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Bird Assemblages in Anthropogenic Habitats: Identifying a Suitability Gradient for Native Species in the Atlantic Forest

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ABSTRACT

Traditional approaches to the study of species persistence in fragmented landscapes generally consider a binary classification of habitat being suitable or unsuitable; however, the range of human-modified habitats within a region may offer a gradient of habitat suitability (or conservation value) for species. We identified such a gradient by comparing bird assemblages among contrasting land uses (pine plantations of different age, annual crops, clear cuts and cattle pastures) in the Upper Parana Atlantic forest. Bird assemblages and vegetation structure were characterized in an extensive area of 4400 km^2 in Argentina and Paraguay during the breeding seasons of 2005–2010. Similarity of bird assemblages between anthropogenic habitats and the native forest and the proportion of forest species increased with vegetation vertical structure, while the proportion of open-area species decreased. As a consequence, mature tree plantations were the most suitable habitats for forest species and were mainly used by frugivores and bark insectivores. In contrast, open habitats were the least suitable habitat for forest species and were used primarily by insectivores. Human-created habitats that are structurally complex can be used by a subset of forest species, and may improve functional connectivity and mitigate edge effects. The conservation of large tracks of native forests, however, is critical for the long-term persistence of the entire bird assemblage, especially for native forest dependent species.

Abstract in Spanish is available in the online version of this article.

Key words: birds; conservation value; feeding guild; habitat specificity; human-modified habitats; land use.

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While traditional models of species persistence in fragmented landscapes consider habitat suitability as either suitable or unsuitable, recent work emphasizes the importance of considering a gradient of habitat suitability for species (Petit *et al.* 1999, Lindenmayer *et al.* 2003, Kupfer *et al.* 2006, Shankar Raman 2006). At a local scale, anthropogenic habitats could provide resources such as food, nesting sites, and territories or refuge for native species (Barlow *et al.* 2007). At a landscape scale, differences in habitat suitability and the distance to the native habitat influence functional connectivity and extinction patterns (Antongiovanni & Metzger 2005, Hansbauer *et al.* 2010, Zurita & Bellocq 2010); human-modified habitats that can be used, or at least crossed, by native species reduce the effects of habitat loss and fragmentation.

Environmental factors determining habitat use by birds in human-modified habitats are still poorly explored; however, vegetation structure and composition, microclimatic conditions and spatial heterogeneity have shown to be important factors (Gascon *et al.* 1999, Renjifo 2001, Luck & Daily 2003, Heikkinen *et al.* 2004, Tubelis *et al.* 2004, Shankar Raman 2006). In general, anthropogenic habitats preserving—even partially—the original environmental conditions and the structure and composition of native vegetation are more suitable for native species than habitats producing a drastic change (Filloy *et al.* 2010). Two general criteria of classification have been used to analyse the response of bird assemblages to human disturbance: feeding guilds and the degree of habitat specialization (a proxy for ecological niche amplitude). In the former case, in tropical areas forest frugivores, insectivores and nectarivores tend to be absent in agricultural habitats while granivores and omnivores show the opposite pattern (Schulze *et al.* 2004, Sekercioglu *et al.* 2004, Peh *et al.* 2006, Tscharntke *et al.* 2008); in the second case, forest specialist are in general absent from anthropogenic habitats while generalist species are usually found in both native and anthropogenic habitats (Devictor *et al.* 2008). Those differences are probably related to the capability of generalist species of exploiting a large range of resources, while specialist species are generally dependent on specific resources provided by the native habitat.

The Atlantic forest of Brazil, Argentina and Paraguay has a long history of habitat loss and is currently categorized as one of the five most endangered biodiversity hotspots (Myers *et al.* 2000). Most of the remaining 10 percent of the original Atlantic forest is fragmented in small isolated remnants of less than 50 ha (Ribeiro *et al.* 2009). Recent studies of this highly fragmented ecosystem showed that some bird species and small mammals are able to move between forest fragments through anthropogenic habitats (Awade & Metzger 2008, Vieira *et al.* 2009), though gap-crossing distance, varies among land uses (Antongiovanni & Metzger 2005, Umetsu *et al.* 2008, Hansbauer *et al.* 2010). As a direct consequence, identifying differences in suitability or conservation values

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between different human-modified habitats is a priority to improve landscape planning and land management in the region (Renjifo 2001, Hughes *et al.* 2002, Tabarelli *et al.* 2010).

Recently, multiple authors have analysed the response of species and communities to human disturbances in the Atlantic forest (Rice & Greenberg 2000, Marsden *et al.* 2001, Cockle *et al.* 2005, Faria *et al.* 2006, Zurita *et al.* 2006, Fonseca *et al.* 2009, Laurance 2009, Pardini *et al.* 2009, Volpato *et al.* 2010, Zurita & Bellocq 2010). None of these studies have simultaneously compared bird assemblages in habitats that include the most extensive land uses—agriculture, forest tree plantations and cattle pastures. Our objectives are: (1) to describe and compare the structure of bird assemblages (richness, composition and feeding guild) in habitats generated by the main human activities (agriculture, tree plantations and cattle pastures) and in native forests at a regional and landscape scale to infer a gradient of habitat suitability for native birds in the Upper Paraná Atlantic forest; and (2) to examine the influence of vegetation structure on bird assemblages in those human-modified habitats.

METHODS

STUDY AREA AND LAND USES.—The study was conducted in the Upper Paraná Atlantic semideciduous forest of Argentina and Paraguay, the largest eco-region in the Atlantic forest. The area has a subtropical climate with a cold season between June and August and no dry season (Oliveira-Filho & Fontes 2000). Total mean annual rainfalls are 2000 mm, and mean annual temperature is 20°C. Forest structure has three to five strata with emergent trees. Ferns and bamboos are dominant in the understory, while the canopy stratum is composed of Lauraceae, Fabaceae and others (Campanello *et al.* 2007).

Sampling sites (birds and vegetation) were distributed in an extensive area of 4400 km^2 (3300 km^2 in Argentina and 1100 km^2 in Paraguay) including native forest in large remnants (more than 10,000 ha) and fragments, tree plantations of different age (from clearcuts to mature plantations), annual crops (mainly soy bean, tobacco and corn) and cattle pastures (Fig S1). Four major protected areas were sampled to describe native bird assemblages in continuous forest: the Iguazú National Park (544 km^2) and the Urugua-í Provincial Park (840 km^2) in Argentina and the Mbaracayu Natural Reserve (591 km^2) and the Morombí Private Reserve (250 km^2) in Paraguay. Although these protected areas were exploited in the past, they represent the best preserved forest in Argentina and Paraguay. Three general pattern of land use can be identified in the study area (sub-regions from now on) (Zurita & Bellocq 2010): (1) NW Misiones (Argentina), dominated by commercial tree plantations (mainly *Pinus* spp.); (2) NE Misiones, with annual crops, cattle pastures and tree plantations at small scale; and (3) NE Paraguay, with annual crops and cattle pastures in large farms (Fig. S1).

SAMPLING DESIGN.—Five different habitats resulting from different land uses or different stages of the same land use were sampled in the study area of Argentina and Paraguay: (1) mature tree plantations of *Pinus* spp. (> 14 years old, average extent 8.6 ha); (2) intermediate tree plantations of *Pinus* spp. (between 8 and 14 years old); (3) recent tree plantations of *Pinus* spp. (< 8 years old); (4) cattle pastures; and (5) annual crops and clearcuts (open habitats). In addition, we sampled native forest in forest fragments; the average size of fragments was 17.3 ha (95% of the fragments were between 11 and 23 ha). Bird assemblage structure and composition on each human-modified habitat and forest fragments was sampled in 100 bird counting points, and 200 counting points were sampled in continuous native forest, for a total of 800 bird counting points (five human-modified habitats, fragmented forest and continuous forest) (Table 1). Bird counting points were at least 500-m apart and considered as independent observations. In 478 birds counting points we also sampled vegetation structure (see below); the number of vegetation sampling points varied between 45 and 102 per habitat type (Table 1). Vegetation sampling points were randomly selected among bird counting points, because logistic reasons prevent us from sampling vegetation at all points.

TABLE 1. *The number of bird and vegetation sampling points, bird richness and vegetation structure of human-created habitats and native forest in the Upper Paraná Atlantic Forest.*

	Mature plantations	Intermediate plantations	Recent plantations	Cattle pastures	Open areas	Fragmented forest	Continuous forest
Sampling effort and bird richness							
Bird counting points	100	100	100	100	100	100	200
Vegetation points	49	50	50	102	45	95	90
No. recorded species	70	62	61	77	55	100	130
Bird richness Chao I	105	101	86	96	91	129	144
Chao I (95% CI)	(83−161)	(77−165)	(70−127)	(84−130)	(67−158)	(112−172)	(135−169)
Vegetation structure (% cover)							
High-canopy	69.6	16.0	0.1	0.3	0.2	7.2	7.8
Mid-canopy	3.9	59.5	1.5	2.7	0.4	31.7	37.9
Low-canopy	25.9	12.1	68.4	4.9	0.13	70.4	47.9
Understory	71.3	65.4	69.8	93.0	65.0	43.7	58.3

Counting points were randomly distributed among land uses in the regional study area. To explore differences on habitat suitability related to differences in landscape composition and configuration among sub-regions we compared forest cover (%) and the number, the average size and the edge amount (using the SHAPE index, McGarigal *et al.* 2002) of forest patches and the average patch size of different land uses. Landscapes were defined in a 10 × 10 km grid cells based on a previous study (see Zurita & Bellocq 2010). Landscape attributes within cells were calculated using FRAGSTATS (McGarigal *et al.* 2002).

BIRD COUNTS AND VEGETATION SAMPLING.—We sampled birds during the 2005, 2006, 2008 and 2010 breeding seasons (September–January). Counting points were surveyed during 5 min in a 50 m fixed-radius, excluding flyovers (Bibby *et al.* 1998). To avoid the influence of time of day, counting points were sampled randomly between 0600 and 1000 h. Surveys were performed only on sunny days with calm wind, and the same experienced observer performed all observations. We followed the *BirdLife* checklist for species nomenclature (Birdlife 2008).

At each vegetation sampling point we estimated vegetation cover of all strata using an abundance-cover scale. The following vegetation strata were considered: understory (herbs and shrubs below 1.5 m); low-canopy (between 1.5 and 5 m); mid-canopy (5–15 m); and high-canopy (over 15 m). The same observer visually estimated plant cover in each stratum in a circular plot of 20 m radius centered on the counting point location. For each stratum, we assigned plant cover to one of the following categories: 0–20, 20–40, 40–60, 60–80 and 80–100 percent.

DATA ANALYSIS.—We used ANOVA to compare landscape attributes (native forest cover, number, size and shape of native forest patches, and the average patch size of each anthropogenic habitat type) among sub-regions.

We used the Shannon index as a measure of vertical habitat structure (Magurran 2004). We considered vegetation vertical structure because it has been shown to influence bird diversity in natural habitats (MacArthur & MacArthur 1961), and presumably in human-modified habitats as well (Petit *et al.* 1999). We used the equation:

$$Vertical\ Structure = -\sum Pi \times ln(Pi);$$

where Pi represents the proportional cover of each vegetation stratum (understory, low, medium and high canopy). This index ranges from 0 in areas with only one stratum (minimal complexity) to 1.39 in areas with all vegetation strata having the same cover (maximal complexity).

To describe the regional composition of bird assemblages on native forest (continuous and fragmented) and human-created habitats, counting points within habitat types were pooled. We calculated the Chao1 estimator of species richness with 95% confidence intervals, and used the individual counting points to build the species rarefaction curves based on both the observed and the estimated number of species. The relative abundance was the average over the individual counting point in each habitat type. Using these relative abundances, we calculated the quantitative Jaccard index to estimate similarity in bird assemblage composition between each human-created habitat and continuous native forest. Jaccard index ranges from zero (assemblages differing in all species) to one (assemblages sharing all species with the same abundance), and it quantifies differences on bird assemblage composition in relation to the original assemblage (unfragmented forest). The Chao1 estimator and the Jaccard index were calculated using EstimateS 8.2 (Colwell 2006). Additionally, a non-metric multi dimensional scaling (MDS) using the Jaccard similarity index, was used to ordinate land uses based on the relative abundance of species (Orange 2.5).

To explore the influence of landscape structure on the use of anthropogenic habitats by native species we performed a nested ANOVA. In that analysis, the Jaccard index of similarity was calculated for individual point counts in relation to the continuous native forest, and those point counts located within the same anthropogenic habitat type were nested on sub-regions. The analysis allows us to compare the suitability of anthropogenic habitats for native species excluding the effects of landscape structure.

Birds were classified into three categories according to their primary habitat defined by Stotz *et al.* (1996): (1) forest species, mostly found in forest habitats; (2) open-habitat species, typical of open or semi-open habitats; and (3) generalist species, found in both forest and open habitats. For each habitat type we calculated the proportion of species in each category. We also classified bird species into eight feeding guilds based on literature from the Atlantic forest (D. Deregibus, G. A. Zurita & M. I. Bellocq, unpubl. data, Sick 2001, Lopes *et al.* 2005, Durães & Marini 2005): (1) Carnivores (species consuming mainly live or dead vertebrates); (2) Aquatic feeders (consuming fish, arthropods or vegetation, but mainly in aquatic environments); (3) Frugivore–insectivores; (4) Insectivores; (5) Bark insectivores; (6) Granivore-Insectivores; (7) Granivores; and (8) Nectarivores. We conducted simple regression analyses (lineal and exponential models) to examine the influence of vegetation vertical structure on bird richness, the Jaccard index and the proportion of species on each habitat category (forest, open and generalist birds). In cases were both models had a significant fit, we chose the model with the highest coefficient of determination. We compared guild composition (proportion of species among guilds) between continuous and fragmented forest and human-modified habitats by performing *G*-tests based on 2 (habitats) × 8 (feeding guilds) contingency tables. To account for zero proportions in some categories, we used the *G* statistic instead of the standard χ^2. In the analysis, we compared separately guild composition in native continuous forest with each anthropogenic habitat type. Finally, we correlated the abundance of guilds with the ordination resulting from the MDS.

RESULTS

Sub-regions showed no differences in forest cover and the configuration of forest patches (average size, number and shape) (Table 2). When comparing land uses, however, the average size of cattle pastures was higher in NE Paraguay than in NW and NE Misiones, while patches of open habitats were smaller in NE Misiones (Table 2). Besides, patches of tree plantations were larger in NW Misiones than in NE Misiones. Thus, sub-regions differed on the average size of anthropogenic habitats but not in the spatial structure of the remaining native forest (fragmentation pattern).

A total of 4151 individual birds from 201 species were recorded in the overall study. Native forest (both continuous and fragmented) and mature tree plantations showed the highest species richness, followed by cattle pastures, intermediate and recent plantations and finally open habitats (Fig. S2; Table 1). Sampling effort was adequate to represent the structure of bird assemblages at the study sites; rarefaction curves showed a similar pattern of accumulation and tend to reach an asymptote in all cases (Fig. S2), allowing a direct comparison of bird assemblage structure. Percent cover of the different vegetation strata differed between human-modified habitats, resulting in a gradient of vertical structure with the greatest values found in native forest, mature tree plantations, intermediate and recent tree plantations and finally cattle pastures and open habitats (Table 1).

The Jaccard index of similarity on bird assemblage between anthropogenic habitats and the continuous native forest was strongly related to vegetation vertical structure ($R^2 = 0.96$, $F_{1,4} = 38.9$, $P = 0.007$) (Fig. 1). Similarity exponentially decreased from multi-stratified (fragmented forest and mature tree plantations) to mono-stratified habitats (open habitats). The proportion of forest species increased with vegetation vertical structure while the proportion of open habitat species showed the opposite pattern ($R^2 = 0.96$, $F_{1,4} = 39.1$, $P = 0.007$ and $R^2 = 0.91$, $F_{1,4} = 43.0$, $P = 0.002$, respectively). The proportion of generalist species showed no relationship to vegetation vertical structure ($R^2 = 0.09$, $F_{1,4} = 0.40$, $P = 0.56$) (Fig. 2). When comparing land uses among sub-regions (ANOVA nested design), similarity followed a similar pattern, decreasing from fragmented forest and mature plantations to open habitats ($F_{12,585} = 35.7$, $P < 0.001$) (Fig. 3). Moreover, sub-regions differed on the general pattern of habitat suitability; considering the same anthropogenic habitat, similarity was the highest in NE Misiones, followed by NW Misiones and finally NE Paraguay ($F_{12,585} = 11.2$, $P < 0.001$) (Fig. 3).

Consistent with previous results, MDS habitat ordination (Stress = 0.0007) followed a gradient of structural complexity along the principal axis from native forest (both continuous and fragmented) to open habitats (Fig. 4). The abundance of frugivore–insectivores, bark insectivores, granivores and nectarivores decreased with Axis I of the MDS ($R = -0.98$, $R = -0.83$, $R = -0.91$, $R = -0.73$, $P = < 0.05$ in all cases) whereas the

TABLE 2. *Variables describing landscape structure and composition (mean ± ES) in human-created habitats and native forest in three sub-regions of the Upper Paraná Atlantic Forest.*

	NE Misiones	NW Misiones	NE Paraguay	F
Forest cover (%)	61.6 ± 6.9	48.1 ± 3.0	43.3 ± 7.7	2.3
Number forest patches	154 ± 29	183 ± 23	132 ± 37	1.1
Forest patch size (ha)	75.7 ± 32.5	41.4 ± 8.8	75.5 ± 39.4	0.6
Forest SHAPE INDEX	1.42 ± 0.02	1.43 ± 0.01	1.38 ± 0.02	2.3
Open patch size (ha)	3.1 ± 0.6	14.5 ± 5.0	14.0 ± 3.5	5.8**
Pastures patch size (ha)	3.1 ± 0.4	3.0 ± 0.4	34.0 ± 8.4	47.9**
Plantation patch size (ha)	2.9 ± 1.0	11.1 ± 2.7	0.0 ± 0.0	12.6**

**P < *0.001*.

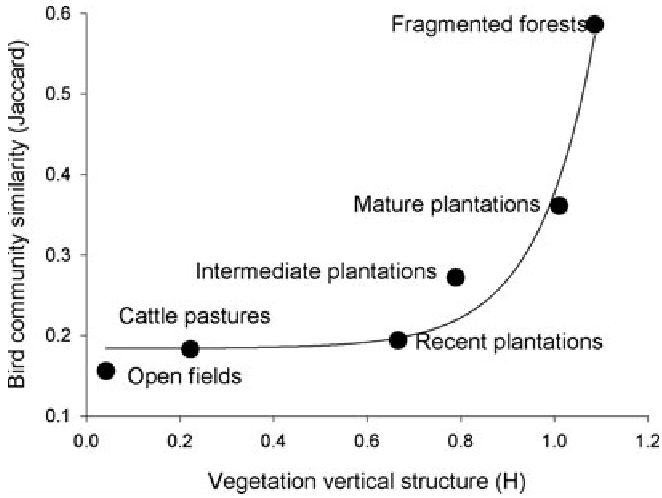

FIGURE 1. The similarity (Jaccard index) in bird community composition between anthropogenic habitats and fragmented forest and the continuous forest in relation to vegetation vertical structure in the Upper Paraná Atlantic Forest.

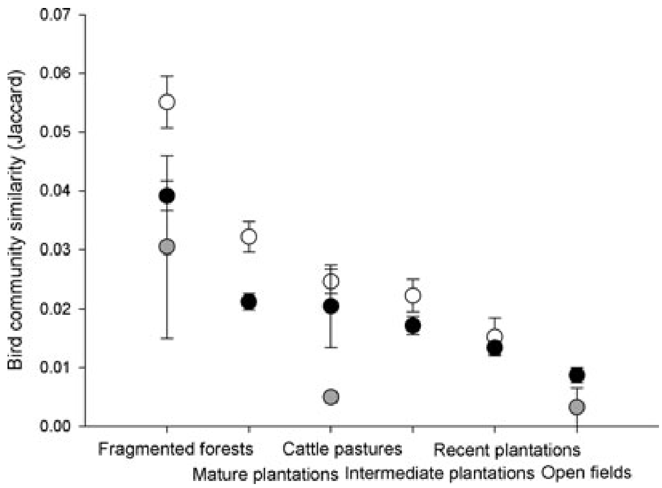

FIGURE 2. Comparison of the similarity (Jaccard index) in bird community composition among anthropogenic habitats nested in sub-regions (ANOVA, nested design) in the Upper Paraná Atlantic Forest. Filled black circles: NW Misiones; Empty circles: NE Misiones and gray filled circles NE Paraguay.

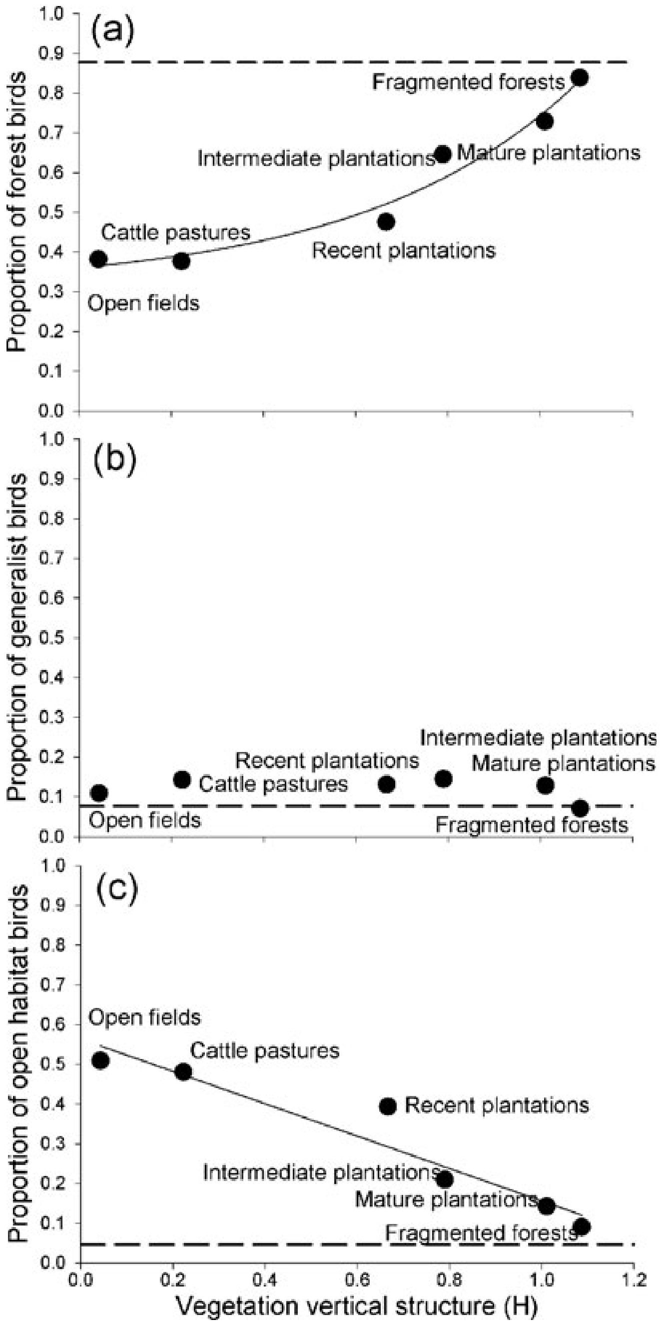

FIGURE 3. Relationship between the proportion of forest birds (a), generalist bird species (b) and open-habitat birds (c) and the vegetation vertical structure in the Upper Paraná Atlantic Forest. Dashed line represents the proportion of species on each category in continuous forest.

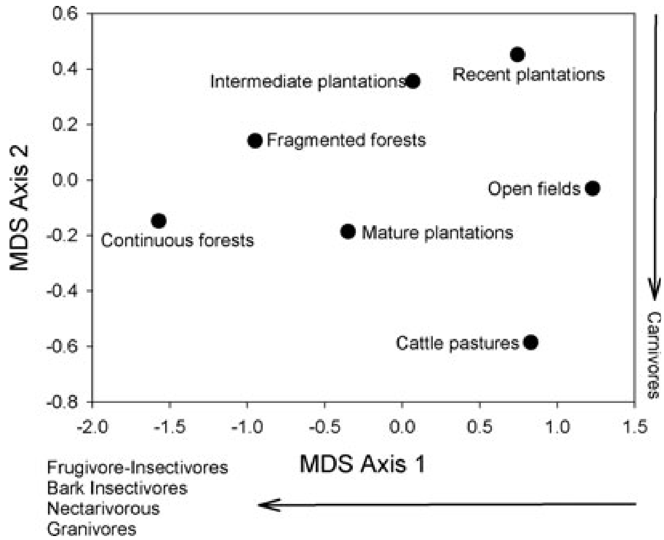

FIGURE 4. Non-metric multidimensional scaling (MDS) analysis of human-modified habitats and native forest based on the relative abundance of birds and the correlation with feeding guilds in the Upper Paraná Atlantic Forest.

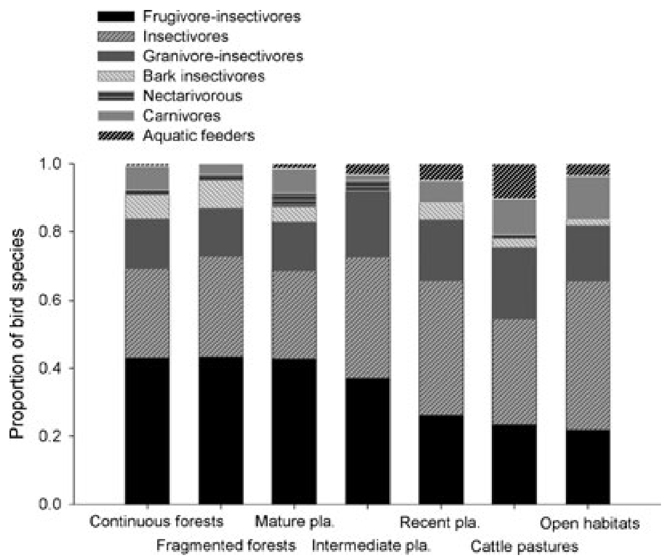

FIGURE 5. Feeding guilds structure (proportion of species) of bird assemblages on human-modified habitats and native forest in the Upper Paraná Atlantic Forest. Pla: Plantations.

abundance of carnivores was negatively correlated to Axis II ($R = -0.75$, $P = 0.05$).

Feeding guild structure of the native continuous forest was similar to that of fragmented forest ($G_7 = 3.4$, $P = 0.84$) and mature tree plantations ($G_7 = 2.2$, $P = 0.94$); but different from intermediate ($G_7 = 17.3$, $P = 0.01$) and recent ($G_7 = 18.7$, $P < 0.01$) tree plantations, cattle pastures ($G_7 = 24.1$, $P < 0.01$) and open habitats ($G_7 = 18.9$, $P < 0.01$). In general, the proportion of frugivore–insectivores decreased from native forest to open habitats while the proportion of insectivores, carnivores and aquatic feeders showed the opposite pattern (Fig. 5).

DISCUSSION

The replacement of the classical view of suitable vs. unsuitable habitat by that considering a gradient of habitat suitability for native species has been advanced by many authors (Kupfer *et al.* 2006, Tabarelli *et al.* 2010). Surprisingly, only a few studies have partially described the suitability gradient (Lawton *et al.* 1998, Petit *et al.* 1999, Petit & Petit 2003, Schulze *et al.* 2004); and no study has been conducted in the Atlantic forest, in spite of the recent number of studies dealing with habitat loss and fragmentation at different scales and on different taxa (Laurance 2009 and references therein, Zurita & Bellocq 2010). As expected, and similar to other studies in tropical and subtropical forests, replacement and degradation of the native Atlantic forests resulted in remarkable (and in some cases drastic) changes in the structure of bird assemblages (both richness and composition) (Lawton *et al.* 1998, Petit *et al.* 1999, Daily *et al.* 2001, Hughes *et al.* 2002, Petit & Petit 2003).

While the transformation of native forests into productive areas resulted in the exclusion of a large proportion of native species, the magnitudes of these changes were highly variable among land uses. This created a gradient of suitability rather than two distinct habitat types that differed in suitability. Our study and previous studies conducted in the Atlantic forest showed that, in general, agro-forestry systems are the most suitable human-created habitat for native species (shade coffee, cacao and yerba mate) (Cockle *et al.* 2005, Faria *et al.* 2006, Pardini *et al.* 2009), followed by mature tree plantations of Pine and Araucaria (with the exception of Eucalypt) (Marsden *et al.* 2001, Zurita *et al.* 2006, Fonseca *et al.* 2009, Volpato *et al.* 2010), and finally open habitats (Hansbauer *et al.* 2010) (for general comparative studies see Lawton *et al.* 1998, Petit *et al.* 1999, Petit & Petit 2003, Schulze *et al.* 2004). In our study, the turnover in species composition was related to the vertical structure of vegetation; forest species tend to use tree plantations which preserve part of the forest vertical structure, whereas non-forest species mainly used open habitat. Those results are consistent with the hypothesis that birds colonize and exploit human-modified habitats that are similar in structure and composition to their original habitats (Gascon *et al.* 1999, Petit *et al.* 1999, Lindenmayer *et al.* 2003, Sodhi *et al.* 2005, Shankar Raman 2006). Differences on bird assemblage structure between small forest fragments and the continuous forest are also expected as a consequence of the species-area relationship and the reduced habitat quality caused by edge effect (Banks Leite *et al.* 2010).

At the landscape scale, differences on habitat suitability among anthropogenic habitats influence functional connectivity among fragments of native habitat (Antongiovanni & Metzger 2005). Although the empirical evidence is still controversial, recent studies suggest that landscape composition (*i.e.*, relative cover of anthropogenic habitats) could be more important than configuration (*i.e.*, fragmentation patterns) in determining spatial patterns of bird diversity at low-intermediate levels of forest cover (*i.e.*, between 20% and 40% of forest cover) (Fahrig 2002, Pardini *et al.* 2010, Zurita & Bellocq 2010, Boscolo & Paul Metzger 2011). At that spatial scale, suitable human matrices may allow the movement of individuals among fragments of native habitats (Awade & Metzger 2008). This gap-crossing capacity is crucial on the response of species to habitat fragmentation; Awade and Metzger (2008) found evidence of birds crossing distances shorter than 100 m through open habitats in the Atlantic forest; consistent with these results, in a recent study we found many Atlantic forest species entering a maximum of 100 m into mature plantations and 50 m into open habitats (G. A. Zurita, G. Pe'er, M. I. Bellocq & M. M. Hansbauer, unpubl. data).

While the results at the regional scale showed a general gradient of habitat suitability for native species, different patterns of land use may results in local differences on the suitability of anthropogenic habitats. Since the distance to the habitat influence the capacity of native species to exploit modified habitat (Antongiovanni & Metzger 2005); differences on the average size of anthropogenic patches among sub-regions and the amount of forest probably explain differences on habitat suitability for native species on similar land uses or habitat type. Smaller patches of human created habitats surrounded by native forest typical from NE Misiones are probably more used by native species than extensive areas of monocultures in NW Misiones and NE Paraguay (such as tree plantation in NW Misiones and cattle pastures and annual crops from NE Paraguay).

Our results showed that frugivores, bark insectivores, nectarivores and granivores were mainly found in native forest and mature plantations and tended to avoid open areas (Tscharntke *et al.* 2008). In contrast, bird assemblages in open areas were mainly composed by insectivores. The dominance of insectivore species in open habitats and frugivores on tree plantations was also found in tropical forests of Malaysia (Peh *et al.* 2006). Differences in resource abundance (low abundance of fleshy fruits and flowers in open areas), predation and parasitism risks, and nesting sites availability are probably the main causes of the observed differences on guild assemblage structure; however specific studies are required to understand the mechanisms driving assemblage composition. Consequences of habitat conversion on ecosystem functioning are not clear; however, recent studies suggest that important ecological functions (such as seed dispersion and pollination) may be drastically affected by replacing or modifying native forest (Sekercioglu *et al.* 2004, Tscharntke *et al.* 2008).

Combining species conservation and economic profits is perhaps one of the major challenges in conservation (Du Toit *et al.* 2004). More detailed information, however, on the mechanisms driving the use of human-modified habitats by species is necessary to improve current patterns of land use at the local and landscape scales (Hill & Hamer 2004). Our study provides a better understanding of the patterns of bird use of human-modified habitats, identifying a gradient of habitat suitability. The suitability of human-modified habitats to native birds within a region will be determined (at least partially) by the similarity between natural and anthropogenic habitats. The range of land uses in the Atlantic forests could be interpreted as a gradient of conservation value (or habitat suitability) for native birds, where multi-stratified human-modified habitats with native vegetation are the most suitable habitat.

Although human-created habitats that are structurally complex (such as mature tree plantations) may be exploited by a subset of native forest species, most forest species depend on the conservation of large tracks of native forest to maintain long-term viable populations. That is particularly relevant for species requiring specific resources only available on native forests. Additionally, complex anthropogenic habitats may provide conservation benefits through increasing functional connectivity and reducing edge effect in forest remnants, and increasing population size of endangered species (*e.g.*, *Leptasthenura setaria* in Araucaria plantations). Adjusting the traditional approach of suitable vs. unsuitable habitat to consider a gradient of habitat suitability will increase the power of ecological models to predict the effects of human activities and improve landscape planning and land management.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Upper Paraná Atlantic forest showing with rectangles the study areas in Paraguay and Argentina.

FIGURE S2. Rarefaction curves based on the observed number of species and the Chao1 estimator of richness of birds in fragmented forest in the Upper Paraná Atlantic Forest.

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