RESEARCH ARTICLE

Spatial patterns of bird community similarity: bird responses to landscape composition and configuration in the Atlantic forest

Gustavo A. Zurita · M. Isabel Bellocq

Abstract Studies dealing with community similarity are necessary to understand large scale ecological processes causing biodiversity loss and to improve landscape and regional planning. Here, we study landscape variables influencing patterns of community similarity in fragmented and continuous forest landscapes in the Atlantic forest of South America, isolating the effects of forest loss, fragmentation and patterns of land use. Using a grid design, we surveyed birds in 41 square cells of 100 km^2 using the point count method. We used multivariate, regression analyses and lagged predictor autoregressive models to examine the relative influence of landscape variables on community similarity. Forest cover was the primary variable explaining patterns of bird community similarity. Similarity showed a sudden decline between 20 and 40% of forest cover. Patterns of land use had a second order effect; native bird communities were less affected by forest loss in landscapes dominated by tree plantations (the most suitable habitat for native species) than in landscapes dominated by annual crops or cattle pastures. The effects of fragmentation were inconclusive. The trade-off between local extinctions and the invasion of extra-regional species using recently created habitats is probably the mechanism generating the observed patterns of community similarity. Limiting forest loss to 30–40% of the landscape cover and improving the suitability of human-modified habitats will contribute to maintain the structure and composition of the native forest bird community in the Atlantic forest.

Keywords Atlantic forest · Birds · Community similarity · Forest loss · Fragmentation · Land use · Thresholds

Introduction

Habitat fragmentation is a worldwide process that has been extensively studied in different ecosystems and taxa over the last two decades (see reviews by Fahrig 2003; Fischer and Lindenmayer 2007). In spite of the large number of studies, biological effects of fragmentation remain as a central issue of debate. Three aspects of fragmentation have recently become the focus of the debate (Fahrig 2003; Ewers and Didham 2006; Koper et al. 2007). First, habitat fragmentation is a landscape process, but most studies are conducted at the patch scale and are unable to distinguish between the independent effects of habitat loss and habitat fragmentation (Fahrig 2003; McGarigal and

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Cushman 2002). Second, recent efforts to isolate the independent effects of habitat loss and fragmentation in real landscapes lead to confusing conclusions due to statistical problems and confounding factors (McGarigal and Cushman 2002; Koper et al. 2007). The most robust studies concluded that habitat fragmentation per se has a much weaker effect on species abundance and richness than habitat loss (Fahrig 2003). Third, the classical approach to the study of habitat fragmentation considers a binary situation of suitable and unsuitable habitat; nevertheless, differences in the suitability of "unsuitable habitats" for native species may drastically influence landscape connectivity and, in consequence, the effects of habitat fragmentation (Gobeil and Villard 2002; Castellón and Sieving 2005; Wiegand et al. 2005; Ewers and Didham 2006; Stouffer et al. 2009).

The traditional approach to the study of spatial changes in biological diversity (including those dealing with habitat loss and fragmentation) focused on species richness (or α-diversity) as the main response variable (Cook 1998). A more comprehensive approach includes the analysis of similarities or differences (β-diversity) in community composition that arise from landscape spatial arrangement (configuration) and relative composition of landscape elements (Koleff et al. 2003; Dormann et al. 2007; Soininen et al. 2007). Although similarity is less intuitive to interpret than species richness, it is more sensitive to changes in the composition of natural communities caused by natural disturbances or human activities (Steinitz et al. 2005). It also allows exploration of mechanisms involved in landscape and regional ecological processes such as biotic homogenization (produced by species invasions and local extinctions) or the exchange of species between local communities (influenced by fragmentation and the suitability for native species of human-modified habitats composing the landscape). Furthermore, similarity in community composition between landscapes allows the identification of areas that maximize regional biodiversity, and can be used as the basis for regional conservation planning (Steinitz et al. 2005; McDonald et al. 2005).

Most studies dealing with similarity in community composition were conducted in regions with a long history of habitat alteration where natural habitat remnants are scarce, such as some temperate ecosystems in Europe or North America (Steinitz et al.

2006; Dormann et al. 2007). In general, species occurring in those regions are adapted to landscapes generated by traditional cultural practices such as farming, and particularly to the mosaic of small scale habitats created by different land uses (Benton et al. 2003; Heikkinen et al. 2004); hence, community similarity is mainly related to the type and intensity of land use (Dormann et al. 2007). In highly diverse regions where many native species are still dependent on natural habitats, such as tropical and subtropical forests, similarity may be influenced by the interaction between species loss (mainly native habitat specialist) associated with forest conversion and fragmentation, and the invasion of extra-regional species using recently created habitats. In the Atlantic forest of Argentina and Paraguay a relatively large proportion of natural habitat remains in protected and non-protected areas, creating a gradient of forest cover. Besides, human activities are diverse (including annual and perennial crops, cattle raise, tree planting, etc.) and the general patterns of land use resulting from the regional political economy generate landscapes differing in the composition of human-modified habitats.

In this study we examine spatial patterns of bird community similarity between fragmented and continuous landscapes in the Atlantic forest of Argentina and Paraguay. We quantify the independent effects of forest loss, fragmentation and patterns of land use on native bird communities through a combination of statistical approaches. The Atlantic forest of Argentina and Paraguay offers an outstanding setting for the study because natural habitat remnants create a gradient of forest cover that allows distinguishing the effects of habitat loss and fragmentation, and the patterns of land use generate landscapes differing in the composition of human-modified habitats.

Methods

Study area

The study was conducted in the Upper Paraná Atlantic forest of Argentina and Paraguay covering approximately 4,400 km^2 (Fig. 1). The Upper Paraná Atlantic forest is the largest ecoregion of the Atlantic forest, which is one of the top five biodiversity

Fig. 1 Study area in the Upper Paraná Atlantic of Argentina and Paraguay (**a**). Sub-regions differing in the general pattern of land use were studied. **b** SE Paraguay and **c** NE Argentina used mainly for annual crops and cattle pastures (Agricultural sub-region) and **d** NW Argentina (*left lower square*) dominated by tree plantations (Forestry sub-region). Modified from Di Bitetti et al. (2003)
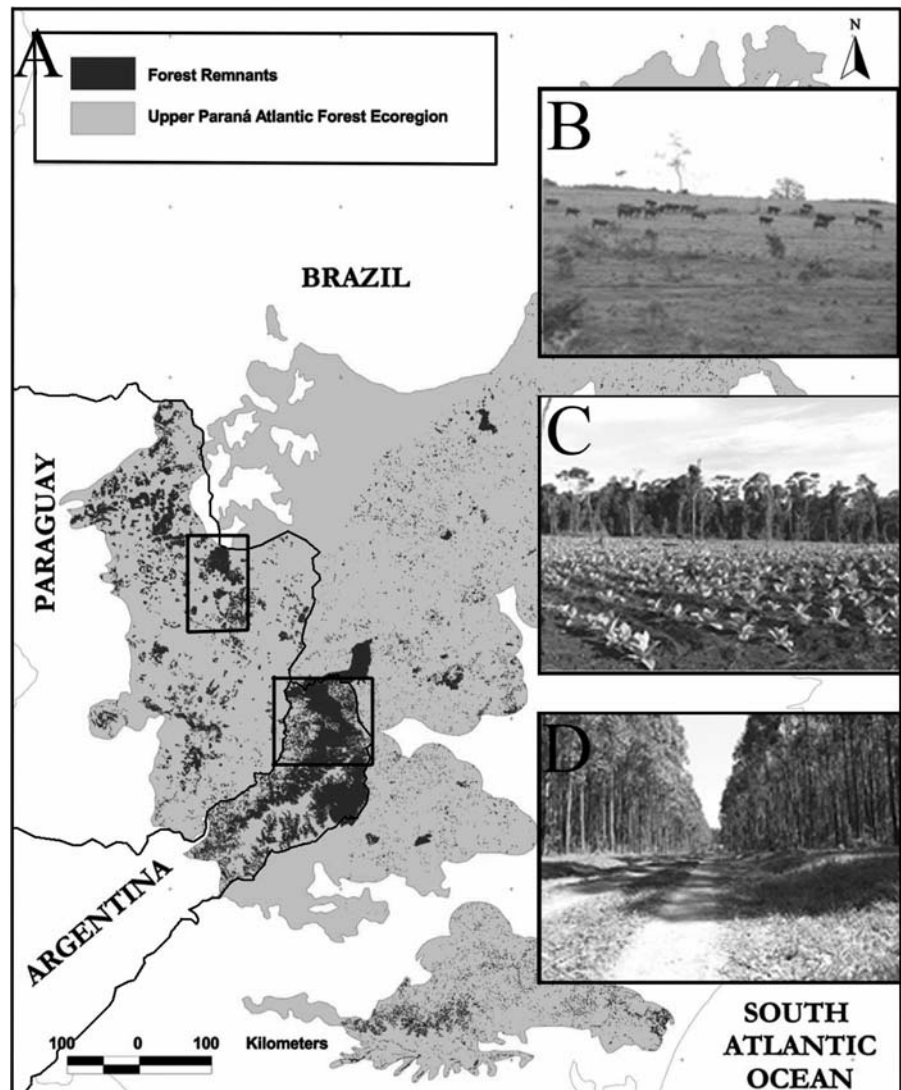
hotspots worldwide (Myers et al. 2000). Currently, on average, 45 and 17% of the original forest cover remains as protected areas or fragments in private lands in Argentina and Paraguay, respectively (Galindo-Leal and Câmara 2003).

Within the study area, we identified different patterns of land use. In the Northeast of Misiones province in Argentina and in Southeastern Paraguay, the most intensive land uses are pastures for raising cattle and annual crops (set in large properties in Paraguay and in small properties in Argentina). In Northwestern Misiones, land is primarily devoted to tree planting (mainly *Pinus* spp. but also *Araucaria angustifolia* and *Eucalyptus* spp.) for wood and pulp

production established in large properties. In a previous study, the human-modified habitats considered here have been shown to differ in the suitability for native forest birds; tree plantations had the highest suitability compared to other land uses (Zurita and Bellocq unpublished data). Based on those results, we a priori divided the study area into two sub-regions defined by the general pattern of land use: (1) Northwestern Misiones dominated by tree plantations (from now on called the Forestry sub-region) and (2) Northeastern Misiones and Southeastern Paraguay dominated by annual crops and cattle pastures (the Agricultural sub-region) (Fig. 1).

Sampling design

The study area was divided into a grid of 10×10 km UTM (Universal Transverse Mercator) cells. Each cell was considered a landscape. Within the study area we selected landscape units to provide a range of native forest cover from the lowest value (7%) up to 80%. Thus, a total of 37 landscapes were selected and sampled for birds: 17 in the Agricultural sub-region (10 in NE Misiones and 7 in SE Paraguay, 7–80% forest cover) and 17 in the Forestry sub-region (30–80% forest). Additionally, five and two landscapes having 100% forest cover (continuous forests) were sampled in Argentina and Paraguay, respectively. In each of the 41 landscapes, we established 20 bird point counts (for a total of 820 point counts). The number of bird point counts was assigned proportionally to the area covered by native forest and productive lands; for example, in landscapes having 60% of forest cover, 12 bird point counts were located in native forest and 8 in human modified habitats. Bird point counts were established at least 500-m apart and 1,000-m from the landscape boundary.

Bird counts

Birds were surveyed during the breeding season (September–January) of 2004–2006 using the point-count technique with a 50 m fixed radius (Bibby et al. 1998). Each point count was sampled between 6:00 and 10:00 am. The same experienced observer performed all bird counts, recording all birds heard and seen in a 5 min period within the 50 m radius. Given that the study was conducted at the regional scale, we decided to maximize the number of point counts instead of the time spent on each sampling point (Koper and Schmiegelow 2006; Dormann et al. 2007). But to ensure that all birds singing during the observation time were recorded, song recordings were taken using a directional microphone at all point counts during the observation time, and later compared with bird song databases. This method has been shown to increase the accuracy of the sampling protocol (Haselmayer and Quinn 2000).

Landscape configuration and composition

To describe landscape composition, we quantified the area covered by each habitat type (human-modified habitats and native forest) within each landscape; and to describe landscape spatial configuration we quantified the number and size of forest fragments,, and the relative length of edge in the landscape (Gustafson 1998). We used Landsat TM images (taken during the period of field sampling) that were classified using an isodata non-supervised algorithm with 20 classes. We then grouped the resulting classes into native forest and human-modified habitats (annual crops, perennial crops, tree plantations, clearcuts, and cattle pastures) based on their spectral signatures, high-resolution IKONOS images and personal field experience. Due to the complexity of classification associated with a variety of cultural practices performed in perennial and annual crops across the region, each landscape was classified independently. To validate the classifications, we calculated the accuracy of each category (native forest and land uses) as the proportion of the 20 field points that were correctly classified; because of distinct vegetation cover and structure, habitat categories were clearly identified in Landsat images.

The FRAGSTATS software (McGarigal et al. 2002) was used to quantify variables describing landscape composition and configuration. We described composition on each landscape by quantifying the proportion of the landscape covered by native forest and human-modified habitats. To describe landscape spatial configuration we (1) counted the number of forest fragments, (2) estimated the average size of forest fragments, and (3) estimated the landscape shape index (LSI). LSI equals the total length of forest edge in the landscape divided by the minimum length of edge if forest where maximally aggregated in a single patch. LSI ranges from one (minimum edge effect) to increasing values and has been used as a measure of edge at the landscape scale (McGarigal et al. 2002). These three attributes of landscape configuration have been frequently used to measure habitat fragmentation at the landscape scale (Trzcinski et al. 1999; Fahrig 2003; Koper et al. 2007).

Bird community similarity

We used the Morisita–Horn index to estimate similarity in bird community composition between fragmented and continuous forest landscapes (Magurran 2004). This index quantifies the number and relative abundance of species shared by two communities and

ranges from zero (communities sharing no species) to one (communities sharing all species with the same abundance). We estimated bird abundance in each landscape by counting the number of bird point counts where the species was registered divided by the total number of birds point counts in that landscape (20); this number was used as the relative frequency of occurrence of a species in a given landscape. The procedure was repeated for all species and landscapes. The composition of the native forest bird community in continuous forest landscapes was estimated by combining the bird abundance values of all landscapes having 100% of native forest cover in both Argentina and Paraguay. To minimize possible effects associated with spatial dependence and biogeographic patterns within each country (landscapes in Paraguay and Argentina were separated by more than 200 km), similarity indices for landscapes in Paraguay and Argentina were calculated using continuous forest landscapes in Paraguay (two) and Argentina (five), respectively.

Statistical analysis

We selected the statistical procedures to achieve the objectives of: (1) exploring the spatial patterns of bird community similarity between fragmented and continuous landscapes, and (2) separating the relative influence of forest loss, patterns of land use, and forest fragmentation on bird community similarity. As stated above, we defined two sub-regions differing mainly in the general pattern of land use (Forestry and Agricultural). To validate this grouping, we performed a principal component analysis (PCA) to examine whether landscapes were grouped based on the relative coverage of each human-modified habitat (annual crops, perennial crops, cattle pastures and tree plantations). The first axis of this PCA was also used later as a single measure summarizing patterns of land use in a multiple regression analysis (Land use index).

To explore the general pattern of bird community similarity between fragmented and continuous landscapes, we first conducted a simple regression analysis between forest cover and community similarity. We then fitted the similarity data to linear and logarithmic models to examine these two different potential patterns of response of bird community similarity to forest loss. When both models were statistically

significant, we selected the model with the highest coefficient of determination.

We used a combination of statistical procedures to separate the effects of forest loss, fragmentation, and patterns of land use. Following Trzcinski et al. (1999), we first performed a PCA (with the number and average size of forest fragments and landscape shape index) to represent patterns of forest fragmentation with a single value (Fragmentation index). Because axes of this PCA are expected to correlate with forest cover, we performed a simple regression analysis between the fragmentation index and forest cover. Residuals from that regression represent an independent estimate of forest fragmentation (Fahrig 2003). Finally, we performed a lagged autoregressive predictor analysis (instead of the classical multiple regression analysis, see below) to examine the independent effects of forest cover, land use index, and the residuals of fragmentation index on bird community similarity (the Forest cover model).

Using the residuals of fragmentation against forest cover may bias results towards finding effects of forest loss over forest fragmentation (Koper et al. 2007); so we also conducted the opposite analysis. We performed a simple regression analysis between forest cover and fragmentation index and used the residuals as an independent measure of forest cover. Similar to the Forest cover model, we performed a lagged autoregressive predictor analysis to examine the independent effects of forest cover residuals, land use index, and fragmentation index on bird community similarity (the Fragmentation model).

An additional alternative approach was also explored to separate the effects of fragmentation and patterns of land use (independent of forest cover). We grouped landscapes into three categories: (1) 30–40% (9 landscapes), (2) 40–50% (9 landscapes) and (3) 70–80% (6 landscapes) forest cover. These categories correspond to the threshold range in the spatial pattern of community similarity (20–40%), and to two points in the plateau (40–50% and 70–80%) (see Fig. 4). Then, we performed lagged autoregressive predictor analysis within each category of forest cover using fragmentation and land use indices as explanatory variables. Finally, we performed an ANCOVA analysis, using fragmentation and land use indices as covariables, to compare similarity among the three categories of forest cover (independent of patterns of land use and fragmentation).

To examine the potential spatial autocorrelation in explanatory variables and bird community similarity, we constructed correlograms of Moran's I and tested the significance on 1,000 Monte Carlo permutations using SAM software (Rangel et al. 2006). Autocorrelations were performed between variables (similarity and explanatory variables) and the spatial proximity of sampling landscapes. When a significant spatial structure was found, we used lagged predictor autoregressive models instead of the classical regression analysis (Rangel et al. 2006). Lagged predictor models use a matrix of neighbor weights based on geographical distance between landscapes to explicitly define spatial structure of dependent and explanatory variables. The classical linear multiple regression model

$$Y = aX + bZ + e$$

where X and Z are the predictor variables and a and b the slopes, becomes

$$Y = \alpha WY + aX + \alpha_1 W_1 X + bZ + \alpha_2 W_2 Y + e$$

where α represents the autoregressive parameters for each variable (both dependent and independent) and W the matrix of neighbor weights. To select between different autoregressive models (given by different weight matrices) we looked for the highest Akaike Information Criteria (AIC) (for further details on autoregressive models see Rangel et al. 2006).

We tested for normality of the dataset through the Kolmogorov–Smirnov test and the homogeneity of variances through a Spearman rank correlation between the absolute values of residuals and the observed values of the dependent variable. When necessary, variables were log transformed.

Results

We recorded a total of 4,910 individuals birds from 203 species in the 41 sampled landscapes (820 bird point counts). The large majority of individual were identified by songs (more than 95% of records). Of the total recorded species, 138 were recorded in the Forestry sub-region and 172 in the Agricultural sub-region. The number of bird species recorded per point count was highly variable, ranging from zero (mainly in annual crops) to 17 (in protected areas) reflecting the variability in species richness among different habitats. The accumulated number of species per

landscape tended to reach an asymptote at an average of 45 species; showing that the number of bird point counts was sufficient to have a representative sample of bird community composition in the landscape (Fig. 2).

Landscape composition and configuration

The landscape map was deemed to have high accuracy; the proportion of pixels that were correctly classified was 0.98 for native forest, 0.88 for annual crops, 0.92 for cattle pastures, 0.80 for perennial crops, 0.88 for clearcut areas and 0.91 for tree plantations.

The PCA (based on the relative cover of human-modified habitats) and ANOVA analysis validated our assumption that the two sub-regions differ in the general pattern of land use. The first and second axes of the PCA accounted for 54 and 27% of the variation among landscapes, respectively. Cover of tree plantations increases with axis I ($R = 0.92$) while cover of cattle pastures and annual crops decreases along the axis ($R = -0.78$ and $R = -0.84$, respectively). The second axis separated landscapes with and without perennial crops (Fig. 3a). Because the first axis separated landscapes dominated by tree plantations from those with annual crops and cattle pastures, it represents a single measure of land use pattern (Land use index). Cover of tree plantations was higher in the Forestry sub-region while covers of
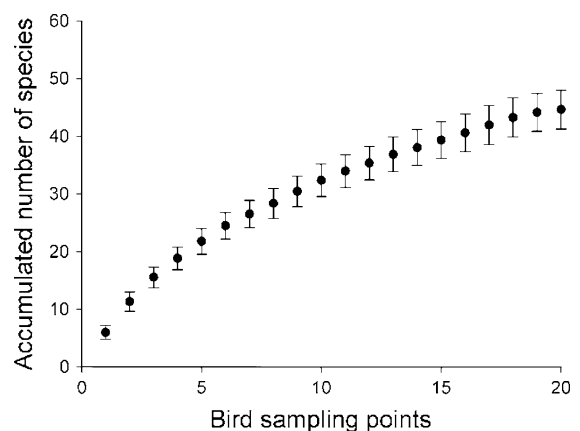

Fig. 2 Accumulated number of species (95.5% confidence intervals) per sampling landscape in the Upper Paraná Atlantic forest
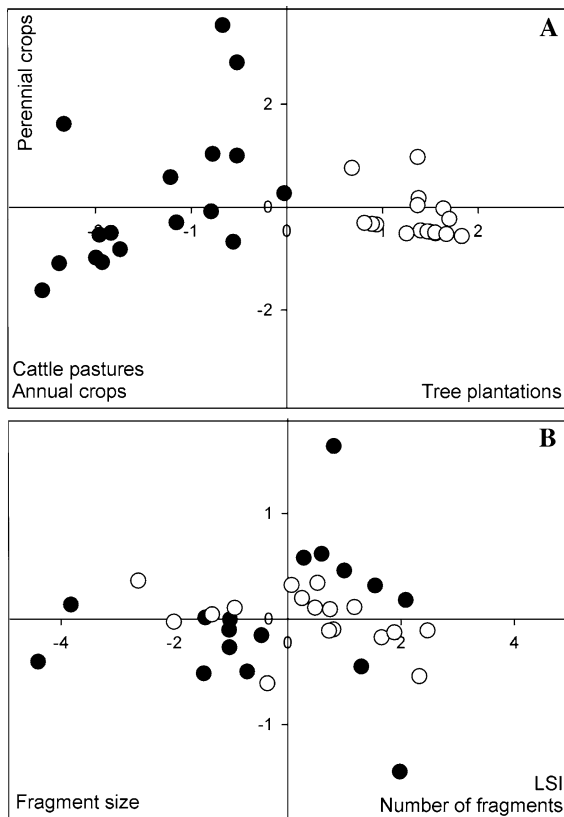
Fig. 3 Principal component analysis of landscapes in the Upper Paraná Atlantic forest based on the composition of human-modified habitats (**a**) and fragmentation pattern (**b**). *Empty circles* represent landscapes in the Forestry sub-region and *filled circles* represent landscapes in the Agricultural sub-region

Table 1 Landscape composition and configuration in the defined sub-regions in the Upper Paraná Atlantic forest

	Agricultural	Forestry	$F_{1,32}$
Forest cover (%)	54.5	47.1	1.4
Tree plantations cover (%)	0.4	47.5*	252.0
Annual crops cover (%)	8.4*	0.0	34.5
Cattle pastures cover (%)	26.3*	1.1	24.1
Perennial crops cover (%)	9.8	3.5	2.6
No. of forest fragments	174	231	1.8
Size of fragments (has)	72	39	1.8
Landscape shape index	16.3	17.7	0.3

* $P < 0.05$, ANOVA

analysis (Fragmentation index). The number and average size of forest fragments and landscape shape index were similar between sub-regions (Table 1).

Landscape effects on community similarity

Correlograms of Moran's I showed no evidence of spatial autocorrelation in community similarity, forest cover or fragmentation index ($P > 0.05$ at most distances). However, as expected, land use index showed a clear spatial structure: landscapes with similar pattern of land use grouped into a maximum distance of 32 km (Table 2).

In all simple regression analyses between forest cover and community similarity both the logarithmic and the lineal models were significant, but the logarithmic model showed the highest coefficient of determination in most cases (Fig. 4). In general, the curves showed an abrupt change in community similarity between 20 and 40% of forest cover, more evident at the regional scale (when pooling both sub-regions) and in the Forestry sub-region. At the regional scale, simple regression analysis revealed that a logarithmic model was the best predictor of similarity as a function of native forest cover ($F_{2,31} = 21.6$, $P < 0.001$, $R^2 = 0.58$ vs. $R^2 = 0.48$ in the linear model) (Fig. 4a). After excluding two points of very low similarity (lower than 0.1) that could modify the regional pattern, the logarithmic model remained the best to explain the regional pattern of bird community similarity ($F_{2,29} = 16.2$, $P < 0.001$, $R^2 = 0.52$ vs. $R^2 = 0.37$ in the linear model). Similar to the regional pattern, the logarithmic model was the best predictor of bird community

annual crops and cattle pastures were higher in the Agricultural sub-region (Table 1).

Although landscape composition differed between sub-regions, results from the ANOVA and the PCA describing fragmentation patterns (based on the number, the average size of fragments and the landscape shape index) showed that landscape configuration was similar between the Forestry and Agricultural sub-regions. The first and second axis of the PCA explained 90 and 8% of the variation among landscapes, respectively. Axis I was positively related to the landscape shape index and the number of fragments ($R = 0.92$ and $R = 0.97$) and negatively related to the average size of fragments ($R = -0.95$) (Fig. 3b). The second axis was not related to variables measuring fragmentation. The first axis will be used as a single measure of fragmentation pattern in further

Table 2 Spatial autocorrelation among landscapes (Moran's I index) in forest cover, fragmentation index (Axis I of a PCA with number and average size of forest fragments and landscape shape index), land use index (Axis I of a PCA with cover of human-modified habitats) and the similarity in bird community composition between fragmented and continuous forest landscapes in the Upper Paraná Atlantic forest

Distance (km)	Forest cover	Fragmentation index	Land use index	Similarity
9	0.10	0.11	0.85*	0.17
23	0.17	0.11	0.66*	0.11
32	0.17	0.11	0.42*	0.08
44	−0.08	0.11	0.08	0.07
56	−0.27*	0.11	−0.50*	0.04
102	−0.22*	0.10	−0.62*	−0.07
163	−0.01	0.09	−0.68*	−0.34*
195	−0.13	0.10	−0.15	−0.34*
240	0.00	0.08	−0.34*	0.01

* $P < 0.05$, Mantel test with 1,000 permutations

Fig. 4 Spatial patterns of bird community similarity between fragmented and continuous forest landscapes in relation to forest cover at the regional scale (**a**) and in the Forestry and Agricultural sub-regions (**b** and **c**, respectively) in the Upper Paraná Atlantic forest

similarity in the Forestry sub-region ($F_{2,14} = 27.6$, $P < 0.001$, $R^2 = 0.79$ vs. $R^2 = 0.55$ in the linear model) (Fig. 4b). Finally, in the Agricultural sub-region both the logarithmic and lineal models explained a similar proportion of bird community similarity ($F_{2,14} = 14.6$, $P < 0.001$, $R^2 = 0.68$ and $R^2 = 0.62$ in the linear model) (Fig. 4c).

We performed lagged predictor autoregression analysis instead of multiple regression analyses because of the spatial autocorrelation on land use index. As expected, fragmentation index was negatively related to forest cover ($F_{1,32} = 31.1$, $P < 0.001$, $R^2 = 0.49$); to avoid colinearity problems in autoregression analysis, we used the residuals from the regression between forest cover and fragmentation index (Forest cover model) and its inverse (Fragmentation model). We directly used land use index as an explanatory variable because this variable was not related either to forest cover ($R = −0.04$, $P = 0.80$) or fragmentation index ($R = 0.11$, $P = 0.52$).

Explanatory variables accounted for 66% of the total variation in community similarity between fragmented and continuous forest landscapes in the Forest cover model. Similarity increases with forest cover ($t_{31} = 6.7$, $P < 0.001$) and land use index ($t_{31} = 3.1$, $P < 0.004$) and was not related to fragmentation index residuals ($t_{31} = 1.7$,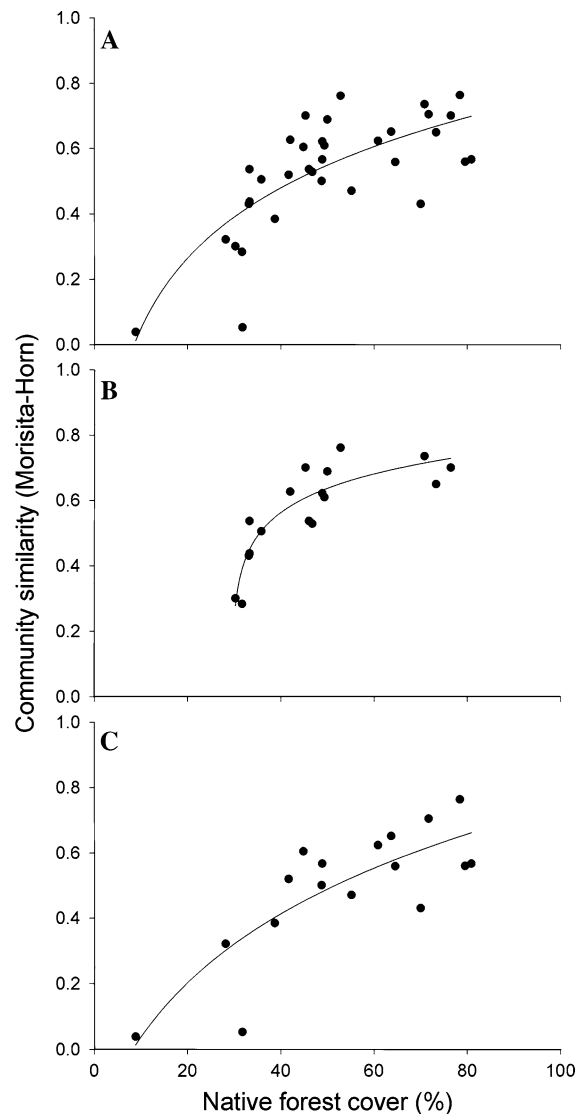 $P = 0.09$). In this model, bird community similarity increases with forest and tree plantation cover and decreases with cover of annual crops and cattle pastures (Table 3). In the Fragmentation model, 64% of total variation in community similarity was explained by independent variables. Similar to the Forest cover model, similarity increases with forest cover residuals ($t_{31} = 5.8$, $P < 0.001$) and land use index ($t_{31} = 3.0$, $P = 0.005$); however,

Table 3 Contribution of individual explanatory variables in lagged predictor autoregression analyses (standardized regression coefficients) to the spatial pattern of bird community similarity between fragmented and continuous forest landscapes in the Upper Paraná Atlantic forest

Model	R^2	Forest cover (or residuals)	Fragmentation index (or residuals)	Land-use index
Forest cover residuals	0.64	0.64*	−0.35*	0.34*
Fragmentation residuals	0.66	0.71*	NS	0.33*

NS non significant

* $P < 0.01$

similarity also decreases with fragmentation index in this model ($t_{31} = -3.2$, $P = 0.003$) (Table 3). Both models showed consistent results regarding the independent contribution of forest loss and land use pattern to the spatial pattern of bird community similarity, but differed in the relative contribution of forest fragmentation (Table 3).

The ANCOVA analysis comparing the three forest cover categories (30–40, 40–50 and 70–80%) and controlling by fragmentation pattern and landscape composition (covariables) was significant ($F_{2,22} = 20.3$, $P < 0.001$), indicating that bird community similarity differs among landscapes having similar fragmentation pattern and land use but different forest cover. Bird community similarity in landscapes having 30–40% forest cover was lower than that in landscapes with 40–50 and 70–80% forest cover (Fisher post-hoc comparisons, $P < 0.001$ in both cases); however, similarity between landscapes having 40–50% forest cover and 70–80% forest cover was similar ($P = 0.22$). In landscapes with 30–40% of forest cover, the lagged predictor autoregression analysis showed that fragmentation and land use indices explained 59% of bird community similarity; also, similarity increased with land use index ($t_9 = 2.6$, $P = 0.04$) and was not related to fragmentation index ($t_9 = -0.9$, $P = 0.39$). In landscapes within the 50–60 and 70–80% forest cover range, bird community similarity was related neither to fragmentation nor to land use index ($t_{11} = 1.6$, $P = 0.14$, $t_{11} = -0.09$, $P = 0.92$ and $t_7 = 1.0$, $P = 0.37$, $t_7 = 1.5$, $P = 0.23$, respectively). These analyses showed that patterns of land use, unlike fragmentation, influence bird community similarity between continuous and fragmented landscapes; and that the influence occurs at low-to-moderate, but not at moderate-to-high, natural forest cover.

Discussion

Determinants of bird community similarity: landscape composition or configuration?

Understanding the independent effects of landscape composition and configuration on biological communities and populations is essential to predict changes in species diversity (loss of native species and the invasion of extra-regional species) and abundance associated with human disturbances. However, because composition and configuration of landscapes usually change simultaneously, the interpretation of mechanisms determining spatial patterns of species diversity and abundance is controversial. As suggested by McGarigal and Cushman (2002), manipulative field experiments are probably the best approach to understand mechanisms influencing population and communities at the landscape scale. However, in real landscapes and especially in highly threatened ecosystems, such as the Atlantic forest, the experimental approach is no longer feasible due to both logistic and ethical reasons. Alternative approaches include measurative field experiments, fixing one variable (e.g. forest cover) and varying others (e.g. fragmentation patterns or landscape composition); however in some real situations (such as tropical and subtropical forests) patterns of land use lead to complex and highly variable landscapes (both in composition and configuration) making this approach infeasible. Instead of using these approaches, we sampled a large number of landscapes and used a combination of statistical techniques to explore mechanisms influencing spatial patterns of community similarity at the landscape scale in the Atlantic forest.

We found habitat loss and patterns of land use to have a consistent effect in the composition of forest

bird communities in fragmented landscapes in the Atlantic forest. At the landscape scale, deforestation and land uses creating open habitats (such as annual crops and cattle pastures) resulted in a decline in the similarity with the native forest bird community. However, the effects of forest fragmentation differed depending on the model used. As suggested by Koper et al. (2007), using the residuals of fragmentation on forest cover (Forest cover model) probably biased the results toward finding effects of forest loss and hiding effects of forest fragmentation. However, in the opposite model, that is, using the residual of forest covers on fragmentation index (Fragmentation model), forest loss still had a strong influence in explaining changes in native bird communities (more than twice the effect of fragmentation). These results reinforce the idea that habitat fragmentation per se has a second order effect (or no effect) compared to habitat loss (Haila 2002; Fahrig 2003). The analysis of landscapes grouped by similar forest cover but differing in the general patterns of land use and fragmentation pattern lead to similar conclusions: landscape composition had a consistent influence on bird community composition (especially in the range of 30–40% forest cover) while fragmentation had no significant effect. Consequently, differences in community similarity at a similar proportion of forest cover (Fig. 4) are likely due to different patterns of land use, rather than different levels of fragmentation. Similar results were found in previous studies; after removing the effects of forest cover, fragmentation had only a marginal or no effect on bird diversity (Cushman and McGarigal 2003; Fahrig 2003). However, these previous studies focused on alpha diversity (overall abundance) whereas we studied spatial patterns of community composition. Nevertheless, the low effect of forest fragmentation on bird community composition is probably valid only for landscapes with intermediate to low levels of deforestation. In highly deforested landscapes (<20% of native habitat remaining), small changes in the fragmentation pattern may have a strong influence on native communities and populations (Wiegand et al. 2005).

The response of bird communities to habitat loss and fragmentation is influenced by the general pattern of land use because human-modified habitats differ in their suitability for native bird species, influencing landscape functional connectivity (Gascon et al. 1999; Ricketts 2001; Dunford and Freemark 2004;

Antongiovanni and Metzger 2004). In the Upper Paraná Atlantic forest, tree plantations are the most suitable human-modified habitat for native forest birds while annual crops and cattle pastures are mainly used by open area species (Petit and Petit 2003; Zurita et al. 2006; Zurita and Bellocq unpublished data). These differences in suitability are mainly explained by the similarity of tree plantations (both structure and composition) to that of native forest. At the landscape scale, modified habitats such as tree plantations may allow movements by native species, enhance landscape connectivity, and thereby reduce the effects of forest loss (Bélisle et al. 2001).

We sampled a relatively large number of landscapes compared to similar recent studies (Koper et al. 2007, 2006). A key assumption of our study was that field sampling effort per landscape was great enough to reliably estimate bird community composition. Field sampling effort (both the number of bird point counts and the time spent at each point count) was similar to recent studies conducted at landscape and regional scales (for example, we used one bird point count per 5 km^2 and Koper et al. 2007 used one bird point count per 8 km^2) (Dormann et al. 2007; Koper et al. 2007). We have confidence in this assumption because the accumulation species curve tends to reach an asymptote, which shows that the number of bird point counts and the time spent at each point per landscape was likely sufficient to capture the real number of species per landscape.

Spatial patterns of bird community similarity

Spatial patterns of similarity have been related to land use type and production intensity in highly modified ecosystems, such as those commonly found in temperate ecosystems (Steinitz et al. 2006; Dormann et al. 2007). In those ecosystems the majority of species currently depends on habitats generated by cultural practices (Heikkinen et al. 2004). In the Atlantic forest, we found that spatial patterns of bird community similarity are primarily determined by forest cover and secondarily by the land use pattern (and probably fragmentation). A large proportion of species are still dependent on native forest (Brooks et al. 1999), unlike the situation found in temperate ecosystems with a long history of landscape modification. As a consequence, the trade-off between local extinctions of

native species caused by habitat loss and the invasion of extra-regional species using the new habitats created by human activities probably generate the observed patterns of similarity between fragmented and continuous forest landscapes.

We found evidence for a potential threshold in the relationship between community similarity and forest cover somewhere between 20 and 40% of forest cover. In recent years, extinction thresholds have been studied as a mechanism to explain species extinctions associated with habitat loss and fragmentation. The theory, and the scarce empirical evidence, suggests that a high number of native species (mainly specialists) become locally extinct when natural habitat decreases below 10–30% of the original cover (Fahrig 2002; Wiegand et al. 2005), producing a major reduction in species richness (Radford et al. 2005). Landscape composition (patterns of land use) was a good predictor of bird community similarity around the threshold range; however after reaching the plateau of bird community similarity, none of the studied variables (forest cover, patterns of land use and fragmentation pattern) seemed to have a strong influence on similarity. In landscape planning, the identification of threshold points could be important to reduce the effects of human disturbances on natural ecosystems. Maintaining forest cover above the threshold point may be the most effective measure to preserve native communities.

We found that habitat loss is the major determinant of changes in forest bird community composition in the Atlantic forest whereas the general pattern of land use had a second order effect. At the landscape scale and in the range of forest cover included in this study (30–80%), the effects of fragmentation on native bird communities were inconclusive. Based on our results, it seems that landscape composition strongly influence the composition of native bird communities, but mainly in the threshold range (20 or 30–40%). From a landscape planning perspective, landscapes preserving at least 30–40% of the native forest cover will maintain bird communities relatively similar to those of native forests, representing a key threshold range in landscape and regional planning. The current debate on the relative influence of landscape composition and configuration explaining landscape patterns of species diversity is mostly based on evidence from temperate ecosystems, while studies from tropical and subtropical forests are lacking. Through our work we expect to contribute to the debate, and to encourage more research in highly diverse ecosystems to improve our understanding of the mechanisms behind intermediate scale patterns.

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