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BIODIVERSITY RESEARCH

Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation

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ABSTRACT

Aim Most of the Atlantic Forest in Brazil occurs in fragments of various sizes. Previous studies indicate that forest fragmentation affects fruit-feeding butterflies. Conservation strategies that seek to preserve organisms that are distributed in high-fragmented biomes need to understand the spatial distribution of these organisms across the landscape. In view of the importance of understanding the fauna of these forest remnants, the objective of the present work is to investigate the extent to which the diversity of this group varies across spatial scales ranging from within-forest patches to between landscapes.

Location South America, south-eastern Brazil, São Paulo State.

Methods We used bait traps to sample fruit feeding butterflies at 50 points in 10 fragments in two different landscapes during a period of 12 months. Total species richness and Shannon index were partitioned additively in diversity at trap level, and beta diversity was calculated among traps, among forest patches, and between landscapes. We used permutation tests to compare these values to the expected ones under the null hypothesis that beta diversity is only a random sampling effect.

Results There was significant beta diversity at the smallest scale examined; however, the significance at higher scales depends on the diversity measurement used. Beta diversity with Shannon index was smaller than expected by chance among fragments, whereas species richness was not. Among landscapes, only beta diversity in richness was higher than expected by chance.

Main conclusions The results observed occur because there is great variability in species composition among forest patches in the same landscape, changing this diversity even though the communities are formed from the same pool of species. At the largest scale evaluated (between landscapes), these pattern changes and differences in beta diversity in richness were detectable. This difference is probably caused by the presence of rare species. Thus, a conservation strategy that seeks to preserve as many species as possible per unit of area in high-fragmented biomes should give priority to protecting fragments in different landscapes, rather than more fragments in the same landscape.

Keywords

Additive partitioning, Atlantic forest, fruit-feeding butterflies, land use, landscape structure, Nymphalidae.

INTRODUCTION

Biological diversity is not homogeneously distributed on the Earth's surface; an understanding of the distribution patterns of organisms is crucial in making effective decisions in conservation actions. Some habitats, such as coral reefs and tropical rain forests, have an exceptional concentration of biodiversity (Gaston, 2000). Tropical rain forests in particular have received much

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attention, since this biome harbours nearly half of the world's species diversity (Olson & Dinerstein, 2002).

Among the Brazilian rain forests, the Atlantic Forest deserves special attention because of its high level of endemism and degree of threat (Brown & Brown, 1992; Tabarelli *et al*., 2005), making this a primary hotspot for conservation (Myers *et al*., 2000). The massive destruction of the Atlantic Forest started with the arrival of the first European colonizers in the 16th century, and since that time about 92% of the natural vegetation in this biome has been modified or replaced by anthropogenic environments (Dean, 1997; Tabarelli *et al*., 2005).The remaining forest occurs mostly as small, disturbed and isolated patches, scattered through matrices of various land uses. In these severely fragmented landscapes, most forest patches are under serious risk of disappearing (Viana *et al*., 1997; Morellato & Haddad, 2000).

The process of forest fragmentation results in a substantial alteration of natural systems, changing local and regional diversity and causing extinction of many native species, which are frequently replaced by invasive organisms (Brown, 1997a; Tabanez & Viana, 2000; Metzger, 2001; Brown & Freitas, 2002; Fahrig, 2003). Additionally, fragmentation interacts synergistically with other factors, such as logging, hunting and fire (Tabanez & Viana, 2000; Laurance & Cochrane, 2001; Brown & Freitas, 2002), causing profound and irreversible changes in local communities (Brown, 1997b).

In areas with a high degree of habitat loss, such as the Brazilian Atlantic Forest, conservation strategies focusing on the effective protection of the remaining habitats must consider the distribution patterns of the organisms in the fragmented landscape (Brown & Freitas, 2000; Fahrig, 2003). This new conservation vision requires a refined knowledge of how biological diversity is organized across different spatial scales (Summerville *et al*., 2003).

The additive partitioning of species diversity is a promising approach to understanding the patterns described previously. It was proposed by some authors in the 1960s (reviewed by Veech *et al*., 2002) and, as analytically demonstrated by Lande (1996), it consists of partitioning total species diversity (γ) into additive components representing within-community diversity (α) and between-community diversity (β), where diversity can be measured as species richness or by using either the Simpson or Shannon index. The additivity allows the analysis of the proportion of total diversity (γ) found in a hierarchy of different scales. In this approach γ-diversity at a given scale is equal to the α diversity at the next scale; thus, total diversity can be conveniently expressed as $\gamma = \alpha + \beta_1 + \beta_2 + \beta_3 + \beta_4 + \dots \beta_n$, where n is the number of scales in the study (Veech *et al*., 2002). The additive partitioning of species diversity is a promising approach to analysing patterns of diversity in hierarchical studies with multiscale sampling (Lande, 1996) because it identifies the most important sources of diversity in a sampling design of nested spatial scales. This is useful for understanding the processes behind the spatial patterns of biodiversity and for helping to target conservation efforts accordingly (Veech *et al*., 2002; Gering *et al*., 2003).

Among the several taxa that can be used in diversity studies, butterflies are considered an excellent model because of their relatively large size, conspicuity, ease of sampling and relatively well-known taxonomy (Brown, 1991, 1992; DeVries *et al*., 1997; Veddeler *et al*., 2005). This combination of factors in such a well-known group of insects suggests an enormous potential for their use as templates for conservation of species and habitats (Brown, 1991; New, 1991, 1997; Steffan-Dewenter & Tscharntke, 1997; Brown & Freitas, 2000; Schulze *et al*., 2004).

Adult butterflies are normally divided into two major guilds: nectar-feeding and fruit-feeding (DeVries, 1987). Fruit-feeding butterflies gain most of their nutritional requirements from rotting fruits, plant sap and decaying material, and they are represented mainly by the Satyroid lineage of Nymphalidae (*sensu* Freitas & Brown, 2004; including the subfamilies Satyrinae, Brassolinae, Morphinae, Charaxinae and Biblidinae) and the tribe Coeini (Nymphalinae), comprising 50–75% of all neotropical Nymphalidae (Brown, 2005). Species of this guild can be easily sampled with bait traps using rotting fruits, allowing sampling in several areas simultaneously with a relatively similar sampling effort. Additionally, local richness and diversity in this group is correlated with total diversity of butterflies (Brown & Freitas, 2000; Horner-Devine *et al*., 2003), forest trees (Uehara-Prado, unpublished data) and birds (Schulze *et al*., 2004).

The objective of the present study is to characterize the diversity of fruit-feeding butterflies in a severely fragmented landscape in the Brazilian Atlantic Rain forest and verify how it is distributed across hierarchies of spatial scales. We compared this partition with the null hypothesis that butterfly assemblages are uniform across all spatial scales investigated, and that observed beta diversity among samples is simply a sampling effect. We expect that environmental heterogeneity and dispersion limitations would create nonrandom patterns of diversity partition.

METHODS

Study site

Field work was carried out in the São Luiz do Paraitinga municipality (Fig. 1), São Paulo State, south-eastern Brazil (centred in 23°20′ S, 45°20′ W), near the cliffs of the 'Serra do Mar' mountain range. The average altitude in this region is 740 m; the relief is composed of a complex landscape with rolling hills, steep escarpments and narrow deep valleys (MME, 1983). The climate is humid without a marked dry season; the annual average temperature is 20 °C (monthly min 12 °C, max 27 °C) and the average annual rainfall is 1340 mm (MME, 1983).

The original vegetation of this area was mainly a dense humid forest (MME, 1983); however, the process of forest fragmentation drastically changed the land cover in the region (Schmidt, 1949; Petrone, 1959; Dean, 1997). Human activity in this landscape started with the replacement of native rain forest by ranch areas and small crop fields at the middle of the 18th century. Around the year 1850, intensive coffee farming started in this region with an increase in deforestation rates. Extensive milk ranching starting in 1930 (Petrone, 1959) further contributed to deforestation. Today, a large part of the native vegetation has been removed, with small patches of disturbed forest scattered in a matrix of

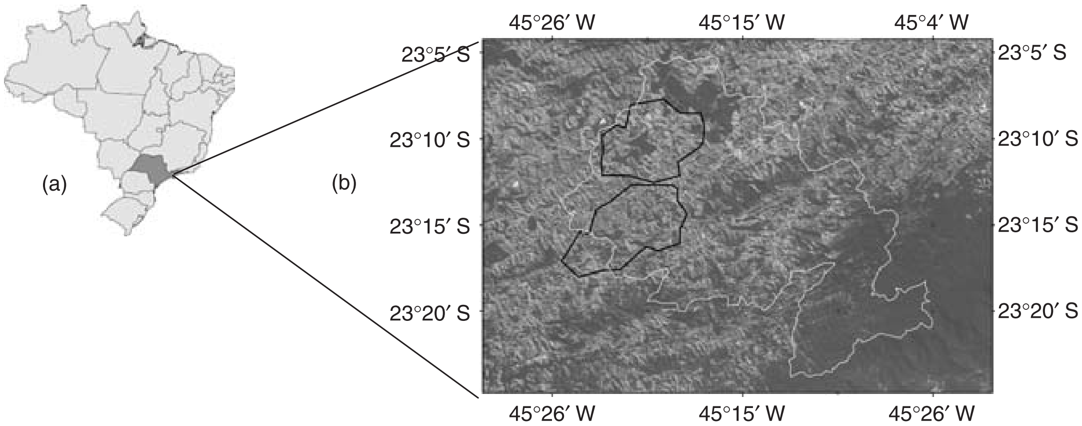

Figure 1 São Luiz do Paraitinga Municipality. (a) Location in Brazil; (b) Satellite image from SPOT (2002) with 5 × 5 m resolution. The white line in the image indicates the limits of São Luiz do Paraitinga Municipality, and the black lines indicate the studied landscapes.

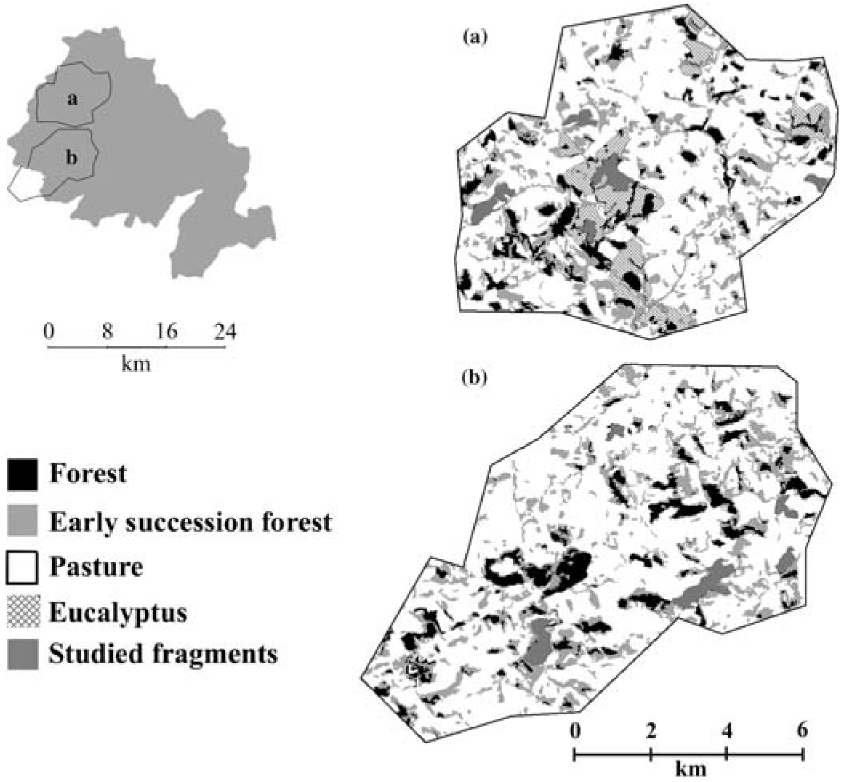

Figure 2 Localization of studied landscapes (a and b) and forest fragments sampled in São Luiz do Paraitinga municipality and land cover classification of landscapes. Note that all studied fragments are also classified as 'forests'.

ranching areas and abandoned pastures with some areas of *Eucalyptus* plantations (Fig. 2).

Sampling methods

In order to test the influence of the matrix on butterfly diversity, 10 fragments with similar structural characteristics (size, shape and normalized difference vegetation index (NDVI)) were chosen at random from two landscapes in adjacent river basins of similar area according to matrix composition. The landscapes (hereafter landscapes A and B) have about 7000 ha each, and the main difference between them is the area occupied by *Eucalyptus* plantations, which is higher in landscape A compared with landscape B (Fig. 2). The area covered with *Eucalyptus* is about 10% of the total area of landscape A, versus less than 1% of landscape B. Forest fragments are more isolated in landscape A according to all connectivity metrics calculated by the Fragstat Software (McGarigal & Marks, 1995). The connectivity index (Gustafson & Parker, 1992), for example, was 82 for landscape B and 210 for landscape A. On the other hand, landscape A has more early forest cover (22% against 19%), partly because in *Eucalyptus* plantations the riparian vegetation has not been removed in the past few years in accordance with Brazilian laws. This creates strips of early secondary vegetation along creeks that can act as connection structures for forest patches. Hence, differences in forest connectivity are related to differences in land use among the studied landscapes.

The butterfly sampling method followed Uehara-Prado *et al.* (2005, 2007), where each fragment received five portable traps baited with a mixture of banana and sugar cane juice fermented for 48 h. The traps were deployed along a linear transect, 30 m apart from each other, suspended from low branches such that the platform hung between 1 m and 1.5 m above the ground. The distance from the forest edge and water bodies, vegetation structure, terrain declivity and logistic aspects were standardized as much as possible to aid in the comparison among traps.

The butterflies were sampled from June 2004 to May 2005. In each month the traps remained open in the field for eight days and were visited at 48 h intervals (following Uehara-Prado *et al.*, 2005). During each visit the bait was replaced, and each individual captured was identified, marked and released. Species not identified in the field were taken for later identification.

Data analyses

The null hypothesis that fruit-feeding butterfly diversity is uniform in all spatial scales was tested by additive partitioning of total diversity, expressed by species richness and Shannon information index. In all comparisons, both measures of diversity were used.

To assess the spatial structure in species diversity, the pooled data for all sampling months were aggregated by trap, forest patch and landscape, thus resulting in a hierarchy with 50, 10 and 2 units, respectively. Average diversities (alpha) at each level were calculated, and the differences between them express beta diversity (Lande, 1996). Thus, alpha diversity at the trap level is the mean of the diversities of the 50 sampling traps, at the patch level the mean of the 10 sampled forest patches and so on. Beta diversity among traps is the difference between alpha diversity of patches and the alpha diversity of the traps. Beta diversity among patches is the difference between alpha of landscapes and alpha of patches, and so on. Note that in additive partitioning alpha and beta diversity have the same units and both are means. For species richness, for example, alpha diversity is the mean number of species in a given level, and beta is the mean number of species added if we move to the next level (Veech *et al.*, 2002).

It is quite improbable that two samples contain the same species in the same abundances even if they came from the same community; thus, part of beta diversity is the result of sampling variation. Hence, to attribute beta diversity to some ecological process, we first have to prove that it is larger or smaller than the value expected by random variation due to the sampling design. In other words, we have to test the null hypothesis that all samples came from the same community and that beta diversity is a sampling artefact. If so, the observed beta value would not differ from the value obtained if data were shuffled among samples at random. Hence, the significance of observed beta can be estimated through permutation tests by which the diversity expected at each level is simulated by shuffling the units of the inferior level (Crist *et al.*, 2003). In this way, captured individuals are shuffled among traps within each forest patch in order to test for significance of beta at the trap level. Then, in separate randomizations, traps are shuffled within the patches of a landscape to test beta at the patch level; and finally, patches are shuffled among the two landscapes to test beta at the landscape level. Because whole lower-level units are permuted within higher-level units, intraspecific aggregation in each scale is preserved. Crist *et al.* (2003) named this procedure 'sample-based randomization' to contrast to a single randomization of individuals independently among units in all levels, which they call 'individual-based randomization'.

The randomization process is then repeated many times to obtain null distributions of the beta diversity estimates at each hierarchical level (Crist *et al.*, 2003). The null hypothesis is tested by determining how often a larger value than the observed value was obtained in the randomizations. If this occurs in less than 5% of randomizations, say less than 50 times in 1000 randomizations, and then we assume that the observed value is significantly greater than expected and report a P-value of 0.05. Alternatively, if only 5% of randomizations are less than the observed value then we conclude that the observed value is significantly less than expected at a P-value of 0.05 (Gotelli & Graves, 1996). For the randomization at each level, we carried out 1000 trials using a routine written in the R Language 2.4.0 (R Development Core Team, 2006), using the package boot 1.2–27 (Canty & Ripley, 2006). The code is available from the authors upon request.

RESULTS

In all, 6488 individuals of 73 species of butterflies were captured in the 12 sampling periods, representing all groups of fruit-feeding Nymphalidae: Satyrinae, Brassolinae, Morphinae, Charaxinae, Biblidinae and the tribe Coeini (Nymphalinae). In all sites the subfamilies Satyrinae and Biblidinae were the most abundant.

The spatial partitioning of species diversity showed that each trap (α), on average, retains less diversity than expected by the null hypothesis ($P < 0.001$ in both diversity measures, Table 1). In consequence, the β-diversities among traps within fragment ($\beta 1$) are significantly higher ($P < 0.001$ for the two diversity measures). The observed β diversity for species richness among fragments within landscape ($\beta 2$: S = 17.2) was not different from that expected by the null hypothesis (mean value from the 1000 randomizations S = 16.7). On the other hand, beta diversity among fragments expressed by the Shannon diversity index ($\beta 2$: $H' = 0.19$) was significantly higher (expected $H' = 0.089$; $P < 0.001$). In the largest scale analysed (landscapes), the observed richness between landscapes was higher than expected ($P = 0.017$); however, the observed $\beta 3$ Shannon diversity ($H' = 0.043$) was not significantly different from that expected by chance ($H' = 0.038$).

DISCUSSION

Both diversity indexes showed higher beta diversity among traps within each fragment than expected by chance. This means that butterflies are not randomly distributed inside forest fragments,

Table 1 Spatial partitioning of species diversity of the assemblage of fruit-feeding Nymphalidae in Upper Paraíba River basin, São Paulo State, Brazil. Results in bold type indicate that the observed diversity is significantly different from that expected in a random distribution. S = species richness, H′ = Shannon diversity Index, n.s. = non significant. For all diversity measures (S and H′) the expected value is the mean of the null distribution (for more details, see Methods section).

Diversity		Observed	(%)	Expected	*P*
S					
α	Within traps	27.10	37.1	27.88	**< 0.001**
β1	Among traps	17.40	23.8	16.62	**< 0.001**
β2	Among fragments	17.25	23.6	16.69	n.s.
β3	Between landscapes	11.26	15.4	8.706	**0.017**
γ	Total	73.00		69.90	
H′					
α	Within traps	2.670	86.4	2.723	**< 0.001**
β1	Among traps	0.186	6.0	0.133	**< 0.001**
β2	Among fragments	0.192	6.2	0.089	**< 0.001**
β3	Between landscapes	0.043	1.4	0.038	n.s.
γ	Total	3.09		2.983	

which can be explained by intraspecific aggregation on a very small scale (the mean distance among traps). The distribution of larval and adult resources could contribute much to explaining these grouped patterns. The vegetation inside the forest fragments is not homogeneous, but approaches a floristic mosaic of habitats with different compositions of larval and adult resources, resulting in concentration of some species at the sites where their resources are concentrated. Hamer *et al.* (2006) showed that adult food resources affect the diversity of fruit feeding butterflies. Besides food resources, vegetation structure is also correlated with microhabitat characteristics like temperature, humidity and luminosity. These microhabitat changes are exacerbated by the constant anthropogenic pressures, from hunting, wood extraction, ox invasion and fire, present in the studied fragments. The relatively small size of these fragments (11–83 ha) increases the importance of these human activities in changes to vegetation structure.

DeVries *et al.* (1997, 1999), in their work in Ecuador, found a pattern of vertical distribution of fruit-feeding butterflies that can be explained in part by differences between forest strata. This pattern of diversity distribution in the lower hierarchical levels (traps, stands) was recorded in beetles and moths in North America (Gering & Crist, 2002; Crist *et al.*, 2003; Summerville *et al.*, 2003). The process that generates this distribution pattern is probably the aggregate distribution of resources on a local scale and the great variability that exists among sample points on small scales. The correlation between beta diversity and spatial aggregation is logically straightforward and has good empirical support. Veech (2005) compiled 28 data sets from different communities and showed that all had α diversities smaller than expected (and thus higher β-diversity), and that the departure from the expected values increased with the mean of Morisita aggregation indexes of the species in each community.

The beta diversity for species richness among fragments (β2) was not significantly different from the expected value, indicating that all butterfly assemblages of fragments are subsamples of the same species pool, but the differences observed in the Shannon index suggest that structural differences among fragments affect the dominance patterns in these communities. The Shannon index gives more weight for common species than species richness; thus, their significant beta diversity among forest patches suggests that they differ in their populations of some of the most abundant species.

Characteristics of forest fragments, such as size, relief, connectivity, succession stage and matrix composition, can also influence the local structure of fruit-feeding butterfly assemblages. Even if size is an obvious feature explaining the occurrence of some species, in the present work this could not be tested since the fragments studied had a small range of sizes (11–83 ha). The orientation of the fragments could be important in the region (next to the Tropic of Capricorn), since fragments orientated as northward slopes receive more solar energy during the year than fragments orientated southward. Therefore, north-orientated fragments are hotter and drier than south-orientated fragments, certainly affecting the vegetation and consequently the local community of fruit-feeding butterflies.

The composition of the surrounding matrix can also influence butterfly communities in the fragments by directly modifying their patterns of migration and colonization (Summerville & Crist, 2001; Veddeler *et al.*, 2005) and in an indirect way changing local microclimate and vegetation structure (Saunders *et al.*, 1991; Laurance *et al.*, 2007). The differences in resource distribution (e.g. host plants) among the fragments could also explain in part the high beta diversity (H′) found on this scale.

The beta diversity expressed by the Shannon index between landscapes (β3) was not significantly different from that expected by chance. However, the beta diversity for species richness at the same scale (β3) was higher than expected by chance. This result indicates that dominant species are the same in both landscapes and that the main difference between butterfly assemblages is the rare species. This is in accordance with the 'Landscape – Divergence Hypothesis' (Laurance *et al.*, 2007), which proposes that fragments within the same landscape will tend to have similar dynamics and trajectories of change in species composition, which will often differ from those in other landscapes. Over time, this process will act as a homogenizing force for fragments within the same landscape and will promote increasing ecological divergence among fragments in different landscapes. The landscapes still support subsets of the same high-diversity species pool found in intact habitats (Laurance *et al.*, 2007), which may include a common core of the most tolerant and abundant species. A similar pattern was reported in several large scale studies (Hamer & Hill, 2000) because despite the structural similarity among sampled areas, there are limits in dispersal capacity in most butterfly species, resulting in grouped patterns in these high-scale approaches.

Scale dependent differences in spatial patterns of diversity, such as those detected for beetles (Crist *et al.*, 2003; Gering *et al.*, 2003) have rarely been observed in Lepidoptera. DeVries & Walla

(2001) showed that there is only a fundamental horizontal stratification in fruit-feeding butterflies in Ecuador. Additionally, Summerville *et al.* (2003) found that moth species showed strong beta diversity at all levels. The present study is the first to document that fruit-feeding butterflies showed high beta diversity, perhaps as a result of spatial aggregation of species, in fragmented landscapes, among forest patches and also among different landscapes.

Even if the results found in Lepidoptera show no clear patterns, beta diversity at larger scales has huge importance for several taxa, such as ants, crickets and fresh water invertebrates (Stendera & Johnson, 2005; Veech, 2005; Hamer *et al.*, 2006). Because of the great importance of beta diversity on local and regional scales, a promising approach for future studies is to investigate which processes maintain these spatial patterns of diversity in order to provide a better understanding of the ecological processes that sustain a widely distributed pattern.

Additionally, conservation efforts need to consider the great importance of beta diversity when proposing the creation of new parks and protected areas. In cases of strongly fragmented landscapes such as those of the present study, decisions about what to do to preserve as many species of fruit-feeding butterflies per area as possible should preferentially focus on fragments distributed through different landscapes, rather than nearby fragments in the same landscape. In our study's case, the increase in assemblage species richness is only the result of the increase of the sampling effort, in contrast with the inclusion of a fragment from another landscape. This pattern occurs because dominant species are the same in both landscapes, and the greater differences between butterfly assemblages are explained by the less abundant species. We think this is a sensible criterion, because the species that deserve more conservation efforts are the rarer ones, especially when habitat loss is severe.

Although most conservation efforts seek to preserve pristine areas of continuous forest, we cannot neglect the importance of preserving local fragmented landscapes. These heterogeneous mosaics efficiently maintain populations of many small arthropods, including fruit-feeding butterflies (Brown & Freitas, 2002; Veddeler *et al.*, 2005), and could additionally act as corridors or 'stepping-stones' for several other organisms. This is especially important considering the highly fragmented nature of the landscapes in some threatened biomes such as the Brazilian Atlantic Forest (Morellato & Haddad, 2000), where the protection of the few large forest remnants will not assure the persistence of populations of most species in the long run (Tabarelli *et al.*, 2005).

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