BIODIVERSITY RESEARCH

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

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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.

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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; 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 relationships, 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, geographical range size of tropical species can differ enormously between taxa. Species with a wide range size are often more abundant, and this combination of wide distribution and large number of individuals makes them less likely to go extinct, while narrow-ranged species tend to have smaller populations. The rarity of narrow-ranged species has been linked to traits such as low growth rates, low reproductive output, poor dispersal ability, greater tendency towards asexual reproduction, and little persistent seed banks (Kruckeberg & 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 (or narrow plasticity to a specific set of conditions broadly distributed), 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 assumption that narrow-ranged species are particularly sensitive to habitat alteration (Kruckeberg & Rabinowitz, 1985). However, Kessler (2001) found that the representation of endemic plant species in Bolivian montane forest 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 species and therefore contribute with more records. For this reason, studies analysing geographical variation in species richness based only on overall species richness patterns might not give a representative picture for the majority of taxa. Jetz & Rahbek (2002), Rahbek *et al.* (2007), and Kreft *et al.* (2006) addressed this problem when analysing the potential determinants of species richness of birds 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 topographical heterogeneity increases. They concluded that both scientific analyses and conservation programmes 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 analyse 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.

Our hypothesis is that narrow-ranged species are more sensitive to anthropogenic disturbance than broad-ranged species. Specifically, we asked: (1) How does land-use intensity affect total species richness and abundance? (2) How does land-use intensity affect partitioning of species over different range-size quartiles? (3) How does species composition, especially for narrow-ranged species, change 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 & 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 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 the high-impact landscape) is situated in the vicinity of the town of Jipijapa (1°20′ S, 80°35′ W) in Manabí Province, mid-west Ecuador, with an elevation range of 100–500 m. The original vegetation is semideciduous 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 & 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 6 months (INAMHI, 2004). Agricultural practices in the high-impact landscape were promoted by the land reform programmes initiated in the early 1960s (Dodson & Gentry, 1991) and therefore it is possible to find agroforestry 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, agroforestry systems with coffee, and arable crops such as 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 the low-impact landscape) is located to the north of the high impact landscape, in the neighbourhood of the village of Cabo San Francisco (0°39′ N, 80°05′ W) in Esmeraldas Province, 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* ssp. *eggersii* (Standl.) C.C.Berg (Moraceae), *Exarata chocoensis* A.H. Gentry (Bignoniaceae), *Virola dixonii* Little (Myristicaceae), and *Protium ecuadorense* Benoist (Burseraceae) (Jørgensen & León-Yánez, 1999). The climate is characterized by mean annual rainfall exceeding 3000 mm and the absence of a distinct dry season (INAMHI,

2004). In this landscape, natural forest accounts for approximately 50% of the total surface (INEC-MAG-SICA, 2002) since the expansion of the agricultural frontier reached the Cabo San Francisco area much later than 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. Currently, due to commercialization problems that are mainly related to a lack of road maintenance, cacao and banana have lost economic importance and most agroforestry has been abandoned during the last 15 years. To counterbalance the decreased income, arable crops and pastureland 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 established by manual sowing without mechanical soil tillage; managed agroforestry systems (hereafter called *managed agroforest*) based on 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*). These land-use types represent different sets of environmental conditions, such as light intensity and soil characteristics, which we expect to be the determining factors for species richness, abundance and composition.

As mentioned, the landscapes differed in time and intensity of management practices. In the high-impact landscape, agro-ecosystems had been in cultivation for over 8 years and urea fertilizer is occasionally applied to rice crops, whereas in the low-impact landscape, only recently have intensive management practices become more widespread. For instance, rice fields previously had been cultivated for only 2 to 3 years without the use of fertilizers. In both landscapes, pesticides are seldom applied.

Six plots (replicates) were selected for each land-use type. In each plot, nine fixed points were positioned in a regular 3×3 grid with 25 m between adjacent points within a 50×50 m area. All herb specimens (including ferns) were collected in 2.5×2.5 m fixed quadrats 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.

Species richness and abundance of a plot were defined as the total number of species and individuals, respectively, counted in the nine quadrats, averaged over the two sampling dates. For species identification, fertile voucher specimens were collected for each plant species found in the quadrants or, when this was not possible, sterile specimens were gathered. Specimens were first classified as morphospecies and then identified 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 were extracted from the W³TROPICOS 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 the southern-most record. To compare diversity patterns between landscapes, we combined the species lists obtained from the sampling in the high- and the low-impact regions. Afterwards, we partitioned the final species list into four latitudinal range size quartiles (as performed by Jetz & Rahbek, 2002). Hence, the first range size quartile included 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 analysis

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

To avoid misleading results due to differences in total species richness and abundance, 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 separately for each range size quartile. For each landscape, the effect of land-use type on relative species richness and relative abundance per plot was analysed with one-way analysis of variance (ANOVA) and post-hoc Tukey's pairwise comparisons on data with normally distributed modal 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 & 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 were then made with Wilcoxon matched-pairs tests. We carried out all statistical analyses using STATISTICA 6.1 (StatSoft, Tulsa, OK, 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
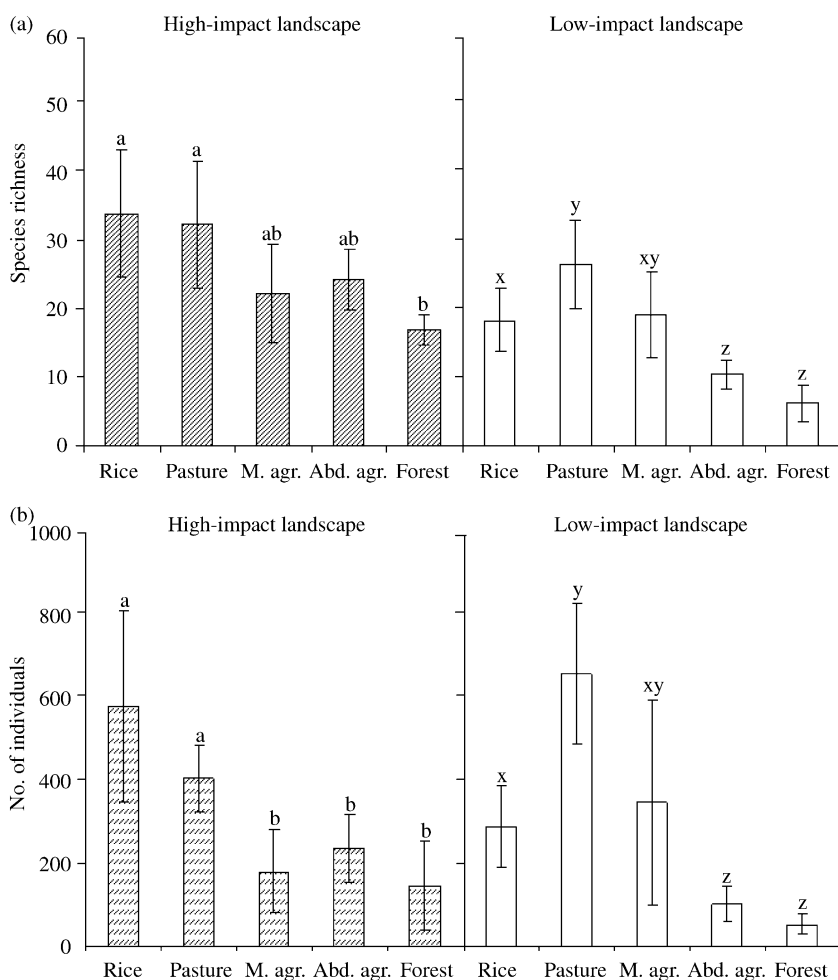
Figure 1 Effect of land-use type on overall species richness (a) and abundance – number of individuals per plot – (b) of terrestrial herbs (numbers per plot, based on twice mapping of nine 2.5 × 2.5 m quadrats). Means with same letter are not significantly different ($P > 0.05$), based on Tukey's test. Error bars represent 1 SD. M. agr., managed agroforest; Abd. agr., abandoned agroforest.

in terms of species richness, abundance, and frequency (i.e. recorded at least once per land-use type). The 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, the 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 analysed. 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).

Partitioning of species into range size quartiles (with 55 species each) revealed patterns of species richness that differed from that of all species taken together. 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). Although this pattern was true for both landscapes, differences among land-use types 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
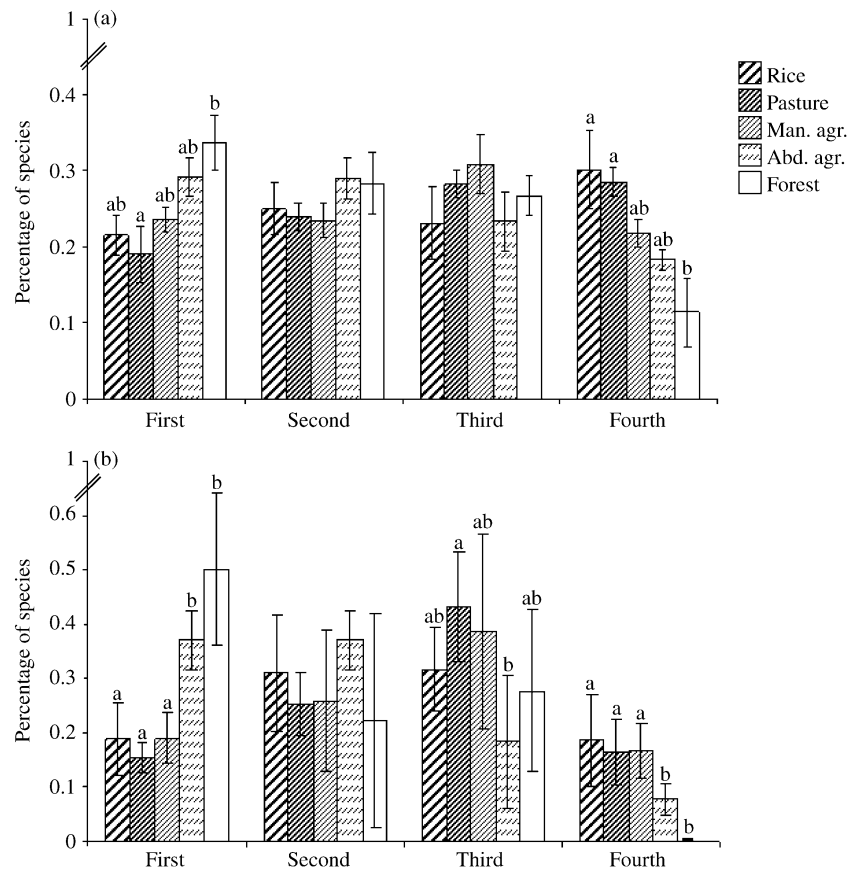
Figure 2 Effect of land-use type on patterns of species richness of terrestrial herbs for each range size quartile separately in a high-impact landscape (a) and a low-impact landscape (b). Overall species richness is divided in four range size quartiles representing 25% of the latitudinal distribution (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. Man. agr., managed agroforest; Abd. agr., abandoned agroforest.

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).

Species composition

Patterns of floristic similarity 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.

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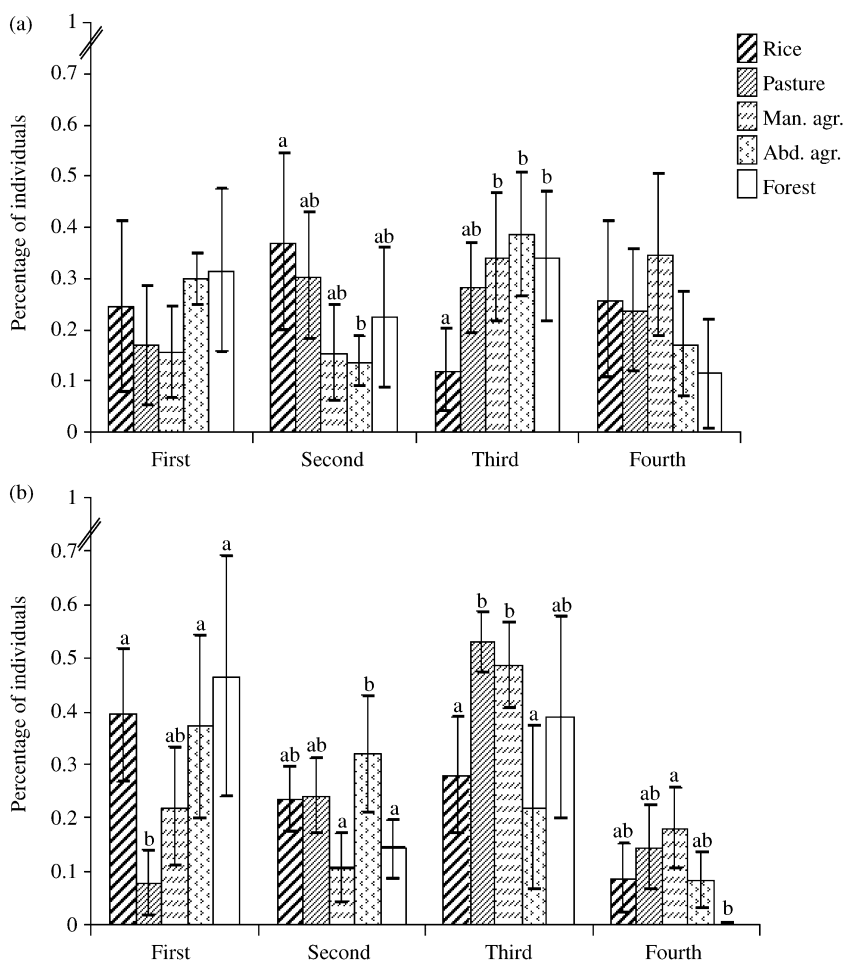
Figure 3 Effect of land-use type on patterns of species abundance of terrestrial herbs for each range size quartile separately in a high-impact landscape (a) and a low-impact landscape (b). Overall abundance divided in four range size quartile representing 25% of the latitudinal distribution. Means with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

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. 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.

Table 1 Partitioning of relative species richness in range size quartiles, indicated as fractions. 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). Bold numbers indicates significant differences. Forest plots of the low-impact landscape were not included in the analysis.

|	First	Second	Third	Fourth	χ^2	*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
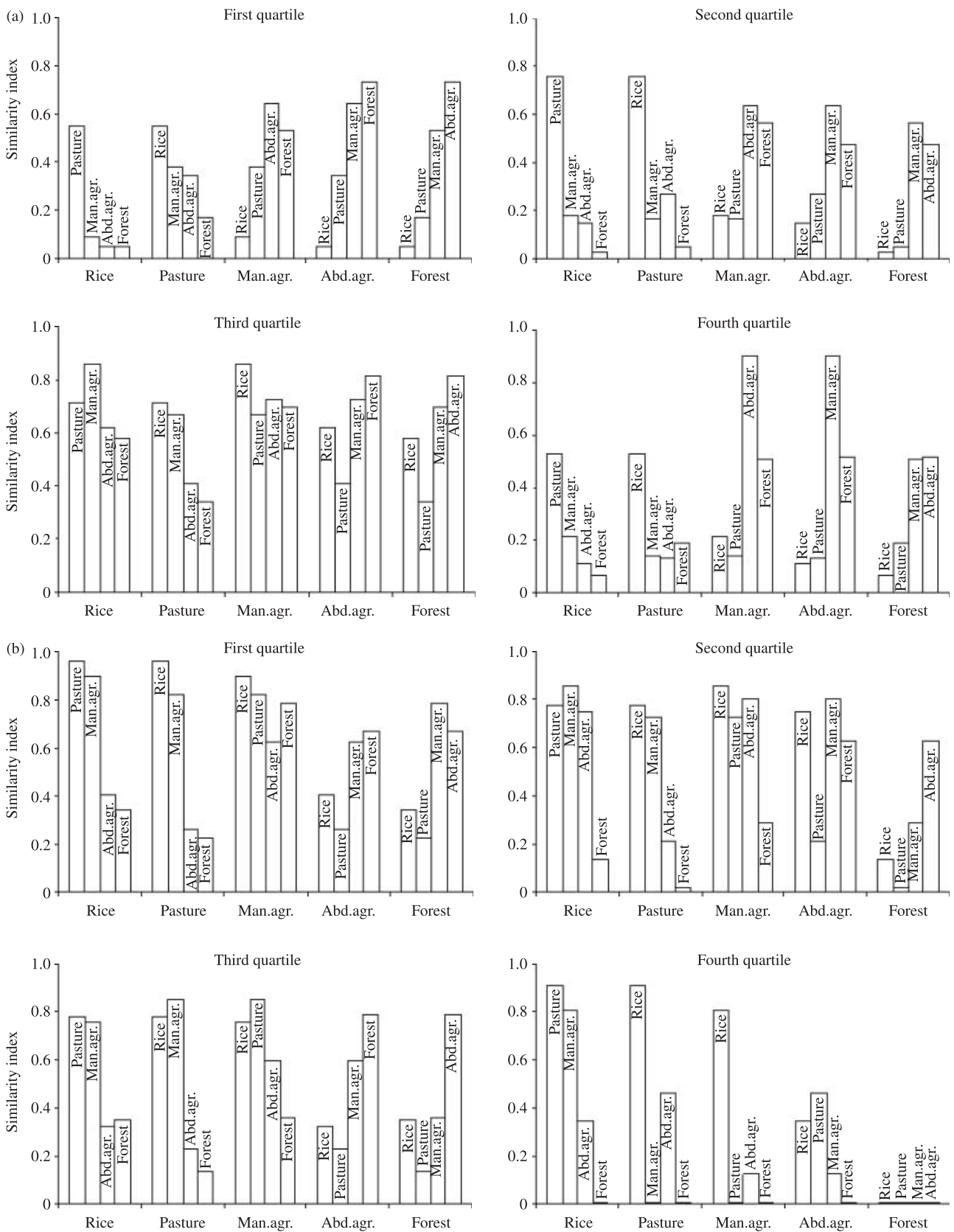
Figure 4 Floristic similarities (abundance-based Jaccard's index) of terrestrial herb communities among land-use types for each range size quartile in the high-impact landscape (a) and the low-impact landscape (b). Man. agr., managed agroforest; Abd. agr., abandoned agroforest.

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; Lozada, unpubl. data). Likewise, several studies have investigated environmental factors that might determine the range size of plants species (Kessler, 2002a,b; Hunter, 2003; Kreft *et al.*, 2006). However, the importance of range size in the response of species to anthropogenic disturbance in human-dominated landscapes, 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 & Rahbek, 2002; Kreft *et al.*, 2006; Rahbek *et al.*, 2007). 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 analysed data for each range size quartile, we found the opposite pattern for the narrowest range size quartile. This contrasting outcome confirms that studies analysing 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 & Rabinowitz, 1985; Balmford & 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 (Kessler, 2001). 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 showed the same pattern for the two landscapes with respect to the narrow-ranged species: abandoned agroforest and forest contained the highest number of narrow ranged species. However, in the high-impact landscape the difference between rice and forested land-use types was not significant. This could be due to the fact that the forested land-use types were more intervened and disturbed over a longer period of time than those in the low-impact landscape.

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 & 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 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, the 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 & 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. It should be noticed that our landscapes not only differed in management practices but also in climatic and other environmental conditions that can have an influence on species composition.

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 makes them a priority in conservation programmes (Brooks *et al.*, 2002). Our results suggest that the preservation of forest fragments in western Ecuador should be a 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 & 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 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 kilometres, is necessary but not sufficient (Pimm & 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.

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