Contributed Paper

Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance

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Abstract: *Theoretical and empirical studies demonstrate that the total amount of forest and the size and connectivity of fragments have nonlinear effects on species survival. We tested how habitat amount and configuration affect understory bird species richness and abundance. We used mist nets (almost 34,000 net hours) to sample birds in 53 Atlantic Forest fragments in southeastern Brazil. Fragments were distributed among 3 10,800-ha landscapes. The remaining forest in these landscapes was below (10% forest cover), similar to (30%), and above (50%) the theoretical fragmentation threshold (approximately 30%) below which the effects of fragmentation should be intensified. Species-richness estimates were significantly higher (F = 3715, p = 0.00) where 50% of the forest remained, which suggests a species occurrence threshold of 30–50% forest, which is higher than usually occurs (<30%). Relations between forest cover and species richness differed depending on species sensitivity to forest conversion and fragmentation. For less sensitive species, species richness decreased as forest cover increased, whereas for highly sensitive species the opposite occurred. For sensitive species, species richness and the amount of forest cover were positively related, particularly when forest cover was 30–50%. Fragment size and connectivity were related to species richness and abundance in all landscapes, not just below the 30% threshold. Where 10% of the forest remained, fragment size was more related to species richness and abundance than connectivity. However, the relation between connectivity and species richness and abundance was stronger where 30% of the landscape was forested. Where 50% of the landscape was forested, fragment size and connectivity were both related to species richness and abundance. Our results demonstrated a rapid loss of species at relatively high levels of forest cover (30–50%). Highly sensitive species were 3-4 times more common above the 30–50% threshold than below it; however, our results do not support a unique fragmentation threshold.*

Keywords: Atlantic Forest, corridors, fragmentation, fragment size, thresholds, tropical landscapes.

Asociaciones de la Cobertura Forestal, Superficie del Fragmento y Conectividad con la Riqueza y Abundancia de Aves Neotropicales de Sotobosque

Resumen: *Estudios teóricos y empíricos demuestran que la cantidad total de bosque y el tamaño y la conectividad de los fragmentos tienen efectos no lineales sobre la supervivencia de especies. Probamos el efecto de la cantidad y configuración de hábitat sobre la riqueza y abundancia de especies de aves de*

sotobosque. Utilizamos redes de niebla (casi 34,000 horas red) para muestrear aves en 53 fragmentos del Bosque del Atlántico en el sureste de Brasil. Los fragmentos se distribuyeron en tres paisajes de 10,800 ha. El bosque remanente en estos paisajes era menor (10% cobertura forestal), similar (30%) y superior (50%) al umbral de fragmentación teórico (aproximadamente 30%) por debajo del cual se intensifican los efectos de la fragmentación. Las estimaciones de riqueza de especies fueron significativamente mayores (F = 3715, p = 0.00) donde permanecía 50% del bosque, lo que sugiere un umbral de ocurrencia de especies de 30–50% que es mayor a lo que ocurre usualmente (<30%). Las relaciones entre la cobertura de bosque y la riqueza de especies difirieron dependiendo de la sensibilidad de la especie a la conversión y fragmentación del bosque. Para especies menos sensibles, la riqueza de especies decreció a medida que incrementó la cobertura de bosque, mientras que ocurrió lo contrario para especies altamente sensibles. Para especies sensibles, la riqueza de especies y la cantidad de cobertura de bosque estuvieron relacionados positivamente, particularmente cuando la cobertura del bosque fue 30–50%. El tamaño del fragmento y la conectividad se relacionaron con la riqueza y abundancia de especies en todos los paisajes, no solo debajo del umbral de 30%. Cuando permanecía 10% del bosque, el tamaño del fragmento estaba más relacionado con la riqueza y abundancia de especies que la conectividad. Sin embargo, la relación entre la conectividad y la riqueza y abundancia de especies fue mayor donde 30% del paisaje tenía bosques. Donde 50% del paisaje tenía bosques, el tamaño del fragmento y la conectividad se relacionaron con la riqueza y abundancia de especies. Nuestros resultados demostraron una pérdida rápida de especies en niveles relativamente altos de cobertura forestal (30–50%). Especies altamente sensibles fueron 3–4 veces más comunes por encima del umbral de 30–50% que por debajo de él; sin embargo, nuestros resultados no sustentan un umbral de fragmentación único.

Palabras Clave: Bosque del Atlántico, corredores, fragmentación, paisajes tropicales, tamaño del fragmento, umbrales

Introduction

The effects of habitat quantity and spatial configuration on species persistence in fragmented landscapes and the existence of thresholds in species' occurrence and abundance relative to these variables are challenging ecological questions (Fahrig 2003; Fischer & Lindenmayer 2007; Hanski 2011). Anthropogenic changes in land cover may lead to reductions in the amount of habitat and changes in its configuration, both of which affect ecological processes (Bruun 2000; Borgella & Gavin 2005), including those related to species persistence (Hill & Curran 2003).

Results of theoretical studies suggest that habitat loss exerts strong effects on species extinctions in landscapes and that a distinct threshold may exist in this relation beyond which species disappear abruptly (Metzger & Décamps 1997; With & King 1999). This landscape species-extinction threshold could be related to rapid changes in landscape configuration below the percolation threshold. The percolation threshold is the amount of habitat at which there is at least one patch (or fragment) of habitat that is as wide as the landscape and thus spans (i.e., percolates) the landscape from one side to the other (Swift & Hannon 2010). Below this threshold, there is a sharp increase in number and isolation of patches and a decrease in the average patch size and thus a decrease in individual movements among habitat patches (Fahrig 2003). This pattern has been observed in simulated and real landscapes, and the amount of habitat at the percolation threshold varies on the basis of land-use patterns (Oliveira Filho & Metzger 2006).

Habitat fragmentation also affects species' extirpations and colonizations (Fahrig 2003; Fischer & Lindenmayer

2007). Size of a habitat patch is usually related to population size and is therefore associated with the probability of local extinctions (Temple & Cary 1988). Connectivity, which is a measure of the capacity of a landscape to allow species movements among habitat patches (Fischer & Lindenmayer 2007), is closely related to colonization dynamics, rescue effects (Brown & Kodrick-Brown 1977), and the movement of individuals among different patches (Martensen et al. 2008).

The effects of habitat configuration may vary along gradients of habitat loss (Flather & Bevers 2002; Fahrig 2003). Results of some studies suggest that the threshold of remaining habitat below which population persistence is affected by habitat loss and by habitat configuration (Lindenmayer et al. 2005; Radford et al. 2005) is 10-30% (Andrén 1994; Fahrig 2003). However, such thresholds are not always consistent among taxonomic groups and land-cover types (Lindenmayer et al. 2005; Swift & Hannon 2010).

Land-use changes can simultaneously change land cover and fragment habitat. Therefore, there is a correlation between how much habitat is lost and how the remainder is configured (Gustafson & Parker 1992; Andrén 1994). Disentangling the effects of land cover and configuration is contentious and challenging (Fahrig 2003), particularly because, even when highly correlated, these variables have been shown to increase support for models used to explain species occurrence (Cushman & McGarigal 2004). Investigators who have at least partially disentangled the confounding effects of habitat loss and configuration suggest that the amount of habitat is the primary driver of species abundance and occurrence (Trzcinski et al. 1999; Fahrig 2003). Others present data

that indicate species occurrence affected by habitat configuration and amount (Villard et al. 1999). The relation between habitat configuration and species occurrence and how it varies on the basis of the amount of habitat in landscapes are still open questions with limited empirical support (Fahrig 2003; Swift & Hannon 2010).

We focused on the relation between forest amount and configuration and richness and abundance of bird species in fragmented landscapes with high species diversity in southeastern Brazil (Ribeiro et al. 2009). In particular, we examined the relation between habitat amount and bird species richness; the relation between fragment size and connectivity and bird species richness and abundance; and whether these relations changed as habitat amount changed. We also tested whether the relations between habitat amount, fragment size, and connectivity and species richness and abundance varied on the basis of species sensitivity to habitat conversion and fragmentation.

Methods

Studied Landscapes

We selected 3 Atlantic Forest landscapes of 10,800 ha each in the Atlantic Plateau of São Paulo. From the nearest edges, the landscapes were separated by <122 km. Landscapes represented variations in total amount of forest cover (Fig. 1 & Supporting Information): low (Ribeirão Grande, 11% forest cover, hereafter 10%), intermediate (Caucaia do Alto, 31%, hereafter 30%), and high (Tapiraí, 49%, hereafter 50%). Respectively, these levels of forest cover, represented proportions less than, similar to, and above the proposed fragmentation threshold of approximately 30% habitat (Andrén 1994; Swift & Hannon 2010). The landscapes had similar relief, floristic composition, and climate (Supporting Information); however, they had different land-use histories. The existing spatial configuration of the studied landscapes resulted from dynamic land-use changes that occurred over the last decades. For example, there has been a recent decrease in forest cover in Caucaia do Alto (46% forest cover in 1981 to 31% in 2000), while forest cover has increased in the other 2 landscapes (Ribeirão Grande: 7% in 1980 and 11% in 2000; Tapiraí: 28% in 1978 and 49% in 2005 [Lira et al. 2012]).

We used Spot-5 images from 2005 with a 10-m resolution to classify land cover in Ribeirão Grande and Tapiraí. We established 3 land-cover classes that represented forest successional stages: early (canopy height 5–10 m), intermediate (canopy height 10–15 m), and late (canopy height >15m). Only the late-successional class was habitat for the species we surveyed; thus, we considered only this class as forest in our analyses. Land use was also classified from the Spot images and included pasture,

agricultural fields, non-native tree plantations, water bodies, urban areas, and rural buildings. In Caucaia do Alto, where birds were sampled in 2001 and 2002, we used aerial photographs with a 5-m resolution from the year 2000 to classify land cover and land use. To derive comparable fragment area and connectivity metrics between landscapes, we transformed the pixel resolution of the classified map from Caucaia do Alto to 10 m with nearest-neighbor resampling. We checked land-cover classes exhaustively across all the landscapes to validate and improve map quality. Checking was performed by visually surveying all existing roads and pathways, which allowed us to verify classifications over all the landscapes. We corrected all detected errors on the maps (for method details see Silva et al. 2007).

Studied Forest Fragments

We sampled 53 forest fragments: 17 in Ribeirão Grande and Caucaia do Alto and 19 in Tapiraí. We selected only fragments with similar vegetation structure (advanced successional stage with forest canopy height ≥15 m and >40 years of regeneration [Lira et al. 2012]) that had approximately circular shapes and a surrounding matrix of open vegetation (agriculture or pasture). The fragments were selected to encompass the complete range of fragment sizes and connectivity (explained below) within each landscape. Across all studied landscapes, the fragment sizes ranged from 2.1 to 158.5 ha (mean [SD] = 29.9 ha [36.8]): 4.7–92.3 ha in Ribeirão Grande (mean = 21.8 [22.6]), 2.1–158.5 ha in Caucaia do Alto (mean = 30.8 [39.9]), and 2.8–156.5 ha in Tapiraí (mean = 36.3 [44.1]). The sampled fragment sizes did not differ significantly among landscapes ($F = 0.23$, df = 52, $p = 0.63$). Distances between the centers of studied fragments were also similar in all landscapes (mean, minimum, and maximum distances respectively: Ribeirão Grande, 4951 m, 1010 m, 10,623 m; Caucaia do Alto, 3443 m, 423 m, 9845 m; and Tapiraí, 4255 m, 898 m, 10,160 m). However, the amount of forest surrounding the fragments within 500 m of the edge (300-m radii $F = 0.90$, $p = 0.41$; 500-m radii $F = 7.72$, $p = 0.001$) differed among landscapes, as did one connectivity metric (large crossing gaps) ($F = 9.02$, $p = 0.04$).

Dependent Variables

We used mist nets to sample the understory bird community (total effort 33,945 net hours). In each fragment, we established a 120-m-long transect with 10 2.5-m-high mist nets placed at ground level. Sampling effort in all fragments was >50% above the minimum estimated to be necessary for characterizing understory bird communities in Atlantic Forest fragments (Banks-Leite et al. 2012); however, due to logistical constraints there were some small differences in effort among landscapes. Total effort was 11,888 net hours (mean [SD] = 700 net
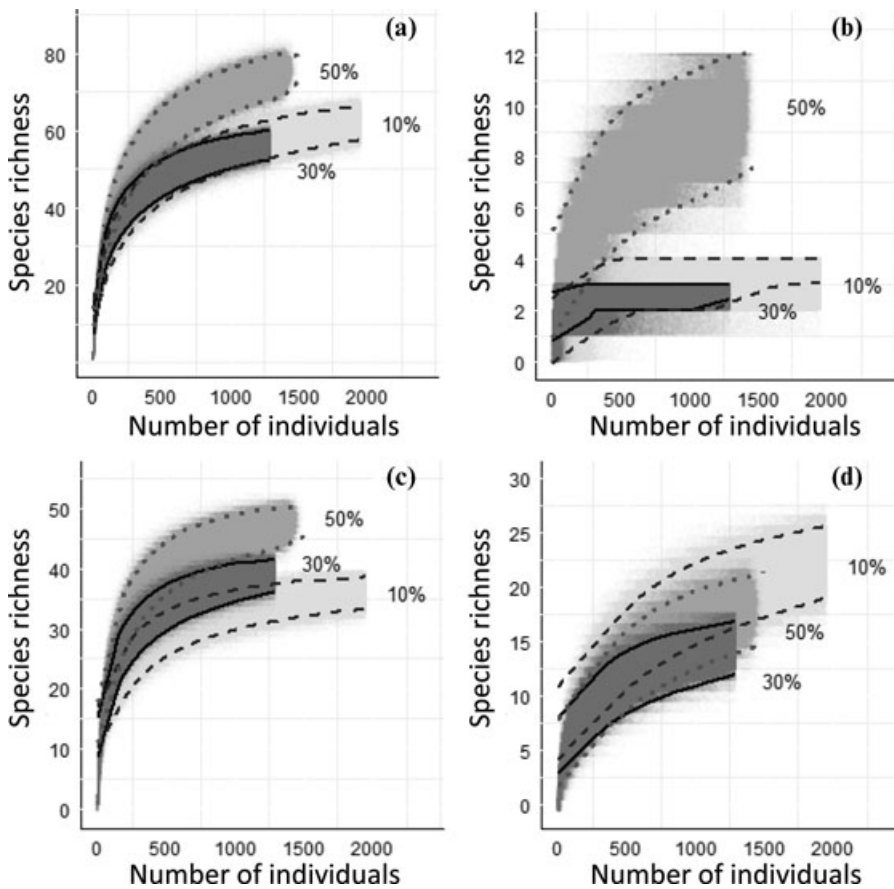
Figure 1. Accumulation curves of species richness (a) of individual birds (b) of birds that are highly sensitive species to human disturbance, (c) of birds that are moderately sensitive to human disturbance, and (d) of birds that are least sensitive to human disturbance sampled in areas with 3 different levels of forest cover (10%, 30%, and 50%) for each studied landscape (lines [dashed, dotted, solid], 95% CI of the simulations).

hours/fragment [21]) in Ribeirão Grande; 9137 net hours (mean = 540 net hours/fragment [6]) in Caucaia do Alto; and 12,920 net hours (equally distributed effort of 680 net hours/fragment) in Tapiraí. In all landscapes, effort was balanced between dry and wet seasons (Caucaia do Alto: 2001–2002; Ribeirão Grande: 2004–2005; and Tapiraí: 2005–2006) and was very similar between fragments within the same landscape (see SDs above); thus, we avoided possible systematic biases.

We used observed species richness per fragment as a measure of actual species richness and observed number of individuals as a measure of total abundance. We also inspected spatial autocorrelation of the dependent variables between landscape fragments with Mantel tests ("vegan" package in R version 2.8.0). We did not consider differences in species capture probabilities. We conducted exploratory analyses when abundances were included as explanatory variable of species richness. However, we did not consider abundance in the models because the results (model ranking, see below) were highly correlated with those obtained without its inclusion (Pearson's correlations > 0.8, with only one < 0.8, however > 0.7).

To test whether a species' response to forest cover, fragment area, and connectivity varied as a function of its sensitivity to habitat conversion and fragmentation, we classified each captured species into 3 disturbance

groups on the basis of what Stotz et al. (1996) refers to as forest species "sensitivity to human disturbance."

Independent Variables

Fragment areas exclude corridor area. Corridors were arbitrarily defined as forested areas ≤100 m wide that linked ≥2 fragments. We used 100 m because this value is commonly suggested by Brazilian environmental agencies as a corridor of sufficient width (CONAMA 1996). We used graph theory to calculate fragment connectivity (Urban & Keitt 2001; Martensen et al. 2008) and considered the capacity of species to use corridors and cross the matrix between patches. We considered 3 levels of connectivity: corridors (CA00), crossing gaps of 20 m through the matrix, and crossing gaps of 40 m through the matrix. We calculated the area of forest linked by corridors (area did not include the focal fragment but did include the corridor area and the area of the connected fragment); the area of forest surrounding the focal fragment that could be reached by crossing a 20-m gap in the forest (area of the focal fragment excluded); and the area of forest surrounding the focal fragment that could be reached by crossing a 40-m gap in the forest. We used a maximum distance of 40 m because most understory species will not cross more than 50 m of open vegetation in their daily movements (Hansbauer et al. 2008).

Data Analyses and Modeling

Because sampling efforts differed among landscapes, we compared species richness among landscapes on the basis of 20 bootstrap species-accumulation curves. The curves varied from one individual recorded to the total number of individuals recorded for each landscape. Because more fragments were sampled in Tapiraí (19) than in the other 2 landscapes (17 each), each bootstrap iteration for Tapiraí included data from 17 randomly selected fragments. Therefore, for each landscape we obtained bootstrapped curves for the total number of species, the number of species in each of the 3 sensitivity classes, and the associated 95% CIs for all of these cases. We used analysis of variance for between-landscape comparisons and a standardized sample of 1000 individuals.

To investigate the effects of fragment area and connectivity on species richness and abundance, we built 20 models (Table 1). Species richness (overall and per sensitivity class) was modeled with a Poisson error structure, whereas mean abundance values were modeled as Gaussian functions. In both cases, the expected values of the response variables were modeled as power functions of the dependent variables to detect nonlinear responses.

We did not include strongly correlated variables (Spearman $r > 0.50$) in the same model. The models were fitted by minimizing their negative likelihoods. The log-likelihood of the models was then used to calculate the Akaike information criterion corrected for small samples (AIC_c) (Burnham & Anderson 2002) and Akaike weights (w), which we used in model comparisons. We considered an AIC_c difference of <2 an indicator of equal weights of evidence. All analyses were conducted in R version 2.8.0, and all the likelihood analyses were run with the "bbmle" package (Bolker 2008).

To understand whether responses of richness and abundance to fragment area and connectivity varied among landscape (i.e., among different amounts of forest), we combined models with different combinations of the area and connectivity variables, one for each of the 3 landscapes, by summing their log likelihood to obtain the support for models for all landscapes. We then analyzed how the independent variables associated with bird richness and abundance differed among landscapes by ranking these models by their AIC_c values.

Results

We captured 4818 individual birds: 1952 in Ribeirão Grande, 1293 in Caucaia do Alto, and 1573 in Tapiraí. We recorded 118 species: 70 in Ribeirão Grande, 62 in Caucaia do Alto, and 87 in Tapiraí. Of the captured species, 55 (approximately 47%) were observed in 1 landscape, 25 (21%) were observed in 2 landscapes, and 38 (32%) were observed in all 3 landscapes. Of the 55 species observed

in 1 landscape, 18 were captured at Ribeirão Grande, 8 at Caucaia do Alto, and 29 at Tapiraí. Most of the species captured exclusively in Tapiraí, such as White-collared Foliage-Gleaner (*Anabazenops fuscus*), Variegated Antpitta (*Grallaria varia*), and the Sharp-billed Treehunters (*Heliobletus contaminatus*), were classified as highly sensitive to human disturbance. The species recorded only in Ribeirão Grande, such as Swainson's Flycatcher (*Myiarchus swainsoni*) and Orange-headed Tanager (*Thlypopsis sordida*), were mainly classified as least sensitive to human disturbance. We recorded 12 highly sensitive species in Tapiraí, 4 in Ribeirão Grande, and 3 in Caucaia do Alto, whereas 27 species in the least sensitive class were recorded in Ribeirão Grande, 23 in Tapiraí, and 17 in Caucaia do Alto. Of the moderately sensitive species, 39 were recorded in Ribeirão Grande, 42 in Caucaia do Alto, and 52 in Tapiraí.

The bootstrap curves presented similar expected species richness for 1000 individuals sampled in Caucaia do Alto (54.36 [SD 2.15]) and Ribeirão Grande (55.23 [2.64]), but species richness was over 25% higher in Tapiraí (70.95 [3.09], $F = 3715$, $P = 0.00$) (Fig. 1a). The results from the groups of species classified by their sensitivity to human disturbance showed that Tapiraí had 3 times the number of highly sensitive species (9 [1.3]) and more species that were classified as moderately sensitive to human disturbance (45.6 [1.9]) than Caucaia do Alto (3 [0.2] and 37.9 [1.6], highly and moderately sensitive respectively) and Ribeirão Grande (3.3 [0.6] and 33.2 [1.6], highly and moderately sensitive respectively). Differences in species richness of highly and moderately sensitive species richness were statistically significant between landscapes ($F = 4729.4$, $p = 0.00$ [Fig. 1b]; $F = 3912.4$, $p = 0.00$ [Fig. 1c]). Ribeirão Grande had the highest ($F = 658.61$, $p = 0.00$) (Fig. 1d) richness of least sensitive species (18.7 [1.9]) compared with Caucaia do Alto (13.5 [1.3]) and Tapiraí (16.3 [1.9]). There was a monotonic decrease in the richness of moderately sensitive species as forest cover decreased (Fig. 1c).

Forest-Configuration Effects and Forest Amount

The spatial correlations of our dependent variables were weak, particularly for Ribeirão Grande and Tapiraí (Ribeirão Grande: $r = -0.02$, $p = 0.58$ for richness and $r = -0.02$, $p = 0.55$ for abundance; Caucaia do Alto: $r = 0.19$, $p = 0.05$ for richness and $r = 0.19$, $p = 0.07$ for abundance; Tapiraí: $r = 0.04$, $p = 0.25$ for richness and $r = -0.05$, $p = 0.65$ for abundance); thus, there appeared to be no underlying spatial process that could have affected our results.

Fragment area and species richness and abundance were related in the landscapes with low (10%, $w = 0.33$ for richness and $w = 0.34$ for abundance) and high (50%, $w = 0.21$ for richness and $w = 0.45$ for abundance) forest cover. Where forest cover was 30%, corridors (CA00) and

Table 1. Models of the relation between forest area (fragment size) and connectivity on understory bird species richness and abundance in the Atlantic Forest, Brazil.

Model*	Effect tested
$E[Y] = a1 * (\text{area})^{a2}$	Fragment size
$E[Y] = a1 * (\text{CA00})^{a2}$	Corridor connectivity
$E[Y] = a1 * (\text{CA20})^{a2}$	Small crossing gaps
$E[Y] = a1 * (\text{CA40})^{a2}$	Large crossing gaps
$E[Y] = a1 * (\text{area})^{a2} * (\text{CA00})^{a3}$	Fragment size and corridor connectivity
$E[Y] = a1 * (\text{area})^{a2} * (\text{CA20})^{a3}$	Fragment size and small crossing gaps
$E[Y] = a1 * (\text{area})^{a2} * (\text{CA40})^{a3}$	Fragment size and large crossing gaps
$E[Y] = a1 * (\text{area})^{a2} * (\text{CA00})^{a3} * (\text{area} * \text{CA00})^{a4}$	Fragment size and corridor connectivity and their interaction
$E[Y] = a1 * (\text{area})^{a2} * (\text{CA20})^{a3} * (\text{area} * CA20)^{a4}$	Fragment size and small crossing gaps and their interaction
$E[Y] = a1 * (\text{area})^{a2} * (\text{CA40})^{a3} * (\text{area} * \text{CA40})^{a4}$	Fragment size and large crossing gaps and their interaction

E [Y], estimated species richness and abundance of all species or species richness and abundance of species classified on the basis of sensitivity to human disturbance (low, intermediate, and high sensitivity to human disturbances [Stotz et al. 1996]); area, area of habitat fragment; CA00, connectivity provided by corridors; CA20, areas with small crossings gaps (20 m); CA40, areas with larger crossing gaps (40 m); a1, a2, a3, a4, estimated parameters of the power functions.

areas accessible by small crossing gaps (CA20) were retained in the most strongly supported model for species richness (CA00, $w = 0.38$; CA20, $w = 0.25$) and abundance (CA00, $w = 0.64$) (Fig. 2 & Supporting Information). Connectivity provided by corridors helped explain richness and abundance ($w = 0.21$, $w = 0.20$ respectively) in the landscape with low forest cover, and fragment area associated with corridor connections helped explain abundance ($w = 0.22$) in landscapes with 50% forest cover (Fig. 2 & Supporting Information).

The models with the same variable for all landscapes (e.g., area for all landscapes) were less supported than those that included different variables among landscapes (e.g., area for the 10%, CA00 for the 30%, and CA20 for the 50% forested landscape) (Table 2) because $\Delta \text{AIC}_c = 3.32$ for the best supported model of species richness with the same variables in any landscape and $\Delta \text{AIC}_c = 7.58$ for the best supported model of abundance with the same variables in any landscape. For models that included the same variable for all landscapes (Table 2), the models that included only corridors (CA00) were supported for explaining species richness ($w = 0.37$) and bird abundance ($w = 0.31$). The corridor and fragment area (area * CA00) model was the best supported model for bird abundance ($w = 0.58$) for any of the landscapes, whereas the model with corridors alone (CA00) was the best supported for species richness. For species richness, the corridor model (CA00) was followed by small gaps (CA20, $w = 0.35$) and then fragment area ($w = 0.18$). For abundance, only the fragment area and corridor model (area * CA00) and the corridor (CA00) model were supported ($\Delta \text{AIC}_c < 2$).

The relation between fragment area and species richness was strong for birds in all 3 classes of sensitivity to human disturbance, regardless of the landscape (Tables 3 & 4). For highly sensitive species, fragment area was highly related to species richness, especially where forest cover was 10% ($w = 1.00$), and small crossing gaps

were also strongly related to species richness where forest cover was 30% ($w = 0.34$) and 50% ($w = 0.45$). For moderately sensitive species, fragment area in landscapes with 10% forest cover ($w = 0.46$) and corridors (CA00, $w = 0.40$) and short gap crossings (CA20, $w = 0.49$) in landscapes with 30% or 50% forest cover were related to species richness (Tables 3 & 4). For the least sensitive species, connectivity was more closely related to species richness than area where forest cover was 10% (CA20, $w = 0.26$) and 30% (CA00, $w = 0.28$), whereas area ($w = 0.30$) was more closely related to species richness where forest cover was 50%.

Abundance of species in the highly sensitive class differed from abundance of species in the other sensitivity classes (Tables 3 & 4). The most strongly supported models for highly sensitive species included both fragment area and connectivity in landscapes with 30% (area * CA00 * [area * CA00], $w = 0.98$) and 10% forest cover (area * CA40 * [area * CA40], $w = 0.44$ and area * CA20 * [area * CA20], $w = 0.38$), but only the model with fragment area was supported where forest cover was 50% (area, $w = 0.41$). For moderately sensitive species, the most strongly supported models included fragment area for 10% ($w = 0.28$) and 50% forest cover ($w = 0.44$), whereas only the model with corridors was supported for 30% forest cover ($w = 0.73$). The model containing corridors and fragment area (area * CA00) was supported where forest cover was 50% ($w = 0.23$). Where forest cover was 10%, models with 20-m gaps and 40-m gaps were also supported. For the least sensitive species, connectivity models were more strongly supported than models with fragment area where forest cover was 10% (CA00, CA20 and CA40) and 50% (CA20, $w = 0.32$ and CA40, $w = 0.27$). In the 30% forested landscape, models that included fragment area and corridors were more strongly supported (area * CA00, $w = 0.41$ and area * CA00 * [area * CA00], $w = 0.20$), followed by models with corridors alone (CA00, $w = 0.18$).
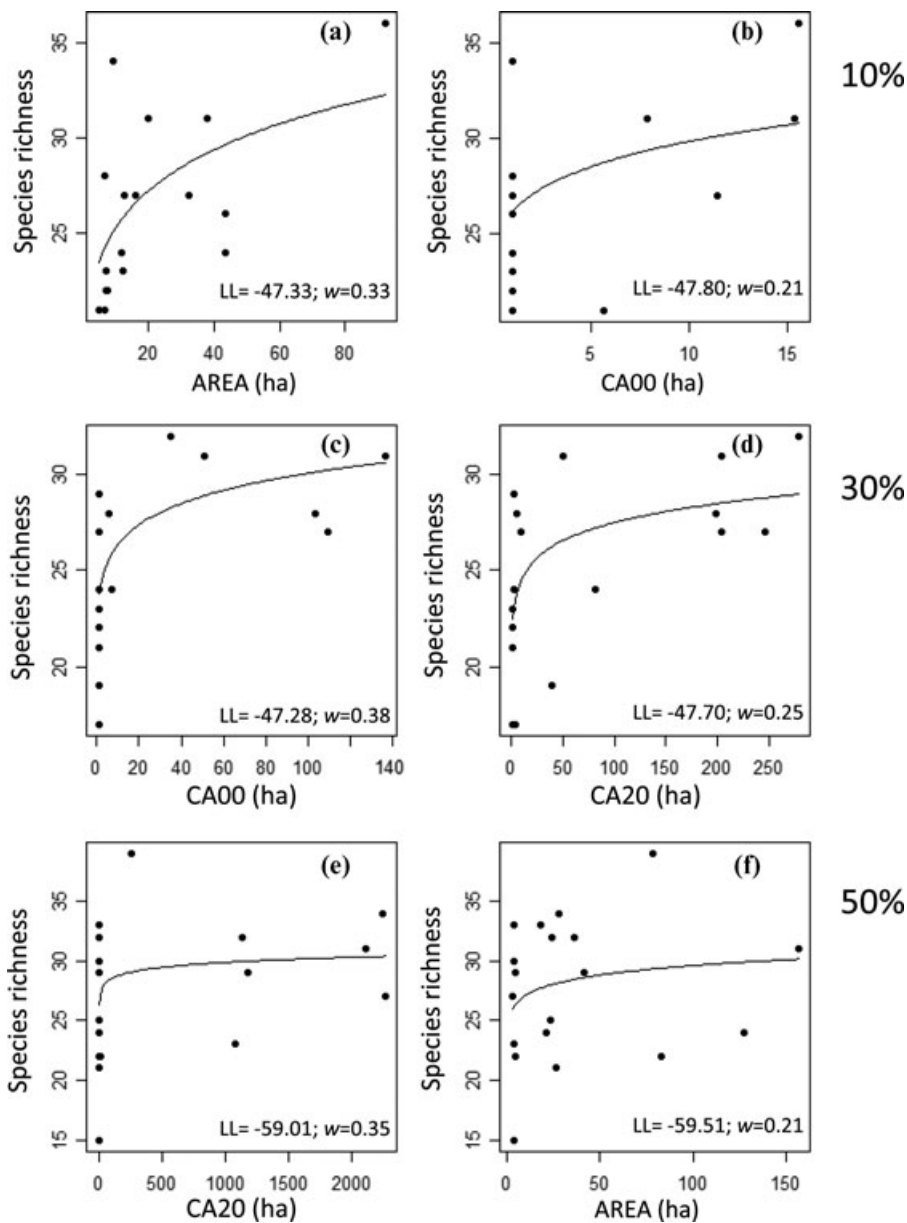
Figure 2. Best-supported models of the relation between bird species richness and abundance and the 3 levels of forest cover: (a, b) species richness in Ribeirão Grande, (c, d) species richness in Caucaia do Alto, (e, f) species richness in Tapiraí, (g, h) species abundance in Ribeirão Grande, (i) species abundance in Caucaia do Alto, and (j) species abundance in Tapiraí (area, area of forest fragment; CA00, corridor connections; CA20, area accessible by small crossing gaps; LL, log-likelihood; w, Akaike information criterion [AIC] weight; 10%, 30%, 50%, levels of forest cover). For the entire model ranking and likelihoods, AICs and model weights, see Supporting Information.

Discussion

The relation between bird species richness and amount of forest cover in the landscape was strong; when forest cover was reduced from 50% to 30%, the number of species declined abruptly to 75%. Our results suggest that species richness decreased sharply as a function of habitat amount (Fig. 1a), where forest cover was 50% there were 3 times more highly sensitive species than in the other landscapes (Fig. 1b). The number of moderately sensitive species decreased along a gradient of decreasing forest cover, whereas an opposite trend was observed with the least sensitive species. Furthermore, we found a threshold beyond which species richness declined abruptly: 30–50% forest cover. This range of forest

cover may represent a higher forest-cover threshold than suggested by previous researchers.

Pardini et al. (2010), who sampled nonvolant small mammals in the same landscapes as we sampled, observed a similar pattern of abrupt declines in species richness, but at lower levels of forest cover (10–30%). The difference in threshold values between our study and Pardini et al. (2010) suggests that highly sensitive bird species require more forest and higher connectivity to survive than forest-dependent small mammal species. Similar results have been observed for temperate birds and mammals, where an abrupt loss of species usually occurs between 10% and 30% forest cover (e.g., Andrén 1994; Cushman & McGarigal 2003; Radford et al. 2005). One possible reason for the higher threshold values we
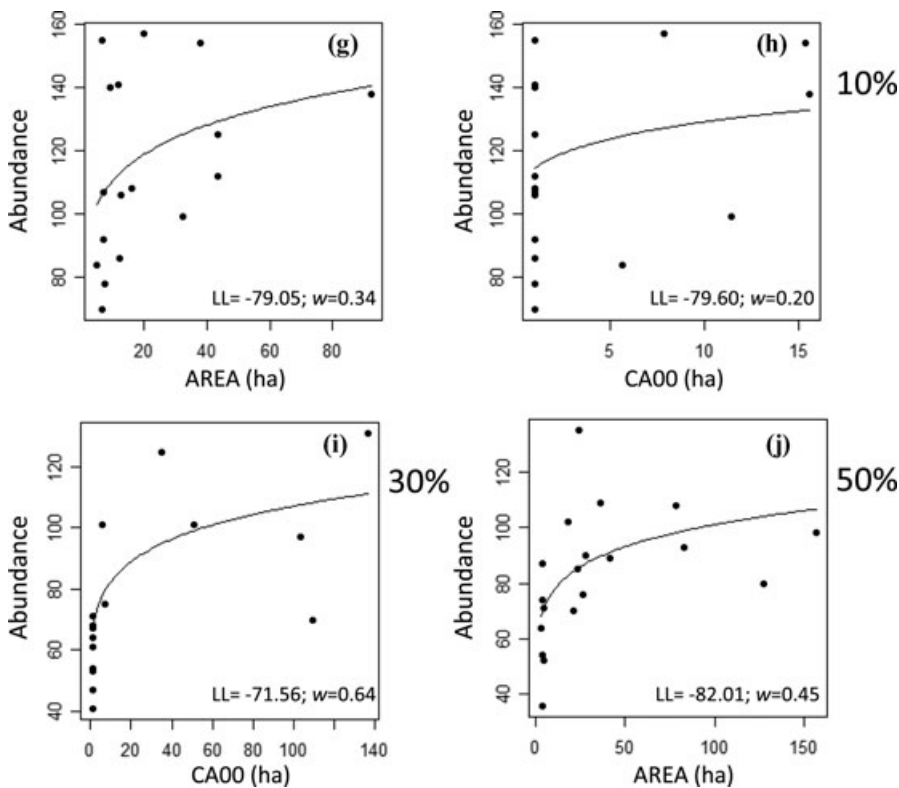
Figure 2. Continued

found is that the composition of most tropical bird communities is characterized by a large proportion of rare and specialized species. These specialized species are typically more sensitive to alterations in their habitat than generalist species and have lower mobility through non-habitat areas and are thus expected to be affected quickly when habitat decreases.

Our results do not support the existence of a single "fragmentation threshold," which would be a certain (constant) amount of forest below which habitat configuration has a stronger influence than above. Rather, our results indicate that in landscapes with an intermediate proportion of remaining forest, such as 30%, connectivity provided by corridors, which is essentially a landscape configuration parameter, could be more important than fragment size (i.e., the local amount of habitat) in determining species richness and abundance.

The importance of fragment size and connectivity varies as a function of forest amount at the landscape scale, especially when considering species abundance. A fragmentation threshold seemed to occur for highly sensitive species because the model that combined fragment area and connectivity best accounted for species abundance in landscapes with 30% and 10% forest cover, whereas fragment area alone predicted abundance in 50% forest cover. Moderately sensitive species were particularly affected by connectivity in landscapes with 30% forest cover. The least sensitive species appeared to have an inverse pattern; their abundances were more strongly related to fragment area in landscapes with 10% forest cover

and to corridors or areas with small crossing gaps where forest cover was 50%. These results suggest that spatial configuration may have a greater influence in landscapes with greater proportions of forest than would have been expected on the basis of results from earlier studies.

Although simulated landscapes have demonstrated an intrinsically high correlation between habitat amount and configuration (Gustafson & Parker 1992), real patterns of land use show a certain independence between these 2 variables, which can be particularly important in situations with intermediate amounts of habitat. For instance, in landscapes where 10% of habitat remains, the distances between fragments are greater (Fahrig 2003), and, even if a similar range of fragment sizes is maintained, connectivity is severely compromised relative to landscapes with more habitat (Venier & Fahrig 1996). We found that under these circumstances fragments with low overall connectivity were strongly affected by local conditions, such as fragment size and corridor connections.

As habitat amount increases (to approximately 30%), landscapes contain fragments that are close to each other (Fahrig 2003) and usually containing forest corridors or "stepping stones," both of which improve connectivity (Boscolo et al. 2008; Martensen et al. 2008; Uezu et al. 2008). In these cases, movements of individuals between fragments are more common, which directly reduces the probability of species extirpations (Hanski 1999, 2011). This is especially true for moderately sensitive species, which are better able to use structures such as corridors (Martensen et al. 2008) and stepping stones (Boscolo

Table 2. Best supported models (AIC$_c$ ≤ 2) of the relation between forest area (fragment size) and connectivity and species richness and abundance of understory bird species in landscapes with 3 levels of forest cover in the Atlantic Forest, Brazil.[a]

Richness[b]

Forested 10%	Forested 30%	Forested 50%	AIC$_c$	delta1	delta2	w_1	w_2
Area	CA00	CA20	321.69	0.00		0.21	
Area	CA20	CA20	322.53	0.84		0.14	
CA00	CA00	CA20	322.63	0.94		0.13	
Area	CA00	Area	322.69	1.00		0.13	
CA00	CA20	CA20	323.47	1.78		0.08	
Area	CA20	Area	323.53	1.84		0.08	
CA00	CA00	Area	323.63	1.94		0.08	
CA00			325.01	3.32	0.00	0.04	0.37
CA20			325.14	3.45	0.13	0.04	0.35
Area			326.46	4.77	1.45	0.02	0.18

Abundance[b]

Forested 10%	Forested 30%	Forested 50%	AIC$_c$	delta1	delta2	w_1	w_2
Area	CA00	Area	488.54	0.00		0.29	
CA00	CA00	Area	489.63	1.09		0.17	
Area	CA00	area*CA00	489.97	1.43		0.14	
CA40	CA00	Area	490.51	1.97		0.11	
CA20	CA00	Area	490.54	2.00		0.11	
	Area*CA00		496.12	7.58	0.00	0.01	0.58
	CA00		497.40	8.86	1.28	0.00	0.31

[a] Each model combines independent effects of patch metrics on the expected richness in each landscape, fitted as separate power functions (see Methods and Table 1 for model equations).

[b] Abbreviations: AIC$_c$, Akaike information criterion with small sample correction; delta1, difference between the minimum observed AIC$_c$ and any other AIC$_{ci}$; delta2, difference between the minimum observed AIC$_c$ for the same model for all landscapes and any other AIC$_{cf}$ for the same model for all landscapes; w_1, model weights for all models; w_2, model weights for the same model for all levels of forest amount; area, area of forest fragment; CA00, connectivity provided by corridors; CA20, small gap crossings (20 m); CA40, large gap crossings (40 m).

et al. 2008) or to cross short gaps in the matrix (Awade & Metzger 2008) than more sensitive species (Hansbauer et al. 2008). In these situations, we found that connectivity was related to species richness and abundance; even small fragments often supported high species richness and abundance of understory bird species when they were well connected.

In landscapes with higher amounts (approximately 50%) of remaining forest, the relation between connectivity and species richness and abundance was strong. Moreover, given the presence of an additional pool of highly sensitive species (Fig. 1a,b), the relation between fragment area and species richness and abundance was also strong. This reflects the distribution patterns of highly sensitive species, such as the Variegated Antpitta (*Grallaria varia*) and the Rufous-capped Ant Thrush (*Formicarius colma*), which are ground insectivores that are highly sensitive to openings in the forest canopy and require large areas relative to other understory species (Kattan et al. 1994).

Pardini et al. (2010) suggest that the effects of fragment size on nonvolant small mammals varies depending on the amount of forest in the landscape. Our results show that the effects of both area and connectivity vary as a function of the amount of forest, depending on the species group (30–50% for birds in our study vs. 10–30% for nonvolant small mammals in Pardini et al.'s 2010 study). For instance, patch size may not affect small mammals where the landscape is 50% habitat because connectivity is sufficient to allow movement between patches (Pardini et al. 2010), which may not be possible for highly sensitive bird species.

Although our results lend some support to a nonlinear relation between habitat amount and patterns of species richness and abundance, our results should be interpreted with care because we examined only 3 landscapes. Nevertheless, the habitat-amount threshold we found could be related to an extinction threshold for the most sensitive species, which are present in larger numbers in the tropics. For these species, it is important to conserve large and well-connected fragments, which are more frequent in landscapes with higher amounts of habitat. Thus, our results suggest that landscapes with large proportions of remaining habitat (>50%) should be targeted for conservation because they may maintain and serve as source areas for highly sensitive species, which depend on particular configuration conditions that do not occur in landscapes with lower amounts of forest. Furthermore, Brazil is currently modifying its environmental legislation, and these efforts may result in <20% of each property being protected (Metzger et al. 2010). Our results suggest that this alteration may lead to additional species losses in Brazil's landscapes.

The general response pattern of the understory bird community of the Atlantic Forest does not support a unique fragmentation threshold. Rather, habitat

Table 3. Best supported models (ΔAIC$_c$ < 2) of the relation between forest area (fragment size) and connectivity and species richness and abundance of birds with different levels of sensitivity to human disturbances (Stotz et al. 1996) in landscapes with 3 levels of forest cover in the Atlantic Forest, Brazil.[a]

Variable and forest cover (%)		*high*					*medium*					*low*			
		Model	LL	AIC$_c$	Δ	w	Model	LL	AIC$_c$	Δ	w	model	LL	AIC$_c$	Δ	w
Species richness	10	Area	−23.92	52.71	0	0.26	Area	−43.75	92.36	0.00	0.29	CA20	−37.46	79.78	0.00	0.22
							CA00	−44.00	92.86	0.50	0.22	CA40	−37.49	79.84	0.05	0.21
							Area*CA00	−43.20	94.25	1.89	0.11	Area	−37.53	79.92	0.13	0.20
												CA00	−37.61	80.07	0.29	0.19
	30	CA20	−25.36	55.58	0	0.27	CA00	−45.53	95.91	0.00	0.29	CA00	−33.01	70.88	0.00	0.24
		Area	−25.72	56.30	0.72	0.19	CA20	−46.02	96.90	0.99	0.18	CA20	−33.20	71.26	0.38	0.24
		CA40	−25.81	56.48	0.90	0.17	Area	−46.31	97.47	1.56	0.13	CA40	−33.38	71.62	0.74	0.17
		CA00	−25.85	56.55	0.97	0.17	CA40	−46.34	97.54	1.63	0.13	Area	−33.44	71.74	0.86	0.16
												Area*CA00	−32.44	72.72	1.84	0.10
	50	CA20	−33.50	71.75	0	0.30	CA20	−51.97	108.69	0.00	0.31	Area	−42.59	89.92	0.00	0.23
		Area	−33.75	72.25	0.50	0.24	Area	−52.38	109.50	0.81	0.21	CA40	−42.69	90.13	0.21	0.20
		Aea*CA20	−32.90	73.40	1.65	0.13	CA40	−52.92	110.60	1.91	0.12	CA20	−42.72	90.20	0.28	0.20
												CA00	−43.22	91.18	1.26	0.12
Species abundance	10	Area*CA40 (area*CA40)	−34.47	84.39	0	0.44	Area	−76.01	159.87	0	0.28	CA00	−61.60	131.05	0	0.22
		Area*CA20 (area*CA20)	−34.63	84.71	0.32	0.38	CA00	−76.17	160.18	0.31	0.24	CA20	−61.63	131.10	0.05	0.22
	30	Area*CA00 (area*CA00)	−27.46	70.37	0	0.98	CA40	−76.71	161.27	1.40	0.14	CA40	−61.64	131.12	0.06	0.21
							CA20	−76.72	162.28	1.41	0.14	Area	−61.65	131.14	0.09	0.21
							CA00	−65.98	139.81	0	0.73	Area*CA00	−54.37	120.07	0.00	0.41
	50	Area	−51.7	111.0	0.0	0.41	Area	−77.48	162.56	0.00	0.44	Area*CA00* (area*CA00)	−53.03	121.52	1.45	0.20
							Area*CA00	−76.48	163.83	1.26	0.23	CA00	−56.92	121.70	1.63	0.18
												CA20	−62.62	132.85	0.00	0.32
												CA40	−62.80	133.20	0.36	0.27

[a] See Table 1 for model equations.

[b] LL, model log likelihood; AIC$_c$, Akaike information criterion with small-sample correction; Δ, differences between the minimum observed AIC$_c$ and the AIC$_{c,i}$ (define i); w, model weights; area, fragment area; CA00, connectivity provided by corridors; CA20, small crossing gaps (20 m); CA40, large crossing gaps (40 m).

Table 4. Average model weights ($\bar{w}$) of all models for which $\triangle AIC_c < 2$ for species richness and abundance of species classified on the basis of sensitivity to human disturbance (low, medium, and high [Stotz et al. 1996]) in landscapes with 3 levels of forest cover in the Atlantic Forest, Brazil.

Variable and forest cover (%)		Species sensitivity to human disturbances and model weights					
		Low	*w*	*Medium*	*w*	*High*	*w*
Species richness	10	CA20	0.26	Area	0.46	Area	1.00
		CA40	0.26	CA00	0.36		
		Area	0.25	Area * CA00	0.18		
		CA00	0.23				
	30	CA00	0.28	CA00	0.40	CA20	0.34
		CA20	0.23	CA20	0.24	Area	0.24
		CA40	0.19	Area	0.18	CA40	0.22
		Area	0.18	CA40	0.18	CA00	0.21
		Area * CA00	0.11				
	50	Area	0.30	CA20	0.49	CA20	0.45
		CA40	0.27	Area	0.32	Area	0.35
		CA20	0.26	CA40	0.19	Area * CA20	0.20
		CA00	0.16				
Abundance	10	CA00	0.26	Area	0.35	Area * CA40 * (area * CA40)	0.54
		CA20	0.25	CA00	0.30	Area * CA20 * (area * CA20)	0.46
		CA40	0.25	CA40	0.17		
		Area	0.24	CA20	0.17		
	30	Area * CA00	0.52	CA00	1.00	Area * CA00 * (area * CA00)	1.00
		Area * CA00 * (areaA * CA00)	0.25				
		CA00	0.23				
	50	CA20	0.54	Area	0.65	Area	1.00
		CA40	0.46	Area * CA00	0.35		

Abbreviations: area, fragment area; CA00, connectivity provided by corridors; CA20, short crossing gas (20 m); CA40, large crossing gaps (40 m).

configuration was related to species richness and abundance along the entire gradient of habitat amount, particularly for intermediate proportions of forest cover, independent of species sensitivity to anthropogenic disturbance.

Acknowledgments

Supporting Information

Descriptions of the sample region, sampling effort, and its distribution (Appendix S1), maps of the study areas and a graphical representation of the connectivity index (Appendix S2), and complete AIC_c tables for every model and a species list (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of the material) should be directed to the corresponding author.

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