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Spatial heterogeneity and habitat configuration overcome habitat composition influences on alpha and beta mammal diversity

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Abstract

The effects of habitat fragmentation on different taxa and ecosystems are subject to intense debate, and disentangling them is of utmost importance to support conservation and management strategies. We evaluated the importance of landscape composition and configuration, and spatial heterogeneity to explain α- and β-diversity of mammals across a gradient of percent woody cover and land use diversity. We expected species richness to be positively related to all predictive variables, with the strongest relationship with landscape composition and configuration, and spatial heterogeneity, respectively. We also expected landscape to influence β-diversity in the same order of importance expected for species richness, with a stronger influence on nestedness due to deterministic loss of species more sensitive to habitat disturbance. We analyzed landscape structure using: i) landscape metrics based on thematic maps and ii) image texture of a vegetation index. We compared a set of univariate explanatory models of species richness using AIC, and evaluated how dissimilarities in landscape composition and configuration and spatial heterogeneity affect β-diversity components using a Multiple Regression on distance Matrix. Contrary to our expectations, landscape configuration was the main driver of species richness, followed by spatial heterogeneity and last by landscape composition. Nestedness was explained, in order of importance, by spatial heterogeneity, landscape configuration, and landscape composition. Although conservation policies tend to focus mainly on habitat amount, we advocate that landscape management must include strategies to preserve and improve habitat quality and complexity in natural patches and the surrounding matrix, enabling landscapes to harbor high species diversity.

Resumo

Os efeitos da fragmentação de habitats em diferentes táxons e ecossistemas estão sujeitos a intenso debate, e esclarecê-los é de extrema importância para subsidiar estratégias de conservação e manejo. Avaliamos a importância da composição e configuração da paisagem em escala grossa e da heterogeneidade espacial dentro do habitat para explicar a diversidade α e β de mamíferos em um gradiente de porcentagem de cobertura de vegetação lenhosa e de diversidade de uso da terra. Esperamos que a riqueza de espécies seja positivamente relacionada a todas as variáveis explanatórias, sendo a relação mais forte com medidas de composição, com medidas de configuração da paisagem em escala grossa e com a heterogeneidade espacial dentro do habitat, respectivamente. Também esperamos que a paisagem influencie ambos os componentes da diversidade β (substituição e aninhamento), na mesma ordem de importância esperada para a riqueza de espécies, e com uma forte influência no componente de aninhamento devido à perda determinística de espécies mais sensíveis ao distúrbio no habitat. Registramos ocorrências de mamíferos de pequeno, médio e grande porte em 20 paisagens no Brasil e analisamos a estrutura da paisagem usando: i) métricas da paisagem baseadas em mapas temáticos de cobertura da terra e ii) medidas de textura de imagem de um índice de vegetação calculadas a partir de imagens não classificadas. Comparamos um conjunto de modelos explicativos univariados de riqueza de espécies usando o Critério de Informação de Akaike e avaliamos como as diferenças entre pares de paisagens em medidas de composição e configuração da paisagem e medidas dentro de habitat de heterogeneidade espacial afetam os componentes da diversidade β usando uma regressão múltipla em uma matriz de distância. Descobrimos que, contrário às nossas expectativas, a configuração da paisagem foi o principal fator que afeta a riqueza de espécies, seguido pela heterogeneidade espacial e, por último, pela composição da paisagem. O aninhamento das espécies foi explicado, em ordem de importância, pela heterogeneidade espacial, configuração da paisagem e composição da paisagem. Embora as políticas de conservação tendem a se concentrar principalmente na quantidade de habitat, defendemos que o manejo da paisagem deve incluir estratégias para preservar e melhorar a qualidade do habitat em manchas naturais e a incrementar a complexidade da vegetação na matriz circundante, permitindo que as paisagens abriguem maior diversidade de espécies.

Keywords: biodiversity conservation, image texture, fragmentation, habitat modeling, habitat quality, landscape, Mato Grosso do Sul, species losses

1 | INTRODUCTION

The modern biodiversity crisis has been mainly attributed to the process of habitat fragmentation (Haddad et al. 2015), which changes landscape composition, configuration, and habitat quality, by affecting both natural vegetation patches and the anthropogenic matrix (Fahrig 2003, Fischer and Lindenmayer 2007, Driscoll et al. 2013). The harmful effects of habitat loss on biodiversity are widely recognized among the scientific community, but the importance of habitat fragmentation *per se* and habitat degradation is subject to debate due to differences in conceptual foundations, statistical models, study systems, and resulting interpretations (Villard and Metzger 2014, Fahrig 2017, Fletcher et al. 2018). Habitat fragmentation *per se* is the sub-division of habitat patch (Fischer and Lindenmayer 2007) and habitat degradation is the deterioration of habitat quality (Mortelliti et al. 2010). Some researchers have proposed that the effects of fragmentation *per se* are notable under certain levels of habitat cover, which is called fragmentation threshold (Andrén 1994, Swift and Hannon 2010). Others have hypothesized that the effects of the process of habitat fragmentation depend exclusively of the amount of habitat within the landscape (Fahrig 2013, Melo et al. 2017). However, studies assessing the role of habitat quality are still largely unexplored (Mortelliti et al. 2010), so the importance of the variability of vegetation heterogeneity within-habitat is possibly underestimated (Kupfer et al. 2006, Driscoll et al. 2013). Consequently, conservation recommendations beyond reducing habitat loss have not reached a consensus, posing significant challenges for landscape management and biodiversity conservation (Fletcher et al. 2018). In Neotropical regions, nature management is particularly more challenging due to i) high ecosystem complexity associated to a mega biodiversity (Lewinsohn and Prado 2005), ii) the highest global rates of forest loss (Hansen et al. 2013), and iii) lack of consistency in environmental policies, especially in Brazil (Brancalion et al. 2016). Thus, it is critical that we understand how structural modifications in fragmented landscapes drive the organization of assemblages in tropical ecosystems.

Historically, landscape ecology theories and models were strongly influenced by Island Biogeography and Metapopulation theories, wherein patches of native vegetation are considered as islands of habitat immersed in an inhospitable matrix, and, consequently, patch area and isolation drive metapopulation dynamics (MacArthur and Wilson 1967, Hanski 1998, Kupfer et al. 2006, Fahrig 2013). Based on this approach, conservation strategies have been focused on the preservation of large remnants of natural vegetation, and, eventually, on enhancing the matrix to connect these areas through ecological corridors (Fischer and Lindenmayer 2006). This paradigm, however, has been challenged by recent studies, emphasizing the importance of explicitly considering differences between land cover types, contrary to the simplistic classification of habitat and non-habitat (Boscolo et al. 2016). Classifying different land use types is important because species occurrence may be driven by ecological requirements of non-substitutable resources from different habitat types (landscape complementation) and by substitutable resources from more than two habitat types (landscape supplementation; Dunning et al. 1992). The degree of matrix permeability also differs among land cover types because of variation in provision of food resources, water, shelters, and the presence of stepping stones (Russel et al. 2007, Brady et al. 2011, Ferreira et al. 2018). Thus, the anthropogenic matrix is not uniformly inhospitable for survival and reproduction of many species, nor an impenetrable barrier to its movement and dispersal (Kupfer et al. 2006, Driscoll et al. 2013). Nevertheless, the matrix permeability varies from species to species, once landscape perception itself is species-traits dependent (Gehring and Swihart 2003, Goheen et al. 2003, Hansbauer et al. 2010, Kellner et al. 2019). In this regard, even patches of natural vegetation can differ in habitat quality due to natural variation or anthropogenic degradation, producing spatial heterogeneity within habitat patches (Mortelitti et al. 2010). Therefore, explicitly incorporating spatial heterogeneity gradients in landscape analysis approaches can improve our understanding of the relationship between species diversity and landscape/environmental conditions, leading to management and conservation strategies that combine natural environments and human land use in an integrated and functional way (Fischer and Lindenmayer 2006, Fahrig et al. 2011, Boscolo et al. 2015).

The intensity of anthropogenic land use is a primary concern for the conservation of terrestrial mammal worldwide (Pekin and Pijanowski 2012). Mammalian species are highly diverse in terms of diet, trophic levels, body mass, and habitat use patterns, and are key components of tropical ecosystem (Paglia et al. 2012, Dirzo et al. 2014). Mammalian species richness has been shown to be sensitive to changes in landscape structure (Goheen et al. 2003, Russel et al. 2007, Brady et al. 2011, Haddad et al. 2015, Melo et al. 2017, Regolin et al. 2017, Berl et al. 2018), allowing the modeling of this diversity component using distinct scenarios of land use. Other components of species diversity, however, have different responses to environmental variation and change (e.g. Dornelas et al. 2014), but are understudied in comparison with alpha diversity (Mori et al. 2018). Although measures of alpha diversity (such as richness, abundance, and occurrence probability) are the main response variables in most studies, recent research has shown that beta diversity (dissimilarity between communities) is an essential variable to understand the processes that shape assemblage differences (Baselga 2010). The beta diversity reflects two different phenomena: turnover and nestedness. The turnover component measures species replacement between communities, whereas nestedness refers to a non-random process of species loss between communities (Baselga 2010). Therefore, understanding how beta diversity varies within a spatially heterogeneous system can contribute to our understanding of landscape functioning (Mori et al. 2018).

In this study, we assessed how mammalian communities are structured over heterogeneous fragmented landscapes, by combining analyses of landscape structure with measures of fine spatial heterogeneity. Specifically, we quantified the importance of coarse-scale measures of landscape structure with measures of within-habitat spatial heterogeneity in explaining mammal species richness, and the role of landscape variables in species compositional dissimilarity. We defined landscape composition as the amount of different land cover types present in the study landscapes, and landscape configuration as the spatial arrangement of landscape units (Villard and Metzger 2014), while spatial heterogeneity was quantified using proxies of vegetation structural complexity (Wood et al. 2012). We expected a positive relationship between species richness and landscape composition, configuration and spatial heterogeneity, with decreasing contributions from the former to the last respectively (Figure 1A). We also expected that β-diversity components (nestedness and turnover) would increase linearly with the differences among predictive variables between pairs of landscapes, with the same order of importance expected for species richness. Nestedness should be more strongly influenced by landscape differences than turnover due to deterministic losses of species more sensitive to environmental modifications (Figure 1B). Our expectations were based on the following assumptions: i) natural vegetation cover captures resource availability and environmental conditions that produce species occupancy (Fischer and Lindenmayer 2007); ii) higher composition heterogeneity (diversity of land use types) increases the occurrence probability for species that use two or more vegetation types (landscape supplementation and complementation, Dunning et al. 1992); iii) Landscape supplementation and complementation also depend on landscape configuration, and are favored in patchy landscapes due to higher incidence of abrupt transitions between different land use types (edge areas, Fahrig 2017); iv) edge areas have biotic and abiotic conditions that are different from both the matrix and the patch core region, with either positive or negative effects on species (Murcia et al. 1995, Berl et al. 2018); and v) structural complexity is positively related to resource and shelter availability for both habitat patches and the matrix, and ultimately affect species movement capacity (Russel et al. 2007, Driscoll et al. 2013).

[Figure 1 here]

2 | METHODS

2.1 | Study areas

Our study was conducted on 20 landscapes located in Mato Grosso do Sul State, western Brazil, covering an area of 534,598 hectares. We distributed the landscapes across a gradient of seasonal Atlantic Forest, *Cerradão* and Cerrado *stricto sensu* cover (hereafter ‘woody cover’), while also considering land use composition heterogeneity (Figure 2). The sampled landscapes are within an ecotonal region, with biogeographic influences from the Atlantic Forest, Cerrado and a small portion of the dry Chaco in the southwest. Both Atlantic Forest and Cerrado are biodiversity hotspots for conservation priorities (Myers et al. 2000). Some landscapes are also biogeographically influenced by Amazon forest (Chiquitana forest). The study region is under constant anthropogenic pressure and has been undergoing intensive conversion of natural areas to anthropogenic land uses, especially croplands and pastures (Klink and Machado 2005, Roque et al. 2016). The deforestation ranges from 22,000 to 30,000 km^2/year, which is higher than rates in Amazon (Klink and Machado 2005).

[Figure 2 here]

2.2 | Mammal diversity data

We performed four field expeditions in April 2009, August 2009, May and June 2010, and July and August 2010. This effort was carried over 20 landscapes, distant from each other between 20 km to 634 km, yielding 20 independent samples of terrestrial mammal occurrence with body sizes varying from small (>1 kg) to large (Figure 2). On each expedition, we sampled mammals in five landscapes during five consecutive days and four nights using the following complementary methods: i) identification of vestiges, such as tracks (identified according to Angelo et al. 2008), feces, teeth, and others bones (bones were collected and compared to collection material for identification); ii) direct observation; iii) camera trapping; and iv) capture of small mammals with live traps. The sampling goal was not to estimate abundances, but to get a tally of species in each landscape for calculating species richness and composition.

For the first two methods, we performed walks on foot or by car at different periods of day and night, covering the different environments within each landscape. For the third method, we installed between 11 and 16 camera traps (Tigrinus®, Timbó, Santa Catarina State, Brazil) at

30-40 cm above the ground, in tree trunks of forest or Cerrado patches in each landscape. Cameras were placed on transect lines of 110 m in length containing two cameras in each extremity (in the border and in the interior of each forest fragment), operating 24 hours a day, during four consecutive days and nights. Transect lines were distant at least 150 m from each other (in small areas), but usually a minimum distance of 300 m was set. The total sampling effort was of 1,128 traps-night, with the mean effort per landscape being 56 ± 7 traps-night. We captured rodents and marsupials (<1 kg, Cricetidae, Echimyidae and Didelphidae families) using 65 wire (33x12x12 cm) and Sherman live-traps (30x9x7 cm). Traps were installed in forest ground (wire) and understory (Sherman), between 1.5 and 2 meters above the ground, during four consecutive nights, totaling 6,800 trap-night overall and 340 traps-night per landscape. We baited the traps with a mixture of pumpkin, bacon, peanut butter and cod liver oil. In each landscape, we installed the traps along transects between the camera trap sampling points, 10 m apart from each other in the same transect, separated at least 150 m from each other transect line and at least 20 m from the nearest patch edge. Captured animals were identified and subsequently released. When necessary, we collected voucher specimens for identification, which were deposited in the mammalian collection of the Universidade Federal de Santa Maria (UFSM).

2.3 | Land use and land cover maps

We generated an 8-km buffer around the camera trap sampling points within each landscape to delimit landscape extent. We chose this extent based on previous studies reporting landscape structure effects on small-, medium- and large-sized mammal assemblage composition within the Atlantic Forest (e.g. Lyra-Jorge et al. 2010, Beca et al. 2017, Melo et al. 2017, Regolin et al. 2017), as well as to avoid spatial overlap (Jackson and Fahrig 2015). We mapped land cover for each landscape using orthorectified images from the RapidEye satellite constellation, with 5m spatial resolution. Images were selected preferably from the dry season, due to lesser cloud cover and greater contrast between land use classes (47 images acquired between January 2011 and August 2013). Image processing was performed over all five spectral bands (blue, green, red, red edge and near infrared) and included: i) atmospheric correction using the 'Quick Atmospheric Correction – QUAC' algorithm implemented in the ENVI 5.0 software and ii) unsupervised classification using the 'Auto Class' software (github.com/JohnWRRC). Auto Class uses the GRASS function 'i.segment' to generate image segments and the K-means Clustering function of the 'foreign' R package (R Core Team 2017) to group the segments into classes according to the mean and standard deviation of pixel values. We then converted this unsupervised map into a thematic classification by supervised visual interpretation and manual editing, based on image visualization at 1:2,500 cartographic scale, generating a final map with 11 classes (Figure 2).

2.4 | Landscape structure metrics

The produced land cover maps in raster format were used as inputs for landscape structure metric calculations. We used the 'raster' R package (Hijmans et al. 2017) to load the raster data and define custom functions to calculate the following landscape structure metrics: (i) woody cover — percent woody (forest plus cerrado) cover in the landscape, (ii) patch density — ratio between the number of woody patches and total landscape area, (iii) edge density — ratio between area of woody patch edges and landscape area, and (iv) landscape diversity — Shannon index for mosaic of patches including all cover types. Woody cover and landscape diversity are used as measures of woody habitat composition, whereas edge density and patch density are measures of woody habitat configuration (Villard and Metzger 2014).

2.5 | Within-habitat spatial heterogeneity

We estimated within-habitat spatial heterogeneity by calculating image texture measures from the normalized difference vegetation index (NDVI). NDVI is a spectral index sensitive to photosynthetically active vegetation, which is related to plant biomass productivity (Justice et al. 1998). We calculated NDVI using the red and near-infrared spectral bands of RapidEye images (5-m spatial resolution) using the ‘spatial.tools’ R package (Greenberg 2018). Image textures are statistical descriptors of the spatial relationship among pixel values within an image region, thus capturing spatial heterogeneity (St-Louis et al. 2009, 2014). When calculated using NDVI, texture therefore represents spatial variability in photosynthetically active vegetation within a given area (Wood et al. 2012). Texture measures calculated from high resolution images have been related with descriptors of vegetation heterogeneity such as leaf-area index and foliage height diversity (Colombo et al. 2003, Wood et al. 2012). Particularly, textures can yield larger explanatory power for species richness than classified images because it captures fine-scale variability within coarse habitat classes in areas of gradual transition between vegetation types (St-Louis et al. 2009, Wood et al. 2013).

We calculated 12 texture measurements from NDVI, using the ‘r.texture’ GRASS GIS function, being seven first order metrics: (i) sum average, (ii) entropy, (iii) difference entropy, (iv) sum entropy, (v) variance, (vi) difference variance, (vii) sum variance; and five second-order metrics based on a pairwise matrix of spatial relationships among pixels (grey-level co-occurrence matrix; Haralick 1979), (viii) angular second moment, (ix) inverse difference moment, (x) contrast, (xi) correlation, and (xii) information measures of correlation. Each texture was calculated in four directions (0, 45, 90 and 135 degrees) considering a central pixel and its neighbors within the specified window, and then average of texture metrics were calculated to summarize all directions. We derived textures using four different moving window sizes on each pixel (3x3, 5x5, 7x7 and 9x9 pixels of 5m).

2.6 | Data analysis

We first evaluated potential spatial autocorrelation and multicollinearity among explanatory variables (Supplementary material Appendix 1, Figs. A1, A2 and A3), and then selected seven uncorrelated predictive variables (|r|<7, as suggested by Dormann et al. 2013); two representing woody habitat composition: wood cover and landscape diversity; two representing woody habitat configuration: edge density and patch density; and three representing within-habitat spatial heterogeneity (texture measurements): correlation, sum entropy and difference entropy of the 3x3 moving window size that represents more local environmental information (Table 1).

[Table 1 here]

Mammal species richness− We fitted generalized additive models (GAMs) to quantify how mammalian species richness relate to heterogeneous fragmented landscapes, using the ‘gam’ function of the ‘mgcv’ R package (Wood 2011) and assuming a Poisson distribution for count data (Zuur et al. 2009). We choose GAMs as they are able to capture non-linear and linear effects (Zuur et al. 2009). We computed seven univariate models, each including one of the four landscape structure metrics or the three spatial heterogeneity variables as predictors. We also included a null model representing a neutral response of richness to landscape structure (intercept only), totalizing eight competing models. We then compared the set of models using Akaike’s Information Criterion corrected for small samples (AICc), to select the best explanatory model using the ‘Ictab’ function of the ‘bbmle’ R package (Bolker and R Development Core Team 2017). All models with ΔAICc <2 were considered equally plausible to explain the patterns, i.e., a given landscape predictor influences species richness as much as the other included on best model list (Burnham and Anderson 2002). We evaluated model weight (w_i) of plausible models as a proxy of predictor importance, since model weight can be interpreted as the probability of a model to be the best among competing models (Wagenmakers and Farrell 2004). We also reported deviance explained to access model fit.

β-diversity−We estimated total β-diversity and partitioned it in two components – turnover and nestedness – using a presence-absence assemblage matrix as input to the ‘beta.pair’ function of the ‘betapart’ R package (Baselga 2010, Baselga and Orme 2012). Total β-diversity was calculated as Sorensen’s dissimilarity index (β_{sor}), turnover as Simpson dissimilarity index (β_{sim}), and nestedness (β_{nes}) as the difference between total β-diversity (β_{sor}) and turnover (β_{sim}). We used a multivariate linear regression (Multiple Regression on distance Matrix − MRM) (Linchstein 2007) using the dissimilarities matrices (beta diversity components), using the ‘adonis’ function of the ‘vegan’ R package (Oksanen et al. 2017) with 9,999 permutations to test the effect of predictive variables (landscape structural metrics and spatial heterogeneity) on β-diversity measures (turnover and nestedness). We considered that predictors affected beta diversity components where the significance levels of the coefficients were equal or lower than 0.05. We calculated the adjusted coefficient of multiple determination (R^2), which is the ratio of the sum of squares of distances of the estimated values to the mean, to the sum of squares of distances of the original response variable values to the mean — adjusted by the numbers of degrees of freedom of the numerator and denominator of the coefficient of multiple determination **(**Legendre & Legendre 2012). We opted to analyze the effect of the landscape on beta diversity through a frequentist approach - evaluating the p-value and the R^2 - as recent research has criticized the use of model selection for multivariate data on genetics and beta diversity (Franckowiax et al. 2017, Rocha et al. 2019)

3 | Results

3.1 | Overview

We recorded a total of 48 species of terrestrial mammals from 20 families and nine orders (Supplementary material Appendix 1, Table A1). Species richness per landscape ranged from eight to 25 (16 ± 4; mean ± sd). The richest groups registered were rodents and carnivores, both with 12 species, followed by marsupials, with eight species. We recorded six ungulates, of which the most frequently were brocket deers (*Mazama gouazoubira* and *M. americana*) and the lowland tapir (*Tapirus terrestris*). The yellow bearded capuchin (*Sapajus cay*) was frequently detected, while three other primate species were rarely recorded. Regarding Xenarthra, we recorded three species of armadillos and two of anteaters. Finally, we verified the occurrence of the tapeti rabbit (*Sylvilagus brasiliensis*) in most studied landscapes.

3.2 | Landscape structure influence on mammal richness

Among the set of eight competing models, three were equally plausible to explain species richness (Table 2): landscape configuration – edge density (ΔAICc = 0.0; $w_i = 0.374$), spatial heterogeneity – sum entropy (ΔAICc = 0.3; $w_i = 0.316$), and landscape composition – woody cover (ΔAICc = 1.1; $w_i = 0.211$). We found a positive linear relationship between species richness and landscape configuration – edge density (Figure 3A) and also for spatial heterogeneity – sum entropy (Figure 3B). In addition, we also observed a positive relationship of woody cover on species richness below 30% of woody cover, with no effect above this threshold (Figure 3C).

[Table 2 here]

[Figure 3 here]

3.3 | Patterns of β-diversity

Total β-diversity was composed mainly by turnover (0.78±0.13 sd) with a small proportion of nestedness (0.22±0.10 sd). Nestedness (β_{nes}) was driven by spatial heterogeneity (sum entropy), landscape configuration (edge density), and landscape composition (landscape heterogeneity and woody cover) – see Table 3 and Figure 4. Turnover (β_{sim}) was not explained by any predictive variable.

[Table 3 here]

[Figure 4 here]

4 | Discussion

Species assemblage in heterogeneous fragmented landscapes of tropical ecosystems are shaped by many ecological processes acting simultaneously. Consequently, identifying the main drivers of changes in mammalian species richness (α-diversity) and variation in communities' composition (β-diversity) is challenging (Mori et al. 2018). Our results contradicted our expectations; landscape configuration (edge density) was the main driver of species richness, followed by spatial heterogeneity (sum of entropy) and landscape composition (woody cover). The order of importance of predictive variables explaining β-diversity was also different from our expectations; loss of species between communities (β_{nes}) was driven mainly by spatial heterogeneity (sum of entropy), followed by landscape configuration (edge density) and landscape composition (woody cover and landscape heterogeneity). In accordance to our third prediction, β_{nes} responded more strongly than β_{sim} to differences in predictive variables.

Although several studies have reported that landscape composition – especially the amount of natural vegetation – as the main drivers of biodiversity patterns (Fahrig 2013), the role of landscape configuration [such as fragmentation *per se* (Fahrig 2003)] beyond the effect of landscape composition has been recently debated. While some studies highlight the predominant effect of habitat amount (Fahrig 2003, 2013), others advocate that habitat configuration has an important additional effect on biodiversity (Villard and Metzger 2014, Hanski 2015, Fletcher *et al.* 2018). Furthermore, some authors also advocate that the effects of habitat fragmentation and loss on biodiversity are mediated by habitat quality (Kupfer et al 2006, Driscoll et al. 2013). We corroborate here the importance of habitat quality by showing how spatial heterogeneity in fragmented landscapes strongly contributes to explain mammalian species richness and changes in species composition.

4.1 | Reliability of field data

Although a higher sampling effort on each landscape would decrease our variability resulting in a smaller error in species detection, a larger sample size (more landscapes) would result in a higher statistical power by increasing our degrees of freedom. We choose to increase sample units in detriment of a larger sampling effort in each landscape considering that the predictors (landscape metrics and measurements of spatial heterogeneity) were logistical easier and financial cheaper to measure than the response variable (Brennan et al. 2002). In this way, we were able to sample 20 independent landscapes, which is a high number of independent sample units in comparison to other studies sampling mammals at landscapes scale (see examples in the review of Presley et al. 2019). Although our sampling effort in each landscape could limit the detection of rare or cryptic species, we used an equal sampling effort along the landscapes, so we consider our results are not bias and represent the relationship of the most representative local mammal species and landscape patterns.

4.2 | Habitat composition influence

Species richness was positively associated with landscape configuration and spatial heterogeneity, but the relationship with percent woody cover was nonlinear. Richness was positively influenced by woody cover up to approximately 30% of total cover, followed by a slow decline of species above this threshold. This pattern is consistent with empirical studies showing similar thresholds of species diversity, where decreases of habitat amount result in abrupt decreases of species richness (*e.g.* Radford et al. 2005, Banks-Leite et al. 2014, Ochoa-Quintero et al. 2015). Our results indicate that, for landscapes below this 30% threshold, increasing native vegetation cover must be the main strategy to improve mammal diversity.

Woody cover, which we expected to be the strongest predictor of β-diversity, had the weakest effect on species richness and β_{nes}. The contribution of landscape composition to explain species richness and loss of species between communities seems to be larger in other landscapes with ample differences in habitat amount (e.g. 5-95%) and low landscape use diversity. An example is the study by Beca et al. (2017), who related mammals occurrence and richness to measures of landscape structure of forest patches immersed in a homogeneous matrix of biofuel plantation within the Brazilian Atlantic Forest. However, our study had a limited range of variation in habitat amount (5-55%) and higher heterogeneity of both native vegetation and matrix components than Beca et al. (2017), who classified land use types in two classes, forest and matrix. Therefore, the simpler view that habitat amount can alone support landscape management is unlikely to be applicable to heterogeneous landscapes under intense anthropic use in tropical ecosystems.

The positive relationship between landscape heterogeneity (Shannon index) and β_{nes}, which reflects natural and human land use diversity, refers to the processes of landscape complementation and landscape supplementation (*sensu* Dunning et al. 1992). The former occurs when species persistence depends on non-substitutable resources that are available in two or more different habitat types. For example, the crab-eating raccoon (*Procyon cancrivorus*) feeds in water bodies and shelters in the forest interior. On the other hand, landscape supplementation exists when species occurrence is favored by the provision of substitutable resources in different habitat types. It occurs, for example, when jaguars (*Panthera onca*) and pumas (*Puma concolor*) prey on cattle and sheep livestock in addition to wild mammals. Therefore, mammalian species loss can be related to a lack of structurally complex matrices where species can find complementary or supplementary resources. However, species-specific responses to landscape structure must be noted (Goheen et al. 2003, Hasbauer et al. 2010) and, consequently, effects of landscape composition may vary according to species traits (e.g. niche breadth and mobility; Kellner et al. 2019) and temporal variation in matrix structure (e.g. crop cycles within agriculture matrix; Berl et al. 2018).

4.3 | Habitat configuration effects

Our results go beyond the paradigms of habitat composition, and evidence the role of the configuration of natural vegetation patches for the maintenance of species richness. We found a positive relationship between edge density and the number of mammalian species, which suggests a positive effect of habitat fragmentation *per se* (Fahrig 2003). Our studied system encompassed a range of small to intermediate proportions of woody cover, where the variation in possibilities of landscape configuration is highest (Villard and Metzger 2014), possibly increasing the influence of landscape configuration on species richness. The positive response of species richness and β_{nes} to landscape configuration (edge density) is also related to the processes of landscape complementation and landscape supplementation (*sensu* Dunning et al. 1992), which depend on landscape configuration (Fahrig 2017). Species movement among land cover types is favored in patchy landscapes due to decreased distances between each land use type. Nonetheless, movement decisions also depend on vegetation structure similarity among natural vegetation and matrix (Russel et al. 2007, Berl et al. 2018).

4.4 | Within-habitat spatial heterogeneity matters

The relationship between spatial heterogeneity (sum entropy) and both α- and β- diversity results from deterministic losses of the most sensitive species due to reduction in vegetation structural complexity within both native vegetation patches and anthropogenic matrices. Larger vegetation structural complexity within habitat patches increases niche availability, and consequently, patch capacity to host high species diversity (Brady et al. 2011). Furthermore, high similarity between patch and matrix vegetation structure favors species movement through the landscape (Kupfer et al. 2006). By providing habitat breeding and food resources, the anthropogenic matrix can guarantee (re)colonization of habitat patches by species, increasing population size and reducing the risk of extinction (Driscoll et al. 2013). For example, polyculture and agroforestry systems are wildlife-friendly matrices, as they are more structurally complex than pasturelands, intensive cereal cropping, and other annual monocultures, which in turn erode mammal diversity (Ferreira et al. 2018).

Previous studies have shown that within-habitat spatial heterogeneity, measured using image texture measures, explain bird species richness in ecosystems where vegetation heterogeneity is high and transitions between land-use classes are gradual (St-Louis et al. 2009, Wood et al. 2013). Within-habitat spatial heterogeneity also drives compositional variation of tropical anuran communities (Sugai et al. 2019). In contrast, our study region comprises a set of landscapes that vary in the amount of woody cover and in the diversity of land uses, with sharp boundaries delineating the different land cover types. Therefore, even in a region characterized by less diversity of vegetation formations, spatial heterogeneity played an important role in shaping the patterns of species diversity, possibly reflecting the availability of resources, shelters and structures that favor dispersal. Qualitative thematic mapping obscures differences in landscape structure that are potentially essential to species survival, and land cover mapping procedures are susceptible to subjective bias and errors in image segmentation (the delineation of boundaries of landscape units) and classification (St-Louis et al. 2009).

4.5 | Concluding remarks

As far as we know, this is the first study that reports the role of landscape spatial heterogeneity as one of the main drivers on mammals assemblages. The effects of spatial heterogeneity on human-modified landscapes will be better understood by calculating texture metrics per land cover type. Thus, it will be possible to distinguish the effects of spatial heterogeneity by land cover types, i.e. “functional heterogeneity” framework proposed by Boscolo et al. (2016).

The effects of spatial heterogeneity and habitat configuration overcame the influence of habitat composition on alpha and beta mammal diversity in heterogeneous fragmented landscapes within western Brazil. Patch configuration may influence species movement and, consequently, habitat (re)colonization rates. Vegetation structural complexity in the anthropogenic matrix may also affect species movement, as it defines the matrix capacity to provide breeding and food resources. Therefore, landscape composition alone should not be used to support landscape management strategies aimed at mammalian conservation, that should also include strategies to preserve and improve vegetation structural complexity in both habitat patches and the matrix, enabling landscapes to harbor high species diversity by increasing niche availability.

DECLARATIONS

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Author contributions - ALR and MCR conceived study aim and hypothesis. TSFS, LFCC and LSSM contributed with remote sensing mapping and image texture quantification theory. ALR wrote the manuscript with input from LSSM, GLM, TSFS and FM. GLM, JS and NCC designed data collection and carried out field work. ALR, MCR and FM analyzed the data. ALR, LFCC and FM quantified landscape structure indices. LSSM calculated all the image textures. All the authors revised the manuscript. Proof reading by TSFS.

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Tables

Table 1. Description of the seven non-correlated predictive variables of landscape structure measurements assessed to explain mammalian species richness and changes in species composition in 20 fragmented landscapes in western Brazil.

Metric type	Landscape metric name	Landscape metric description
Landscape composition	Woody cover	Percentage of Atlantic Forest, *Cerradão* and Cerrado *stricto sensu* in the landscape area.
	Landscape diversity	Shannon index for mosaic of patches including all cover types.
Landscape configuration	Edge density	Ratio between area of woody edges and landscape area.
	Patch density	Ratio between the number of patches of woody and total landscape area.
Within-habitat spatial heterogeneity	Correlation	Linear dependency of pixel values on those of neighboring pixels (Haralick 1973, Wood *et al.* 2012).
	Sum entropy	Entropy is the system level disorder. The greater the entropy, the greater the heterogeneity. Measures the disorder related to the gray level-sum distribution of the image (Haralick 1973, Wood *et al.* 2012).
	Difference entropy	Measures the disorder related to the gray level difference distribution of the image (Haralick 1973, Wood *et al.* 2012).

Table 2. Set of eight competing univariate models to explain mammalian species richness in 20 fragmented landscapes in western Brazil. Two models refer to landscape composition (woody cover, landscape heterogeneity), two to habitat configuration (edge density, patch density), three to spatial heterogeneity (correlation, sum entropy, and difference entropy), and a null model with intercept-only that represents absence of effect. Model selection statistics include: ΔAIC is the relative difference in AIC values compared with top-ranked model; K is the number of parameters; w_i is the AIC model weight; and Deviance explained is proportion of null deviance explained by the model.

Model	ΔAICc	K	w_i	Deviance explained
Landscape configuration (edge density)	**0.0**	**2**	**0.374**	**38.7%**
Spatial heterogeneity (sum entropy)	**0.3**	**2**	**0.316**	**37.1%**
Landscape composition (woody cover)	**1.1**	**4.04**	**0.211**	**61.9%**
Landscape composition (landscape heterogenity)	4.4	2	0.041	17.7%
Spatial heterogeneity (correlation)	5.4	2.73	0.025	22.5%
Null	5.7	1	0.021	<< 0.0001%
Landscape configuration (patch density)	7.6	2	0.008	2.84%
Spatial heterogeneity (difference entropy)	8.8	2.78	0.004	7.26%

Table 3. Coefficients of determination (R^2) using Multiple Regression on distance Matrix for each predictive variable to explain β diversity components (turnover and nestedness) of mammalian communities within twenty fragmented landscapes of western Brazil. Significant p-values (<0.05) are in bold.

Predictive variables	β diversity	
	Nestedness (β_{nes})	Turnover (β_{sim})
Landscape composition		
Woody cover	**0.278 (p=0.025)**	0.052 (p=0.475)
Landscape heterogeneity	**0.314 (p=0.028)**	0.075 (p=0.233)
Landscape configuration		
Patch density	0.023 (p=0.438)	0.069 (p=0.286)
Edge density	**0.412 (p=0.008)**	0.023 (p=0.821)
Spatial heterogeneity		
Correlation	0.176 (p=0.10)	0.040 (p=0.574)
Sum Entropy	**0.565 (p<0.001)**	-0.037 (p=0.998)
Difference Entropy	0.097 (p=0.243)	0.032 (p=0.709)

Figures legends

Figure 1. Expected patterns between α (A) and β-diversity (B) of mammalian species and predictive variables of landscape composition, configuration and spatial heterogeneity in 20 heterogeneous fragmented landscapes in western Brazil.

Figure 2. Land use maps of 20 study landscapes in south-western Brazil where terrestrial mammals were studied to understand the effects of landscape composition (woody cover,

landscape heterogeneity), configuration (edge density, patch density), and spatial heterogeneity (satellite image texture) on α- and β-diversity.

Figure 3. Best-supported models for explaining mammalian species richness in heterogeneous fragmented landscapes of western Brazil: (A) landscape configuration (edge density), (B) spatial heterogeneity (sum entropy), and (C) landscape composition (woody cover). Green shading is the confidence interval.

Figure 4. Relationship between mammalian species nestedness and (a) spatial heterogeneity (sum entropy), (b) landscape configuration (edge density), (c) landscape composition (landscape heterogeneity), and (d) landscape composition (woody cover) in heterogeneous fragmented landscapes of western Brazil. Blue shading is the confidence interval. The x-axes represent absolute differences in explanatory variables.

Figures

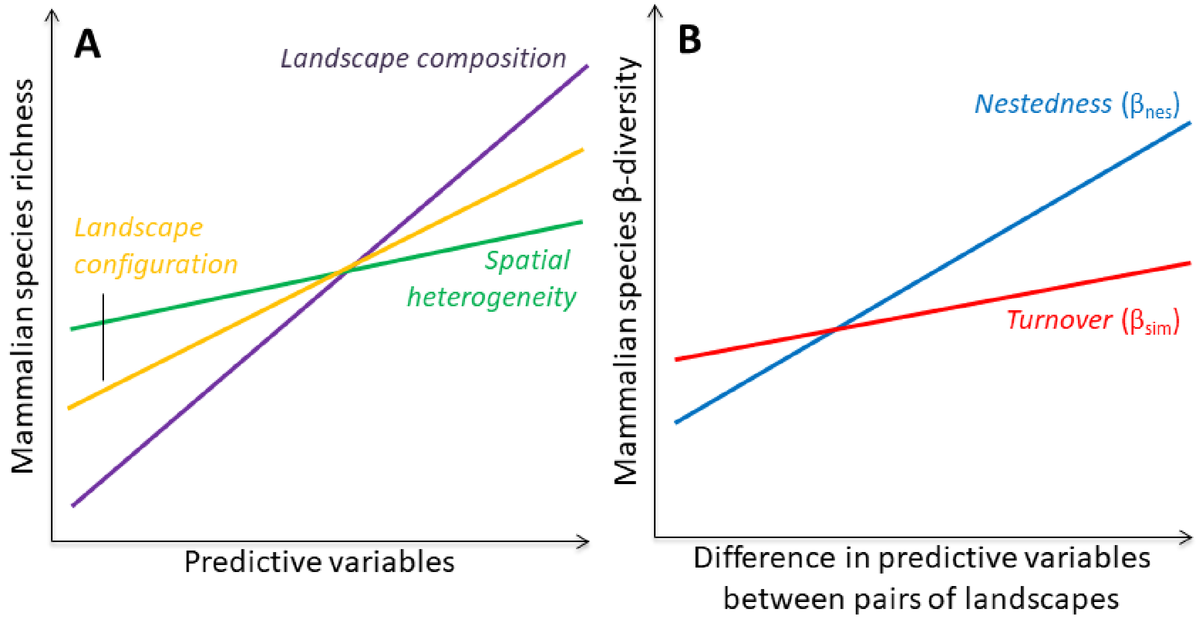

Figure 1.

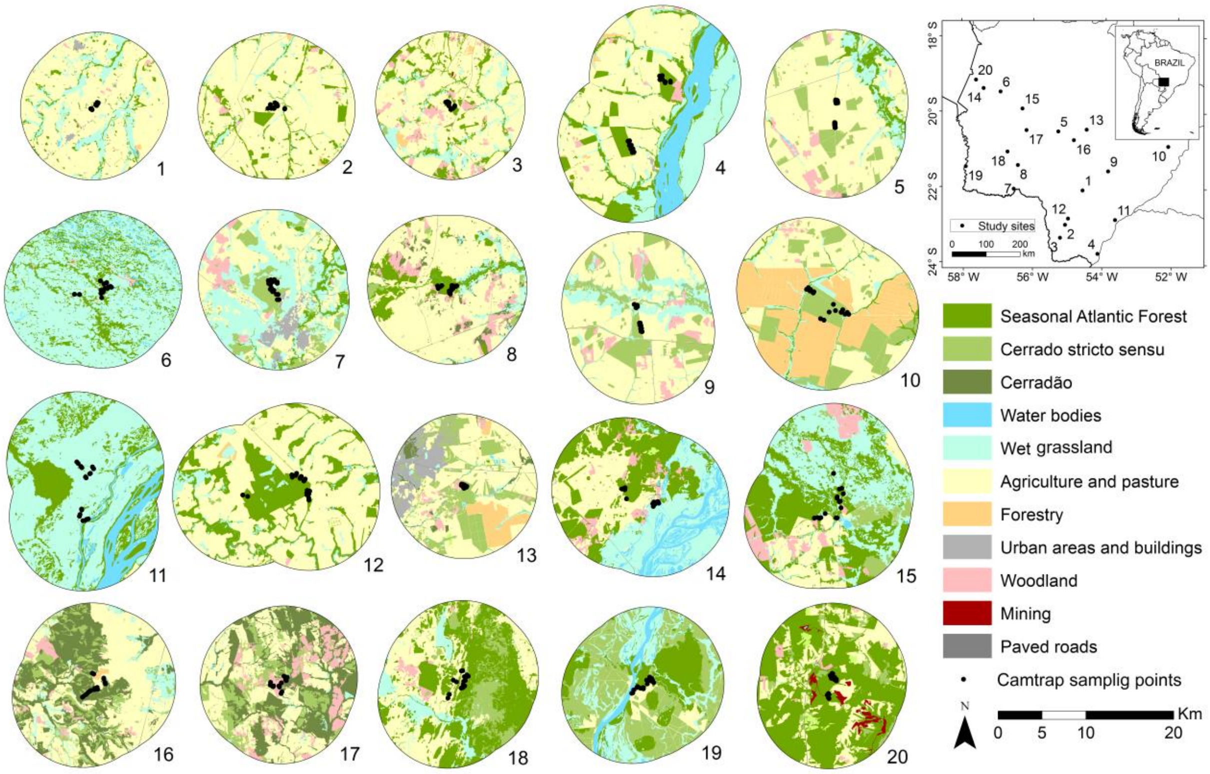

Figure 2.

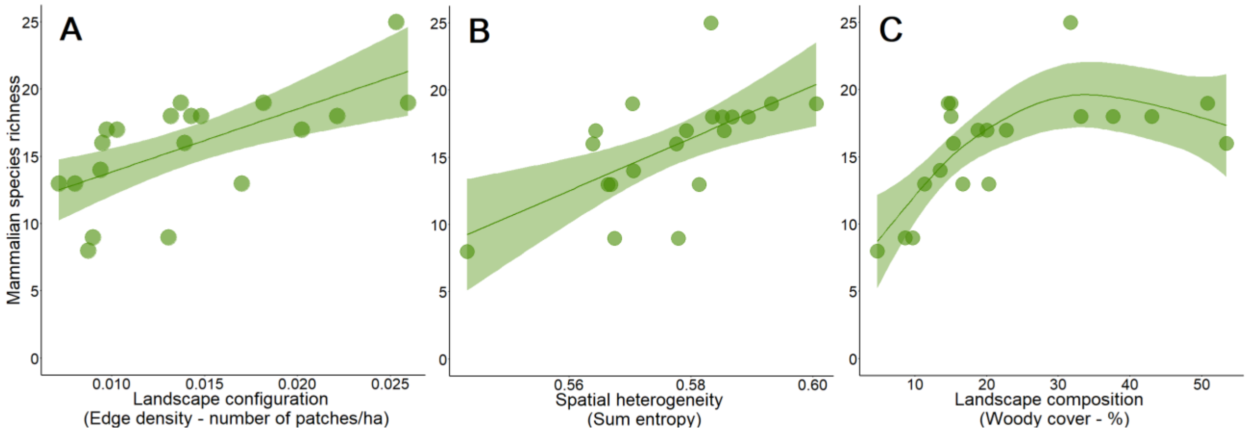
A
B
C
Mammalian species richness
0
5
10
15
20
25
0.010
0.015
0.020
0.025
Landscape configuration
(Edge density - number of patches/ha)
0.56
0.58
0.60
Spatial heterogeneity
(Sum entropy)
10
20
30
40
50
Landscape composition
(Woody cover - %)

Figure 3.

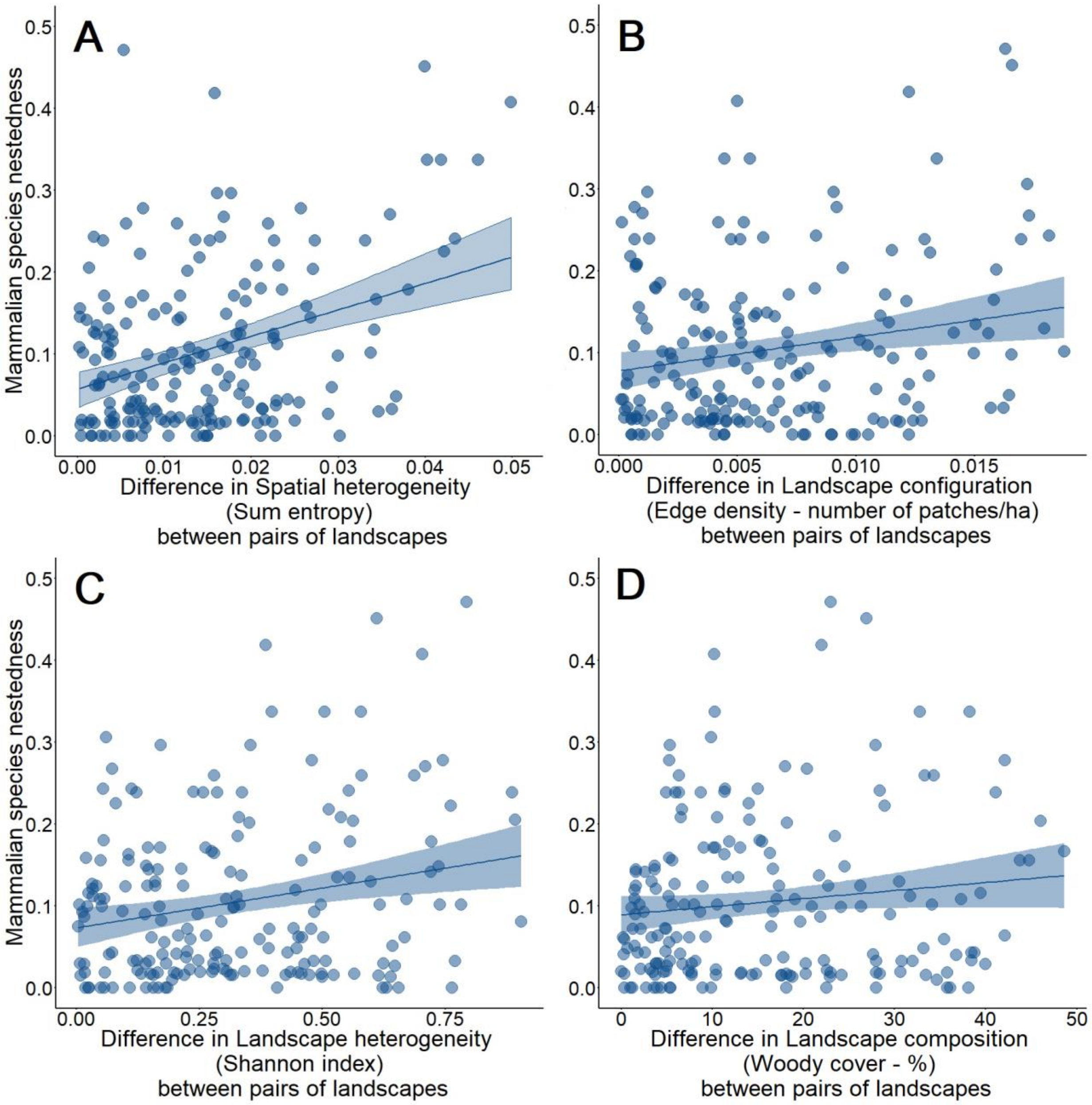
A
B
C
D
Mammalian species nestedness
0.0
0.1
0.2
0.3
0.4
0.5
0.00
0.01
0.02
0.03
0.04
0.05
Difference in Spatial heterogeneity
(Sum entropy)
between pairs of landscapes
0.000
0.005
0.010
0.015
Difference in Landscape configuration
(Edge density - number of patches/ha)
between pairs of landscapes
0.00
0.25
0.50
0.75
Difference in Landscape heterogeneity
(Shannon index)
between pairs of landscapes
0
10
20
30
40
50
Difference in Landscape composition
(Woody cover - %)
between pairs of landscapes

Figure 4.

SUPPLEMENTARY INFORMATION

Spatial autocorrelation– We evaluated spatial autocorrelation between species assemblage composition and landscape geographic coordinates applying the Mantel test (Fortin and Dale 2009) using the 'mantel' function of the 'vegan' R package (Oksanen et al. 2017). Spatial correlation was weak (r=0.224; P-value=0.014), indicating a low level of spatial autocorrelation (Fig. S1).

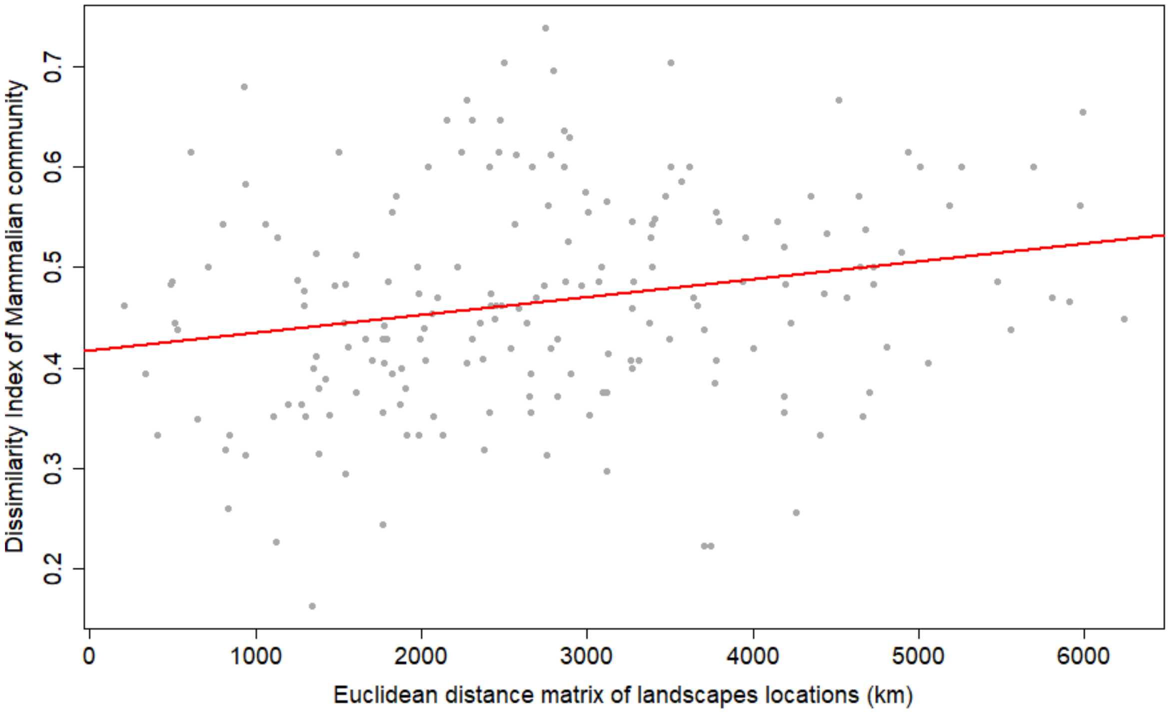

Figure S1. Correlation between mammalian assemblage and landscapes locations. Spatial correlation was negligible (r=0.224; P-value=0.014).

Multicollinearity– We evaluated multicollinearity of predictive variables using Pearson's correlation, considering less correlated variables where absolute $r < 0.7$. We verified high correlation between the four sizes of moving windows for all the twelve NDVI texture measurements. Thus, we only used textures computed with the 3x3 window size for subsequent analysis, and performed a second round of correlation analysis among all textures calculated with this extent. As expected, we found that just three of the twelve texture measurements were poorly correlated: correlation, sum entropy, and difference entropy (Fig. S2). In a third round of correlation analysis, we compared the three non-correlated texture measurements with the four landscape metrics and found no correlation between them (Fig. S3). Thus, we selected seven uncorrelated predictive variables, two representing landscape composition (woody cover and landscape heterogeneity) two representing landscape configuration (edge density, and patch density) and three representing spatial heterogeneity (texture measurements of correlation, sum entropy and difference entropy, Table 1).

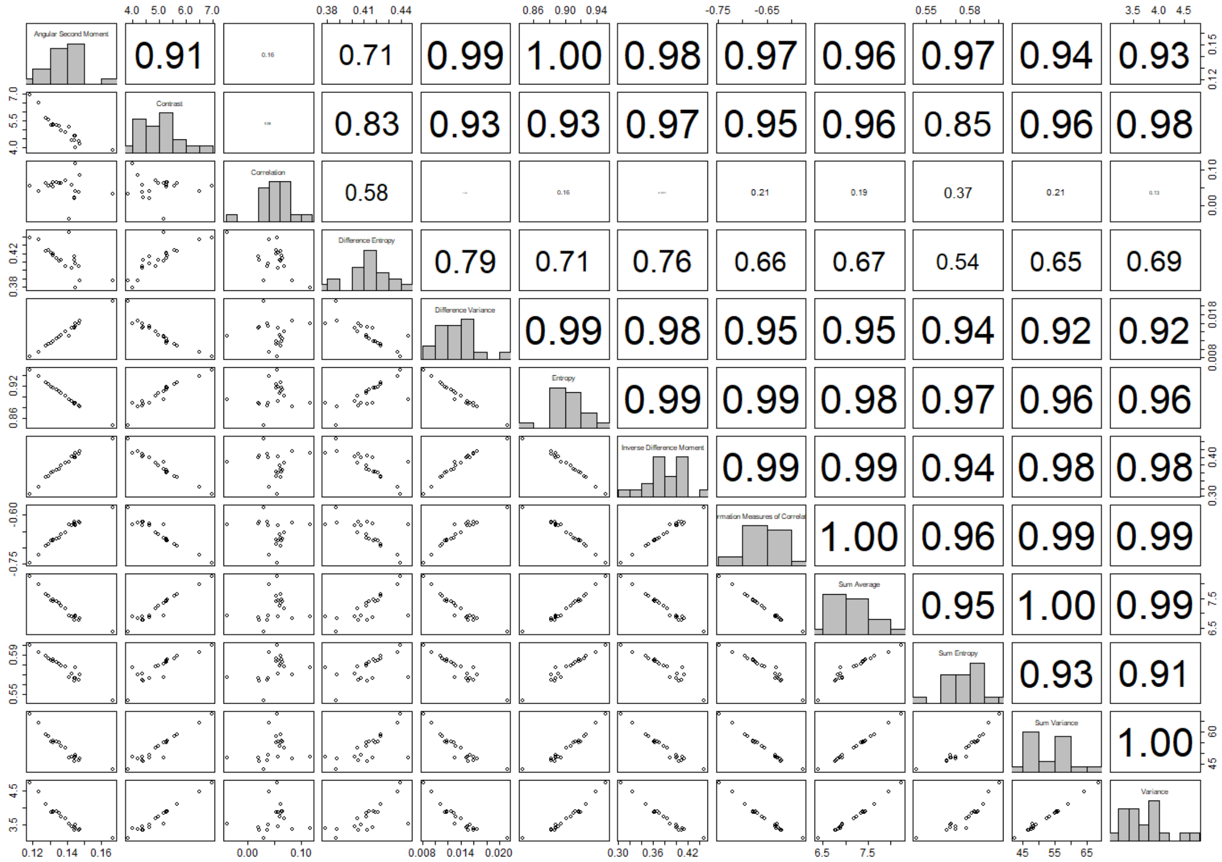

Figure S2. Scatter plot matrices of correlation between twelve measurements of spatial heterogeneity. The diagonal panels present the frequency histograms of data distribution. The upper panels show the value of the Pearson correlations among metrics. Lower panels include the point plots with data for the pairs of metrics. Three of twelve texture measurements are not correlated: correlation, sum entropy and difference entropy.

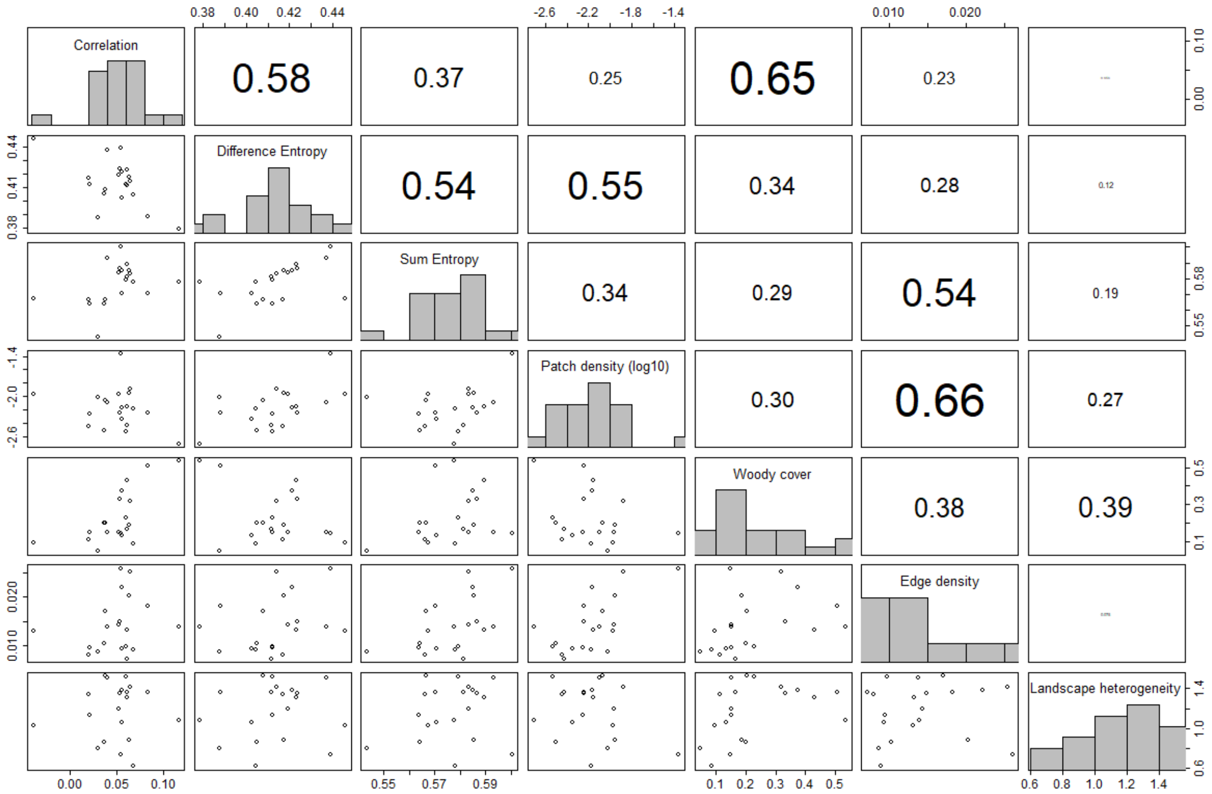

Figure S3. Scatter plot and correlation between three measurements of spatial heterogeneity and four metrics of landscape structure. The diagonal panels present the frequency histograms of data distribution. The upper panels show the value of the Pearson correlations among paired metrics. Lower panels include the scatterplots with data for the pairs of metrics.

Mammalian species check list

Table S1. Check list of mammalian species detected in 20 heterogeneous fragmented landscapes in south west Brazil.

Order	Family	Genus	Species
Artiodactyla	Tayassuidae	Pecari	*Pecari tajacu*
		Tayassu	*Tayassu pecari*
	Cervidae	Blastocerus	*Blastocerus dichotomus*
		Mazama	*Mazama americana*
			Mazama gouazoubira
Carnivora	Felidae	Leopardus	*Leopardus pardalis*
		Panthera	*Panthera onca*
		Puma	*Puma concolor*
			Puma yagouaroundi
	Canidae	Cerdocyon	*Cerdocyon thous*
		Chrysocyon	*Chrysocyon brachyurus*
		Lycalopex	*Lycalopex vetulus*
	Mustelidae	Eira	*Eira barbara*
		Pteronoura	*Pteronura brasiliensis*
		Lontra	*Lontra longicaudis*
	Procyonidae	Nasua	*Nasua nasua*
		Procyon	*Procyon cancrivorus*
	Dasypodidae	Dasypus	*Dasypus novemcinctus*
		Euphractus	*Euphractus sexcinctus*
		Cabassous	*Cabassous tatouay*
Didelphimorphia	Didelphidae	Didelphis	*Didelphis albiventris*
		Gracilinanus	*Gracilinanus agilis*
		Marmosa	*Marmosa murina*
		Marmosops	*Marmosops ocelatus*
		Micoreus	*Micoreus constantiae*
		Monodelphis	*Monodelphis domestica*
		Philander	*Philander opossum*
		Thylamys	*Thylamys macrurus*
Lagomorpha	Leporidae	Sylvilagus	*Sylvilagus brasiliensis*
Perissodactyla	Tapiridae	Tapirus	*Tapirus terrestris*
Pilosa	Myrmecophagidae	Myrmecophaga	*Myrmecophaga tridactyla*
		Tamandua	*Tamandua tetradactyla*
Primates	Cebidae	Sapajus	*Sapajus cay*
	Atelidae	Alouatta	*Alouatta caraya*
	Pitheciidae	Callicebus	*Callicebus pallescens*
	Aotidae	Aotus	*Aotus azarae*

Order	Family	Genus	Species
Rodentia	Caviidae	Hydrochoerus	*Hydrochoerus hydrochaeris*
	Dasyproctidae	Dasyprocta	*Dasyprocta azarae*
	Cuniculidae	Cuniculus	*Cuniculus paca*
	Echimyidae	Proechimys	*Proechimys longicaudatus*
		Thrichomys	*Thrichomys pachyurus*
	Sigmodontinae	Akodon	*Akodon montensis*
		Cerradomys	*Cerradomys scotti*
		Hylaeamys	*Hylaeamys megacephalus*
		Oecomys	*Oecomys bicolor*
		Rhipidomys	*Rhipidomys macrurus*
		Oligoryzomys	*Oligoryzomys* sp.
		Calomys	*Calomys* sp.