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On the similarity among bird communities: Testing the influence of distance and land use

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ABSTRACT

The search for mechanisms determining community composition is currently in the core of ecological research. Human land use may promote species invasions or local extinctions by altering the environmental conditions, which can drastically change the composition of local communities. Understanding community responses to human activities will help develop sound land use strategies. Our main question is whether particular human activities lead to bird communities similarly composed regardless of the distance between the sites where those activities are placed. We examined bird community composition and the number of native species in two land uses (soybean cropfields and eucalypt plantations) in two different biomes (Pampean grassland and Atlantic forest). Birds were surveyed with point counts, and ordination analysis, similarity indices and factorial ANOVA were used to analyse and compare bird assemblages. Within each biome, the composition of bird communities differed between soybean cropfields and eucalypt plantations. The composition of bird communities within the same land use type (either soybean or eucalypt) but in different biomes was similar. In the forest, eucalypt plantations held a higher proportion of forest bird species (i.e., native species) than soybean cropfields. The opposite pattern was observed in the grassland sites where a higher proportion of grassland species (i.e., native species) recorded in cropfields than in plantations. The composition of local communities in human-modified ecosystems seems to be strongly influenced by local conditions derived from the particular land use. Eucalypt plantations and soybean cropfields were less detrimental to both forest and grassland birds in contexts dominated by forest and grasslands, respectively. Our results suggest that a better persistence of native species to a certain habitat may be achieved by taking into account the regional context in which human activities are developed. These findings should be useful for land use strategies and regional planning.

1. Introduction

The last decade experienced a shift in the approach to biodiversity problems by emphasizing the relevance of the identity of species composing communities, and not the number of species alone. Typically, two distant communities are expected to differ in species composition stating certain taxonomic similarity between them or, its inverse, certain beta diversity (Nekola and White, 1999; Soininen et al., 2007). The focus in the composition of communities shed light into the mechanisms driving spatial biodiversity patterns. Soininen et al. (2007) stated that similarity between communities may be determined by at least three mechanisms: 1) the environmental distance between sites and the differences in species capability of adapting to different environmental conditions (i.e. niche differentiation), 2) the spatial context dictating dispersal rates among sites, and 3) species dispersal limitations.

Typically, local communities will show a certain degree of similarity depending on the geographical (Nekola and White, 1999) and environmental distances between the sites where they occur (Steinitz et al., 2006). The change in environmental distances between sites caused by human activities may modify the original values of similarity among local assemblages from different places. As a consequence of the conversion of natural habitat into lands dominated by agriculture or other human activities, some species might enlarge their geographical ranges whereas other species may suffer reductions in their ranges or even get locally extinct (McKinney and Lockwood, 1999; Olden and Poff, 2003; Olden and Rooney, 2006). The dynamics of invasions and local extinctions resulting from human disturbances may either promote an increase in taxonomic similarity between distant sites (decrease in β-diversity), known as biotic homogenization, or a decrease in taxonomic similarity (increase in β-diversity), known as biotic differentiation

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(Olden and Poff, 2003; Qian et al., 2008). Thus, habitat changes may lead to changes in bird community composition. On the one hand, habitat conversion to a particular monoculture increases habitat similarity between sites that previously had contrasting vegetation types, thus homogeneous assemblages would be expected. On the other hand, habitat conversion to different monocultures decreases habitat similarity between sites that had similar original vegetation, thus different assemblages should be observed.

The effects of alternative land uses on a particular species assemblage may be different depending on the environmental conditions offered by the managed systems. Vegetation structure is a key factor driving bird species composition within communities (Cody, 1985); those modified habitats preserving, at least partially, the structure of the natural habitat are more often used by native species than those modified habitats changing drastically the original structure (Gascon et al., 1999; Zurita and Bellocq, unpublished data).

Our main question is whether particular monocultures lead to bird communities similarly composed regardless of the distance between the sites where human activities are placed (i.e., regardless the original species pools). We surveyed birds in sites transformed into soybean cropfields or eucalypt plantations and placed in different biomes, forest and grassland. If bird community composition in monocultures responded primarily to land use, we would expect bird community similarity between soybean cropfields placed in different biomes to be equivalent to the similarity between soybean cropfields in a given biome. A similar pattern would be expected for eucalypt plantations. We also evaluated the relative effects of monocultures on forest bird species in sites located in the forest biome, and on grassland birds in sites located in the grassland biome (referred to as native species from here). Each type of human activity will potentially preserve some specific resources (e.g. for feeding, nesting, shelter), even monocultures with extremely low levels of internal complexity. Because of similarities in vegetation structure, we expect that eucalypt plantations will be more favourable for forest birds than soybean cropfields whereas the opposite is expected for grassland birds.

2. Materials and methods

2.1. Study area

The work was conducted in soybean cropfields and eucalypt plantations in southeastern Paraguay (54°51′–54°39′ from W to E and 25°16′–25°23′ from N to S) and central-eastern Argentina (58°03′–58°22′ from W to E and 31°51′–31°58′ from N to S) (Fig. 1). Eastern Paraguay is part of the Interior Atlantic Forest (Dinerstein et al., 1995), characterised by a canopy dominated by Myrtaceae, Lauraceae and Leguminoseae trees, and an understory covered mostly by ferns and bamboos (Oliveira Filho and Fontes, 2000). Mean annual rainfall is 2000 mm with no dry season, and mean annual temperature is 20 °C with a cold season during June–August. Grasslands from central-eastern Argentina were originally dominated by *Paspalum*, *Axonopus*, *Stipa*, *Bromus*, and *Piptochaetium* (Landi et al., 1987). The region has a temperate climate with mean annual temperature ranging 13–17 °C. Precipitations occur all year round ranging from 1100 mm yr^{-1} in the North to 600 mm yr^{-1} in the South. Native trees are virtually absent in the region but small and isolated woodlots are often found in edaphic communities or associated with cattle-shelter or windbreaks (Cabrera, 1971). Soybean has been the main commercial crop in both the Atlantic forest (Fearnside, 2001) and the Pampean grasslands (Paruelo et al., 2006) over the last decade. Currently, both ecoregions also encompass intensively forested areas where exotic species of *Eucalyptus* are commonly used in commercial plantations (Brizuela et al., 2003; Galindo-Leal and Camara, 2003).

Fig. 1. Location of study eucalypt plantations and soybean cropfields in the Atlantic forest (upper ecoregion) and the Pampean grasslands (lower ecoregion). Photographs illustrate the original vegetation physiognomy and internal structure of both biomes.

2.2. Study design and bird surveys

We selected five internally homogeneous and at least 1 km^2 eucalypt plantations and five soybean cropfields per region, for a total of twenty sites. Within each region sites were at least 1-km apart to ensure different local bird communities and homogeneous context. All sites had a long history of land use. The silvicultural or agricultural management practices were similar, determining similar habitat internal structure, in all plantations and cropfield sites from both regions. Eucalypt plantations were approximately seven years old and soybean cropfields were surveyed approximately two months after sowing.

To survey birds, we located ten observation points in each site. Observation points were 200-m apart to promote non-overlapped subsamples (Bibby et al., 1998), and were located at least 200-m away from the plantation or cropfield edges to minimize edge effect. To increase reliability of species identification, bird surveys were made by two trained independent observers from sunrise to approximately 10:30 on sunny calm days. At each observation point we fixed a 100 m radius, which is less than the maximum recommended for forests, to minimize detectability biases due to different habitat openness. All heard and seen birds were recorded for a 5-min period (Ralph et al., 1996; Bibby et al., 1998). Birds flying overhead were not considered. We controlled for the adequacy of experimental unit size and confirmed that six to eight observation points per site were enough to detect 75–100% of the total species recorded in ten 5-min-observation points. Sample sites were surveyed once during the breeding season, during late December 2007–early January 2008. Thus, all identified species were recorded and the abundance of each one per point was registered.

2.3. Data analysis

To address whether the composition of local bird assemblages in soybean cropfields and eucalypt plantations were primarily determined by land use, we first performed a correspondence analysis (CA) to explore site grouping based on species composition and their relative abundances. We further examined the similarity in species composition between bird assemblages by analyzing similarity indices between pairs of sites. To estimate similarity between sites we used the Morisita–Horn quantitative index, based on both species occurrence and relative abundances (Magurran, 2004). The index ranges from zero to one; an index value of one indicates two sites sharing all species with the same abundance, and a value of zero indicates two sites with no bird species in common. The Morisita–Horn index of similarity was calculated between all soybean cropfields (SS), all eucalypt plantations (EE) and between soybean cropfields and eucalypt plantations (SE) in either the forest (F) or the grassland (G). We used InfoStat (2004) software.

We compared similarity between 1) soybean cropfields within and between contexts (S_FS_F vs. S_FS_G and S_GS_G vs. S_FS_G), to test whether bird assemblages in soybean cropfields from a unique environmental context were more similar among them than those from different contexts; 2) eucalypt plantations within each region and between regions (E_FE_F vs. E_FE_G and E_GE_G vs. E_FE_G), to test if the composition of bird assemblages in eucalypt plantations from a unique region were more similar among them than those from different regions; and 3) soybean cropfields and eucalypt plantations within each region and a) between soybean cropfields from different regions (S_FE_F vs. S_FS_G and S_GE_G vs. S_FS_G), and b) between eucalypt plantations from different regions (S_FE_F vs. E_FE_G and S_GE_G vs. E_FE_G), to test if the composition of bird assemblages in soybean cropfields and eucalypt plantations within a unique context were more similar than either cropfields or plantations from different contexts. Because the Morisita–Horn index of similarity may be indirectly affected by the number of species and then cannot be assumed to be normally distributed; we used a permutational multivariate analysis of variance (PERMANOVA) to perform comparisons within and between contexts and land use types (PERMANOVA 1.6 Anderson, 2001; McArdle and Anderson, 2001). Different to the traditional ANOVA, PERMANOVA tests the significance of comparisons using a permutation procedure and does not have explicit assumptions regarding data distribution. We ran 10.000 permutations to calculate the overall significance and for post hoc pair comparisons. The experimentwise error rate (alpha inflation due to large number of tests) was controlled using the Bonferroni correction ($0.05/8$ comparisons $= 0.006 = \alpha$) (Roback and Askins, 2005).

We evaluated the relative effects of soybean cropfields and eucalypt plantations on native birds; that is, the effects on forest species (F species from now on) in the forest context and on grassland species (G species) in the grassland. The analysis was based on the presence of each species in sample sites. To obtain an independent species classification, we followed Stotz et al. (1996) to classify species based on both the biogeographical area of origin and the preferred habitat (see Table 1). Species with biogeographical areas covering all study sites and species exploiting both open and forested habitats were excluded from the classification. We also excluded from the analysis those species inhabiting atypical habitats within biomes (that is, in open habitats within forests or forested habitats within grasslands). Thus, we compared the proportion of F species occurring in soybean cropfields and eucalypt plantations in the forest and the proportion of G species occurring in soybean cropfields and eucalypt plantations in the grassland, using a 2 × 2 factorial ANOVA and Fisher-post hoc comparisons (InfoStat, 2004).

Table 1
Recorded bird species in eucalypt plantations and soybean cropfields in two different biomes (forest and grassland). Species were classified based on their native zoogeographic region (AF: Atlantic forest, PG: Pampas grassland) and preferential original habitat (F: forests, G: grasslands) following Stotz et al. (1996). The type of monoculture where each species was recorded is included (S: soybean cropfields, E: eucalypt plantations).

Species	Common name	Zooregion/ habitat	Recorded
Rhea americana	Greater Rhea	PG/G	S
Rhynchotus rufescens	Red-winged Tinamou	AF–PG/G	S
Crypturellus parvirostris	Small-billed Tinamou	AF/G	S
Nothura maculosa	Spotted Tinamou	PG/G	S
Buteo magnirostris	Roadside Hawk	AF–PG/F	E
Falco sparverius	American Kestrel	AF–PG/G	S
Circus buffoni	Long-winged Harrier	PG/G	S
Tringa solitaria	Solitary Sandpiper	PG/G	S
Claravis pretiosa	Blue Ground-Dove	AF/F	E
Zenaida auriculata	Eared Dove	AF–PG/G	S
Leptotila verreauxi	White-tipped Dove	AF–PG/F	E
Patagioenas picazuro	Picazuro Pigeon	PG/F–G	E
Columbina talpacoti	Ruddy Ground-Dove	AF–PG/G	E–S
Patagioenas maculosa	Spot-winged Pigeon	PG/F–G	E
Myiopsitta monachus	Monk Parakeet	PG/F	E
Guira guira	Guira Cuckoo	AF–PG/F	E
Crotophaga ani	Smooth-billed Ani	AF–PG/G	E
Athene cunicularia	Burrowing Owl	PG/G	S
Chlorostilbon lucidus	Glitterin-bellied Emerald	AF–PG/F–G	E
Colaptes campestris	Field Flicker	AF–PG/G	S–E
Colaptes melanochloros	Green-barred Woodpecker	AF–PG/F	E
Anumbius annumbi	Firewood-gatherer	AF–PG/G	S
Furnarius rufus	Rufous Hornero	AF–PG/G	S–E
Myiodynastes maculatus	Streaked Flycatcher	AF–PG/F	E
Tyrannus melancholicus	Tropical Kingbird	AF–PG/F–G	S–E
Machetornis rixosa	Cattle Tyrant	AF–PG/G	E
Megarynchus pitangua	Boat-billed Flycatcher	AF/F	E
Tyrannus savana	Fork-tailed Flycatcher	AF–PG/G	S–E
Pitangus sulphuratus	Great Kiskadee	AF–PG/F–G	S–E
Empidonomus varius	Variegated Flycatcher	AF/F	E
Xolmis irupero	White Monjita	PG/G	S
Cyanocorax chrysops	Plush crested Jay	AF/F	E
Progne tapera	Brown-chested Martin	AF–PG/G	S
Troglodytes aedon	House Wren	AF–PG/G	E
Mimus triurus	White-banded Mockingbird	PG/G	S
Anthus lutescens	Yellowish Pipit	PG/G	S
Turdus rufiventris	Rufous-bellied Thrush	AF–PG/F–G	E
Cyclarhis gujanensis	Rufous-browned Peppershrike	AF–PG/F	E
Vireo olivaceus	Red-eyed Vireo	AF–PG/F	E
Basileuterus culicivorus	Golden-crowned Warbler	AF/F	E
Euphonia chlorotica	Purple-throated Euphonia	AF–PG/F	E
Thraupis sayaca	Sayaca Tanager	AF–PG/F	S–E
Ammodramus humeralis	Grassland Sparrow	AF–PG/G	S
Sicalis flaveola	Saffron Finch	AF–PG/G	E
Volatinia jacarina	Blue-black Grassquit	AF–PG/G	S
Zonotrichia capensis	Rufous-collared Sparrow	AF–PG/G	S–E
Cacicus haemorrhous	Red-rumped Cacique	AF/F	E
Sturnella superciliaris	White-browed Blackbird	AF–PG/G	S
Agelaioides badius	Bay-winged Cowbird	PG/G	S
Molothrus bonariensis	Shiny Cowbird	AF–PG/G	S

3. Results

We recorded a total of 638 individual birds from 50 species (Table 1). Of the 30 bird species recorded in eucalypt plantations, 27 were found in plantations located in the forest context and nine in the grassland context; and of the 28 species recorded in soybean cropfields, 14 were in cropfields from the forest context and 21 in the grassland context.

The exploratory CA showed clear separation by land use and a second order effect given by biome (Fig. 2). First and second axes of the CA explained 40% of the variation in bird assemblage composition among sites ($\lambda_1 = 0.90$ and $\lambda_2 = 0.52$, respectively). The first axis separated soybean cropfields from eucalypt plantations. Soybean sites grouped at the right of the first axis, far separated from eucalypt plantations. The second axis separated sites located in the grassland, grouped at the top of the axis, from sites in the forest, grouped at the bottom. Only one eucalypt plantation from the grassland grouped together with forest plantations, probably due to the presence of Sayaca Tanager (*Thraupis sayaca*) that was very common in forest sites.

The PERMANOVA, used to test whether monocultures lead to bird communities similarly composed regardless of the distance between the sites, showed that bird community composition depended primarily on land use and secondly on the biome. First, comparisons among similarity indices showed that bird assemblages from different biomes but under a particular human use were more similarly composed than bird assemblages from a given biome but under different human uses (Fig. 3). Bird composition was more similar between soybean cropfields within forests and within grasslands than between soybean cropfields and eucalypt plantations within either the forest (S_FS_G vs. S_FE_F: $P = 0.0001$) or the grassland (S_FS_G vs. S_GE_G: $P = 0.0001$). Bird composition was more similar between eucalypt plantations within the forest and the grassland than that from soybean cropfields and eucalypt plantations within either the Atlantic forest (E_FE_G vs. S_FE_F: $P = 0.0002$) or the Pampean grasslands (E_FE_G vs. S_GE_G: $P = 0.0002$). Second, the performed comparisons also showed that similarity in bird assemblages between soybean cropfields within the Atlantic forest or within Pampean grasslands was higher than the similarity between soybean cropfields from both ecoregions (S_FS_F vs. S_FS_G: $P = 0.0001$ and S_GS_G vs. S_FS_G: $P = 0.0003$). Similar results were found for eucalypt plantations, as bird composition between plantations within ecoregions was more alike than that between plantations from different ecoregions (E_FE_F vs. E_FE_G, $P = 0.0001$ and E_GE_G vs. E_FE_G: $P = 0.0003$).

The two land uses had opposite effects on native birds (G species and F species for grassland and forest sites, respectively), depending on the biome where the sites were located (ANOVA interaction: $F = 268.7$, $P < 0.001$) (Fig. 4). Fisher-post hoc comparisons revealed that the proportion of G species was higher in soybean cropfields than in eucalypt plantations in the grassland ($df = 16$, $P < 0.001$), whereas the proportion of F species was higher in eucalypt plantations than in soybean cropfields in the forest ($df = 16$, $P < 0.001$).

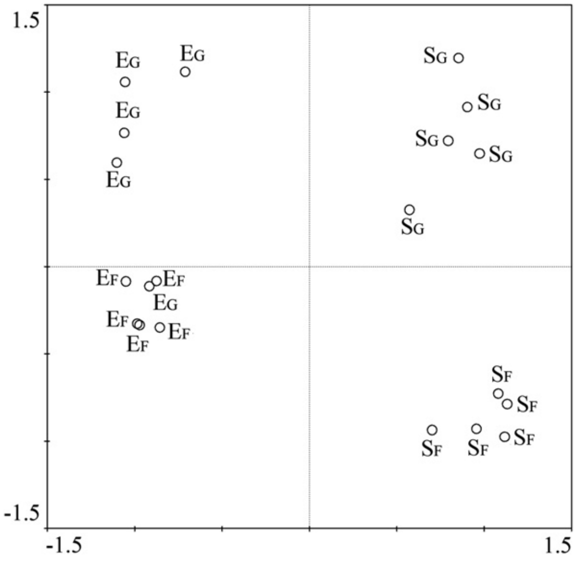

Fig. 2. Biplot showing site ordination obtained from a Correspondence Analysis (E = eucalypt plantations, S = soybean cropfields, F = Forest, G = Grassland).

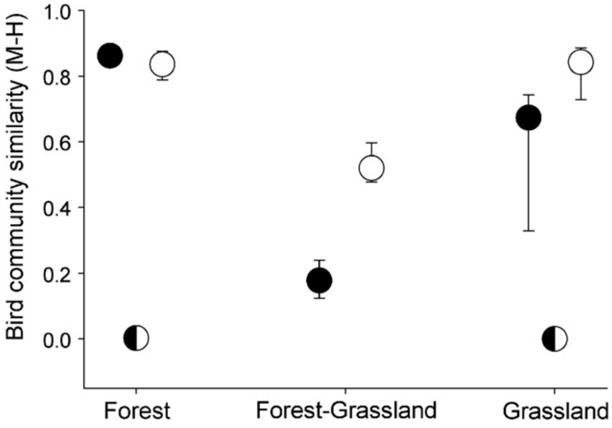

Fig. 3. Median (±25–75 quartiles) community similarity (Morisita–Horn index) among sites. The PERMANOVA and comparisons among similarity indices showed that bird assemblages from different biomes but under a particular human use were more similarly composed than bird assemblages from a given biome but under different human uses. Filled circles: eucalypt plantations, empty circles: soybean cropfields and semi-filled circles: eucalypt plantations–soybean cropfields.

4. Discussion

Land use promotes both the similarity between assemblages from distant places and the difference between assemblages from nearby sites. That generalization was previously discussed within the conceptual framework of biotic homogenization/differentiation (Olden and Poff, 2003), challenging the so-called “first law in geography” which refers to the distance decay of biotic similarity (see Nekola and White, 1999, and references therein). Assuming that nearby communities were originally similarly composed whereas distant communities were very different, our work suggests that habitat conversion to monocultures led to major changes in local species composition, either homogenizing bird

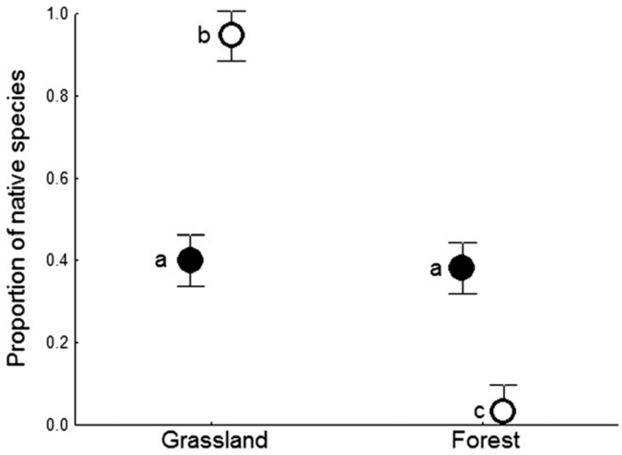

Fig. 4. Mean (±SE) proportion of native species (G species and F species for grassland and forest, respectively) in soybean cropfields (empty circle) and eucalypt plantations (filled circle) in the forest and grassland biomes. Different letters indicate statistically significant differences ($P < 0.05$).

assemblages from distant sites (which leads to decreasing global diversity) or enhancing differences among communities from nearby sites (increasing regional diversity). However, results also indicated some level of differentiation between distant communities in either soybean cropfields or eucalypt plantations. The structural similarity between original habitats and monocultures would ultimately favor the persistence of some native species in transformed environments.

Our results support the hypothesis that human land use determines community similarity through habitat similarity. Previous studies have shown that habitat similarity strongly influences community similarity (Harrison et al., 1992; Dormann et al., 2007), and that low-intensity agriculture and heterogeneous landscapes enhance beta diversity (Tscharntke et al., 2008). Our sampling sites, currently used for tree plantations or cropfields, were modified from the original subtropical forest or temperate grassland. Habitat conversion to monocultures increased habitat similarity between sites that previously had contrasting vegetation types, and decreased habitat similarity between sites that originally had similar vegetation type. Habitat changes probably led to changes in bird community composition. Nekola and White (1999) proposed that community similarity could be determined by niche-based processes because species may show different levels of coincidence in their abilities to perform under given environmental conditions (Tuomisto et al., 2003; Gilbert and Lechowicz, 2004). As plantations and cropfields in both Paraguayan and Argentinean sites showed different bird species composition, it is possible that those species strongly differed in their abilities to perform under the environmental conditions settled by both human land uses. Cottenie (2005) also emphasized the role of niches and environmental constraints in structuring communities.

The high community similarity that we found among cropfields and among plantations from distant sites, together with the low similarity between cropfields and plantations from nearby sites, indicate that niche-based rather than dispersal-based processes is likely a primary factor determining species occurrence and consequently community composition. Soininen et al. (2007) concluded that the spatial structure of species composition unites several ecological phenomena including environmental structuring and species dispersal propensity. Nonetheless, niche-based and dispersal-based processes may act hierarchically: when dispersal is not a limitation, the ability of species to perform in the environment will determine the composition of local assemblages; but when dispersal is a limitation for species to colonize new areas, the environmental similarity between the original and the new site will be insufficient to predict similar communities simply because species will not be able to reach those sites.

Several species occurred only at plantations or cropfields in either grassland or forest sites, possibly indicating that different regional pools of species contributed to partially differentiate distant assemblages under a given local environment (i.e. plantation or crop). In urban environments, for instance, Sorace and Gustin (2008) found higher similarity between bird communities of different habitats in the same town than between bird communities of the same habitat in towns from different Italian regions. Ecoregions differ not only on the original vegetation type but also in factors such as climate and soil type (Olson et al., 2001). The sites we surveyed were approximately 800-km apart and immersed in two different ecoregions with no geographical barriers for bird dispersal. It is likely that many species from one ecoregion were unable to colonize the other ecoregion due to unsuitable conditions given by factors such as climate. Thus, these findings support that local niche-based processes (i.e. species abilities to perform under a given set of climatic conditions) are major determinants of community composition.

It is known that birds are sensitive to vegetation structure (Cody, 1985). Our results indicated that the similarity in vegetation structure between the original and human-modified habitats allows the persistence of some native species in human-modified habitats. In sites located in the forest, we found that eucalypt plantations held more forest species than soybean cropfields. In contrast, soybean cropfields showed more grassland bird species than eucalypt plantations in the grassland sites. Although detectability biases may occur even using a 100-m radius, they would eventually lead to overestimations of richness and abundance in the open habitat (i.e., soybean cropfields) and to miss individuals and species in forests. Thus, results suggest that preserving vertical components instead of creating open environments when replacing native forests would be less detrimental to the occurrence of forest birds. In contrast, when replacing grasslands, the preservation of open areas with a low herbaceous stratum instead of plantations where trees become dominant and vegetation structure is more complex would produce less negative effects on the occurrence of grassland birds. However, even when some monocultures can promote the occurrence of native species, the associated environmental conditions could negatively affect the performances of those species. A recent study showed that, within a particular land use, the maintenance of a high and diverse cover of original plant species would enhance the occurrence of specialists and endemics (Abrahamczyk et al., 2008). If species distributions across space were primarily determined by the availability of suitable habitat (Pulliam, 2000), a given land use activity preserving at least one niche dimension of the natural habitat would be more suitable to native species than activities that changes all niche dimensions.

In summary, 1) bird communities in cropfields and plantations in nearby sites were composed by different species, 2) bird communities in distant cropfields and distant tree plantations were similarly composed, and 3) plantations were less detrimental to forest bird species than cropfields in the forest sites, whereas cropfields were less detrimental to grassland birds in the grassland sites. Even when cropfields and tree plantations are detrimental to forest and grassland birds (Mardsen et al., 2001; Zurita et al., 2006; Filloy and Bellocq, 2007) and species loss might have strong implications for ecosystem functioning (Sekercioglu, 2006), both land uses showed some contrasting effects on (at least some) native bird species. Our findings suggest that locating each land use in the best possible environmental context will tend to preserve beta diversity, whereas the location of a variety of land uses within a particular context will promote alpha diversity. Although results are based on a simple field design (two land uses and contexts) and limited sample size, they show strong patterns that may have significant implications for land use planning; more exhaustive confirmatory studies are required to include the range of land uses and ecoregions to explore the generality of our conclusions. In a world with increasing need for land services and with a considerable extension of land transformed for providing those needs, our findings might be useful for future land use strategies and regional planning.

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