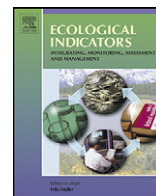




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The confounded effects of habitat disturbance at the local, patch and landscape scale on understorey birds of the Atlantic Forest: Implications for the development of landscape-based indicators

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ABSTRACT

The search for surrogates of changes in species richness and community structure in fragmented landscapes involves not only the selection of predictors, such as landscape metrics or environmental variables, but also the identification of the spatial scale that is most relevant to the taxa in question. However the heavily intercorrelated nature of many structural features in fragmented landscapes complicates analyses, and the wide variation in species responses prevents the identification of a general trend. In this study, we used a two-tiered hierarchical variation partitioning to identify the unique and shared effects of: 1 – changes in vegetation structure at the plot scale, patch structure (size and shape), and forest cover at the landscape scale; and 2 – variables within these scales; as predictors of species richness and species' abundances of birds in a fragmented landscape of Atlantic Forest; with the goal of aiding to the development of biodiversity indicators. Birds were sampled with mist-nets with a constant effort of 680 net-h at each of 23 sites, which resulted in almost 2600 captures. At the community level, regression models showed that changes in plot, patch and landscape scale variables explained a large proportion of the variation in species richness, but results from variation partitioning showed that the intercorrelation among predictors was so high that the unique contribution of each was non-significant. Our results point to a relatively large unique effect of local and landscape scale variables at the community level, but we also show that results vary greatly depending on the trophic guild being analysed. At the species level, multiple scale models also presented high explanatory power, however, species responses were so varied that we could not detect a general trend. We conclude that there is no single 'best' scale that could function as a proxy for changes in bird communities because each species and functional guild is uniquely affected by the environment, and suggest that efforts should be focused on finding indicators that encompasses all scales and the needs of different taxa.

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1. Introduction

The use of landscape-based indicators can be a reliable, powerful, as well as time- and cost-effective approach for remotely assessing community structure and integrity (Banks-Leite et al., 2011). One of the reasons underlying the efficacy presented by landscape-based indicators is that habitat loss, fragmentation and degradation are the main causes of biodiversity loss (Gardner et al., 2009); thus, indicators built from landscape metrics and environmental variables representing anthropogenic disturbances have a

causal relationship with species and communities. While it is undisputed that most species are strongly influenced by habitat cover, patch structure and/or habitat quality (see Barlow et al., 2007; Fahrig, 2003; Gardner et al., 2009), there are many examples of idiosyncratic biological responses to each of these factors. For this reason, it is still largely unknown how the combination of these factors structure natural communities and therefore which of these factors would be most effective as biodiversity indicators.

There is an extended literature on the importance of habitat quality, patch structure and habitat loss for species of various taxa (Banks-Leite et al., 2010; Banks-Leite and Cintra, 2008; Barlow et al., 2007; Coreau and Martin, 2007; Ewers and Didham, 2007; Fahrig, 2002; Fleishman and Mac Nally, 2007; Laurance et al., 2002; Saab, 1999; Trzcinski et al., 1999). However, vegetation structure and composition are highly influenced by patch size and edge effects (Laurance et al., 2006; Santos et al., 2008), and patch configuration is

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usually correlated with the amount of forest cover in the landscape (Andr  n, 1994; Fahrig, 2003). Moreover, the variables described above represent three distinct hierarchical scales; the plot, patch and landscape scale (Cushman and McGarigal, 2004). Given that these factors are both causally associated and nested in space, it is not surprising that they are also highly inter-correlated, and that researchers have encountered so many difficulties separating their effects (Koper et al., 2007).

In one of the first attempts to partition the effects of environmental variables at the plot, patch and landscape scales, Cushman and McGarigal (2004) found that the conditions at the plot scale had larger unique effects (e.g. effects that can be attribute to only one predictor) than variables at the patch and landscape scales in structuring bird communities. Cushman and McGarigal's (2004) results framed what they termed the "proximity-influence hypothesis", which postulates that species should be more strongly affected by conditions at the vicinity of individual organisms (plot scale), rather than diffuse influences at larger spatial scales (patch and landscape scales).

Nonetheless, there is accumulating evidence showing that different taxa respond in diverse ways to environmental variables and spatial scales (Barlow et al., 2007; Boscolo and Metzger, 2009; Gardner et al., 2008). Boscolo and Metzger (2009), for instance, searched for the optimum landscape scale to predict the occurrence of three bird species of the Atlantic Forest, and their findings show that each of the three species investigated were more strongly correlated to a particular spatial scale, a result believed to be related to the variation in species' area requirements due to their dietary needs. Boscolo and Metzger (2009) suggest that omnivorous species should be affected by conditions at smaller spatial scales because these species feed on a wide range of resources (Hasui et al., 2007) and therefore may be able to shift between fruits and arthropods without having to move long distances. By contrast, insectivorous species have a more restricted diet and may have to forage through very large areas to secure their required intake of energy (Develey and Peres, 2000). If this is true, then hummingbirds, which have very exclusive diets and which can track resources through very large areas (Altshuler, 2006; Cotton, 2007), should be expected to respond more strongly to conditions at large spatial scales. This hypothesis is further supported by a recent review showing that the feeding guild of Neotropical vertebrates is one of the main predictor of responses to habitat loss and fragmentation (Vetter et al., 2011).

In this study, we used data from an understory bird community of the Atlantic Forest to identify (1) the spatial scale at which biodiversity indicators would be most effective and (2) which landscape metric or measure of habitat structure would be the most effective indicator within each scale. We used a two-tiered variation partitioning approach to first assess the unique and shared effects of variables across scales; and then, within each spatial scale we aimed to assess the effects of scale-specific variables that act as a proxy for describing the environment at that scale. We discuss the results in the light of the proximity-influence hypothesis, also searching for trends in the unique effects of each spatial scale across different trophic guilds and one habitat specialisation guild. For the latter, we chose the group of sensitive species; those that are highly affected by all levels of human disturbances (Stotz et al., 1996). Because many of these species have been shown to be affected by habitat quality, edge effects and patch size, and forest cover at several spatial scales (Banks-Leite et al., 2010; Develey and Metzger, 2006; Van Houtan et al., 2007; Zurita and Bellocq, 2010), we hypothesised that sensitive species should show strong responses to all spatial scales. We looked for patterns at the community level, as these results could provide us with a framework for finding general trends in species-rich communities; however, we also conducted the same set of analyses on the abundances of the most

common species from each trophic guild. Although we expected community and species-level patterns to be somewhat matched, we anticipated to find variation among the two trends as the variables that determine the number of species in an assemblage do not necessarily impact the abundances of all species in the same way.

2. Methods

2.1. Study area

The study was conducted in the Atlantic Plateau of the State of S  o Paulo, Brazil. Part of the sampling was conducted in a 10,000 ha fragmented landscape (23  50'S, 47  20'W), which has nearly 50% of native forest cover. We also sampled in an adjacent forested area, the State Park of Jurupar  , which is located just 5 km from the fragmented landscape (see Banks-Leite et al., 2010 for more details on the study area).

We sampled a total of 19 patches in the fragmented landscape and an additional four sites in the State Park (Fig. 1). Forest patches were chosen to reflect the natural variation in patch size and connectivity present in the fragmented landscape. Thus, we selected seven small patches ranging from 3 to 5 ha, eight medium-sized patches from 8 to 30 ha and four large patches of 90–150 ha. The four control sites in Jurupar   State Park were separated by at least

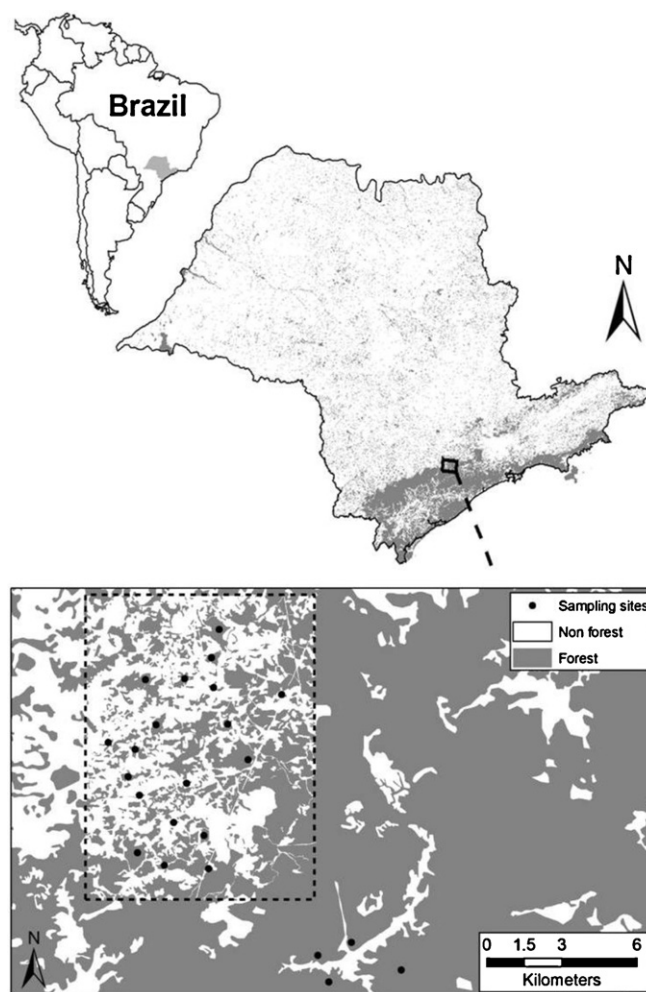


Fig. 1. Location of the study area in the State of S  o Paulo, south-eastern Brazil, showing the location of the fragmented landscape (dotted lines) and adjacent control forest and the sampling sites where understory birds were captured (circles).

1.5 km, were located at least 400 m from the nearest forest edge, and situated in two large blocks of forest of approximately 6700 ha and 14,800 ha each.

2.2. Sampling the bird community

Understory birds were sampled using 10 mist nets (12 m length, 2.5 m high, 31 mm mesh) positioned in a single line. We sampled each of the 23 sites in four surveys of two consecutive days from 2005 to 2007, totalling 680 net-h per site. The capture of birds with mist-nets was authorised by the Brazilian Center of Research for Conservation of Wild Birds (CEMAVE – IBAMA under the Registry Number 522117), which also provided numbered aluminium bands for individual marking.

Birds were categorised into three trophic groups and one habitat specialisation category that divided bird species according to their sensitivity to human disturbances (Develey, 2004; Hasui et al., 2007; Narosky and Yzurieta, 2003; Stotz et al., 1996). The groups were: insectivorous species, omnivorous species, nectarivorous species and sensitive species. We analysed the total number of species captured and individual assemblages (hereafter referred to as species richness), and abundances of the most common species (species with ≥ 50 individuals captured) within each trophic guild.

2.3. Measuring variables at the plot, patch and landscape scales

At all 23 sites, we assessed habitat conditions at the plot scale by measuring vegetation structure in a 300 m² plot (2.5 m \times 120 m) along the mist net line. Inside this plot we measured variables related to forest integrity (Catharino et al., 2006) and that are known to be related to bird community structure (Hasui et al., 2007; Pearson, 1975; Piacentini and Varassin, 2007). Specifically, we recorded the diameter at breast height of all trees (above 5 cm DBH) and the number of tank bromeliads in bloom at up to 4 m high above ground. We also quantified understory vegetation stratification with 42 foliage height profiles in each plot. Every 6 m along the plot, we sampled two points (one on each side of the path) with a 2.5 m vertical pole and recorded the 50-cm height intervals which had vegetation touching the pole. Habitat conditions at plot scale were quantified as (1) the mean of the DBH, (2) the number of bromeliads inside each plot (log scale), and (3) the understory vegetation stratification represented by the first axis of a principal components analysis (PCA) performed on the 42 profiles of foliage height distribution at each site. PCA axis 1 captured 40% of the variation in foliage height profiles and was negatively related to areas with denser foliage vegetation at 1–2 m from the ground. Disturbed forest sites are known to have lower mean DBH and lower numbers of tank bromeliads, but a higher foliage density in the understory (low values of PCA axis 1) (Brown, 2003; Tabarelli et al., 1999).

To measure forest cover and patch structure, we classified a Spot 5 image from 2005 into forest and non-forest with a 10 m resolution, with exhaustive field checking performed to validate and improve map accuracy. Patch and landscape metrics were calculated using Fragstats 3.3 (McGarigal and Marks, 1995) and were also chosen for their known effects on several taxa (Banks-Leite et al., 2011; Boscolo and Metzger, 2009; Ewers and Didham, 2007). Patch level metrics related to habitat configuration were: (1) patch size, (2) perimeter to area ratio of the patch, and (3) distance from the sampling point to the nearest edge; with all variables being log-transformed. Landscape variables related to the landscape context around a patch, represented by the proportion of forest cover in circles of radii of 300 m, 800 m and 1300 m around the sampling point.

2.4. Statistical analyses

We first performed a Mantel test with 1000 permutations to check for spatial autocorrelation in the bird community composition among sites in the fragmented landscape. We also used Pearson's correlations to check the underlying correlation structure among predictors.

We used hierarchical variation partitioning (Cushman and McGarigal, 2002) to assess the unique and shared contribution of each factor to the models explaining patterns of spatial variation in the bird community, while accounting for the correlated nature of predictors and their nested structure in space. Starting with the single scale models (Tier 2), we used simple and multiple linear regressions to partition the variation among the (1) predictors at the plot scale: mean DBH, foliage stratification and number of tank bromeliads; (2) predictors at the patch scale: patch area, perimeter to area ratio, distance to edge; and (3) predictors at the landscape scale: percentage of forest cover in a radius of 300, 800 and 1300 m from the sampling point. Then, we performed a separate principal components analysis (PCA) on each set of plot, patch and landscape variables to restrict the number of explanatory variables in multiple scale models into just one PCA axis for each scale. Plot scale PCA was performed directly on mean DBH, number of bromeliads and the profiles of foliage height distribution at each site. We partitioned the variance across plot, patch and landscape scales by using the PCA axes representing each scale (Tier 1). We report the coefficient of determination, R^2 , as a measure of explanatory power representing: (1) the unique effects (i.e. the contribution on the response variable that can be attributed to just one predictor) and (2) the shared effects (i.e. the contribution on the response variable that is shared by two or more predictors). Large unique effects from single variables or single scales would indicate the potential efficacy of such predictors as biodiversity indicators.

Inspection of model residuals showed that normal errors provided the best fit to community level regression models, but Poisson errors provided the best fit for models of species abundances. Consequently, we used linear models for community level analyses and generalised linear models for species level analyses. For the latter, we report instead the pseudo- R^2 (explained deviance) as the measure of explanatory power of the models, and the Wald χ^2 test as a measure of statistical significance (Crawley, 2007). The use of GLMs did not alter the variation partitioning procedure. The statistical significance of unique effects was assessed with residual regressions (Koper et al., 2007). All analyses were performed in R v2.11.0 (R Development Core Team, 2009).

3. Results

In total, we captured 2166 individuals belonging to 109 bird species (Table S1). The bird community was typical of rich tropical areas with some abundant species (30 species with more than 30 individuals), but numerous rare species (73 species with less than 10 individuals). A Mantel test showed that there was no spatial autocorrelation in species composition among sites ($r=0.058$, $P=0.252$).

The first axis of the PCA performed on patch and landscape-scale variables explained 90 and 88% of the variation, respectively, and were highly correlated (Table S2). The PCA performed on plot-scale variables explained 33.5% of the variation, but was not significantly correlated with either patch or landscape scale axes. The second PCA axis explained a further 15% of the variation and was a better predictor of the bird community than PCA1 (Table S2).

Table 1
Coefficients of determination (R^2) for single-scale and multiple-scale regression models on the number of species captured from different assemblages with PCA variables representing the plot, patch and landscape scale (Tier 1). Regression models significant at $P \leq 0.05$ are marked in bold. Results from variation partitioning, reported inside parentheses, refer to the R^2 of the unique contribution specific to each scale and the shared contribution across scales. None of the unique contributions were significant at $P \leq 0.05$. Shared contributions cannot be tested for significance and may show negative R^2 when explanatory variables joined in a multiple regression explain the response variable better than the sum of the individual effects.

	Single scale regressions (unique contributions)			Multiple scale regressions (shared contributions)			
	Plot	Patch	Landscape	Plot and patch	Plot and landscape	Patch and landscape	Plot and patch and landscape
Whole assemblage	0.33 (0.10)	0.28 (0.02)	0.34 (0.06)	0.39 (−0.01)	0.43 (0.01)	0.35 (0.05)	0.44 (0.23)
Omnivores	0.16 (0.12)	0.03 (0.03)	0.05 (0.03)	0.16 (−0.02)	0.16 (0.01)	0.07 (−0.03)	0.19 (0.04)
Insectivores	0.35 (0.09)	0.33 (0.02)	0.41 (0.08)	0.43 (−0.01)	0.49 (0.01)	0.42 (0.06)	0.51 (0.26)
Hummingbirds	0.09 (0.00)	0.18 (0.02)	0.16 (0.00)	0.19 (0.00)	0.17 (0.00)	0.18 (0.08)	0.19 (0.08)
Sensitive species	0.45 (0.03)	0.79 (0.00)	0.83 (0.04)	0.83 (0.01)	0.87 (0.01)	0.84 (0.38)	0.87 (0.41)

3.1. Community-level analyses

3.1.1. The effects of habitat disturbance across plot, patch and landscape scales (Tier 1)

Total species richness and species richness of insectivores and sensitive species were strongly correlated with variation at the plot, patch and landscape scales; full models including all scales had coefficients of determination varying from $R^2 = 0.44$ to 0.87 (Table 1), suggesting that such predictors could indeed be used as indicators of bird species richness. Hummingbirds were only significantly influenced by the patch scale, and none of the models for omnivorous species were significant, although there was a weak tendency for the plot scale to have a larger effect. Variation partitioning results showed that none of the unique effects were significant at $P < 0.05$ (Table 1), and that most of the explained variance was in the shared contributions among effects. The unique effects of plot- and landscape-scale predictors were of similar size and were higher than patch-scale predictors at explaining the variation in total species richness (Fig. 2) and richness of insectivores and sensitive species. However, the unique effects of each scale on the number of sensitive species were small, with 92% of the total explained variance being captured in shared effects across scales.

3.1.2. The effects of habitat disturbance within scales (Tier 2)

3.1.2.1. Plot scale. Full regression models containing the three predictors at the plot scale explained a large proportion of the variation in species richness from all assemblages (R^2 varying from 0.37 to 0.63) except for hummingbirds (Table 2a). Variation partitioning showed that the foliage stratification was the most important variable for the whole assemblage, omnivores and insectivores; whereas richness of sensitive species was more strongly related to mean DBH (Table 2a, Fig. 2). At the plot scale, the contribution shared among predictors was not very large, mirroring the weak correlation structure among these variables (Pearson r among predictors varied from 0.06 to 0.32, Table S2).

3.1.2.2. Patch scale. Full models explained a large variation in species richness from all assemblages (R^2 varying from 0.35 to 0.82) but for omnivorous species (Table 2b). However, due to the high correlation among variables (Pearson r among predictors varied from 0.71 to 0.92, Table S2), unique effects all had $R^2 \leq 0.1$ and were therefore non-significant. Altogether this means that most of explained variance at the patch scale was captured by the shared effects across variables.

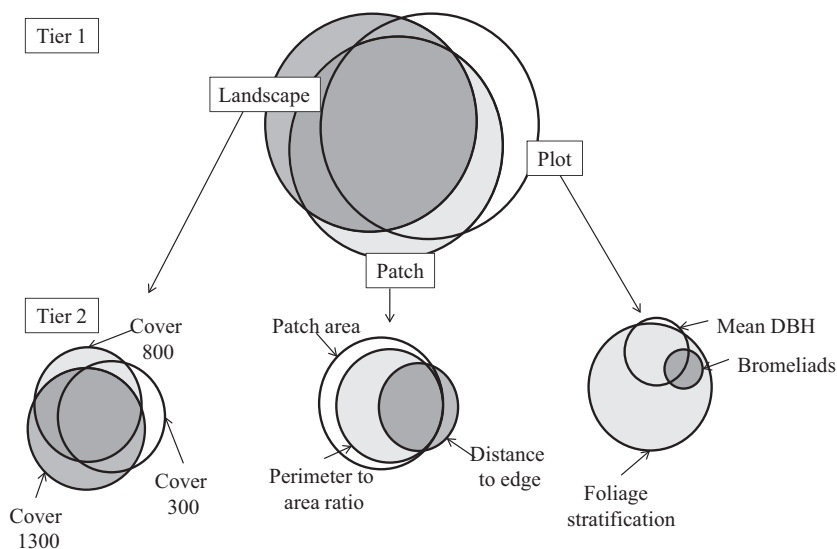


Fig. 2. Venn diagram representing the variation partitioning results achieved for models explaining the total number of species captured (whole assemblage). Large central circles represent results across plot, patch and landscape scales (Tier 1), and small outer circles represent results from variation partitioning performed within each scale (Tier 2). Circle size is proportional to the R^2 obtained for each variable in a simple regression of that variable on the response variable (for values see Table 1), and overlapping sections represent the shared contribution between two or more variables.

Table 2

Coefficients of determination (R^2) for simple and multiple regression models on the number of species captured from the different assemblages with explanatory variables representing the plot (panel a), patch (panel b) and landscape scale (panel c) (Tier 2). Inside parentheses are reported the results from the variation partitioning in which we computed the R^2 of the unique contribution specific to each variable and the shared contribution across variables. Results significant at $P \leq 0.05$ are marked in bold and effects are marked as positive (+) or negative (–) on the response variable, irrespectively of their size or significance.

	Single regressions (unique contributions)			Multiple regressions (shared contributions)			
	Mean DBH	Foliage stratification	Bromeliads	Mean DBH and foliage stratification	Mean DBH and bromeliads	Foliage stratification and bromeliads	Mean DBH and foliage stratification and bromeliads
(a) Plot scale							
Whole assemblage	0.11 (0.01) +	0.41 (0.34) –	0.02 (0.02) +	0.43 (0.09)	0.12 (0.01)	0.44 (–0.02)	0.45 (0.01)
Omnivores	0.01 (0.01) +	0.36 (0.35) –	0.01 (0.00) –	0.37 (0.01)	0.02 (0.00)	0.36 (0.01)	0.37 (–0.01)
Insectivores	0.13 (0.01) +	0.37 (0.31) –	0.08 (0.08) +	0.40 (0.08)	0.17 (0.02)	0.48 (–0.04)	0.49 (0.02)
Hummingbirds	0.10 (0.07) +	0.05 (0.02) –	0.00 (0.00) –	0.12 (0.04)	0.11 (0.00)	0.05 (0.00)	0.12 (0.00)
Sensitive species	0.48 (0.23) +	0.29 (0.13) –	0.09 (0.04) +	0.59 (0.18)	0.50 (0.07)	0.39 (–0.02)	0.63 (0.00)
	Patch area	Perimeter to area ratio (PARA)	Distance to nearest edge (EDGE)	Patch area and PARA	Patch area and EDGE	PARA and EDGE	Patch area and PARA and EDGE
(b) Patch scale							
Whole assemblage	0.32 (0.09) +	0.26 (0.00) –	0.12 (0.03) +	0.32 (0.14)	0.35 (–0.03)	0.26 (0.00)	0.35 (0.12)
Omnivores	0.05 (0.06) +	0.02 (0.02) –	0.01 (0.01) +	0.07 (–0.01)	0.06 (–0.01)	0.02 (0.00)	0.08 (0.01)
Insectivores	0.37 (0.09) +	0.30 (0.00) –	0.16 (0.02) +	0.37 (0.14)	0.39 (–0.02)	0.30 (0.00)	0.39 (0.16)
Hummingbirds	0.18 (0.01) +	0.26 (0.08) –	0.02 (0.10) +	0.27 (0.26)	0.29 (0.01)	0.36 (0.01)	0.37 (–0.10)
Sensitive species	0.77 (0.03) +	0.79 (0.04) –	0.45 (0.00) +	0.81 (0.30)	0.77 (0.00)	0.79 (0.00)	0.82 (0.45)
	Single regressions (unique contributions)			Multiple regressions (shared contributions)			
	Cover 300 m	Cover 800 m	Cover 1300 m	Cover 300 and cover 800	Cover 300 and cover 1300	Cover 800 and cover 1300	Cover 300 and cover 800 and cover 1300
(c) Landscape scale							
Whole assemblage	0.25 (0.05) +	0.31 (0.03) +	0.34 (0.07) +	0.32 (–0.03)	0.36 (–0.04)	0.34 (0.04)	0.39 (0.27)
Omnivores	0.03 (0.01) +	0.05 (0.01) +	0.06 (0.02) +	0.05 (–0.01)	0.06 (–0.01)	0.07 (0.01)	0.07 (0.04)
Insectivores	0.32 (0.08) +	0.36 (0.04) +	0.39 (0.09) +	0.38 (–0.04)	0.43 (–0.06)	0.39 (0.02)	0.47 (0.34)
Hummingbirds	0.08 (0.01) +	0.15 (0.03) +	0.19 (0.07) +	0.15 (–0.01)	0.19 (–0.01)	0.21 (0.04)	0.22 (0.10)
Sensitive species	0.56 (0.02) +	0.82 (0.00) +	0.81 (0.02) +	0.82 (0.02)	0.84 (–0.01)	0.83 (0.26)	0.84 (0.53)

3.1.2.3. *Landscape scale.* Full models explained a large amount of variance in the number of species captured for the whole assemblage, insectivores and sensitive species, but not for omnivores and hummingbirds (Table 2c). Similarly to patch scale models, all unique effects had $R^2 \leq 0.1$ (Table 2c, Fig. 2), as these variables were strongly correlated (Pearson r among predictors varied from 0.67 to 0.96, Table S2).

3.2. Species-level analyses

In total, 15 species were used for species-level analyses, comprising four omnivores, nine insectivores and two hummingbirds. Only one of the sensitive species, the omnivore *Habia rubica*, had total abundance ≥ 50 individuals and was included in analyses (Table S1).

Species showed a wide range of responses to plot, patch and landscape scales; full models including all scales had explained deviance varying from pseudo- $R^2 = 0.01$ to 0.78 (Table S3). However, in contrast to the results obtained at the community level, variation partitioning showed that many species had significant unique effects of a particular scale (Tier 1, Table S3) or environmental variable (Tier 2, Table S4). Nonetheless, species responses were remarkably idiosyncratic, with no clear indication of an overall 'most' important scale or environmental variable. There was also no trend for species within the same guild to show similar patterns, or for responses at the species level to match those at the community level. Interestingly, many species were strongly affected by interactions among variables, as indicated by unique contributions that were larger than the explanatory power of the single regression (Legendre and Legendre, 1998). PCA does not capture interaction

among variables, which may explain why multiple-scale models built with PCA axes (Table S3) often had lower explanatory power than single-scale multiple regressions (Table S4).

4. Discussion

4.1. The effects of habitat disturbance across scales

4.1.1. Community level patterns

In this study, we used data from the highly imperilled Atlantic Forest of Brazil to identify the spatial scale at which indicators of bird species richness would be most effective, and for that, we assessed the unique and shared effects of variables measured at the plot, patch and landscape scales. At the community level, our results point to a large unique effect of habitat quality at the plot scale, giving some support for the proximity-influence hypothesis (Cushman and McGarigal, 2004). We also found that species richness of omnivores was mostly affected by local spatial scales, whereas species richness of insectivores showed a relatively large effect of environmental variables at the landscape scale; results which corroborate previous findings that the relative effect of variables at different spatial scales varies with the feeding group to which a species belongs (Boscolo and Metzger, 2009).

However, the similarities between our findings and the predictions from previous studies end there. For instance, Cushman and McGarigal (2004) showed that, in the Oregon Coast region, the unique effects of plot-scale variables were significantly larger than those at either patch or landscape scale, but in the Atlantic Forest, none of the unique effects were significantly larger than the others (Fig. 2). It is possible that, as species have different biological

needs (Pearson, 1975), the inclusion of further plot scale variables into models (e.g. presence of standing logs or bamboos) would represent new axes of variation in habitat quality, which would possibly increase the influence of the plot scale as a whole. But also, unlike the results presented by Boscolo and Metzger (2009), species richness of omnivorous birds was not related to landscape metrics at any landscape radius, and richness of the insectivorous assemblage also had equally sized unique effects of plot-scale variables. Furthermore, richness of hummingbirds, that was expected to be mostly affected by variables at the landscape scale, was only significantly related to patch-scale variables.

Richness of sensitive species, expectedly, was so strongly influenced by all three scales that all unique effects were low and non-significant. However, this result does not mean that none of the variables were important, as full models containing all variables explained 87% of the variation in species richness. When predictors are highly correlated in nature and also have a strong effect on the response variable, variation partitioning can often yield very low unique effects which complicates the statistical detection of the independent effects of each variable (Koper et al., 2007). Given the explanatory power of the full model and the large sizes of the shared contributions, the best interpretation for this result is that although it is impossible to identify which of the variables are most influential, all variables have a strong joint effect on the spatial patterns of occurrence of sensitive species, and indicators built with such variables would be both powerful and reliable. The use of landscape metrics and environmental variables as indicators of richness of sensitive species is even more important given that such species are often so rare and inconspicuous. For instance, most sensitive species were so rare that only one out of 41 species considered sensitive was captured frequently enough to allow us to conduct species-level analyses (Table S1). Nonetheless, some of them are listed as vulnerable and require specific management actions if extinction is to be avoided.

4.1.2. Species level patterns

Species level models yielded results that were just as strong as those found for community level analyses, explaining up to 78% of the variation in the species' abundances (Table S3). However, unlike community level analyses, we have no evidence whatsoever to corroborate the proximity-influence hypothesis, or that the importance of each scale varies systematically with feeding habits (Boscolo and Metzger, 2009; Cushman and McGarigal, 2004). In fact, our results did not corroborate the findings from Boscolo and Metzger (2009) even when we compared the same three species tested in their paper: *Chiroxiphia caudata*, *Pyriglena leucoptera* and *Xyphorhynchus fuscus*. Boscolo and Metzger (2009) reported that the omnivore *C. caudata* responded to small scales, but in our study the species only showed a significant effect of the interaction between patch and landscape scale. The insectivore *P. leucoptera*, on the other hand, was reported as influenced by landscape metrics at large spatial scales (Boscolo and Metzger, 2009), and in our study the species showed a significant unique effect from the landscape scale, but at only at small landscape radii. And finally, the insectivore *X. fuscus*, that Boscolo and Metzger (2009) found to respond to larger spatial scales, in our study was not significantly affected by any scale.

Although our results at the species level are quite distinct to those presented in Boscolo and Metzger (2009) study, we do not believe our data contradicts their findings. Instead, we believe that the largest difference lies on the choice of response variable. Cushman and McGarigal (2002) used species composition as their response variable, Boscolo and Metzger (2009) used species occurrence, while in this study we used species richness and species' abundances. While we could speculate on the reasons for the disparity in results between response variables, we cannot

find defensible reasons to decide which response variable is more important for conservation. For this reason, we believe the most important result is that all scales were important to at least one assemblage or one species.

4.2. The effects of habitat disturbance within scales

All environmental variables within the plot, patch and landscape scales were significantly related to either species richness of one or more bird assemblage or species' abundances. In general, our results suggest that none of the analysed factors is consistently more important than the others and therefore could not act as an indicator for other variables within the same scale. Furthermore, the many cases at the species level in which we found a strong interaction among variables, provides us with further reasons to discourage the use of just one variable to represent each scale; as two, or more, variables together in the same model explain species' abundances much better than the sum of individual effects (Banks-Leite et al., 2011; Legendre and Legendre, 1998).

4.3. Implications for the development of indicators

Studies conducted on one taxon have often reported one most important scale determining the presence of that taxon (Bauerfeind et al., 2009; Binzenhöfer et al., 2008; Franken and Hik, 2004); however, such clear-cut results have eluded researchers working on multiple taxa (Boscolo and Metzger, 2009; Gardner et al., 2009). Our results mirror this problem, with our main finding being that all scales are influential, at least for one species or group of species, and that a high efficacy of landscape-based indicators is dependent on the use of landscape metrics and environmental variables at multiple scales. These results corroborate previously published findings in which many landscape metrics were needed to be included in the model to obtain strong results (Banks-Leite et al., 2011).

5. Conclusion

In this study, we could not identify one single landscape metric or spatial scale that could function as an indicator for changes in the bird community of the Atlantic Forest as all spatial scales were found to be highly influential, and within spatial scales, none of the analysed factors was consistently more important than others. Such findings stem from the highly idiosyncratic responses observed across species and across functional guilds, but also from the fact that sensitive species, those which are of conservation concern, responded strongly to all landscape metrics and all scales. Thus, our results show that landscape-based indicators are most efficient when built with several variables measured at multiple scales.

It is important to note that the fact that landscape-based indicator models might need to contain a large number of variables at varying scales is not as problematic as it would be for models of indicator species. Firstly, complex models consisting of landscape-based indicators still present high transferability to other landscapes or scales (e.g. remain effective), a trend that is not observed with indicator species models (Banks-Leite et al., 2011). Secondly, the use of indicator species requires the detection of species in the field, so there is a strong practical need to restrict indicator groups as much as possible, as very complex species models would make the task of detecting those species almost as hard as sampling the whole community. On the other hand, dozens of landscape metrics can be simultaneously calculated from satellite imagery (while measures of habitat structure can be quickly assessed in situ) with not much extra cost or time, allowing the use of more complex models.

Given the ubiquitous nature of intercorrelations among variables impacting diverse communities in modified landscapes, and that conservation actions at one scale may inadvertently generate benefits at a different scale, it seems that the best way forward for conservation strategies is to develop multi-scale approaches that will maximise the benefits for multiple assemblages.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2012.04.015>.

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