

1 LRH: Regolin *et al.*

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

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29 **Abstract**

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

48 include strategies to preserve and improve habitat quality and complexity in natural patches and
49 the surrounding matrix, enabling landscapes to harbor high species diversity.

50

51 **Resumo**

52 Os efeitos da fragmentação de habitats em diferentes táxons e ecossistemas estão sujeitos a
53 intenso debate, e esclarecê-los é de extrema importância para subsidiar estratégias de
54 conservação e manejo. Avaliamos a importância da composição e configuração da paisagem em
55 escala grossa e da heterogeneidade espacial dentro do habitat para explicar a diversidade α e β de
56 mamíferos em um gradiente de porcentagem de cobertura de vegetação lenhosa e de diversidade
57 de uso da terra. Esperamos que a riqueza de espécies seja positivamente relacionada a todas as
58 variáveis explanatórias, sendo a relação mais forte com medidas de composição, com medidas de
59 configuração da paisagem em escala grossa e com a heterogeneidade espacial dentro do habitat,
60 respectivamente. Também esperamos que a paisagem influencie ambos os componentes da
61 diversidade β (substituição e aninhamento), na mesma ordem de importância esperada para a
62 riqueza de espécies, e com uma forte influência no componente de aninhamento devido à perda
63 determinística de espécies mais sensíveis ao distúrbio no habitat. Registramos ocorrências de
64 mamíferos de pequeno, médio e grande porte em 20 paisagens no Brasil e analisamos a estrutura
65 da paisagem usando: i) métricas da paisagem baseadas em mapas temáticos de cobertura da terra
66 e ii) medidas de textura de imagem de um índice de vegetação calculadas a partir de imagens não
67 classificadas. Comparamos um conjunto de modelos explicativos univariados de riqueza de
68 espécies usando o Critério de Informação de Akaike e avaliamos como as diferenças entre pares
69 de paisagens em medidas de composição e configuração da paisagem e medidas dentro de
70 habitat de heterogeneidade espacial afetam os componentes da diversidade β usando uma
71 regressão múltipla em uma matriz de distância. Descobrimos que, contrário às nossas

72 expectativas, a configuração da paisagem foi o principal fator que afeta a riqueza de espécies,
73 seguido pela heterogeneidade espacial e, por último, pela composição da paisagem. O
74 aninhamento das espécies foi explicado, em ordem de importância, pela heterogeneidade
75 espacial, configuração da paisagem e composição da paisagem. Embora as políticas de
76 conservação tendem a se concentrar principalmente na quantidade de habitat, defendemos que o
77 manejo da paisagem deve incluir estratégias para preservar e melhorar a qualidade do habitat em
78 manchas naturais e a incrementar a complexidade da vegetação na matriz circundante,
79 permitindo que as paisagens abriguem maior diversidade de espécies.

80

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

83

84 **1 | INTRODUCTION**

85 The modern biodiversity crisis has been mainly attributed to the process of habitat
86 fragmentation (Haddad et al. 2015), which changes landscape composition, configuration, and
87 habitat quality, by affecting both natural vegetation patches and the anthropogenic matrix (Fahrig
88 2003, Fischer and Lindenmayer 2007, Driscoll et al. 2013). The harmful effects of habitat loss on
89 biodiversity are widely recognized among the scientific community, but the importance of
90 habitat fragmentation *per se* and habitat degradation is subject to debate due to differences in
91 conceptual foundations, statistical models, study systems, and resulting interpretations (Villard
92 and Metzger 2014, Fahrig 2017, Fletcher et al. 2018). Habitat fragmentation *per se* is the sub-
93 division of habitat patch (Fischer and Lindenmayer 2007) and habitat degradation is the
94 deterioration of habitat quality (Mortelliti et al. 2010). Some researchers have proposed that the
95 effects of fragmentation *per se* are notable under certain levels of habitat cover, which is called

96 fragmentation threshold (Andr n 1994, Swift and Hannon 2010). Others have hypothesized that
97 the effects of the process of habitat fragmentation depend exclusively of the amount of habitat
98 within the landscape (Fahrig 2013, Melo et al. 2017). However, studies assessing the role of
99 habitat quality are still largely unexplored (Mortelliti et al. 2010), so the importance of the
100 variability of vegetation heterogeneity within-habitat is possibly underestimated (Kupfer et al.
101 2006, Driscoll et al. 2013). Consequently, conservation recommendations beyond reducing
102 habitat loss have not reached a consensus, posing significant challenges for landscape
103 management and biodiversity conservation (Fletcher et al. 2018). In Neotropical regions, nature
104 management is particularly more challenging due to i) high ecosystem complexity associated to a
105 mega biodiversity (Lewinsohn and Prado 2005), ii) the highest global rates of forest loss (Hansen
106 et al. 2013), and iii) lack of consistency in environmental policies, especially in Brazil
107 (Brancalion et al. 2016). Thus, it is critical that we understand how structural modifications in
108 fragmented landscapes drive the organization of assemblages in tropical ecosystems.

109 Historically, landscape ecology theories and models were strongly influenced by Island
110 Biogeography and Metapopulation theories, wherein patches of native vegetation are considered
111 as islands of habitat immersed in an inhospitable matrix, and, consequently, patch area and
112 isolation drive metapopulation dynamics (MacArthur and Wilson 1967, Hanski 1998, Kupfer et
113 al. 2006, Fahrig 2013). Based on this approach, conservation strategies have been focused on the
114 preservation of large remnants of natural vegetation, and, eventually, on enhancing the matrix to
115 connect these areas through ecological corridors (Fischer and Lindenmayer 2006). This
116 paradigm, however, has been challenged by recent studies, emphasizing the importance of
117 explicitly considering differences between land cover types, contrary to the simplistic
118 classification of habitat and non-habitat (Boscolo et al. 2016). Classifying different land use
119 types is important because species occurrence may be driven by ecological requirements of non-

120 substitutable resources from different habitat types (landscape complementation) and by
121 substitutable resources from more than two habitat types (landscape supplementation; Dunning
122 et al. 1992). The degree of matrix permeability also differs among land cover types because of
123 variation in provision of food resources, water, shelters, and the presence of stepping stones
124 (Russel et al. 2007, Brady et al. 2011, Ferreira et al. 2018). Thus, the anthropogenic matrix is not
125 uniformly inhospitable for survival and reproduction of many species, nor an impenetrable
126 barrier to its movement and dispersal (Kupfer et al. 2006, Driscoll et al. 2013). Nevertheless, the
127 matrix permeability varies from species to species, once landscape perception itself is species-
128 traits dependent (Gehring and Swihart 2003, Goheen et al. 2003, Hansbauer et al. 2010, Kellner
129 et al. 2019). In this regard, even patches of natural vegetation can differ in habitat quality due to
130 natural variation or anthropogenic degradation, producing spatial heterogeneity within habitat
131 patches (Mortelitti et al. 2010). Therefore, explicitly incorporating spatial heterogeneity
132 gradients in landscape analysis approaches can improve our understanding of the relationship
133 between species diversity and landscape/environmental conditions, leading to management and
134 conservation strategies that combine natural environments and human land use in an integrated
135 and functional way (Fischer and Lindenmayer 2006, Fahrig et al. 2011, Boscolo et al. 2015).

136 The intensity of anthropogenic land use is a primary concern for the conservation of
137 terrestrial mammal worldwide (Pekin and Pijanowski 2012). Mammalian species are highly
138 diverse in terms of diet, trophic levels, body mass, and habitat use patterns, and are key
139 components of tropical ecosystem (Paglia et al. 2012, Dirzo et al. 2014). Mammalian species
140 richness has been shown to be sensitive to changes in landscape structure (Goheen et al. 2003,
141 Russel et al. 2007, Brady et al. 2011, Haddad et al. 2015, Melo et al. 2017, Regolin et al. 2017,
142 Berl et al. 2018), allowing the modeling of this diversity component using distinct scenarios of
143 land use. Other components of species diversity, however, have different responses to

144 environmental variation and change (e.g. Dornelas et al. 2014), but are understudied in
145 comparison with alpha diversity (Mori et al. 2018). Although measures of alpha diversity (such
146 as richness, abundance, and occurrence probability) are the main response variables in most
147 studies, recent research has shown that beta diversity (dissimilarity between communities) is an
148 essential variable to understand the processes that shape assemblage differences (Baselga 2010).
149 The beta diversity reflects two different phenomena: turnover and nestedness. The turnover
150 component measures species replacement between communities, whereas nestedness refers to a
151 non-random process of species loss between communities (Baselga 2010). Therefore,
152 understanding how beta diversity varies within a spatially heterogeneous system can contribute
153 to our understanding of landscape functioning (Mori et al. 2018).

154 In this study, we assessed how mammalian communities are structured over
155 heterogeneous fragmented landscapes, by combining analyses of landscape structure with
156 measures of fine spatial heterogeneity. Specifically, we quantified the importance of coarse-scale
157 measures of landscape structure with measures of within-habitat spatial heterogeneity in
158 explaining mammal species richness, and the role of landscape variables in species
159 compositional dissimilarity. We defined landscape composition as the amount of different land
160 cover types present in the study landscapes, and landscape configuration as the spatial
161 arrangement of landscape units (Villard and Metzger 2014), while spatial heterogeneity was
162 quantified using proxies of vegetation structural complexity (Wood et al. 2012). We expected a
163 positive relationship between species richness and landscape composition, configuration and
164 spatial heterogeneity, with decreasing contributions from the former to the last respectively
165 (Figure 1A). We also expected that β -diversity components (nestedness and turnover) would
166 increase linearly with the differences among predictive variables between pairs of landscapes,
167 with the same order of importance expected for species richness. Nestedness should be more

168 strongly influenced by landscape differences than turnover due to deterministic losses of species
169 more sensitive to environmental modifications (Figure 1B). Our expectations were based on the
170 following assumptions: i) natural vegetation cover captures resource availability and
171 environmental conditions that produce species occupancy (Fischer and Lindenmayer 2007); ii)
172 higher composition heterogeneity (diversity of land use types) increases the occurrence
173 probability for species that use two or more vegetation types (landscape supplementation and
174 complementation, Dunning et al. 1992); iii) Landscape supplementation and complementation
175 also depend on landscape configuration, and are favored in patchy landscapes due to higher
176 incidence of abrupt transitions between different land use types (edge areas, Fahrig 2017); iv)
177 edge areas have biotic and abiotic conditions that are different from both the matrix and the
178 patch core region, with either positive or negative effects on species (Murcia et al. 1995, Berl et
179 al. 2018); and v) structural complexity is positively related to resource and shelter availability for
180 both habitat patches and the matrix, and ultimately affect species movement capacity (Russel et
181 al. 2007, Driscoll et al. 2013).

182

[Figure 1 here]

184

185 **2 | METHODS**

186 **2.1 | Study areas**

187 Our study was conducted on 20 landscapes located in Mato Grosso do Sul State, western
188 Brazil, covering an area of 534,598 hectares. We distributed the landscapes across a gradient of
189 seasonal Atlantic Forest, *Cerradão* and Cerrado *stricto sensu* cover (hereafter ‘woody cover’),
190 while also considering land use composition heterogeneity (Figure 2). The sampled landscapes
191 are within an ecotonal region, with biogeographic influences from the Atlantic Forest, Cerrado

192 and a small portion of the dry Chaco in the southwest. Both Atlantic Forest and Cerrado are
193 biodiversity hotspots for conservation priorities (Myers et al. 2000). Some landscapes are also
194 biogeographically influenced by Amazon forest (Chiquitana forest). The study region is under
195 constant anthropogenic pressure and has been undergoing intensive conversion of natural areas
196 to anthropogenic land uses, especially croplands and pastures (Klink and Machado 2005, Roque
197 et al. 2016). The deforestation ranges from 22,000 to 30,000 km²/year, which is higher than rates
198 in Amazon (Klink and Machado 2005).

199

200 [Figure 2 here]

201

202 **2.2 | Mammal diversity data**

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

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

216 30-40 cm above the ground, in tree trunks of forest or Cerrado patches in each landscape.
217 Cameras were placed on transect lines of 110 m in length containing two cameras in each
218 extremity (in the border and in the interior of each forest fragment), operating 24 hours a day,
219 during four consecutive days and nights. Transect lines were distant at least 150 m from each
220 other (in small areas), but usually a minimum distance of 300 m was set. The total sampling
221 effort was of 1,128 traps-night, with the mean effort per landscape being 56 ± 7 traps-night. We
222 captured rodents and marsupials (<1 kg, Cricetidae, Echimyidae and Didelphidae families) using
223 65 wire (33x12x12 cm) and Sherman live-traps (30x9x7 cm). Traps were installed in forest
224 ground (wire) and understory (Sherman), between 1.5 and 2 meters above the ground, during
225 four consecutive nights, totaling 6,800 trap-night overall and 340 traps-night per landscape. We
226 baited the traps with a mixture of pumpkin, bacon, peanut butter and cod liver oil. In each
227 landscape, we installed the traps along transects between the camera trap sampling points, 10 m
228 apart from each other in the same transect, separated at least 150 m from each other transect line
229 and at least 20 m from the nearest patch edge. Captured animals were identified and
230 subsequently released. When necessary, we collected voucher specimens for identification,
231 which were deposited in the mammalian collection of the Universidade Federal de Santa Maria
232 (UFSM).

233

234 **2.3 | Land use and land cover maps**

235 We generated an 8-km buffer around the camera trap sampling points within each
236 landscape to delimit landscape extent. We chose this extent based on previous studies reporting
237 landscape structure effects on small-, medium- and large-sized mammal assemblage composition
238 within the Atlantic Forest (e.g. Lyra-Jorge et al. 2010, Beca et al. 2017, Melo et al. 2017,
239 Regolin et al. 2017), as well as to avoid spatial overlap (Jackson and Fahrig 2015). We mapped

240 land cover for each landscape using orthorectified images from the RapidEye satellite
241 constellation, with 5m spatial resolution. Images were selected preferably from the dry season,
242 due to lesser cloud cover and greater contrast between land use classes (47 images acquired
243 between January 2011 and August 2013). Image processing was performed over all five spectral
244 bands (blue, green, red, red edge and near infrared) and included: i) atmospheric correction using
245 the ‘Quick Atmospheric Correction – QUAC’ algorithm implemented in the ENVI 5.0 software
246 and ii) unsupervised classification using the ‘Auto Class’ software (github.com/JohnWRRC).
247 Auto Class uses the GRASS function ‘i.segment’ to generate image segments and the K-means
248 Clustering function of the ‘foreign’ R package (R Core Team 2017) to group the segments into
249 classes according to the mean and standard deviation of pixel values. We then converted this
250 unsupervised map into a thematic classification by supervised visual interpretation and manual
251 editing, based on image visualization at 1:2,500 cartographic scale, generating a final map with
252 11 classes (Figure 2).

253

254 **2.4 | Landscape structure metrics**

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

264

265 **2.5 | Within-habitat spatial heterogeneity**

266 We estimated within-habitat spatial heterogeneity by calculating image texture measures
267 from the normalized difference vegetation index (NDVI). NDVI is a spectral index sensitive to
268 photosynthetically active vegetation, which is related to plant biomass productivity (Justice et al.
269 1998). We calculated NDVI using the red and near-infrared spectral bands of RapidEye images
270 (5-m spatial resolution) using the ‘spatial.tools’ R package (Greenberg 2018). Image textures are
271 statistical descriptors of the spatial relationship among pixel values within an image region, thus
272 capturing spatial heterogeneity (St-Louis et al. 2009, 2014). When calculated using NDVI,
273 texture therefore represents spatial variability in photosynthetically active vegetation within a
274 given area (Wood et al. 2012). Texture measures calculated from high resolution images have
275 been related with descriptors of vegetation heterogeneity such as leaf-area index and foliage
276 height diversity (Colombo et al. 2003, Wood et al. 2012). Particularly, textures can yield larger
277 explanatory power for species richness than classified images because it captures fine-scale
278 variability within coarse habitat classes in areas of gradual transition between vegetation types
279 (St-Louis et al. 2009, Wood et al. 2013).

280 We calculated 12 texture measurements from NDVI, using the ‘r.texture’ GRASS GIS
281 function, being seven first order metrics: (i) sum average, (ii) entropy, (iii) difference entropy,
282 (iv) sum entropy, (v) variance, (vi) difference variance, (vii) sum variance; and five second-order
283 metrics based on a pairwise matrix of spatial relationships among pixels (grey-level co-
284 occurrence matrix; Haralick 1979), (viii) angular second moment, (ix) inverse difference
285 moment, (x) contrast, (xi) correlation, and (xii) information measures of correlation. Each texture
286 was calculated in four directions (0, 45, 90 and 135 degrees) considering a central pixel and its
287 neighbors within the specified window, and then average of texture metrics were calculated to

288 summarize all directions. We derived textures using four different moving window sizes on each
289 pixel (3x3, 5x5, 7x7 and 9x9 pixels of 5m).

290

291 **2.6 | Data analysis**

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

300

301 [Table 1 here]

302

303 **Mammal species richness**—We fitted generalized additive models (GAMs) to quantify how
304 mammalian species richness relate to heterogeneous fragmented landscapes, using the ‘gam’
305 function of the ‘mgcv’ R package (Wood 2011) and assuming a Poisson distribution for count
306 data (Zuur et al. 2009). We choose GAMs as they are able to capture non-linear and linear
307 effects (Zuur et al. 2009). We computed seven univariate models, each including one of the four
308 landscape structure metrics or the three spatial heterogeneity variables as predictors. We also
309 included a null model representing a neutral response of richness to landscape structure
310 (intercept only), totalizing eight competing models. We then compared the set of models using
311 Akaike’s Information Criterion corrected for small samples (AICc), to select the best explanatory

312 model using the ‘Ictab’ function of the ‘bbmle’ R package (Bolker and R Development Core
313 Team 2017). All models with $\Delta AICc < 2$ were considered equally plausible to explain the
314 patterns, i.e., a given landscape predictor influences species richness as much as the other
315 included on best model list (Burnham and Anderson 2002). We evaluated model weight (w_i) of
316 plausible models as a proxy of predictor importance, since model weight can be interpreted as
317 the probability of a model to be the best among competing models (Wagenmakers and Farrell
318 2004). We also reported deviance explained to assess model fit.

319

320 **β -diversity**—We estimated total β -diversity and partitioned it in two components – turnover and
321 nestedness – using a presence-absence assemblage matrix as input to the ‘beta.pair’ function of
322 the ‘betapart’ R package (Baselga 2010, Baselga and Orme 2012). Total β -diversity was
323 calculated as Sorensen’s dissimilarity index (β_{sor}), turnover as Simpson dissimilarity index (β_{sim}),
324 and nestedness (β_{nes}) as the difference between total β -diversity (β_{sor}) and turnover (β_{sim}). We
325 used a multivariate linear regression (Multiple Regression on distance Matrix – MRM)
326 (Linchstein 2007) using the dissimilarities matrices (beta diversity components), using the
327 ‘adonis’ function of the ‘vegan’ R package (Oksanen et al. 2017) with 9,999 permutations to test
328 the effect of predictive variables (landscape structural metrics and spatial heterogeneity) on β -
329 diversity measures (turnover and nestedness). We considered that predictors affected beta
330 diversity components where the significance levels of the coefficients were equal or lower than
331 0.05. We calculated the adjusted coefficient of multiple determination (R^2), which is the ratio of
332 the sum of squares of distances of the estimated values to the mean, to the sum of squares of
333 distances of the original response variable values to the mean — adjusted by the numbers of
334 degrees of freedom of the numerator and denominator of the coefficient of multiple
335 determination (Legendre & Legendre 2012). We opted to analyze the effect of the landscape on

336 beta diversity through a frequentist approach - evaluating the p-value and the R^2 - as recent
337 research has criticized the use of model selection for multivariate data on genetics and beta
338 diversity (Franckowiak et al. 2017, Rocha et al. 2019)

339

340 **3 | Results**

341 **3.1 | Overview**

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

351

352 **3.2 | Landscape structure influence on mammal richness**

353 Among the set of eight competing models, three were equally plausible to explain species
354 richness (Table 2): landscape configuration – edge density ($\Delta AICc = 0.0$; $w_i = 0.374$), spatial
355 heterogeneity – sum entropy ($\Delta AICc = 0.3$; $w_i = 0.316$), and landscape composition – woody
356 cover ($\Delta AICc = 1.1$; $w_i = 0.211$). We found a positive linear relationship between species
357 richness and landscape configuration – edge density (Figure 3A) and also for spatial
358 heterogeneity – sum entropy (Figure 3B). In addition, we also observed a positive relationship of

359 woody cover on species richness below 30% of woody cover, with no effect above this threshold
360 (Figure 3C).

361

362 [Table 2 here]

363

364 [Figure 3 here]

365

366 **3.3 | Patterns of β -diversity**

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

372

373 [Table 3 here]

374

375 [Figure 4 here]

376

377 **4 | Discussion**

378 Species assemblage in heterogeneous fragmented landscapes of tropical ecosystems are
379 shaped by many ecological processes acting simultaneously. Consequently, identifying the main
380 drivers of changes in mammalian species richness (α -diversity) and variation in communities'
381 composition (β -diversity) is challenging (Mori et al. 2018). Our results contradicted our
382 expectations; landscape configuration (edge density) was the main driver of species richness,

383 followed by spatial heterogeneity (sum of entropy) and landscape composition (woody cover).
384 The order of importance of predictive variables explaining β -diversity was also different from
385 our expectations; loss of species between communities (β_{nes}) was driven mainly by spatial
386 heterogeneity (sum of entropy), followed by landscape configuration (edge density) and
387 landscape composition (woody cover and landscape heterogeneity). In accordance to our third
388 prediction, β_{nes} responded more strongly than β_{sim} to differences in predictive variables.

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

400

401 **4.1 | Reliability of field data**

402 Although a higher sampling effort on each landscape would decrease our variability
403 resulting in a smaller error in species detection, a larger sample size (more landscapes) would
404 result in a higher statistical power by increasing our degrees of freedom. We choose to increase
405 sample units in detriment of a larger sampling effort in each landscape considering that the
406 predictors (landscape metrics and measurements of spatial heterogeneity) were logistical easier

407 and financial cheaper to measure than the response variable (Brennan et al. 2002). In this way,
408 we were able to sample 20 independent landscapes, which is a high number of independent
409 sample units in comparison to other studies sampling mammals at landscapes scale (see
410 examples in the review of Presley et al. 2019). Although our sampling effort in each landscape
411 could limit the detection of rare or cryptic species, we used an equal sampling effort along the
412 landscapes, so we consider our results are not bias and represent the relationship of the most
413 representative local mammal species and landscape patterns.

414

415 **4.2 | Habitat composition influence**

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

424 Woody cover, which we expected to be the strongest predictor of β -diversity, had the
425 weakest effect on species richness and β_{nes} . The contribution of landscape composition to explain
426 species richness and loss of species between communities seems to be larger in other landscapes
427 with ample differences in habitat amount (*e.g.* 5-95%) and low landscape use diversity. An
428 example is the study by Beca et al. (2017), who related mammals occurrence and richness to
429 measures of landscape structure of forest patches immersed in a homogeneous matrix of biofuel
430 plantation within the Brazilian Atlantic Forest. However, our study had a limited range of

431 variation in habitat amount (5-55%) and higher heterogeneity of both native vegetation and
432 matrix components than Beca et al. (2017), who classified land use types in two classes, forest
433 and matrix. Therefore, the simpler view that habitat amount can alone support landscape
434 management is unlikely to be applicable to heterogeneous landscapes under intense anthropic
435 use in tropical ecosystems.

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

451

452 **4.3 | Habitat configuration effects**

453 Our results go beyond the paradigms of habitat composition, and evidence the role of the
454 configuration of natural vegetation patches for the maintenance of species richness. We found a

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

466

467 **4.4 | Within-habitat spatial heterogeneity matters**

468 The relationship between spatial heterogeneity (sum entropy) and both α - and β - diversity
469 results from deterministic losses of the most sensitive species due to reduction in vegetation
470 structural complexity within both native vegetation patches and anthropogenic matrices. Larger
471 vegetation structural complexity within habitat patches increases niche availability, and
472 consequently, patch capacity to host high species diversity (Brady et al. 2011). Furthermore, high
473 similarity between patch and matrix vegetation structure favors species movement through the
474 landscape (Kupfer et al. 2006). By providing habitat breeding and food resources, the
475 anthropogenic matrix can guarantee (re)colonization of habitat patches by species, increasing
476 population size and reducing the risk of extinction (Driscoll et al. 2013). For example,
477 polyculture and agroforestry systems are wildlife-friendly matrices, as they are more structurally

478 complex than pasturelands, intensive cereal cropping, and other annual monocultures, which in
479 turn erode mammal diversity (Ferreira et al. 2018).

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

493

494 **4.5 | Concluding remarks**

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

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

511

512 **DECLARATIONS**

513 **Permits** - Data collection followed ASM guidelines (Sikes, 2016) and was authorized by the
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527 wrote the manuscript with input from LSSM, GLM, TSFS and FM. GLM, JS and NCC designed
528 data collection and carried out field work. ALR, MCR and FM analyzed the data. ALR, LFCC
529 and FM quantified landscape structure indices. LSSM calculated all the image textures. All the
530 authors revised the manuscript. Proof reading by TSFS.

531

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688

689

690 **Tables**

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

Metric type	Landscape metric name	Landscape metric description
Landscape composition	Woody cover	Percentage of Atlantic Forest, <i>Cerradão</i> and Cerrado <i>stricto sensu</i> 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 <i>et al.</i> 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 <i>et al.</i> 2012).
	Difference entropy	Measures the disorder related to the gray level difference distribution of the image (Haralick 1973, Wood <i>et al.</i> 2012).

694

695

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

Model	$\Delta AICc$	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 heterogeneity)	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%

704

705

706 Table 3. Coefficients of determination (R^2) using Multiple Regression on distance Matrix for
 707 each predictive variable to explain β diversity components (turnover and nestedness) of
 708 mammalian communities within twenty fragmented landscapes of western Brazil. Significant p-
 709 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)

710
 711 **Figures legends**
 712 Figure 1. Expected patterns between α (A) and β -diversity (B) of mammalian species and
 713 predictive variables of landscape composition, configuration and spatial heterogeneity in 20
 714 heterogeneous fragmented landscapes in western Brazil.

715
 716 Figure 2. Land use maps of 20 study landscapes in south-western Brazil where terrestrial
 717 mammals were studied to understand the effects of landscape composition (woody cover,

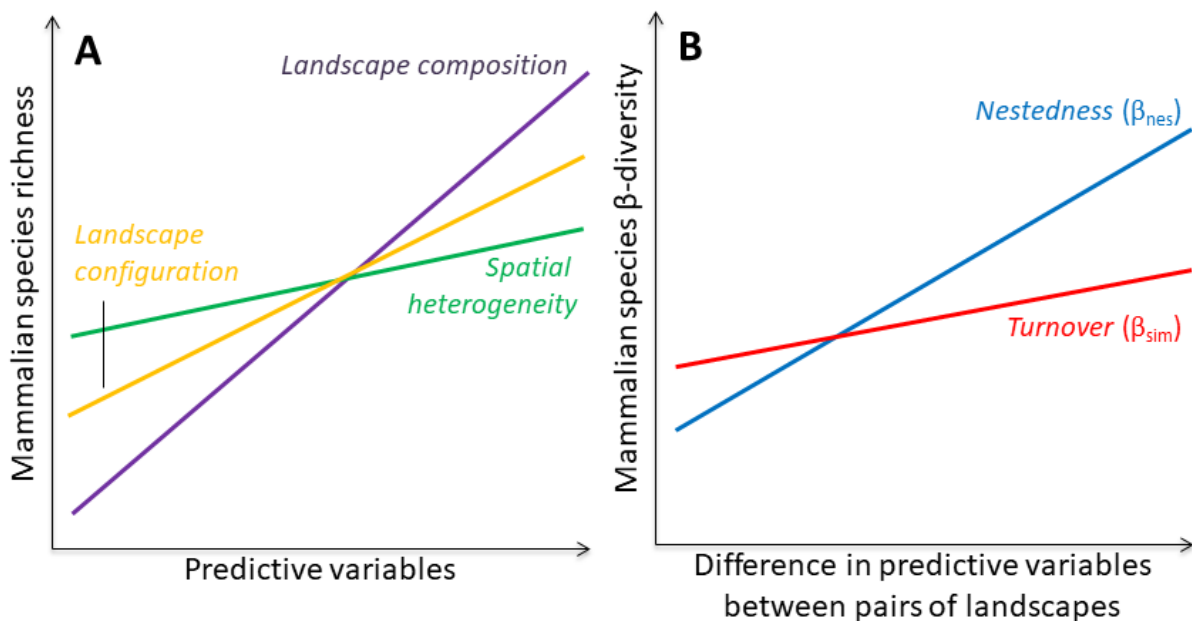
718 landscape heterogeneity), configuration (edge density, patch density), and spatial heterogeneity
719 (satellite image texture) on α - and β -diversity.

720
721 Figure 3. Best-supported models for explaining mammalian species richness in heterogeneous
722 fragmented landscapes of western Brazil: (A) landscape configuration (edge density), (B) spatial
723 heterogeneity (sum entropy), and (C) landscape composition (woody cover). Green shading is
724 the confidence interval.

725
726 Figure 4. Relationship between mammalian species nestedness and (a) spatial heterogeneity
727 (sum entropy), (b) landscape configuration (edge density), (c) landscape composition (landscape
728 heterogeneity), and (d) landscape composition (woody cover) in heterogeneous fragmented
729 landscapes of western Brazil. Blue shading is the confidence interval. The x-axes represent
730 absolute differences in explanatory variables.

731

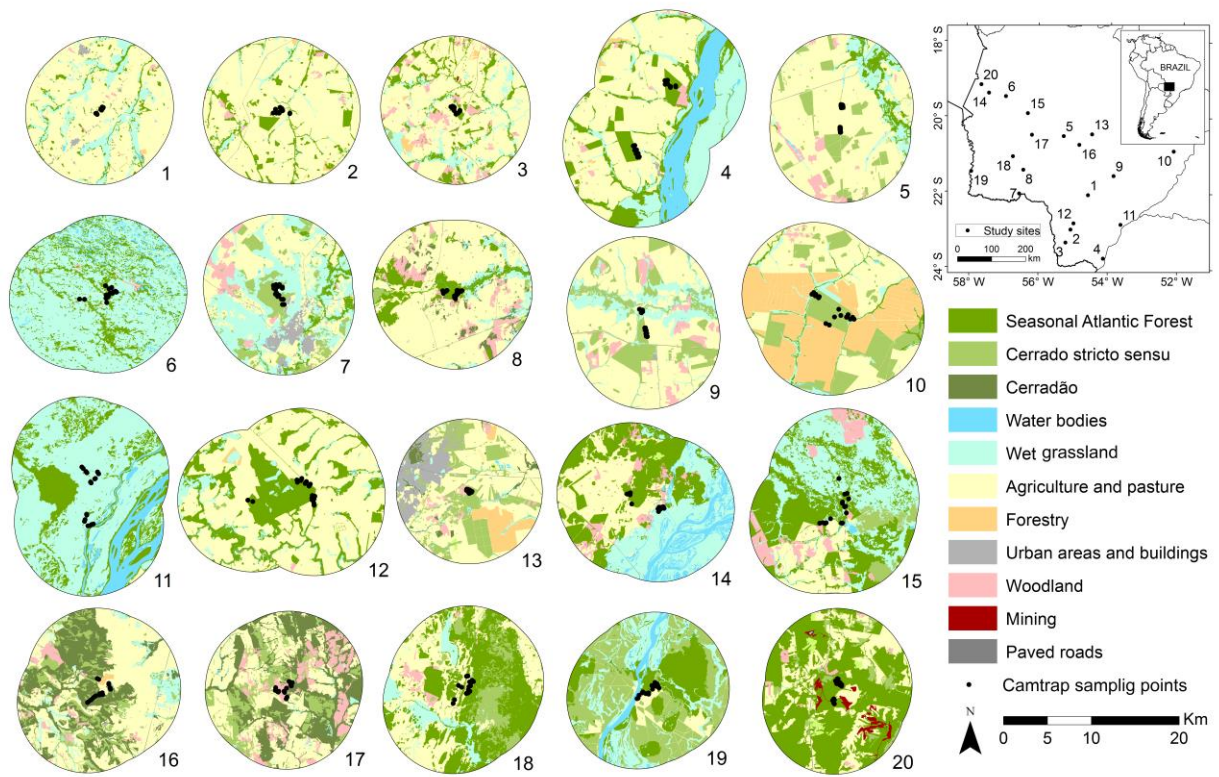
732 **Figures**



733

734 Figure 1.

735

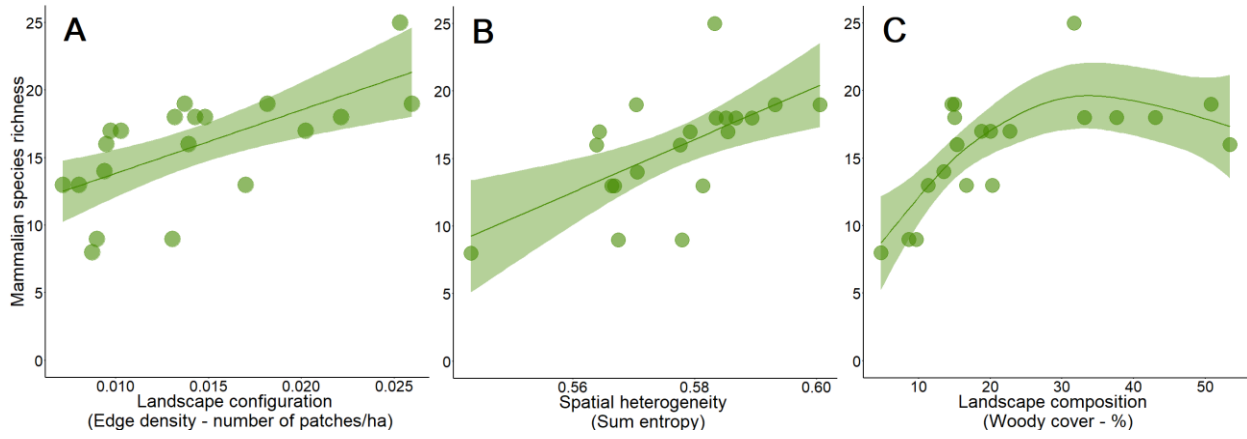


736

737 Figure 2.

738

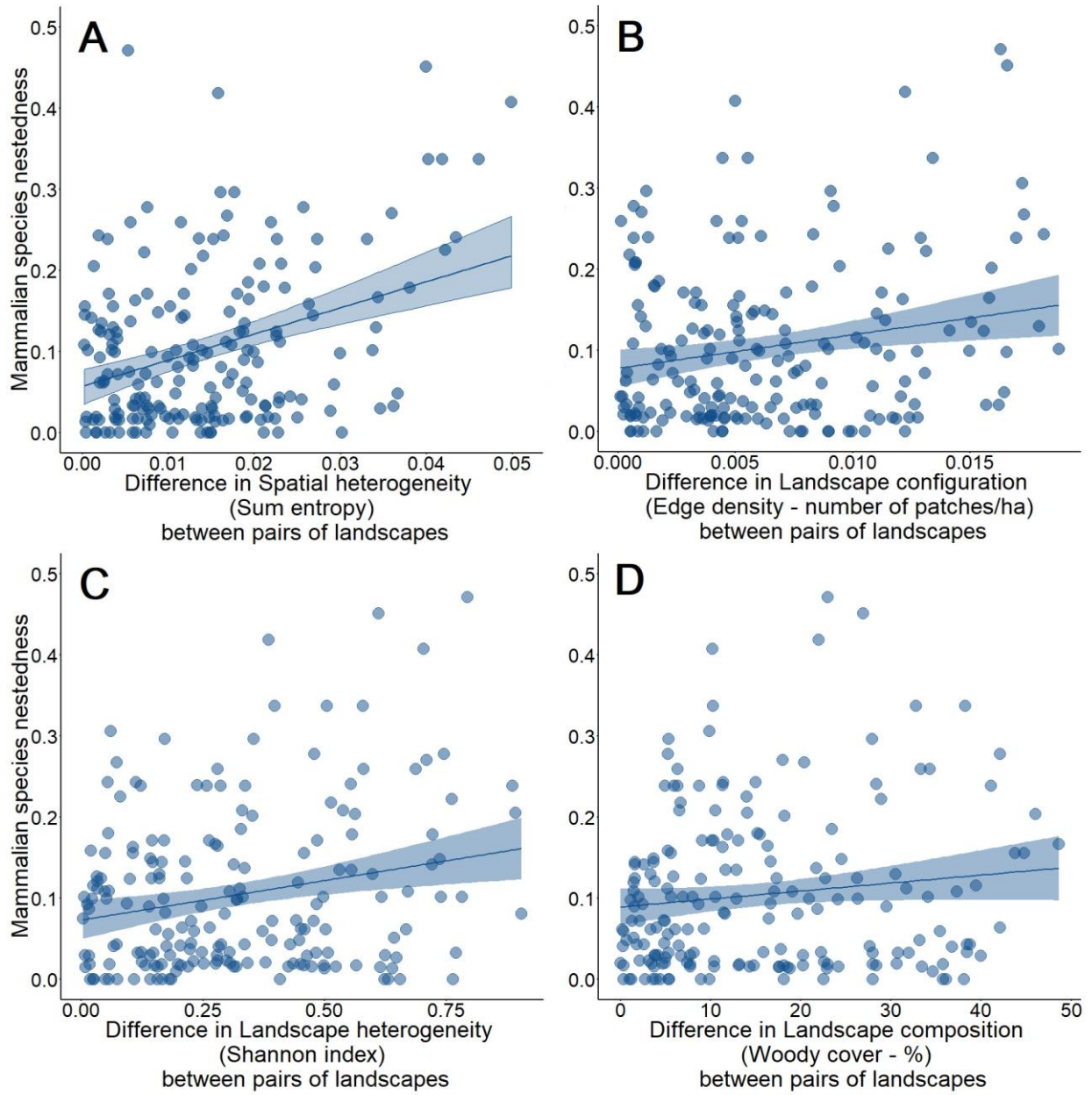
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740

741 Figure 3.

742



743

744 Figure 4.

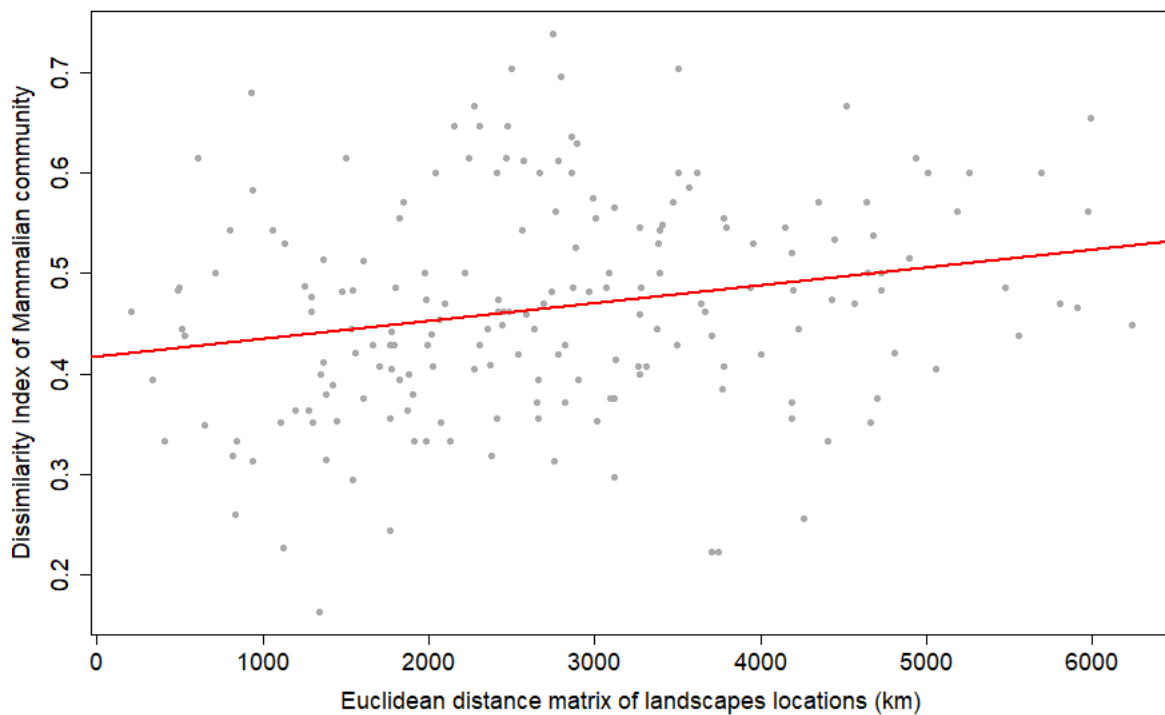
745

746 **SUPPLEMENTARY INFORMATION**

747

748 **Spatial autocorrelation**– We evaluated spatial autocorrelation between species assemblage
749 composition and landscape geographic coordinates applying the Mantel test (Fortin and Dale
750 2009) using the ‘mantel’ function of the ‘vegan’ R package (Oksanen et al. 2017). Spatial
751 correlation was weak ($r=0.224$; $P\text{-value}=0.014$), indicating a low level of spatial autocorrelation
752 (Fig. S1).

753



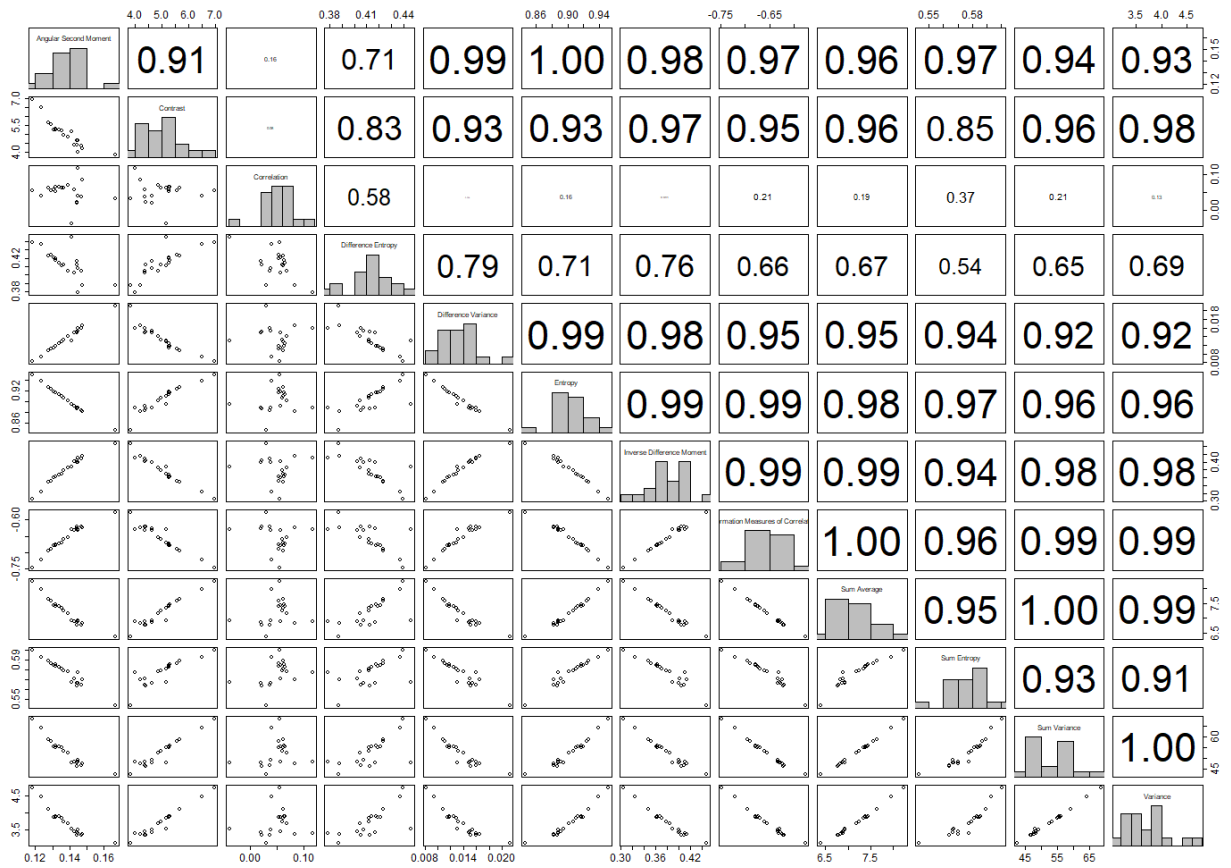
754

755 Figure S1. Correlation between mammalian assemblage and landscapes locations. Spatial
756 correlation was negligible ($r=0.224$; $P\text{-value}=0.014$).

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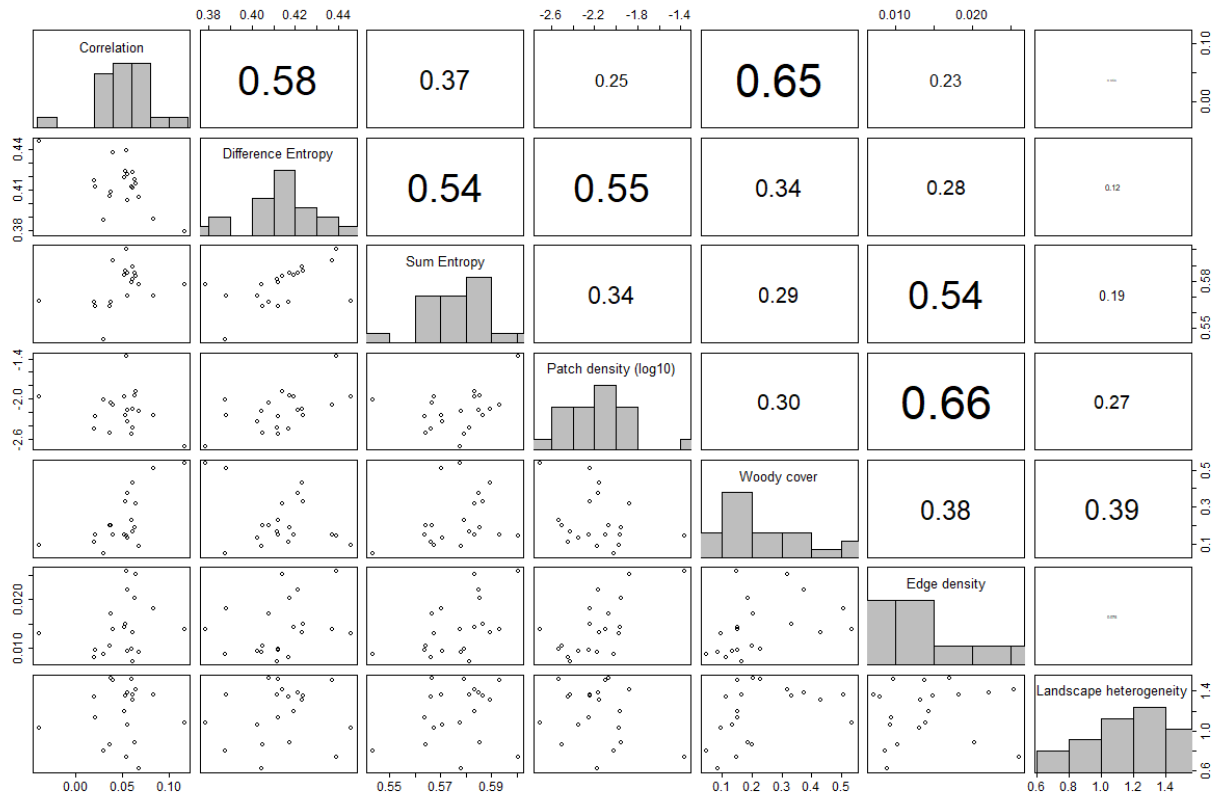
1 **Multicollinearity**– We evaluated multicollinearity of predictive variables using Pearson’s
2 correlation, considering less correlated variables where absolute $r < 0.7$. We verified high
3 correlation between the four sizes of moving windows for all the twelve NDVI texture
4 measurements. Thus,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

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

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 2 Figure S3. Scatter plot and correlation between three measurements of spatial heterogeneity and
 3 four metrics of landscape structure. The diagonal panels present the frequency histograms of data
 4 distribution. The upper panels show the value of the Pearson correlations among paired metrics.
 5 Lower panels include the scatterplots with data for the pairs of metrics.
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1 **Mammalian species check list**

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

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

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

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