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# Local randomness, vegetation type and dispersal drive bird and mammal's diversity in a tropical South American region

N. C. CÁCERES,<sup>1</sup> C. S. DAMBROS,<sup>2,†</sup> G. L. MELO,<sup>3</sup> J. SPONCHIADO,<sup>1</sup> F. DELLA-FLORA,<sup>1</sup> AND M. O. MOURA<sup>4</sup>

<sup>1</sup>*Department of Biology, CCNE, Universidade Federal de Santa Maria, Camobi, Santa Maria, RS 97110-970 Brazil*

<sup>2</sup>*Department of Biology, University of Vermont, Burlington, Vermont 05405 USA*

<sup>3</sup>*Universidade Federal de Mato Grosso do Sul, Campo Grande, MS 79070-900 Brazil*

<sup>4</sup>*Departamento de Zoologia, Universidade Federal do Paraná, UFPR, Curitiba, PR 81531-980 Brazil*

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**Abstract.** How dispersal, environmental filters, and local extinctions affect species diversity depends on the species requirements for habitat, dispersal limitations, and abundance. Few studies have been able to properly separate these processes and to show how they affect the beta diversity patterns for multiple organisms. We investigated how the composition of birds and mammals changed along geographical and environmental gradients in an environmentally complex South American region. Using mantel tests and a null model approach we disentangled the effects of dispersal, environment, and stochastic processes in the species beta diversities. The similarity on species composition was negatively associated with the geographical distance separating areas for both groups. The changes in bird species composition likely resulted from their dispersal limitation over large geographical regions. In contrast, the composition of mammals in a given area was a partially random subset of the regional species pool, to some extent, filtered by the vegetation. Small communities tended to have more variable species composition, whereas dispersal limited birds showed a stronger distance-decay pattern. Neither local randomness nor dispersal limitation prevented species from being filtered by the environment. Other groups are likely to show similar patterns depending on their dispersal abilities, environmental requirements and community size.

**Key words:** dispersal limitation; distance decay; ecological drift; neutral theory; niche theory; species richness; vegetation effect.

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† **E-mail:** Cristian.Dambros@uvm.edu

## INTRODUCTION

The decay of similarity in species composition with geographical distance has been extensively reported for many organisms and geographical regions (Nekola and White 1999, Steinitz et al. 2006). The distance-decay in species similarity can be caused by dispersal or environmental filters sorting species from the regional pool into local communities. When the species are dispers-

al limited, the similarity in species composition is higher in neighboring areas because they have a higher flux of individuals compared to areas farther apart (Hubbell 2001). However, the environment might also determine which species will establish in the local communities because some species can be better adapted to certain environments. Because the environment is usually spatially structured (Soininen et al. 2007, Chang et al. 2013), areas that are near to each

other also tend to share more species due to environmental filtering.

One approach to disentangle the effect of environmental and dispersal filters on species composition is to compare organisms with different dispersal abilities and environmental requirements. Despite some attempts to compare different groups of species (e.g., Soininen et al. 2007), the samples are usually taken in much finer scales for dispersal limited organisms, which prevent correct comparisons (Barton et al. 2013). Moreover, multiple groups have rarely been investigated in the same areas using the same sampling design, limiting the investigation of the beta diversity patterns among groups (Thompson and Townsend 2006, Qian and Ricklefs 2012).

Neutral processes (e.g., dispersive) are more likely to affect the diversity of dispersal limited communities and have been shown mainly for sessile organisms that are strongly dispersal limited (Gilbert and Lechowicz 2004, Steinitz et al. 2006). Mammals comprehend many large sized species that are generally widely distributed, but some small mammals can be highly restricted to their natal sites (Fonseca et al. 1996). Birds also have great variation in dispersal strategies but are usually slightly more dispersal limited than mammals (Sutherland et al. 2000). Therefore, it is not clear which group is expected to be more strongly associated with geographical distance (Barton et al. 2013).

Besides their similarities in dispersal, mammals are much less abundant than birds, and mammals are more affected by human disturbance, like hunting (Cullen et al. 2000) and species-area effects (Chiarello 1999). Through ecological drift, small communities might experience higher extinction rates of species (Rosindell et al. 2011). The predictions of drift and randomness due to small population sizes have long been incorporated to determine the dynamics of allele fixation or lost in population genetics (Kimura and Crow 1964). However, local randomness in species diversity has been poorly explored in community ecology and biogeography, particularly the effects in the species beta diversity. Ecological drift can cause differences in species composition even in the absence of dispersal limitation, leading to higher beta diversity, and a random composition of species

in small communities. However, commonly used tests cannot properly separate the effects of local and regional processes in the species beta diversity (Jost 2007, Baselga 2010). Using a null model approach proposed by Chase et al. (2011), we disentangled the role of regional (dispersal) and local random processes in the communities' beta diversities. We then compared the deviations from the null model with the predictions based on species dispersal, community size and association with non-spatially structured environmental gradients.

Within this framework, we asked (1) whether birds and mammals differ in their response to geographical isolation and local environmental conditions, as expected for groups with different dispersal capabilities; (2) how environmental filtering and dispersal limitation affect the alpha and beta diversities of birds and mammals; and (3) whether mammals have a distribution closer to a random expectation than birds, given that smaller communities are expected to be more affected by random processes (Chase et al. 2011).

## METHODS

### *Study area*

The sampled area is located in the state of Mato Grosso do Sul, west of Brazil, which includes vast portions of Pantanal wetlands and Cerrado (dominated mostly by woodland savannah), and smaller portions of semi-deciduous forests of Chaco and Atlantic domains, forming ecotonal zones. Atlantic forest patches occur in the southeastern part of the study region, the Cerrado vegetation in the center, southwest and northeast, the Pantanal wetlands in the northwest, and the semi-deciduous Chiquitan forest and the Chaco thorny vegetation in the far west (Veloso et al. 1991). The areas of Cerrado, Pantanal and Chaco eco-regions in this study refer to the “diagonal of open areas” described by Ab'Saber (1977), separating the Amazon of the Atlantic Forest domains (Fig. 1).

The climate in the region is seasonal, with rains occurring during the wet season between October and March, and drought occurring in the dry season from April to September.

### *Data sampling*

In total, 20 fragments were extensively sam-

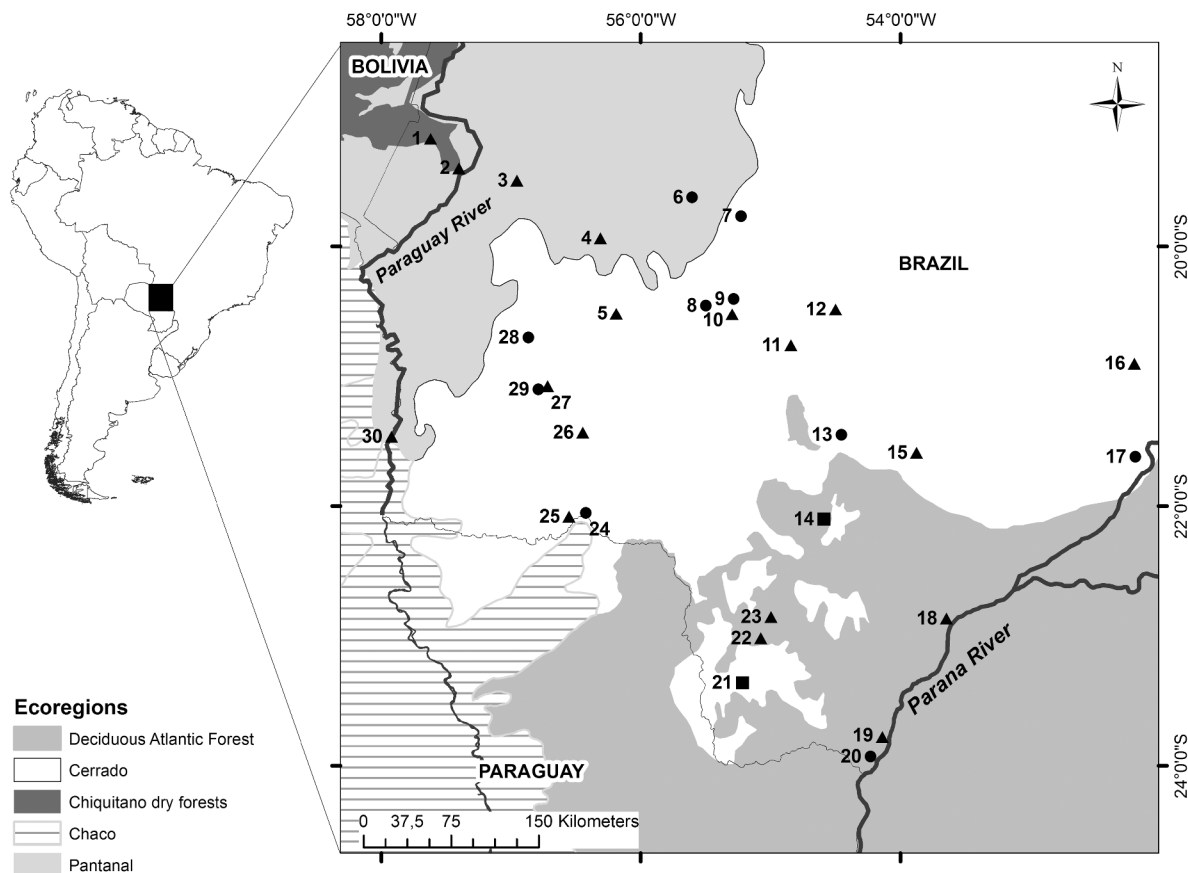


Fig. 1. Map showing the study region in central South America, with the sampling areas. Triangles are areas where both birds and mammals were sampled ( $n = 18$ ); circles are areas where only mammals were sampled (10); and squares are areas where only birds were sampled (2).

pled for birds and 28 for mammals. Eighteen common fragments from both groups were sampled simultaneously. The maximum distance between fragments was 634 km (Fig. 1). These fragments are variable in terms of geographic location, altitude, and vegetation structure (Table 1), and are representative of each eco-region within the study area. We used the largest forest fragments found in each locality, with an adequate level of conservation, which well represented the regional landscape. The largest remnant sampled had around 5,000 ha and the smaller one, 22 ha. In each area, we sampled all existing forested landscapes, such as semideciduous forest, gallery forest, woodland savanna, riparian forest, and woodland Chaco. In order to standardize the sampling effort, grassland and shrub land habitats were not sampled. All

sampled fragments are forest remnants created by human activity.

The surveyed areas for birds and non-volant mammals occurred during four field phases of 25 days between April and August, 2009 and 2010. Due to the difficulty of access to the Pantanal wetland areas during the rainy season, the sampling covered only the dry season (April to September) for standardization (avoiding seasonal effects). Following the same sampling protocol, eight additional areas were sampled for mammals before 2009 and were included in the analyses. Each field phase for each sampled location was performed during four days and nights. We opted to compare resident birds (see below) and non-volant mammals following Greenwood et al. (1996), whose have separated both birds and mammals according to flying

Table 1. Characteristics of the sampling areas. Latitude (Lat) and longitude (Long) are shown in decimals; altitude in meters above sea level; vegetation is in a scale from 1 to 5, where 1 means predominance of grasslands and 5 indicates predominance of deciduous forests; fragment size was measured in ha and log transformed prior to the analyses.

Code (map)	Fragment	Lat	Long	Elevation	Vegetation	Area	Bird richness	Mammal richness
1	Corumbá/Urucum	19.17	57.62	372	5	650	42	13
2	Corumbá/Albuquerque	19.38	57.4	152	2	800	58	13
3	Corumbá/Xaraés	19.48	56.92	94	1	150	48	18
4	Miranda/Caiman	19.93	56.32	113	3	5600	62	21
5	Miranda/Borboleta	20.5	56.18	225	3	70	45	17
6	Aquidauana/Pantanal	19.62	55.6	135	1	150	no data	18
7	Corguinho	19.77	55.23	300	3	200	no data	16
8	Aquidauana/Piraputanga	20.45	55.5	180	3	600	no data	16
9	Terenos	20.4	55.27	280	3	600	no data	15
10	Dois Irmãos do Buriti	20.52	55.28	280	3	400	31	13
11	Sidrolândia	20.77	54.85	469	3	3000	47	16
12	Campo Grande	20.48	54.5	624	3	600	27	11
13	Nova Alvorada do Sul/Bela Vista	21.45	54.45	480	4	450	no data	14
14	Douradina	22.1	54.58	338	5	22	15	no data
15	Nova Alvorada do Sul/Laranjeira	21.58	53.87	344	3	340	28	15
16	Três Lagoas	20.88	52.18	320	3	1000	48	10
17	Santa Rita do Pardo	21.67	52.17	330	4	170	no data	9
18	Naviraí	22.87	53.63	232	1	1200	53	17
19	Eldorado	23.77	54.12	298	4	620	38	10
20	Mundo Novo	23.92	54.25	290	5	140	no data	9
21	Sapuçaia	23.35	55.22	407	4	22	31	no data
22	Amambai	23.02	55.07	383	5	60	22	9
23	Laguna/Campanário	22.85	55	409	5	3520	52	14
24	Bela Vista/Redomão	22.05	56.43	236	3	200	no data	16
25	Bela Vista/Exército	22.07	56.55	236	3	600	51	18
26	Jardim	21.43	56.43	257	4	500	41	15
27	Bonito/Santa Tereza	21.08	56.73	610	2	100	67	15
28	Bonito/Princesinha	21.08	57.48	550	2	350	no data	22
29	Bodoquena/Califórnia	20.7	56.85	470	2	100	no data	12
30	Porto Murtinho	21.47	57.9	85	2	2000	41	19

capacity, body size and migration capacity.

In each area, birds were sampled during four days of observation using binoculars. In each field phase, birds were recorded in interior and edges of forest fragments, with observations starting at 07:00 h in the morning and finishing 3–4 h later. Different sites were sampled each day in a given area, and there was not variation in the starting time between sites or areas. Eagles, hawks and owls, being underestimated in forested habitats, and long-dispersal migratory bird species (non-residents; Figueira et al. 2006) were not included in the study.

Marsupials and rodents (<1 kg; families Cricetidae, Echimyidae and Didelphidae), and large non-volant mammals were sampled. In each area five 120-m transect lines were used. The transect lines were at least 150 m apart from one another and at least 20 m from the nearest

border inside the forest fragments. For sampling small mammals, 65 cage traps were used. Thirteen traps were installed in each transect line, alternately between the ground and under-story levels, 10 m from one another. The bait used was a mixture of pumpkin, bacon, peanut butter and codfish liver oil. Specimens captured were identified and released to the field. Voucher specimens were collected and maintained in the mammal collection of the Santa Maria Federal University.

For sampling large sized mammals, we used the following methods: (1) direct field observations (sightings and sounds); (2) track analysis; (3) other vestiges such as feces, skull remains and road-kill in the surroundings.

#### *Explanatory variables*

For each area, we measured the vegetation



type on a scale from 1 to 5, where 1 represents the predominance of grasslands and 5 represents the predominance of semi-deciduous forests in the landscape (the predominance of woodland savanna averages a score of 3). Fragment size was measured in ha based on satellite images taken during the sampling period (Table 1). When small fragments surrounding the sampled fragment were present (25% of the fragments), the total area was calculated as the sum of all fragments. These additional fragments were small and did not increase significantly the edge size for the covered area. The pairwise Euclidean distance between fragments was measured by the fragments geographical position and the altitude in meters above sea level (m asl).

### *Statistical analyses*

Data on species richness and composition, using presence and absence data, was recorded in each fragment (Fig. 1, Table 1). For the similarity analyses, we considered only species occurring in at least two areas.

We correlated the number of bird and mammal species (richness) with the explanatory variables of vegetation type and fragment size. We performed a multiple linear regression analysis of the observed number of species in each fragment against the fragment size and vegetation type, and compared the models with and without each variable based on Akaike Information Criteria values (AIC).

To analyze the effect of geographical distance on community composition of birds and mammals, we performed Mantel tests using Pearson's correlation of community similarity against geographical distance, similarity in fragment size and vegetation type, and all variables combined. The similarity of species composition was measured by the Jaccard similarity index.

Tuomisto et al. (2003) showed that in certain distances it is possible that the general pattern of distance-decay disappears due to absence of correlation between distance and environmental similarity. To account for this, we used a partial Mantel correlogram to assess spatial correlation in different classes of distance for both groups.

To analyze the effect of random processes in the local species diversity related to fragment size and community size, we created a null model where species in local communities are randomly

drawn with the same observed proportions from the regional species pool (Gotelli and Graves 1996, Chase et al. 2011). The species occupancy among sites was kept constant and the differences in species composition in our model were created by differences in community size alone. The null model was created by pooling the species from all sites, and recording the frequency of occurrence of each species. From this regional species pool, we draw a random species sample for each area maintaining the original number of species observed locally. The random draw was based on the frequencies in which the species were observed in the regional pool, so that the overall frequency of occurrence for each species remained constant. In each random sample, we recorded the number of shared species between all pairs of samples. This procedure was generated 10,000 times. We then compared the actual similarity in each pair of communities with those in the simulated communities. This procedure was conducted for birds and mammals independently and had the following predictions: (1) if local random processes are responsible for the changes in species composition, then the similarity in current communities will not differ from the null model; and (2) if dispersal limitation associated with geographical distance exists (spatial structure) or if the environment determines species composition, then communities should be more dissimilar or similar than expected by chance, depending on the geographical distance and vegetation differences between areas under comparison (Chase et al. 2011).

Diagrams of community change across the areas were generated by summarizing species composition of birds and mammals using the first axis of a Principal Coordinates Analysis (PCoA). Jaccard similarity index was used again to measure species composition differences between areas.

All analyses were carried out using the R program (R Development Core Team 2013) and the package Vegan (Oksanen et al. 2012). For the null model, the R functions are provided in Chase et al. (2011) and we used the non-standardized results to compare birds and mammals. Additional functions used are available at [www.uvm.edu/~cddambro](http://www.uvm.edu/~cddambro) and by request to the authors.

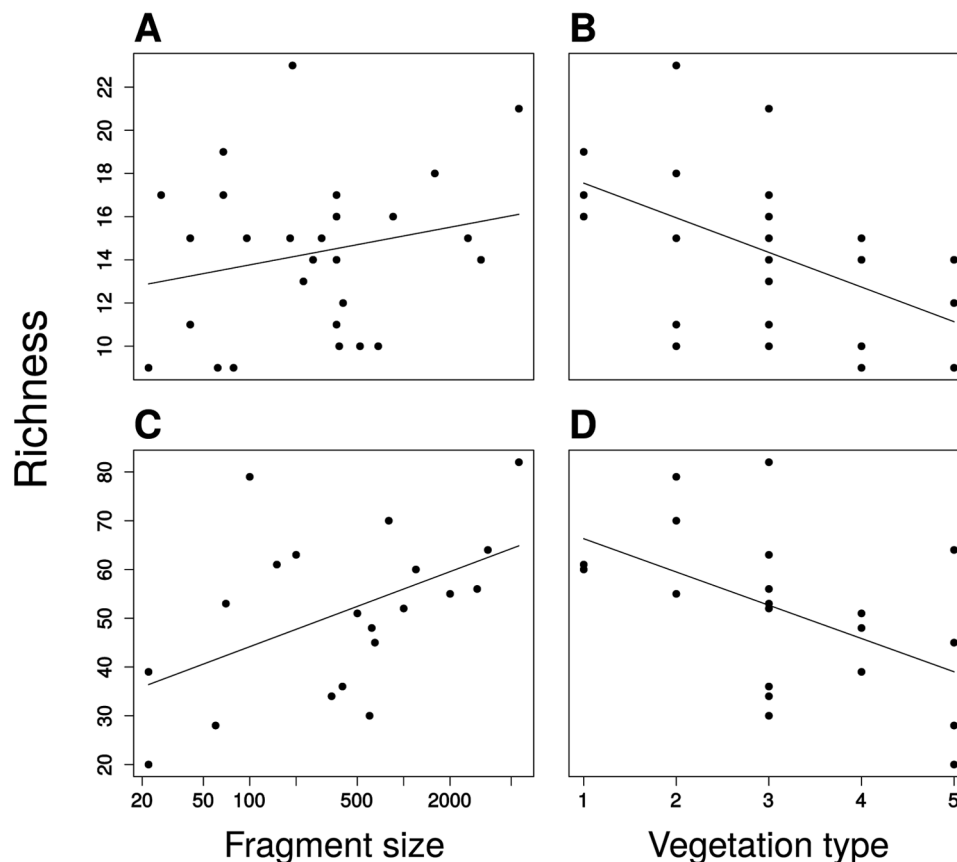


Fig. 2. Relationships of species richness against fragment size and vegetation type for mammals (A; B) and birds (C; D). Fragment size is shown in log scale and vegetation types represent the change from grasslands (1), savannas (3), and forests (5).

## RESULTS

After 235 hours of sighting for birds and large mammals, and 7,280 trap-nights for small mammals, 200 bird and 59 mammal species were sampled. One hundred fifty-six bird and 49 mammal species were present in at least two areas for similarity analyses (Table 1).

In the regression model of the predictor variables against species richness, the best-fitting model, based on AIC values, included a positive association of fragment size and a negative association of vegetation type as predictors both for birds ( $P < 0.001$ ,  $F_{2,17} = 9.32$ ,  $R^2 = 0.52$ ) and mammals ( $P < 0.001$ ,  $F_{2,25} = 8.33$ ,  $R^2 = 0.40$ ) (Fig. 2).

The similarity of species composition was negatively associated with geographical distance

(distant areas share less species) both for birds and mammals (Fig. 3, Table 2). Bird species composition was more strongly associated with the geographical distance between areas than differences in local ecological conditions (fragment size or vegetation type) (Table 2), and the model with just geographical distance had the highest correlation with species similarity. The inclusion of additional variables in the model did not increase the ability to explain species composition (Table 2). For mammals, vegetation type was more strongly associated with species composition than fragment size or geographical distance. However, there was a strong correlation between geographical distance and species composition (Table 2).

When analyzed by distance classes, the pattern of distance-decay disappeared in distances higher than ~400 km for birds and higher than ~250

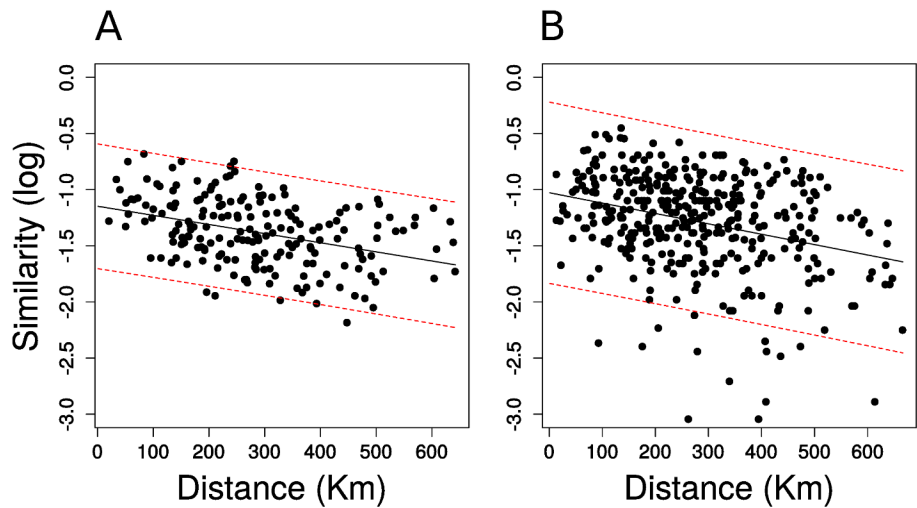


Fig. 3. Relationships between the similarity in species composition and geographical distance for birds (A) and mammals (B). Dashed lines represent the 95% confidence interval. Mammal species composition was much more variable than the bird species composition. This pattern is likely caused by differences in community sizes.

km for mammals. Comparing distant areas, there were positive associations between distance and similarity. For example, areas 500 km far from one another were more similar than areas 400 km apart for mammals (Table 2, Fig. 4).

When analyzed against a null expectation that simulates local randomness, the similarity in species composition differed from the null expectation more strongly for birds (mean = -0.38) than mammals (mean = -0.21) ( $P < 0.01$

for both groups). The departure of similarity in bird communities was mostly associated with the geographical distance (distant areas were more dissimilar than expected;  $P < 0.001$ ;  $r = 0.45$ ). Mammals also differed from the null expectation and the differences were associated with vegetation type ( $P < 0.001$ ;  $r = 0.30$ ).

Besides the fact that the overall vegetation structure was weakly associated with species composition in birds, some bird species were just present in some vegetation formations (Fig. 5A). For mammals, the change in species composition was not as easily defined and directional as for birds, but there were considerable changes in species composition within the areas (Fig. 5B).

Table 2. Correlation coefficients ( $r$ ) of Mantel tests between similarity of species composition and geographical distance and/or local conditions (fragment size and vegetation type).

Independent variable	Bird similarity	Mammal similarity
Geographical distance	-0.38**	-0.30**
Correlation by distance classes (km)		
0.0–54.9	-0.33**	-0.12*
54.9–123.9	-0.15*	-0.07
123.9–193.0	-0.03	-0.06
193.0–262.0	-0.07	0.15**
262.0–331.0	0.08	0.02
331.0–400.0	0.23*	0.19**
400.0–469.0	0.22*	0.14*
469.0–538.1	0	0.14**
538.1–607.1	0.08	...
Fragment size	0.12	0.19
Vegetation	-0.19*	-0.32**
Local conditions and distance	-0.24*	-0.38**

\* $P < 0.05$ , \*\*  $P < 0.01$ .

DISCUSSION

Neutral and niche processes are likely to play important roles on species distribution (Rosindell et al. 2011) and our results clearly indicate that both processes affect the species diversity along a broad range of habitats and across multiple geographical scales. More importantly, our results highlight that the magnitude of neutral and niche processes differ among taxonomic groups even in the same geographical region.

The species diversity in local fragments (alpha diversity) was very similarly associated to the area of fragments and vegetation type both for



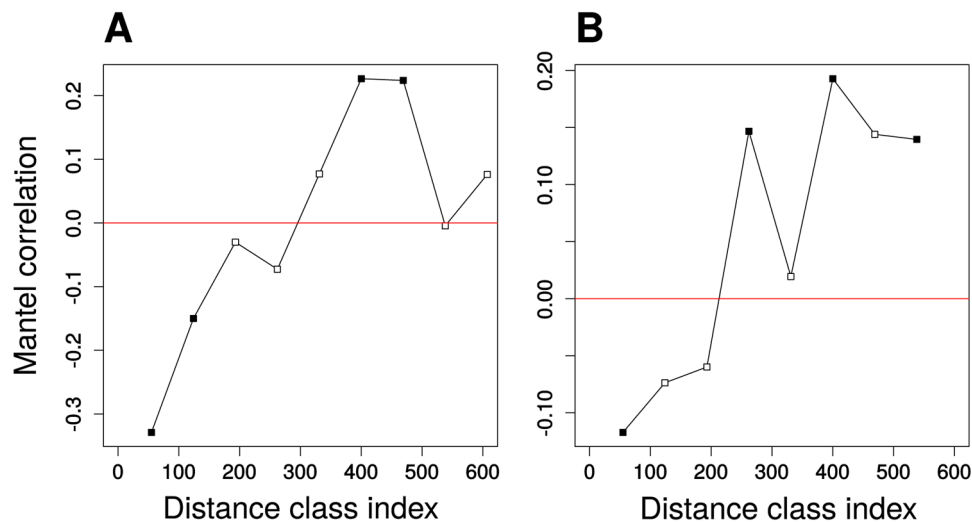


Fig. 4. Mantel correlograms showing the relationships of Pearson's correlations according to distance classes (in km) for birds (A) and mammals (B). Black points are significant associations of distance and species similarity at the  $\alpha = 0.05$ .

mammals and birds. This pattern might be associated with the higher environmental heterogeneity and vegetation complexity in larger fragments (MacArthur and MacArthur 1961) or a balance between high immigration (target effect; Lomolino 1990) and lower extinction rates (MacArthur and Wilson 1967). At local scales, niche processes are more likely to influence species distribution than neutral processes because, at local scales, species compete (Silvertown et al. 1999) and can reach all areas where they are able to survive (Ozinga et al. 2005). It is also in this scale that local random extinctions are more likely to occur due to the reduced number of individuals in local populations. In this study, larger fragments harbored more species of birds and mammals but we were unable to distinguish between niche and neutral processes by just observing the alpha diversity patterns. The reduction of fragment area can cause species loss due to the reduced number of habitats (MacArthur and MacArthur 1961) or through random local extinctions that are more prominent in small communities (MacArthur and Wilson 1967, Hubbell 2001). Similarly, different vegetation types can have more or less environmental complexity, or support communities with different sizes, affecting local diversity through neutral and non-neutral processes. Usually forests are

more complex than shrublands and grasslands (August 1983) and will have more species if niche availability is determinant (Cáceres et al. 2011). However, we observed just the opposite, possibly because in our field sites, areas dominated by grasslands are highly heterogeneous compared to forests.

Although niche and neutral processes can have very similar predictions for the number of locally co-existing species, the identity of these species (composition) depends on which processes are assembling the local communities. At regional scales, differences in the dispersal capability between birds and mammals could affect the species ability to occupy suitable habitats (Ozinga et al. 2005), causing differences in species similarity between areas. For both birds and mammals, the similarity in species composition was highly correlated with the geographical distance between areas, and a deeper decay was observed in shorter distances (Table 2, Fig. 3). The comparisons against a null model revealed that mammals are more likely to be affected by local random processes (e.g., ecological drift) because the mammal species composition is more similar to a random simulated community than birds. Small communities tend to have random species composition due to several reasons, such as rapid extinctions or

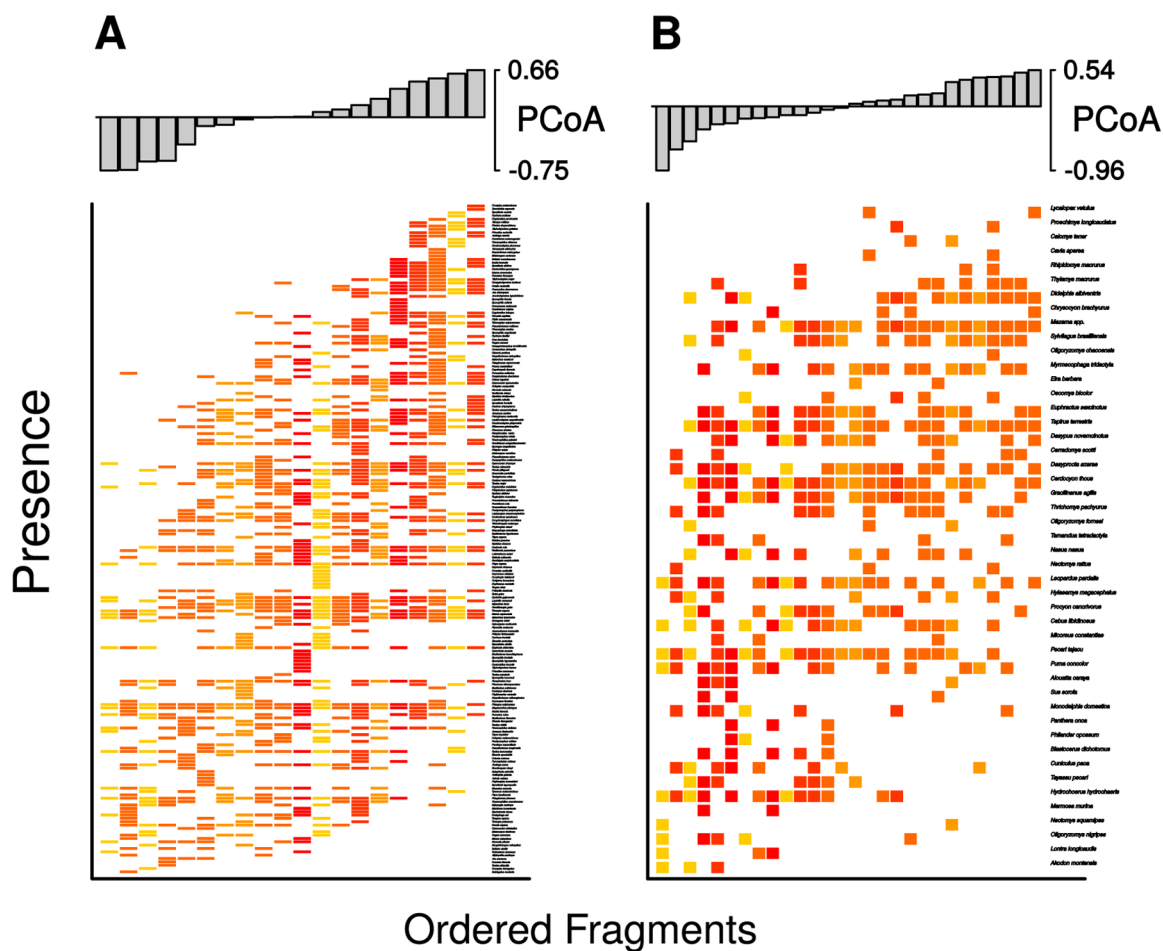


Fig. 5. Ordination histograms representing the species presence in the fragments and similarity in species composition among fragments for birds (A) and mammals (B). Fragments were ordered by the first ordination axis of a Principal Coordinates Analysis (PCoA) using the Jaccard index of species similarity. Species were ordered by their mean of distribution along the ordination axis. Adjacent columns represent fragments with similar species composition and adjacent species represent species with similar distribution. Colors represent fragments' vegetation heterogeneity from the most (yellow) to the less heterogeneous (red).

natural sampling processes (Chase et al. 2011). This randomness can increase the beta-diversity in mammal communities even if they are not dispersal limited or in homogeneous environments (Chase et al. 2011). Conversely, the similarity of birds among fragments strongly differed from the random expectation, and the bird composition was much more spatially structured. These results are in accordance with expectations because birds have larger populations than mammals in tropical ecosystems (Parry et al. 2007), and resident birds might be more dispersal limited than mammals (Suther-

land et al. 2000). At the same body size, non-volant mammals also produce more offspring per time than birds (Greenwood et al. 1996), which could be related to a higher dispersal capacity for mammals. Dispersal limited organisms are known to be more strongly associated with geographical distance, while communities of species with intermediate dispersal ability decay in similarity both due to geographical isolation and environmental filtering (Thompson and Townsend 2006), as observed for mammals.

Although the overall patterns of species distribution met the neutral expectations, it is

usually difficult to disentangle the influences of dispersal limitation and environmental filters because many important environmental variables are naturally spatially structured (Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Chang et al. 2013). We have not detected a strong association between vegetation type and geographical distance (results not shown), but unmeasured variables are likely to be spatially structured. The Mantel correlogram test, which makes independent correlations in several classes of distance, showed that the decay in species similarity was strong only in small and intermediate scales (Table 2, Fig. 4). In these scales, the separation between areas is small enough to encompass a sole vegetation type and the spatial autocorrelations involving nearby sites is strong (Legendre 1993, Steinitz et al. 2006). However, when comparing areas far apart, more than 400km for birds and 300km for mammals, there was a positive correlation between geographical distance and community similarity, which is not expected based on the distance decay of community similarity (Nekola and White 1999) and neutral assumptions (Hubbell 2001). This indicates that ecological factors are in part determining the species composition over large scales (Tuomisto et al. 2003). In fact, the northwestern forests (Pantanal wetlands or Chiquitanean Forest) were more similar to the southeastern forests (Atlantic Forest) than to the central areas with savannahs (Fig. 1). Therefore, the species composition changed in response to geographical distance when the environment was not strong enough to drastically affect species composition.

Our results indicate that local environments were predictors of the species identity for birds and mammals over larger scales even when neutral processes might be occurring. This is the first study attempting to compare two vertebrate groups in light of neutral and niche theory under the same sampling extent and grain size, which brings new insights about how dispersal limitation might affect the association of diversity and environment. Despite the fact that neutral processes have a strong potential to make communities diverge, this does not mean that just isolation and distance from source areas are mandatory. Larger areas can maintain a larger pool of species whereas vegetation type might be an important predictor both of species

richness and composition (Parry et al. 2007, Cáceres et al. 2011). The species composition was affected both by dispersal limitation and local ecological conditions, indicating that interconnected fragments and areas with high environmental variation harbor more species. Mammals were more dependent on local processes (deterministic or not) than birds, which seemed to be limited by dispersal. Dispersal limitation also regulated how species were affected by the environment but did not prevent environmental filtering to act. Highly mobile organisms are likely to reach all areas where they are able to survive and adapt to various environmental conditions.

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