



The challenge of maintaining Atlantic forest biodiversity: A multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia

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ABSTRACT

Recent developments have highlighted the importance of forest amount at large spatial scales and of matrix quality for ecological processes in remnants. These developments, in turn, suggest the potential for reducing biodiversity loss through the maintenance of a high percentage of forest combined with sensitive management of anthropogenic areas. We conducted a multi-taxa survey to evaluate the potential for biodiversity maintenance in an Atlantic forest landscape that presented a favorable context from a theoretical perspective (high proportion of mature forest partly surrounded by structurally complex matrices). We sampled ferns, butterflies, frogs, lizards, bats, small mammals and birds in interiors and edges of large and small mature forest remnants and two matrices (second-growth forests and shade cacao plantations), as well as trees in interiors of small and large remnants. By considering richness, abundance and composition of forest specialists and generalists, we investigated the biodiversity value of matrix habitats (comparing them with interiors of large remnants for all groups except tree), and evaluated area (for all groups) and edge effects (for all groups except trees) in mature forest remnants. Our results suggest that in landscapes comprising high amounts of mature forest and low contrasting matrices: (1) shade cacao plantations and second-growth forests harbor an appreciable number of forest specialists; (2) most forest specialist assemblages are not affected by area or edge effects, while most generalist assemblages proliferate at edges of small remnants. Nevertheless, differences in tree assemblages, especially among smaller trees, suggest that observed patterns are unlikely to be stable over time.

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1. Introduction

Habitat loss and fragmentation are two closely linked anthropogenic threats with a significant influence on extant patterns of spe-

cies distribution and abundance (Pimm and Raven, 2000). Today a significant part of the terrestrial biodiversity is found in fragmented landscapes, and since the landmark publication of island biogeography theory (MacArthur and Wilson, 1967), a growing body of research has allowed ecologists to start disentangling the main effects of habitat loss and fragmentation upon biological assemblages (Fahrig, 2003; Ewers and Didham, 2006; Fischer and Lindenmayer, 2007).

Habitat loss and fragmentation adversely affect species persistence mainly through reduction in available native core habitat, increase in isolation among remnant patches and edge effects (Laurance et al., 2002; Fahrig, 2003; Kupfer et al., 2006). In general, habitat reduction increases the likelihood of stochastic extinction in fragments; an effect that is rarely offset by migrants due to increased patch isolation (Hanski, 1998). The influence of the modified habitats that surround remnants, the so called edge effect, is known to affect forest microclimate (Didham and Lawton, 1999),

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vegetation structure (Laurance et al., 2006) and, thus the structure of animal communities (Didham et al., 1998; Laurance et al., 2002). The interaction between fragmentation and other human-induced pressures (hunting, logging, fire) further threatens species in fragmented landscapes (Gascon et al., 2000; Silva and Tabarelli, 2000; Laurance, 2004).

Most of the conceptual framework of habitat fragmentation studies, derived from the island biogeography theory, was built under the assumption that only two components of a given landscape are important in determining species persistence: remnants of native forest or habitat and non-forest/non-habitat areas (Kupfer et al., 2006). This simplification emphasizes the importance of native remnants for the maintenance of native biodiversity while underestimates the role of landscape structure and composition, including the amount and spatial arrangement of remaining habitats and the structure and quality of the intervening matrix (Haila, 2002; Ewers and Didham, 2006).

Given the non linear relationship between habitat loss at the landscape scale and the characteristics of remaining patches (such as mean patch size or mean distance among patches, see Andr en, 1994; Fahrig, 1997; Fahrig, 2003), the likelihood of species extinction is expected to increase drastically when the area of remaining habitat is suppressed below a threshold value. This fragmentation threshold, however, has been demonstrated to vary among taxa, regions and spatial scales (With and Crist, 1995; Huggett, 2005; Lindenmayer and Luck, 2005; Radford et al., 2005).

The importance of heterogeneous anthropogenic habitats in the intervening matrix is not limited to their potential for promoting species movements across landscapes, but also in providing suitable habitat and resources for the native biota (Ewers and Didham, 2006; Fischer and Lindenmayer, 2007). These surrounding modified habitats can be of particular importance for species persistence when they present low structural contrast with the primary habitat (Collinge and Palmer, 2002). In tropical landscapes, although second-growth forests are not surrogates for primary forest, they can provide suitable habitat for a component of local assemblages (Barlow et al., 2007). The potential of modified habitats to harbor forest species, however, varies among biological groups (Schulze et al., 2004; Pineda et al., 2005; Harvey et al., 2006; Faria et al., 2006, 2007). Considering the rapid pace of deforestation, it is important to establish the actual conservation value of these modified habitats for biodiversity conservation (Gardner et al., 2007).

In the light of these recent research developments it is expected that fragmented landscapes comprising high amounts of remaining habitat, and heterogeneous anthropogenic habitats that are relatively structurally complex, may harbor an appreciable component of the native biota. This would allow, therefore, the potential for reducing biodiversity loss in altered tropical landscapes through the maintenance of a relatively high percentage of forest combined with sensitive management of anthropogenic areas. However, few attempts have been made to test this prediction in fragmented tropical forest landscapes (Lindenmayer and Luck, 2005), especially for multiple taxonomic groups.

The Atlantic forest stretched along most of the Brazilian coast and has been reduced, except for few large conservation units, to small remnants (<100 ha), mainly composed of second-growth forest, and immersed in agricultural or urban matrices (Ribeiro et al., 2009). An exception to this pattern is observed in some regions of the cacao-producing zone of southern Bahia, where mature forest remnants are inserted in a mosaic of cleared land, second-growth forests and cacao plantations shaded by native trees.

We conducted a large-scale, multi-taxa, standardized survey in a landscape in the cacao-growing region of southern Bahia to evaluate its potential for maintaining native biodiversity. Using standardized field protocols we sampled ferns, frugivorous butterflies, leaf-litter frogs and lizards, bats, small mammals and birds in six replicates

of six habitat categories – second-growth forests, shade cacao plantations, interiors and edges of large (>1000 ha) and small (<100 ha) mature forest remnants, as well as trees in a subset of these habitats (interiors of large and small mature forest remnants). We investigated the biodiversity value of matrix habitats (shade cacao plantations and second-growth forest) compared to mature forest (interiors of large mature forest remnants) for ferns and all animal groups. By comparing habitat categories within mature forest remnants, we also evaluated the effects on biodiversity of area reduction (for ferns, trees and all animal groups), and edge proximity (for ferns and all animal groups). For each taxonomic group we considered the richness, abundance and composition of two distinct sets of species, forest specialists and habitat generalists, that vary in their dependence to humid forest, an thus, extinction proneness.

2. Methods

2.1. Study area and sites

Southern Bahia encompasses some of the largest remnants of Atlantic forest in northeastern Brazil. The study was carried out in the Una municipality (15°17'S, 39°04'W), located in the coastal zone of the cacao-growing region. By the time the project was carried out, 7000 ha of forest was protected as a conservation unit (Una Biological Reserve – RebioUna). The forest is classified as tropical lowland rainforest, the mean annual temperature is 24 °C and mean rainfall is around 2000 mm year⁻¹, with no clear seasonality, though a period of 1–3 months with reduced rainfall may occur from December to March (Faria et al., 2006).

The study was carried out in three replicated sampling blocks (6 × 6 km) to minimize the influence of covariates that were not measured (e.g. block-wise variability in soil, relief, etc.) (Fig. 1). Considering the total area of the three blocks, mature forest represents 49% and is distributed in irregularly-shaped remnants with a high proportion of edges. These forests are interdigitated with the modified matrix, which is dominated by pastures, second-growth forests and shade cacao plantations, covering 27%, 15% and 6%, respectively (Pardini, 2004).

In each of the three blocks, two replicates of six habitat categories were selected: IL – interiors of large mature forest remnants (>1000 ha), EL – edges of large mature forest remnants, IS – interiors of small mature forest remnants (<100 ha), ES – edges of small mature forest remnants, SF – second-growth forests, and SCP – shade cacao plantations (Fig. 1). Sites in second-growth forests were located in areas that had been clear-cut less than 12 year before sampling. Sites located in edges of small and large mature forest remnants were 20 m or less from open areas, mainly pastures, while sites in interiors were at least 100 m from the forest-open area boundary.

2.2. Data collection

Tree surveys were limited to interiors of large and small mature forest remnants (IL and IS), comprising 12 sampling sites, while all other groups were sampled in all 36 sites. Although the size of the sampling unit and the sampling procedure varied among taxonomic groups, the area sampled in each site overlapped across all taxa and all fieldwork was carried out between September 1997 and August 2000.

Trees – In each of the 12 sites, trees were sampled separately in three classes of diameter at breast height (DBH): dominant trees (DBH > 15 cm) were sampled in ten 20 × 10 m plots, understory trees (DBH between 15 and 5 cm) in ten 10 × 10 m plots, and tree saplings (plants with a stem at breast height and DBH <5 cm) in ten 5 × 5 m plots. Smaller plots were nested within larger plots, which were randomly placed within a 100 × 120 m area.

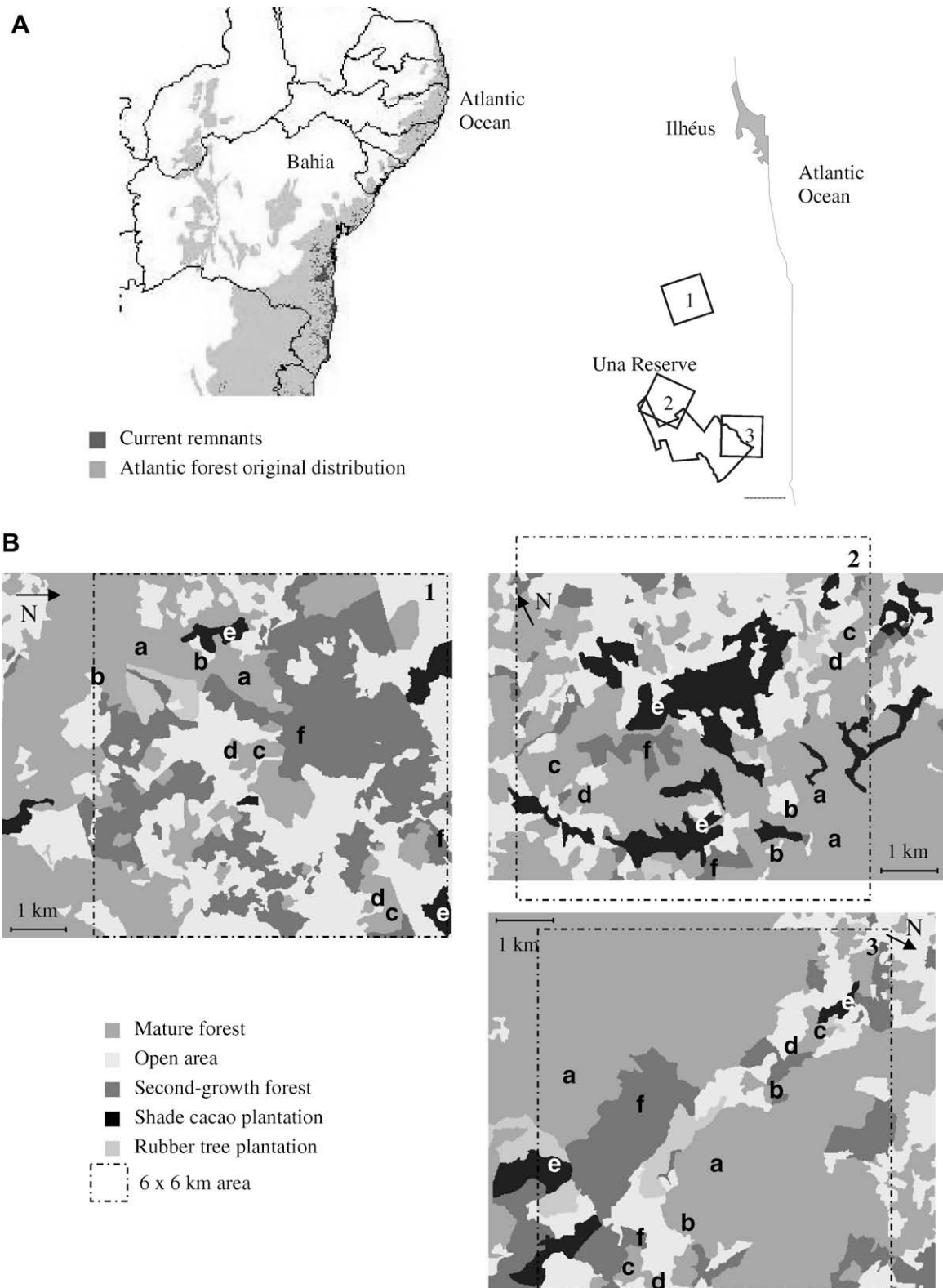


Fig. 1. A-Map of northeastern Brazil, showing the original distribution and the current remnants of Atlantic forest, the location of the Una Biological Reserve and the three study blocks. B-Distribution of the main habitat types and the position of the 12 study sites in each of the three study blocks: a-interior of large remnants (IL), b-edge of large remnants (EL), c-interior of small remnants (IS), d-edge of small remnants (ES), e-shade cacao plantations (SCP), f-second-growth forests (SF). Redrawn from Pardini (2004).

Ferns – All ferns up to 2 m above the ground, including herbaceous, climbers, tree ferns, and epiphytes, were sampled in a 0.12 ha plot (120 × 10 m) in each of the 36 sites (Paciencia and Prado, 2005).

Frugivorous butterflies – In each site, three trap stations, each containing one trap hanging in the understory (3–5 m high) and one ground trap, were set at 120-m intervals. Traps were baited with fermented banana and sugar cane juice. Each site was sam-

pled for 15 non-rainy days equally distributed in three different capture sessions carried out every four months.

Leaf-litter frogs and lizards – In each site, we used three 25-m long arrays of pitfall traps placed 50 m apart, each containing four 35-l plastic buckets 8 m from each other connected by a 50-cm high fence. Each site was sampled twice, for 12 consecutive days, and captured animals were marked before release (Dixo and Martins, 2008).

Small mammals – Small mammals were sampled using pitfall traps (see above) and Sherman traps of two different sizes placed along two parallel 165-m long lines, 20 m from each other, in 24 trap stations spaced every 15 m. One small and one large trap were set in each station, one on the forest floor and one 1.5-m high in the understory vegetation, alternating the height of small and large traps between adjacent stations. Three capture sessions with Sherman traps of seven days each were conducted in each site and animals were marked at first capture (Pardini, 2004).

Bats – In each site, bats were mist-netted using eight, 2.5-m high ground mist nets of length 12 m (2), 9 m (2) and 6 m (4), totaling a sampling area of 165 m² of nets open for 5 h after sunset. Each site was equally sampled on four non-consecutive, moonless and rainless nights. Captured bats were released at the end of the sampling night (Faria et al., 2007).

Birds – Birds were monitored using fixed-radius point count surveys of 15 min each, in three points 100 m apart from each other in each site. Each point was sampled at five hourly intervals (the first starting at sunrise). Points sampled during the same interval of the same day were at least 200 m apart and surveys in the same site occurred in 7–12 different days (Faria et al., 2007).

2.3. Classification of species

The variability of responses to habitat or landscape modification is usually significant both among (Barlow et al., 2007) and within taxonomic groups (Uehara-Prado et al., 2007). In the absence of *a priori* detailed information on the level of dependence of all sampled species to mature forest, we classified species into forest specialist and habitat generalist species using independent criteria, i.e. not based on species distribution among habitats in Una, that we assumed were correlated with dependence to native forest. All classifications were based on the best available information, considering the reliability and coverage of the information available in the literature, and the natural history of each group (see details and sources used to classify species in [Supplementary material S1](#)). Trees were classified as shade tolerant or intolerant, and forest specialist assemblage of ferns included those species exclusively registered in native forest habitats, while generalist species were those occurring also or exclusively in open habitats in floristic-taxonomic studies. We categorized as forest specialists the gleaning animalivorous bats, since they are more strictly related to undisturbed forests. For the remaining animal groups, classification was based on species distribution in relation to the major neotropical biomes or forest types, assuming that species that are restricted to forest at larger spatial scales are also more dependent on forest on a local scale.

2.4. Data analysis

To investigate the biodiversity value of matrix habitats, we compared mean richness and abundance of forest specialist and generalist species of each taxonomic group (except trees, which were not sampled in the matrices) among interiors of large mature forest remnants (IL), second-growth forests (SF) and shade cacao plantations (SCP) using factorial ANOVAs (habitat types and blocks as factors), followed by *a posteriori* comparisons with Tukey test. Data were tested for homogeneity of variances with Bartlett test and when re-

quired, data were rank-transformed. For each analyzed taxonomic group (except bats, for which the forest specialist assemblage encompassed few rare species preventing the use of multivariate analysis), we also compared the composition of forest specialist assemblages among the three habitat types through analyses of similarity (ANOSIM) and Non-metric Multidimensional Scaling (NMS, two axes), using Bray–Curtis similarity index on the abundance (standardized by sample unit totals) of forest specialist species.

To evaluate the effects of area reduction and edge proximity on biodiversity in mature forest remnants, the same statistical procedure as described above was used to compare interiors of large and small mature forest remnants (IL and IS) in the case of trees, and among interiors and edges of large and small mature forest remnants (IL, EL, IS and ES) for the remaining groups.

3. Results

We found a total of 431 species in the 36 sites in Una – 60 species of ferns, 86 frugivorous butterflies, 15 leaf-litter frogs, 13 leaf-litter lizards, 39 bats, 19 small mammals and 199 birds. From those, 151 were classified as forest specialists and 280 as generalists. Among the 498 species of trees recorded in the 12 sites in Una (260 among dominant trees, 309 among understory trees and 397 among tree saplings), 334 were classified as shade tolerant, 126 as shade intolerant and 38 could not be classified due to lack of information.

3.1. The value of second-growth forest and shade cacao plantations for biodiversity

Considering the total number of species found per habitat type, the number of forest specialist species decreased from mature forests to shade cacao plantations to second-growth forests, while the number of generalist species increased from mature forests to second-growth forests to shade cacao plantations (Fig. 2). Therefore, shade cacao plantations harbored not only a higher proportion of forest specialists (57.6%) but also of generalist species (77.1%) compared to second-growth forest (47% and 66.4%, respectively). The value of these matrix habitats, however, varied among taxonomic groups (Fig. 2). For ferns, the single plant taxa considered here, the proportion of forest specialists present in each matrix habitat was lower than that observed for most animal groups.

The factorial ANOVAs showed more significant differences among habitats (16) than among blocks (6), with few significant interactions between these two factors (4) (Table 1). Thus, in general, most differences in forest specialist or generalist assemblages among habitats were independent from the spatial location of sampling sites within the landscape.

The abundance of forest specialist assemblages of ferns, birds and bats varied significantly among habitats (Table 1, Fig. 3). For ferns and birds, forest specialist abundance was significantly or marginally significant higher in mature forests compared to both matrix habitats. On the other hand, the abundance of forest specialist bats differed among the three habitat types, being absent from second-growth forests, and higher in shade cacao plantations than in mature forest. The richness of forest specialist assemblages of ferns, butterflies and bats varied significantly among habitats (Table 1, Fig. 3). For ferns, forest specialist richness was higher in mature forests, while for butterflies it was higher in mature forests compared only to shade cacao plantations. For bats, forest specialist richness differed among habitats, following the same pattern observed for abundance.

On the other hand, significant changes in forest specialist composition among habitats were observed for most groups (ferns, butterflies, lizards, and birds) (Fig. 4). The composition of forest

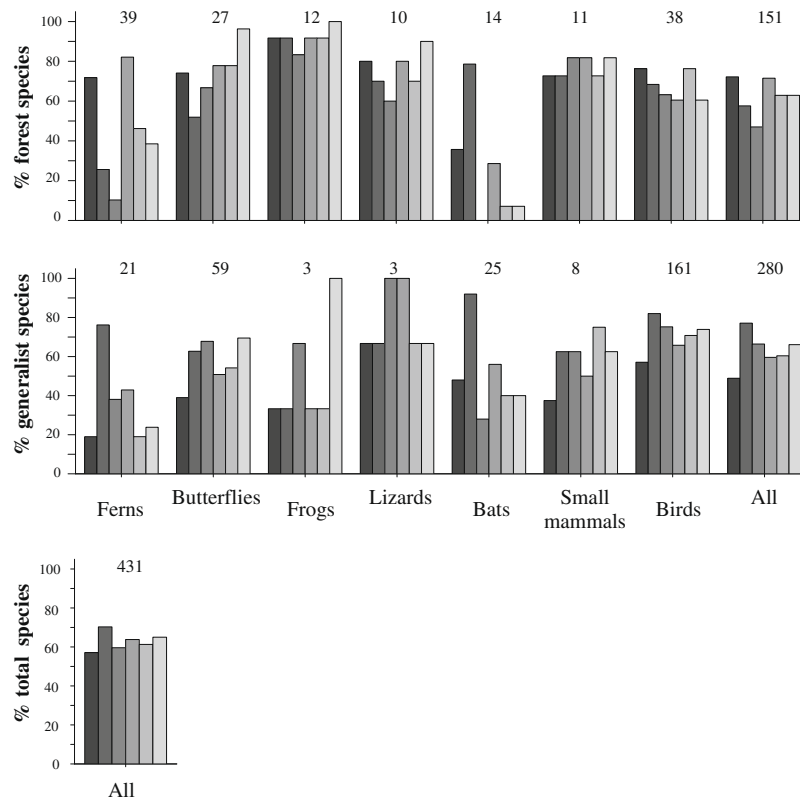


Fig. 2. Percentage and total number (over the bars) of forest and generalist species of ferns, frugivorous butterflies, leaf-litter frogs and lizards, bats, small mammals and birds found in interiors of large remnants, shade cacao plantations, second-growth forests, interiors of small remnants, edges of large remnants and edges of small remnants (in this order, from darker to grayish bars) in the Una region, South Bahia, Brazil.

specialist ferns in shade cacao plantations differed from that in mature forests (Fig. 4, ANOSIM pairwise comparisons: $IL \times SCP P = 0.002$, $IL \times SF P = 0.060$, $SCP \times SF P = 0.080$). For butterflies, lizards and birds, forest specialist composition differed among the three habitats, with the composition observed in shade cacao plantations being the most distinct from that observed in mature forests (Fig. 4, ANOSIM pairwise comparisons: for butterflies, $IL \times SCP P = 0.002$, $IL \times SF P = 0.006$, $SCP \times SF P = 0.020$; for lizards, $IL \times SCP P = 0.002$, $IL \times SF P = 0.020$, $SCP \times SF P = 0.004$; and for birds, $IL \times SCP P = 0.002$, $IL \times SF P = 0.010$, $SCP \times SF P = 0.002$).

Considering the generalists, abundance and richness varied significantly among habitats for most groups (Table 1, Fig. 3). For butterflies and small mammals, the abundance of generalists was lower in mature forests than in both matrix habitats, while for birds it was lower in mature and second-growth forests compared to shade cacao plantations. Again, the abundance of generalist bats differed significantly among habitats, following the same pattern observed for forest specialists: a decreasing abundance from shade cacao plantations to mature forests to second-growth forests. The richness of generalists was lower or tended to be lower in mature forests than in both matrix habitats for butterflies and small mammals. For birds, generalist richness varied among the three habitat types, being lower in mature forests, followed by second-growth forest and shade cacao plantations. For ferns and bats, a lower number of generalist species was found in mature and second-growth forests compared to shade cacao plantations.

3.2. The effects of area reduction and edge proximity on biodiversity in mature forest remnants

Considering the total number of species of ferns and animals found per treatment within mature forest remnants, although the number of forest specialists decreased from interiors to edges of

remnants, regardless of remnant size, a greater increase in the number of generalist species was observed over a gradient from interiors of large remnants to edges of small remnants (Fig. 2). Thus, considering both assemblages of species (forest specialist and generalists) together, the number of species was higher at edges of small remnants (65%) compared to interiors of large remnants (57.1%) (Fig. 2). The pattern of decreasing forest specialists at edges was mainly attributable to ferns and bats, while that of increasing generalist species was associated with patterns of butterflies, small mammals and birds (Fig. 2). In contrast, considering the total number of species of trees found per treatment within mature forest remnants, the number of shade tolerant tree species decreased from large to small remnants for all three forest strata considered, while the number of shade intolerant species increased from large to small remnants for understory trees only (Fig. 5).

Again, ANOVAs comparing assemblages of ferns and animal groups among interiors and edges of small and large remnants (Table 2) and those comparing tree assemblages between interiors of small and large remnants (Table 3) resulted in a higher number of significant differences among treatments (12) than among blocks (4), with two interactions between factors.

For fern and animal assemblages, there was no significant difference in forest specialist abundance or richness among interiors and edges of large and small remnants (Table 2, Fig. 3). The composition of forest specialist ferns and butterflies, however, differed slightly among treatments (Fig. 4). Composition of forest specialist ferns differed between interiors (of both small and large remnants) and the edges of large remnants (Fig. 4, ANOSIM pairwise comparisons: $IL \times EL P = 0.035$, $IL \times IS P = 0.639$, $IL \times ES P = 0.123$, $EL \times IS P = 0.011$, $EL \times ES P = 0.537$, $IS \times ES P = 0.173$). For butterflies, composition of forest specialist in the interior of large remnants differed from that found in both the edges (of small and large remnants) and in the interior of small remnants (Fig. 4, ANOSIM

Table 1

Results from the two-way ANOVAs (blocks and treatments: interiors of large remnants – IL, shade cacao plantations – SCP and second-growth forest – SF) and *a posteriori* comparisons (Tukey test) for the richness and abundance of forest and generalist species of ferns, frugivorous butterflies, leaf-litter frogs and lizards, bats, small mammals and birds in the Una region, South Bahia, Brazil.

	Block		Treatment		Interaction		Tukey test		
	F	P	F	P	F	P	IL/SCP	IL/SF	SCP/SF
<i>Forest species</i>									
Abundance									
Ferns	0.674	0.534	8.342	0.009	2.650	0.103	0.066	0.008	0.377
Butterflies	2.003	0.191	2.296	0.156	0.313	0.862			
Frogs	1.446	0.285	0.018	0.982	2.789	0.093			
Lizards	14.258	0.002	61.642	<0.001	5.226	0.019			
Bats ^a			14.494	0.001					
Small mammals	0.175	0.842	0.561	0.589	0.854	0.526			
Birds	4.063	0.055	5.143	0.032	0.425	0.787	0.045	0.060	0.982
Richness									
Ferns	3.756	0.065	22.794	<0.001	0.692	0.616	0.004	0.000	0.146
Butterflies	0.981	0.412	7.838	0.011	0.010	1.000	0.009	0.112	0.267
Frogs	2.724	0.119	1.069	0.383	4.586	0.027			
Lizards	12.875	0.002	0.875	0.450	2.000	0.178			
Bats ^a			14.494	0.001					
Small mammals	7.000	0.015	0.538	0.601	4.231	0.034			
Birds	4.956	0.035	2.882	0.108	0.787	0.562			
<i>Generalist species</i>									
Abundance									
Ferns	5.029	0.034	24.471	<0.001	4.353	0.031			
Butterflies	0.331	0.727	16.692	0.001	1.108	0.410	0.001	0.006	0.448
Frogs	2.824	0.112	0.706	0.519	1.941	0.188			
Lizards	0.920	0.433	0.376	0.697	0.684	0.621			
Bats	1.048	0.390	35.216	<0.001	1.508	0.279	0.002	0.018	<0.001
Small mammals	0.427	0.665	15.265	0.001	0.946	0.481	0.005	0.002	0.719
Birds	8.962	0.007	56.018	<0.001	3.247	0.066	<0.001	0.082	<0.001
Richness									
Ferns	3.552	0.073	33.552	<0.001	1.276	0.348	<0.001	0.648	<0.001
Butterflies	1.009	0.402	17.095	0.001	1.810	0.211	0.005	0.001	0.455
Frogs	4.000	0.057	1.000	0.405	2.000	0.178			
Lizards	0.467	0.641	0.467	0.641	0.967	0.471			
Bats	2.714	0.120	92.592	<0.001	1.918	0.192	<0.001	0.381	<0.001
Small mammals	1.867	0.210	7.467	0.012	0.567	0.693	0.075	0.011	0.448
Birds	2.404	0.146	28.428	<0.001	2.336	0.134	<0.001	0.009	0.013

^a Variables analyzed by a median test.

pairwise comparisons: IL × EL $P = 0.017$, IL × IS $P = 0.024$, IL × ES $P = 0.022$, EL × IS $P = 0.136$, EL × ES $P = 0.602$, IS × ES $P = 0.821$).

On the contrary, both the abundance and richness of shade tolerant trees was significant or marginally significant higher in interior of large versus small remnants for all three forest strata considered (Table 3, Fig. 3). For the abundance of shade tolerant dominant trees, however, there was a significant interaction between treatments and blocks (Table 3). For understory trees, the composition of shade tolerant trees was also significantly different between interiors of large and small remnants (Fig. 4).

Considering the generalists, abundance was lower in interiors of large remnants compared to edges of small remnants for butterflies and small mammals (Table 2, Fig. 3). Similarly, the richness of generalist was lower in interiors of large remnants compared to edges of small remnants for butterflies, and was lower or tended to be lower in interiors of large remnants compared to edges of both small and large remnants for birds (Table 2, Fig. 3). For dominant trees, only the abundance of shade intolerant species was higher in interiors of small compared to interiors of large remnants, while for understory trees both the abundance and richness of shade intolerant species was higher in small remnants (Table 3, Fig. 3).

4. Discussion

The results of studies designed to investigate the effects of habitat or landscape modification on biodiversity depend strongly on

which taxonomic groups are sampled as well as on which metric is used to analyze assemblage responses (Barlow et al., 2007). With the exception of small mammals and ferns, the six remaining taxonomic groups considered in this study were shown to be among the seven best ecological indicators of coarse-scale changes in habitat integrity as suggested by a recent cross-taxa study on the cost-effectiveness of biodiversity surveys in tropical forests (Gardner et al., 2008, which did not sample ferns).

Although commonly used, the total number of species (richness) provides only a coarse summary of biodiversity responses as it does not include any information on abundance and does not distinguish between vulnerable and disturbance-adapted species (Laurance et al., 2006; Uehara-Prado et al., 2007). In fact, contrary to the assumption of models underlying most studies on the effects of habitat fragmentation, i.e. that species are equally affected, most taxonomic groups encompass a range of species-specific responses (Fischer and Lindenmayer, 2006). By dividing each taxon into forest specialist and generalist species we appear to have captured the major trends in variation in species response within taxonomic groups, with forest specialist and shade tolerant assemblages having predominantly negative responses, and generalist or shade intolerant assemblages having predominantly positive responses to habitat modification.

Thus, as reported recently by Barlow et al. (2007) from work in the Amazon, our results also suggest that accounting for the variability in species responses within taxonomic groups can reveal a higher level of cross-taxon congruence in disturbance responses.

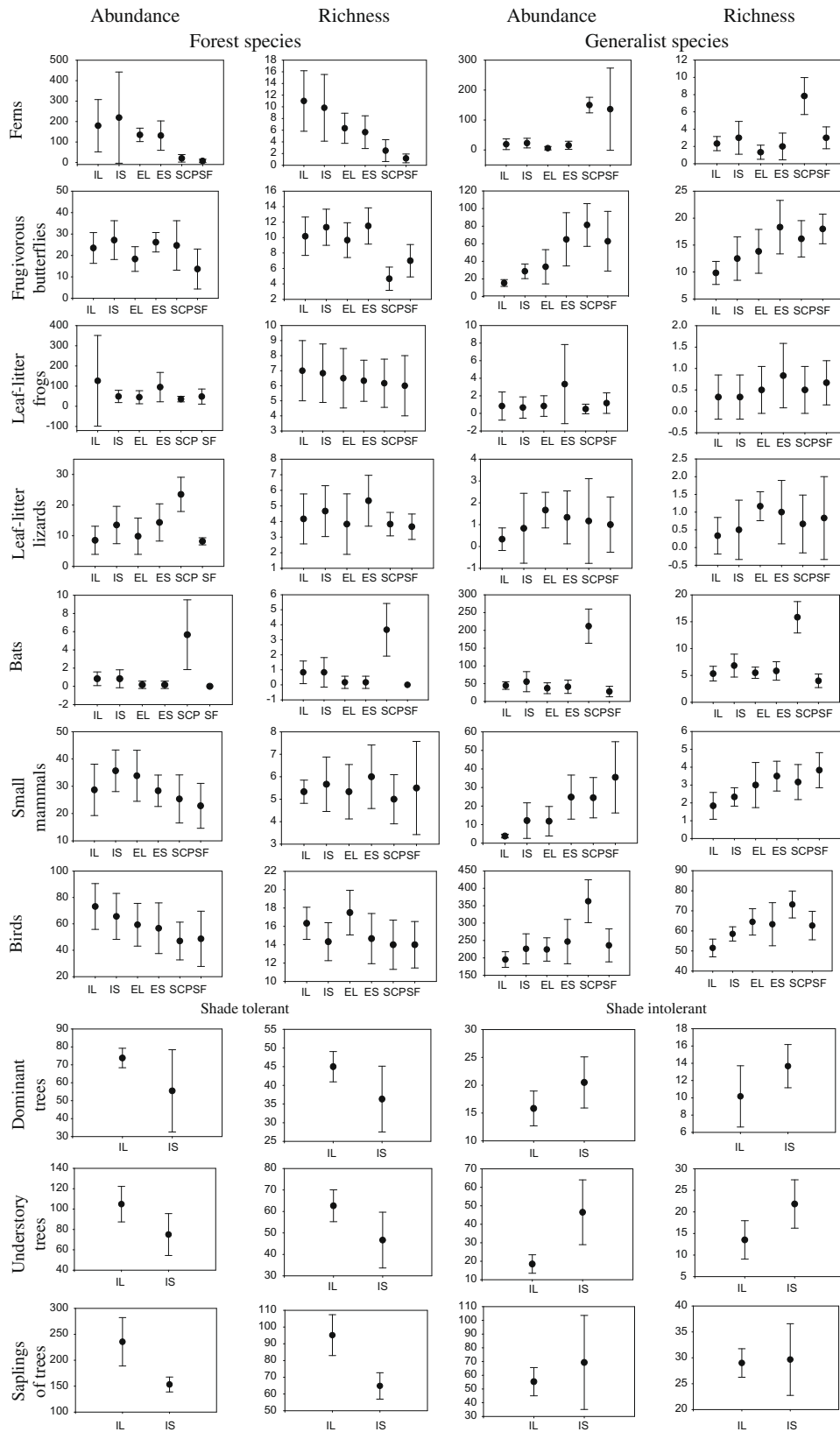


Fig. 3. Mean and standard deviation of the richness and abundance of forest and generalist species of ferns, frugivorous butterflies, leaf-litter frogs and lizards, bats, small mammals and birds, as well as shade tolerant and intolerant species of trees in three forest strata (dominant, understory and saplings) in interiors (IL) and edges (EL) of large remnants, interiors (IS) and edges (ES) of small remnants, shade cacao plantations (SCP) and second-growth forest (SF) in the Una region, South Bahia, Brazil.

Moreover, our results reinforce the findings of earlier studies by indicating that shade tolerance in tropical trees (Benitez-Malvido,

1998; Tabarelli et al., 1999; Metzger, 2000; Laurance et al., 2002), and the degree of endemism or size of geographical range,

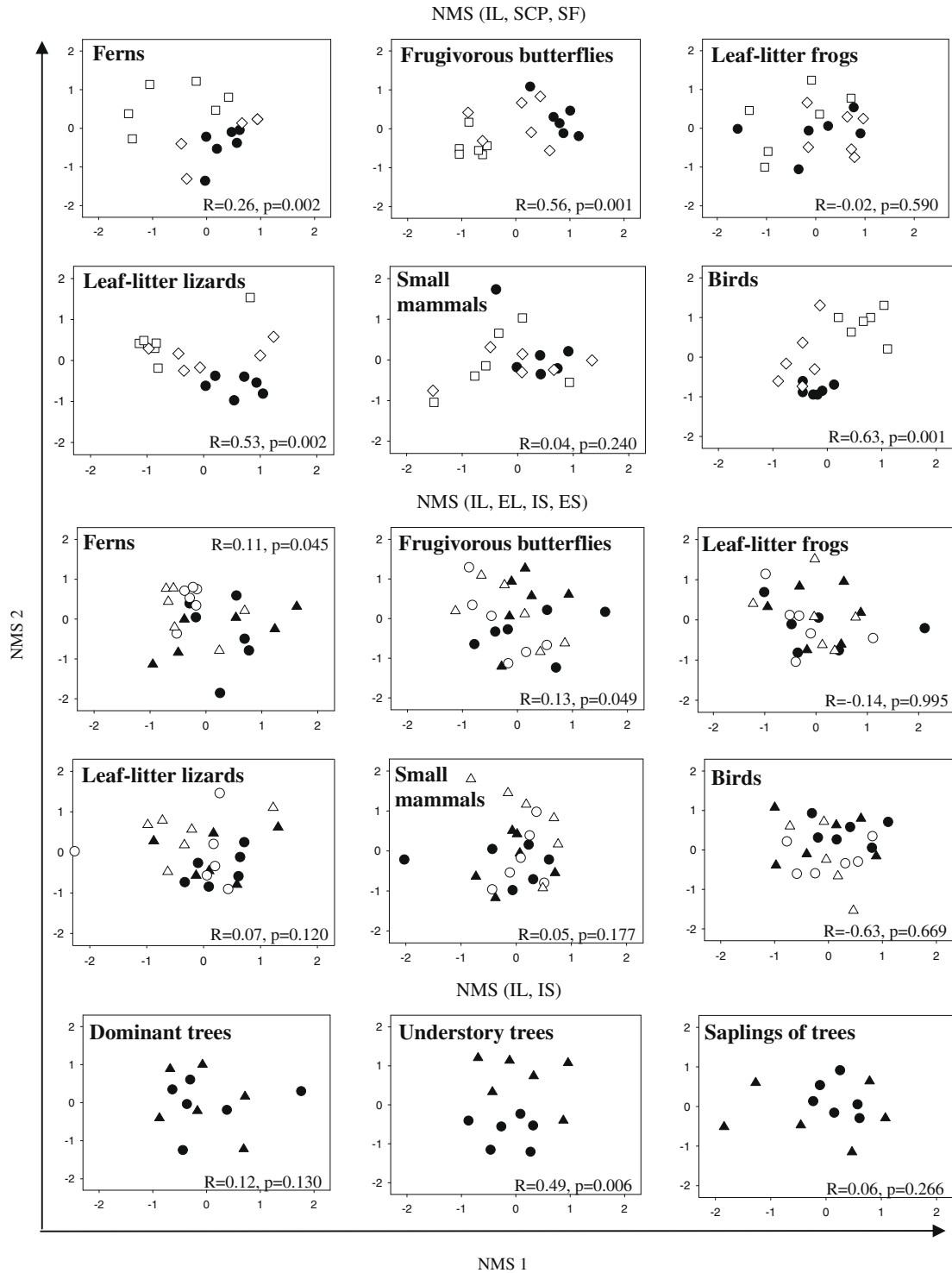


Fig. 4. Biplots of 2D NMS ordinations, and results from the global ANOSIM comparison, of the species-abundance matrices of forest species of ferns, frugivorous butterflies, leaf-litter frogs and lizards, small mammals and birds, as well as shade tolerant trees in three forest strata (dominant, understory and saplings) in the Una region, South Bahia, Brazil. Interiors (IL – black dot) and edges (EL – white dot) of large remnants, interiors (IS – black triangle) and edges (ES – white triangle) of small remnants, shade cacao plantations (SCP – white square) and second-growth forest (SF – white diamond).

for animals (Dunn and Romdal, 2005; Bobo et al., 2006; Fridley et al., 2007; Umetsu and Pardini, 2007), are good predictors of species vulnerability to habitat change. It is important to highlight, however, that although species categorized as generalists here may be less vulnerable to habitat or landscape modification, they are nevertheless all native taxa.

4.1. The value of second-growth forest and shade cacao plantations for biodiversity

Considering ferns and animal assemblages and all study sites within each habitat, both shade cacao plantations and second-growth forests harbored a higher number of species than the inte-

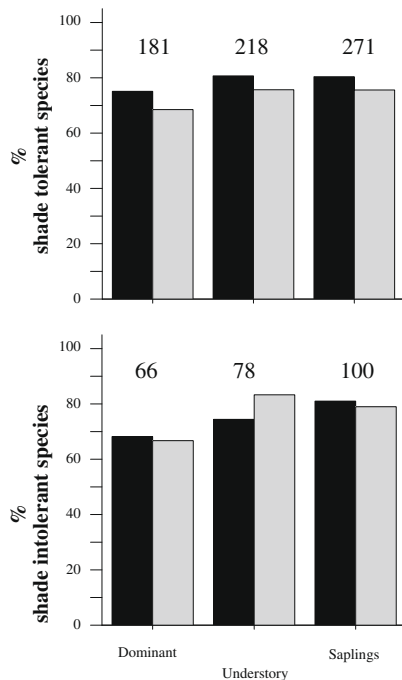


Fig. 5. Percentage and total number (over the bars) of species of shade tolerant and shade intolerant trees found in three different forest strata (dominant, understory and saplings) in interiors of large remnants (black bars) and interiors of small remnants (gray bars) in the Una region, South Bahia, Brazil.

rior of large mature forest remnants. Despite the fact that mature forests harbored, as expected, the highest number of forest specialists and lowest of generalists, this result shows that these altered habitats are able to harbor an extremely high diversity of native species in Una.

Among these habitats, shade cacao plantations harbored a higher number of both forest specialist and generalist species than second-growth forests. Although comparisons and generalizations are difficult to make given the paucity of information on the biodiversity value of tree plantations and second-growth forest in the neotropics (Gardner et al., 2007), it is interesting that many fewer primary forest species were observed in *Eucalyptus* plantations than in 12–18 year second-growth forest in the Amazon (Barlow et al., 2007). The value of shade cacao plantations is probably due to, on one hand, the maintenance of vertical stratification and the partial retention of native trees (Sambuichi and Haridasan, 2007), making these shade crops more structurally and floristically complex than tree monocultures (see Schroth et al., 2004), and, on the other hand, the culling of trees, promoting the colonization of open-area species that would avoid the dense vegetation that characterizes second-growth forest (Faria et al., 2006).

These structural and floristic differences between shade cacao plantations and second-growth forest seem to be correlated to the distinct value of these habitats among taxonomic groups. As we expected given the suppression of native vegetation in shade plantations, ferns were more impacted than animal assemblages within this habitat. Changes in vertical stratification can also have a strong influence on the disturbance responses of animal groups. For example, while bat abundance and richness are inversely correlated to understory density in Atlantic forest patches (Faria, 2002), the abundance and richness of non-volant small mammals are often positively correlated with understory density in neotropical forests (Malcolm, 1995; Pardini et al., 2005). Thus shade cacao plantations may facilitate the flight, maneuver or hunting of bats, while the dense understory of second-growth forests may offer

higher food availability to non-volant small mammals (Malcolm, 1997).

Nevertheless, when considering the composition of forest specialist assemblages (ferns and animal groups) per site, we found markedly consistent responses among taxonomic groups to habitat change. Across all groups except frogs and small mammals, the composition of forest specialists varied significantly among habitats, indicating that shade cacao plantations harbor the most distinct species assemblages compared to mature forests. Decreases in mean abundance (e.g. ferns, bats and birds) or richness (e.g. ferns, butterflies and bats) of forest specialists between mature forests and at least one of the matrix habitats was observed for fewer groups – indicating the importance of considering patterns of assemblage composition (Barlow et al., 2007). On the other hand, for most taxonomic groups (ferns, butterflies, bats, small mammals and birds) there was a significant increase in both mean abundance and richness of generalist assemblages from mature forests to one of the matrix habitats, indicating that the conversion of mature forest results mainly in a proliferation of disturbance-adapted native species.

Comparisons of our results with research from the same region that was conducted in a landscape dominated by shade cacao plantations and relatively few forest remnants (Faria et al., 2006, 2007) indicate, however, that the conservation value of tree plantations depends strongly on the proportion of mature forest remaining in the landscape, as suggest by Lindenmayer and Hobbs (2004). In fact, several studies have shown that the distance to remnant forest strongly influences biodiversity found in tree plantations (reviewed in Lindenmayer and Hobbs, 2004). Thus the best-case scenario for the value of second-growth forest or tree plantations seems to be the situation where small patches of altered habitats are surrounded by mature forest, avoiding the creation of large tracts of homogeneous altered habitats.

4.2. The effects of area reduction and edge proximity on biodiversity in mature forest remnants

Considering all taxonomic groups sampled in interiors and edges of small and large forest remnants (i.e. ferns and animal groups) and all study sites within each treatment, edge effects seem to be the most important process altering biodiversity in forest remnants in Una: the total number of forest specialist species decreased at edges compared to interiors irrespective of remnant size, while the number of generalist species gradually increased from the interior of large remnants to the edge of small remnants. However, once again taxonomic groups were differentially affected. The taxa for which both specialist and generalist species were poorly represented in second-growth forest (ferns and bats) were predominantly responsible for the loss of forest specialists at edges, while those taxa that exhibited relatively diverse assemblages in second-growth forest (butterflies, small mammals and birds) were predominantly responsible for the increase in generalist species. Edge effects in tropical forest remnants are known to increase the mortality of canopy trees (Laurance et al., 1998), inducing the proliferation of the understory vegetation (Laurance et al., 2001) and resulting in a vegetation structure at forest edges similar to that found in second-growth forests (Malcolm, 1994). The increase in generalist species, however, more than compensated for the decrease in forest specialists, as the total number of species was higher at the edges of small remnants.

In fact, when considering the variation in fern and animal assemblages among sites per treatment, almost all significant responses to edges and remnant size in our study region were associated with an increase in either mean richness or abundance of generalist assemblages. These effects on generalist species were more marked in smaller remnants, i.e. differences were found

Table 2

Results from the two-way ANOVAs (blocks and treatments: interiors (IL) and edges (EL) of large remnants and interiors (IS) and edges (ES) of small remnants) and *a posteriori* comparisons (Tukey test) for the richness and abundance of forest and generalist species of ferns, frugivorous butterflies, leaf-litter frogs and lizards, bats, small mammals and birds in the Una region, South Bahia, Brazil.

	Block		Treatment		Interaction		Tukey test					
	F	P	F	P	F	P	IL/EL	IL/IS	IL/ES	EL/IS	EL/ES	IS/ES
<i>Forest species</i>												
Abundance												
Ferns	0.363	0.703	0.197	0.896	1.787	0.185						
Butterflies	0.800	0.472	1.554	0.252	0.319	0.915						
Frogs	4.655	0.032	1.382	0.296	1.715	0.201						
Lizards	1.373	0.290	2.807	0.085	3.942	0.021						
Bats	0.750	0.493	1.778	0.205	0.861	0.549						
Small mammals	0.691	0.520	1.056	0.404	0.652	0.689						
Birds	11.378	0.002	2.069	0.158	0.776	0.604						
Richness												
Ferns	2.251	0.148	2.232	0.137	0.617	0.714						
Butterflies	0.143	0.868	0.585	0.636	0.218	0.964						
Frogs	1.274	0.315	0.215	0.884	1.941	0.155						
Lizards	1.350	0.296	1.022	0.417	1.439	0.278						
Bats	0.750	0.493	1.778	0.205	0.861	0.549						
Small mammals	0.667	0.531	0.611	0.621	2.111	0.128						
Birds	3.033	0.086	2.566	0.103	0.355	0.894						
<i>Generalist species</i>												
Abundance												
Ferns	1.105	0.363	1.251	0.335	0.230	0.959						
Butterflies	0.007	0.993	7.835	0.004	0.229	0.959	0.124	0.194	0.002	0.992	0.129	0.081
Frogs	0.074	0.929	1.341	0.307	0.892	0.530						
Lizards	0.838	0.456	1.324	0.312	0.405	0.862						
Bats	0.327	0.727	0.789	0.523	0.570	0.747						
Small mammals	0.472	0.635	5.549	0.013	0.210	0.967	0.276	0.232	0.007	0.999	0.187	0.224
Birds	2.757	0.103	1.694	0.221	1.019	0.458						
Richness												
Ferns	0.437	0.656	1.083	0.393	0.146	0.986						
Butterflies	0.577	0.576	4.316	0.028	0.758	0.616	0.387	0.695	0.019	0.944	0.294	0.128
Frogs	3.500	0.063	1.333	0.310	1.500	0.259						
Lizards	0.857	0.449	1.619	0.237	0.476	0.814						
Bats	0.608	0.561	0.823	0.506	0.456	0.828						
Small mammals	0.500	0.619	2.974	0.074	0.244	0.953						
Birds	1.578	0.246	4.233	0.029	0.682	0.668	0.033	0.354	0.055	0.479	0.991	0.644

mainly between interiors of large remnants and edges of small remnants, as it would be expected if edge effects are more drastic in smaller remnants (Malcolm, 1994). By contrast mean abundance and richness of forest specialist assemblages were not affected by edge or area effects for any of the taxonomic groups and the differences in forest specialist composition were slight and observed just for ferns and butterflies, mainly between interiors and edges. However, several of the same taxonomic groups are known to be negatively affected by the size of remnants in more fragmented Atlantic forest landscapes (e.g. Ribon et al., 2003; Gorresen and Willig, 2004; Pardini et al., 2005; Becker et al., 2007; Uehara-Prado et al., 2007; Metzger et al., 2009; Vieira et al., 2009), suggesting that, given the amount of remaining forest and/or the relative suitability of the matrix habitats, most populations of forest specialists are not critically isolated in the Una region.

The only taxonomic group for which there was a clear response between the interior of large and small remnants was trees. Considering all sites per treatment, the richness of shade tolerant species decreased in all forest strata, and that of shade intolerant species increased in the understory, from large to small forest remnants. Indeed, considering the variation among sites per treatment, not only mean richness and abundance of shade intolerant trees in the dominant and understory strata increased, but, more importantly, mean richness and abundance of tolerant trees decreased in all forest strata from large to small remnants. Similar drastic alterations in tree communities have been found elsewhere in the Atlantic forest (Tabarelli et al., 1999; Oliveira et al., 2004; Lopes

et al., 2009) and in Amazonian fragments (Laurance et al., 2006; Michalski et al., 2007), and have been associated with a synergetic interaction of different factors, including deeply-penetrating edge-induced tree mortality (Laurance et al., 1998), increased incidence of fire and logging in fragmented areas (Tabarelli et al., 2004; Laurance et al., 2006; Michalski et al., 2007), and the loss of pollinators or dispersers (Silva and Tabarelli, 2000; Tabarelli et al., 2004; Laurance et al., 2006; Lopes et al., 2009). The relative importance of these different factors is difficult to assess as both the intensity of edge effects (Malcolm, 1994) and the frequency of cryptic disturbances such as logging, hunting or fire are all likely to be higher in small versus large patches (Laurance, 2004). Nevertheless, our results are congruent with those found in experimental fragments in the Amazon where a rapid and drastic effect of fragmentation has been found on tree assemblages, suggesting that despite being long-lived and requiring small areas for survival, tropical trees are probably more vulnerable to fragmentation than most animal groups (Laurance et al., 2006).

Two lines of evidence suggest that alterations in tree assemblages in Una may be even more pronounced in the future promoting cascading effects on other groups. Observed changes in tree assemblages within smaller remnants appeared to be more drastic among understory trees, for which we observed changes in mean abundance, richness and composition of shade tolerant, and mean abundance and richness of shade intolerant species. In contrast no differences were found in the composition of shade tolerant or mean richness of shade intolerant species among the dominant

Table 3
Results from the two-way ANOVAs (blocks and treatments: interiors of large remnants – IL and interiors of small remnants – IS) for the richness and abundance of shade tolerant and shade intolerant trees found in three different forest strata (dominant, understory and saplings) in the Una region, South Bahia, Brazil.

	Block		Treatment		Interaction	
	F	P	F	P	F	P
<i>Shade tolerant</i>						
Abundance						
Dominant	0.661	0.550	9.763	0.020	5.949	0.038
Understory	1.221	0.359	7.195	0.036	0.669	0.547
Saplings	0.500	0.630	24.000	0.003	0.389	0.694
Richness						
Dominant	1.793	0.245	6.090	0.049	1.550	0.287
Understory	0.297	0.753	4.897	0.069	0.269	0.773
Saplings	0.032	0.969	18.651	0.005	0.541	0.608
<i>Shade intolerant</i>						
Abundance						
Dominant	2.984	0.126	6.426	0.044	1.607	0.276
Understory	1.164	0.374	32.507	0.001	5.104	0.051
Saplings	8.313	0.019	0.690	0.438	0.342	0.724
Richness						
Dominant	1.523	0.292	3.973	0.093	0.568	0.595
Understory	0.079	0.925	10.331	0.018	3.277	0.109
Saplings	5.614	0.042	0.091	0.773	0.841	0.476

trees. Hunting pressure in Una is high and several large mammals are extremely rare or locally extinct probably due to over hunting (R. Pardini and G.S. Rodrigues, unpublished data). Given the importance of some of these animals as seed predators and dispersers in tropical forests, it is likely that their demise provides one of the explanations for the already observed pattern of impoverishment of tree assemblages, as well as will exacerbate alterations in tree communities in the long run (Cramer et al., 2007; Wright et al., 2007).

4.3. Implications for conservation

In an Atlantic forest landscape dominated by mature forest partly surrounded by altered, but forested habitats, shade cacao plantations and second-growth forest harbored rich assemblages of multiple taxa, which encompassed part of the forest specialist species and generalist native species that proliferate in those altered habitats. Moreover, a positive effect on the generalist assemblages was the main alteration observed in the remaining mature forest patches for most groups, excepting trees. These results reflect the fact that native species vary in their response to habitat and landscape modification, and are in agreement with the idea that landscape heterogeneity, i.e. the number of habitat types, is an important process in determining patterns of biodiversity by increasing the availability of different resources in space and time (Benton et al., 2003). In fact, models underlying the study and management of altered landscapes that take into account the variability in taxon-wide and individual species responses lead to conservation guidelines of increasing landscape heterogeneity, while those that assume that all species are equally and negatively affected lead to strategies of preserving large tracts of native habitats (Fischer and Lindenmayer, 2006; Lindenmayer et al., 2006).

Nevertheless, comparisons with studies carried out in more fragmented Atlantic forest landscapes corroborate the fact that the amount of remaining native forest is important in determining the fate of forest specialist species, not only in forest remnants (Andrén, 1994; Metzger and Décamps, 1997; Radford et al., 2005) but also in other habitats within the landscape (Lindenmayer and Hobbs, 2004). Thus our results strongly suggest that productive tropical landscapes can be managed to maintain an appreciable component of native biodiversity by avoiding the creation of large

tracts of homogeneous converted land. Achieving this goal within Brazil could be at least partly accomplished simply by ensuring compliance with the federal Forest Code (Código Florestal), which states that each property should maintain a proportion (varying from 20% to 80%) of land covered by native habitats.

Our results emphasize the finding that tropical trees are likely to be the most vulnerable species group to landscape modification (Laurance et al., 2006). Strong and probably long-standing alterations in species assemblages occur rapidly, even with low levels of deforestation, probably as a result of multiple factors that are exacerbated by fragmentation such as edge effects, fire, logging and hunting (Silva and Tabarelli, 2000; Tabarelli et al., 2004; Laurance et al., 2006; Michalski et al., 2007; Lopes et al., 2009). We therefore recommend that in order to promote the long-term persistence of biodiversity in anthropogenic tropical landscapes particular attention should be given to the development of techniques that avoid the use of fires and minimize edge effects, as well as the control of illegal logging and hunting.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2009.02.010](https://doi.org/10.1016/j.biocon.2009.02.010).

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