

Spatial autocorrelation of mammalian richness and abundance along the Cerrado-Pantanal corridor, Central Brazil

Autocorrelação espacial da riqueza e da abundância de mamíferos ao longo do corredor Cerrado-Pantanal, Brasil Central

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Abstract

In this paper, we evaluated spatial patterns in mammalian fauna obtained using 75,000 camera-trap hours in 33 fragments at the Cerrado-Pantanal border, along an east-west axis and flanked by two relatively large preserved areas. This region has been proposed as an ecological corridor, connecting these two large ecosystems. The richness of species obtained (total = 33) was explained by the area and the number of habitats in each fragment. The abundance of small-bodied species tends to have significant spatial patterns, whereas variation in the abundance of large-bodied species is randomly distributed in the geographical space. No faunal transition (changes in species compositions) between the two ecosystems was identified.

Key words: camera trap, Cerrado, ecological corridor, Pantanal, mammals.

Resumo

Neste trabalho, avaliamos o padrão espacial da mastofauna através de 75.000 horas de esforço amostral obtidas por armadilhas fotográficas instaladas em 33 fragmentos em uma região de transição entre o Cerrado e o Pantanal, ao longo de um eixo Leste-Oeste, entre duas áreas relativamente grandes e bem preservadas. Esta região tem sido proposta como um corredor ecológico, conectando estes dois grandes ecossistemas. A riqueza de espécies obtida (total de 33 espécies) foi explicada pela área e pelo número de habitats em cada fragmento. A abundância de espécies de pequeno porte tende a apresentar padrões espaciais significativos, enquanto a variação na abundância de espécies de grande porte é aleatoriamente distribuída no espaço geográfico. Não foi identificada uma transição faunística (mudança na composição de espécies) entre os dois ecossistemas.

Palavras-chave: armadilha fotográfica, Cerrado, corredor ecológico, Pantanal, mamíferos.

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Introduction

Understanding the spatial structure of abundance and species richness has been traditionally one of the main concerns of ecological research (Krebs, 1994), both to understand ecological and evolutionary processes underlying these patterns and, more recently, to use these pieces of information to drive conservation efforts (Nichols *et al.*, 1998; Rouget *et al.*, 2003; Dark, 2004). Handling spatial data, thus, becomes a central issue in conservation programs worldwide, at different scales.

More specifically, spatial autocorrelation measures the similarity between samples for a given variable as a function of spatial distance (Sokal and Oden, 1978a,b; Griffith, 1987; Legendre, 1993). This way, autocorrelation analyses can be used as a powerful tool to describe spatial patterns in ecological variables. At the same time, testing statistical hypotheses using standard methods (e.g., ANOVA, correlation and regression) in the presence of spatially autocorrelated data deserves special concern, since the standard errors of estimates are usually underestimated and, consequently, Type I errors may be strongly inflated (Legendre, 1993; Dark, 2004). Recent papers have discussed the importance of measuring spatial autocorrelation when evaluating problems in different fields of ecological research, including the analysis of latitudinal gradients in species richness, the relationship between local and regional richness, spatial patterns in community structure, spatial synchrony in population dynamics and conservation biology (see Koenig, 1998, 1999; Koenig and Knops, 1998; Diniz-Filho and Telles, 2002; Manel *et al.* 2003; Diniz-Filho *et al.* 2003 and Escudero *et al.*, 2003, for recent reviews).

In the last 10 years the use of camera-trapping has become popular as an efficient non-invasive method for faunal inventories, especially for cryptic animals and also for population studies of species for which individuals can be individually recognized by marks (Karanth, 1995;

Carbone *et al.*, 2001; Karanth and Nichols, 1998; Kucera and Barret, 1993; Mace *et al.*, 1994; Silveira *et al.*, 2003). Considering the urgent need for data for conservation purposes and decision-making, camera-trapping becomes a very efficient method for rapid faunal assessment (RAP) (Fonseca, 2001). Indeed, one of the advantages of this approach is to generate data for richness and abundance quickly (photographic rate – see Carbone *et al.*, 2001) across broad scales with relatively little effort and costs, thus making it useful for understanding spatial structures using autocorrelation analyses.

In this paper, we used data from camera-trapping for a RAP evaluation of spatial patterns in mammalian fauna along fragments at the Cerrado-Pantanal border. The region studied stretches approximately 400 km along an east-west axis following the Taquari river, linking the Emas National Park (ENP), one of the most representative Conservation Units in the Cerrado Biome, and the protected area in the Fazenda Rio Negro, within the Pantanal. This region has been proposed as a broad-scale ecological corridor connecting the Cerrado and the Pantanal ecosystems (Cavalcanti and Joly, 2002; see also www.conservation.org) and, after further conservation efforts, it could work under a structural definition of ecological corridor, with multiple functions (see Hess and Fischer, 2001). Because of its relatively large size, this corridor would link the two ecosystems mainly by supporting the complete range of ecological and microevolutionary processes that enable species to persist and disperse over a period of many generations, maintaining the evolutionary processes through time (Myers and Knoll, 2001; Sechrest *et al.*, 2002). This way, conservation efforts in this corridor must be mainly focused on the reduction of the current levels of habitat fragmentation (by restoration programs supported by private landowners and public agencies; Cavalcanti and

Joly, 2002), on establishing coherent patterns of corridor dynamics avoiding increased extinction risks (Earn *et al.*, 2000; Graves *et al.*, 2007) and on defining optimal networks linking patches (Jordan, 2000; Fuller *et al.*, 2006; Rouget *et al.*, 2003; Vogt *et al.*, 2007). In this context, a detailed evaluation of spatial patterns of richness and abundance may be useful to define ecological and life-history traits related to these spatial patterns for different mammal species and at the same time to understand processes that may be linked with population persistence of this faunal component along the fragmented landscape.

Material and methods

Between March 2002 and February 2003, a total of 30 infrared-triggered camera-traps, accumulating 75.834 trapping hours, were randomly moved among 33 fragments of the Cerrado distributed along the ca. 400 km of the Cerrado-Pantanal Corridor, ranging from ENP to the limit of the Pantanal area (Figure 1). To minimize upward bias in abundance estimates by camera-trapping due to multiple recaptures, we eliminated photos close in time or for which individual recognition was possible (e.g. marked animals). The goal of the procedure was to have a rapid diagnosis of the variation in terrestrial medium-large sized mammal fauna in the region. Considering that the detectability of small species (< 500 g) by camera-traps is highly variable (see Silveira *et al.*, 2003), we only considered photographs of species with average body mass higher than 500 g for the analyses. The number of camera units per fragment ranged from 1 to 11, installed at a distance of at least 1.5 km apart.

Estimates of total abundance and abundance for 32 mammal species (see Table 1) were expressed as regression residuals of the number of photographs (at logarithmic scale) against camera exposition time (in hours) across sampling units (fragments), creating

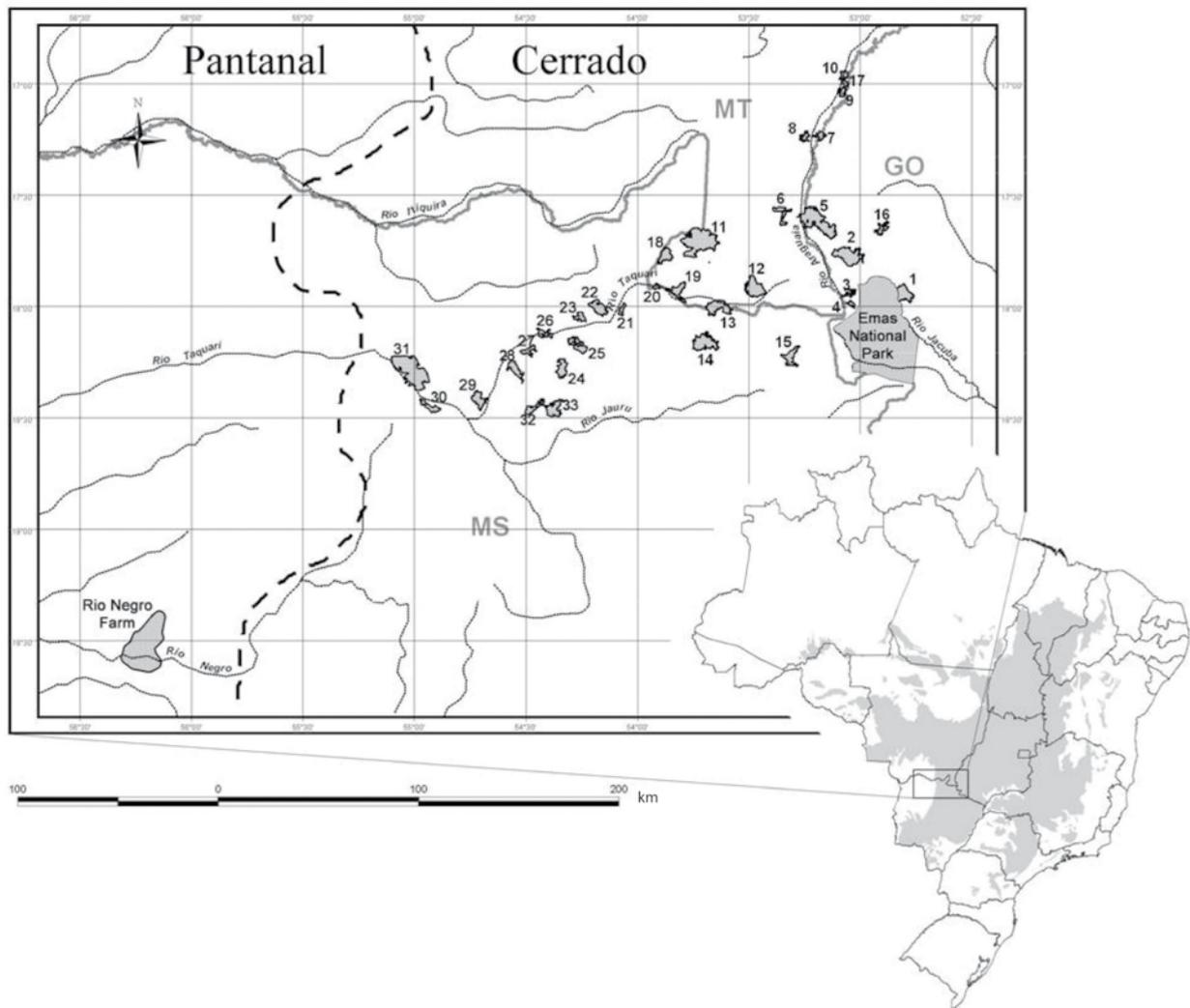


Figure 1. Study area showing the distribution of the 33 fragments sampled across the Cerrado-Pantanal Corridor and the two large extreme units, the Emas National Park, in the Cerrado, and the Rio Negro farm, in the Pantanal. The dashed line shows the approximate border between the Cerrado and the Pantanal.

an estimate that is independent of variations in efforts. We used rarefaction (Gotelli and Graves, 1996) to ensure that variations in species richness among fragments were not due solely to differences in the total number of photographs recorded and cameras at each fragment.

Spatial autocorrelation in species richness and abundance (total and for each species) was analyzed using Moran's I coefficients, given as

$$I = \left(\frac{n}{S} \right) \left[\frac{\sum_i \sum_j (y_i - \bar{y})(y_j - \bar{y})w_{ij}}{\sum_i (y_i - \bar{y})^2} \right]$$

where n is the number of spatial units (fragments), y_i and y_j are the values of the species richness or abundance in the fragments i and j , \bar{y} is the average of y and w_{ij} is an element of the matrix \mathbf{W} . In this \mathbf{W} matrix, $w_{ij} = 1$ if the pair i, j of fragments is within a given distance class interval (indicating fragments that are "connected" in this class), and $w_{ij} = 0$ otherwise. S indicates the number of entries (connections) in the \mathbf{W} matrix. The value expected under the null hypothesis of absence of spatial autocorrelation is $-1 / (n-1)$. Detailed computations of the standard error of this coefficient are given in Legendre and Legendre (1998).

Moran's I coefficients usually vary between -1.0 and 1.0 , for maximum negative and positive autocorrelation, respectively. The geographic distances can be partitioned into discrete classes, creating successive \mathbf{W} matrices and allowing computation of different Moran's I values for the same variable. This allows one to evaluate the behavior of autocorrelation as a function of spatial distance, in a graph called spatial correlogram, which furnishes a descriptor of the spatial pattern in data.

In this paper, spatial correlograms were constructed using Moran's I coefficients at five distance classes, whose upper

Table 1. Type I error of spatial correlograms after Bonferroni correction, diet, amplitude of habitat use and coefficient of determination of multiple regression models of abundance index against fragment characteristics (see Table 2) for each species. **Abbreviations:** B, browser; CAR, carnivore; INS, insectivore; GR, granivore; OM, omnivore; GRZ, grazer; FRUG, frugivore; G, generalist; S, specialist.

Species	Type I error	Diet	Habitat	R ²
Agouti – <i>Dasyprocta agouti</i>	0.29	FRUG	G	0.19
Capybara – <i>Hydrochaeris hydrochaeris</i>	0.55	GRZ	S	0.05
Coati – <i>Nasua nasua</i>	0.72	OM	S	0.06
Collared peccary – <i>Tayassu tajacu</i>	0.24	OM	G	0.16
Crab-eating fox – <i>Cerdocyon thous</i>	0.41	OM	G	0.06
Crab-eating raccoon – <i>Procyon cancrivorus</i>	0.55	OM	G	0.03
Feral pig – <i>Sus crofa</i>	0.25	OM	G	0.22
Giant anteater – <i>Myrmecophaga tridactyla</i>	0.16	INS	G	0.13
Giant armadillo – <i>Priodontes maximus</i>	0.45	INS	G	0.09
Giant otter – <i>Pteronura brasiliensis</i>	0.13	CAR	S	0.06
Grey brocket deer – <i>Mazama gouazoubira</i>	0.01	GR	S	0.02
Grison – <i>Gallictis cuja</i>	0.13	CAR	G	0.07
Hairy armadillo – <i>Euphractus sexcinctus</i>	0.37	OM	S	0.07
Hoary fox – <i>Dusicyon vetulus</i>	0.13	OM	S	0.02
Hog-nosed skunk – <i>Conepatus semistriatus</i>	0.08	OM	S	0.07
Jaguarundi – <i>Puma yagouarundi</i>	0.91	CAR	G	0.05
Lesser anteater – <i>Tamandua tetradactyla</i>	0.08	INS	S	0.06
Maned-wolf – <i>Chrysocyon brachyurus</i>	0.76	OM	G	0.12
Margay cat – <i>Leopardus wiedii</i>	0.76	CAR	S	0.16
Marsh deer – <i>Blastocerus dichotomus</i>	0.77	GR	S	0.09
Nine-banded armadillo – <i>Dasybus novencinctus</i>	0.21	OM	S	0.06
Ocelot – <i>Leopardus pardalis</i>	0.93	CAR	G	0.03
Opossum – <i>Didelphis albiventris</i>	0.47	OM	S	0.06
Paca – <i>Agouti paca</i>	0.77	FRUG	S	0.06
Pampas cat – <i>Leopardus colocolo</i>	0.01	CAR	S	0.22
Pampas deer – <i>Ozotocerus bezoarticus</i>	0.13	GR	S	0.06
Puma – <i>Puma concolor</i>	0.75	CAR	G	0.12
Rabbit – <i>Sylvilagus brasiliensis</i>	1.00	B	G	0.09
Red brocket deer – <i>Mazama Americana</i>	0.32	B	S	0.06
River otter – <i>Lutra longicaudis</i>	0.13	CAR	S	0.12
Tapir – <i>Tapirus terrestris</i>	1.00	B	G	0.11
Tayra – <i>Eira Barbara</i>	0.71	OM	G	0.18
White-lipped peccary – <i>Tayassu pecari</i>	0.46	OM	G	0.09

limits (in km) were 40.1, 67.6, 102.4, 149.6 and 244.3. These classes were chosen to maximize the similarity in the S values (number of connections) for the different Moran's I coefficients that thereby become more comparable. Since Moran's I coefficients at a single correlogram are based on the same data (variable), their significance test are not self-independent, so a Bonferroni correction is necessary. Correlograms were considered significant at $\alpha = 0.05$ only if at least one of their coefficients was significant at α / k , where k is the number of distance classes ($0.05/5 = 0.01$). Spatial autocorrelation analyses were performed using SAAP 4.3 (Wartenberg, 1989).

We used the Type I error of the entire correlograms as an indication of the magnitude of spatial structure in the abundance estimates for each species. In an attempt to explain variation in the spatial patterns among the species, these Type I errors were then correlated with body mass, habitat use (i.e., generalist when it occurs in more than one type of habitat and specialist if the species uses a single type of habitat) and diet categories (browser; carnivore; insectivore; omnivore; grazer; granivore; frugivore) across species, using regression (for body mass) and ANOVA (for habitat use and diet categories). These data were obtained from the literature (Eisenberg, 1989; Redford and Eisenberg, 1992, 1999; Emmons, 1997) and from our personal field observations.

Data on abundance were also used to construct a pairwise dissimilarity matrix between the 33 fragments, using Morisita-Horn coefficients. Abundance data were also transformed into presence/absence data for species in the fragments and a Jaccard similarity matrix was constructed (Krebs, 1998). These two matrices expressing similarity in faunal composition among fragments were correlated with the geographic distances among fragments and the significance of the matrix correlation was assessed using 10,000 permutations in a Mantel

test (Legendre and Legendre, 1998). Similarity/dissimilarity matrices and Mantel tests were performed using the NTSYS 1.5 (Rohlf, 1989).

We also performed multiple regressions of species richness and abundance (total and for each species) as a response variable in order to try to explain its variation along the corridor. Predictors used included fragment area (in ha), after log-transformation (LnA), and number of habitat types within the fragment (HABITAT, with a total of six different habitat types: deciduous forest, gallery forest, "cerrado", "cerradão", open and shrub fields). Fragment selection for analyses, their areas and other landscape characteristics (i.e., distance among fragments) were initially derived using remote sensing techniques based on Landsat 7 ETM images for the year 2002, which were processed using ERDAS 8.6 and ArcGIS 3.2. These landscape characteristics and the habitat classification were confirmed by fieldwork on the fragments. Finally, since Type I errors of these multiple regressions could be biased by the presence of spatial autocorrelation, we also estimated Moran's I coefficients for regression residuals when significant effects were detected for richness and abundance (Diniz-Filho *et al.*, 2003).

Results

Species richness (expected values derived by rarefaction) showed a significant autocorrelation pattern along the corridor ($p = 0.033$) with positive significant Moran's I coefficients in the first distance class that decreases up to the third distance class and then stabilizes (Figure 2). However, there is not a simple linear pattern and correlations with latitude and longitude were not significant. Autocorrelation analyses indicated that fragments situated up to around 50 km tend to be similar for species richness and that this similarity decreases to a maximum negative coefficient (indicating dissimilarity) at around 100 km, which is approximately half of the maximum distance among fragments. For total abundance, none of the individual autocorrelation values was significant at the 5 % level.

Multiple regression showed that variation in species richness can be significantly explained by fragment descriptors ($r^2 = 0.34$; $F = 3.52$, $p = 0.019$) with significant partial coefficients for both LnA and HABITAT (Table 2). In general, fragments with larger and more heterogeneous fragments (i.e., with

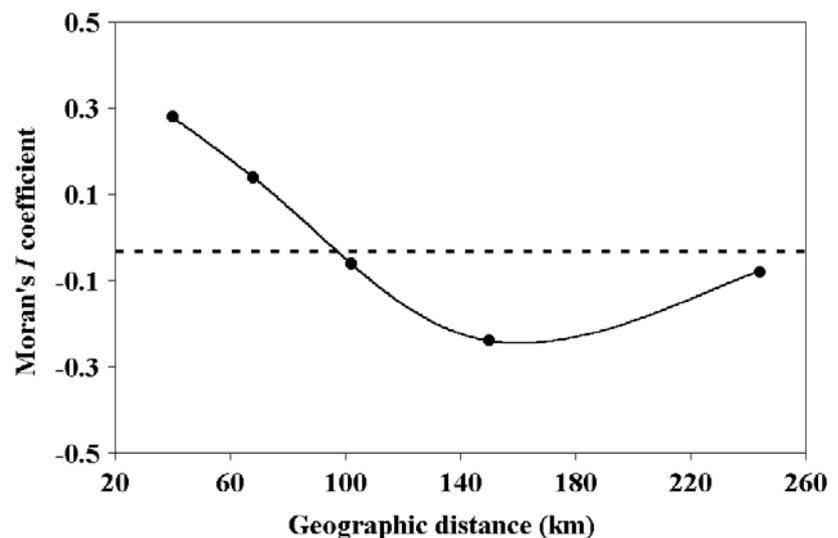


Figure 2. Spatial correlogram of rarefied species richness. The dashed line indicates the expected values under the null hypothesis of absence of autocorrelation $\{E(I) = -1/(n-1)\}$.

Table 2. Multiple regression analysis results evaluating the effects of fragment characteristics on species richness (rarefied). Conventional partial regression coefficients, standard error for these coefficients, standard partial regression coefficients, t tests and P values are shown for each predictor.

Predictors	Coefficients	Standard Error	Standard coefficients	t	P
Intercept	-5.63	± 3.07	0.00	-1.83	0.0780
LnA	1.03	± 0.34	0.50	3.07	0.0050
HABITAT	0.49	± 0.22	0.38	2.22	0.0340

more habitat types) possess more species (Figure 3). Spatial autocorrelations are not biasing these results, since regression residuals are not spatially autocorrelated (Bonferroni's $p = 0.125$ for the correlogram).

Of the 32 terrestrial medium-large sized mammal species found in the corridor, significant spatial correlograms at 5% level were found only for abundance of two species (tapir *Tapirus terrestris* and marsh-deer *Blastocerus dichotomus*). For the first, there is a gradient-like pattern of variation across the corridor. However, the Bonferroni criterion can be too conservative and, after increasing overall Type I error to 10%, spatial patterns appeared for 2 other species (hog-nosed skunk, *Conepatus semistriatus*, and the lesser anteater, *Tamandua tetradactyla*).

Abundance of each species was not significantly explained by any of the fragment descriptors (Table 1). However, the magnitude of spatial pattern of the species, measured by the Bonferroni probability of the spatial correlograms, tends to be correlated with body mass ($r = 0.33$; $p = 0.063$). Thus, large-bodied species tend to have no spatial structure of abundance, whereas reduction in body size tends to reveal spatial patterns in some species (Figure 4A). This relationship, however, is strongly influenced by the very high Type I errors for autocorrelation in abundance of *Tapirus* and *Blastocerus*.

There is also a significant difference between generalist and specialist species for the Type I errors of spatial autocorrelation analyses ($F = 5.12$; $p = 0.031$) with some tendency for spatial

patterns in specialist species (Figure 4B). On the other hand, the magnitude of spatial patterns across species was not significantly associated with variations in diet (ANOVA's $F = 1.01$; $p = 0.457$). Multivariate analyses match in part the results previously described. Dissimilarity between fragments measured by Morisita index based on abundance was not significantly correlated with geographic distances ($r = -0.042$; $p = 0.238$). In contrast, there was a significant (but weak) correlation between Jaccard's coefficients and geographic distances ($r = -0.13$; $p = 0.028$) indicating that geographically close fragments tend to be more similar in species composition than expected by chance alone.

Discussion

The spatial analyses of abundance and richness in the corridor Cerrado-Pantanal indicated few spatial components in the overall data set. Thus, there is no clear ecological gradient in these variables along the corridor. Spatial patterns detected for species richness (and for Jaccard matrix expressing turnover) are in fact short-distance autocorrelation effects indicating that geographically close fragments tend to have more similar richness and composition, but this cannot be expanded to larger geographic distances creating broad-scale patterns such as gradients. The low broad scale spatial component in richness and abundance in the area studied could be explained if the overall spatial difference between the Cerrado and the Pantanal fauna formed a clear steep gradient with an abrupt transition occurring outside the area studied (slightly beyond the Pantanal border used here). Another possibility is that differences between the two ecosystems (the Cerrado and the Pantanal) are not very pronounced for the faunal components studied here, and in fact for some conservation purposes and because of their spatial contiguity, these two major ecosystems are sometimes treated as a unit (Brasil, 1999; see also Oliveira and Marques,

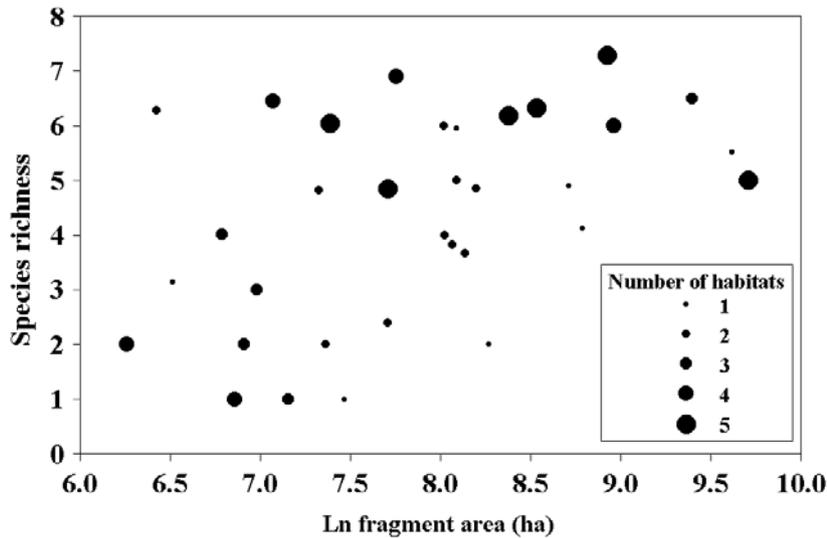


Figure 3. Relationship between species richness and fragment area revealing also that more heterogeneous fragments have more species richness at a fixed area.

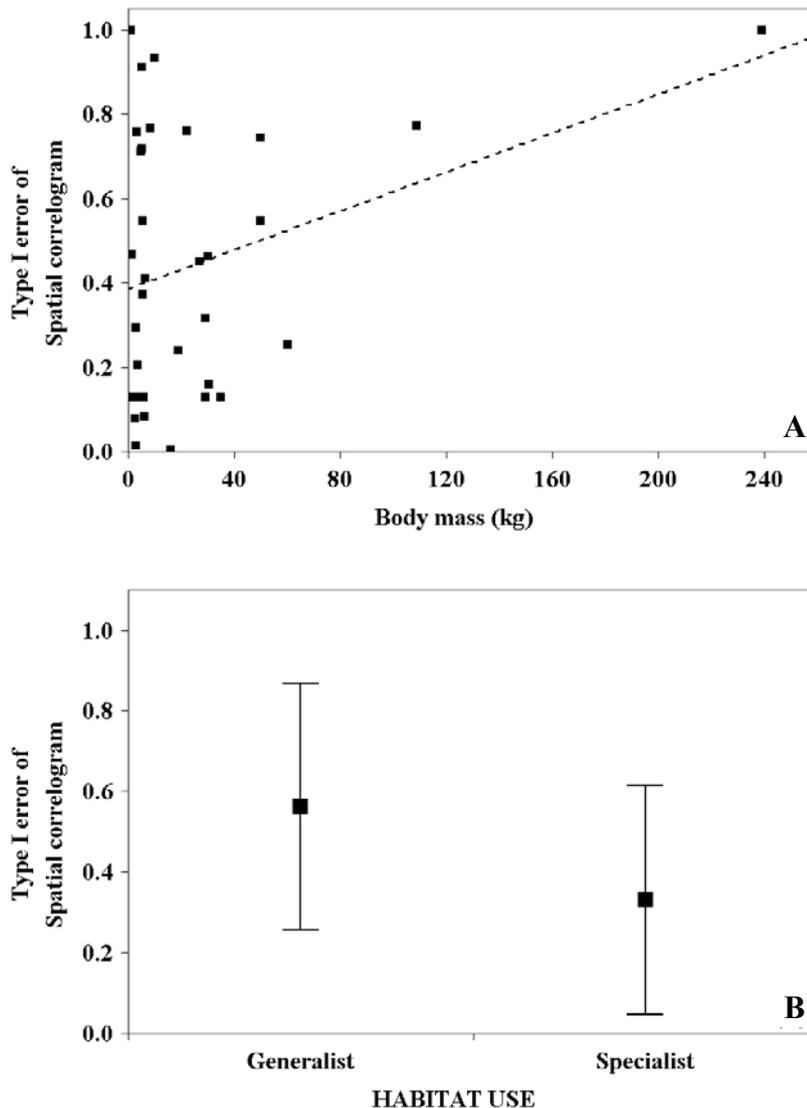


Figure 4. Explanations for the magnitude of spatial autocorrelation across species, expressed by Type I error of the correlograms in terms of (A) species body mass and (B) habitat use.

2002). Our unpublished studies in two protected areas of the Cerrado and of the Pantanal that flank the region studied here (Fazenda Rio Negro and Emas National Park, ENP) show that the composition and the abundance patterns for large and medium mammals are indeed similar, which is also consistent with the relatively low endemism for animal species in the Cerrado (see Marinho-Filho *et al.*, 2002 for a review).

For conservation purposes, the absence of strong spatial patterns in the region may also indicate that the main preserved areas on the east and

the west sides of the corridor (i.e., ENP and Pantanal, respectively) apparently do not control the dynamics of species populations along the corridor. Also, this suggests that the high level of landscape fragmentation (see below) may restrict any “rescue effect” that would be provided by both main preserved areas at the extremes of the corridor. So, further conservation efforts at landscape level decreasing fragmentation level are still necessary to improve the region as an ecological corridor linking the Cerrado and the Pantanal.

The viability of this region as a broad-scale structural and functional corridor may also be partially supported by the correlation between the Type I error of spatial correlograms with body mass across species (although the relationship is influenced by two large-bodied species, tapir and marsh-deer). Large-bodied species tend to have no spatial pattern at all, whereas some smaller species tend to show significant patterns. This is indeed expected if large-bodied species disperse more frequently through the fragmented landscape creating a relative homogeneity and randomness in their relative abundance estimates across the corridor. On the other hand, a few small-bodied species are more restricted to a few close fragments and tend to show more spatial structure in abundance. Since most of the mammalian fauna of the Cerrado region is composed by small-bodied species (ca. 85% of the species is smaller than 5 kg; Marinho *et al.*, 2002), these tendencies for aggregation in abundance suggest that ecological components of population persistence in the proposed corridor (see below) must be carefully investigated. The significant association between magnitude of spatial patterns and habitat use by species also supports this interpretation, as predicted by Ziv’s (2000) model (see also LaBarbera, 1989; Brown, 1995). In principle, these trends for more spatial structure in small-bodied species could also be explained by sampling errors caused by variable camera-trapping efforts, since our previous comparative analyses in ENP showed that the different methods used to estimate abundance and richness only converge to very similar results when large-bodied species are analyzed (Silveira *et al.*, 2003). It is difficult to separate these two explanations for the relationship observed in Figure 4A, but since the magnitude of spatial pattern is not significantly correlated with the overall abundance estimate for each species ($r = 0.14$; $p = 0.444$), it is plausible to assume that this relationship reflects life-history and demographic characteristics of the species, not

sampling bias. Anyway, the conclusion about the absence of broad-scale spatial patterns is conservative in relation to the method used here to estimate abundance (Silveira *et al.*, 2003).

Finally, it is interesting to note that despite the absence of strong spatial patterns across species, our results also show that variation among the fragments along the corridor can be explained by standard ecological theory matching the well-known ecological predictions for fragmented landscapes (e.g., MacArthur and Wilson, 1967; Ricklefs, 1990). Species richness can be explained both by fragment area and its habitat heterogeneity, but it is important to note that regression analysis showed that these two effects were partially independent of each other (a non-trivial finding), so they are not redundant explanations for variations in species richness in the region. Because area effects are easier to measure and are usually correlated with other explanatory variables (including habitat heterogeneity), most ecological research tends to converge to simple classical species-area relationship (Rosenzweig, 1995; see also Taniguchi *et al.*, 2003 for a recent discussion). However, in the region studied habitat effects also occur independently of the area and may be linked with more complex dispersion functions in the region (see Malanson and Cramer 1999). Thus, the region studied cannot be considered necessarily a transition zone between the two large ecosystems Cerrado and Pantanal, but surely it works as a fragmented Cerrado landscape, in which species occurrence follows well-known “island rules”. Abrupt transitions between the two ecosystems or an influence of Pantanal conditions on the western border of the corridor were not detected in the present study.

Our spatial analysis of RAP data from camera-trapping of terrestrial mammals along the Cerrado-Pantanal corridor indicates no clear gradient between the two ecosystems in the

region. Although further studies are necessary to see if ecological gradients can be detected beyond the Pantanal border limiting our area studied, the region was clearly characterized, at least for this faunal component, as a fragmented Cerrado landscape. Thus, fundamental ecological relationships between species abundance and richness on one hand, and area and habitat heterogeneity effects on the other hand should clearly be explored further for future conservation efforts in the region, improving possibilities for population persistence and for the long-term dynamic function of this region as an ecological corridor linking the Cerrado and the Pantanal ecosystems.

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