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Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation

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ABSTRACT

It is known that large fragment sizes and high connectivity levels are key components for maintaining species in fragments; however, their relative effects are poorly understood, especially in tropical areas. In order to test these effects, we built models for explaining understory birds occurrence in a fragmented Atlantic Rain Forest landscape with intermediate habitat cover (3%). Data from over 9000 mist-net hours from 17 fragments differing in size (2–175 ha) and connectivity (considering corridor linkages and distance to nearby fragments) were ranked under a model selection approach. A total 1293 individuals of 62 species were recorded. Species richness, abundance and compositional variation were mainly affected by connectivity indices that consider the capacity of species to use corridors and/or to cross short distances up to 30 m through the matrix. Bird functional groups were differently affected by area and connectivity: while terrestrial insectivores, omnivores and frugivores were affected by both area and connectivity, the other groups (understory insectivores, nectarivores, and others) were affected only by connectivity. In the studied landscape, well connected fragments can sustain an elevated number of species and individuals. Connectivity gives the opportunity for individuals to use multiple fragments, reducing the influence of fragment size. While preserving large fragments is a conservation target worldwide and should continue to be, our results indicated that connectivity between fragments can enhance the area functionally connected and is beneficial to all functional groups and therefore should be a conservation priority.

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1. Introduction

Habitat loss and fragmentation are pointed as main threats to biodiversity conservation (Wilcox and Murphy, 1985; Fahrig, 2003). These two processes create landscapes where fragments are relatively small and poorly connected (With, 1997; Fahrig, 2003). In these situations, fragment size and landscape connectivity are suggested as key structural features influencing species persistence (Fahrig and Merriam, 1985, 1994; Taylor et al., 1993; Hanski and Simberloff, 1997;

Metzger and Décamps, 1997; Beier and Noss, 1998; Metzger, 2000; Antongiovanni and Metzger, 2005). Fragment size is considered to be related to population size, and thus is associated with the extinction probability in a given patch (Temple and Cary, 1988; Roth and Johnson, 1993; Jules, 1998; but see Debinski and Holt, 2000; Bowman et al., 2002). Landscape connectivity, which is a measure of the capacity of the landscape to facilitate biological flows among habitat patches (for a complete discussion of this terminology, see Fischer and Lindenmayer, 2007), is related with (re)colonization (Fahrig

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and Merriam, 1985; Hanski and Simberloff, 1997; Franken and Hik, 2004) and rescue effects (Brown and Kodrick-Brown, 1977), key processes determining population maintenance in fragmented landscapes (Fahrig and Merriam, 1985; Hanski and Simberloff, 1997; Fahrig, 2003; Ewers and Didham, 2006; Fischer and Lindenmayer, 2007).

Few studies have compared the relative importance of connectivity and fragment size for the maintenance of species in fragmented landscapes (Turner, 1996; Ewers and Didham, 2006). Usually, fragment size is the most significant predictor of species richness for all taxa, and connectivity is only a secondary predictor (Drinnan, 2005). However, there are situations where connectivity is as important as or even more important than size, especially for small fragments situated near large ones (Metzger, 2000) or when inter-habitat matrix permeability is high (Pardini, 2004; Faria et al., 2006). Some authors argued that below a 30% habitat cover threshold, habitat configuration, i.e. the spatial distribution of habitat in the landscape, including its structural connectivity, becomes particularly relevant the species persistence (Andr n, 1994; Fahrig, 2003; Radford et al., 2005). It has also been hypothesized that connectivity can modulate species-area relationships (Bender and Fahrig, 2005; Ewers and Didham, 2006; Metzger, 2006). Apparently, in less connected landscapes, the loss of species with fragment area reduction is intensified when compared with well connected ones (Metzger, 2006).

To address these problems and to provide a more concrete support for management and conservation actions, in this study we analyzed the relative effects of patch size and connectivity for the understory bird community richness and abundance in a fragmented Atlantic Rain Forest region. Particularly, we considered three sets of hypotheses: (i) higher importance of area; (ii) higher importance of connectivity; and (iii) importance of both aspects. We discuss the implications of our results for biodiversity conservation not only for the Atlantic Rain Forest but also for other regions.

2. Methods

2.1. Study area

The studied landscape has 10,063 ha (SW 47°07'27"23°47'12" and NE 47°02'10"23°40'47") and is located in the crystalline Plateau of Ibi na (Pon ano et al., 1981), state of S o Paulo, south-eastern Brazil (Fig. 1). This is part of the Atlantic Rain Forest, one of the most rich (Myers et al., 2000) and threatened regions of the world, where less than 8% of the original vegetation cover is left (Myers et al., 2000; SOS Mata Atl ntica/INPE, 2002). Altitude ranges from 850 to 1100 m asl and the climate type is temperate warm and rainy (K ppen, 1948). The mean monthly temperature varies from 17 °C to 22 °C. The average annual rainfall is around 1 340 mm, with monthly means ranging from 60 to near 200 mm (Metzger et al., 2006).

The original forest in the region is defined as a transition between the highly humid coastal forests and the drier forests of the interior of S o Paulo (Catharino et al., 2006). It is classified as a Lower Montane Rainforest (Oliveira-Filho and Fontes, 2000). The most common tree families are Myrtaceae,

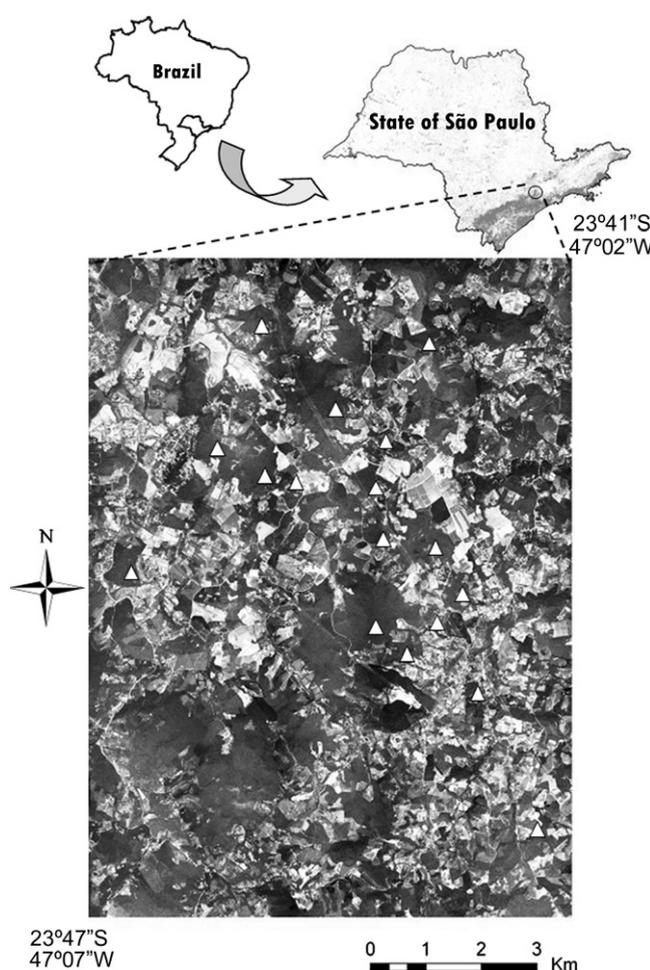


Fig. 1 – Localization of the study sites in the Ibi na Plateau, State of S o Paulo, Brazil. The more detailed map shows the landscape mosaic (aerial photographs from April 2000), containing different land cover types. Dark grey denotes forest cover and Δ represents the 17 sampled forest fragments.

Lauraceae, Fabaceae “sensu lato” and Rubiaceae (Bernacci et al., 2006; Catharino et al., 2006; Durigan et al., 2008).

Forest at an intermediate to advanced stage of succession (dense arboreal vegetation with canopy height >10–15 m, and occasional to frequent emerging species >25 m) corresponds to 31% of the landscape and is distributed in 358 fragments. Natural vegetation in early stages of succession (low arboreal vegetation, <8 m high, and/or shrub-arboreal formation) covers additional 17% of the landscape. Horticultural properties, pastures and abandoned fields correspond to 36% of the landscape, and human settlements and other types of more intense human occupations cover 16% of the area.

2.2. Study fragments

A total of 17 fragments varying in size from 1.95 to 175.09 ha were sampled. Selection of fragments in three size classes (<5 ha; 10–40 ha; >50 ha) was done randomly in order to cover a large fragment size range and presenting different connec-

tivity degrees. Only fragments with similar forest structure (intermediate to advanced successional stages), without severe disturbance (such as understory cleaning or cattle use) and with similar surrounding matrix permeability for bird species were considered.

2.3. Bird survey

Birds are one of the most studied taxonomic group in the Atlantic Rain Forest (Brooks and Balmford, 1996; Goerck, 1997; Marini and Garcia, 2005). In the present study, we considered the understory bird community. Mist-nets were used mainly because of their suitability for comparisons, since they are less influenced by observer-bias, they minimize identification errors, and they allow marking individuals for detection of movements through recaptures (Karr, 1981; Pearman, 2002).

At each fragment we set up a trail of 120 m of mist-nets. They were located at least 50 m from the nearest forest edge (except in some small fragments, where this was not possible), and in similar relief, luminosity and vegetation structure conditions (Silva et al., 2007). We used 10 mist-nets placed from the ground level up to 2.5 m of height (12 × 2.5 m, 36 mm mesh). 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. We opened the nets at sunrise (≈06:00) and closed it at sunset or mid-day. All captured birds were marked with numbered metal tags.

2.4. Dependent variables

Since sampling efforts were similar at all fragments, we analyzed differences among fragments based on total species richness (observed number of species), abundance (number of individuals captured) and composition. Bird community compositional aspects were obtained using a Non-metric Multidimensional Scaling, with Bray-Curtis dissimilarity in-

dex. We used abundance data and reduce the data set in to two compositional axes. All composition analyses were performed with vegan package, R 2.5.1. We also divided the bird species in to functional groups. The division was based on sensitivity to human disturbance (low, medium and high sensitivity; Stotz, 1996) and diet and habitat use (Willis, 1979; Table 1).

2.5. Area and connectivity indices

Aerial photograph from April 2000, on a scale of 1:10,000, were used to map forest cover (accuracy >88%; Silva et al., 2007) and to calculate landscape metrics. For the purpose of this study, we defined corridors as linear forest structures measuring ≤100 m of width. The studied corridors ranged from 25 to 100 m in width and from 50 to 1071 m in length. The area of the fragment (AREA) was then measured without considering the corridors.

Landscape connectivity has been measured in different ways and this has led to confusions and different interpretations (Tischendorf and Fahrig, 2000; Fischer and Lindenmayer, 2007). We opted to measure connectivity in a multi-scale approach considering the capacity of the species to use corridors and to cross the inter-habitat matrix. These measurements were done using the graph theory (Gross and Yellen, 1999). This theory is becoming popular in ecology where it has been used to define clusters of functional linked fragments (Keitt et al., 1997; Urban and Keitt, 2001). Connectivity was measured for each studied fragment and was defined as the area of forest linked according to six different rules: the area of forest linked by corridors, not considering the area of the focal fragment, but including corridor area (CA00); the area of forest surrounding the focal fragment that can be reached crossing 10 m of matrix (CA10); and similarly for the other linkage distances (CA20, CA30, CA40 and CA50). Fifty meters was the maximum used linkage distance considered because most of the understory species would not cross more than 50 m of open vegetation (Awade and Metzger, in

Table 1 – Bird species richness and abundance per fragment considering the whole community and the bird functional groups (Plateau of Ibiúna, SE Brazil)

	Species richness				Bird abundance			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Total community	17	32	25.12	4.76	41	131	76.06	26.04
<i>Habitat and diet functional groups</i>								
Edge species	1	7	3.82	1.42	3	19	9.88	5.04
Understory insectivores	6	14	11.11	2.73	13	58	32.64	12.57
Trunk and twig insectivores	2	5	3.35	0.93	3	18	8.76	3.84
Terrestrial insectivores	0	3	1	1	0	7	2.11	2.52
Nectarivores	0	3	1.41	0.79	0	10	3.35	2.69
Omnivores, frugivores and seed eaters	2	5	3.76	0.90	7	49	18.47	10.82
<i>Disturbance sensitivity</i>								
High	1	3	1.76	0.75	3	20	6.65	4.62
Medium	11	24	17.76	3.88	25	80	51.06	16.62
Low	3	9	5.41	1.28	7	39	18.18	8.42

SD: standard deviation.

press) and larger distances would clump most of the fragments together (Uezu et al., 2005).

In a preliminary analysis we found that connectivity by corridors and by gap-crossing presented distinct patterns from fragment to fragment. Besides the intrinsic relation of these variables in natural landscapes they varied somehow independently of AREA (Spearman correlation between AREA and CA00 to CA50 were, respectively, 0.63, 0.45, 0.35, 0.51, 0.39, and 0.04). This indicates that we could analyze AREA and connectivity variables independently.

2.6. Vegetation structure quantification

To control for variations in vegetation structure between the studied fragments, we quantified foliage stratification in 26 points along each mist-net line. In each point, we recorded the percentage of vegetation cover inside each height class (1 m) of an imaginary cylinder of 30 cm of diameter from the ground level to the canopy. The average frequencies, i.e. average percentage of leaf density at each height class of each study site, were then considered in a principal component analysis (PCA). The first three PCA axes correspond to 61.85% of the data variation (respectively 31.23%, 17.18% and 13.44%). Spearman correlation analyzes of these three axes with AREA and connectivity indices were not significant ($p > 0.05$) and presented low correlation values (< 0.50). These first two PCA axes had small influence in the model selection process, given proper fragment selection in order to control for vegetation variation, and thus we opted for not including these variables in further analyses. Variation in forest structure was then considered as homogeneous throughout fragments or clusters of linked fragments with different sizes, allowing testing the effects of size and connectivity independently of the forest structure.

2.7. Data analyses

We opted to use a model selection framework since this approach is considered more appropriate for complex observational experiments than traditional null hypothesis testing (Burnham and Anderson, 1998). The obtained results, a rank of the suitability of the pre-existing models, can be understood as an approximation of the explainable information in the empirical data.

For each dependent variable (total species richness, total bird abundance, and richness and abundance of each functional group) we built 13 models. These models contained different combinations of the independent variables:

- $DV = a + f \log_AREA + f \log_CAxx$
- $DV = a + f \log_AREA$
- $DV = a + f \log_CAxx$

where: DV = dependent variable; a = intercept; AREA = area of the fragment, $CAxx$ = fragment connectivity for a xx linkage distance ($xx = 00-50$ m); Poisson error distributions were assumed.

The models were transformed to the log scale (log of the variable +1) in order to allow analysis with linear models.

The best fit models were obtained by likelihood with Poisson error distribution with the General Linear Model (GLM) package in R 2.3.1.

To compare the 13 models, we used the Akaike Information Criterion (AIC, Burnham and Anderson, 1998) with the small sample correction (AICc) proposed by Hurvich and Tsai (1989), generating a rank from the best to the worst model. We also used the AICc weight (w_i), which is the selection probability of a given model in the cases of re-sampling the available data (Akaike, 1979). The evidence ratio ($wAICc_max/wAICc_i$) was used to visualize differences between models.

We cautiously prevented for multicollinearity and auto-correlation problems by avoiding the use of variables that were found highly correlated (for example two connectivity variables in the same model), as well as by avoiding the use of spatial auto-correlated data. We inspected for spatial dependence with Mantel tests (Mantel, 1967), using Sorensen distance for the biological (species or functional group abundance data) and Euclidian distance for the geographical matrix. After 1000 permutations in PC-ORD 4.14 (McCune and Mefford, 1999), all the tested variables presented low and non-significant correlation values.

3. Results

3.1. Community structure

A total of 1293 individuals of 62 species were recorded during 9137 net/hours of sampling at the 17 fragments. Observed species composition, richness and abundance per site varied considerably, both for all species and within each of the functional groups (Table 1).

3.2. Community models

The three best models to explain total community richness with evidence ration < 1.5 summed 51% of the $wAIC$ and contained only connectivity variables by short linkage distances (≤ 20 m) and corridor connections (Table 2). AREA was only included in the sixth best model, however, together with a connectivity metric. AREA alone was the eleventh best model to explain variation in richness with low support (evidence ration > 7) and $wAIC$ (3%). Models that include both AREA and connectivity variables accounted for 24% of the $wAIC$, while the ones only with connectivity variables accounted for 73% of the $wAICc$.

For abundance, a single model containing connections through corridors (CA00) was supported far better than others (Table 3). The second best model presented again the corridor variable, this time together with AREA. AREA alone was only the eleventh best model, with very low evidence ratio, only better than the models with longer linkage distances.

Compositional axes were particularly influenced by the large amount of species with occurrence in a unique site, but the axes appear to be related with species sensitivity to human disturbances. Compositional variation followed the same pattern of richness and abundance, with a higher influence of the connectivity variables (Table 4). AREA was within the best models only jointly with a connectivity variable.

Table 2 – Models of bird community richness variation in the 17 studied forest fragments from the Ibiúna Plateau (SE Brazil)

Rank	Area variable	Connectivity variables	AICc	Δ AICc	wAIC	Evidence ratio
1		CA10	98.79	0.00	0.19	1.00
2		CA20	98.98	0.19	0.17	1.10
3		CA00	99.21	0.42	0.15	1.23
4		CA40	99.76	0.97	0.11	1.62
5		CA30	100.47	1.68	0.08	2.32
6	AREA	CA20	101.08	2.29	0.06	3.15
7	AREA	CA10	101.18	2.40	0.06	3.31
8	AREA	CA00	101.80	3.01	0.04	4.51
9	AREA	CA40	101.92	3.13	0.04	4.79
10		CA50	102.45	3.66	0.03	6.24
11	AREA		102.76	3.98	0.03	7.31
12	AREA	CA30	102.85	4.06	0.02	7.61
13	AREA	CA50	103.05	4.27	0.02	8.45

Models are ranked from best to worst according to Akaike's Information Criterion weight (wAICc). Δ AICc is the difference between AICc from a considered model to the model with the lowest AICc value.

Table 3 – Models of bird community abundance variation in the 17 studied forest fragments from the Ibiúna Plateau (SE Brazil)

Number of model	Area variable	Connectivity variables	AICc	Δ AICc	wAIC	Evidence ratio
1		CA000	186.11	0.00	0.51	1.00
2	AREA	CA000	187.51	1.40	0.25	2.01
3	AREA	CA020	187.66	1.55	0.23	2.18
4	AREA	CA010	196.46	10.35	0.00	176.64
5		CA020	197.37	11.26	0.00	278.95
6	AREA	CA030	198.95	12.85	0.00	615.72
7		CA030	203.46	17.35	0.00	>5800
8		CA010	203.60	17.49	0.00	
9	AREA	CA040	206.42	20.31	0.00	
10	AREA	CA050	207.22	21.12	0.00	
11	AREA		212.33	26.22	0.00	
12		CA040	219.67	33.56	0.00	
13		CA050	233.62	47.51	0.00	

Models are ranked from best to worst according to Akaike's Information Criterion weight (wAICc). Δ AICc is the difference between AICc from a considered model to the model with the lowest AICc value.

Table 4 – Models for bird compositional variables presenting evidence ratio <2.0, considering abundance and presence/absence ordinations axes

First axis				Second axis			
Number of model	Area variable	Connectivity variables	Δ AICc	Number of model	Area variable	Connectivity variables	Δ AICc
1		CA040	0.00	1		CA010	0.00
2		CA000	1.19	2		CA030	0.24
3		CA010	1.40	3	AREA	CA010	1.45
4		CA020	1.84	4		CA020	1.98
5	AREA	CA040	1.94	5	AREA	CA030	1.99
6		CA050	2.25	6	AREA	CA020	2.63
7		CA030	2.87	7		CA040	2.76
8	AREA	CA000	3.16	8	AREA	CA040	3.64
9	AREA	CA050	3.19	9	AREA	CA050	6.99
10	AREA	CA010	3.33	10	AREA		7.65
11	AREA	CA020	3.60	11		CA000	8.10
12	AREA		3.74	12		CA050	8.68
13	AREA	CA030	4.72	13	AREA	CA000	9.06

AREA: area of the studied fragments; CA00: area connected by corridors; CAxx: area connected by linkage distances of xx m according to a graph theory approach. For each dependent variable, models are ranked from the highest to the lowest evidence ratio.

Table 5 – Models for richness and abundance of bird in the 17 studied forest from the Ibiúna Plateau (SE Brazil) presenting evidence ration <2.0, considering the whole community and the bird functional groups

	Richness	Abundance
Total	CA10, CA20, CA00, CA40	CA00
High sensitive	CA10, CA30, CA20, CA40	AREA + CA20, AREA + CA00, AREA + CA10
Medium sensitive	CA00, CA10, CA30, CA20, CA40	CA00
Low sensitive	CA20, CA00, CA10, CA50, CA30, CA40, AREA	CA20, CA00
Edge species	CA20, CA50, CA40, CA10, CA30, CA00, AREA	AREA + CA50
Understory insectivores	CA10, CA20, CA00, CA30, CA40, CA50	CA00
Terrestrial insectivores	CA30	AREA + CA20, AREA + CA10, AREA + CA40
Trunk and twig insectivores	CA00, CA20, CA10, AREA + CA30	CA00
Nectarivores	CA30, CA20, CA40, CA10, CA00	CA40, CA10
Omnivores, frugivores and seed eaters from lower strata	AREA, CA30, CA10, CA20, CA00, CA40	AREA + CA20

AREA: area of the studied fragments; CA00: area connected by corridors; CAxx: area connected by linkage distances of xx m according to a graph theory approach. For each dependent variable, models are ranked from the highest to the lowest evidence ratio.

3.3. Sensitivity by functional groups

The richness of most functional groups followed the general trend and was best explained by connectivity indices through short distances (<30 m; Table 5). Only edge species showed stronger relationships with longer distance linkages, and the trunk and twig insectivores with corridors. Omnivores, frugivores and seed eaters from lower strata were the unique group to be more sensitive to the AREA of the fragment than to connectivity indices (Table 5; see supplementary material for a full results table). For abundance, a different trend was observed: four groups were particularly sensitive to a combination of AREA with a connectivity index, and three to the linkage by corridors (Table 5 and supplementary material). Only connectivity indices were selected as best model for five of the nine functional groups.

4. Discussion

4.1. Relative importance of connectivity and area

Contrary to the expected from the literature, connectivity was more important than fragment area in predicting community and functional group richness. Landscapes with high connectivity, where fragments are close to each other and/or linked by corridors, provide the possibility for birds to use more than one fragment to obtain the necessary resources to survive, in daily or occasional movements (Andrade and Marini, 2001; Lees and Peres, 2008). Such landscape complementation (sensus Dunning et al., 1992) should result in larger re-colonization rates (Levins, 1969; Fahrig and Merriam, 1985; Hanski and Simberloff, 1997; Franken and Hik, 2004) and rescue effects (Brown and Kodrick-Brown, 1977), maintaining larger populations and richer communities, even in relatively small fragments. In this high connectivity condition, the area of habitat available is therefore not the fragment area but the total area of the fragments that are functionally connected.

The landscape connectivity can possibly explain when fragment area is an important factor acting on species richness, abundance and composition. In the Atlantic Forest, all evidences of a positive relationship of species richness with fragment size were obtained in landscapes with highly iso-

lated fragments (Willis, 1979; Christiansen and Pitter, 1997; Machado and Fonseca, 2000; Ribon et al., 2003), while no clear relationships were observed in a study in Espírito Santo where the connectivity was elevated (Marsden et al., 2001).

Furthermore, connectivity provided by short movements thru the matrix (≤ 30 m) or by corridors were particularly more effective to explain community variation than connectivity provided by larger linkage distances. Models that use long linkage distances variables were only important to explain results obtained for edge species, which are known as able for using and crossing matrix, are less affected by loss of forest quality, and thus, are less affected by fragmentation (Willis, 1979; Stouffer and Bierregaard, 1995). These results are supported by empirical evidences produced by play-back induced gap-crossing experiments in the same region, which suggested that for more sensitive understory bird species, gap crosses of 40 m through non-forest habitats are avoided (Awade and Metzger, in press). When crossing larger gaps, birds tend to use stepping-stones, as isolated trees in agricultural matrix (Boscolo et al., 2008). Previous studies also demonstrated that daily movements could be inhibited by open areas of 50–75 m (Laurance and Gómez, 2005), and even shorter gaps, as road interruptions, can prevent bird movements (Develey and Stouffer, 2001). Theoretically, as gap size increases, connectivity decreases (Hanski, 1994; Haddad, 1999).

The importance of corridors was particularly high for species with low capacity to move through the matrix: the species moderately sensitive to human disturbances, the understory insectivores and especially the trunk and twig insectivores. These species are considered sensitive to habitat fragmentation (Willis, 1979; Aleixo and Vielliard, 1995; Soares and Anjos, 1999; Anjos, 2001). They were mainly affected in their abundances, suggesting that corridors act directly in increasing fragment size or facilitating daily movements, maintaining populations by rescue effect, what do not influence richness but influences abundance. For these species, crosses throughout longer distances of open habitat would be infrequent (Boscolo et al., 2008; Hansbauer et al., 2008), thus insufficient for sustaining higher abundances rates. Corridor use was previously detected as a relevant factor for understory species (Anjos, 2001; Uezu et al., 2005), suggesting

that both aspects, area and connectivity, could be important for these species conservation (Anjos, 2001).

The unique group to be more affected by area than by connectivity was the omnivore/frugivore group. The importance of area for those species was registered previously (Willis, 1979; Ribon, 2003), and can be explained by the fact that food resources for those species tend to be temporally and spatially aggregated, and thus less frequent in smaller patches (Willis, 1979; Levey, 1988; Loiselle and Blake, 1991; McCarty et al., 2002). While large frugivorous from the upper canopy can obtain such patchy resources by having larger dispersal capacities, thus being capable of crossing large open areas (Anjos, 2001; Pizo, 2001), the studied understory species, such as *Schiffornis virescens* and *Mionectes rufiventris*, present a lower movement capacity, thus being more affected by fragment area (Willis, 1979; Ribon, 2003). The abundance of terrestrial insectivorous was also affected by fragment area. This group is considered as one of the most sensitive bird group to habitat fragmentation worldwide (Kattan et al., 1994; Borges and Stouffer, 1999; Beier et al., 2002; Sekercioglu et al., 2002; Watson et al., 2004) and in the Atlantic Rain Forest region (Willis, 1979; Aleixo and Vielliard, 1995; Ribon, 2003; Anjos, 2004), especially because of their low dispersal capacity. Thus, besides the higher importance of connectivity for most species, some groups were also affected by the size of the fragment, especially in their abundance, suggesting that the preservation of large size fragments should also be a target in order to preserve these species.

4.2. Conservation implications

Connectivity, either provided by corridors and/or by crossing small gaps between fragments, appears as a key element in the studied landscape, allowing species to explore the mosaic in different ways, permitting their maintenance in this landscape and in fragmented landscapes in general. Our results suggest a larger importance of connectivity over size of the fragment. This pattern can be particularly relevant in the studied conditions, where habitat cover is at an intermediate amount in the landscape (31%), and where fragments are separated by small distances and several fragments are linked by corridors. It is expected that in landscapes where fragments are more isolated, patch size would have a larger importance (Marini, 2001). From our and previous results, it is expected that relative effects of fragment size and connectivity would vary according to the amount of habitat. In landscapes with an intermediate proportion of habitat, connectivity would appear as the best predictor of bird abundance and richness, while in landscapes with a low amount of habitat, fragment size would probably be a better predictor. These results do not support a fragmentation threshold (Fahrig, 2003), because it suggests that configuration (including connectivity) would be particularly important at an intermediate amount of habitat (around 30%), and not only in conditions with lower habitat cover. Furthermore, the relative importance of area and connectivity will also vary according to the capacity of the species to move through the matrix, i.e. when their capacity is lower, the importance of the area of the fragment is higher, and vice-versa.

Several authors suggest as a “rule of thumb” for biodiversity conservation the selection of larger areas for preservation (e.g. Fahrig, 1997; Trzcinski et al., 1999). Large fragments should be a target, given their aptitude in preserving species of low dispersal capacity, larger area requirements and habitat demands; which are particular difficult to be preserved in this actual highly fragmented scenario of the Atlantic Rain forest. For some specialist groups, such as ground insectivorous and understory frugivorous/omnivorous, the size of the fragment is important and should be taken into account to preserve these species. However, our results suggest that connectivity is the key factor for the whole understory species persistence in the studied landscape. The short distance between fragments and the physical linkage through corridors allow the maintenance of a large number of species even in small fragments, because individuals are capable of using different fragments nearby or do occasional longer movements, maintaining marginal populations by rescue effects or re-colonization. Therefore, conservation management actions and restoration programs in landscapes with intermediate amount of forest should not only focus on large fragments, but also in promoting higher levels of connectivity among fragments, decreasing distances between them, and enhancing corridor connections. This general conservation guideline is particularly important for landscapes where no large fragment is left, which is the most common situation in the Atlantic Rain Forest region.

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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.2008.06.008](https://doi.org/10.1016/j.biocon.2008.06.008).

REFERENCES

- Akaike, H., 1979. A Bayesian extension of the minimum AIC procedure of autoregressive model fitting. *Biometrika* 66, 237–242.
- Aleixo, A., Vielliard, J.M.E., 1995. Composição e dinâmica da comunidade de aves da Mata de Santa Genebra, SP. *Revista Brasileira de Zoologia* 12, 493–511.
- Andrade, R.D., Marini, M.A., 2001. Movement of birds in natural forest patches in southeast Brazil, in: Albuquerque, J.L.B.,

- Cândido Jr., J.F., Straube, F.C., Ross, A.L. (Eds.), *Ornitologia e Conservação: da Ciência às Estratégias*. Editora UNISUL, Tubarão, pp. 125–136.
- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Anjos, L. dos, 2001. Bird communities in five Atlantic Forest fragments in southern Brazil. *Ornitologia Neotropical* 12, 11–27.
- Anjos, L. dos, 2004. Species richness and relative abundance of birds in natural and anthropogenic fragments of Brazilian Atlantic forest. *Anais da Academia Brasileira de Ciências* 76, 429–434.
- Antongiovanni, M., Metzger, J.P., 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation* 122, 441–451.
- Awade, M., Metzger, J.P., in press. Importance of functional connectivity to evaluate the effects of habitat fragmentation for three Atlantic Rainforest birds. *Austral Ecology* 33.
- Beier, P., Noss, R.F., 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12, 1241–1252.
- Beier, P., Drielen, M.V., Kankam, B.O., 2002. Avifaunal collapse in West African forest fragments. *Conservation Biology* 16, 1097–1111.
- Bender, D.J., Fahrig, L., 2005. Matrix spatial structure can obscure the relationship between inter-patch movement and patch size and isolation. *Ecology* 86, 1023–1033.
- Bernacci, L.C., Franco, G.A.D.C., Arbocz, G., Catharino, E.L., Durigan, G., Metzger, J.P., 2006. O efeito da fragmentação florestal na composição e riqueza de árvores na região da Reserva Morro Grande (Planalto de Ibiúma, SP). *Revista do Instituto Florestal* 18, 121–166.
- Borges, S.H., Stouffer, P.C., 1999. Bird communities in two types of anthropogenic successional vegetation in Central Amazonia. *Condor* 101, 529–536.
- Boscolo, D., Candia-Gallardo, C., Awade, M., Metzger, J.P., 2008. Importance of inter-habitat gaps and stepping-stones for a bird species in the Atlantic Forest, Brazil. *Biotropica* 40, 273–276.
- Bowman, J., Cappuccino, N., Fahrig, L., 2002. Patch size and population density: the effect of immigration behavior. *Conservation Ecology* 6 (1), 9 [online] URL: <http://www.consecol.org/vol6/iss1/art9/>.
- Brooks, T., Balmford, A., 1996. Atlantic forest extinctions. *Nature* 380, 115.
- Brown, J.H., Kodrick-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Catharino, E.L., Bernacci, L.C., Franco, G.A.D.C., Durigan, G., Metzger, J.P., 2006. Aspectos da composição e diversidade do componente arbóreo das florestas da Reserva Florestal do Morro Grande, Cotia, SP. *Biota Neotropica* 6 (2) [on line] URL: <http://www.biotaneotropica.org.br/v6n2/pt/abstract?article+bn00306022006>.
- Christiansen, M.B., Pitter, E., 1997. Species loss in a forest bird community near Lagoa Santa in Southeastern Brazil. *Biological Conservation* 80, 23–32.
- Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14, 342–355.
- Develey, P.F., Stouffer, P.C., 2001. Effects of roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil. *Conservation Biology* 15, 1416–1422.
- Drinnan, I.N., 2005. The search for fragmentation thresholds in a southern Sydney suburb. *Biological Conservation* 124, 339–349.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Durigan, G., Bernacci, L.C., Franco, G.A.D.C., Arbocz, G., Metzger, J.P., Catharino, E.L., 2008. Similaridade florística entre fragmentos florestais no Planalto Atlântico, estado de São Paulo, Brasil. *Acta Botânica Brasileira* 22, 51–62.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117–142.
- 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 Review of Ecology, Evolution and Systematics* 34, 487–515.
- Fahrig, L., Merriam, G., 1985. Habitat patch connectivity and population survival. *Ecology* 66, 1762–1768.
- Fahrig, L., Merriam, G., 1994. Conservation of fragmented populations. *Conservation Biology* 8, 50–59.
- Faria, D., Laps, R.R., Baumgarten, J., Cetra, M., 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. *Biodiversity and Conservation* 15, 587–612.
- Fischer, J., Lindenmayer, D.B., 2007. Tackling the habitat fragmentation panchreston. *Trends in Ecology and Evolution* 22, 127–132.
- Franken, R.J., Hik, D.S., 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *Journal of Animal Ecology* 73, 889–896.
- Goerck, J.M., 1997. Patterns of rarity in the birds of the Atlantic forest of Brazil. *Conservation Biology* 11, 112–118.
- Gross, J., Yellen, J., 1999. *Graph Theory and its Applications*. CRC Press, Florida.
- Haddad, N.M., 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* 9, 612–622.
- Hansbauer, M.M., Storch, I., Leu, S., Nieto-Holguin, J-P., Pimentel, R.G., Knauer, F., Metzger, J.P., 2008. Movements of neotropical understory passerines affected by anthropogenic forest edges in the Brazilian Atlantic Rainforest. *Biological Conservation* 141, 782–791.
- Hanski, I., 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63, 151–162.
- Hanski, I., Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski, I., Gilpin, M. (Eds.), *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London, pp. 5–26.
- Hurvich, C.M., Tsai, C.L., 1989. Regression and time series model selection in small samples. *Biometrika* 76, 297–307.
- Jules, E.S., 1998. Habitat fragmentation and demographic change for a common plant: trillium in old-growth forest. *Ecology* 69, 1645–1656.
- Karr, J.R., 1981. Surveying birds with mist nets. In: Ralph, C.J., Scott, J.M. (Eds.), *Studies in Avian Biology*, Cooper Ornithological Society, vol. 6. Allen Press Inc., Lawrence, pp. 62–67.
- Kattan, G.H., Alvarez-López, H., Giraldo, M., 1994. Forest fragmentation and bird extinction: San Antonio eighty years later. *Conservation Biology* 8, 138–146.
- Keitt, T.H., Urban, D.L., Milne, B.T., 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1 (1), 4 [on line] URL: <http://www.consecol.org/vol1/iss1/art4>.
- Köppen, W., 1948. *Climatologia*. Ed. Fondo Cultura Economica, Mexico City.

- Laurance, S.G.W., Gómez, M.S., 2005. Clearing width and movements of understory rainforest birds. *Biotropica* 37, 149–152.
- Lees, A.C., Peres, C.A., 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology* 22, 439–449.
- Levey, D.J., 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58, 251–269.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237–240.
- Loiselle, B.A., Blake, J.G., 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72, 180–193.
- Machado, R.B., Fonseca, G.A.B., 2000. The avifauna of Rio Doce Valley, southeastern Brazil, a highly fragmented area. *Biotropica* 32, 914–924.
- Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27, 209–220.
- Marini, M.A., 2001. Efeitos da fragmentação florestal sobre as aves em Minas Gerais, in: Alves, M.A.9S., Silva, J.M.C., Sluys, M.V., Bergallo, H.G., Rocha, C.F.D. (Eds.), *A Ornitologia no Brasil: Pesquisa Atual e Perspectivas*. Editora Uerj, Rio de Janeiro, pp. 41–54.
- Marini, M.A., Garcia, F.I., 2005. Bird conservation in Brazil. *Conservation Biology* 19, 665–671.
- Marsden, S.J., Whiffin, M., Galetti, M., 2001. Bird diversity and abundance in forest fragments and *Eucalyptus* plantations around an Atlantic forest reserve, Brazil. *Biodiversity and Conservation* 10, 737–751.
- McCarty, J.P., Levey, D.J., Greenberg, C.H., Sargent, S., 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. *Forest Ecology and Management* 164, 277–291.
- McCune, B., Mefford, M.J., 1999. *Multivariate Analysis on the PC-ORD System, Version 4*. MjM Software, Gleneden Beach.
- Metzger, J.P., 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. *Ecological Applications* 10, 1147–1161.
- Metzger, J.P., 2006. *Ecologia de paisagens fragmentadas*. Habilitation thesis. University of São Paulo, São Paulo, Brazil.
- Metzger, J.P., Décamps, H., 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Oecologica* 18, 1–12.
- Metzger, J.P., Alves, L.F., Goulart, W., Teixeira, A.M.G., Simões, S.J.C., Catharino, E.L.M., 2006. Uma área de relevante interesse biológico, porém pouco conhecida: a Reserva Florestal do Morro Grande. *Biota Neotropica* 6 (2) [on line] URL: <http://www.biotaneotropica.org.br/v6n2/pt/abstract?article=bn00406022006>.
- 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* 34, 793–810.
- Pardini, R., 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodiversity and Conservation* 13, 2567–2586.
- Pearman, P.B., 2002. The scale of community structure: habitat variation and avian guilds in tropical forest understory. *Ecological Monographs* 72, 19–39.
- Pizo, M.A., 2001. A conservação de aves frugívoras, in: Albuquerque, J.L.B., Cândido Jr., J.F., Straube, F.C., Ross, A.L. (Eds.), *Ornitologia e Conservação: da Ciência às Estratégias*. Editora UNISUL, Tubarão, pp 49–60.
- Ponçano, W.L., Carneiro, C.D.R., Bistrichi, C.A., Almeida, F.F.A., Prandini, F.L., 1981. Mapa geomorfológico do Estado de São Paulo. IPT Monografias No. 5, vol. I, São Paulo.
- Radford, J.Q., Bennett, A.F., Cheers, G.J., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124, 317–337.
- Ribon, R., 2003. *Aves em fragmentos de Mata Atlântica: incidência, abundância e associação à topografia*. Ph.D. Thesis. Federal University of Minas Gerais, Belo Horizonte, Brazil.
- Ribon, R., Simon, J.E., Mattos, G.T., 2003. Bird extinctions in Atlantic Forest fragments on the Viçosa region, southeastern Brazil. *Conservation Biology* 17, 1827–1839.
- Roth, R.R., Johnson, R.K., 1993. Long-term dynamics of a Wood Thrush population breeding in a forest fragment. *Auk* 110, 37–48.
- Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandi, R., 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Science* 99, 263–267.
- Silva, W.G.S., Metzger, J.P., Simões, S., Simonetti, C., 2007. Relief influence on the spatial distribution of the Atlantic Forest cover at the Ibiúna Plateau, SP. *Brazilian Journal of Biology* 67, 631–640.
- Soares, E.S., Anjos, L., 1999. Efeito da fragmentação florestal sobre aves escaladoras de tronco e galho na região de Londrina, norte do estado do Paraná, Brasil. *Ornitologia Neotropical* 10, 61–68.
- SOS Mata Atlântica/INPE, 2002. *Atlas da evolução dos remanescentes florestais da Mata Atlântica no período de 1995–2000*. Fundação SOS Mata Atlântica, São Paulo, Brazil.
- Stotz, D., 1996. *Neotropical Birds: Ecology and Conservation*. Chicago University Press, Chicago.
- Stouffer, P.C., Bierregaard Jr., R.O., 1995. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* 9, 1086–1095.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573.
- Temple, S.A., Cary, J.R., 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2, 340–347.
- Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. *Oikos* 90, 7–19.
- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9, 586–593.
- Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33, 200–209.
- Uezu, A., Metzger, J.P., Vielliard, J.M., 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological Conservation* 123, 507–519.
- Urban, D.L., Keitt, T.H., 2001. Landscape connectivity and metapopulation persistence: a graph-theoretic perspective. *Ecology* 82, 1205–1218.
- Watson, J.E.M., Whittaker, R.J., Dawson, T., 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography* 31, 1791–1807.
- Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125, 879–887.
- Willis, E.O., 1979. The composition of avian communities in remanescent woodlots in southern Brazil. *Papéis Avulsos de Zoologia* 33, 1–25.
- With, K.A., 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* 11, 1069–1080.