

# The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape

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## Abstract

Using the abundance and distribution of small mammals at 26 sites in an Atlantic forest landscape, we investigated how species abundance and alpha and beta diversity are affected by fragment size and the presence of corridors. To account for the variability in forest structure among fragments, we described and minimized the influence of foliage density and stratification on small mammal data. Sites were distributed among three categories of fragment size and in continuous forest. For small and medium-sized categories, we considered isolated fragments and fragments connected by corridors to larger remnants. Small mammal abundance and alpha and beta diversity were regressed against site scores from the first axis of a Principal Component Analysis on forest structure variables. Residuals were used in analyses of variance to compare fragment size and connectivity categories. Forest structure influenced total abundance and abundance of some species individually, but not the diversity of small mammal communities. Total abundance and alpha diversity were lower in small and medium-sized fragments than in large fragments and continuous forest, and in isolated compared to connected fragments. Three species were less common, but none was more abundant in smaller fragments. At least one species was more abundant in connected compared to isolated fragments. Beta diversity showed an opposite relationship to fragment size and corridors, increasing in small and isolated fragments. Results highlight the importance of secondary forest for the conservation of tropical fauna, the hyper-dynamism of small isolated fragments and the potential of corridors to buffer habitat fragmentation effects in tropical landscapes.

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**Keywords:** Habitat loss and fragmentation; Corridors; Connectivity; Alpha and beta diversity; Forest structure; Hyper-dynamism

## 1. Introduction

The negative consequences of habitat loss and fragmentation to different aspects of biodiversity have been shown by a large number of theoretical and empirical

studies, in different environments, and for a large array of taxa (Fahrig, 2003). By decreasing population size and thus increasing the influence of stochastic processes, habitat loss and fragmentation should increase extinction rates, leading to a decrease in alpha diversity in remnants (Wilcox and Murphy, 1985) and an increase in beta diversity among them (Harrison, 1997; Loreau, 2000; Chase, 2003). Although species loss has been observed for different taxa in fragmented tropical

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landscapes (Laurance and Bierregaard, 1997), few studies focused on the increase in spatial variability in community composition among fragments (Harrison, 1997; Gilbert et al., 1998).

Moreover, recent studies have brought to light the synergism between habitat fragmentation and a series of impacts induced by human activities in altered landscapes (Laurance and Cochrane, 2001). In tropical forests in particular, forest structure, an important factor determining the occurrence of species and the structure of animal communities (Tews et al., 2004), is drastically altered in human landscapes by edge effects, selective logging, fire and the regeneration process (Malcolm, 1994; Malcolm and Ray, 2000; Cochrane, 2001; DeWalt et al., 2003).

On the other hand, landscape elements that enhance functional connectivity among fragments, i.e., which increase the flow of individuals or genes, should favor recolonization or immigration rates and decrease local extinctions through the rescue effect (Brown and Kodric-Brown, 1977). Corridors are an evident aspect of the degree of structural connectivity among fragments, representing a clear and attainable strategy for the management of fragmented landscapes. For this reason, a number of studies have tested the effectiveness of corridors (Simberloff et al., 1992; Beier and Noss, 1998). Corridors may increase movement of individuals (Gonzalez et al., 1998; Haddad, 1999; Mech and Hallett, 2001), gene flow (Aars and Ims, 1999; Hale et al., 2001; Mech and Hallett, 2001) and population size (Dunning et al., 1995; Haddad and Baum, 1999; Uezu et al., *in press*), and may facilitate animal–plant interactions (Tewksbury et al., 2002; Orrock et al., 2003). Few studies, however, focused on the effects of corridors on the composition, richness (alpha diversity) and spatial variability (beta diversity) of communities (Beier and Noss, 1998).

The Brazilian Atlantic forest is one of the richest but also most endangered tropical forests in the world (Myers et al., 2000). Covering less than 8% of its original distribution, conservation strategies for the Atlantic forest depend on information on how biodiversity is maintained and affected in the remaining small and altered patches, and on information to help establish restoration plans. Small mammals, rodents and marsupials, may be considered a good group to help answer this type of question. They play an important ecological role in the Atlantic forest, influencing forest regeneration through the differential predation on seeds and seedlings (Pizo, 1997; Vieira et al., 2003a) and the dispersal of seeds (Grelle and Garcia, 1999; Vieira and Izar, 1999; Pimentel and Tabarelli, 2004). They also represent the most diverse ecological group of mammals in the Atlantic forest, where more than 90 species are found, of which around 43 are endemic (Fonseca et al., 1996).

Despite the reduced number of studies that focused on the effects of the long-standing fragmentation on Atlantic forest small mammals (Fonseca and Robinson, 1990; Pires et al., 2002; Castro and Fernandez, 2004; Pardini, 2004), there are good indications that these animals clearly respond to habitat and landscape alterations. Atlantic and Amazonian small mammals occupy a series of habitats that retain a forest structure, including secondary forest (Stallings, 1989; Fonseca and Robinson, 1990; Pardini, 2004), shade cocoa plantations (Pardini, 2004), linear corridors (Lima and Gascon, 1999) and forest edges (Malcolm, 1997a; Pardini, 2004). The abundance of several species, however, is affected by foliage density and stratification (Malcolm, 1995; Gentile and Fernandez, 1999; Pardini, 2001; Grelle, 2003). Some of the species that are found mainly on the canopy as well as some of those that occupy the ground level decrease in abundance, while those found predominantly on the understory increase in abundance, in more disturbed or younger forest, where the understory is denser and the canopy is more open (Malcolm, 1995; Pardini, 2001, 2004; Vieira et al., 2003b). With few exceptions, however, the great majority of Atlantic forest small mammals do not occur in natural or anthropogenic open habitats (Stallings, 1989; Stevens and Husband, 1998; Feliciano et al., 2002), and the rates of movement of individuals among Atlantic forest fragments surrounded by open fields are low (Pires et al., 2002), leading to extinctions in small fragments (Castro and Fernandez, 2004).

Using the abundance and distribution of small mammals in 26 sites of an Atlantic forest landscape, we investigated how species abundance and alpha and beta diversity are affected by fragment size and the presence of corridors. To account for the variability in forest structure among fragments, we described and minimized the influence of foliage density and stratification on small mammal data.

## 2. Methods

### 2.1. Study area

Our study was carried out in Caucaia do Alto, located in the Cotia and Ibiúna municipalities, State of São Paulo, Brazil, in a continuous forest and in a fragmented landscape (Fig. 1). The altitude in the region varies from 850 to 1100 m and the relief is characterized by denudation, convex hills and inclinations of more than 15% (Ross and Moroz, 1997). Mean maximum temperature is 27 °C and mean minimum temperature is 11 °C. Rainfall is around 1300–1400 mm/year and it is seasonally variable, with the driest and coldest months between April and August. The vegetation in the region is a transition between the coastal Atlantic rain forest

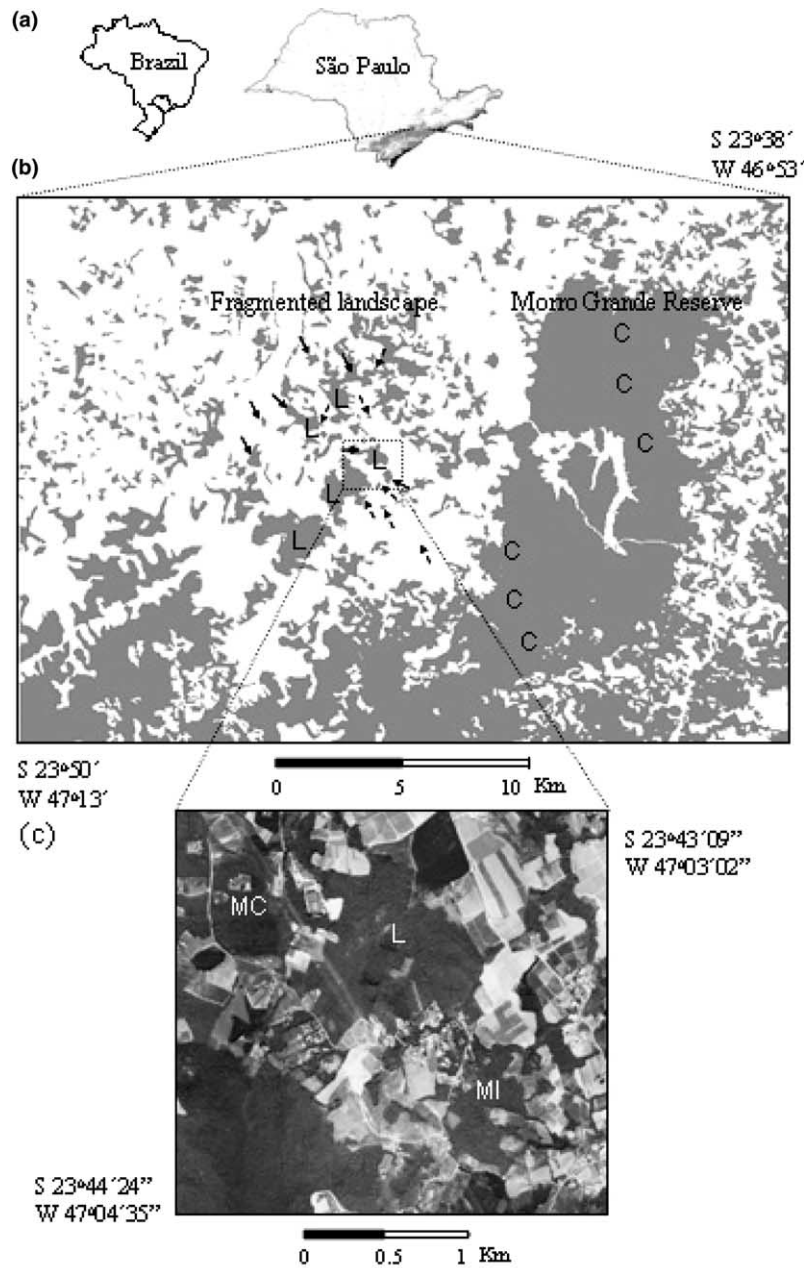


Fig. 1. (a) Map of the State of São Paulo, Brazil, showing the distribution of current remnants of Atlantic Forest and the location of the Caucaia do Alto region; (b) distribution of forest remnants in Caucaia do Alto and the position of the 26 study sites: C, control sites; L, large fragments; arrow, medium-sized fragments; and dashed arrow, small fragments; (c) Aerial photograph showing one large fragment (L), one medium-sized isolated fragment (MI) and one medium-sized fragment connected by a corridor to the large one (MC).

and the Atlantic semi-deciduous forest, being classified as “Lower Montane Atlantic Rain Forest” (Oliveira-Filho and Fontes, 2000).

The continuous forest is the Morro Grande Reserve, which comprises 9400 ha of secondary and mature forest. In its southern limits, the reserve is connected to other large forested areas (Fig. 1). The fragmented landscape extends southwestwards from the reserve and is dominated by open habitats, which cover 58% of the landscape (agricultural fields – 33%, areas with rural

buildings or urban areas –15%, and native vegetation in early stages of regeneration –10%). Native forests (e.g., secondary vegetation) cover 31% of the landscape, and pine and eucalyptus plantations, 7%. The study region was chosen because of its homogeneity in terms of type of forest, relief, altitude and climate, the existence of a continuous area composed mainly of secondary forest comparable to that of fragments and the relative low amount of remaining forest and of forested matrix habitats in the fragmented landscape.

## 2.2. Study sites

All sites were located in secondary forest from 50 to 80 years old, except three sites in the reserve located in mature forest. Selection of study sites was performed as follows. To assure a large range of fragment size, we selected the five largest patches in the fragmented landscape (>50 ha). Among smaller fragments, we systematically selected sites based on the presence/absence of corridors to large fragments (corridors were of native vegetation, in most cases mainly of secondary forest, and varied from 25 to 100 m in width), fragment size considering two categories (small – <5 ha, and medium-sized – 10–50 ha), and distance to large fragments (corridor length varied from 37 to 1071 m and isolated fragments covered approximately the same range of distance to large fragments, i.e., 125–1955 m between the limits of the secondary forests of the two fragments, Fig. 1). In continuous forest, we randomly selected six sites at least 2.2 km apart to avoid differences in the distance between sites among different fragment categories. Mean distance between one site and the nearest surveyed neighbor was 1398 m (SD = 769, range = 491 to 3217) and was not significantly different among fragment categories (ANOVA,  $F_{5, 20} = 0.786$ ,  $p = 0.572$ ). Thus, in order to avoid a strong spatial segregation among sites from different categories (Fig. 1) and prevent initial or inherent variability among samples to invalidate results (Hurlbert, 1984), we systematically selected sites in fragments and randomly spaced out sites in the continuous landscape.

Because landowners' permission was not always obtained and highly disturbed fragments were avoided, we chose to maximize the number of replicates when possible at the expense of a complete even distribution of replicates among categories. In total, we studied 26 sites: six continuous forest sites, five large fragments, four medium-sized connected fragments, four medium-sized isolated fragments, four small connected fragments and three small isolated fragments (Fig. 1).

## 2.3. Data collection

We used a standardized sampling protocol in each of the 26 sites, using the same type, number and arrangement of traps and sampling the same area for the same number of days, regardless of the size of the fragment. Unlike protocols in which an equivalent proportion of the area of the fragments is sampled, this approach allows for direct comparison of results and minimizes the chance that differences in habitat heterogeneity affect comparisons among fragments. At each site, we set a 100-m sequence of 11 pitfall traps (60 L) 10 m from each other and connected by a 500-mm high plastic fence. Sequences of large pitfall traps are effective in capturing not only terrestrial, but also scansorial and arboreal

small mammal species (Lyra-Jorge and Pivello, 2001; Hice and Schmidly, 2002; Pardini and Umetsu, in press), capturing a larger number of species (Pardini and Umetsu, in press) and individuals (Lyra-Jorge and Pivello, 2001; Pardini and Umetsu, in press) than conventional live traps in Neotropical habitats. Because our main objective was to investigate spatial and not temporal patterns, we concentrated a large sampling effort during summer (wet season), the time of the year when capture success is higher for pitfall traps (capture rates are very low during the dry season, Hice and Schmidly, 2002). Adding different sampling periods could obscure spatial patterns of diversity, since small isolated fragments are probably hyper-dynamic (Laurance, 2002) and may present a high turnover of species (Hinsley et al., 1995; Schmiegelow et al., 1997; Terborgh et al., 1997). Two capture sessions of eight days each were conducted during January and February 2002, totaling sixteen days of sampling for each of the 26 sites. Thirteen sites were sampled at the same time to prevent temporal fluctuations from influencing the comparison among sites. Animals were marked with numbered tags at first capture (Fish and small animal tag-size 1 – National Band and Tag Co., Newport, Kentucky).

Forest structure was described by measuring foliage density and stratification, important features determining forest quality for rain forest small mammals. Foliage density and stratification are good indicators of forest regeneration stage (DeWalt et al., 2003) and of level of forest disturbance, such as edge effect intensity (Malcolm, 1994) and selective logging (Malcolm and Ray, 2000). They are correlated with arthropod biomass (Malcolm, 1997b), understory fruit availability (DeWalt et al., 2003) and the abundance of several Neotropical small mammal species (Malcolm, 1995; Gentile and Fernandez, 1999; Pardini, 2001; Vieira et al., 2003b). At each site, 12 stations spaced every 15 m were set in each of two parallel lines of 165 m in length and 20 m apart from each other, which overlay the pitfall sequence. At each station, we used a 4-meter pole to help establish an imaginary vertical column of 150 mm in diameter. The height of the inferior and superior limits of all foliage which stretched along the imaginary column was measured in the field and afterwards used to calculate the length in meters occupied by foliage in five strata (0–1, 1–5, 5–10, 10–15, >15 m). For each site, we calculated the mean of foliage length in each stratum considering the 24 sampling stations. This is a modification of the method described in Malcolm (1995).

## 2.4. Data analysis

Since the sampled area and capture protocol were the same for all sites, the number of captured individuals was used as an index of relative abundance (Slade and Blair, 2000). For each site, we calculated abundance



(number of individuals), alpha diversity (number of species) and beta diversity. We calculated beta diversity for pairs of sites, considering each site in relation to all others from the same category of size and connectivity. To obtain one value for each site, we calculated the mean of the paired beta values. This approach is better than comparing the composition of the focal site with that of the entire set of sites of the same category of size and connectivity, which results in the comparison of areas of different size. This is undesirable especially when the number of sites per category is unequal (Koleff et al., 2003). We used two metrics, Beta w calculated as  $a + b + c / [(2a + b + c) / 2]$  (Whittaker, 1960) and Beta sim calculated as  $\min(b, c) / [\min(b, c) + a]$  (Lennon et al., 2001), where  $a$  is the total number of species which are found in both sites,  $b$  is the number of species which are present in the other site but not in the focal site, while  $c$  is the number present in the focal site but not in the other site. Beta w is considered a 'broad sense' beta diversity metric which incorporates differences in composition attributable to species richness gradients, and Beta sim is considered a 'narrow sense' metric that focuses on compositional differences independent of such gradients (Koleff et al., 2003). For each fragment category, we also calculated gamma diversity (total number of species considering all spatial replicates). Because the number of replicates was unequal among fragment categories, gamma diversity was calculated using the non-parametric estimator Jackknife 2.

A Principal Component Analysis was performed using the foliage density for five forest strata in the 26 sites in a correlation matrix (centered and standardized per species) using the package CANOCO for Windows 4.0 (ter Braak and Smilauer, 1998). Small mammal total abundance, species abundance and alpha diversity were regressed against the 26 sites scores of the first axis of the Principal Component Analysis. Beta diversity, which is a measure of community composition variability among sites, was regressed against a measure of forest structure dissimilarity calculated as the linear distance between site scores on the first axis of the Principal Component Analysis. After translating the scale (the smallest score was set to zero), we calculated the mean of the modular differences between the score of each site and the scores of all other sites in the same category of size and connectivity.

We used one-way analysis of variance (one-way ANOVA) to compare total abundance, species abundance and alpha and beta diversity among the four categories of size (continuous forest and large, medium-sized isolated and small isolated fragments, totaling 18 sites). Tukey's pairwise comparisons were run a posteriori when significant variations were found. To test the effects of corridors, we used two-way analysis of variance (two-way ANOVA), considering fragment size (medium-sized

and small) and presence/absence of corridors (connected and isolated) as factors (15 sites).

To minimize the influence of forest structure differences among sites, analyses of variance were run using the residuals from the regressions of small mammal variables against the first axis of the Principal Component Analysis described above. Homogeneity of variance among categories was tested using Bartlett's test and, when necessary, data were rank-transformed. Variation in species abundance was analyzed statistically only for species captured in more than 20% of the sites and for which more than 10 individuals were captured in the group of sites considered in each of the analysis described above. All analyses were run in the package SYSTAT 5.03 for Windows (SYSTAT, 1993).

### 3. Results

As a result of the total sampling effort, 915 individuals belonging to 21 species (7 marsupials and 14 rodents) were captured in Caucaia. No individual was captured in more than one site. The most common species were the terrestrial rodents *Oligoryzomys nigripes* (172 individuals, 25 sites), *Akodon montensis* (102, 21), *Delomys sublineatus* (75, 22), *Oryzomys russatus* (35, 9), *Bucepattersonius* aff. *iheringi* (29, 14) and *Thaptomys nigrita* (22, 6); the terrestrial marsupial *Monodelphis americana* (43, 16); the scansorial rodent *Oryzomys angouya* (72, 18); the scansorial marsupials *Marmosops incanus* (165, 25) and *Didelphis aurita* (64, 21); and the arboreal marsupial *Gracilinanus microtarsus* (18, 9). Fewer than 20 individuals were captured of the terrestrial rodents *Oxy-mycterus* cf. *dasitrychus*, *Calomys tener*, *Cavia aperea*, *Bibimys labiosus* and *Nectomys squamipes*; the terrestrial marsupial *Monodelphis macae*; the scansorial marsupials *Philander frenata* and *Marmosops paulensis*; and the arboreal rodents *Juliomys pictipes* and *Phillomys nigripinus*.

With the exception of the rodents *C. tener*, *C. aperea*, *B. labiosus* and *N. squamipes*, all species were captured in control sites and are considered Atlantic forest species (Fonseca et al., 1996). While *C. tener* and *C. aperea* are more characteristic of open habitats, *B. labiosus* is a rare species whose habitat preference is not known and *N. squamipes* is a common Atlantic forest species which was not frequently captured because of its semi-aquatic habit.

#### 3.1. Forest structure

The first axis of the Principal Component Analysis explained 43.5% of the total variation in forest structure among the 26 sites. It represented a gradient of increasing foliage density in the lower stratum (descriptor score<sub>0-1 m</sub> = 0.850) and decreasing foliage density in

the higher strata (descriptor score<sub>10–15 m</sub> = -0.775, descriptor score<sub>>15m</sub> = -0.680), with forests in earlier stages of regeneration or subjected to higher levels of disturbance (lower canopy and denser understory) located on the right side of the axis.

Small mammal alpha diversity was not significantly related to the main gradient of vegetation variation among the 26 sites in Caucaia ( $R^2 = 0.000$ ,  $p = 0.522$ , Fig. 2). Small mammal beta diversity between one site and all others from the same category of size and connectivity was also not significantly influenced by vegetation structure dissimilarity between the same sites (Beta w -  $R^2 = 0.000$ ,  $p = 0.972$ , Beta sim -  $R^2 = 0.000$ ,  $p = 0.586$ , Fig. 2). On the other hand, small mammal total abundance was significantly related to the first axis of the Principal Component Analysis, increasing towards the forests in earlier stages of regeneration or subjected to higher levels of disturbance ( $R^2 = 0.159$ ,  $p = 0.025$ , Fig. 2).

Eleven species had more than 10 individuals captured and occurred in more than 20% of the 26 sites (Fig. 3). Among those, three rodents (*A. montensis*, *D. sublineatus* and *O. angouya*) were significantly more common, and one marsupial (*M. incanus*) tended to be more common, in forests in earlier stages of regeneration or subjected to higher levels of disturbance ( $R^2 = 0.300$ ,  $p = 0.002$ ;  $R^2 = 0.340$ ,  $p = 0.001$ ;  $R^2 = 0.304$ ,  $p = 0.002$ ,  $R^2 = 0.112$ ,  $p = 0.053$ , respectively). Alternatively, the

rodent *T. nigrita* was significantly more common in more preserved and mature forests ( $R^2 = 0.179$ ,  $p = 0.018$ ). The other six analyzed species did not present significant relationships with the variation in forest structure.

### 3.2. Fragment size and corridors

Small mammal total abundance and alpha diversity decreased with decreasing fragment size. Total abundance was significantly lower in medium-sized isolated fragments – and tended to be lower in small isolated fragments, compared to control sites (Fig. 4 and Table 1). Alpha diversity was significantly lower in medium-sized isolated fragments than in control sites and in small isolated fragments in comparison to large fragments and control sites (Fig. 4 and Table 1).

On the contrary, the two measures of beta diversity were higher in smaller fragments. Beta w was significantly higher in medium-sized and small isolated fragments than in large fragments and control sites and Beta sim was significantly higher in small isolated fragments than in medium-sized isolated fragments, large fragments and control sites (Fig. 4 and Table 1).

Eleven species had more than 10 individuals captured and occurred in more than 20% of the 18 sites located in continuous forest, large fragments and smaller isolated fragments (Fig. 5 and Table 1). Two of those (*O. russatus*

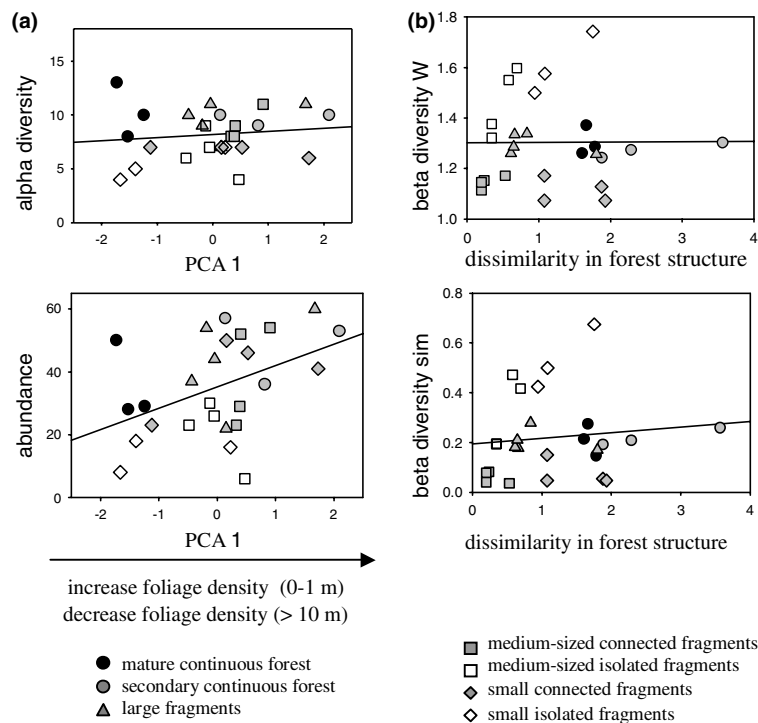


Fig. 2. Relationship of: (a) small mammal total abundance and alpha diversity with forest structure, summarized by site scores on the first axis of a Principal Component Analysis (PCA) on foliage density in five forest strata and (b) small mammal beta diversity and dissimilarity in forest structure between one site and all others from the same category, considering the 26 sites of Caucaia do Alto, Brazil.

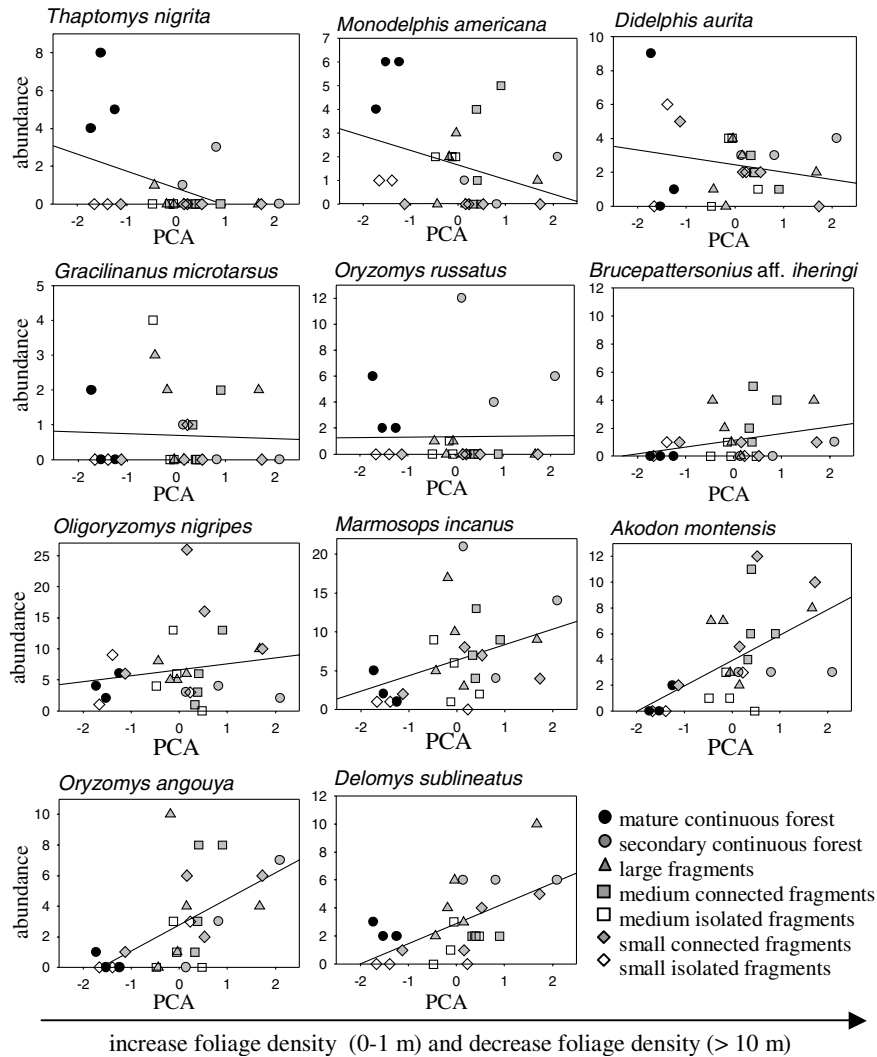


Fig. 3. Relationship of the abundance of small mammal species and forest structure, summarized by site scores on the first axis of a Principal Component Analysis (PCA) on foliage density in five forest strata, considering the 26 sites of Caucaia do Alto, Brazil.

and *T. nigrita*) were significantly less common in large, medium-sized and small fragments compared to control sites and *D. sublineatus* was significantly less common in medium-sized and small isolated fragments than in large fragments and control sites (Fig. 5 and Table 1). The abundance of *Brucepattersonius* aff. *iheringi* varied significantly among fragment size categories, but Tukey a posteriori pairwise comparisons revealed only marginal significant differences between control sites and large fragments (Fig. 5 and Table 1). The abundance of none of the analyzed species significantly increased with decreasing fragment size (Fig. 5 and Table 1).

Small mammal total abundance and alpha diversity were significantly higher in connected compared to isolated fragments (Fig. 4 and Table 2). Again, beta diversity showed an opposite relationship to that observed for alpha diversity: it was significantly lower in connected than in isolated fragments (Fig. 4 and Table 2). For none of these four variables, there were significant

differences between small and medium-sized fragments or significant interactions between size and connectivity (Fig. 4 and Table 2).

Eight species had more than 10 individuals captured and occurred in more than 20% of the 15 sites located in smaller isolated and connected fragments (Table 2). One of those (*A. montensis*) was significantly more common in connected than in isolated fragments (Fig. 5, Table 2). For *Brucepattersonius* aff. *iheringi*, there was a significant interaction between fragment size and the effect of corridors (Table 2). The abundance of this species was higher in connected compared to isolated fragments just when considering medium-sized fragments (Fig. 5). On the other hand, the abundance of *M. americana* did not vary significantly among connected and isolated fragments, but was significantly higher in medium-sized than in small fragments (Fig. 5 and Table 2). None of the analyzed species was more common in isolated than in connected fragments (Fig. 5 and Table 2).

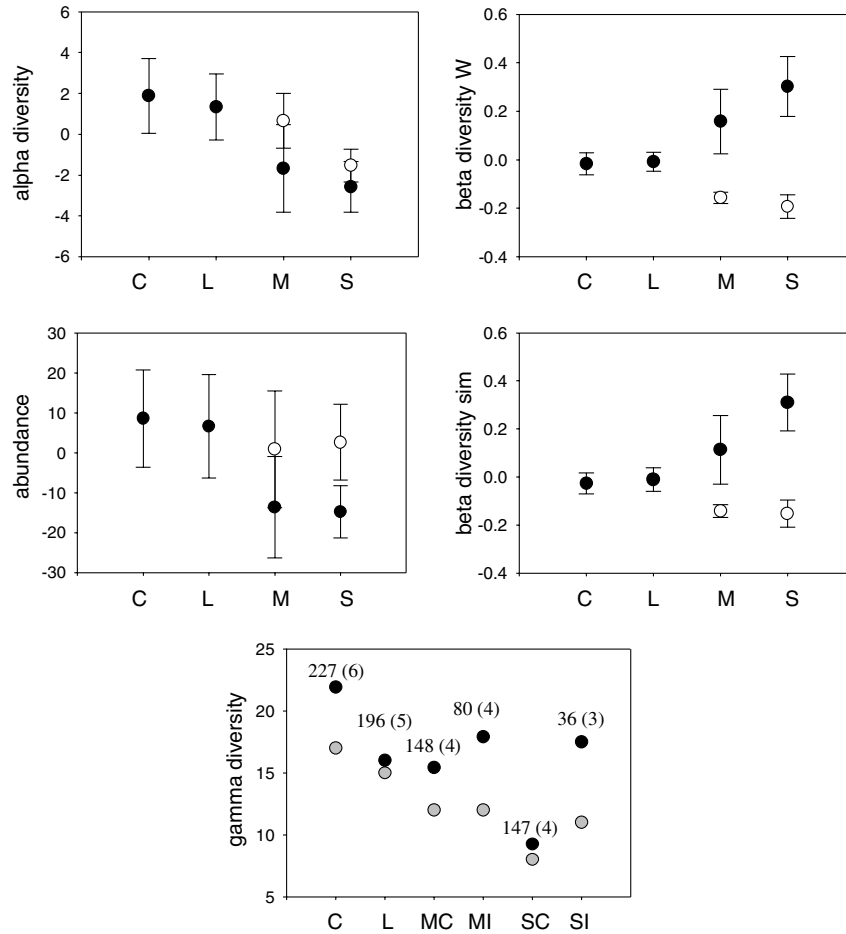


Fig. 4. Mean and standard deviation of small mammal abundance and alpha and beta diversity for the six fragment categories in Caucaia do Alto, Brazil, after excluding the effect of the first axis of a Principal Component Analysis on forest structure. C, control sites; L, large; M, medium-sized and S, small (black, isolated and white, connected). Gamma diversity is represented by Jackknife 2 estimated richness (black) and observed richness (gray) for the total number of replicates (in parentheses) and total number of individuals captured per fragment category. SI, small isolated; SC, small connected; MI, medium-sized isolated and MC, medium-sized connected.

Table 1

Results from the analyses of variance (ANOVA) and Tukey's tests comparing species abundance, total abundance and alpha and beta diversity of small mammals among four classes of fragment size (C, control sites; L, large fragments; MI, medium-sized isolated fragments; and SI, small isolated fragments) in Caucaia do Alto (São Paulo, Brazil)

	ANOVA		Significance level of Tukey's test					
	F	p	C × L	C × MI	C × SI	L × MI	L × SI	MI × SI
<i>Marmosops incanus</i>	1.076	0.391						
<i>Oligoryzomys nigripes</i>	0.636	0.604						
<i>Delomys sublineatus</i>	6.199	0.007*	0.998	0.040*	0.044*	0.037*	0.041*	0.998
<i>Didelphis aurita</i>	0.220	0.881						
<i>Akodon montensis</i>	2.678	0.087						
<i>Oryzomys angouya</i>	0.672	0.584						
<i>Oryzomys russatus</i>	9.454	0.001*	0.003*	0.004*	0.012*	0.999	1	0.999
<i>Monodelphis americana</i>	3.179	0.057						
<i>Thaptomys nigrita</i>	11.893	<0.001*	0.015*	0.002*	0.001*	0.613	0.228	0.835
<i>Gracilinanus microtarsus</i>	0.683	0.577						
<i>Brucepattersonius aff. iheringi</i>	3.333	0.050*	0.055	1	0.902	0.089	0.358	0.916
Total abundance	4.829	0.016*	0.993	0.050*	0.063	0.097	0.109	0.999
Alpha diversity	6.461	0.006*	0.958	0.034*	0.015*	0.096	0.039*	0.906
Beta diversity w	12.445	<0.001*	0.999	0.029*	<0.001*	0.047*	0.001*	0.166
Beta diversity sim	11.627	<0.001*	0.991	0.109	<0.001*	0.196	0.001*	0.048*

\* p ≤ 0.05.



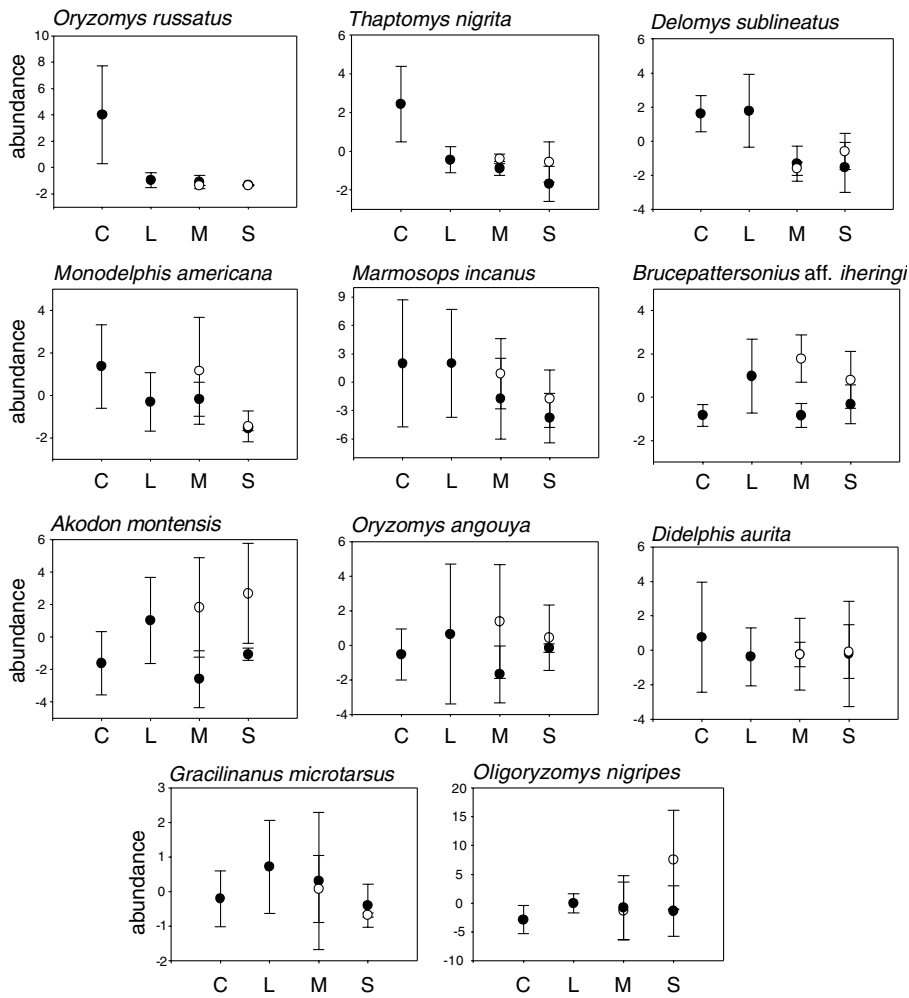


Fig. 5. Mean and standard deviation of the abundance of small mammal species for the six fragment categories in Caucaia do Alto, Brazil, after excluding the effect of the first axis of a Principal Component Analysis on forest structure. C, control sites; L, large fragments; M, medium-sized fragments and S, small fragments (black, isolated and white, connected).

Table 2

Results from the two-way analyses of variance considering the presence/absence of corridors and fragment size (small and medium-sized) for species abundance, total abundance and alpha and beta diversity of small mammals in Caucaia do Alto (São Paulo, Brazil)

	Corridors		Size		Interaction	
	F	p	F	p	F	p
<i>Marmosops incanus</i>	1.614	0.230	1.606	0.231	0.026	0.874
<i>Oligoryzomys nigripes</i>	1.676	0.222	1.645	0.226	2.120	0.173
<i>Delomys sublineatus</i>	0.364	0.558	0.566	0.468	1.339	0.272
<i>Didelphis aurita</i>	0.004	0.953	0.010	0.922	0.005	0.944
<i>Akodon montensis</i>	10.254	0.008*	0.863	0.373	0.066	0.802
<i>Oryzomys angouya</i>	1.621	0.229	0.552	0.473	0.281	0.606
<i>Monodelphis americana</i>	0.364	0.558	14.374	0.003*	0.099	0.759
<i>Brucepattersonius aff. iheringi</i>	3.840	0.076	1.987	0.186	5.243	0.043*
Total abundance	6.999	0.023*	0.002	0.965	0.058	0.814
Alpha diversity	4.835	0.050*	4.054	0.069	0.699	0.421
Beta diversity w	72.260	<0.001*	1.267	0.284	3.547	0.086
Beta diversity sim	51.817	<0.001*	3.447	0.090	4.360	0.061

\*  $p \leq 0.05$ .

Gamma diversity estimated by Jackknife 2 was higher for continuous forest, followed by medium-sized and small isolated fragments, despite the low number of individuals captured in these fragments (Fig. 4).

#### 4. Discussion

##### 4.1. Forest structure

Fragments in Caucaia presented a large variation in forest structure, which was associated with an increase in foliage density in the lower stratum and a decrease in foliage density in the higher strata of the forest. This gradient in the vertical stratification is observed not only among tropical forest chronosequences (Guariguata and Ostertag, 2001; Pardini, 2001; DeWalt et al., 2003), but also among tropical forests that have suffered different intensities of edge effects (Malcolm, 1994; Pardini, 2001) and of human disturbances such as selective logging (Malcolm and Ray, 2000).

For small mammals, this structural gradient may represent a gradient of forest quality. In general, earlier regeneration stages present higher productivity and higher proportion of biomass on leaves than on wood (Guariguata and Ostertag, 2001), probably offering higher food availability to small mammals, which feed mainly on fruits and arthropods. In fact, foliage density is positively related to arthropod biomass (Malcolm, 1997b) and the availability of fleshy fruits is higher in earlier regeneration stages (DeWalt et al., 2003). The increased abundance of small mammals in forests in earlier stages of regeneration or subjected to higher levels of disturbance in Caucaia is probably due to an increase in the productivity and availability of food to species not restricted by specific resources. The same relationship between the abundance of Neotropical small mammals and changes in the vertical structure of the forest was observed in the Amazon forest (Malcolm, 1995) and in the Atlantic forest (Vieira et al., 2003b).

Because of this, Neotropical small mammal species were considered to be adapted to secondary habitats, or to be highly resilient to changes in habitat structure (Malcolm, 1997a). As observed for other groups such as birds (Aleixo, 1999), however, the results from Caucaia suggest that there are some small mammal species clearly associated with mature Atlantic forest. This is the case for relatively common species such as *T. nigrita* and, possibly, *M. americana*, which increase in abundance in mature forest sites.

##### 4.2. Fragment size and corridors – small mammal abundance and alpha diversity

Regardless of the variation in forest structure, fragment size influenced not only small mammal total abun-

dance, but also small mammal diversity. Fragments smaller than 50 ha (small and medium-sized) structurally isolated from other forest tracts presented a small mammal community with fewer individuals and species than would be expected from their local forest structure, indicating that these fragments are below their carrying capacity.

On the contrary, previous studies in Neotropical forests found an increase in small mammal richness and/or total abundance with decreasing fragment size in Manaus, Amazonia (Malcolm, 1995) and in Una, South Bahia (Pardini, 2004). These increases were related to edge-induced vegetation changes in smaller fragments, which in both landscapes were of mature forest. Increased mortality rate of large trees due to an increased wind impact is the main cause of the altered vertical structure at edges in tropical remnants of mature forest (Malcolm, 1994; Laurance et al., 1998). Because of the small number of large trees characteristic of secondary forest, edge effects on forest structure are probably less intense in secondary remnants, like those sampled in Caucaia. Moreover, in Una and Manaus, the proportion of remaining habitat in the landscape is well above the theoretical threshold at which the importance of spatial configuration of remnants to species maintenance drastically increases (fragmentation threshold – Andr n, 1994; Fahrig, 1997; Develey and Metzger, in press), while this proportion in Caucaia (31%) is close to the threshold. The permeability of the matrix in both landscapes was also probably higher than in Caucaia, containing a larger proportion of altered habitats with a forested structure. Thus, the low proportion of forested habitats (both forest and forested habitats of the matrix) in Caucaia could explain the increase in the relative importance of fragment size in determining animal communities in comparison to previously studied landscapes.

Among species, the effect of fragment size reduction in Caucaia seems to be especially important to three terrestrial rodents (*O. russatus*, *T. nigrita* and *D. sublineatus*), which are the dominant rodent species in continuous forest sites representing 31% of the individuals captured there. The idea that these common terrestrial rodents are the small mammals most vulnerable to Atlantic forest fragmentation is supported by the sparse information in the literature. Community studies conducted in large forest tracts indicate that one of the most common small mammal species in continuous Atlantic forest is a terrestrial rodent from the genus *Oryzomys* (Bergallo, 1994; Bergallo and Magnusson, 1999; Vieira and Monteiro-Filho, 2003; Pardini, 2004). In small or altered Atlantic forest remnants, however, *Oryzomys* is not the dominant species or is not present (Stallings, 1989; Paglia et al., 1995; Stevens and Husband, 1998; Pires et al., 2002; Pardini, 2004). The few studies considering several Atlantic forest fragments in the same

landscape found that terrestrial forest-dwelling small mammals are the most vulnerable to forest fragmentation (Castro and Fernandez, 2004; Pardini, 2004) and rodents from the genera *Oryzomys* and *Thaptomys* are associated with the interior of large mature remnants decreasing in abundance in smaller remnants, edges or secondary forest and cocoa plantations (Pardini, 2004).

In agreement with several studies that have shown a positive effect of corridors on population density or size and on the rate of animal movement for an array of taxa (see Section 1), results from Caucaia showed that, regardless of the local forest structure, small mammal total abundance is significantly higher in connected than in isolated fragments. Corridors thus seem to be effective in increasing or facilitating the arrival of genes or individuals in small fragments, otherwise isolated from other forest tracts. However, with the small number of replicates considered in this study, the positive effects of corridors are significant for the abundance of one terrestrial rodent (*A. montensis*), although another four of the eight analyzed species (two marsupials – the terrestrial *M. americana* and the scansorial *M. paulensis*, and two rodents – the terrestrial *B. aff. iheringi* and the scansorial *O. angouya*) presented higher mean abundance in connected than in isolated patches (Fig. 5).

More importantly, our data support the idea that corridors increase species richness in tropical forest fragments. Connected forest fragments in Caucaia harbored a significantly higher number of small mammal species than isolated fragments. This increase in alpha diversity is expected to derive from the positive effects of corridors on the abundance or on population density or size and has been poorly tested (Beier and Noss, 1998). In tropical forests, most studies describe the presence of forest species in corridors, but do not evaluate the effects of corridors on animal communities in fragments (Lima and Gascon, 1999; Laurance and Laurance, 1999; Estrada et al., 2000; Estrada and Coates-Estrada, 2001). However, a positive effect of corridors on the richness of micro-arthropods in artificial landscapes (Gilbert et al., 1998), and on the richness of arboreal marsupials in an Australian fragmented landscape (Laurance, 1990), have already been shown.

#### 4.3. Fragment size and corridors – small mammal beta and gamma diversity

Beta diversity in Caucaia is higher in medium-sized and, specially, in small isolated fragments compared to large fragments and control sites, irrespective of the degree of dissimilarity in forest structure. As expected, decreasing fragment size increases spatial variability in community composition (Harrison, 1997). These results are congruent with the idea that fragmented landscapes are hyper-dynamic, i.e., present increased range and/or

frequency of the dynamics of most ecological processes (Laurance, 2002).

This hyper-dynamism would be related to two main factors: the higher vulnerability of small habitat portions, firstly, to stochastic processes and, secondly, to influences coming from the neighboring altered areas, i.e., to increased environmental heterogeneity (Laurance, 2002). In fact, several studies have found an increase in beta diversity associated with an increase in environmental heterogeneity caused by fragmentation (Didham et al., 1998; Lomolino and Perault, 2000; Pardini, 2004). However, this is one of the few empirical studies that has investigated and found support for the role of fragment size and isolation in increasing the spatial variability in community composition in fragmented landscapes.

It is noteworthy that from all 915 records of individuals in Caucaia only five are from species characteristic from open areas (*C. tener* and *C. aperea*), three of which occurred in large fragments, one in a medium-sized isolated fragment and one in a small isolated fragment. Thus, the higher variability in community composition among smaller fragments cannot be attributed to the arrival of opportunistic or generalist species. It is probably related to stochastic extinctions of small populations of forest-dwelling species in fragments.

In fact, eleven from the twelve forest-dwelling species present in more than one fragment (considering large and smaller isolated fragments) occurred in a higher proportion of the large than of the smaller isolated fragments. Moreover, the higher beta diversity in fragments is related to the fact that occurrences or absences were not observed in the same smaller isolated fragments for all species. In agreement with several studies that have shown variation in extinction proneness among species (Henle et al., 2004), including a long term demographic study for Atlantic forest small mammals (Castro and Fernandez, 2004), there was a large variation in the number of occurrences in smaller fragments among species in Caucaia.

Besides buffering the decrease in abundance and alpha diversity, corridors in Caucaia led to a decrease in beta diversity. Connected fragments presented lower beta diversity than isolated fragments, irrespective of forest structure dissimilarity. Theoretically, the increased influx of individuals or genes should raise the synchronicity of the dynamics among sub-populations from a meta-population (Earn et al., 2000) and the temporal stability in population size (Reddingius and den Boer, 1970; Roff, 1974), which in turn, should facilitate the increase in spatial homogeneity in community composition, i.e., decrease beta diversity.

Few empirical studies have investigated the influence of connectivity on beta diversity. Nonetheless, the decrease in beta diversity with increasing rates of movement of potential dispersal vectors (increasing rates of

transfer) has already been shown in an experiment with artificial zooplankton meta-communities (Forbes and Chase, 2002). Comparing species composition among groups of ponds from distinct regions with similar environmental characteristics, Chase (2003) showed that beta diversity increases in regions with increasing distance among ponds – distance which is assumed to be a surrogate of dispersal rate.

Gilbert et al. (1998) studied the effects of corridors on gamma diversity of micro-arthropods in artificial landscapes, but not on beta diversity. They found a significant increase in the total number of species in connected compared to fragmented landscapes, as well as an increase in alpha diversity. Alternatively, Forbes and Chase (2002) found a decrease in gamma diversity with increasing rates of movement of potential dispersal vectors among artificial zooplankton meta-communities, mainly due to a decrease in beta diversity. Although our sampling design does not allow statistical comparison of gamma diversity among categories of fragment size and connectivity, our data suggest that smaller isolated fragments may present gamma diversity similar to larger fragments or to smaller connected fragments. Although smaller isolated fragments harbor a lower number of species locally, they are spatially more variable than larger or connected fragments.

Finally, in a recent modeling and simulation work, Hudgens and Haddad (2003) showed that the benefits of corridors should increase with increasing carrying capacity of fragments and thus with fragment size. We found no evidence from the two-way analysis of variance that the effects of corridors are greater in medium-sized than in small fragments.

## 5. Conclusions

This study suggests that habitat structure gradients associated with the disturbance or regeneration of tropical forests are more important to the abundance than to the diversity of small mammal communities. This highlights the importance of secondary forest and the potential of vegetation regeneration in restoration techniques for the conservation of fragmented tropical forest landscapes.

Our results are congruent with the idea that habitat loss and fragmentation lead to less abundant, less rich and more spatially variable communities. More importantly, they suggest that corridors may attenuate habitat loss and fragmentation effects by increasing the abundance and thus the richness and spatial homogeneity of animal communities in small patches of tropical forest. These results indicate that maintenance and restoration of corridors are effective management strategies to improve the chance of persistence of animal species in small patches in tropical landscapes that have already

suffered high levels of deforestation as the Atlantic forest. Comparisons with other studies indicate that the importance of fragment size and corridors is higher in landscapes with a lower amount of habitat or with reduced matrix permeability.

The opposite trends of alpha and beta diversity in relation to fragment size and presence of corridors suggests that, as a group, smaller isolated patches may harbor a similar number of species (gamma diversity) as larger or more connected fragments. The consequences of these patterns are important for conservation strategies. Because most algorithms for selecting sites for conservation are based on composition complementarity (Margules and Pressey, 2000), they may tend to prioritize small isolated fragments given their higher beta diversity. However, small isolated habitat patches are probably not only spatially, but also temporally variable (Hinsley et al., 1995; Schmiegelow et al., 1997; Terborgh et al., 1997). Selection of small isolated patches may not guarantee the long term persistence of species, and the results from complementarity algorithms should be tested for correlation with fragment size.

It is important to highlight, however, that this study focused on the distribution of species in a fragmented tropical landscape over a small period of time. It indicates that small isolated fragments are subjected to local extinctions, harboring a smaller number of species and being spatially variable. This, in turn, suggests that they could be highly variable in time. It is important that future studies investigate the dynamics of small remnants in comparison to larger areas and compare spatial patterns observed in different years.

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## References

- Aars, J., Ims, R.A., 1999. The effects of habitat corridors on rates of transfer and interbreeding between vole demes. *Ecology* 80, 1648–1655.
- Aleixo, A., 1999. Effects of selective logging on a bird community in the Brazilian Atlantic Forest. *Condor* 101, 537–548.

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–364.
- Beier, P., Noss, R.F., 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12, 1241–1251.
- Bergallo, H.G., 1994. Ecology of small mammal community in an Atlantic Forest area in southeastern Brazil. *Studies on Neotropical Fauna and Environment* 29, 197–217.
- Bergallo, H.G., Magnusson, W.E., 1999. Effects of climate and food availability on four rodent species in southeastern Brazil. *Journal of Mammalogy* 80, 472–486.
- Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449.
- Castro, E.B.V., Fernandez, F.A.S., 2004. Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. *Biological Conservation* 119, 73–80.
- Chase, J.M., 2003. Community assembly: when should history matter? *Oecologia* 136, 489–498.
- Cochrane, M.A., 2001. Synergetic interactions between habitat fragmentation and fire in evergreen tropical forests. *Conservation Biology* 15, 1515–1521.
- Develey, P.F., Metzger, J.P., in press. Birds in Atlantic forest landscapes: effects of forest cover and configuration. In: Laurance, W.F., Peres, C.A. (Eds.), *Emerging Threats to Tropical Forests*. University of Chicago Press, Chicago.
- DeWalt, S.J., Maliakal, S.K., Denslow, J.S., 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management* 182, 139–151.
- Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P., Stork, N.E., 1998. Beetle species response to tropical forest fragmentation. *Ecological Monographs* 68, 295–323.
- Dunning, J.B., Borgella, J.R., Clements, K., Meffe, G.K., 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9, 542–550.
- Earn, D.J.D., Levin, S.A., Rohani, P., 2000. Coherence and conservation. *Science* 290, 1360–1364.
- Estrada, A., Cammarano, P., Coates-Estrada, R., 2000. Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 9, 1399–1416.
- Estrada, A., Coates-Estrada, R., 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography* 24, 94–102.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61, 603–610.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Reviews in Ecology, Evolution and Systematics* 34, 487–515.
- Feliciano, B.R., Fernandez, F.A.S., Freitas, D., de Figueiredo, M.S.L., 2002. Population dynamics of small rodents in a grassland between fragments of Atlantic Forest in southeastern Brazil. *Mammalian Biology* 67, 304–314.
- Fonseca, G.A.B., Herrmann, G., Leite, Y.L.R., Mittermeier, R.A., Rylands, A.B., Patton, J.L., 1996. Lista anotada dos mamíferos do Brasil. *Occasional Papers in Conservation Biology* 4, 1–38.
- Fonseca, G.A.B., Robinson, J.G., 1990. Forest size and structure: competitive and predatory effects on small mammal communities. *Biological Conservation* 53, 265–294.
- Forbes, A.E., Chase, J.M., 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. *Oikos* 96, 433–440.
- Gentile, R., Fernandez, F.A.S., 1999. Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. *Mammalia* 63, 29–40.
- Gilbert, F., Gonzalez, A., Evans-Freke, I., 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 265, 577–582.
- Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M., Evans-Freke, I., 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281, 2045–2047.
- Grelle, C.E.V., 2003. Forest structure and vertical stratification of small mammals in a secondary Atlantic forest, southeastern Brazil. *Studies on Neotropical Fauna and Environment* 38, 81–85.
- Grelle, C.E.V., Garcia, Q.S., 1999. Potential dispersal of *Cecropia hololeuca* by the common opossum (*Didelphis aurita*) in Atlantic forest, southeastern Brazil. *Revue D'Ecologie – La Terre et La Vie* 54, 327–332.
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148, 185–206.
- Haddad, N.M., 1999. Corridor use predicted from behaviors at habitat boundaries. *The American Naturalist* 153, 215–227.
- Haddad, N.M., Baum, K.A., 1999. An experimental test of corridors on butterfly densities. *Ecological Applications* 9, 623–633.
- Hale, M.L., Lurz, P.W.W., Shirley, M.D.F., Rushton, S., Fuller, R.M., Wolff, K., 2001. Impact of landscape management on the genetic structure of red squirrel population. *Science* 293, 2246–2248.
- Harrison, S., 1997. How natural habitat patchiness affects the distribution of diversity in Californian Serpentine Chaparral. *Ecology* 78, 1898–1906.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivities to fragmentation. *Biodiversity and Conservation* 13, 207–251.
- Hice, C.L., Schmidly, D., 2002. The effectiveness of pitfall traps for sampling small mammals in the Amazon basin. *Mastozoologia Neotropical/Journal of Neotropical Mammalogy* 9, 85–89.
- Hinsley, S.A., Bellamy, P.E., Newton, I., 1995. Bird species turnover and stochastic extinction in woodland fragments. *Ecography* 18, 41–50.
- Hudgens, B.R., Haddad, N.M., 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. *The American Naturalist* 161, 808–820.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 184–201.
- Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367–382.
- Laurance, W.F., 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. *Journal of Mammalogy* 71, 641–653.
- Laurance, W.F., 2002. Hyperdynamism in fragmented habitats. *Journal of Vegetation Science* 13, 595–602.
- Laurance, W.F., Bierregaard, R.O., 1997. *Tropical Forest Remnants – Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago.
- Laurance, S.G., Laurance, W.F., 1999. Tropical forest corridors: use of linear rainforest remnants by arboreal mammals. *Biological Conservation* 91, 231–239.
- Laurance, W.F., Cochrane, M.A., 2001. Synergetic effects in fragmented landscapes. *Conservation Biology* 15, 1488–1489.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79, 2032–2040.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D., Gaston, K.J., 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966–979.
- Lima, M.G., Gascon, C., 1999. The conservation value of linear forest remnants in Central Amazonia. *Biological Conservation* 91, 241–247.



- Lomolino, M.V., Perault, D.R., 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology* 81, 1517–1532.
- Loreau, M., 2000. Are communities saturated? On the relationship of alpha, beta and gamma diversity. *Ecological Letters* 3, 73–76.
- Lyra-Jorge, M.C., Pivello, V.R., 2001. Combining live trap and pitfall to survey terrestrial small mammals in savanna and forest habitats, in Brazil. *Mammalia* 65, 524–530.
- Malcolm, J.R., 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75, 2438–2445.
- Malcolm, J.R., 1995. Forest structure and the abundance and diversity of Neotropical small mammals. In: Lowman, M.D., Nadkarni, N.M. (Eds.), *Forest Canopies*. Academic Press, San Diego, pp. 179–197.
- Malcolm, J.R., 1997a. Biomass and diversity of small mammals in Amazonian forest fragments. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants*. University of Chicago Press, Chicago, pp. 207–221.
- Malcolm, J.R., 1997b. Insect biomass in Amazonian forest fragments. In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), *Canopy Arthropods*. Chapman & Hall, London, pp. 510–533.
- Malcolm, J.R., Ray, J.C., 2000. Influence of timber extraction routes on Central African small-mammal communities, forest structure, and tree diversity. *Conservation Biology* 14, 1623–1638.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Mech, S.G., Hallett, J.G., 2001. Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology* 15, 467–474.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Oliveira-Filho, A.T., Fontes, M.A.L., 2000. Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. *Biotropica* 32, 793–810.
- Orrock, J.L., Danielson, B.J., Burns, M.J., Levey, D.J., 2003. Spatial ecology of predator–prey interactions: corridors and patch shape influence seed predation. *Ecology* 84, 2589–2599.
- Paglia, A.P., Marco, P., de Costa, F.M., Pereira, R.F., Lessa, G., 1995. Heterogeneidade estrutural e diversidade de pequenos mamíferos em um fragmento de mata secundária de Minas Gerais, Brasil. *Revista Brasileira de Zoologia* 12, 67–79.
- Pardini, R., 2001. Pequenos Mamíferos e a Fragmentação da Mata Atlântica de Una, Sul da Bahia – Processos e Conservação. PhD Thesis, Universidade de São Paulo, São Paulo.
- Pardini, R., 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodiversity and Conservation* 13, 2567–2586.
- Pardini, R., Umetsu, F., in press. Small mammals from the Morro Grande Reserve – distribution of species and diversity in an Atlantic Forest area. *Biota Neotropica*.
- Pimentel, D.S., Tabarelli, M., 2004. Seed dispersal of the palm *Attalea oleifera* in a remnant of the Brazilian Atlantic Forest. *Biotropica* 36, 74–84.
- Pires, A.S., Lira, P.K., Fernandez, F.A.S., Schittini, G.M., Oliveira, L.C., 2002. Frequency of movements of small mammals among Atlantic Coastal Forest fragments in Brazil. *Biological Conservation* 108, 229–237.
- Pizo, M.A., 1997. Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic Forest of south-eastern Brazil. *Journal of Tropical Ecology* 13, 559–578.
- Reddingius, J., den Boer, P., 1970. Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia* 5, 240–284.
- Roff, D., 1974. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. *Oecologia* 15, 259–275.
- Ross, J.L.S., Moroz, I.C., 1997. Mapa Geomorfológico do Estado de São Paulo: escala 1:500.000. FFLCH-USP, IPT and FAPESP, São Paulo.
- Schmiegelow, F.K.A., Machtans, C.S., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* 78, 1914–1932.
- Simberloff, D., Farr, J.A., Cox, J., Mehlman, D.W., 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6, 493–504.
- Slade, N.A., Blair, S.M., 2000. An empirical test of using counts of individuals as indices of population size. *Journal of Mammalogy* 81, 1035–1045.
- Stallings, J.R., 1989. Small mammal inventories in an eastern Brazilian park. *Bulletin Florida State Museum* 34, 153–200.
- Stevens, S.M., Husband, T.P., 1998. The influence of edge on small mammals: evidence from Brazilian Atlantic Forest fragments. *Biological Conservation* 85, 1–8.
- SYSTAT, Inc. 1993. Systat 5.03 for Windows.
- ter Braak, C.J.F., Smilauer, P., 1998. CANOCO for windows version 4.0. Center for biometry Wageningen CPRO-DLO, Wageningen, The Netherlands.
- Terborgh, J., Lopez, L., Tello, J., 1997. Bird communities in transition: the lago Guri islands. *Ecology* 78, 1494–1501.
- Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.L., Townsend, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 99, 12923–12926.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31, 79–92.
- Uezu, A., Metzger, J.P., Vielliard, J.M.E., in press. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological Conservation*.
- Vieira, E.M., Izar, P., 1999. Interactions between aroids and arboreal mammals in the Brazilian Atlantic rainforest. *Plant ecology* 145, 75–82.
- Vieira, E.M., Monteiro-Filho, E.L.A., 2003. Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil. *Journal of Tropical Ecology* 19, 501–507.
- Vieira, E.M., Pizo, M.A., Izar, P., 2003a. Fruit and seed exploitation by small rodents of the Brazilian Atlantic forest. *Mammalia* 67, 533–539.
- Vieira, M.V., Faria, D., Fernandez, F., Ferrari, S., Freitas, S., Gaspar, D.A., Moura, R., Olifiers, N., de Oliveira, P.P., Pardini, R., Pires, A., Ravetta, A., de Mello, M.A.R., Ruiz, C., Setz, E., 2003b. Mamíferos. In: Rambaldi, D.M., Oliveira, D.A.S. (Eds.), *Fragmentação de Ecossistemas: Causas, Efeitos sobre a Biodiversidade e Recomendações de Políticas Públicas*. MMA/SBF, Brasília, pp. 125–151.
- Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: effects of fragmentation on extinction. *The American Naturalist* 125, 879–887.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30, 279–338.