

1 **Short title:** Patterns of taxonomic, functional and phylogenetic β -diversity variation of
2 Neotropical small mammals

3

4 **Exploring patterns of taxonomic, functional and phylogenetic β -diversity variation**
5 **of Neotropical small mammals in a highly fragmented landscape**

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8 Wellington Hannibal^{1, *}, Nicolay Leme da Cunha²

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10 ¹Laboratório de Ecologia e Biogeografia de Mamíferos, Universidade Estadual de
11 Goiás, Quirinópolis, Goiás, Brazil

12 ²Grupo de Ecología de la Polinización, INIBIOMA, CONICET-Universidad Nacional
13 del Comahue, San Carlos de Bariloche, Río Negro, Argentina

14

15 * Corresponding author

16 E-mail: wellingtonhannibal@gmail.com (WH)

17

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19

20 **Abstract**

21 Diversity can be partitioned in several components and dimensions that are affected in
22 different ways by habitat loss and fragmentation. However, these partitions and
23 dimensions are rarely investigated on human-modified landscapes. In this study, we
24 investigated different partitions (Hill numbers) and dimensions (taxonomic [T β D],
25 functional [F β D] and phylogenetic [P β D]) of small mammal β -diversity in a fragmented
26 landscape of central Brazil using a multi-scale approach. T β D was estimated
27 considering rare, common and abundant species. Tolerance to disturbed habitat,
28 assessed via the traits “habitat use”, “tail length” and “use of vertical strata”, and trophic
29 guild, defined by the “diet”, were used to estimate F β D. P β D was based on phylogenetic
30 relatedness of the sampled species. The association between different partitions and
31 dimensions of β -diversity with habitat and landscape attributes were investigated using
32 Mantel tests. We found a significant positive effect of geographical distance on all
33 partitions and dimensions of β -diversity. NDVI was the second most important variable
34 affecting abundance based T β D, and all phylogenetic and functional β -diversity
35 dimensions. Habitat characteristics, such as fallen logs and canopy cover were
36 positively associated with all β -diversity dimensions. Our findings support the
37 hypothesis that even in a highly modified landscape, small mammal’s β -diversity is
38 determined by different environmental factors and spatial disposition of forest patches.
39 However, the relatively higher importance of space appears to be related to dispersal
40 limitation of this group.

41 **Keywords:** abundance; geographical distance; NDVI; vegetation structure

42 **Introduction**

43 Biological diversity is a topic of great interest for biologists and can have different
44 connotations [1,2]. There are several ways to describe biological diversity, and among
45 them the definition of three main components: alpha diversity (α) - diversity on a local
46 scale, beta diversity (β) - the variation of species between locations, and gamma
47 diversity (γ) - diversity on a regional scale [3] have been largely employed.
48 Nevertheless, the traditional definition of β -diversity is dependent on α -diversity [3,4],
49 leading to spurious results when researchers compare β -values of regions with different
50 α -diversities [5]. Therefore, to avoid misinterpretation, α and β components should be
51 ideally transformed into their number equivalents [6,7]; for example ${}^qD_\beta$ for β -diversity,
52 where q -number could determine a diversity measure's sensitivity to rare or common
53 species [5,8]. In this approach, species richness, Hill-Shannon diversity and Hill-
54 Simpson diversity [6] are the three forms of Hill diversity most commonly used in
55 ecological studies [8] and are generally known as the "Hill numbers".

56 In a community dynamic viewpoint, β -diversity increases (heterogenization)
57 when common species do not co-occur from some or all sites, or when new species
58 arrive at some sites; and β -diversity decrease (homogenization) when rare, non-common
59 species become extinct, or when formerly rare or absent species become widespread [9].
60 Variation on the trajectory of β -diversity can be caused by different effects of human
61 disturbance [9–11]. Between these human disturbances, habitat loss has a consistently
62 negative effect on biodiversity, while habitat fragmentation has been associated with the
63 concept of habitat spatial heterogeneity, generally considered to have a positive
64 influence on population and community-level ecological response [12,13]. In this

65 scenario of habitat fragmentation, β -diversity should increase due mainly the effects of
66 environmental variation among patches.

67 Nonetheless, the accrued evidence showed that the patterns of β -diversity in
68 fragmented landscapes can result in homogenization or differentiation depending on the
69 landscape heterogeneity and the spatial scale of analysis [14–17], highlighting the
70 importance of isolation by distance on determining patterns of β -diversity variation
71 [18]. Functional and phylogenetic β -diversity have been relatively less investigated on
72 fragmented landscapes when compared to traditional taxonomic metrics [19], but
73 despite less used, some studies show that a decrease in such dimensions of β -diversity
74 was associated with land use intensification [20,21]. On the other hand, in a gradient of
75 habitat complexity, the increase of all dimensions of β -diversity can be driven by β -
76 replacement (T β D and F β D) or β -richness (P β D) [22]. So, ecological drives of
77 biodiversity can differ among different biotas, scales and diversity facets [23]. Thus,
78 decomposition of biodiversity into different dimensions may allow the identification of
79 the main aspects of communities that are affected by forest conversion and
80 fragmentation [24]. Therefore, in the abovementioned examples, habitat loss and
81 fragmentation can lead to contrasting effects on β -diversity depending on the scale and
82 dimension investigated.

83 Previous studies in the Neotropical region have shown that small mammals are
84 good model organisms for testing the influence of landscape heterogeneity and habitat
85 complexity on community ecology [25–30]. However, studies conducted in a multi-
86 scale approach pointed contrasting scale-effects on small mammal β -diversity. For
87 instance, in an Atlantic Forest fragmented landscape, small mammal β -diversity
88 increased in small and isolated fragments [25], whereas, in Amazonian land-bridge
89 islands, small mammal β -diversity was more strongly related to environmental variation

90 (habitat quality) among sites than to spatial distance, patch scale and landscape scale
91 [31]; further, in this ecoregion, all dimension of β -replacement decreased, while β -
92 richness increased with forest area [32]. In the Brazilian Savanna, spatial configuration
93 of the landscape and the extent, and quality of habitat strongly influence the rate of
94 species turnover [30]. So, there is no consensus of the effects of landscape variation on
95 structuring the Neotropical small mammals β -diversity, clearly demonstrating the need
96 of further studies exploring different community dimensions to better understand the
97 effects of habitat fragmentation on this important group of vertebrates.

98 In this study, we evaluated the response of species richness, Shannon's entropy
99 and Simpson's dominance on T β D (multiplicative partitioning of Hill numbers) [5] to
100 understand the relative importance of rare and dominant species on determining patterns
101 of β -diversity in a highly fragmented landscape. We also investigated which are the
102 main predictors of habitat (local) and landscape (regional) scales affecting the partitions
103 of taxonomic, functional and phylogenetic β -diversity. Dispersal ability and habitat
104 selectivity have been described as the main processes related to change on species
105 composition [28], functional structure [29] and species turnover [30] of small mammal
106 community in highly fragmented landscapes. Considering the relative low dispersal
107 ability of small mammals [33–35], and the effect of habitat and landscape scale on
108 structuring small mammal composition in Neotropical region [26,28,30,31], we would
109 expect a positive effect of space, habitat and landscape quality on influencing all
110 partitions and dimensions of β -diversity.

111

112 **Materials and Methods**

113 **Study area**

114 The study was conducted in southern Goiás State, central Brazil (18°25' – 18°43' S,
115 50°48' – 50°22' [28]), a highly fragmented landscape with about 13% of forest cover
116 (<https://mapbiomas.org/>), dominated by semi-deciduous forest connected to riparian
117 forest in a transitional region between Atlantic Forest and Cerrado ecoregion [36]. The
118 climate is Tropical semi-humid - Aw (Köppen) with markedly dry season (April to
119 September) and wet season (October to March), and mean annual temperature and mean
120 annual rainfall around 23 °C and 1600-1900 mm, respectively [37].

121

122 **Sampling design**

123 The sampling was carried out between January and December 2015. We captured small
124 mammals, and quantified the vegetation structure and food resources in 24 trapping
125 grids, distant 0.5 to 1 km within the same patch. Each trapping grid was composed of 20
126 trap stations, representing an area of 45 x 60 m (see, [28] for details about trapping
127 grids). For landscape characterization, we estimated landscape metrics in 13 buffers of 1
128 km radius from the edge of sampled forest patches. The average forest patch size was
129 84.1 ha, with the smallest patch with 39.5 ha and the largest one with 142 ha. The
130 average Euclidean distance among them was 22,588 m, being the closest distant 389 m
131 and the farthest 51,978 m.

132

133 **Small mammal surveys**

134 We captured small mammals using live traps (wire-cage traps and Sherman traps) and
135 pitfall traps. We set Sherman and wire-cage traps in 16 trap-stations arranged in four
136 linear transects, with 15-m intervals between the nearest trap stations. Each trap-station
137 was composed by one wire-cage and one Sherman trap disposed on ground and
138 understory (1.5 to 2 m height), alternatively. Pitfall traps was arranged in a
139 perpendicular transect distant 15 m of each live trapping-grid, composed by four
140 buckets (30 liters) connected by a fence of 0.8 m height (see, [28] for methodological
141 detail). We made the captures under the collection license SISBIO n° 46985-1 and in
142 accordance with guidelines provided by the American Society of Mammalogists [38].

143

144 **Habitat and landscape characterization**

145 We used 23 variables to describe habitat and landscape characterization (S1 Data). For
146 habitat characterization, we measured six variables related to vegetation structure
147 (numbers of trees, shrubs, lianas, fallen logs, canopy cover and litter cover) and two
148 variables that depict food resource availability (arthropods and fruits and seeds
149 composition) in 10 selected trap stations of each trapping grid. We reduced the
150 dimensionality of food resource availability using a Principal Coordinates Analysis
151 (PCoA) separately for the matrix of arthropods and fruits-seeds resources. We
152 associated the both matrices with the “horn” dissimilarity index, the one that presented
153 higher variance recovery in relation to the original distances. As for the patch scale, we
154 used four variables (i.e., forest area, core area, perimeter and NDVI), whereas for
155 landscape scale, we used nine variables (i.e., mean isolation, water distance, shannon
156 diversity, shape, mean perimeter area, core area, index core area, total edge and

157 connectivity). The attributes related to patch and landscape scales were obtained via
158 satellite images (methodological details can be found in [28]).

159

160 **Functional traits and phylogeny building**

161 We selected four functional traits associated with tolerance to habitat disturbance: 1)
162 habitat use [nominal trait: generalist or forest specialist], 2) tail length [quantitative trait
163 in mm: arboreal species tend to be long tailed], 3) understory use [quantitative trait in
164 %: based on the percentage of capture in the understory]; and trophic guild: 4) diet
165 [multi-choice: insectivore, frugivore, granivore and omnivore, according to Annotated
166 Checklist of Brazilian Mammals [41] (see, [29] for functional traits interpretation
167 details). Traits were measured in the field from captured specimens or obtained from the
168 literature [26,39–42].

169 We derived a phylogeny for our data set using the VertLife.org phylogeny subset
170 on-line tool. We used as backbone the "Mammal's birth-death node-dated completed
171 trees (all 5911 species, set of 10k trees)" tree. Despite the criticisms regarding the use of
172 synthesis-based phylogenies in evolutionary community studies, mostly because the
173 relative low resolution and higher number of polytomies [43,44] demonstrated that this
174 method of generating phylogenetic trees is sufficiently robust for community
175 phylogenetic analysis.

176

177 **Data analysis**

178 We initially tested for multicollinearity among all the 23 predictor variables described
179 above using the Variance Inflation Factor (VIF) approach. For this, we used a stepwise

180 procedure, where all data set was tested for collinearity, and when a variable showed
181 VIF value above the threshold of 10, it was excluded and the procedure repeated with
182 remaining variables until no variable was excluded. After such procedure, a total of 15
183 variables remained to be used as predictors in our models (S1 Table).

184 We used various distance-based metrics at the taxonomic, functional and
185 phylogenetic dimensions to test for variation of β -diversity along the predictor variables
186 selected above. For the taxonomic dimension, we partition the diversity of the
187 metacommunity into β -components weighting different orders of diversity: species
188 richness [$q = 0$], Shannon's diversity [$q = 1$] and Simpson's dominance [$q = 2$] (Hill
189 numbers, [5-7]). For each Hill number, we did such partition for each pair of grids; thus,
190 we estimate the β -diversity variation among all possible pairs of grids to generate a
191 distance-based triangular matrix of β -diversity.

192 As for the functional dimension, we associated each pair of species by the eight
193 continuous traits using the "Gower" distance. We then used this distance-based
194 triangular matrix to estimate the Rao's quadratic entropy [45], a measure of diversity in
195 ecological communities accounting for species differences (functional or phylogenetic).
196 We estimate two metrics of F β D: D_{kl}, which is the pairwise functional distance, and H,
197 which is the D_{kl} standardized to account for within-community diversity. Both metrics
198 return distance-based triangular matrix of F β D among pair of grids. For the
199 phylogenetic dimension, we used the phylogenetic relationship of the captured species
200 of small mammals to calculated the mean phylogenetic distance among all pairwise
201 combinations of species co-occurring in a sample (MPD), which is a basal measure of
202 the phylogenetic relatedness, and phylogenetic distance between each species and its
203 nearest neighbor on the phylogenetic tree (MNTD), which is can be interpreted as a
204 terminal metric of the phylogenetic relatedness of co-occurring species [46,47].

205 To test the association between each of the explanatory variables with the
206 different dimensions of β -diversity, we used Mantel tests with 9999 permutations. For
207 this, we used each of the β -diversity distance based on the triangular matrix as a
208 response matrix, and a Euclidean distance-based on a matrix associating each sample
209 unit by each predictor as a predictor matrix. We have also used a triangular matrix based
210 on the Euclidean distance among grids to test for spatial autocorrelation. Moreover,
211 given that our dataset is composed by 13 forest patches, being 12 of them with two
212 grids, for testing the effect of the landscape metrics, we sampled one trapping grid per
213 forest patch, thus reducing the number of sampling units to 13 to avoid pseudo-
214 replication at a landscape scale. In the end, we did a total of 16 mantel tests for each β -
215 diversity dimension described above. Finally, we tested for the spatial autocorrelation of
216 each of the 15 predictor variables, and whenever we found an association between a β -
217 diversity metric and any metric spatial autocorrelated, we did partial mantel tests in
218 order to account for any potential confounding effect between explanatory variables.

219 We did all our analyses and graphics in R version 4.0.5 [48]. For calculating
220 the VIF we used the package "*usdm*" [49]. To calculate the pairwise β -diversity at the
221 taxonomic level, we used the function "*DivPart*" of the package "*entropart*" [50]. To
222 associate our functional matrix based on "Gower" distance, we used the function
223 "*vegdist*", and to perform the Mantel tests, we used the "*mantel*" function, both from the
224 package "*vegan*" [51]. To estimate the Rao's quadratic entropy, we used the function
225 "*raoD*", and to calculate "MPD" and "MNTD" we used the functions "*mpd*" and "*mntd*",
226 respectively, all from the "*picante*" package [52].

227

228 **Results**

229 **Small-mammal diversity**

230 With an effort of 12,096 trap-night, we had 624 captures, resulting in a trap success of
231 5.2%. We captured 408 individuals (mean \pm standard deviation (SD), 16.67 ± 8.76
232 individuals per trapping grid), belonging to 12 small mammal species (4.58 ± 1.50
233 species per trapping grid). The most common species were the arboreal marsupial
234 *Gracilinanus agilis* (124 individuals, 20 trapping grids); the arboreal rodents
235 *Rhipidomys macrurus* (55, 14), *Oecomys bicolor* (52, 16) and *Oecomys catherinae* (27,
236 6); the scansorial marsupials *Didelphis albiventris* (49, 20) and *Marmosa murina* (28,
237 8); and the terrestrial rodent *Calomys expulsus* (55, 13), comprising 96.1% of all
238 individuals captured. The rarest species represented by less than 20 individuals were the
239 terrestrial rodent *Calomys tener* (6 individuals, 4 trapping grid); the scansorial
240 marsupial *Cryptonanus chacoensis* (5, 4); the scansorial rodent *Oligoryzomys*
241 *matogrossae* (2, 2); the terrestrial marsupial *Monodelphis kunsi* (2, 2); and the arboreal
242 marsupial *Caluromys philander* (1, 1).

243

244 **Explanatory variables variation**

245 For habitat characterization – vegetation structure and food resource availability, we
246 found the following amplitude variation: “no. of shrubs” (min = 62, max = 1027), “no.
247 of lianas” (min = 86, max = 418), “no. of fallen logs” (min = 3, max = 58), “canopy
248 cover” (min = 41%, max = 98%) and “litter cover” (min = 85%, max = 99%). We
249 considered the first two PCoA axes obtained from “arthropods” resource matrix

250 (variance recovery, $r^2 = 0.85$), and the first two PCoA axes from the “fruit-seed”
251 resource matrix ($r^2 = 0.87$) to represent “food resource availability” (S2 Table).
252 Landscape characterization was based on patch and landscape metrics, according to
253 following amplitude variation parameters: “forest area of focal patch” (min = 39.6, max
254 = 142.3 ha), “perimeter length of focal patch” (min = 2749, max = 21136 m), “NDVI”
255 (min = 0.2800, max = 0.3370), “patch isolation” (min = 99, max = 4102 m), “water
256 distance” (min = 171.6, max = 1258.4 m) and “total edge of landscape” (min = 6410,
257 max = 60766 m). Average values for all variables patch and landscape variables can be
258 found elsewhere (S2 Table). Within the 15 predictor variables, we have only found
259 evidence that “forest area” was spatially autocorrelated (Mantel test, $r = 0.48$, $p <$
260 0.001). All other variables showed no signal of spatial structure (S3 Table).

261

262 **Functional and phylogenetic variation**

263 The small mammal community represented a range of different ecological traits, seven
264 species were classified as habitat generalist (e.g., marsupials [*C. chacoensis*, *D.*
265 *albiventris*, *G. agilis* and *M. kunsi*] and rodents [*C. expulsus*, *C. tener*, *O.*
266 *mattogrossae*]), and five species were forest specialist (marsupials [*C. philander* and *M.*
267 *murina*] and rodents [*O. bicolor*, *O. catherinae* and *R. macrurus*]). In relation to tail
268 length, the shorter and longer tails were found in the terrestrial *M. kunsi* (36.1 mm) and
269 scansorial *D. albiventris* (297.8 mm) marsupials, respectively. Thus, tail length of
270 marsupials ranged from 36.1 to 297.8 (mean \pm SD, 156 ± 87.8 mm), while the tail
271 length of rodents ranged from 58.6 to 148.2 (96.8 ± 34.3 mm). The use of understory
272 ranged from 0 (*M. kunsi*, *C. expulsus*, *C. tener* and *O. mattogrossae*) to 100% (*C.*
273 *philander*), with little variation within each small mammal group (marsupials: min = 0,

274 max = 100, 52.3 ± 41.7 ; rodents: min = 0, max = 93.1, 42.2 ± 47 frequency). We found
275 no association between tail length and understory use ($r = 0.44$, $df = 10$, $p = 0.15$),
276 showing that these traits are complementary to described use of vertical stratum. For
277 trophic guild, the small mammals captured species were assigned to a diet category
278 representing a combination of feeding guilds, such as: frugivore-omnivore (*C. philander*
279 and *D. albiventris*) and insectivore-omnivore (*C. chacoensis*, *G. agilis*, *M. murina* and
280 *M. kungsi*); while rodents were classified as: frugivore-granivore (*C. expulsus*, *C. tener*
281 and *O. mottogrossae*) and frugivore-seed predator (*O. bicolor*, *O. catherinae* and *R.*
282 *macrurus*). Categories were based on Paglia et al. [41].

283 The marsupial species captured in our study belong to the family Didelphidae,
284 and are distributed into two subfamilies: Caluromyinae (i.e., *C. philander*) and
285 Didelphinae that can be sub-divided in three tribes: Marmosini (*M. murina* and *M.*
286 *kungsi*), Didelphini (*D. albiventris*) and Thylamyini (*C. chacoensis* and *G. agilis*). The
287 six rodent species comprised the suborder Myomorpha, family Cricetidae, subfamily
288 Sigmodontinae, belonging to three tribes: Oryzomyini (*O. bicolor*, *O. catherinae* and *O.*
289 *mottogrossae*), Phyllotini (*C. expulsus* and *C. tener*) and Thomasomyini (*R. macrurus*).
290 The phylogenetic and functional relationships of the captured small mammal
291 community can be found in Fig 1.

292

293 **Taxonomic β -diversity**

294 The comparison of T β D variation with our predictor variables showed consistent results
295 when weighting the species richness ($q = 0$) and Shannon entropy ($q = 1$). We found
296 evidence of geographical distance ($q = 0$: $r = 0.38$, $p = 0.008$ [13 sample units]; $q = 0$: r

297 = 0.32, $p = 0.001$ [24 sample units]; $q = 1$: $r = 0.27$, $p = 0.047$ [13 sample units]; $q = 1$: r
298 = 0.34, $p = 0.001$ [24 sample units]; Fig 2a and b) on the patterns of β -diversity (Table
299 1). We have not found any other association with else predictor variables for these β -
300 diversity metrics. For the β -diversity weighting the dominant species ($q = 2$), we found
301 that geographical distance ($r = 0.27$, $p = 0.042$ [13 sample units]; $r = 0.26$, $p = 0.004$ [24
302 sample units]; Table 1, Fig 2c), “no. of fallen logs” ($r = 0.22$, $p = 0.014$; Table 1; Fig
303 2d) and “canopy cover” ($r = 0.19$, $p = 0.038$; Table 1, Fig 2e) were important predictors
304 on determining the patterns of β -diversity turnover. Despite occurring all over the
305 gradient, higher fallen logs frequency seems to determine the higher incidence of *C.*
306 *tener*, *M. murina* and *R. macrurus*, and lower fallen logs frequency appears to
307 associated to *G. agilis* and *C. philander* (S1 Fig). As for the canopy cover, most of the
308 species were relatively abundant along the entire gradient, but some species like *M.*
309 *kunsi*, *O. mattogrossae* and *C. philander* were exclusively found in grids with higher
310 canopy cover, and *C. expulsus* was more frequently capture in low canopy cover sites
311 (S2 Fig).

312

313 **Functional and phylogenetic β -diversity**

314 The functional turnover represented by D_{kl} was positively associated with “no. of fallen
315 logs”, “canopy cover” and “NDVI” ($r = 0.15$, $p = 0.030$; $r = 0.18$, $p = 0.004$; $r = 0.25$, p
316 = 0.018, respectively; Table 1, Fig 3a-c). In the other hand, the standardized H was
317 related only to geographical distance ($r = 0.36$, $p = 0.013$; Table 1, Fig 3d). Higher
318 values of D_{kl} and H were associated with species like *O. mattogrossae*, *D. albiventris*,
319 *C. chacoensis* and *O. bicolor*; species with a wide range of variation in their traits

320 related to use of habitat, tail length, and diet, which have determined such high values
321 of functional diversity variation (S3 Fig).

322 The P β D represented by MPD showed a positive association with geographical
323 distance and “forest area” ($r = 0.36$, $p = 0.006$ [13 sample units]; $r = 0.34$, $p = 0.001$ [24
324 sample units]; $r = 0.42$, $p = 0.017$; Table 1, Fig 4a and b). The effect of “forest area” is
325 consistently significant even when accounting for the variability captured by the
326 geographical disposition of the grids (Partial mantel, $r = 0.31$, $p = 0.04$). The MNTD
327 showed significant associations with geographical distance and “canopy cover” ($r =$
328 0.51 , $p = 0.007$ [13 sample units]; $r = 0.46$, $p = 0.001$ [24 sample units]; $r = 0.32$, $p =$
329 0.030 ; Table 1, Fig 4c and d). Marsupials, Marmosini tribe (*M. murina* and *M. kunsii*)
330 and arboreal rodents, tribes Oryzomyini (*O. bicolor*) and Thomasomyini (*R. macrurus*)
331 were more frequent in habitats with high “canopy cover” values (S2 Fig).

332

333 **Discussion**

334 **Overview**

335 Our findings revealed that *i*) small mammal communities sampled in this highly
336 fragmented landscape Neotropical region were dominated by commonly found
337 marsupials and rodent’s species with arboreal-scansorial habits. *ii*) In spite of being
338 highly fragmented, our landscape presented a wide variation of habitat quality, mostly
339 driven by vegetation structure, food resource and landscape attributes, which harbor
340 functionally and phylogenetically diverse small mammal communities in central Brazil.
341 *iii*) Geographical distance was the main variable correlated to all partitions and all

342 dimensions of β -diversity. Habitat quality gradient was an important predictor for T β D
343 (partition of dominant species), and F β D and P β D. We discuss below such findings in
344 the light of dispersal limitation and environmental filters on driving the patterns of β -
345 diversity in small mammals of Central Brazil.

346

347 **Taxonomic β -diversity**

348 Geographical distance was positively correlated with all partitions of T β D,
349 corroborating our initial hypothesis. Marsupials and small rodents have a low dispersal
350 ability [33,35,51,52] that limit the continuous replacement of small mammal species
351 between distant localities. Further, small mammal communities in the Cerrado domain
352 have been discussed elsewhere to be mainly driven by dispersal limitation and habitat
353 selectivity [28,30]. Geographical distance also has been the most important predictor of
354 small mammal dissimilarity in Atlantic Forest [52]. This finding can be explained by
355 the idea that fragmented landscapes are hyper-dynamically influenced by environmental
356 heterogeneity [12]. Small mammals are able to disperse between relatively closer
357 fragments (\sim 485 m in average, according to [55]), but homing behavior can be much
358 higher for larger species like *Philander frenatus*, which crossed an area of 1050 m of
359 fragmented landscape in the Atlantic Forest [56]. In our study, although the landscape is
360 mainly composed by homogeneous semideciduous forest fragments, strong
361 heterogeneity at small scales can be found between forest patches (e.g., vegetation
362 structure). Such variability may reflect different levels of habitat quality, which
363 certainly influence the potential source pools and species establishment for each patch
364 with different degrees of isolation.

365 When weighting abundant species ($q = 2$ Hill number), T β D was also positively
366 associated to habitat quality (e.g., fallen logs and canopy cover). We captured an
367 expressive number of individuals in such highly fragmented landscape of central Brazil,
368 within these only *C. philander*, *M. kunsii* and *O. mattogrossae* were rarely recorded in
369 our study (1 to 2 individuals). On the other hand, 96% of the captured individuals -
370 seven of the twelve captured species - occurred in 6 to 20 trapping grids. This finding
371 may be caused by the variation in vegetation structure between different sampling sites,
372 which by consequence determine abundance patterns for the most common species.
373 Thus, the higher values of T β D based on the abundance of species of small mammals
374 can be resulted from the higher variability in small mammal community structure along
375 this habitat quality gradient. In the Cerrado domain, the abundance (not richness) of
376 small mammals is known to be correlated with different types of vegetation cover (e.g.,
377 herbaceous, shrub, and tree density) [57], a variable that is commonly associated with
378 habitat heterogeneity and complexity [58].

379

380 **Functional and phylogenetic β -Diversity**

381 In overall terms, the small mammals communities sampled in our study is relatively
382 species poor when compared to other communities of the same group in Central Brazil
383 [59], a pattern that seems to related to the elevated habitat loss in the region. Large
384 bodied rodents that are specialists in forested habitats (e.g., tribe Oryzomyini [*Hylaemys*
385 *megacephalus*], Family Echimyidae, Eumysopinae [*Proechimys longicaudatus* and *P.*
386 *roberti*]) generally represent the first functional group and respective phylogenetic
387 lineages to disappear in highly fragmented landscapes [25,60]. Such group is intimately
388 associated with continuous forests and landscapes with high percentual of vegetation

389 cover [25,27,39,60,61]. In the other hand, species of marsupials (e.g., *G. agilis* e *C.*
390 *chacoensis*) and rodents (e.g., *C. expulsus* e *C. tener*) that have a broad ecological niche
391 and are able to use both forested and open field environments, as present an
392 opportunistic feeding habitat [29,60], commonly represent the species that are capable
393 to be successful even in such disturbed environments. Small sized rodent species that
394 use the understory (e.g., *O. bicolor* e *R. macrurus*) seems also to be weakly affected by
395 habitat fragmentation in the region, perhaps the smaller scale of niche requirements of
396 these species protected them of the negative effects of habitat fragmentation [29].
397 However, despite high co-occurrence of such resistant species between forest fragments
398 in the region, variation in abundance patterns are common for these species, which may
399 be related to different niche requirements and responses to habitat modification [29].

400 Despite the relatively modest phylogenetic and functional variation of our
401 sampled small mammals' communities, we found a turnover for these community
402 dimensions in relation to geographical distance and habitat quality gradient (i.e., no.
403 fallen logs and canopy cover). In the Amazonian habitat, F β D and P β D of bat
404 communities were highest between continuous forest and *campinarana*, two highly
405 contrasting environments, and these patterns in β -diversity were associated with
406 functional richness and lineage richness differences, respectively [22]. An study with
407 bird and ant assemblages, in Atlantic Forest and Pampas Grassland showed that land
408 uses and biomes seems to promote assemblage differentiation in traits and lineages that
409 occurred in anthropogenic habitats, further in this landscape both animal groups were
410 similarly sensitive to changing in vegetation structure [63]. Therefore, habitat quality
411 seems to be an important driver of functional and phylogenetic turnover in biological
412 communities in the Neotropics independent of the biological group or sampled region.
413 Nevertheless, understanding what are the most important traits and functional lineages

414 that readily respond to habitat disturbance, as what are the most resilient ones that
415 persist in disturbed fragments, are of utmost importance for providing information for
416 conservation initiatives.

417 Little is known about the dispersibility of small mammals among forest patches
418 in the Neotropics [55]. Despite reasonable to expect, a positive relation between body
419 size and dispersiveness is not always the rule for this group of mammals. For instance,
420 the mid-bodied size nocturnal marsupial *P. frenatus* (400-600 g) has a relatively small
421 living area (2.8 ha). Thus, even being a larger species for a small-mammal, the apparent
422 inability of this species to occupy different types of habitats (e.g. less forested patches
423 or open fields), may limit its dispersion to equivalent nearby fragments, letting this
424 species susceptible to local extinctions [64], which may similarly be the case for other
425 large bodied terrestrial small rodents that was expected to be reported in our study, but
426 were not captured [e.g. *Cerradomys scotti*, *C. maracajuensis*, *C. marinhui*, *C.*
427 *subflavus*, *P. longicaudatus*, *P. roberti*]. The capacity of using the landscape matrix as
428 a secondary habitat, confers more flexibility to overcome the negative effects of habitat
429 fragmentation [65,66]. Therefore, the prevalence of mostly generalist's species that can
430 occupy different portions of the landscape found here may explain the low F β D e P β D
431 in the sampling region.

432

433 **Conclusion**

434 To the best of our knowledge, this is the first study that shows the effect of geographical
435 distance, habitat and landscape variation on all partitions and dimensions of small
436 mammals' β -diversity. Considering that we have a depleted small mammal community

437 due to high habitat loss in central Brazil, we conclude that only abundance-weighted β -
438 diversity values responded to the predictors of habitat quality. In this sense, a
439 homogeneous environment results in poor communities, where abundance was more
440 important than richness, therefore, studies that seek to investigate the effect of habitat
441 loss and fragmentation on biodiversity need to consider species abundance and not just
442 species richness. Abundance was also a more important attribute than richness in anuran
443 assemblages in Pantanal, a region naturally disturbed by floods in South America, since
444 most species co-occurred in all sampled ponds but varied in their abundance [67]. Thus,
445 we summarize that taxonomic, functional and phylogenetic replacement of the small
446 mammal communities in the fragmented landscape of central Brazil is determined by
447 dispersal limitation and habitat selection, driven by species-specific responses in the
448 communities' arrangements.

449

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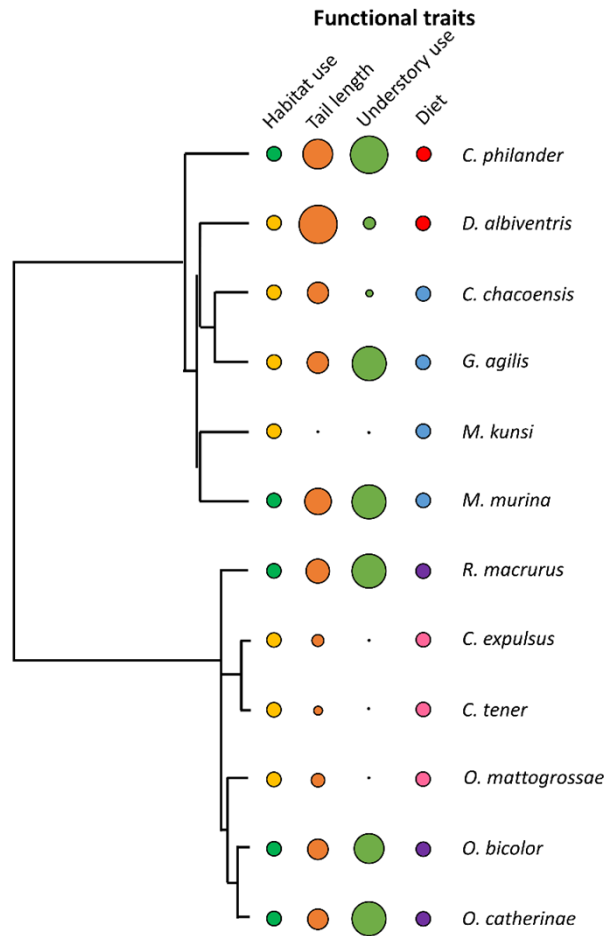
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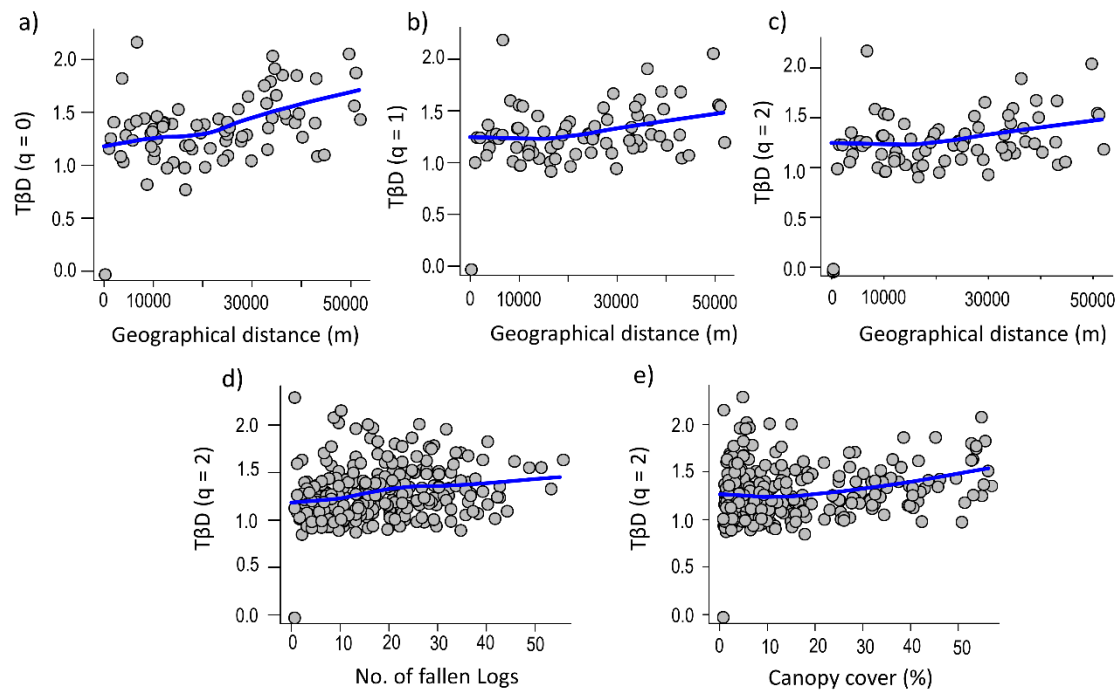
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644 Figures.



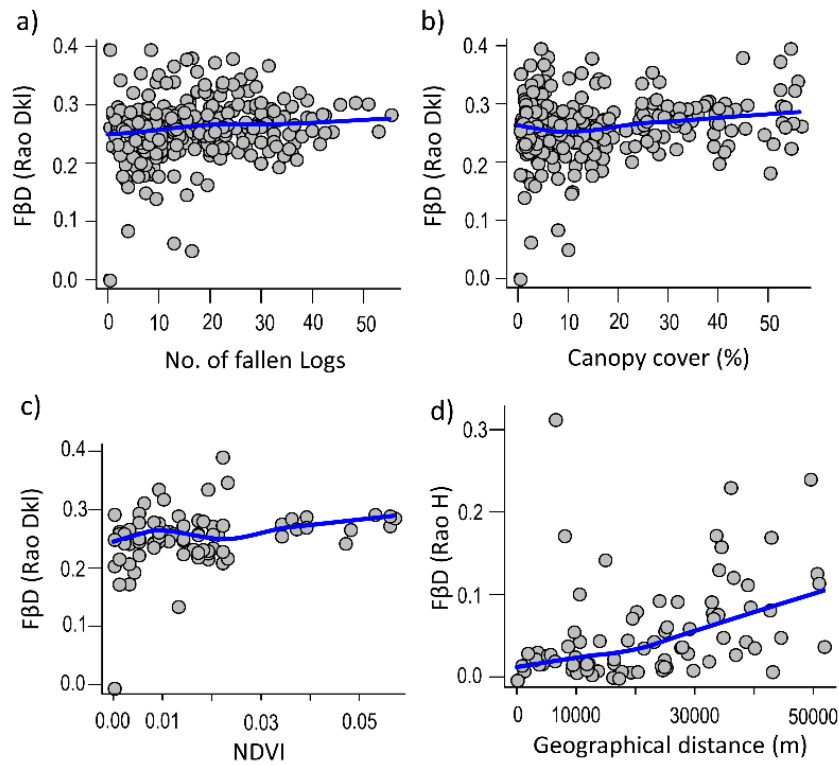
645

646 **Fig 1: Phylogenetic hypothesis derived from the “VertLife.org phylogeny subset**
 647 **on-line tool”**, using as backbone the "Mammal’s birth-death node-dated completed
 648 trees [all 5911 species, set of 10k trees]" and the functional traits used in our study:
 649 habitat use [nominal trait: generalist [orange circle] or forest specialist [green circle]],
 650 tail length [quantitative trait ranging from 31.6 to 297.8 mm], use of vertical strata
 651 [quantitative trait ranging from 0 to 100% and diet [multi-choice: frugivore-omnivore
 652 [red circle], insectivore-omnivore [blue circle], frugivore-granivore [pink circle] and
 653 frugivore-seed predator [purple circle]], based on relative capture success in traps set in
 654 the understory] [see, Hannibal et al. 2020 for functional traits interpretation details].



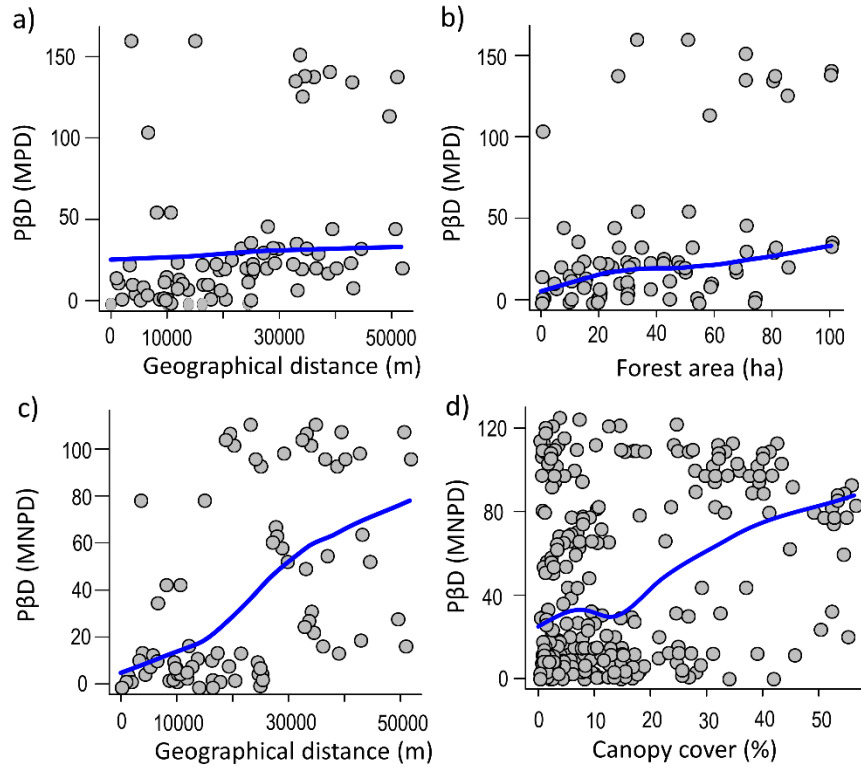
655

656 **Fig 2. Correlation between small mammal taxonomic β -diversity and geographical**
657 **distance [a-c], no. of fallen logs [d] and canopy cover [e] in a highly fragmented**
658 **landscape in central Brazil.** The Hill numbers associated represent rare [$q = 0$],
659 common [$q = 1$] and abundant [$q = 2$] species, respectively. The tendency line is fitted
660 using Locally Estimated Scatterplot Smoothing [LOESS].



661

662 **Fig 3. Correlation between small mammal functional β -diversity and no. of fallen**
663 **logs [a], canopy cover [b], NDVI [c] and geographical distance [e] in a highly**
664 **fragmented landscape in central Brazil. The tendency line is fitted using Locally**
665 **Estimated Scatterplot Smoothing [LOESS].**



666

667 **Fig 4. Correlation between small mammal phylogenetic β -diversity and**
668 **geographical distance [a and c], forest area [b] and canopy cover [d] in a highly**
669 **fragmented landscape in central Brazil. The tendency line is fitted using Locally**
670 **Estimated Scatterplot Smoothing [LOESS].**

671 Table.

672 **Table 1. Pearson correlation between geographical distance, habitat**
 673 **characterization [vegetation structure and food resource availability] and**
 674 **landscape characterization [patch and landscape metrics] with taxonomic,**
 675 **functional and phylogenetic small mammal β -diversity. The significance of the**
 676 **relation was tested via Mantel-tests.**

	Taxonomic [Hill numbers]			Functional Rao		Phylogenetic	
	q = 0	q = 1	q = 2	Dkl	H	MPD	MNTD
Geographical distance [13 sample units]	0.38*	0.27*	0.27*	0.19	0.36*	0.36*	0.51*
Geographical distance [24 sample units]	0.32**	0.34**	0.26**	0.19*	0.36**	0.34**	0.46**
Vegetation structure							
No. shrubs	-0.15	-0.08	-0.02	0.07	0.01	-0.06	-0.05
No. lianas	-0.06	-0.05	-0.02	-0.02	-0.12	0.00	-0.12
No. fallen logs	-0.08	0.13	0.22*	0.15*	0.05	-0.08	0.02
Canopy cover	0.01	0.15	0.19*	0.18**	0.15	-0.06	0.32*
Litter cover	-0.06	-0.02	-0.01	0.01	-0.03	0.06	0.17
Food resource availability							
PCoA Arthro1	-0.05	-0.04	-0.03	-0.04	-0.02	0	0.12
PCoA Arthro2	-0.04	-0.09	-0.06	0.03	-0.08	-0.07	-0.13
PCoA Fruit1	-0.03	0.00	-0.02	-0.04	-0.05	-0.04	-0.07
Patch metrics							
Forest area	0.17	0.06	0.09	-0.14	0.23	0.42*	0.16
Perimeter	0.08	0.09	0.05	0.04	-0.13	-0.13	-0.11
NDVI	-0.06	0.13	0.13	0.25*	0.18	-0.00	0.39

Landscape metrics

Isolation	-0.22	-0.25	-0.25	-0.16	-0.14	-0.15	-0.09
Water distance	-0.19	-0.29	-0.29	-0.13	-0.19	-0.17	-0.10
Total edge	0.05	0.01	0.01	0.07	-0.07	-0.10	-0.12
Connectivity	0.05	0.02	0.02	-0.05	-0.02	0.01	0.04

677 Significant p-value = *<0.05, **<0.01

678

679 **Supporting Information**

680 **S1 Table. VIFs of the remained variables after stepwise procedure, based on 23**
681 **variables that characterized habitat and landscape scales.**

Variables	VIF
No. shrubs	3.196
No. lianas	2.673
No. fallen logs	3.750
Canopy cover	2.594
Litter cover	2.741
PCoA Arthro1: Arthropods resources according to axis 1 of PCoA	2.464
PCoA Arthro2: Arthropods resources according to axis 2 of PCoA	3.561
PCoA Fruit-Seed1: Fruit-seed resources according to axis 1 of PCoA	2.620
Forest area of patch [ha]	3.184
Perimeter of focal patch [m]	8.916
NDVI	3.557
Isolation: mean isolation of the five nearest patches [m]	1.957
Water distance: distance to water course [m]	3.780
Total edge in the landscape [m]	5.172
Connectivity [connected <i>versus</i> isolated patch, considering riparian forest]	4.424

682

683

684 **S2 Table. Habitat, patch and landscape metrics that characterization fragmented**
 685 **landscape studied.**

Parameter	Type of parameter	Description	Range	Mean ± SD
No. shrubs	Vegetation structure	Number of shrubs in trapping-grid	62-1027	228.60±193.01
No. lianas	Vegetation structure	Number of lianas in trapping-grid	86-418	224.27±80.04
No. fallen logs	Vegetation structure	Number of fallen logs in trapping-grid	3-58	33.63±14.41
Canopy cover	Vegetation structure	Canopy cover in trapping-grid	41-98%	85.92±14.70
Litter cover	Vegetation structure	Litter cover in trapping-grid	85-99%	95.55±3.32
PCoA Arthro1	Food resource	PCoA axis 1 of arthropods in trapping-grid	-	-
PCoA Arthro2	Food resource	PCoA axis 2 of arthropods in trapping-grid	-	-
PCoA Fruit-Seed1	Food resource	PCoA axis 1 of fruit and seed in trapping-grid	-	-
PCoA Fruit-Seed2	Food resource	PCoA axis 2 of fruit and seed in trapping-grid	-	-
Forest area	Patch metric	Total area of sampled patch [ha]	39.6-142.3	81.52±36.23
Perimeter	Patch metric	Perimeter of sampled patch [m]	2749-21136	6189.2±4733.7
NDVI	Patch metric	Normalized difference vegetation index	0.28-0.33	0.32 ±0.01

Isolation	Landscape	Mean distance of the 4	99-4102	1603.1±1311.5
	metric	nearest patches [m]		
Water	Landscape	Distance of trapping grid to	171.6-1258.4	628.7±344.7
distance	metric	water course [m]		
Total edge	Landscape	Total edge measured in the	6410-60766	23679.9±15560.5
	metric	landscape [m]		

686

687

688 **S3 Table. Correlation between predictors variables and spatial distribution of the**
689 **sampled forest patches.**

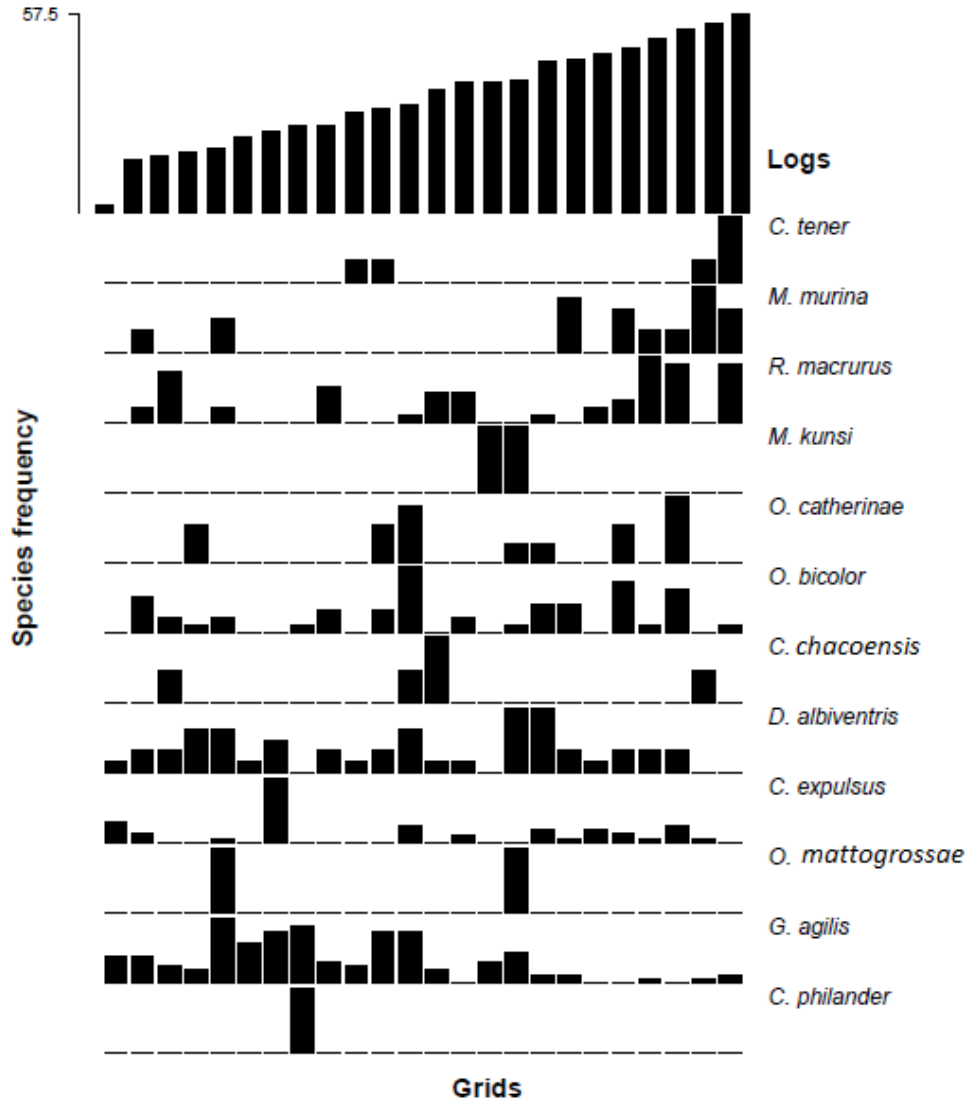
Group	Method	Statistic	N	P.value
No. shrubs	Pearson	0.0666	276	0.315
No. lianas	Pearson	-0.0088	276	0.509
No. fallen logs	Pearson	0.0312	276	0.317
Canopy cover	Pearson	0.0759	276	0.205
Litter cover	Pearson	0.0167	276	0.401
PCoA Arthro1	Pearson	0.0229	276	0.292
PCoA Arthro2	Pearson	-0.1020	276	0.837
PCoA Fruit-Seed1	Pearson	-0.0567	276	0.752
Forest area	Pearson	0.4495	78	0.007*
Perimeter	Pearson	-0.1249	78	0.745
NDVI	Pearson	-0.0000	78	0.458
Isolation	Pearson	-0.0210	78	0.502
Water distance	Pearson	-0.0370	78	0.572
Total edge	Pearson	-0.0896	78	0.721
Connectivity	Pearson	-0.0836	78	0.831

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692 Supporting Information:

693 Figures:



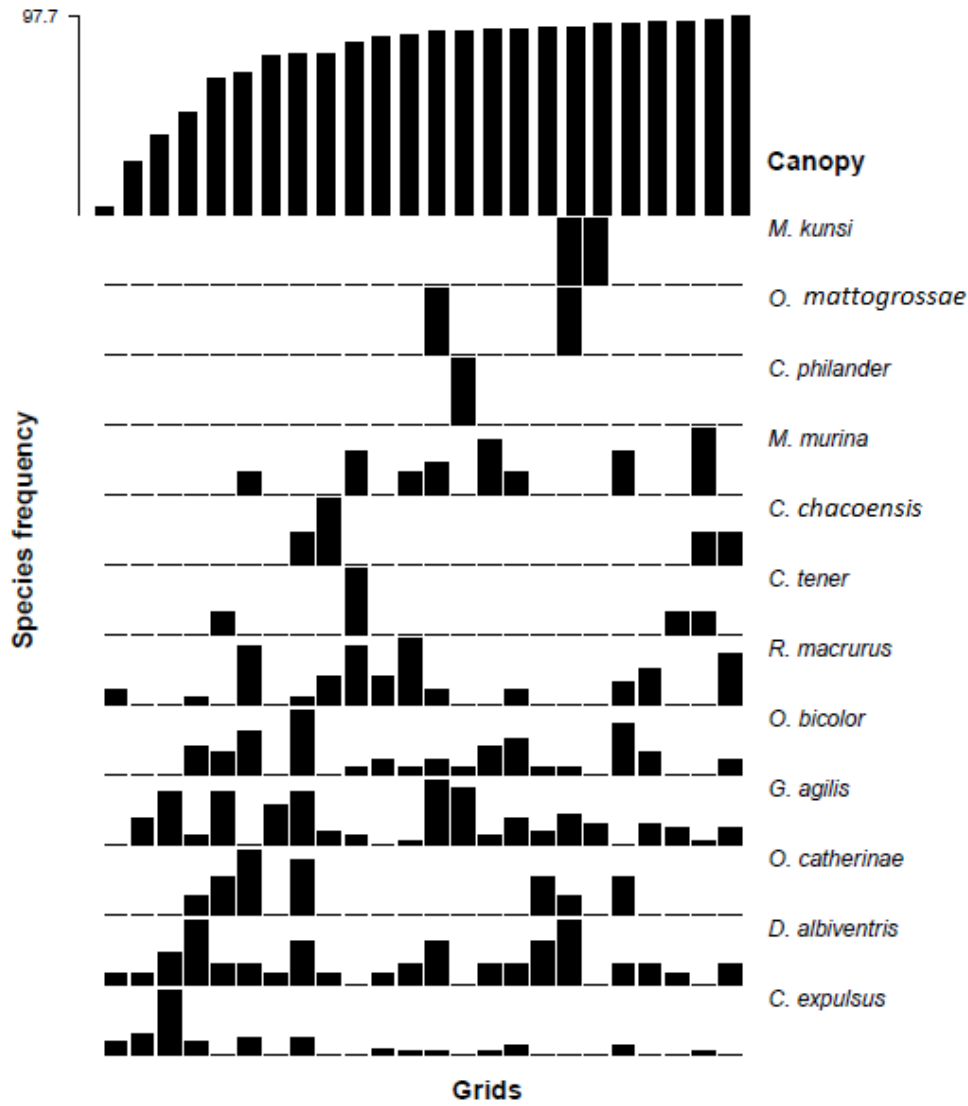
694

695 **S1 Fig. Direct ordination of small mammal species' frequency associated with no.**

696 **of fallen logs in fragmented landscape studied.**

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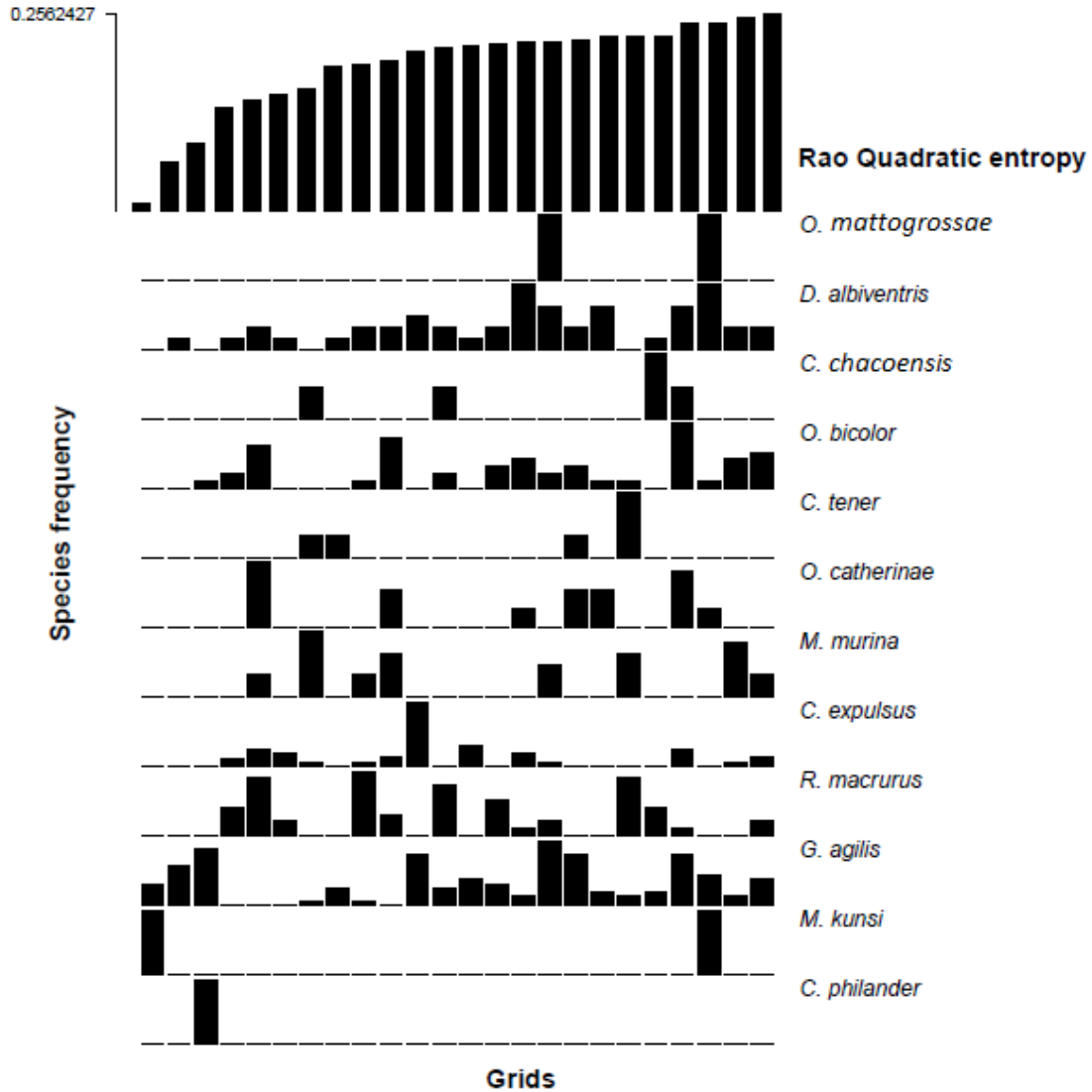


699

700 **S2 Fig. Direct ordination of small mammal species' frequency associated with**
701 **canopy cover in fragmented landscape studied.**

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705 **S3 Fig. Direct ordination of small mammal species' frequency associated with Rao**

706 **Quadratic Entropy in fragmented landscape studied.**

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