore, to conserve biodiversity in fragmented landscapes, it might be beneficial to maintain many different land-use types, as it is the combination of different land-use types that preserves overall herb species richness.

Intermediate and fine scale effects

Through additive partitioning of plant diversity in agricultural landscape, Wagner *et al.* (2000) conclude that beta diversity among land-use types is more critical than beta diversity among patches of the same land-use types in generating plant species richness. Our analysis at the biogeographical scale mirrored this result. When our analysis of additive partitioning was confined to the landscape level, variability among plots of the same land-use type become important in explaining herb, but not woody species diversity, in the low impact landscape. In fact, the observed variability of herb diversity among plots of the same land-use type suggests that even "intensively" managed land-use types (e.g. rice) are not simply homogeneous in terms of plant communities. This is in contrast with studies that report low species diversity in intensive management practices, as for example shown by Krebs *et al.* (2002) for Western Europe. In our study area even the annual crop rice is rather heterogeneous probably due to lack of mechanization and relatively low chemical inputs and therefore little eradication of the crop-associated vegetation. The high species turnover we found supports the conclusion that plots can be highly heterogeneous. Since beta diversity is partially determined by variability at the next lower scale, high values of beta diversity among quadrants will contribute to a high variability between plots of the same land-use type.

We expected different patterns among herb and woody species, because of their different life-history traits, including dispersal modes, resource requirements, and life-span (Kolb and Diekmann 2004). Overall herb diversity was explained by the same spatial scales in both landscapes, whereas critical spatial scales for woody species differed between the two landscapes.

Dispersal or migration between habitats may act as a homogenizing force, which tends to reduce beta diversity and to increase alpha diversity (Loreau 2000). Seed dispersal may have worked as a homogenizing force among plots in the low impact landscape, but this appeared to be much less important in the high impact landscape. A possible reason is the fact that landscape fragmentation was higher and intensive management practices was more important in the high impact, relative to the low impact landscape, in particular as management also affected abandoned agroforest and forest by selective logging and introduction of timber species such as *Schizolobium parahybum* (Vell.) Blake (Tannya Lozada unpublished data). In line with this idea of enhanced dispersal as a homogenizing force in low-impact landscapes, we found the expected decrease of beta diversity with land-use intensity only in the high-impact landscape (from forested to open land-use types), but not in the low-impact landscape.

The plant species were more equally distributed on small than large spatial scales, so the smaller scales (quadrants within plots) were more import for the Shannon diversity (explaining the combined effect of species richness and abundance) than for overall plant species richness. This supports findings that species evenness is mainly affected by fine spatial scales (Wagner et al. 2000, Gering et al. 2003). This is presumably due to the fact that most rare species can be found only when including the high heterogeneity which comes in through larger spatial scales.

Communities were more or less diverse than expected by chance, depending on the scale of observation. Through diversity partition we might determine and thus assist in the selection of “important” sites for the preservation of plant communities. Further studies are necessary to identify all the possible ecological process operating at different spatial scales. In our study region, landscape composition and land-use history appeared to have a major effect on species diversity and distribution among spatial scales. Our study clearly shows that scale of observation influences conclusions on diversity in heterogeneous landscapes. If our study includes only large scale factors, we might overlook the influence of management practices (i.e., differences among plots of the same land-use type) on biodiversity and therefore ignoring the effect of seed dispersal as a homogenizing force.

Conservation implications

Although our landscapes were located within the same biogeographical area (the Chocó region of coastal Ecuador), which has been recognized as a hotspot for biodiversity (Myers et al. 2000), important differences in vegetation structure were found within and between landscapes at relatively small distances. This suggests that conservation programs to identify biocorridors or habitats for important ecosystem services, a more detailed look at the variation within and between landscapes needs to be taken into account. In tropical countries the potential role of agroecosystems in the maintenance of plant diversity at a landscape has been less studied than in industrialized countries (Tscharntke et al. 2005). Our results suggest that human-intervened agroecosystems should not be disregarded when regional vegetation diversity is considered in tropical areas because they can contribute significantly to overall diversity. Conservation efforts should therefore not only focus on little disturbed ecosystems of which little surface areas remain, but also find strategies to maintain diversity in human-dominated landscapes. This inevitably calls for the inclusion of land owners in biodiversity conservation and in identifying trade-offs between conservation and welfare.

Chapter

4

Geographical range size of tropical plants influences their response to anthropogenic activities

T. Lozada, G.H.J. de Koning, M. Kessler, A.-M. Klein & T. Tscharntke

Abstract

Biodiversity patterns may be influenced by the species' geographical range sizes, but this is rarely shown. We used a highly replicated and large-scale study in coastal Ecuador to determine for the first time the importance of latitudinal range size of plant species in their response to land-use activities. We examined herbaceous plant communities of five land-use types with decreasing anthropogenic disturbance (from the most intervened rice and pasture to the less intervened managed agroforest, abandoned agroforest, and forest) in a low and a high impact human-dominated landscape. All species were classified in four latitudinal range size quartiles, from the 25% species with the narrowest to the 25% with the widest range size. We found notable differences between patterns of total species richness and those of individual range size quartiles. Whereas total species richness was higher in more intervened land-use types, percentages of narrow ranged species were significantly higher in less intervened land-use types. In contrast, percentages of wide-ranging species were higher in more intervened land-use types. Hence, responses of plant species to human activities were influenced by traits that determine their range sizes. An analysis of floristic similarity between land-use types revealed that narrow ranged species were mainly preserved in forest fragments, but the other land-use types supported many unique narrow ranged species and therefore made an important contribution to their preservation at the landscape level. Conservation efforts should combine protection of natural habitats with strategies to maintain a diversity of low-intensity land-use types, looking for win-win solutions or trade-offs between biodiversity conservation and human welfare in human-dominated landscapes.

Keywords: Chocó biogeographical region, disturbance, biodiversity, land-use management, endemism, Ecuador.

Introduction

For a wide spectrum of taxonomic groups (including groups as different as trees, ants, lizards, mammals, and birds) species richness increases with decreasing latitude (Stevens 1989). However, a growing number of studies indicate that latitude *per se* is not the primary determinant of species richness, but a proxy of environmental factors (Gaston 2000). The strikingly high diversity of many tropical ecosystems when compared with their counterparts at high latitudes has generated a plethora of hypotheses about possible determinants of large scale patterns of species richness (Hughes et al. 1996; Kreft et al. 2006). This includes explanations based on chance, historical perturbation, environmental stability, habitat heterogeneity, species-energy relationship, and interspecific interactions (Gaston 2000).

It has been suggested that latitude and the geographical range size of species are related, with narrower range sizes predominating at lower latitudes (Stevens 1989). This pattern might result from the fact that tropical species tend to live under localized conditions characterized by distinctively different microhabitats, and thereby, exhibit narrower environmental tolerances (Stevens 1989; Brown et al. 1996; Gaston 1996). However, also tropical species differ in their geographical range sizes exhibited by individual species can differ enormously between taxa. Species with wide range sizes often exhibit high local abundance, and this combination of wide distribution and abundance makes them less likely to go extinct, while narrow range species tend to have smaller populations. The rarity of narrow-ranged species has been linked to traits such as low grow rates, low reproductive output, poor dispersal ability, greater tendency towards asexual reproduction, and little persistent seed banks (Kruckeberg and Rabinowitz 1985; Gaston 1996; Walck et al. 1999). A better understanding of the factors influencing species range size is necessary to identify the environmental and anthropogenic factors that determine the origin and current patterns of species diversity, to predict the likely response of species diversity to global environmental changes, and to identify the most effective schemes for in situ conservation and sustainable land use (Gaston 2000; Hunter 2003).

Several studies explore the relationships between patterns of species range size and environmental factors (e.g., Gaston 1996, Kessler 2002a, b, Hunter 2003, Lennon et al. 2004, Kreft et al. 2006). These studies suggest that species with wide ranges are characterized by a broad ecological plasticity, whereas species with narrower range size are adapted to local environmental conditions. Surprisingly, few studies link these patterns to the responses of endemic vs. widespread species to human habitat disturbances. The reason for this gap in knowledge is perhaps the commonly assumption that endemic species are particularly sensitive to habitat alteration (Kruckeberg and Rabinowitz 1985). However, Kessler (2001) found that the representation of endemic plant species may be higher in slightly anthropogenically disturbed forests than in adjacent mature forests. The competitively inferior species with narrow ranges appeared to depend on natural habitat disturbances to disrupt competitive interactions with other species and therefore profit from a certain level of anthropogenic disturbance (Kessler 2001). If this pattern holds true in other tropical habitats and for other groups of organisms, then moderate land-use activities might be compatible with the conservation of endemic species, creating the opportunity for a win-win-situation profiting both nature and humans.

Previous studies on total species richness patterns at a broad spatial scale (Currie 1991; Guegan et al. 1998) tend to be biased towards wide ranging species, because these are more abundant than narrow ranged size species, and therefore contribute with more records. For this reason, studies analyzing geographical variation in species richness based only on overall species richness patterns might not give a representative picture for the majority of taxa. Jetz and Rahbek (2002) and Kreft et al. (2006) addressed this problem when analyzing the potential determinants of species richness of bird species richness in Africa and of palms in America. Through the partitioning of overall species richness in four range size quartiles, they demonstrated that the apparent role of net primary productivity as a determinant of species richness distribution diminishes with decreasing range size, whereas the effect of topographic heterogeneity increases. They concluded that both scientific analyses and conservation programs based exclusively on the distribution of total species richness and its correlation with environmental factors may neglect the specific requirements of species with narrower range size.

Here, we analyze for the first time the influence of anthropogenic activities on the diversity patterns of terrestrial herb species with different latitudinal range sizes. Our research was carried out in tropical western Ecuador, in two human-dominated landscapes with different degrees of anthropogenic influence. Specifically, we asked (1) how anthropogenic activities affect the species range-size distribution (for different land-use types and at the landscape scale), and (2) how species composition, especially for narrow ranged species, changes from low to high intensity land-use types. We used herbaceous species, because they are highly diverse in human intervened landscapes and contain a higher percentage of endemics than trees (van der Werff and Consiglio 2004).

Methods

Study areas

Fieldwork was carried out in western Ecuador, within the biodiversity-rich region known as Chocó-Darien-Western Ecuador, one of the 25 global "hotspots of biodiversity" (Myers et al. 2000), on private farms spread across two agriculture-dominated landscapes. These landscapes are about 300 km apart and differ in climatic conditions, vegetation formations, and degree and timing of anthropogenic disturbances. The first landscape (hereafter called high-impact landscape) is situated in the vicinity of the village of Jipijapa (UTM 17, 546800 S, 9849274 W) in Manabí Province, mid-west Ecuador, with an elevation range of 100-500 m. The original vegetation is semi-deciduous forest dominated by *Centrolobium ochroxylum* Rudd (Fabaceae), *Erythrina poeppigiana* (Walp.) O.F. Cook (Fabaceae), *Poulsenia armata* (Miq.) Standl. (Moraceae), and *Phytelephas aequatorialis* Spruce (Arecaceae) (Jørgensen and León-Yánez 1999; Sierra 1999). The climate is characterized by mean annual rainfall (excluding El Niño years) of 1170 mm and an annual dry period of about six months (INAMHI 2002). Agricultural practices in the high-impact landscape were promoted by the land reform programs initiated in the early 1960s (Dodson and Gentry 1991) and therefore it is possible to find agroforests or annual crops that have persisted in the area for more than 40 years. More than 60% of the total area is dominated by pasture, coffee agroforests, and the arable crops rice and maize, whereas natural vegetation, found mainly on steep slopes, accounts for less than 25% of the landscape (INEC-MAG-SICA 2002).

The second landscape (hereafter called low-impact landscape) is located in the neighborhood of the village of Cabo San Francisco (UTM 17, 72685 N, 604100 W) in Esmeraldas Province (north of the high impact landscape), at 0-200 m. The natural vegetation classified as lowland evergreen forest is recognized as an extension of the wet Colombian Chocó region with a high proportion of endemic species. Common tree species include *Pseudolmedia rigida* subsp. *eggersii* (Standl.) C.C.Berg (Moraceae), *Exarata chocoensis* A.H. Gentry (Bignoniaceae), *Virola dixonii* Little (Myristicaceae), and *Protium ecuadorense* Benoist (Burseraceae) (Jørgensen and León-Yánez 1999). The climate is characterized by mean annual rainfall exceeding 3000 mm and absence of a distinct dry season (INAMHI 2002). In this landscape, natural forest accounts for approximately 50% of the total surface (INEC-MAG-SICA 2002) as the expansion of the agricultural frontier has reached the surroundings of Cabo San Francisco much later than around Jipijapa. Information provided by the farmers showed that some years ago the main agricultural activities in the region were agroforestry management dominated by cacao and banana. Nowadays, due to commercialization problems, mainly related to lack of road maintenance, cacao and banana have lost economic importance and most of the agroforests have been abandoned during the last 15 years. To counterbalance the decreased farmer's income, the production of arable crops and cattle products of increasing pastures have become more important in recent years.

Field sampling

The study sites were chosen to include the dominant land-use types in the study region that represent a gradient of decreasing anthropogenic disturbance: rice and pasture which have been established by manual sowing without mechanical soil tillage, managed agroforestry systems (hereafter called *managed agroforest*), which result from the replacement of understorey vegetation by coffee plants (in the high-impact landscape) or cacao plants (in the low-impact landscape), abandoned agroforestry systems (hereafter called *abandoned agroforest*) where no agricultural practices have been applied for about 15 years, and near-natural, selectively logged forest (hereafter referred to as *forest*). As mentioned, landscapes differed in time and intensity of management practices. Whereas in the high-impact landscape agroecosystems have been in cultivation for over eight years and urea fertilizer is occasionally applied in rice, in the low-impact landscape only recently intensive management practices are more widespread, for instance rice fields had been cultivated for only two to three years without fertilizers. In both landscapes pesticides are hardly ever applied.

Six plots (replicates) were selected for each land-use type. In each plot, nine fixed points were positioned in a regular 3 x 3 grid with 25 m between adjacent points within a 50 x 50 m area. All herb specimens (including ferns) were collected in 2.5 x 2.5 m fixed quadrants positioned around each of the nine points. To consider possible variation of herb species richness and abundance due to climatic conditions, two plant surveys were conducted in April and October of 2003 for the high impact landscape, and in April and October 2004 for the low-impact landscape.

Total species richness and abundance were calculated for the total of the two sampling dates for each quadrant, and the abundance was used as the mean value of individuals of the two sampling dates. For species identification, fertile voucher specimens were collected for each plant species found in the quadrants and when not possible, sterile specimens were gathered. Specimens were first classified as morphospecies and then identified up to species level with the help of experts at the Ecuadorian herbaria in Quito (QCA, QCNE) and Guayaquil (GUAY). Voucher specimens have been deposited at QCA and GUAY.

Distribution data

The latitudinal distribution data of all species was extracted from the W^{3}TROPICOS of the Missouri Botanical Garden´s VAST nomenclatural database and associated authority files (http://mobot.mobot.org/W3T/Search/vast.html). Latitudinal range size for each species was measured as the latitudinal difference between the northern- and southern most record. To compare diversity patterns among landscapes, we combined the species list obtained from the sampling procedure in the high and the low-impact region. Afterwards, we partitioned the final species list into four latitudinal range size quartiles (as performed by Jetz and Rahbek 2002). Hence, the *first range size quartile* was represented by the 25% of species with the narrowest range sizes whereas the *fourth range size quartile* contained the 25% of the widest latitudinal range sizes. Latitudinal range size was calculated only for those morphospecies that could be identified to species level (= 76% of all species sampled).

Data analyses

In a pre-analysis we assessed the adequacy of our sampling effort by calculating the abundance-based coverage estimator (ACE) of species richness using the Estimate*S* version 7.5, with 500 randomizations (Colwell 2004).

To avoid misleading results due to differences in total species richness and abundance, for each range size quartile separately, we calculated relative species richness (expressed as the number of species records for one specific range size quartile divided by the total number of species recorded per plot) and relative abundance. The effect of land-use type on relative species richness and relative abundance per plot were analyzed with one-way analyses of variance (ANOVA) and post-hoc Tukey's pairwise comparisons on data with normally distributed model residuals. Where necessary, data were log-transformed in order to meet assumptions of homogeneity of variance. All values of $p < 0.05$ are reported as significant throughout (Sokal and Rohlf 1995).

Floristic similarity among land-use types was estimated using the abundance-based Jaccard's index, which is a derivation of the classic incidence-based Jaccard Index (Chao et al. 2005). These tests were performed using Estimate*S* 7.5 (Colwell 2004). To identify patterns of species dominance within the land-use types, we determined whether one range size quartile had on average higher relative species richness than the others, using a nonparametric Friedman ANOVA by ranks. Post hoc pairwise comparisons where then made with Wilcoxon matched-pairs tests. We carried out all statistical analyses using Statistica 6.1 (StatSoft, Tulsa, Oklahoma, USA).

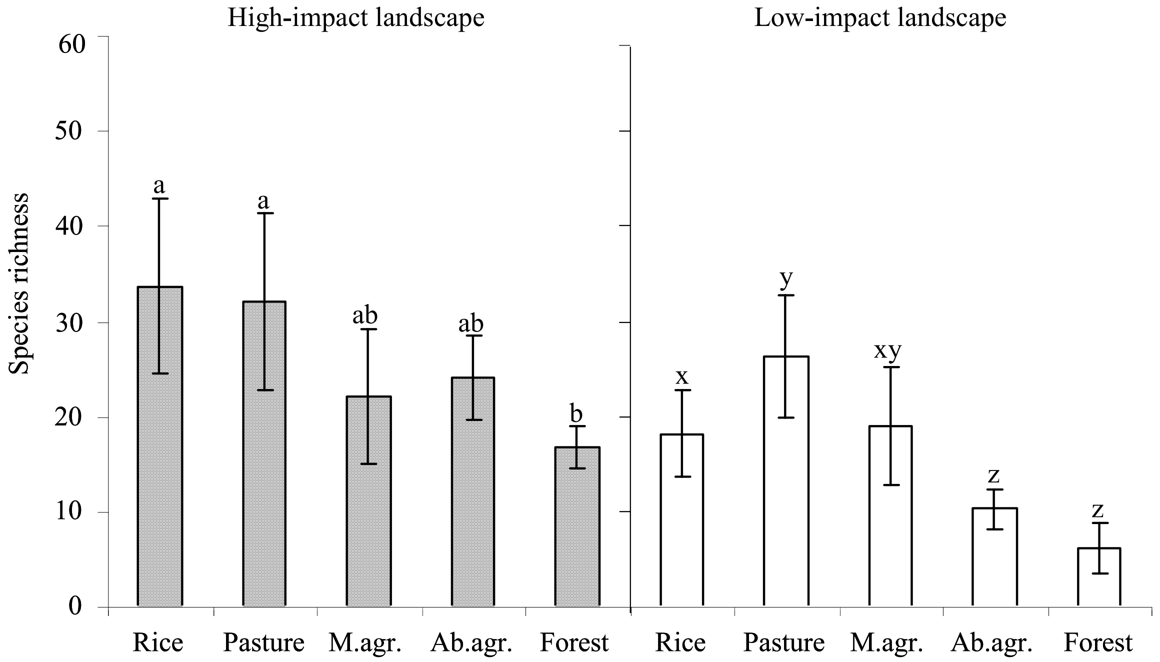
Results

A total of 290 herbaceous plant species belonging to 63 families were recorded in the 60 study plots. Of these, 220 could be identified to species level. As is typical for tropical agricultural areas, Poaceae and Asteraceae were the dominant families in terms of species richness, abundance, and frequency (i.e., recorded at least once per land-use type). Araceae was also important in terms of individual abundance in the low-impact landscape. The degree of species saturation (according to ACE, Colwell 2004), which is expressed by the percentage of observed species richness relative to the estimated species richness was 88% and 96% for herbs in the high and low impact landscapes, respectively, suggesting that sample size and sampling effort were sufficient. Therefore, we decided to perform all our statistical analyses with original species numbers rather than estimated species numbers.

Diversity patterns

In general, overall species richness (species richness not partitioned in range size quartiles) decreased with decreasing anthropogenic disturbance (Fig. 1a). In the high-impact landscape, significantly higher values were recorded for rice and pasture ($F_{(4,25)}=5.6675$; $p=0.003$) than for forest. In the low-impact landscape, pasture was the most species rich land-use type ($F_{(4,25)}=18.83$; $p<0.0001$) whereas abandoned agroforest and forest were the least species rich land-use types. The same pattern was observed when abundance per land-use type was analyzed. In the high-impact landscape, as expected, abundance was significantly higher in rice and pasture than in forested land-use types (i.e., managed agroforest, abandoned agroforest and forest: $F_{(4,25)}=8.0494$; $p<0.0001$).In contrast, in the low-impact landscape, abundance was significantly higher in pasture than in abandoned agroforest and forest and even rice ($F_{(4,25)}=27.024$; $p<0.0001$). Maximum differences were found between pasture (654 individuals) and forest (52 individuals; Fig. 1b).

a. Species richness



b. Species abundance

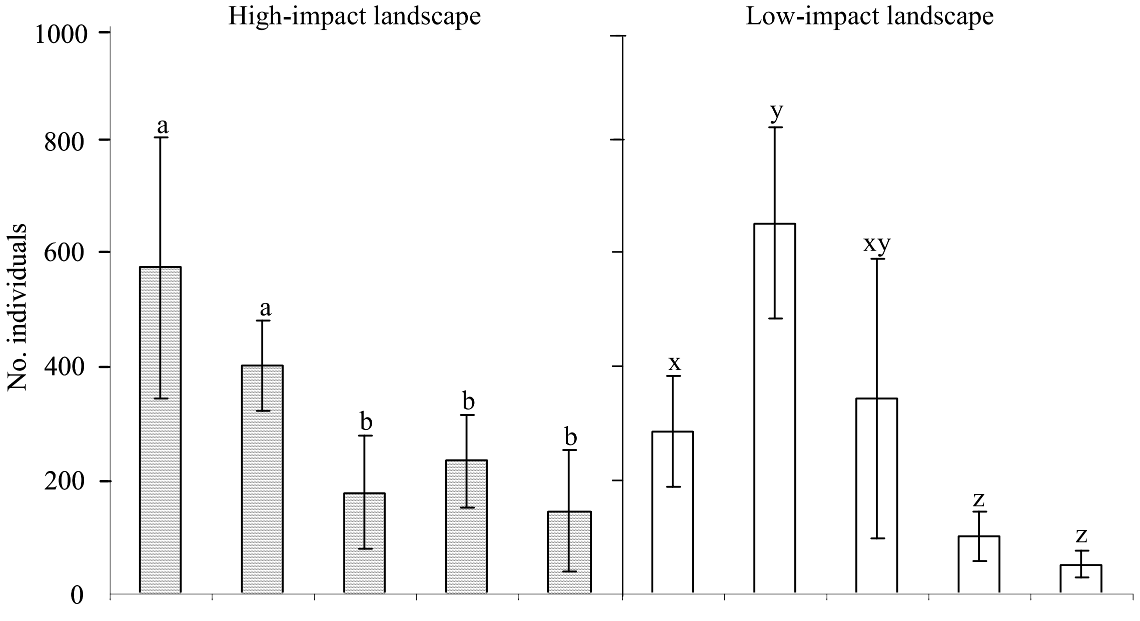
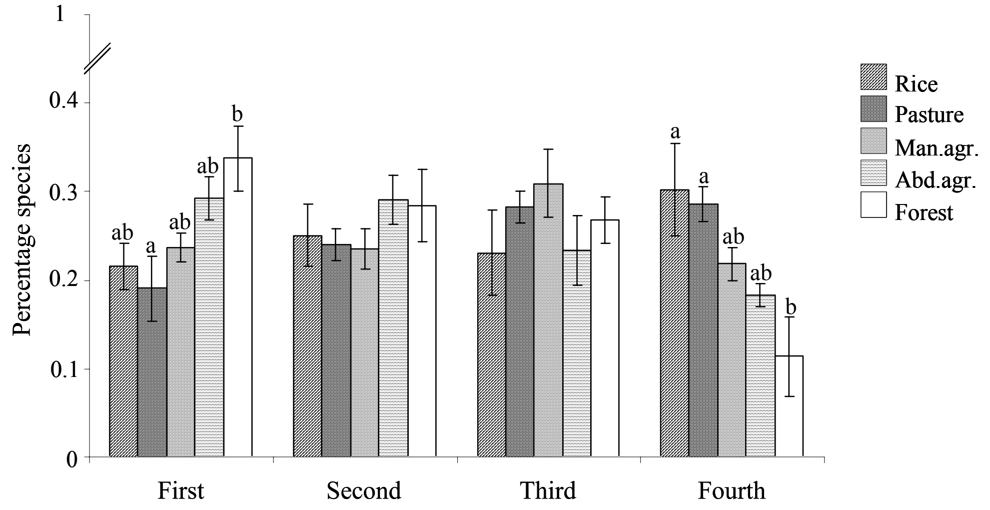


Figure 1. Effect of land-use type on overall species richness (a) and abundance (b) of terrestrial herbs (numbers per plot, based on twice mapping of nine 2.5 x 2.5m quadrants). Means with same letter are not significantly different ($p > 0.05$), based on Tukey's test. Error bars represent 1 SD.

Partitioning of species into range size quartiles (with 55 species each), revealed patterns of species richness that differed from those of all species. The narrowest range size quartile (i.e., first) with a mean latitudinal range size of 13° was significantly more species rich in less intervened land-use types (e.g., abandoned agroforest and forest) than in highly intervened land-use types (e.g., pasture) (Fig. 2).

a. High-impact landscape



b. Low-impact landscape

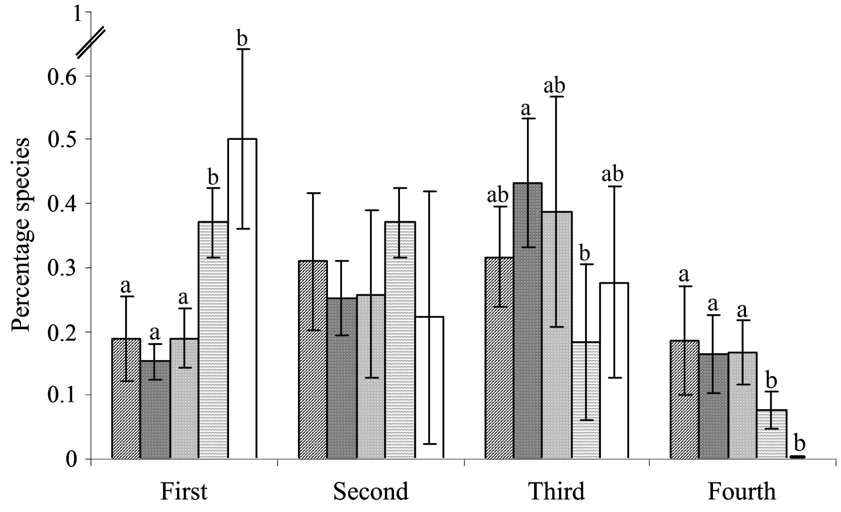
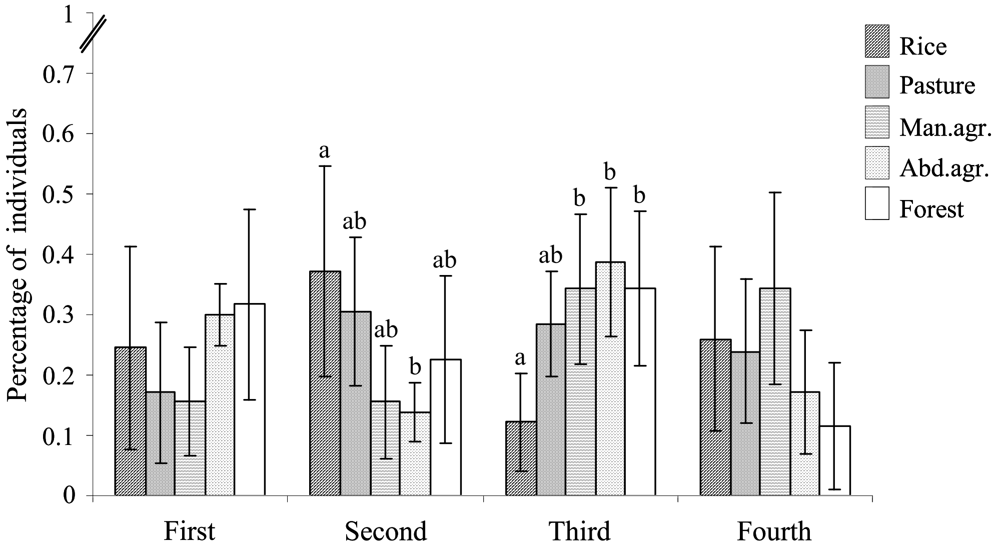


Figure 2. Effect of land-use type on patterns of species richness of terrestrial herbs for each range size quartile separately in a high-impact landscape (a) and a low-impact landscape (b). Overall species richness is divided in four range size quartiles representing 25% of the latitudinal distribution (from small to large range size: first, second, third, and fourth). Means with different letters indicate significant differences ($p > 0.05$), based on Tukey’s. Error bars represent 1 SD.

Although this pattern was true for both landscapes, differences among land-use type were stronger in the low-impact landscape ($F_{(4,25)}$=16.995; p<0.0001) than in the high-impact landscape ($F_{(4,25)}$=3.996; p=0.012). For the second and third range size quartiles (with mean latitudinal range sizes of 30° and 47°, respectively) differences among land-use types were not significant, except for the third range size quartile in the low-impact landscape, where different values of species richness were found between pasture and abandoned agroforest ($F_{(4,25)}$=3.259; p=0.028). The analysis of the fourth range size quartile, with a mean latitudinal value of 65°, revealed the same diversity pattern as the pattern found for all species together. Species richness was significantly higher in the highly intervened land-use types rice and pasture ($F_{(4,25)}$=5.236; p=0.003) for the high-impact landscape. In the low-impact landscape, species richness was significantly higher in intervened land-use types in comparison to abandoned agroforest and forest ($F_{(4,25)}$=8.333; p<0.001).

The analysis of abundance per latitudinal range size showed very heterogeneous patterns (Fig. 3). For the first range size quartile, species abundance was not different among land-use types for the high-impact landscape ($F_{(4,25)}$=2.061; p=0.116), and significant differences were only recorded among land-use types in the low-impact landscape ($F_{(4,25)}$=6.398; p=0.001). Surprisingly, species abundance of the narrowest range size quartile in the low-impact landscape was roughly equal among rice and abandoned agroforest and forest. In both landscapes, considerable differences were found among land-use types for the second and third range size quartiles. However, a consistent pattern of increasing or decreasing species abundance among land-use types was not evident (Fig. 3).For instance, for the second range size quartile, we found that species abundance in the high-impact landscape was highest in rice ($F_{(4,25)}$=3.739; p=0.016) whereas in the low-impact landscape abundance was highest for abandoned agroforest ($F_{(4,25)}$=4.883; p=0.005). Finally, the widest range quartile revealed no significant differences for species abundance among land-use types for the high-impact landscape. In the low-impact landscape, abundance was significantly higher in managed agroforest compared to forest while for rice, pasture and abandoned agroforest intermediate values were found ($F_{(4,25)}$=3.371; p=0.024; fig. 3b).

a. High-impact landscape



b. Low-impact landscape

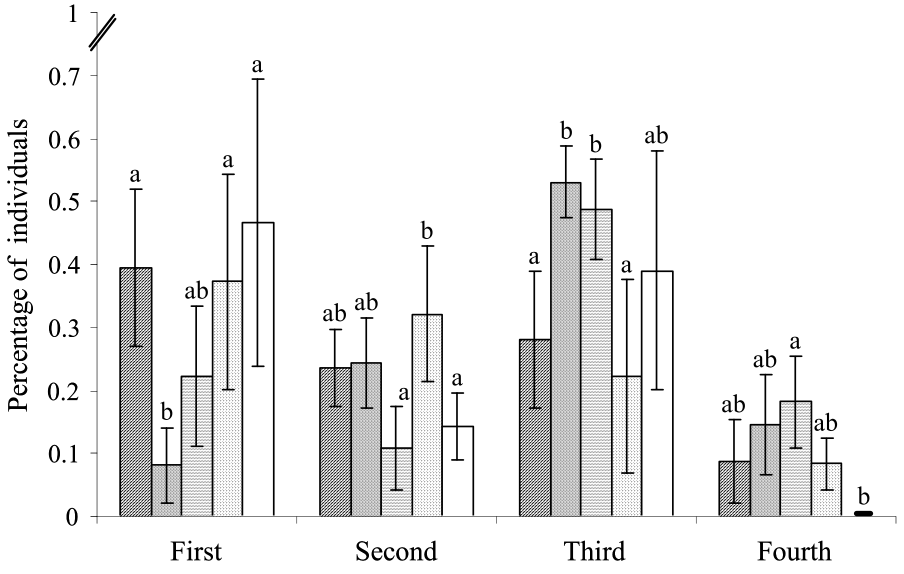
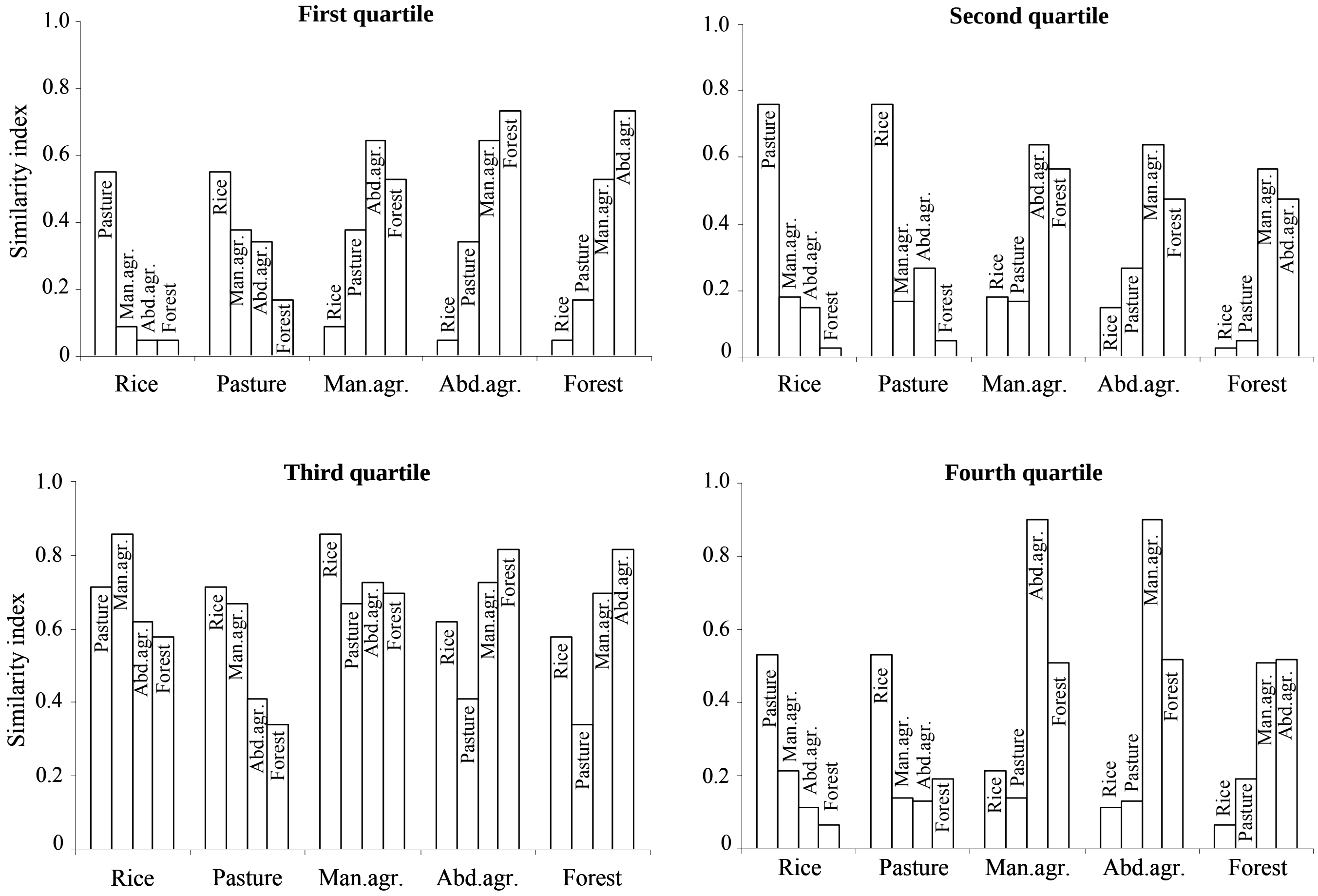


Figure 3. Effect of land-use type on patterns of species abundance of terrestrial herbs for each range size quartile separately in a high-impact landscape (a) and a low-impact landscape (b). Overall abundance divided in four range size quartile representing 25% of the latitudinal distribution. Means with same letter are not significantly different (p > 0.05), based on Tukey's richness. Error bars represent 1 SD.

Species composition

Patterns of floristic similarities differed between range size quartiles and landscapes (Fig. 4). The first range size quartile was characterized by high similarity values among land-use types with comparable intensities of anthropogenic influence such as between rice and pasture and between abandoned agroforest and forest. Extremely high values were recorded between rice and pasture in the low-impact landscape, with plant communities composed of almost the same species, as expressed by a similarity value close to one. Interestingly, in the low impact region, species found in managed agroforest were more similar to highly intervened land-use types than forested land-use types, whereas the opposite occurred in the high-impact landscape.

a. High-impact landscape



b. Low-impact landscape

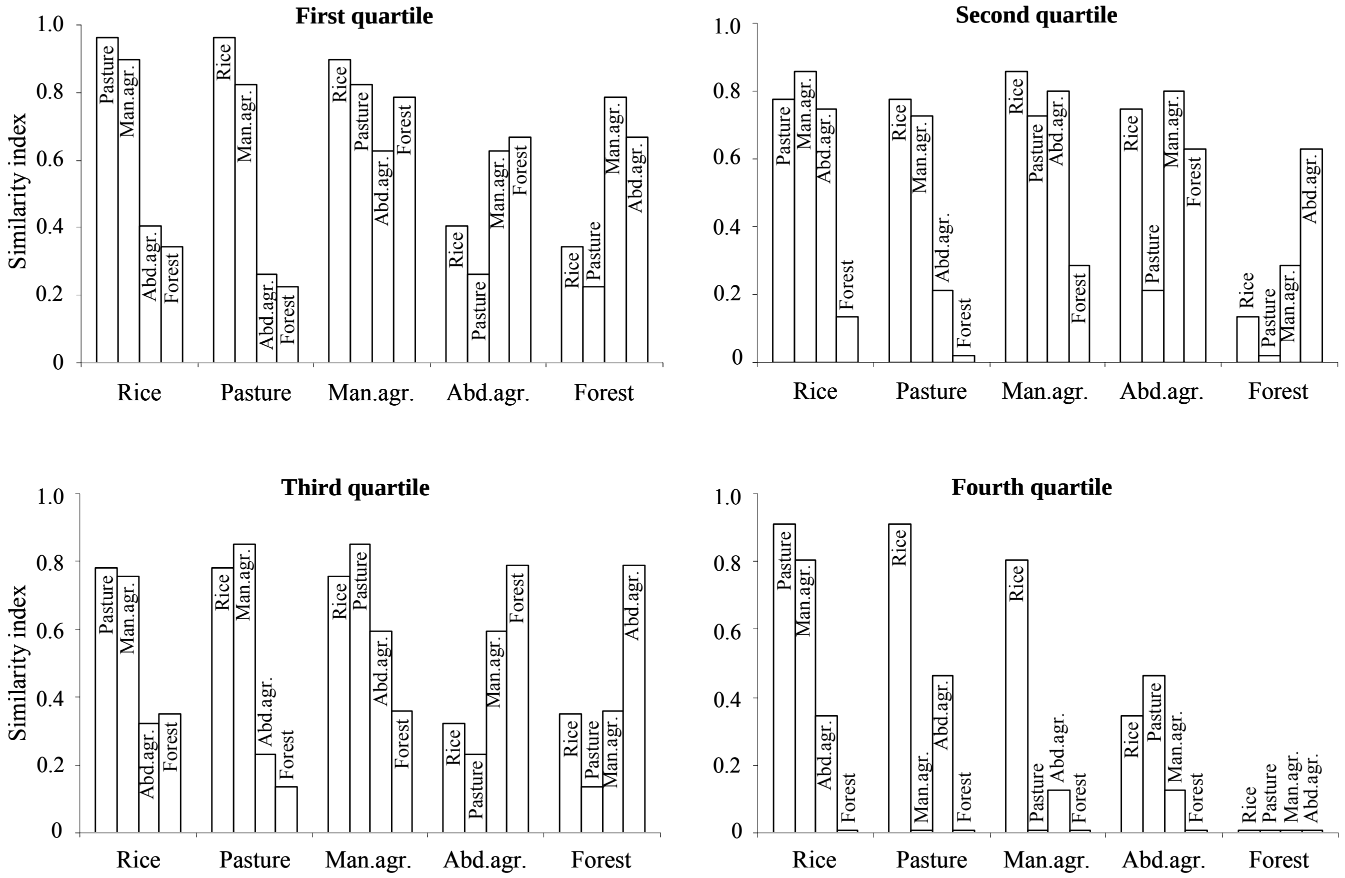


Figure 4. Floristic similarities (abundance-based Jaccard's index) of terrestrial herb communities among land-use types for each range size quartile in the high-impact landscape (a) and the low-impact landscape (b).

For the second range size quartile, we broadly observed the same pattern as for the first range size quartile. However, for the high-impact landscape, similarity values among abandoned agroforest and forest decreased. Again and in contrast to our expectations, in the low-impact landscape similarity values between the highly intervened land-use types rice and pasture, and managed and abandoned agroforest were higher than the values recorded between managed and abandoned agroforest and forest.

For the third range size quartile, patterns of floristic similarity between land-use types in the high-impact landscape were weaker than for the other quartiles. In the low impact landscape, in contrast, strong pattern were observed for the third range size quartile with high similarity values between abandoned agroforest and forest. As expected, high similarity among land-use with similar land management intensity was recorded for species of the widest range size quartile. The analysis of species distribution across range size quartiles within each land-use type revealed interesting patterns (Table 1). In the high-impact landscape, contrary to our expectations, no significant differences existed among range size quartiles for all land-use types.

Table 1. Partitioning of relative species richness in range size quartiles (RSQ). Comparisons within vegetation communities: rice, pasture, managed agroforest (Man. agr.), abandoned agroforest (Abd. agr.), and forest, using a nonparametric Friedman ANOVA by ranks. Post-hoc pairwise comparisons were made with Wilcoxon matched-pairs tests (letters). Forest plots of the low-impact landscape were not included in the analysis.

	First	**Second**	**Third**	**Fourth**	**Chi-square**	**p-value**
High-impact						
Rice	0.21	0.25	0.23	0.30	1.632	0.652
Pasture	0.19	0.24	0.28	0.28	4.404	0.221
Man. agr.	0.24	0.23	0.31	0.22	2.529	0.470
Abd. agr.	0.29	0.29	0.23	0.18	4.737	0.192
Forest	0.33	0.28	0.27	0.11	6.056	0.109
Low-impact						
Rice	0.19 *a*	0.30 *b*	0.31 *b*	0.18 *a*	7.964	*0.047*
Pasture	0.15 *a*	0.25 *b*	0.43 *c*	0.16 *ab*	14.085	*0.003*
Man. agr.	0.18	0.26	0.39	0.16	7.316	0.062
Abd. agr.	0.37 *a*	0.37 *a*	0.18 *b*	0.08 *b*	13.980	*0.003*
Forest	0.50	0.22	0.28	--	4.667	0.097

In the low-impact landscape, significant differences between quartiles were found for rice, pasture, and abandoned agroforest. For rice, the amount of species in the second and third range size quartiles was higher than in the other quartiles, whereas in pasture most species were found in the third range size quartile. For abandoned agroforest higher values of species richness were found for the first and second range size quartiles.

Discussion

The impact of agricultural land-use intensity on species diversity has been frequently examined (e.g., Svenning 1998, Klein et al. 2002, Perfecto et al. 2003, Tylianakis et al. 2005, Lozada unpublished data). Likewise, several studies investigated environmental factors that might determine the range size of plants species (Kessler 2002*a,b*; Hunter 2003; Kreft et al. 2006). However, the importance of range size of species in their response to anthropogenic disturbance in human-dominated landscape, as shown in this study, has largely been neglected. Species with different latitudinal range sizes tend to show patterns of diversity that differ from those of all species (Brown et al. 1996; Jetz and Rahbek 2002; Kreft et al. 2006). If we had only examined patterns of diversity for all species, we would come to the conclusion that more strongly intervened land-use types (rice and pasture) contained higher plant diversity than forested land-use types. However, when we analyzed data for each range size quartile, we found the opposite pattern for the narrowest range size quartile. This contrasting outcome confirms that studies analyzing geographical variation of overall species richness patterns might not give a representative picture for taxa of high conservation interest.

Biological determinants

The response of plant species to agricultural activities is influenced by the traits that determine their range size, including reproductive biology, dispersal mechanisms, life-form, demography, spatial population structure, competitive ability, and susceptibility to disturbance and habitat loss (Kruckeberg and Rabinowitz 1985; Balmford and Long 1994; Walck et al. 1999; Kessler 2001).Wide ranging species tend to show strong competitiveness under highly disturbed habitat conditions, explaining why we found a dominance of wide ranged species in highly intervened land-use types such as rice and pasture. Narrow ranged species, the group most sensitive to disturbance, showed the opposite pattern. Species from the second and third range size quartile were intermediate and did not show a clear tendency or preference to particular land-use types.

This general pattern is similar to the results found by Kessler (2001) in Andean forests. Our results differed among landscapes in respect to the narrow ranged species: in the low-impact landscape, abandoned agroforest and forest contained the highest amount of narrow ranged species, whereas in the high-impact landscape the amount of narrow ranged species was not significantly different between rice and forested land-use types. The general pattern and the differences between landscapes, might be explained by the intermediate disturbance hypothesis (Connell 1978). Forest and abandoned agroforest in the low-impact landscape suffered to some degree of human-induced disturbance. However, and according to the intermediate disturbance hypothesis, increasing disturbance might result in decreasing species richness, which could be shown by the lower diversity of narrow range species in abandoned agroforest and forest plots in the high-impact landscape. Apparently, the degrees to which disturbances affect plant species, and hence the shape of the intermediate disturbance curves, are different for species with different range sizes.

The observed similar richness patterns for wide ranged species and total species in the high-impact landscape confirms that a minority of widespread species dominated the spatial variation in overall species richness (Jetz and Rahbek 2002; Kreft et al. 2006). In contrast, the dominance of widespread species in the low-impact landscape was not that evident. The high species numbers observed in pasture and rice for overall species numbers seem, thus, to emerge from complex spatial interactions of many species with relatively narrow ranges and few species with very wide ranges.

Differences in species richness and composition among landscapes reflect historical and contemporary factors such as productivity, habitat heterogeneity, and isolation dynamics (Jetz et al. 2004), which in turn are the result of alterations of competitive relationship, soil conditions, nutrient availability, light exposure, humidity conditions, and seed sources (Svenning 1998; Dupouey et al. 2002; Fédoroff et al. 2005). However, their effects on species abundance were not always consistent. For instance, similar numbers of narrow ranged individuals were recorded in land-use types with few narrow ranged species, such as in rice, and in land-use types with many narrow ranged species, such as forest. Although narrow range size is often related to poor reproduction and dispersal abilities (Kruckeberg and Rabinowitz 1985; Kessler 2001), the narrow ranged species of our study showed a surprisingly high ability to colonize land-use systems, as expressed by their relatively high abundance. This could be the result of management practices. In both high- and low-impact landscapes, management practices in rice and pasture did not include intensive mechanical tillage, application of synthetic fertilizer, or chemical pest and weed control. Therefore, we expect that seed banks were not highly perturbed and species not able to develop under shade conditions are able to germinate and grow once the original vegetation is removed.

Between-habitat similarity in floristic composition

The fact that species with narrow range sizes tend to have higher extinction risks due to more strict environmental requirements and low population densities, make them a priority in conservation programs (Brooks et al. 2002). Our results suggest that the preservation of forest fragments in western Ecuador should be priority for the conservation of such species. However, our analysis of floristic similarities among land-use types per range size quartile suggests that the other land-use types also make important contributions to the preservation of narrow range size species at the landscape level. Narrow ranged species found in highly intervened land-use types are different to those found in forested land-use types, as is suggested by the low floristic similarity between these categories. This divergence in species composition is more pronounced for the first and fourth range size quartiles. Therefore, from a landscape perspective, the presence of a certain amount of intervened land-use types could increase the overall richness of narrow ranged species. Our study furthermore shows that, opposite to our expectations, highly intervened land-use types were not dominated by wide ranged size species, indicating that plant communities in these land types were composed by a mixture of species with different environmental requirements (Table 1).

Conservation implications

Modern land-use activities can degrade the environment in ways that may ultimately undermine ecosystem services, human welfare, and long-term sustainability of human societies, and speed up species extinction rates (Pimm and Raven 2000; Foley et al. 2005). Since preservation of biodiversity through the establishment of protected areas is often unrealistic (Bawa et al. 2004), conservation efforts have been focused on areas with an agglomerations of vulnerable and endemic species, the so-called “biodiversity hotspots” (Myers et al. 2000). Biodiversity hotspots are areas with exceptional concentrations of endemics (i.e., narrow ranged species) and exceptional losses of habitat. Protecting natural habitats in these areas, which constitute only a little more than one million square kilometers, is necessary but not sufficient (Pimm and Raven 2000; Brooks et al. 2002). Our results suggest that human-intervened agroecosystems should not be excluded when conservation of narrow ranged species is considered, because they can contribute significantly to overall diversity and because many narrow ranged species thrive in agroecosystems. Conservation efforts should therefore combine protection of natural habitats with strategies to maintain a diversity of low-intensity land-use types, looking for win-win solutions or trade-offs between biodiversity conservation and human welfare in human-dominated landscapes.

Chapter

5

Contrasting response of intraspecific aggregation of plant communities to human disturbance at different spatial scales

T. Lozada, G.H.J. de Koning, A.-M. Klein & T. Tscharntke

Abstract

Among the hypotheses to explain the coexistence of plant species, intraspecific aggregation has been proposed as a mechanism that promotes species coexistence by reducing competitive exclusion. We use a highly replicated field study to evaluate, for the first time, the impact of anthropogenic activities on patterns of spatial aggregation at two spatial scales. We examined herbaceous plant communities of five land-use types along a gradient of anthropogenic disturbance, decreasing from rice and pasture to managed agroforest, abandoned agroforest, and forest, in a low and a high impact human-dominated, tropical landscape. We found notable differences among spatial scales. In the high-impact landscape, intraspecific aggregation at the subplot level increased with decreasing anthropogenic disturbance. This appeared to be due to gaps in the forest featuring herbaceous colonizers. Good colonizers are usually poor competitors, but intraspecific aggregation can prolong competitiveness of competitively inferior species over time. In contrast to the subplot pattern, intraspecific aggregation on a plot scale was highest in the most disturbed habitats, because on a larger scale, only the non-forested land-use types are dominated by early-successional colonizers. In the low-impact landscape, where human disturbance was much more recent, plant communities of all land-use types and at both spatial scales were mainly composed by species that grow in aggregated patterns and exhibit high dispersal abilities and low competitiveness. Finally, we found that intraspecific aggregation explained more than 50% of the variation of beta-diversity. We conclude that the effect of human disturbance on patterns of plant diversity is determined by intraspecific aggregation, which allows colonizers with little competitive abilities to persist.

Keywords: beta diversity, intraspecific aggregation, colonization/competition trade-off, plant communities, biodiversity, Ecuador.

Introduction

Explanations for biodiversity patterns in natural communities often emphasize the importance of environmental heterogeneity. Species with different adaptations to physical and biotic conditions, are able to coexist by dominating different “niches” across heterogeneous landscapes, therefore avoiding competitive exclusion (Chesson 1991, Chesson 2000, Crawley 1997). However, maintenance of diversity without traditional niche differences is also possible (Tilman 1997, Barot 2004). One theory to explain coexistence without niche differentiation is based on a “trade-off” between colonization and competition. According to this theory, species with inferior competitive abilities exhibit superior colonization (typically plants that produce a large number of small and wind-dispersed seeds) and, *vice versa,* species with superior competitive abilities are inferior colonizers (Crawley 1997). In a sowing experiment of seven co-occurring annual plant species, Turnbull et al. (1999) described the influence of seed mass in the competition/colonization trade-off. They found that species producing the largest seeds were the best competitors. The fecundity advantage of small-seeded species ensured their presence in a higher fraction of sites, although they lose in direct competition. Therefore, coexistence of species with similar ecological requirements depends critically on this trade-off that prevents species from being both good competitors and good colonizers (Coomes et al. 2002, Levine and Rees 2002). A trade-off between competition and colonization is particularly important in highly disturbed habitats, as disturbances might remove strong competitors and create new gaps for fast colonizers (Connell 1978).

The coexistence of a high number of species might also be explained by the spatial structure of plant communities. Most plant species occur more often in aggregated patterns than in regular or random patterns, as a consequence of limited seed dispersal and/or clonal growth (Hubbell 1979, Stoll and Prati 2001). This aggregated pattern increases the proportion of intra- rather than interspecific interactions between individuals, which in turn is particularly relevant for plant survival and reproduction, because individuals primarily interact with conspecific neighbours (Murrell et al. 2001, Purves and Law 2002).

It has been suggested that the aggregation of conspecifics promotes the coexistence of species by affecting plant competition profoundly. An analysis of aggregation patterns in experimental plant communities showed that inferior competitors increased their performance when intraspecifically aggregated, especially at high densities where competition was greater than at low densities (Stoll and Prati 2001). On the other hand, competitively superior species exhibited lower performance in the aggregated pattern than in the random pattern at high densities. Thus, in aggregated communities inferior competitors increased their fitness while superior competitors might be suppressed; a mechanism that prevents or at least retards the elimination of competitively inferior species (Stoll and Prati 2001). Other studies showed similar patterns. For example, a study performed on four co-existing annual plant species found that poor competitors increased biomass and seed production within neighborhoods of conspecifics, while good competitors showed increased biomass and seed production within neighborhoods of heterospecifics (Monzeglio and Stoll 2005). A diminishment of the speed of competitive exclusion through intraspecific aggregation can tip the balance from competitive exclusion to coexistence and thus promote species diversity (Pacala 1997, Barot 2004).

An increase of intraspecific aggregation can also result in a decline of alpha-diversity within a sample plot (He and Legendre 2002, Veech et al. 2003). Alpha and beta-diversity are both a direct consequence of the way in which individuals are distributed among communities. According to the additive partitioning of diversity, for a given total diversity a decline in alpha-diversity leads to an increase in beta-diversity (Loreau 2000, Wagner et al. 2000). Therefore, a negative effect of intraspecific aggregation on alpha-diversity would result in a positive effect on beta-diversity (Veech 2005). Several studies on additive partitioning of plant diversity found that beta-diversity or the variability among sample units is the key factor for explaining overall species diversity (Wagner et al. 2000), and therefore an increment in beta-diversity would favor overall species diversity.

In western Ecuador, part of the Chocó biogeographical region, one of the world's hotspots of biodiversity (Myers et al. 2000), we used a highly replicated field study to investigate the relationship among patterns of intraspecific aggregation and species diversity. We analyzed the impact of management practices on intraspecific aggregation at two spatial scales: at a micro scale measuring patterns of aggregation within quadrants (2.5x2.5m) within sites and at a meso-scale where patterns of aggregation were estimated for the whole study site. Specifically we asked: (1) whether patterns of intraspecific aggregation differ among spatial scales (2) how anthropogenic activities affect intraspecific aggregation (3) whether differences in land-use history among landscapes influence patterns of intraspecific aggregation (4) to what extent intraspecific aggregation explains beta diversity at a micro scale.

Methods

Study regions

The study plots were located in western Ecuador. They comprise private farms spread across two agriculture-dominated landscapes, about 300 km apart which differ in climatic conditions, vegetation formations, and degree and history of anthropogenic disturbances. The first landscape (hereafter called high-impact landscape) is situated in the vicinity of the village of Jipijapa (UTM 17, 546800 S, 9849274 W) mid-west Ecuador. The climate is characterized by mean annual rainfall (excluding El Niño years) of 1170 mm and an annual dry period of about six months (INAMHI 2002). The original vegetation is semi-deciduous forest (Jørgensen and León-Yánez 1999). More than 60% of the total area is dominated by pasture, agroforestry systems dominated by coffee and the arable crops rice and maize, which have persisted in the area for more than 40 years. Natural vegetation, which is found mainly on steep slopes, accounts for less than 25% of the landscape (INEC-MAG-SICA 2002).

The second landscape (hereafter called low-impact landscape) is located in the neighborhood of the village of Cabo San Francisco (UTM 17, 72685 N, 604100 W) north-west Ecuador. The climate is characterized by mean annual rainfall exceeding 3000 mm and absence of a distinct dry season (INAMHI 2002). The natural vegetation is classified as lowland evergreen forest (Jørgensen and León-Yánez 1999). In this landscape, natural forest accounts for approximately 50% of the total surface (INEC-MAG-SICA 2002). In both landscapes, several coffee and cacao farms have been abandoned for over 15 to 20 years, after the decline of international prices and due to commercialization problems.

Study sites

The study sites were chosen to represent a gradient of decreasing anthropogenic disturbance: rice, pasture, managed agroforestry systems (hereafter called *managed agroforest*), which result from the replacement of understorey vegetation by coffee plants (in the high-impact landscape) or cacao plants (in the low-impact landscape), abandoned agroforestry systems (hereafter called *abandoned agroforest*) where no agricultural practices have been applied for at least 15 years, and near-natural, selectively logged forest (hereafter referred to as *forest*). In the high-impact region 12 replicates of each managed habitat type (rice, pasture, managed agroforest) and six replicates of each non-managed habitat type (abandoned agroforest, forest) were sampled. In the low-impact landscape six replicates for each habitat type were sampled.

In each study site (hereafter called plot) nine fixed points were positioned in a regular 3 x 3 grid with 25 m between adjacent points within a 50 x 50 m area. Herb specimens (including ferns) were collected in 2.5 x 2.5 m fixed quadrants positioned around each of the nine points. Specimens were identified up to species level with the help of experts at the Ecuadorian herbaria in Quito (QCA, QCNE) and Guayaquil (GUAY). Voucher specimens have been deposited at QCA and GUAY.

Data analyses

We measured intraspecific aggregation of each non-singleton species (abundance>1) using the *J* index of Ives (1991): $J = \{[\Sigma\ x_i\ (x_i\text{-}1)/XN]\text{-}X\}^*\ (1/X)$, where x_i is the number of individuals at site *i*, *X* is the mean number of individuals per site, and *N* is the number of sampled sites. If individuals are independently and randomly dispersed among samples, the number of individuals per sample follows a Poisson distribution. The intraspecific aggregation index *J* measures the proportional increase in the mean number of conspecifics encountered relative to the mean number expected based on a Poisson distribution (Ives 1991, Veech et al. 2003). A value of $J = 0$ indicates that individuals are randomly distributed in the sample unit, whereas $J = 1$ indicates a 100% increase (a doubling) in the number of conspecific expected in a sample. Intraspecific aggregation was calculated at two spatial scales. At quadrant scale, we evaluated patterns of species aggregation within a single plot, i.e., we determined how individuals were clumped within quadrants. At plot scale, we examined patterns of aggregation among plots of the same land-use type, i.e., how species are distributed over the landscape.

Species turnover or beta-diversity was estimated at quadrant scale using additive partitioning of species diversity (Veech et al. 2002). Total species richness (γ-diversity) found in a given sampled unit is partitioned into alpha-diversity (average number of species that occur in a sampling unit) and beta-diversity (between community diversity);

so that $\gamma = \alpha + \beta$ or $\beta = \gamma - \alpha$. This technique is a useful tool for quantifying diversity components across multiple spatial scales and it is insensitive to differences in sampling effort among replicates, and therefore does not require rarefaction data prior to analyses (Veech et al. 2002).

The effect of land-use type on intraspecific aggregation at quadrant scale and on relative beta-diversity were analyzed using ANOVA and post hoc Tukey's pairwise comparisons on data with normally distributed model residuals. We used mixed effect models (under the GRM module of Statistica 6.1) to analyze the variability of beta-diversity among quadrants within plots for each landscape separately. Land-use type was included as categorical variable in all models and intraspecific aggregation as a continuous variable. Model residuals were tested for adherence to a normal distribution before this was assumed in analyses. To avoid misleading results due to differences in species richness between land-use types, species turnover was represented by the proportion of total plot diversity explained by beta-diversity. The mixed effect model was only applied for the smallest spatial scale, as at the plot scale replicates are not available.

Floristic similarity among land-use types was estimated using the abundance-based Jaccard's index, which is a derivation of the classic incidence-based Jaccard Index (Chao et al. 2005). These tests were performed using Estimate*S* 7.5 (Colwell 2004). At plot scale we analyzed the effect of management practices on intraspecific aggregation patterns. We performed comparison among land-use types using a nonparametric Kruskal-Wallis ANOVA. To determine whether the plant community had on average higher aggregation in one or more land-use types, we performed Kolmogorov-Smirnov two-sample tests. We carried out all statistical analyses using Statistica 6.1 (StatSoft, Tulsa, Oklahoma, USA).

Results

Spatial structure

The partitioning of overall species richness showed that relative beta-diversity among quadrants within a plot accounted for a high proportion of the total species richness: 72-78% in the high-impact landscapes and 58-72% in the low-impact landscape (Table 1). The effect of land-use type on beta-diversity differed among landscapes. In the high-impact landscape, beta-diversity increased with decreasing anthropogenic disturbances, with significantly higher values for managed agroforest in comparison to rice ($F_{4,43} = 2.804$, $p = 0.037$). Intermediate values were recorded in pasture, abandoned agroforest and forest. In the low impact landscape, in contrast, the highest values of relative beta-diversity were recorded for rice and abandoned agroforest ($F_{4,25} = 3.543$, $p = 0.020$), which were significantly higher than those in pasture. Values for managed agroforest and forest plots were intermediate, and not significantly different from the other land-use types (Table 1).

Table 1. Mean (±1SD) of beta-diversity recorded in rice, pasture, managed agroforest, abandoned agroforest and forest plots in a high- and a low-impact landscape. Beta-diversity represents the percentage of total diversity explained by variability among quadrants within plots. Probability values (p-values) for one-way ANOVA. The letters indicate results of pairwise comparison with Tukey test.

	Rice	Pasture	Man.agr.	Ab.agr.	Forest	p-value
High-impact	71.7 ± 1.2 a	75.2 ± 1.2 ab	77.8 ± 1.3 b	75.6 ± 0.9 *ab*	76.5 ± 2.8 *ab*	0.037
Low-impact	71.6 ± 3.0 a	58.3 ± 2.4 b	66.1 ± 2.2 ab	71.9 ± 2.3 a	69.4 ± 4.2 ab	0.020

Likewise, intraspecific aggregation in the high-impact landscape increased with decreasing anthropogenic disturbances. A significantly higher value was recorded for forest than for the more intervened land-use types rice and pasture ($F_{4,43} = 4.662$, p =

0.003), while for managed and abandoned agroforest intermediate values were found (Fig. 1a). A different pattern was found for the low-impact region (Fig. 1b). The highest value of intraspecific aggregation was recorded for rice, while forest showed the lowest value ($F_{4,25} = 2.997$, $p = 0.037$) and intermediate values were found in pasture, managed and abandoned agroforest of the low-impact region.

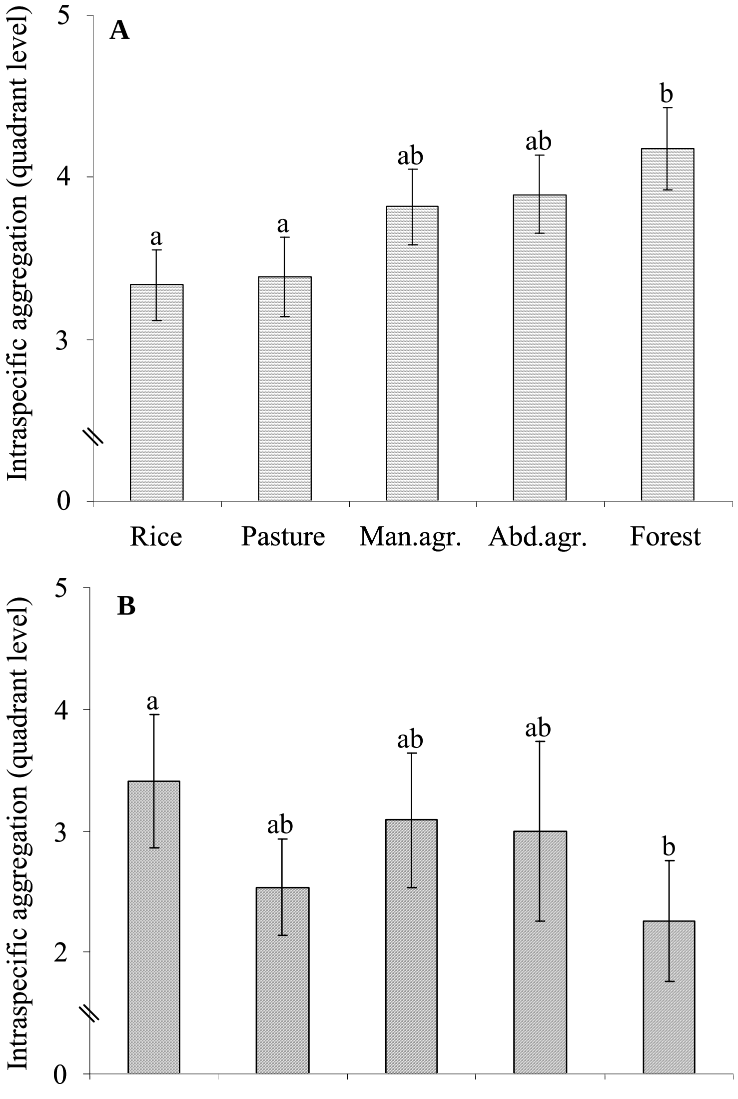


Figure 1. At quadrant scale, mean (±1SD) of intraspecific aggregation for rice, pasture, managed agroforest, abandoned agroforest and forest plots in a high- (A) and a low-impact landscape (B). Differences among land-use types tested with one-way ANOVA. The letters indicate results of pairwise comparison with Tukey test.

As expected, intraspecific aggregation had a positive effect on beta-diversity for all land-use types from both landscapes. In the high-impact landscape intraspecific aggregation ($F_{4,42}$ = 37.348, $p < 0.001$) significantly affected beta-diversity, while land-use type had no significant effect ($F_{4,42}$ = 2.592, p = 0.052; Table 2). In the low-impact landscape, in contrast, both intraspecific aggregation ($F_{4,42}$ = 52.468, $p < 0.001$) and land-use ($F_{4,42}$ = 9.775, $p < 0.001$) significantly affected beta-diversity. Regression coefficients for relative beta-diversity were positive and highly significant ($p< 0.00001$). In the high-impact landscape, 53% of the variation of beta-diversity was explained by patterns of intraspecific aggregation, while in the low-impact landscape the combined effect of land-use type and intraspecific aggregation explained 76% of the variation of beta-diversity, as shown by the adjusted R^2 values in Table 2.

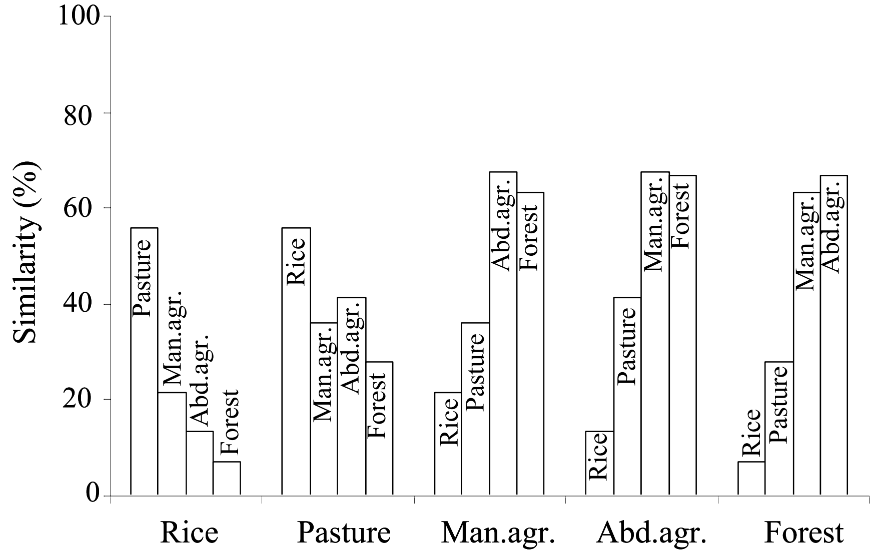
Table 2. Results of mixed effect model analyses of the effect of land-use and intraspecific aggregation in the variability of beta-diversity among quadrants within plots. Land-use was included as a categorical variable and intraspecific aggregation as a continuous variable. Analyses performed for each landscape separately.

Landscape	Response	Extraplanatory	*F*	*p*	*Adj. R^2*
High-impact	Beta - diversity	Intraspecific	37.348	0.000	
		Land-use type	2.592	0.052	
	Model		11.609	0.000	0.53
Low-impact	Beta - diversity	Intraspecific	52.468	0.000	
		Land-use type	9.775	0.000	
	Model		19.163	0.000	0.76

Community composition

In total, 310 plant species belonging to 71 families were encountered across 78 study plots. Richness was not evenly distributed among landscapes. Overall species richness was higher in the high-impact (262 spp.) compared to the low-impact landscape (108 spp.).

a. High-impact landscape



b. Low-impact landscape

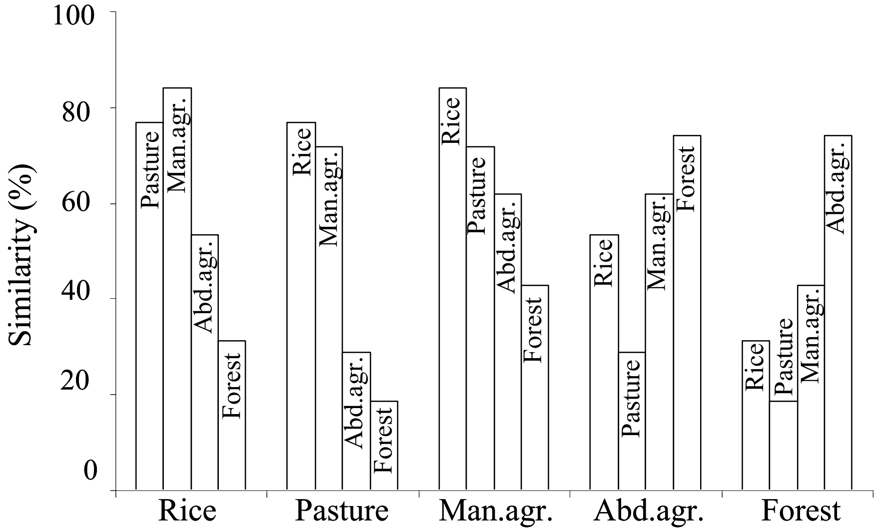


Figure 2. Floristic similarities (abundance-based Jaccard's index) of terrestrial herb communities among land-use types in a high-impact landscape (a) and a low-impact landscape (b).

As is typical for tropical agricultural areas, Poaceae and Asteraceae were the dominant families in terms of species richness and abundance in managed land-use types. Amaranthaceae, Araceae, Pteridaceae and Dryopteridaceae were additionally important in terms of abundance in abandoned agroforest and forest, mainly in the low-impact landscape. Patterns of floristic similarities differed among landscapes. In the high-impact landscape, similar values were recorded among land-use types with comparable intensities of anthropogenic disturbance such as between rice and pasture and between managed agroforest, abandoned agroforest and forest (Fig 2a). In the low-impact landscape, plant communities of rice and pasture were composed of almost the same species, as expressed by a high similarity value close to 80% (Fig. 2b). In contrast to our expectations, in the low impact region, species found in managed agroforest were more similar to highly intervened land-use types than forested land-use types, whereas the opposite occurred in the high-impact landscape.

At plot scale, the analysis of patterns of intraspecific aggregation revealed considerable differences among land-use types: intraspecific aggregation tended to increase with increasing anthropogenic disturbances (high-impact: X^2=96.092, p<0.001; low-impact: $X^2 = 18.260$, p = 0.001) as shown in Figure 3. In the high-impact landscape values of intraspecific aggregation were significantly higher in managed land-use types than in abandoned agroforest and forest (Fig. 3a). In the low impact landscape, in contrast, significantly higher values of intraspecific aggregation were only recorded for rice. Although pasture had higher aggregation values than the less intervened land-use types, managed agroforest, abandoned agroforest and forest, these differences were not significant (Fig. 3b).

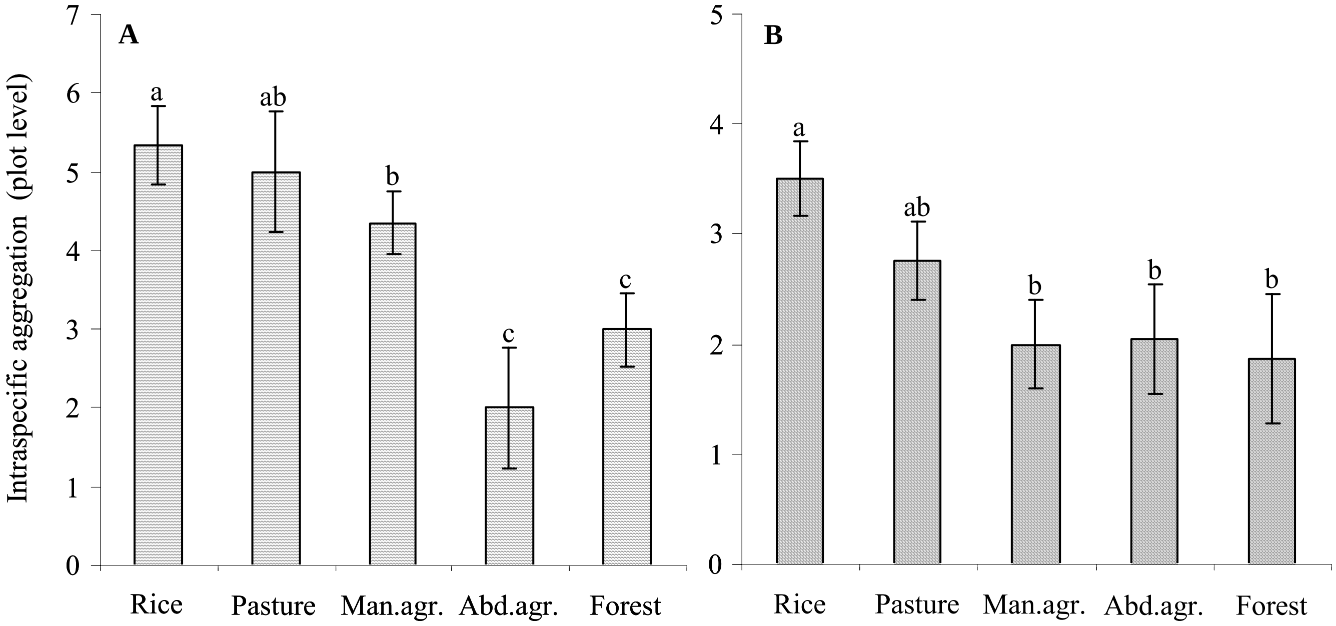


Figure 3. The effect of land-use type on intraspecific aggregation at plot scale, for each landscape separately. Means compared among land-use types using Kruskal-Wallis ANOVA test. Means with same letter are not significantly different ($p > 0.05$), based on Kolmogorov-Smirnov test. Error bars represent 1 SE.: a. high-impact landscape, b. low-impact landscape.

Discussion

The effect of intraspecific aggregation on species dynamics has been primarily tested in theoretical and experimental plant communities, and little is known about these processes in natural communities (Barot 2004, Monzeglio and Stoll 2005). We evaluated patterns of intraspecific aggregation using empirical data collected in 78 study sites of five different habitats types spread across two landscapes, which differ in the impact of anthropogenic disturbance.

Our results revealed contrasting patterns depending on the spatial scale considered. In the high impact landscape, intraspecific aggregation at quadrant scale decreased with increasing anthropogenic disturbance, whereas the exact opposite occurred at plot scale, where aggregation declined with decreasing anthropogenic disturbance. We can explain these patterns by combining intraspecific aggregation and competition/colonization trade-off concepts. The (partial) removement of original vegetation for agricultural activities creates new gaps for colonization. According to the competition/colonization trade-off theory (Chesson 2000) we might expect that immediately after disturbance the plant community would be mainly composed of species with high dispersal rates and therefore a high capacity for colonization, but with low competitive abilities. On the other hand, intraspecific aggregation has been described as a mechanism used by inferior competitors to avoid competitive exclusion (Stoll and Prati 2001). Therefore, the initial colonizers, which are inferior competitors, tend to grow in aggregated patterns to avoid competitive exclusion. However, the influence of intraspecific aggregation on competitive interactions of plant communities has mainly been studied for short periods and the question remains whether or not initial aggregation patterns remain over longer periods of time and promote long-term species co-existence (Rejmánek 2002). The results for our high impact landscape, where rice and pasture have been cultivated for more than 40 years, give insight in these long-term processes. The high values for intraspecific aggregation for rice and pasture at the plot scale and low values at the quadrant scale indicate that these land-use types are dominated by species with low colonization abilities and poor dispersal abilities, but good competition strategies. This in turn suggests that these plant communities were dominated by colonizers shortly after disturbance, but have been replaced by more competitive species over the course of time. The higher presence of colonizers shortly after disturbance is demonstrated by the results for the forest plots, for which we observed low values for intraspecific aggregation at the plot scale (a low proportion of colonizers) and high values for intraspecific aggregation at the quadrant scale (a high proportion of poor competitors). The different characteristics of communities in pasture and rice (good competitors and poor colonizers) versus forest and agroforest (poor competitors and good colonizers) is demonstrated by the low floristic similarity between these groups of land-use types.

In the low-impact landscape, where all land-use types were recently established on former forest land, intraspecific aggregation patterns only slightly differed between spatial scales and between land-use types, which is consistent with our interpretation. The highest values for intraspecific aggregation were found for rice and the lowest values for forest at the plot and quadrant scale. Rice and pasture plots in the low-impact landscape were recently established, in contrast to the high-impact landscape with long-term and more intensive management practices. Therefore, seed banks were probably not highly perturbed and plant communities in this land-use type could be composed by a mixture of competitive species in the seed bank and good colonizers. The fact that all managed land-use types are only recently established and in similar stages of colonization is also demonstrated by the high similarity values among rice, pasture and managed agroforest.

Through the analysis of species diversity of various groups of arthropods, Veech (2005) concludes that intraspecific aggregation significantly limits alpha-diversity within communities and enhances beta-diversity among communities. Our analysis at the quadrant scale mirrored a similar result for plants: intraspecific aggregation explained more than 50% of the variation of beta-diversity. The additive partitioning approach implies that alpha diversity at each spatial scale is the combined effect of heterogeneity or beta diversity at lower scales (Wagner et al. 2000). Although previous studies have shown that overall species diversity is mainly determined by large spatial scales such as variability among land-use types (Gering et al. 2003, Gabriel et al. in press, Lozada et al. submitted), the potential role of beta diversity at quadrant scale is still an important component of overall species diversity. The intraspecific aggregation patterns observed within our plots plays a major role in determining not only species diversity at quadrant scale, but may also be important in explaining species diversity at a landscape scale.

Conclusions

Few studies have simultaneously tested the relative importance of different mechanisms of coexistence in plant communities under field conditions (Barot 2004). With a highly replicated field study, we evaluated the effect of both intraspecific aggregation and colonization/competition trade-off in the maintenance of plant communities in two human-dominated landscapes. Although, the simplistic view of aggregation as a mechanism of coexistence of plant species (Murrell et al. 2001, 2002) has been criticized and the importance of colonization /competition trade-offs in the explanation of plant species coexistence has been stressed (Bolker and Pacala 1999, Chesson and Neuhauser 2002), we suggest that the effect of human disturbance on patterns of plant diversity is determined by both intraspecific aggregation and the trade-off between colonization and competition.

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Summary

Tropical ecosystems are the greatest contributors to global biodiversity. Since preservation of biodiversity can not only be realized through the establishment of protected areas, conservation efforts should not only focus on pristine forest, but also on human-intervened landscapes with a potentially high biodiversity value. This study focuses on the effects of management practices on plant communities and evaluates the contribution of habitat types with various degrees of anthropogenic disturbance to the preservation of plant diversity in landscapes.

We studied 78 private farms of a high human-impacted and a low-human impacted landscapes of western Ecuador. We selected the major land-use systems in these two regions, which were five habitat types representing a gradient of decreasing anthropogenic disturbance: rice, pasture, managed agroforest with coffee or cacao, abandoned agroforest, and near-natural forest.

We investigated forest recovery in managed agroforest, abandoned agroforest, and forest sites including the role of birds in the regeneration process. Analyses of diversity, abundance, and composition of woody species revealed that isolated patches of forest and abandoned agroforest exhibited a similar pattern of forest recovery, with birds as the main seed vectors. In the fragmented landscape, these habitats are stepping stones for birds and - by reducing isolation effects – important for conserving tree diversity.

To determine the critical spatial scales that explain overall plant diversity, starting with quadrants within plots to the landscape level, we analyzed plant diversity patterns at multiple spatial scales in the major land-use types of the landscapes. Plant diversity was mainly determined by the heterogeneity at large spatial scales, and land-use type specifically contributed to overall plant diversity at the landscape level.

We evaluated whether the response of herbaceous plant communities to land-use activities depended on their latitudinal range size. More wide-ranging species were found in more intervened land-use types, while species richness of narrow-ranging species increased with decreasing anthropogenic disturbance. Hence, responses of plant species to human activities were influenced by specific traits that determine their range sizes. Floristic similarity analyses between land-use types revealed that narrow ranging species were mainly preserved in forest fragments, but the other land-use types have also unique narrow ranging species, and therefore made an important contribution to their preservation at the landscape level.

Finally, in order to understand the processes that determine patterns of species richness distribution among land-use types, we investigated intraspecific plant aggregations and the relation between intraspecific aggregation and the spatial distribution of species (mainly beta-diversity). We found that intraspecific aggregation increased with increasing anthropogenic disturbance. Intraspecific aggregation explained more than 50% of beta-diversity and is therefore an important cause for the high diversity observed even in the most intervened land-use types.

In conclusion, our results suggest that human-intervened agroecosystems should not be disregarded when regional plant diversity is considered in tropical areas, because they can contribute significantly to overall diversity. Conservation efforts should therefore combine protection of natural habitats with strategies to maintain diversity of low-intensity land-use types within heterogeneous landscapes, looking for win-win solutions or trade-offs between biodiversity conservation and human welfare.

Appendices

Appendix 1

Herb species found in 78 plots representing a gradient of anthropogenic disturbance: R: rice; P: pasture; M.ag.: managed agroforest; A.ag.: abandoned agroforest, and F: forest, spread across two agricultural landscapes which differ in history and level of human impact.

	High-impact landscape					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
ACANTHACEAE										
Blechum pyramidatum				x						
Elytraria imbricata				x						
Justicia comata	x	x	x	x	x		x	x		
Pseuderanthemum cuspidatum				x					x	
Ruellia brevifolia						x	x	x	x	
Ruellia sp.	x	x	x	x	x	x	x	x	x	
Tumbergia sp.						x				
ALISMATACEAE										
Echinodorus sp.	x	x								
ALSTROEMERIACEAE										
Bomarea obovata		x	x							
Bomarea sp.						x				
AMARANTHACEAE										
Achyranthes aspera	x	x	x	x	x		x	x	x	
Alternanthera areschougii	x		x	x	x					
Alternanthera pubiflora			x	x	x					
Amaranthus gracilis							x			
Amaranthus spinosus	x	x								
Amaranthus sp.	x			x			x			
Cyathula achyranthoides						x	x	x	x	
Iresine angustifolia		x								
Iresine diffusa		x	x	x	x					
APIACEAE										
Eryngium foetidum	x									

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
APOCYNACEAE										
Fosteronia subcordata				x						
Mandevilla subsagittata			x	x						
Mesechites trifida	x		x	x	x					
Prestonia mollis	x	x	x	x	x					
Prestonia rotundifolia		x			x					
Tabernaemontana amygdalifolia	x	x	x							
ARACEAE										
Anthurium brachipodum						x	x	x	x	x
Anthurium lancea						x	x	x	x	x
Anthurium sp.				x	x	x	x	x	x	x
Caladium bicolor		x								
Chlorospatha sp.	x					x		x	x	x
Dieffenbachia harlingii									x	
Philodendron alliodorum					x					
Philodendron grandipes					x					
Philodendron sp.						x		x	x	x
Stenospermation sp.								x	x	x
Syngonium sp.			x		x					
Xanthosoma daguense		x								
Xanthosoma eggersii	x	x	x		x	x	x	x	x	x
ARISTOLOCHIACEAE										
Aristolochia odoratissima	x	x	x							
Aristolochia pilosa	x	x	x	x	x					
Aristolochia sp.									x	
ASCLEPIADACEAE										
Asclepias curassavica		x			x					
Gonolobus sp.			x		x					
Macroscepis sp.		x			x					
Marsdenia sp.	x	x	x	x	x					
Matelea sp.		x								
ASPLENIACEAE										
Asplenium dissectum										x
ASTERACEAE										
Acanthospemum microcarpum	x									
Acmella alba	x	x								
Acmella sp.			x		x					
Adenostemma platyphyllum	x	x	x	x	x					

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
ASTERACEAE										
Adenostemma sp.	x	x	x	x	x	x	x	x		
Ageratina azangaroensis						x	x			
Ageratina sp.	x	x	x	x	x					
Ageratum conyzoides		x								
Ageratum sp.						x				
Austroeupatorium inulaefolium	x	x								
Baccharis trinervis				x						
Baltimora recta		x	x	x			x			
Bidens sp.						x		x		
Brickellia diffusa	x									
Chaptalia nutans		x								
Chromolaena roseorum	x									
Chromolaena scabra		x	x							
Conyza bonariensis	x	x								
Cyanthillium cinereum							x			
Delilia biflora		x								
Eclipta prostrata		x				x	x			
Egletes viscosa	x	x								
Erechtites hieraciifolius		x								
Eupatorium sp.	x	x								
Fleischmannia microstemon	x									
Isocarpha microcephala	x	x								
Jungia sp.	x	x	x	x	x					
Liabum eggersii		x		x						
Mikania cordifolia	x	x		x	x					
Mikania sp.	x	x	x	x	x					
Pseudelephantopus spicatus		x	x	x			x			
Sphagneticola trilobata		x								
Synedrella nodiflora		x	x			x	x	x		
Lycoseris trinervis		x		x	x					
Tridax procumbens	x	x								
Tridax sp.							x			
Wedelia grandiflora						x	x	x		
BEGONIACEAE										
Begonia foliosa						x		x		
Begonia serotina	x				x					

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
BIGNONIACEAE										
Amphilophium paniculatum		x	x	x	x					
Arrabidaea sp.					x					
Macfadyena unguis-cati	x	x	x	x	x					
BLECHNACEAE										
Blechnum occidentale					x					
Blechnum sp.				x	x					
BORAGINACEAE										
Heliotropium rufipillum				x						
CAESALPINIACEAE										
Chamaecrista nictitans		x								
Senna obtusifolia		x	x							
CAMPANULACEAE										
Burmeistera sp.		x								
CAPPARACEAE										
Podandrogyne brachycarpa			x							
CARYOPHYLLACEAE										
Drymaria cordata	x	x	x	x			x	x		
Stellaria ovata		x				x	x			
COMMELINACEAE										
Callisia gracilis			x	x	x					
Commelina erecta	x	x	x	x		x	x	x		
CONVOLVULACEAE										
Ipomoea batatas				x						
Ipomoea meyeri	x									
Ipomoea setosa			x	x						
Ipomoea sp.	x					x		x		
Merremia umbellata	x	x	x	x		x	x	x	x	
Turbina abutiloides				x	x					
CUCURBITACEAE										
Cayaponia macrocalyx						x		x	x	
Cayaponia sp.		x			x					
Cyclanthera sp.						x				
Melothria pendula			x			x	x	x		
Momordica charantia		x	x	x		x	x	x		
Posadaea sphaerocarpa		x								
Rytidostylis carthaginensis			x	x						
Sicyos sp.			x	x						

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
CYCLANTHACEAE										
Carludovica palmata									x	
CYPERACEAE										
Cyperus chalaranthus	x	x					x	x		
Cyperus compressus		x								
CYATHEACEAE										
Cyathea sp.										x
Cyperus hermaphroditus	x	x								
Cyperus iria	x									
Cyperus luzulae						x	x	x		
Cyperus odoratus	x	x								
Cyperus panamensis	x	x				x	x	x		
Cyperus simplex						x	x			
Cyperus surinamensis	x	x								
Cyperus sp.	x	x								
Fimbristylis annua	x									
Fimbristylis dichotoma						x				
Kyllinga brevifolia	x	x								
Kyllinga pumila							x			
Rhynchospora contracta	x	x	x							
Rhynchospora radicans		x					x			
Rhynchospora sp.		x								
Scleria melaleuca	x	x		x		x	x	x		
DENNSTAEDTIACEAE										
Dennstaedtia cicutaria						x	x	x		x
DIOSCOREACEAE										
Dioscorea piperifolia			x		x					
DRYOPTERIDACEAE										
Athyrium sp.			x	x	x					
Bolbitis sp.					x					
Cyclopeltis semicordata			x		x			x		
Diplazium striatastrum										x
Diplazium sp.		x					x		x	
Maxonia apiifolia								x	x	x
Tectaria incisa						x	x	x	x	x
Tectaria sp.			x						x	x
EUPHORBIACEAE										
Acalypha subcastrata	x									

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
EUPHORBIACEAE										
Acalypha sp.						x	x	x	x	x
Chamaesyce hirta	x	x								
Chamaesyce ophtalmica	x	x								
Croton hirtus		x								
Euphorbia graminea	x		x	x	x					
Euphorbia sp.							x			
Phyllanthus caroliniensis		x								
Phyllanthus niruri		x								
FABACEAE										
Aeschynomene sp.	x	x								
Cajanus cajan	x									
Calapagonium mucunoides		x								
Canavalia sp.			x		x					
Coursetia caribaea				x						
Coursetia sp.				x						
Desmodium distortum		x								
Desmodium incanum	x	x	x			x	x	x		
Desmodium scorpiurus	x	x				x	x	x		
Desmodium sp.	x	x	x	x						
Centrosema pubescens		x								
Centrosema sp.				x						
Macroptilium sp.					x		x	x		
Phaseolus sp.	x	x			x					
Rhynchosia minima	x	x			x					
Macroptilium lathyroides	x	x								
GESNERIACEAE										
Diastema racemiferum			x	x	x					
HAEMODORACEAE										
Xiphidium caeruleum						x		x		
HELICONIACEAE										
Heliconia hirsuta				x						
Heliconia latispatha	x	x	x	x	x					x
Heliconia schumanniana						x	x	x	x	x
HYDROPHYLLACEAE										
Hydrolea spinosa		x								
LAMIACEAE										
Hyptis mutabilis		x		x						

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
LAMIACEAE										
Hyptis pectinata	x	x	x							
Hyptis savannarum	x	x				x	x	x		
Ocimum campechianum						x	x	x	x	
Salvia occidentalis		x	x	x						
Salvia sp.	x	x			x					
LOASACEAE										
Klaprothia fasciculata		x	x							
LOGANIACEAE										
Mitreola petiolata	x									
LYTHRACEAE										
Adenaria floribunda		x								
Ammania auriculata	x									
Cuphea strigulosa	x	x					x			
Rotala ramosior	x	x								
MALVACEAE										
Malachra alceifolia	x	x								
Malachra fasciata		x								
Pavonia castaneifolia						x	x	x	x	
Sida repens		x	x	x						
Sida sp.		x	x	x		x	x	x		
MARANTACEAE										
Calathea crotalifera					x					
Calathea metallica						x	x	x	x	x
Calathea sp.		x	x		x					
Ischnosiphon inflatus						x	x	x	x	
MARATTIACEAE										
Danaea nodosa								x	x	x
MENISPERMEACEAE										
Cissampelos tropaeolifolia			x	x						
MORACEAE										
Dorstenia contrajerva			x	x	x					
NYCTAGINACEAE										
Boerhavia coccinea		x								
Mirabilis violacea				x						
ONAGRACEAE										
Eclipta prostrata	x									
Ludwigia erecta	x	x								

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
ONAGRACEAE										
Ludwigia octovalvis							x			
Ludwigia peruviana		x								
OXALIDACEAE										
Oxalis glauca	x	x	x							
PASSIFLORACEAE										
Passiflora filipes		x	x	x	x					
Passiflora foetida		x								
Passiflora punctata		x	x	x	x					
Passiflora sprucei		x		x	x					
PHYTOLACCACEAE										
Gallesia integrifolia					x					
Microtea debilis	x	x	x	x	x					
Petiveria alliacea	x	x	x	x	x	x	x	x	x	
PIPERACEAE										
Peperomia pellucida		x	x				x			
Peperomia rotundifolia			x							
Piper peltatum		x	x							
PLUMBAGINACEAE										
Plumbago scandens				x						
POACEAE										
Axonopus compressus						x	x			
Chloris radiata	x									
Digitaria horizontalis						x	x	x		
Digitaria sp.	x									
Echinochloa colona	x	x								
Echinolaena aequatoriana		x	x	x	x					
Eleusine indica	x	x								
Eragrostis amabilis	x									
Eragrostis ciliaris	x									
Eragrostis japonica	x									
Eragrostis sp.	x									
Guadua angustifolia					x				x	
Ichnanthus pallens							x	x		
Isaemum rugosum	x									
Lasiacis sorghoidea		x		x	x					
Leptochloa mucronata						x	x	x		
Leptochloa virgata	x									

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
POACEAE										
Olyra latifolia				x	x					
Oplismenus burmanii	x	x	x	x	x		x	x		
Oplismenus hirtellus	x	x	x	x	x					
Panicum laxum		x								
Panicum pilosum						x				
Panicum polygonatum	x	x				x	x	x		
Panicum stoloniferum							x			
Panicum trichoides	x		x		x					
Panicum sp.	x									
Paspalum conjugatum	x	x	x							
Paspalum microstachyum	x	x	x							
Paspalum paniculatum	x	x								
Paspalum sp.	x	x	x							
Pharus latifolius						x	x	x	x	x
Rhiphidocladum racemiflorum					x					
Scleria melaleuca	x									
Sporobulus tenuissimus	x									
Urochloa fasciculata	x	x								
POLYGALACEAE										
Monnina denticulada					x					
Securidaca coriacea	x									
POLYPODIACEAE										
Micrograma sp.			x							
PONTEDERIACEAE										
Heteranthera reniformis	x	x								
PORTULACACEAE										
Portulaca oleracea										
Talinum paniculatum	x		x	x						
PTERIDACEAE										
Adiantum alarconianum		x	x	x	x					
Adiantum concinnum	x	x		x	x					
Adiantum macrophyllum					x	x	x	x	x	x
Adiantum sp.	x	x	x	x	x					x
Pityrogramma calomelanos	x	x	x	x				x		
Pteris lechlerii				x	x					
RHAMNACEAE										
Gouania sp.				x						

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
RUBIACEAE										
Borreria ocymoides	x	x								
Borreria sp.	x	x	x	x		x	x	x		
Psychotria sp.			x		x					
Sabicea sp.							x			
SAPINDACEAE										
Cardiospermum sp.				x						
Paullinia sp.				x	x					
Serjania sp.			x	x	x					
SCHIZAEACEAE										
Lygodium venustum	x	x	x	x	x					
SCROPHULARIACEAE										
Bacopa monniera	x									
Lindernia crustacea	x	x	x	x		x	x			
Mecardonia procumbens	x	x								
Scoparia dulcis	x	x	x							
Stemodia durantifolia	x									
SMILACACEAE										
Smilax lappacea	x	x			x					
Smilax siphilitica				x					x	
SOLANACEAE										
Acnistus arborescens			x							
Browallia americana	x	x								
Physalis angulata	x	x	x	x						
Solanum americanum		x	x			x	x			
Solanum anceps			x							
Solanum candidum		x								
Solanum caricaefolium		x								
Solanum pimpinellifolium	x									
Solanum quitoense		x								
Solanum sp.		x								
STERCULIACEAE										
Melochia lupulina	x	x								
THELYPTERIDACEAE										
Macrothelypteris torresiana						x	x			
Thelypteris sp.			x	x	x	x	x	x	x	x

Appendix 1. (continued)	**High-impact landscape**					**Low-impact landscape**				
	R	**P**	**M.ag**	**A.ag**	**F**	**R**	**P**	**M.ag**	**A.ag**	**F**
TILIACEAE										
Corchorus orinocensis	x	x		x						
Triumfetta sp.	x	x		x	x					
URTICACEAE										
Boehmeria ramiflora						x	x			
Laportea aestuans	x		x		x					
Phenax laevigatus		x								
Phenax rugosus	x									
Pilea baurii	x	x	x	x	x					
Pilea pubescens						x	x	x	x	x
Pilea sp.					x					
VERBENACEAE										
Phyla nodiflora	x									
Phyla strigulosa	x									
Priva lappulacea	x	x	x	x						
Stachytarpheta cayennensis	x	x					x			
VIOLACEAE										
Hybanthus attenuatus		x								
VITACEAE										
Cissus fusifolia				x	x					
Cissus microcarpa				x						
Cissus verticillata		x	x	x	x	x	x			
Cissus sp.		x								
ZINGIBERACEAE										
Costus pulverulentus					x					
Costus guanaiensis				x						
Costus sp.						x	x	x	x	

Appendix 2

Tree species found in 42 plots representing a decreasing gradient of management practices: M.ag.: managed agroforest; A.ag.: abandoned agroforest and F: forest, spread across two agricultural landscapes which differ in history and level of human impact. Sampled individuals were classified according to their size: 1: adult tree with a dbh of more than 10 cm; 2: juveniles with a dbh of less than 10 cm and stem taller than 20 cm.

	High-impact landscape				**Low-impact landscape**			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
ANACARDIACEAE								
Mangifera indica	x	x		1,2				
Mauria heterophylla		x	x	1,2				
Mauria suaveolens			x	2				
Spondias mombin					x	x		1,2
Tapirira sp.						x		1
ANNONACEAE								
Annona muricata	x	x		1,2				
Guatteria sp.							x	2
Klarobelia lucida			x	2				
Raimondia cherimolioides							x	2
Raimondia sp.			x	2				
Unonopsis magnifolia							x	1
APOCYNACEAE								
Tabernaemontana columbiensis						x	x	2
ARALIACEAE								
Dendropanax sp.							x	2
ARECACEAE								
Astrocaryum standleyanum	x	x		1,2	x	x	x	1,2
Attalea butyracea						x	x	2
Bactris setulosa							x	1
Bactris sp.						x	x	2
Iriartea deltoidea						x	x	1,2
Oenocarpus bataua							x	1,2
Phytelephas aequatorialis	x	x	x	1,2	x	x	x	1,2
Socratea exorrhiza					x	x	x	1,2

Appendix 2. (continued)	High-impact landscape				Low-impact landscape			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
BIGNONIACEAE								
Crescentia cujete		x		2	x			2
Tabebuia billbergii	x		x	1,2				
Tabebuia chrysantha		x	x	2				
BIXACEAE								
Bixa orellana					x			1
BOMBACACEAE								
Ceiba pentandra					x			1,2
Matisia cordata	x			1,2	x	x		1,2
Matisia grandifolia						x	x	2
Ochroma pyramidale	x	x	x	1,2	x	x	x	1,2
Pseudobombax millei	x	x	x	1,2				
BORAGINACEAE								
Cordia alliodora	x	x	x	1,2	x			1,2
Cordia sp.	x	x	x	1,2		x	x	1,2
Tournefortia macrophylla						x		2
BURSERACEAE								
Protium colombianum					x			2
Protium ecuadorense						x	x	1,2
CAESALPINIACEAE								
Bauhinia aculeate		x		2				
Brownea grandiceps			x	2				
Brownea multijuga		x	x	1,2				
Brownea sp.			x	1,2				
Schizolobium parahyba	x			1				
Senna dariensis						x		2
Senna reticulate		x		2				
Senna spectabilis		x	x	1				
Senna sp.		x		1,2				
CAPPARACEAE								
Capparis osmantha						x	x	1,2
Podandrogyne brevipedunculata					x			2
CARICACEAE								
Carica microcarpa					x	x	x	2
Carica papaya		x	x	1,2	x			2

Appendix 2. (continued)	**High-impact landscape**				**Low-impact landscape**			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
CECROPIACEAE								
Cecropia garciae						x	x	1,2
Cecropia insignis						x	x	1,2
Cecropia litoralis						x		2
Cecropia maxima	x	x	x	1,2	x			1,2
Cecropia sp.							x	2
Coussapoa villosa		x	x	1,2				
Coussapoa sp.						x		1
CHRYSOBALANACEAE								
Hirtella triandra							x	1
Hirtella sp.						x	x	2
CLUSIACEAE								
Chrysochlamys dependens						x	x	1,2
Clusia sp.					x			2
Garcinia intermedia							x	1,2
Mammea americana	x			2				
Symphonia globulifera						x	x	1,2
COCHLOSPERMACEAE								
Cochlospermum vitifolium		x	x	1,2				
EBENACEAE								
Diospyros sp.							x	1
ERYTHROXYLACEAE								
Erythroxylum ruizii			x	2				
EUPHORBIACEAE								
Alchornea sp.		x	x	1,2				
Croton rivinifolius		x	x	2				
Margaritaria nobilis			x	2				
Phyllanthus acidus	x			1				
Phyllanthus juglandifolius			x	1				
Phyllanthus sp.			x	2				
Tetrorchidium andinum						x		1,2
Tetrorchidium macrophyllum					x	x	x	1,2
Tetrorchidium sp.							x	2
FABACEAE								
Centrolobium ochroxylum	x	x		1,2				
Clitoria brachystegia			x	2				
Clitoria sp.						x	x	1,2

Appendix 2. (continued)	High-impact landscape				Low-impact landscape			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
FABACEAE								
Dussia lehmannii						x	x	2
Erythrina edulis						x		2
Erythrina fusca	x			1				
Erythrina smithiana	x	x	x	2	x			2
Gliricidia brenningii	x	x	x	1,2				
Myroxylon balsamum	x			1,2				
Platymiscium pinnatum					x			2
Swartzia haughtii		x		1		x		2
FLACOURTIACEAE								
Casearia decandra			x	1,2				
Casearia sp.		x	x	2				
Pleuranthodendron lindenii		x		1				
Xylosma tessmannii						x	x	2
HIPPOCRATEACEAE								
Salacia sp.							x	2
LAURACEAE								
Aniba sp.					x	x	x	1,2
Cinnamomun triplinerve						x	x	1,2
Nectandra martinicensis		x		2				
Nectandra membranaceae			x	2				
Nectandra purpurea							x	1,2
Nectandra reticulata	x	x	x	1,2				
Nectandra sp.			x	2			x	1,2
Ocotea cernua		x	x	2		x	x	1,2
Ocotea floccifera						x	x	1,2
Ocotea sodiroana						x		2
Ocotea sp.	x	x	x	1,2				
Persea Americana	x			1,2	x			1
Persea sp.							x	2
Pleurothyrium sp.	x			2	x	x	x	2
LECYTHIDACEAE								
Grias peruviana						x	x	1,2
Gustavia angustifolia			x	2				
Gustavia serrata	x	x	x	2				
Gustavia sp.						x		2

Appendix 2. (continued)	**High-impact landscape**				**Low-impact landscape**			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
LOGANIACEAE								
Strychnos sp.							x	2
MALPIGHIACEAE								
Bunchosia cornifolia						x	x	2
Bunchosia sp.						x		2
Malpighia glabra	x			1				
MELASTOMATACEAE								
Conostegia centronioides							x	2
Conostegia dentate							x	2
Conostegia sp.					x	x	x	1,2
Miconia longifolia					x	x	x	1,2
MELIACEAE								
Carapa guianensis					x	x	x	1,2
Cedrela odorata	x	x		1,2				
Guarea glabra			x	1,2				
Guarea silvatica		x	x	1,2				
Guarea sp.		x	x	1,2		x	x	1,2
Swietenia macrophylla	x			1,2	x			1,2
Trichilia pallida		x	x	1,2				1
Trichilia sp.			x	2			x	2
MIMOSACEAE								
Acacia macracantha		x		2				
Albizia sp.		x		2				
Cojoba arborea	x	x		1,2				
Cojoba rufescens			x	2				
Inga coruscans						x		2
Inga edulis	x	x	x	1,2				
Inga sapindoides		x	x	2				
Inga spectabilis	x	x	x	1,2	x			1
Inga sp.	x	x	x	1,2	x	x	x	1,2
Jacaranda copaia	x			1				
Leucaena leucocephala	x			2				
Leucaena trichodes		x		2				
Pseudopiptadenia sp.	x	x	x	1,2				
Pseudosamanea guachapele	x	x		1,2				
Samanea saman	x		x	1				

Appendix 2. (continued)

	High-impact landscape				**Low-impact landscape**			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
MONIMIACEAE								
Siparuna palenquensis							x	2
MORACEAE								
Artocarpus altilis						x		2
Brosimum alicastrum		x	x	1,2				
Castilla elastica	x	x	x	1,2	x	x	x	1,2
Clarisia biflora		x		2	x	x	x	1,2
Clarisia racemosa							x	1,2
Ficus citrifolia			x	1,2				
Ficus cuatrecasana						x	x	1,2
Ficus insipida			x	1				
Ficus macbridei							x	2
Ficus maxima	x			1	x	x	x	1,2
Ficus tonduzii						x	x	1,2
Ficus sp.			x	1,2	x	x	x	1,2
Maclura tinctoria	x	x	x	1,2	x			1,2
Maquira guianensis						x		2
Perebea xanthochyma				1	x	x	x	1,2
Poulsenia armata			x	1,2	x	x		1,2
Pseudolmedia laevigata	x			1				
Pseudolmedia rigida			x	1,2			x	1,2
Sorocea sarcocarpa		x	x	2	x	x	x	2
Sorocea sp.							x	1
Trophis caucana			x	2				
MYRISTICACEAE								
Virola duckei					x	x	x	1,2
Virola elongate					x	x	x	1,2
MYRSINACEAE								
Cybianthus sp.			x	2				
Stylogine sp.						x	x	2
MYRTACEAE								
Eugenia sp.			x	2	x	x	x	1,2
Myrcia splendens						x	x	1,2
Myrcia sp.		x	x	2				
Psidium guajava		x	x	2	x			2

Appendix 2. (continued)	**High-impact landscape**				**Low-impact landscape**			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
NYCTAGINACEAE								
Guapira sp.							x	1
Neea sp.						x	x	2
OLACACEAE								
Heisteria acuminata					x	x	x	1,2
Heisteria latifolia						x	x	2
PASSIFLORACEAE								
Passiflora macrophylla			x	2		x	x	2
PHYTOLACCACEAE								
Gallesia integrifolia		x	x	1,2				
PIPERACEAE								
Piper reticulatum						x	x	1,2
POLYGONACEAE								
Triplaris cumingiana	x	x	x	1,2	x	x	x	1,2
RHAMNACEAE								
Colubrina arborescens	x			1,2				
RUBIACEAE								
Coutarea hexandra		x		1,2				
Faramea occidentalis			x	2				
Genipa Americana							x	2
Genipa sp.							x	2
Guettarda hirsute						x	x	1,2
Palicourea guianensis						x	x	2
Pentagonia grandiflora					x	x	x	1,2
Pentagonia sp.					x	x	x	2
Psychotria grandis					x	x	x	2
Psychotria sp.						x	x	2
RUTACEAE								
Citrus aurantiaca	x			2	x			2
Citrus maxima	x	x		1,2	x			1,2
Citrus medica					x	x		1,2
Citrus reticulate	x			2	x			1,2
Zanthoxylum riedelianum						x	x	1,2
Zanthoxylum sp.	x	x	x	1,2		x		2
SAPINDACEAE								
Allophylus punctatus			x	2				
Allophylus sp.		x	x	2				

Appendix 2. (continued)	High-impact landscape				Low-impact landscape			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
SAPINDACEAE								
Cupania cinerea	x	x	x	1,2				
Sapindus saponaria		x		1,2				
Talisia setigera		x	x	2	x	x	x	1,2
Talisia sp.			x	1,2				
SAPOTACEAE								
Chrysophyllum argenteum		x	x	2		x	x	1,2
Chrysophyllum venezuelanense							x	2
Chrysophyllum sp.	x		x	1,2				
Pouteria caimito					x			1
Pouteria sapota							x	2
Pouteria sp.						x	x	1,2
SIMAROUBACEAE								
Simarouba amara	x			1				
SOLANACEAE								
Brunfelsia sp.			x	2				
Cestrum megalophyllum					x	x		2
Cestrum racemosum					x	x	x	1,2
Cestrum sp.		x		2				
Solanum confertiseriatum						x		2
STERCULIACEAE								
Guazuma ulmifolia	x	x	x	1,2				
Herrania balaensis						x	x	2
THEOPHRASTACEAE								
Clavija eggersiana		x	x	1,2		x	x	2
THYMELAEACEAE								
Daphnopsis sp.							x	1,2
Schoenobiblus panamensis							x	1,2
ULMACEAE								
Celtis schippii							x	2
Trema micrantha		x		2	x	x		1
URTICACEAE								
Myriocarpa stipitata		x	x	1,2				
VERBENACEAE								
Aegiphila alba					x	x	x	1,2
Cornutia pyramidata						x		1
Vitex flavens	x	x	x	1,2				

Appendix 2. (continued)	High-impact landscape				Low-impact landscape			
	M.ag.	**A.ag.**	**F**	**Size class**	**M.ag.**	**A.ag.**	**F**	**Size class**
VIOLACEAE								
Leonia sp.							x	1,2
Rinorea apiculata							x	2
ZAMIACEAE								
Zamia poeppigiana			x	2				

Acknowledgements

I acknowledge the Federal Ministry of Education and Research (BMBF) who, through the BioTEAM research program sponsored this research. I am profoundly grateful to Prof. Dr. Teja Tscharntke for his continuing support and guidance during this study. I also thank Dr. Alexandra Klein for her support. I am indebted to Prof. Dr. Thomas O. Crist for providing the PARTITION program and for his valuable and insightful explanations and Dr. Michael Kessler for guidance and suggestions for Chapter 4. I thank Hugo Navarrete, for providing facilities at the QCA herbarium-Catholic University (PUCE) and Luis Duicela from COFENAC for support provided during our field work in Jipijapa. I gratefully acknowledge the support provided by Betty Pico and Roland Olschewski of the Bio-Sys project. I also thank the Institute of Agroecology of Göttingen University and GTZ (Gesellschaft für Technische Zusammenarbeit) for providing good working facilities and kind collaboration in all respects.

This research could not have been completed without the assistance of Angel Choéz, Jesús Lino, Juan Carlos Narváez, David Trujillo, Xavier Haro, Clara Batioja, Miltón Arboleda, and Nicolas Castaño for fieldwork assistance and data management. Alvaro Pérez, Xavier Cornejo, Nicolás Carrasco, Angel Choéz, and experts from QCNE for their help in plant identification. I am grateful to Jason Tylianakis, Anne Richter, Katja Poveda, Indra Roschewitz, Doreen Gabriel, Carsten Thies and other friends and colleagues from the institute of agroecology for their help in data analyses. I thank Raphael Marché for providing bird data. Specially thanks to my friend Markus Schmidt for all his help and the nice time that we spent in Göttingen. My greatest thanks are reserved for the farmers in Jipijapa and Cabo San Francisco for permission to do research on their land.

Quiero agradecer de manera muy especial a Free de Koning por su apoyo incondicional, su ayuda en el análisis de datos, por las largas horas de conversación y discusión, por enseñarme a escribir artículos y sobretodo por su gran amistad. A Male Torres por su excelente trabajo en el campo y manejo de datos y en especial por su amistad y su apoyo incondicional. También agradezco a Ricardo Montero y Rosalía Paladines por su apoyo a lo largo de la realización de este trabajo.

Finalmente quiero agradecer y dedicar este trabajo a mi familia Gina, José, Elisa, David Diego, Noemí, Daniel, Bernardo y Micaela por su amor, paciencia y apoyo a lo largo de estos largos años de estudio; y a Tati por estar siempre ahí.

GRACIAS.

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Curriculum vitae

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