



Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region

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ABSTRACT

Time-lagged responses of biological variables to landscape modifications are widely recognized, but rarely considered in ecological studies. In order to test for the existence of time-lags in the response of trees, small mammals, birds and frogs to changes in fragment area and connectivity, we studied a fragmented and highly dynamic landscape in the Atlantic forest region. We also investigated the biological correlates associated with differential responses among taxonomic groups. Species richness and abundance for four taxonomic groups were measured in 21 secondary forest fragments during the same period (2000–2002), following a standardized protocol. Data analyses were based on power regressions and model selection procedures. The model inputs included present (2000) and past (1962, 1981) fragment areas and connectivity, as well as observed changes in these parameters. Although past landscape structure was particularly relevant for trees, all taxonomic groups (except small mammals) were affected by landscape dynamics, exhibiting a time-lagged response. Furthermore, fragment area was more important for species groups with lower dispersal capacity, while species with higher dispersal ability had stronger responses to connectivity measures. Although these secondary forest fragments still maintain a large fraction of their original biodiversity, the delay in biological response combined with high rates of deforestation and fast forest regeneration imply in a reduction in the average age of the forest. This also indicates that future species losses are likely, especially those that are more strictly-forest dwellers. Conservation actions should be implemented to reduce species extinction, to maintain old-growth forests and to favour the regeneration process. Our results demonstrate that landscape history can strongly affect the present distribution pattern of species in fragmented landscapes, and should be considered in conservation planning.

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1. Introduction

Broad scale land use and land cover changes are occurring rapidly in the tropics (Mayaux et al., 2005), leading to extreme land cover fragmentation, patch isolation, increased edge effects, and area reduction of the native fragments (Fischer and Lindenmayer, 2007). Some species react immediately to these changes (Adriaens et al., 2006); however, others exhibit a time-lag in their responses (Tilman et al., 1994; Brooks et al., 1999a; Hanski and Ovaskainen, 2002), which results in large extinction debts (Tilman et al., 1994).

Time-lagged responses to landscape modifications are sometimes detected in ecological studies, but are rarely considered in management plans. Although empirical evidence of time-lagged species responses to landscape changes has accumulated in recent

years, these studies are essentially limited to plants in temperate regions (Lindborg and Eriksson, 2004; Ernoult et al., 2006; Helm et al., 2006; Paltto et al., 2006; Ellis and Coppins, 2007), and birds in tropical areas (Brooks and Balmford, 1996; Brooks et al., 1999a). Little is known about time-lagged responses in other taxonomic groups (but see Harding et al., 1998; Petit and Burel, 1998; Hanski and Ovaskainen, 2002; Lövenhaft et al., 2004; Holzhauer et al., 2006) and in different landscape compositions and configurations. This lack of knowledge culminates in a common failure to properly consider the influence of historical changes in landscape structure when studying habitat modification (Metzger, 2008).

The mechanisms involved in time-lagged responses are still poorly understood. The influences of former landscape configuration and structure are not always detected (Adriaens et al., 2006; Honnay et al., 2006; Cousins et al., 2007), and responses are likely to be species-dependent (Ewers and Didham 2006). For example, tree species' longevity and seed bank persistence were shown to

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be linked to differences in the time-lag of responses to fragment area and connectivity among grassland species (Piessens and Hermy, 2006; Lindborg, 2007). The rate of landscape change can also influence the balance between colonization and extinction (Munzbergova et al., 2005). Other species traits such as life span (Metzger, 1998), trophic level, dispersal ability and degree of habitat specialization have also been suggested as important attributes related to time-lagged responses (Ewers and Didham, 2006).

Fragment size and connectivity are among the key landscape factors that affect species survival in fragmented landscapes (Metzger, 2000; Ewers and Didham, 2006; Pardini et al., 2005; Uezu et al., 2005; Fischer and Lindenmayer, 2007; Martensen et al., 2008). Fragment size is usually related to the amount and diversity of resources, which directly influence the size and number of resident populations. Larger fragments usually contain more species and also larger populations, which theoretically increases stability against variations in demographic, genetic and environmental processes. However, the surrounding matrix and habitat configuration can exert a strong effect on the processes occurring inside fragments (Kupfer et al., 2006). As a consequence, landscape connectivity, defined as the capacity of the landscape to facilitate biological fluxes (Taylor et al., 1993), has a strong influence on population persistence and species interactions. Connectivity can facilitate the colonization of empty patches, and, through rescue effects, can reduce extinction probabilities and the risk of inbreeding depression (Metzger and Décamps, 1997; Hanski and Ovaskainen, 2000). Connectivity depends on structural features, such as inter-patch distance, presence of corridors, and matrix type; additionally, it also depends on species behaviour, such as gap-crossing capacities and the ability to use disturbed habitats, corridors and stepping-stones (Tischendorf and Fahrig, 2000; Uezu et al., 2005, 2008; Awade and Metzger, 2008; Boscolo et al., 2008; Umetsu et al., 2008). The relative effects of fragment size and connectivity in determining species persistence in fragmented landscapes are still poorly understood (Fitzgibbon et al., 2007; Martensen et al., 2008). It has been suggested that these two factors have interacting effects on species abundance (Schooley and Wiens, 2005),

and their importance vary according to the amount of habitat available (Andrén, 1994).

Here, we investigate the influence of landscape structure dynamics from 1962 to 2000 on different taxonomic groups in a fragmented secondary forest landscape. Highly dynamic fragmented secondary forest landscapes are commonly found in the Atlantic forest region (Ribeiro et al., 2009). This forest is one of the most threatened and fragmented tropical forests in the world (Myers et al., 2000), where the threat of extinction debt is considered to be particularly high (Brooks et al., 1999b). The importance of secondary forests for conservation has been debated in recent years (Develey and Martensen, 2006; Wright and Muller-Landau, 2006a; Gardner et al., 2007), fuelled by the fact that these forests have been replacing mature forests in several regions, and are now the dominant forest type in the Atlantic forest region and elsewhere (Wright, 2005). This is the first study to consider time-lagged responses to fragment area and connectivity using a multi-taxa approach, allowing investigation of variability in responses among different taxonomic groups and biological traits. We discuss the implications of these results for species conservation in highly dynamic forest landscapes.

2. Methods

2.1. Study region

The study landscape covers 10,000 hectares (ha) and is situated in the Crystalline Plateau of Ibiúna in South-eastern Brazil, 50 km west of the city of São Paulo (23°35' S, 23°50' S and 46°45' W, 47°15' W). It is located between one of the largest remnants of Atlantic Forest, the Paranapiacaba continuum (circa 1.1 million ha; Ribeiro et al., 2009), and the small, sparse fragments of semi-deciduous forest in the interior of the state of São Paulo (Fig. 1). The altitude in the Plateau of Ibiúna varies between 850 and 1100 m with a gently undulating topography (Silva et al., 2007). The climate is mild, warm and humid, with temperatures varying between 11 and 27 °C. The average annual precipitation is about

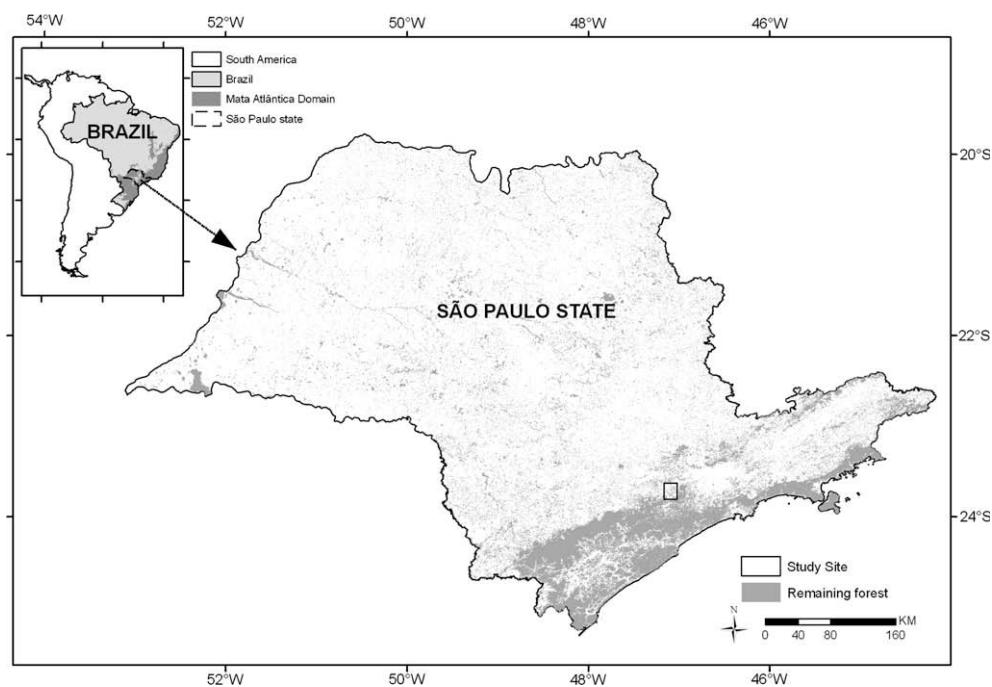


Fig. 1. Map of the study area (Plateau of Ibiúna) in SE Brazil, state of São Paulo.

1300–1400 mm; the driest and coldest months are between April and August.

The original forest in the region is classified as “Lower Montane Rainforest” (Oliveira-Filho and Fontes, 2000), which contains a blend of species from the humid coastal forest, the *Araucaria* mixed forest from the south of Brazil, the semi-deciduous forest of the interior of the country and the Brazilian savannas (Catharino et al., 2006). The most abundant tree families are Myrtaceae, Lauraceae, Fabaceae and Rubiaceae (Bernacci et al., 2006).

The study landscape was intensively deforested and fragmented in the past to supply coal for power generation, and to create agricultural land to support the city of São Paulo. The landscape is now predominantly composed of agricultural fields and pastures (34%), with 31% of secondary forests at intermediate to advanced stages of succession (Silva et al., 2007), mostly between 60 and 80 years of age (unpublished data). There is still strong pressure on these remaining patches due to intense peri-urban expansion, which was recently facilitated by the improvement of the main road linking the study landscape to the city of São Paulo (Teixeira et al., 2009). The existing fragments are also threatened by the expansion of *Eucalyptus* species plantations for cellulose production.

2.2. Selection of study fragments

Twenty-one fragments were selected to include a large range of fragment sizes and connectivity conditions. Fragment selection was conducted following a random-stratified procedure, first considering size and then connectivity attributes. First, the largest five fragments of the landscape (each >50 ha) were chosen; then, eight fragments between 10 and 48 ha and eight fragments <5.5 ha were randomly selected to encompass various connectivity conditions (presence or absence of a corridor to a large fragment). We only considered fragments composed by vegetation in intermediate to advanced stages of succession (Silva et al., 2007), and that lacked any major human disturbances (e.g. without intense cattle use, fire, logging, herb species invasion, or understorey clearing). We selected half of the medium and small fragments linked by a corridor to one of the large fragments of the landscape, while the other half had varying distances (40 m to 2 km) from the nearest fragment.

This sampling design was established to test the effects of both fragment size and connectivity attributes, such as the presence of corridors and varying gap-distances, on biodiversity patterns and processes for different species groups. To prevent auto-correlation problems, we ensured reasonable spatial dispersion of the sampling sites among treatments (fragment size and connectivity), and checked for spatial dependence using Mantel tests. We used the Sorensen distance for the biological abundance matrixes and Euclidian distance for the geographical matrix, and after 1000 permutations, all the tested variables (richness and abundance for all species groups – see below) were non-significant (mostly $p > 0.10$) and exhibited low correlations (<0.18). Furthermore, relief attributes (slope, slope orientation and altitude) were equally distributed among fragments (Silva et al., 2007, 2008), and thus their potential confounding effects were avoided. We also controlled for variation in forest quality by only selecting fragments, and particular study sites in each fragment, in similar stages of succession and levels of disturbance. To validate these measures of forest conditions we recorded different variables of forest structure (including tree density, foliage stratification, herbaceous dominance; Table S1) and disturbance (logging, thinning, fire, hunting; Table S2) in each sampling site. We observed that modifications in forest structure and disturbance were not significantly related to either fragment size or connectivity; that is, large and/or well-connected fragments do not necessarily contain more developed forests than small and/or isolated fragments (Tables S1 and S2).

2.3. Biological sampling

We established one study plot per fragment, randomly situated at least 50 m away from the forest edges, except for some small fragments where meeting this condition was not always possible (minimum distance to edge was 20 m). All taxonomic groups were sampled in the same plot area in each fragment between 2000 and 2002.

From 2000 to 2001, we sampled trees with diameter at breast height >5 cm using the point-centred quarter method (Cottam and Curtis, 1956) in all 21 fragments. We placed 25 vegetation sampling points arranged in two lines separated by at least 10 m (Durigan et al., 2008; Silva et al., 2008). The number of trees analysed per fragment remained constant (100).

Small mammals and frogs were sampled in 20 fragments (all except one small and isolated fragment) using a line of 11 pitfall traps (60 L) situated 10 m from each other and connected by a 50-cm-high plastic fence (100 m total transect length). This method has been shown to be highly efficient for sampling small mammals in the Atlantic forest (Umetsu et al., 2006). Two capture sessions of 8 days each were conducted during the rainy season of January and February 2002, generating a total of 16 days of sampling for each study site (Pardini et al., 2005). Sites were sampled at the same time to prevent temporal fluctuations from influencing the comparison among sites.

Birds were sampled in 17 fragments (four large, three medium and isolated, three medium and well-connected, three small and isolated and four small and connected to large fragments through corridors). In each fragment, we set up 10 mist-nets placed from the ground level up to 2.5 m high (12 × 2.5 m, 36 mm mesh) along a 120 m transect. The sampling effort was approximately 533 net-hours per fragment (standard deviation <10 net-hours), evenly distributed in the dry and wet seasons of 2001 and 2002 (Martensen et al., 2008). We opened the nets at sunrise (≈06:00) and closed them at sunset or mid-day.

We used the observed richness and abundance per fragment for each taxonomic group as dependent variables. We considered the assemblage as a whole, and also divided each taxonomic group into functional categories based on biological characteristics that are thought to affect species' responses to landscape structure and dynamics. For trees, we examined three groups based on light requirements: shade intolerant canopy species (pioneer and early secondary trees from the intermediate and higher strata of the forest); shade tolerant canopy species (late secondary species trees from the intermediate and higher strata of the forest); and shade tolerant understorey species (for details, see Catharino et al., 2006). Small mammals and frogs were divided into forest and non-forest species, defining forest-dependent frog species as those which cannot survive outside forest areas, even if these species can eventually use open matrixes (Dixo, 2005). Forest-dependent small mammal species were defined as those that are endemic to forested biomes and not occurring in open biomes adjacent to the Atlantic forest (Umetsu and Pardini, 2007). Birds were divided into two groups with respect to their preference for edge or interior forest habitats, based on Willis (1979).

2.4. Landscape structure and dynamics

The landscape structure and dynamics analyses were based on aerial photographs from 1962 (1:25,000), 1981 (1:35,000) and 2000 (1:10,000). These photographs were digitalized at a resolution of 1 m, geo-referenced with an RMS error ranging from 5 to 12 m and joined into a mosaic for each year with Erdas Imagine™. Photographs were interpreted visually using stereoscopy, and polygons were digitalized directly over the mosaic in a computer screen with ArcGIS. To avoid bias based on differences in resolution

from different years, all mosaics were transformed to a similar resolution (15 m). The images were interpreted based on five simple land use and land cover classes, which were easily distinguished, even in the 1:35,000 photographs: forest (intermediate/old second growth forest, >15–20 years regeneration); young secondary vegetation (shrub vegetation, typical of an initial forest succession, <10–15 years regeneration); forestry (*Eucalyptus* and *Pinus* plantations); agriculture (annual cultures and pastures) and urban or rural areas with buildings (rural constructions and houses). An accuracy assessment based on the vegetation classes observed at the study sites in 2000 showed an 88% accuracy of the image interpretations (Silva et al., 2007).

Fragment area and connectivity indices for all 21 sampled fragments were calculated for each time period. Connectivity measurements were calculated based on graph theory (Gross and Yellen, 1999), which defines clusters of connected fragments (sub-graphs) according to various linkage rules. Connectivity indices were defined as the sum of the available habitat, that is to say, the sum of the areas of fragments in the same cluster (or sub-graph). For the present study, linkage rules were based on the biological traits of the species analysed, such as the ability to use corridors and gap-crossing capacities (Dixo, 2005; Pardini et al., 2005; Uezu et al., 2005; Awade and Metzger, 2008; Boscolo et al., 2008; Hansbauer et al., 2008a; Martensen et al., 2008; Umetsu et al., 2008).

Thus, we computed the following indices for each fragment (Fig. 2): (i) AREA represents the area of the focal fragment, not considering corridor linkages (≤ 100 m width); (ii) COR includes the area connected by corridors (COR = AREA + area of the corridors + area of the structurally connected fragments); (iii) CLU₂₀ indicates the area of fragments connected by gaps of ≤ 20 m of width (CLU₂₀ = COR + area of fragments at less than 20 m from the COR cluster); and (iv) CLU₄₀ is the area of fragments connected by gaps of ≤ 40 m of width (CLU₄₀ = COR + area of fragments at less than 40 m from the COR cluster). With this approach, all connectivity indices (COR, CLU₂₀ and CLU₄₀) incorporate the focal fragment area (AREA), and thus these indices can be considered an approximation of the functional area for species with different dispersal capacities.

2.5. Data analyses

We built 21 conceptual models to capture present biodiversity patterns, considering five scenarios that incorporate the influence of past and present landscape structure and dynamics. In the equations shown below, DV = dependent variable; a = intercept; b, c and d = power parameters; AREAy_y = area of the fragment for the year yy; CORyy = area of the fragment, plus the area of the corridors

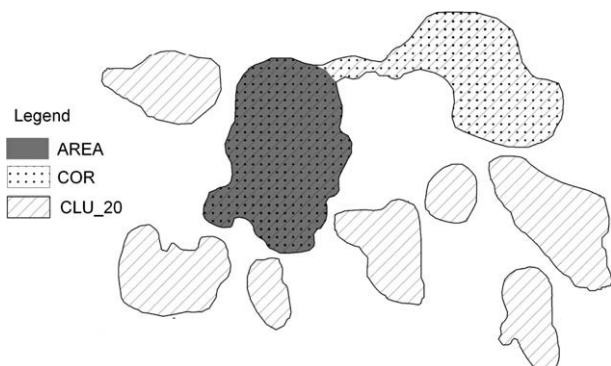


Fig. 2. Schematic representation of the landscape indices for one focal fragment: area of the focal fragment (AREA), area connected by corridors (COR), and area connected by 20 m gap-crossing (CLU₂₀).

and the area of the fragments connected by corridors for the year yy; CLU_{dd} is the connectivity provided by gap-crossing of dd meters for the year 2000; $\Delta AREAy_a - y_b$ is the difference in fragment area between years y_a and y_b ; and $\Delta CORy_a - y_b$ is the difference in area connected by corridors between year y_a and y_b . The five scenarios examined are as follows:

- (i) Present biodiversity is influenced only by the present landscape structure (four models):
 - $DV = a * AREA00^b$;
 - $DV = a * COR00^b$;
 - $DV = a * CLU_{20}^b$;
 - $DV = a * CLU_{40}^b$;
- (ii) Biodiversity is influenced only by past landscape structure (four models):
 - $DV = a * AREA62^b$;
 - $DV = a * COR62^b$;
 - $DV = a * AREA81^b$;
 - $DV = a * COR81^b$;
- (iii) Biodiversity is influenced only by past landscape changes (six models):
 - $DV = a * (\Delta AREA81-62)^b$;
 - $DV = a * (\Delta AREA00-81)^b$;
 - $DV = a * (\Delta AREA81-62)^b * (\Delta AREA00-81)^c$;
 - $DV = a * (\Delta COR81-62)^b$;
 - $DV = a * (\Delta COR00-81)^b$;
 - $DV = a * (\Delta COR81-62)^b * (\Delta COR00-81)^c$;
- (iv) Biodiversity is influenced by a combination of present landscape structure and past changes (six models):
 - $DV = a * AREA00^b * (\Delta AREA81-62)^c$;
 - $DV = a * AREA00^b * (\Delta AREA00-81)^c$;
 - $DV = a * AREA00^b * (\Delta AREA81-62)^c * (\Delta AREA00-81)^d$;
 - $DV = a * COR00^b * (\Delta COR81-62)^c$;
 - $DV = a * COR00^b * (\Delta COR00-81)^c$;
 - $DV = a * COR00^b * (\Delta COR81-62)^c + (\Delta COR00-81)^d$; and
- (v) A neutral model (no effect of past or present landscape structure or dynamics):
 - $DV = a$.

We did not consider a general complete model with all possible model combinations of landscape variables, since some combinations are conceptually improbable (e.g. past landscape structure with past dynamics) and in other cases variables are highly correlated (e.g. past with present landscape structure). In the models that combine present landscape structure and past dynamics, the variables in any one model had relatively low correlations ($N = 21$, Spearman correlation, $0.11 < r < 0.73$). We also did not consider connectivity by 20 and 40 m linkages for years other than 2000 because most of the studied fragments would be clumped in these situations.

We first explored the relationships between biological dependent variables (species richness and abundance) and present and past fragment size and connectivity. We obtained better fits with power models, which were subsequently used in the analyses. We also investigated a set of different residual distributions, and opted to use the Poisson distribution for species richness and the normal distribution for abundance data. We performed all the likelihood analyses with the bbmle package (Bolker, 2008) in R 2.7.1. (R Development Core Team, 2008).

To compare the 21 power models for each species group, we used the Akaike Information Criterion (AIC; Burnham and Anderson, 2002) with the small sample correction (AICc) proposed by Hurvich and Tsai (1998), which generates a rank of the models according to their support of the data. The differences between the lowest AICc and the AICcs from other models were used to

visualize differences in model support, and differences >2 AICc were considered as thresholds for model support (Burnham and Anderson, 2002). This approach was developed in order to test conceptual models of how richness and abundance of different taxonomic groups could be affected by present and past landscape structure and dynamics, and thus, the individual importance of each independent variable was not investigated.

3. Results

3.1. Landscape structure and dynamics

The landscape structure of the study site between 1962 and 2000 was highly dynamic, with changes in land cover in around half of the area in both time periods examined (50.7% between 1962 and 1981; 45.8% between 1981 and 2000; Fig. 3). The dominant change in forest cover was observed from 1981 to 2000, and was mainly related to the development of rural buildings and urban expansion (Fig. 4). Despite the small increase in the amount of forest cover between 1962 and 1981 (Fig. 4), this period was characterized by the re-growth of young native vegetation into forest (1565.9 ha total, or $82.4 \text{ ha year}^{-1}$), and the simultaneous conversion of large forest tracts into agricultural areas (1232.5 ha , $64.9 \text{ ha year}^{-1}$; Fig. 3). Nonetheless, the rate of natural regeneration was higher than the deforestation rate, resulting in a small increase in forest cover. In contrast, the deforestation rate was higher (1543.7 ha , $81.2 \text{ ha year}^{-1}$) in the second period (1981–2000), culminating in an overall reduction of forest cover from 46% to 31% in the landscape.

These intense deforestation and forest regeneration processes produced abrupt changes in the size and connectivity of fragments, including those examined in this study (Fig. 5). Despite the intense deforestation in the second period, the area of most of the studied fragments (15%, or 71%) increased or remained constant (Fig. 5A). Only two fragments were reduced by $>20 \text{ ha}$, and these were among the larger fragments studied.

In contrast to changes in fragment area, the area connected by corridors (COR) was substantially reduced for most of the fragments (13 of 21, or 62%; Fig. 5B). The most common pattern observed was a sharp increase in COR between 1962 and 1981, followed by a substantial reduction in the 1981–2000 periods (12 fragments). Eight other fragments experienced a constant decrease

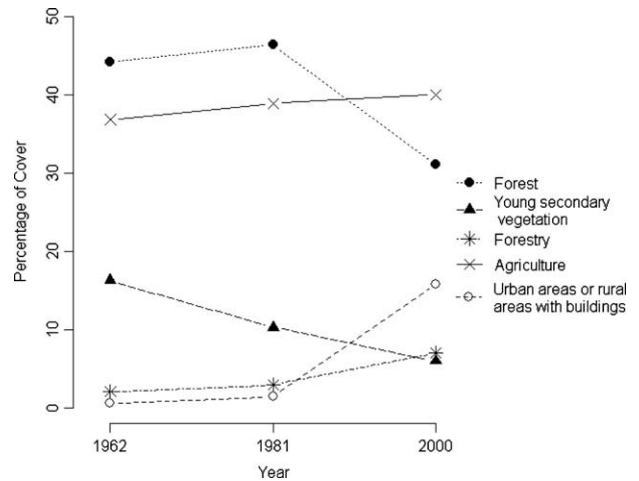


Fig. 4. Land use and land cover of the study area (Plateau of Ibiúna, SE Brazil) from 1962 to 2000.

in the area connected by corridors throughout the entire study period, while only one showed an increase.

When considering connections across 20 or 40 m gaps, almost all fragments were connected in 1962 and 1981 in one unique and large block $>4200 \text{ ha}$, due to the large amount of forest and the close proximity of the patches (Figs. 3, 5C and 5D). In the 2000 landscape (the most deforested), *CLU_20* and *CLU_40* varied between 2 and 1070 ha, with a more heterogeneous distribution of the fragment-clusters. Therefore, a major rupture in the continuity of habitat for species able to cross 20–40 m of the inter-habitat matrix occurred between 1981 and 2000.

3.2. Species-landscape relationships

In total, we registered 6088 individuals from 333 species, including 2100 trees (237 species), 607 small mammals (19), 2088 frogs (15) and 1293 forest birds (62; Table 1). The fragments are mainly composed of shade intolerant trees (51% abundance; 60% richness), forest small mammals (68%; 59%), frogs (67%; 94%), and interior forest bird species (86%; 76%).

Trees exhibited the strongest relationships with past landscape structure, especially with fragment area in 1962 (*AREA62*) and the

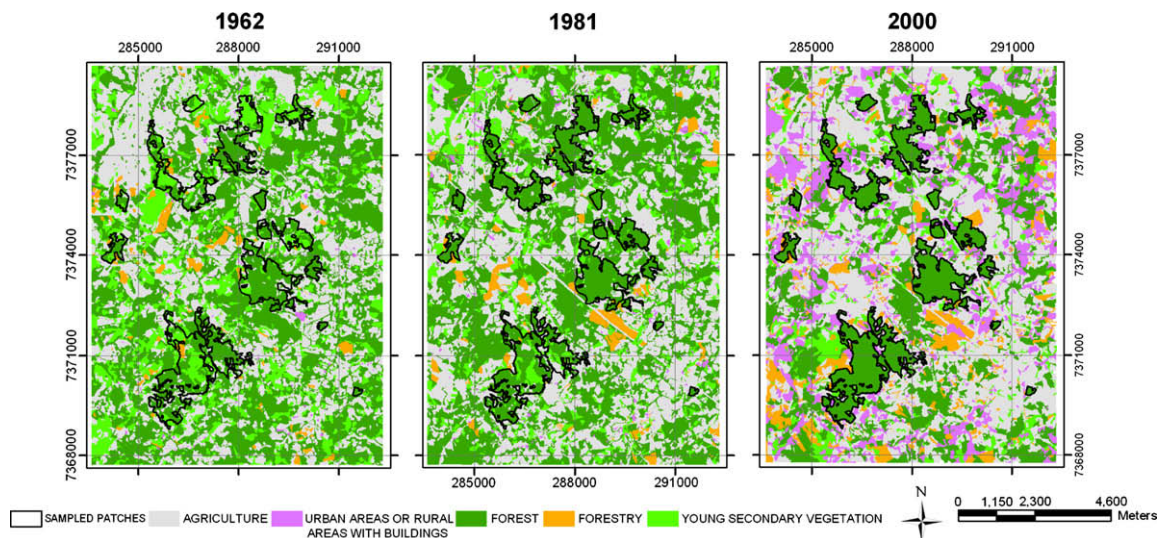


Fig. 3. Land use and land cover maps of the studied landscape for 1962, 1981 and 2000 (Plateau of Ibiúna, SE Brazil).

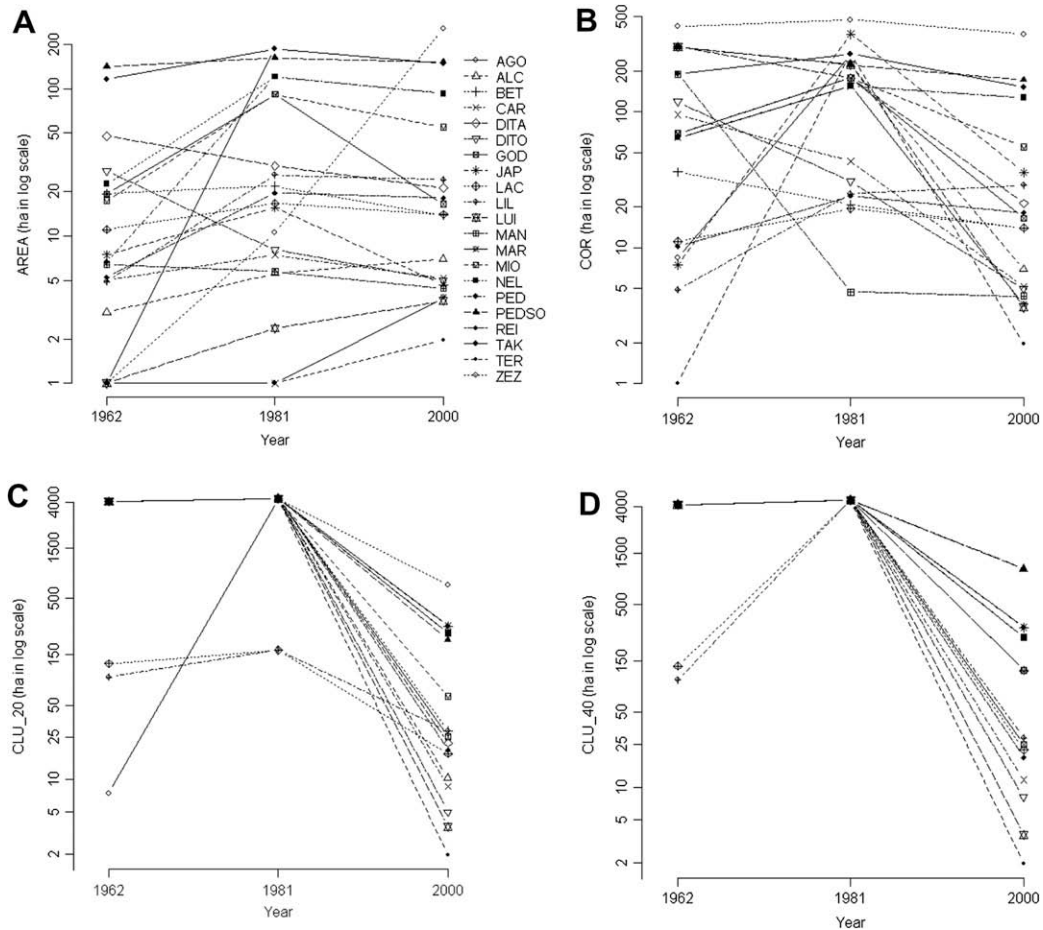


Fig. 5. Variation of AREA (A) and the connectivity indices COR (B), *CLU_20* (C) and *CLU_40* (D) from 1962 to 2000 in each of the 21 fragments studied.

Table 1

Richness and abundance of species assemblages and functional groups sampled in the 21 forest fragments of the Plateau of Ibiúna (SE Brazil).

		Total richness	Total abundance	Richness per fragment				Abundance per fragment			
				Min	Max	Average	Std. Dev.	Min	Max	Average	Std. Dev.
Trees	Total	237	2100	30	53	42.0	7.3	100	100	100	0.0
	Canopy shade intolerant	120	1262	14	30	23.3	5.2	21	95	60.1	20.9
	Canopy shade tolerant	81	538	3	26	13.0	6.8	3	59	25.6	14.6
	Understorey	30	287	1	13	5.3	3.3	1	39	13.7	10.6
Small mammals	Total	19	607	4	11	7.7	2.1	4	54	30.4	15.1
	Forest	13	358	3	9	5.6	1.7	3	38	17.9	9.9
	Non-forest	6	249	1	3	2.1	0.6	1	31	12.5	8.1
Frogs	Total	15	2088	3	10	6.2	1.8	17	343	104.4	88.6
	Forest	10	1954	2	7	4.6	1.5	14	335	97.7	84.3
	Non-forest	5	134	0	3	1.6	0.8	0	37	6.7	8.1
Birds	Total	62	1293	17	32	25.12	4.76	41	131	76.06	26.04
	Interior species	50	1134	13	26	21.59	4.43	35	116	66.71	24.55
	Edge species	12	159	1	7	3.53	1.33	3	19	9.35	4.96

area connected by corridors in 1981 (*COR81*, Tables 2A and 3) Shade intolerant species were related to *AREA62*, suggesting that those species are still responding to the landscape structure of 40 years ago. Shade tolerant species showed a strong relationship between species richness and the area connected by corridors in 1981 (*COR81*), but the association between *COR81* and abundance was weak. Understorey species were related to the past landscape structure and to landscape changes (mainly $\Delta AREA81-62$).

The contributions of past landscape structure and dynamics for small mammal species were weak (Tables 2B and 3). Forest species

abundance and richness were positively related to AREA, COR and *CLU_20* of 2000, and also to fragment area in 1981. The change in fragment area for both periods (1962–1981 and 1981–2000) was also related to forest species abundance. The connectivity landscape index of 40 m gap-crossing (*CLU_40*) was uniquely associated with non-forest small mammal species, which could indicate the higher ability of these species to use or cross areas of matrixes.

Frog species richness was weakly related to past and present area and connectivity (Tables 2C and 3). Both forest and non-forest species had clear relationships between species abundance and

Table 2

Models of species richness and abundance for trees (A), small mammals (B), frogs (C) and birds (D) in the studied forest fragments in the Plateau of Ibiúna (SE Brazil). Models are ranked from best to worst according to Akaike's Information Criterion weight (wAICc). Δi AICc is the difference between the AICc of a given model and the model with the lowest AICc value. For models with more than one independent variable, the individual weights of each variable, obtained from simple model regressions, are presented. Only models with Δi AICc < 2.0 are listed. Relationships between dependent and independent variables are presented visually as follows: + = positive relationship; – = negative relationship; N = neutral (without clear tendency). See variable names in the text.

Variables	AICc	Δi AICc	wAICc	Individual wAICc	Signal
A. Trees (N = 21)					
Canopy shade intolerant species					
Richness					
AREA62	128.32	0.00	0.48		N
Abundance					
AREA62	189.79	0.00	0.32		N
Canopy shade tolerant species					
Richness					
COR81	158.77	0.00	0.94		N
Abundance					
Δ COR00-81	176.41	0.00	0.17		+
NEUTRAL	176.73	0.31	0.14		N
COR62	177.90	1.49	0.08		–
AREA62	178.41	2.00	0.06		N
Understorey species					
Richness					
Δ COR00-81	106.55	0.00	0.46		+
Abundance					
AREA62	161.32	0.00	0.22		+
AREA00 + Δ AREA00-81 + Δ AREA81-62	161.86	0.54	0.17	0.03; 0.02; 0.10	N; N; N
Δ AREA81-62	162.97	1.65	0.10		N
B. Small mammals (N = 20)					
Forest species					
Richness					
AREA00	81.37	0.00	0.19		+
COR00	81.93	0.56	0.14		+
AREA81	83.06	1.69	0.08		+
Abundance					
COR00	146.58	0.00	0.17		+
AREA81	146.62	0.05	0.16		+
AREA00	146.78	0.20	0.15		+
AREA00 + Δ AREA81-62	147.43	0.85	0.11	0.15; 0.10	+; +
Δ AREA81-62	147.60	1.03	0.10		+
CLU_20	147.77	1.19	0.09		+
Non-forest species					
Richness					
NEUTRAL	58.45	0.00	0.20		N
CLU_40	60.37	1.92	0.08		N
Abundance					
CLU_40	141.88	0.00	0.43		+
C. Frogs (N = 20)					
Forest species					
Richness					
NEUTRAL	81.17	0.00	0.19		N
Δ COR00-81	83.09	1.92	0.07		N
Abundance					
COR00 + Δ COR81-62	226.95	0.00	0.77	0.004; 0.01	+; +
Non-forest species					
Richness					
NEUTRAL	63.41	0.00	0.18		N
AREA00	65.19	1.79	0.07		N
COR00	65.20	1.79	0.07		N
Abundance					
Δ COR00-81 + Δ COR81-62	112.66	0.00	0.79	0.02; <0.001	N; +
D. Birds (N = 17)					
Interior species					
Richness					
CLU_40	95.86	0.00	0.39		+
CLU_20	97.33	1.47	0.19		+
Abundance					
COR00 + Δ COR00-81	149.48	0.00	0.58	0.16; 0.001	+; N
Edge species					
Richness					
Δ COR81-62	62.40	0.00	0.15		+
Δ COR00-81	62.57	0.18	0.13		N
NEUTRAL	62.61	0.21	0.13		N
Δ COR00-81 + Δ COR81-62	64.19	1.79	0.06	0.13; 0.15	N; +
CLU_20	64.34	1.92	0.06		+
Abundance					
Δ COR00-81	105.62	0.00	0.19		–

(continued on next page)

Table 2 (continued)

Variables	AICc	Δ_i AICc	wAICc	Individual wAICc	Signal
NEUTRAL	106.53	0.90	0.12		N
AREA00	106.93	1.31	0.10		N
COR81	107.27	1.64	0.08		+

Table 3

Synthesis of the landscape variables related to species richness and abundance indices of small mammals, birds, frogs and trees in the studied forest fragments in the Plateau of Ibiúna (SE Brazil).

		Neutral	Landscape structure			Landscape dynamics	Present structure + past dynamics	Contribution of past landscape	Area or connectivity
			1962	1981	2000				
Canopy shade intolerant tree species	Richness	–	Area	–	–	–	–	High	Area
	Abundance	–	Area	–	–	–	–	High	Area
Canopy shade tolerant tree species	Richness	–	–	Corridor	–	–	–	High	Corridor
	Abundance	Neutral	–	–	–	–	–	–	–
Understorey tree species	Richness	–	–	–	–	Area (1981–2000 dynamics)	–	High	Corridor
	Abundance	–	Area	–	–	Area (1962–1981 dynamics)	Area + (1962–1981, 1981–2000 dynamics)	High	Area
Forest small mammals	Richness	–	–	Area	Area, corridor	–	–	Low	Area and corridor
	Abundance	–	–	Area	Area, corridor, 20 m gap-crossing	Area (1962–1981 dynamics)	Area + (1962–1981 dynamics)	Low	Area, corridor and gap-crossing connections
Non-forest small mammals	Richness	Neutral	–	–	–	–	–	–	–
	Abundance	–	–	–	40 m gap-crossing	–	–	–	Gap-crossing connections
Forest frogs	Richness	Neutral	–	–	–	–	–	–	–
	Abundance	–	–	–	–	–	Corridor + (1962–1981 dynamics)	Intermediate	Corridor
Non-forest frogs	Richness	Neutral	–	–	–	–	–	–	–
	Abundance	–	–	–	–	Corridor (1962–1981, 1981–2000 dynamics)	–	High	Corridor
Interior forest bird species	Richness	–	–	–	20 m and 40 m gap-crossing	–	–	–	Gap-crossing connections
	Abundance	–	–	–	–	–	Corridor + corridor (1981–2000 dynamics)	Intermediate	Corridor
Edge bird species	Richness	Neutral	–	–	–	–	–	–	–
	Abundance	Neutral	–	–	–	–	–	–	–

landscape characteristics. Forest frog species abundance was positively related to the area connected by corridors in 2000 and to past changes in corridor area, suggesting that extinct connections between fragments are still affecting the present abundance of the assemblage. Non-forest species abundance was also sensitive to past dynamics in corridor area, as well as more recent (1981–2000) changes. It is worth noting that abundance patterns are highly affected by only one species, *Rhinella ornata*, which represents 82% of the total forest frog species abundance.

The relationship of bird assemblages to landscape characteristics differed between interior forest species and edge species. The interior species were related to the present landscape structure, especially using models that consider fragment connectivity (COR00, CLU_20, CLU_40), and recent (1981–2000) corridor connection dynamics (Tables 2D and 3). In contrast, edge species were poorly related to present and past landscape structure and dynamics. For interior species, the present landscape structure was the main factor, but past changes in combination with the present structure can also contribute to species abundance variation.

4. Discussion

4.1. Time-lagged responses to dynamic landscapes

The deforestation rates from 1962 to 2000 in the Plateau of Ibiúna (2–3% year⁻¹) were as high as those observed today in the most intense deforestation areas in the Amazon Forest (Ferraz et al., 2005), and higher than those observed in other tropical forest regions (Achard et al., 2002; Brook et al., 2006). Surprisingly, re-growth rates were also particularly high (1–3% year⁻¹), reversing forest loss between 1962 and 1981, and partially balancing the deforestation in the second period (1981–2000). High deforestation rates may be caused by the proximity (circa 50 km) to one of the largest cities in the world, São Paulo. The 2007 population was 12 million within the city, and 18 million in the greater São Paulo area. The city causes deforestation pressure on the Plateau due to its demand for food, charcoal (especially during the Second World War) and more recently, urban expansion (Dean, 1997; Teixeira et al., 2009). On the other hand, re-growth rates are probably affected by more complex processes, and may be related to

fallow periods in agriculture, or with land abandonment after the collapse of the charcoal industry and of the local agricultural cooperative (Teixeira et al., 2009). In highly dynamic conditions, where fragment size and connectivity change considerably within a 20-years period, Fahrig (2005) has suggested that landscape structure should not exhibit a clear effect on species distribution patterns, given the short time for species to adapt to the spatial arrangement of habitat patches. In fact, time-lagged responses to landscape structure were estimated to be between 25 and 100 years for birds (Brooks et al., 1999a; Ferraz et al., 2007), or even longer than 100 years for long-living species such as vascular plants (Leach and Givnish, 1996; Paltto et al., 2006). However, contrary to Fahrig's hypothesis, even in this highly dynamic environment, we observed strong influences of not only present, but also past landscape structure on the contemporary distribution of species and individuals.

One of the most important findings of the present study is that several taxonomic groups, with different biological characteristics and life-cycle durations, were influenced by landscape history. While present landscape structure can be an important factor in explaining species richness and abundance patterns, past landscape structure also contributed considerably to the explanation of richness and abundance models for all groups, apart from small mammals and edge bird species. This result reinforces the conclusions of previous studies that have demonstrated a strong influence of past landscape structure on present biodiversity patterns (Harding et al., 1998; Metzger, 1998; Lindborg and Eriksson, 2004; Ernout et al., 2006). We provide the first evidence that not only is past landscape structure important (especially for trees), but also that the rate of change of fragment area and connectivity can have a strong influence on contemporary biodiversity patterns of understorey trees, interior forest birds and frog species. Therefore, recent changes in landscape structure, particularly the reduction in habitat connectivity observed from 1981 to 2000, can affect species persistence. In some cases, past addition of habitat through AREA or COR increases (mainly between 1962 and 1981), which resulted in intermediate secondary forests (20–40 years old), can positively affect strictly-forest species (such as forest frogs and understorey trees). Less specialized groups are either influenced by current connectivity patterns (such as non-forest small mammal species), or are apparently not influenced by landscape structure in any way (edge bird species). These differences are probably related to the greater capacity of these species groups to utilize the habitat matrix to move between forest fragments, while strictly-forest species will usually require a more structured forest condition, as provided by older re-growths (Barlow et al., 2007; Pardini et al., 2009).

Perhaps unsurprisingly, trees showed the clearest time-lag response, as they were affected by past but not present landscape structure. Due to their longevity, the response of trees to landscape changes is expected to be slow, and thus, the present species distribution should be strongly affected by past events. Previous studies have shown that young trees and plant species with short seed bank persistence and short longevity (annual plants) were less or unaffected by past landscape structure, while old trees and species with long seed bank persistence and long-lived perennial species were particularly affected by historical connectivity and/or area (Metzger, 1998; Lindborg, 2007). In the Ibiúna Plateau, the association between longevity and time-lag response is supported by comparing the responses of different taxonomic groups: in contrast to trees, small mammals, the studied group with the shortest life-cycles, were more affected by present landscape structure than by historical structure or by landscape dynamics. However, an analysis within the tree group did not support the relationship between longevity and time-lagged responses, since initial secondary species were associated with the 1962 landscape structure, while

late secondary and understorey species were associated with landscape structure in 1981.

Another life-history trait that is expected to be associated with time-lagged responses is forest dependence. Strictly-forest species, such as interior forest birds, exhibited stronger relationships with past landscape structure than edge species. Generalist species that do not depend exclusively on forest habitats, and use and/or move through the inter-habitat matrix more frequently, should be less affected by forest fragmentation (Gascon et al., 1999), and more influenced instead by the spatial arrangement of altered, non-forested habitats (Umetsu et al., 2008). On the other hand, strictly-forest species are more affected by forest disruption due to their low capacity to move through or use the matrix, and are thus confined to forest patches even if they do not provide adequate conditions for long-term persistence. In this case, a time-lagged response and an extinction debt should occur (Tilman et al., 1994).

As a consequence, the consistent influence of landscape dynamics supports the notion that diversity patterns in the Atlantic forest are unstable and that the extinction debt is still being paid (Brooks and Balmford, 1996; Brooks et al., 1999b). Due to the elevated deforestation and re-growth rates, the landscape at the Plateau of Ibiúna has progressively become dominated by young forests. If these conditions persist, only generalists and/or edge species will be maintained in the future, as has already been observed in long-term fragmented landscapes in the Atlantic forest region. This is the case in NE Brazil, where an impoverishment in tree assemblages and functional attributes such as reproductive traits and pollination systems has been observed (Santos et al., 2007; Lopes et al., 2009). In our study region, we observed a clear species loss compared to large neighbouring tracts of primary and secondary forests (>10,000 ha, Develey and Metzger, 2006). We also observed a modification in species composition in the fragmented landscape compared to continuous secondary forest (trees: Bernacci et al., 2006 and Durigan et al., 2008; birds: Martensen et al., 2008; frogs: Dixo, 2005; small mammals: Pardini et al., 2005; lizards: Dixo and Metzger, in press). Even if the studied secondary forests are still species-rich, the future loss of species through extinction can possibly not be compensated by the increase of species richness with forest aging (as suggested by Wright and Muller-Landau, 2006b), despite the proximity to large and well-preserved forest tracts (Dunn, 2004; Metzger et al., 2006). The species composition in older fragmented Atlantic forest regions, without large mature forest areas, suggests that contemporary species assemblages resulting from these two processes (extinction debt and re-growth) will only maintain a few generalist and edge-related species, and gradually lose strictly-forest taxa (Christiansen and Pitter, 1997; Ribon et al., 2003; Lopes et al., 2009).

This trend may not be restricted to our study region or to other similar Atlantic forest regions. Tropical forests around the world are progressively becoming dominated by secondary young forests. Almost half of the remaining tropical forest is secondary or disturbed (5,000,000 km²; Wright, 2005). In the Amazon, the largest tropical forest region in the world, the average age of secondary forests is below 5 years (Neeff et al., 2006). The fact that young secondary forests are such a dominant feature in the tropics, coupled with their limited value for long-term conservation, particularly if they are not close to mature forest areas, means that there are strong reasons to be concerned about the future of tropical forest biodiversity, even if the total forest cover is maintained (Brook et al., 2006; Gardner et al., 2007).

4.2. Relative importance of area and connectivity

Independent of a time-lag response, there was a clearly stronger biotic response to the connectivity variables (corridors and/or

gap-crossing connections) versus fragment area. While the area of studied fragments were relatively stable, particularly in the 1981–2000 period, the connectivity indices more clearly reflected the dynamic landscape in the Plateau of Ibiúna. Connectivity, particularly the area connected by corridors, increased when re-growth was higher than deforestation (1962–1981), and decreased when deforestation surpassed forest re-growth (1981–2000). The fact that species are more associated with connectivity indices suggested that species are sensitive to whole-landscape modifications, and not only to changes in fragment area or internal conditions. The results also suggested that the importance of fragment area and connectivity was mediated by the species' capacity to disperse or use altered habitats. Groups with low dispersal capacity, such as some assemblages of trees and forest small mammals, were particularly sensitive to the reduction of fragment area or to connection by corridors. On the other hand, species with a higher capacity to disperse or use altered habitats, which is likely the case for some bird species and non-forest groups, were more sensitive to changes in corridors or to the level of connectivity of the habitat through short gap-crossings, and less sensitive to fragment area. The importance of connectivity was previously reported in the studied region for different taxonomic groups: small mammals (Pardini et al., 2005), frogs (Dixo, 2005) and birds (Martensen et al., 2008). Particularly for small mammals, there was a clear differential response between endemic strictly-forest species and non-endemic generalist species (Umetsu and Pardini, 2007). While the first group is affected by fragment area and presence of corridors, the second group does not respond to forest configuration, but to the quality of the matrix habitats (Pardini et al., 2005; Umetsu et al., 2008). Similarly, we have observed that several small understorey birds species are able to cross short distances through the matrix (up to 80 m; Uezu et al., 2005; Awade and Metzger, 2008; Martensen et al., 2008), use stepping-stones (Boscolo et al., 2008), use corridors (Uezu et al., 2005; Martensen et al., 2008), change their movement behaviour (Hansbauer et al., 2008a) and increase their home range size in fragmented forests (Hansbauer et al., 2008b). These birds were more sensitive to connectivity parameters, which considered the distances among fragments and corridor connections that allow them to explore the functionally connected area (Martensen et al., 2008).

It is also remarkable that all taxonomic groups were related to corridor connections, even if those elements are essentially composed of edge habitats. The importance of corridors has been extensively reported in the literature (for recent examples or synthesis, see Levey et al., 2005; Damschen et al., 2006; Hilty et al., 2006; Lees and Peres, 2008). Despite some controversy, corridors are usually considered to be one of the most important landscape elements to facilitate movement of individuals and gene flow through fragmented landscapes (Simberloff et al., 1992). For the small mammals and frogs studied here, corridor connections increased alpha diversity and decreased spatial variability (beta diversity), probably favoring species movements, (re)colonization and reducing species turnover over time in small fragments (Pardini et al., 2005; Dixo, 2005). In the present study, we showed that different taxonomic groups are sensitive to corridor linkages, and that even old corridor connections (subsequently lost) have an influence on present species distributions.

The importance of fragment area and connectivity are clearly species (or group)-specific, but there are good indications that the remaining habitat cover can also affect this relationship. At an intermediate level of fragmentation and forest cover, as observed in the Plateau of Ibiúna, fragments are usually isolated by short to medium distances (10–150 m), and corridors can easily facilitate the connection among fragments. In these intermediate conditions, the loss of small corridors or fragments can have a disproportionate effect on species persistence by causing a func-

tional rupture in landscape-wide connectivity (Awade and Metzger, 2008).

4.3. Conservation implications

This study shows that a fragmented tropical landscape mainly composed of secondary forest fragments scattered in an agricultural matrix can still harbor a considerable part of the original biodiversity. Long term diversity maintenance requires re-growth to compensate for the extinction debt, while maintaining old-growth areas. Conservation or restoration actions become more urgent when the time-lag response is reduced, such as in highly fragmented landscapes with small and isolated fragments (Ernault et al., 2006). Conservation actions are also urgent when the re-growth process is slow, as in areas without a nearby stable source of species, spores or seeds (Chazdon, 2003; Dunn, 2004).

Furthermore, the observed high rates of deforestation and re-growth, which are relatively common in humid tropical regions (Mayaux et al., 2005), add more complexity and enhance biodiversity conservation possibilities in fragmented landscapes. On one hand, the reduction in the average age of forest fragments in human-dominated landscapes is a great threat, and enormous efforts should be allocated to protect mature and old-growth forests. The role of these forests for the persistence of highly sensitive species and for the maintenance of a large array of ecological processes cannot be offset in the short term with young secondary restored forests (Dunn, 2004; Barlow et al., 2007; Lopes et al., 2009). On the other hand, the high rates of forest re-growth observed in most tropical regions can also be used as a powerful instrument to improve population sustainability in fragmented landscapes through carefully managed restoration strategies (Rodrigues et al., 2009).

Our results also suggest that the effectiveness of conservation actions will depend on our capacity to consider historical landscape structure and dynamics in addition to existing connectivity patterns (primarily provided by corridors). Corridor restoration should be considered a high priority conservation action in highly degraded tropical forest landscapes, especially because this strategy can also be easily coupled with other important measures for species and environmental conservation, such as buffering aquatic environments, and/or the management of the entire landscape mosaic (Bennett et al., 2006; Lindenmayer et al., 2006).

In addition, even if the present landscape structure provides a satisfactory surrogate for species richness and abundance in some taxonomic groups (for example, small mammals and birds), our results (particularly in trees, birds, and frogs) clearly demonstrate for the first time that information on past landscape dynamics can greatly improve our capacity to understand species distribution patterns. As previously stated, the relationship between present landscape structure and species richness can lead to overly optimistic conclusions (Lövenhaft et al., 2004). These conclusions can, in turn, lead to erroneous conservation decisions, such as lack of conservation action where it is necessary, or wasted investment where it is not urgently needed. The temporal dimension should be considered in all conservation steps, from planning to field conservation actions. In particular, temporal parameters can be used as a supplementary proxy for biodiversity, and can thus be used to identify priority areas for conservation actions, including areas with the highest species extinction debts (Uezu, 2007) and the highest potential for future gains of species through restoration of secondary forests.

Our results clearly emphasize that landscapes have history (Lunt and Spooner, 2005; Balée, 2006), and to the extent that this history has a strong influence on the present distribution patterns of species in human-modified landscapes, it is crucial that its effects be considered when planning conservation activities.

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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.2009.01.033.

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