

27

Abstract

28 One of the basics problems in ecology is to understand the factors that shape the spatial
29 patterns in the distribution of the species and the coexistence of close relatives species.
30 Among the most critical factors governing the distributions and the coexistence of
31 species are the spatiotemporal changes occurring in the microhabitat heterogeneity.
32 Here, we assessed the heterogeneity of microhabitats and how they affect the spatial
33 segregation of two species of small mammals (*i. e.*, *Peromyscus difficilis* and *P.*
34 *melanotis*), which coexist in a temperate, mixed forest. We evaluated the microhabitat
35 heterogeneity through multivariate statistics, using onto 23 habitat variables describing
36 horizontal-vertical habitat structure along pluvial seasons. To detect specific
37 microdistribution changes and habitat preferences by two species of small mammals, we
38 used second-order spatial statistics and general linear models. According to their
39 respective morphology and locomotive adaptations, the middle sized, midscansorial *P.*
40 *difficilis* was resident all year long and preferred microhabitats with a high log ground
41 cover, while the opportunistic, small sized, cursorial *P. melanotis* changed its
42 occupancy area, depending on the density of herbaceous and woody plants cover. Under
43 the more benign microhabitat conditions of the rainy season (denser plant coverage,
44 milder temperature), both species showed closer microdistribution patterns; while these
45 became repulsive at the less favorable conditions of the dry season (scarcer plant cover,
46 colder temperature). Thus, we could confirm that seasonal changes of microhabitat
47 heterogeneity promoted *Peromyscus* coexistence, through dispersion patterns reflecting
48 partition of microhabitat resources.

49

50 Keywords: Microhabitat selection, Use of space, Small mammals, Dispersion, Resource
51 partition.

52

53

Introduction

54

55 Spatiotemporal habitat heterogeneity has a substantial impact on coexistence among
56 species since they become spatially segregated, according to niche preferences such as
57 resource requirements (Valladares *et al.* 2015). Model simulations reveal the potentially
58 important role of spatial heterogeneity and its complex and delicate interplay with
59 dispersal in mediating long-term outcomes of species coexistence (Schreiber and
60 Killingback 2013; Valladares *et al.* 2015). For example, an increase in the number of
61 habitat types, resources, and structural complexity should increase the available niche
62 space and thus allow more species to coexist (Currie 1991). Equally crucial for the
63 maintenance of coexistence is the heterogeneity in time, with an influence on natural
64 communities also variable depending upon the temporal scales (Valladares *et al.* 2015).
65 Temporal fluctuations on habitat structure can stabilize coexistence via storage effect
66 (Chesson 2000), when inter-annual variation in climate or resource availability favors
67 alternatively one group of species over the others (Zavaleta *et al.* 2003). For instance,
68 *Peromyscus* mice have been shown to respond to spatiotemporal habitat heterogeneity
69 regarding species coexistence (M'Closkey and Fieldwick 1975; M'Closkey and Lajoie
70 1975), spatial segregation (Monamy and Fox 1999), and competition (Morris 1984;
71 Seagle 1985).

72 Heterogeneous habitats contain patches of varying size, distribution, resources,
73 environmental conditions, and species composition (Fahrig and Merriam 1994) that
74 vary spatiotemporally, depending on observation scale and habitat type under study
75 (Wiens 2000). It is highly likely that small size species such as small mammals perceive
76 spatial habitat heterogeneity at a fine scale (microhabitat). Therefore, both movement

77 and foraging by these kinds of mammals are affected by habitat heterogeneity (Bowne
78 *et al.* 1999), having different responses among species or demographic groups within
79 them (Dooley and Bowers 1996). Here we focus on whether small mammals are
80 capable of perceiving and to respond to spatiotemporal microhabitat heterogeneity.

81 Small mammals use resources selectively, based on their requirements for
82 growth, survival, and reproduction (Johnson and Gaines 1980). Several studies have
83 quantified variation in resource use in heterogeneous environments either among
84 congeneric and co-family mice species within a community (Kaufman and Kaufman
85 1989 and references therein). Indeed, syntopic related species are especially valuable for
86 studies of spatial and resource partitioning, since they are most likely to be current or
87 past competitors (Kalcounis-Rüppell and Millar 2002). Since habitat use varies
88 spatiotemporally (Haim and Rozenfeld 1993) due to distribution and availability of
89 resources, we expect that such variation also affects the use of resources and
90 relationships among non-closely related species. In this study, the primary objective is
91 to analyze how heterogeneity of microhabitats is structured and change through pluvial
92 seasons in a temperate, mixed forest, and how such changes affect the coexistence of
93 two syntopic species of *Peromyscus* (*i. e.*, *P. difficilis* and *P. melanotis*). Therefore, 1)
94 We assess the presence of the spatiotemporal heterogeneity at a fine scale
95 (microhabitat) according to vertical and horizontal structure indicators. 2) We evaluate
96 the ecological dispersion patterns of two species of *Peromyscus* and is tested if the use
97 of space of the two small mammals is affected by the spatiotemporal changes in
98 microhabitat heterogeneity. 3) We determine what kind of spatial relationships occur
99 between both species, depending on seasonal changes in microhabitats heterogeneity (*i.*
100 *e.*, attraction or positive: sharing of same microhabitats and resources; repulsion or
101 negative: not sharing). Finally, we assessed which specific structural elements of each

102 one of the microhabitats better explain the capture frequency of the two *Peromyscus*
103 species between seasons.

104

105 **Material and methods**

106

107 *Ethics statement*

108

109 Animal capture and handling followed guidelines of the American Society of
110 Mammalogists (Sikes *et al.* 2011). If animals died, corpses were prepared as voucher
111 specimens to house them at the Mammal Collection of the Universidad Autónoma
112 Metropolitana-Iztapalapa (UAMI, Ramírez-Pulido *et al.* 1989). Collecting permit,
113 SEMARNAT-08-049-B, was issued by DGVS, SGPA-09712/13, SEMARNAT, to
114 Alondra Castro-Campillo (ACC).

115

116 *Study area*

117

118 The study area was located in a temperate forest of conifers and broad-leaved trees at
119 Parque Nacional Desierto de Los Leones (PNDL, CONANP 2006), Mexico City, within
120 the Transmexican Neovolcanic Range. Temperature averages 12.6 ± 6 °C from April to
121 July, while it descends to 8.1 ± 2 °C from December to February. Rainfalls occur from
122 late spring throughout summer (May to August), with average precipitation of 235 ± 30
123 mm, though this period can go until mid-fall (October). From winter to early spring
124 (December to March), precipitation average becomes 12 ± 4 mm, introducing a dry and
125 cold climate (PNDL, CONANP 2006). Dominating vegetation by strata includes
126 canopy, *Abies religiosa*, *Pinus hartwegii*, *P. leiophylla*, *P. montezumae*, *Prunus*

127 *serotina*, *Garrya laurifolia*, *Salix paradoxa*, and *Buddleia cordata*; understory shrubs,
128 *Baccharis conferta* and *Senecio spp.*, and herbs, *Acaena elongata*, *Sigesbeckia*
129 *zorullensis*, and *Alchemilla procumbens*; ground level, a rich variety of mosses and
130 fungi.

131

132 *Mice sampling*

133

134 We captured mice along ten months (October 2013- August 2014), including the dry
135 and wet seasons within a 2,475 m² surface plot (Fig. 1) at 2289 m. The plot was gridded
136 (12 vertical lines, A-L; 10 horizontal lines, 1-10) marking intersections each 5 m with
137 buried wood stakes (150x2.5x2.5 cm) to construct a coordinate system for independent
138 sampling stations, where we set 120 Sherman live traps (Tallahassee, FL 32303, USA),
139 baited with oat flakes and vanilla scent (Fig. 1). Traps were set for two continuous nights
140 (2400 trap-nights), shortly before dusk, left open overnight, and checked at next day
141 dawn. To avoid bias in the abundance and use of space of both *Peromyscus* during each
142 sampling session, we used a temporal mark (gentian violet applied in the abdomen of
143 the mice) to identify the captures and recaptures. If we saw signals that the gentian
144 violet was disappearing in the abdomen of the mice, we applied it again. This temporal
145 mark enabled us to count the net frequency of the individuals in each microhabitat. We
146 carried out an initial analysis with the recaptures, and we found the same patterns that
147 we obtained with the first frequency (without recaptures). Thus, for the analyses, we
148 used only the first capture data for each of the 120 sampling stations during all trapping
149 sessions. All the traps were cleaned, and bedding was changed at each trap check event.
150 Also, all the traps were set randomly in each sampling station to avoid bias in frequency

151 quantification due to recurrence behavior or shyness of the mice to the trapping.

152 Coordinates of all trapped mice were recorded and the species and sex determined

153 through visual inspection.

154

155 *Microhabitat features*

156

157 To assess spatiotemporal heterogeneity of microhabitat within the entire plot, we

158 delimited an influence zone (sub-plot, Fig. 1; close-up, Fig. 1), drawing a rectangle of

159 2.5 m² around each sampling station. 23 variables were sampled (Table 1) once in each

160 influence zone in both seasons. The sampling of the entire plot took ten days, we

161 sampled one transect per day, starting at 9 am in the second week of the most

162 represented month of rains (July) and in February for the dry season (PNDL, CONANP

163 2006). These variables have been proved to be components of the vertical and

164 horizontal structure of the microhabitat. Also as factors affecting the distribution of

165 small mammals at fine scales (Morris 1984, 1987; Stapp 1997; Jorgensen 2004,

166 Coppeto *et al.* 2006; Villanueva-Hernández *et al.* 2017). Environmental variables

167 include vegetation coverage at different heights (VC10-100 cm), number of herbaceous

168 forms (FH11-15), and number of woody forms (VF21-25) at five different heights: 10,

169 25, 35, 50, and 100 cm, respectively. Rock coverage (RC), logs coverage which include

170 stumps and fallen trunks (CLO); coverage of organic matter (OM); coverage of bare soil

171 (BS); vegetation species richness (VR); total herbaceous plants (TH); total woody plants

172 (TW) and the number of burrows (BW) also were sampled (Table 1). Overall, these

173 variables provide information about possible refuges for the small mammals against

174 predators, some elements of microhabitat also imply spaces for resting, breeding, for

175 food resources and safe roads to move from one place to another, avoiding predation

176 risk (Jorgensen 2004). Detailed information about ecological meanings for each variable
177 appears in Table 1.

178 We adapted Canfield's (1941) method of Line Intercept (LI) to measure all
179 variables in each pluvial station, for it allows sampling within-plot variation and
180 quantifies changes, both in plant species cover and height over time, by using transects
181 located within a plot. We drew eight graduated transects (cm) from the respective
182 influence zone of each station to cover the 2.5 m² sub-plots (Fig. 1); four 2.5 m transects
183 were cardinally oriented (N, S, E, W), while the other four 3.30 m ones were diagonally
184 oriented (NE, NW, SE, SW). Only plants intercepted by diagonal transects were
185 counted for vegetation species richness, number of life forms at different heights
186 (herbaceous and woody plants), and total herbaceous and woody plants; while all
187 transects were used to measure plant coverage at different heights, as well as coverage
188 of fixed elements (*i. e.*, rocks, logs, bare soil, dead organic matter). We calculated
189 coverage percentage of each variable within the sub-plots with the formula $\sum(Xi) \frac{100}{2400}$,
190 where Xi is centimeters occupied by every plant in each transect, and 2400 equals total
191 longitude (sum of the eight transects). We counted the number of woody and
192 herbaceous plant life forms at different heights and burrows within each influence zone
193 of every sampling station. We took each hole in the ground ca. 8-12 cm of diameter as a
194 potential burrow for both *Peromyscus* (Álvarez-Castañeda 2005; Fernandez *et al.* 2010).

195

196 *Statistical data analysis*

197

198 We standardized all variables and run statistical tests at $p \leq 0.05$. We did not found
199 multicollinearity among the 23 variables which was assessed by examining the Variance

200 Inflation Factor (*i. e.*, all values were in a threshold <6) (Zar 1999). To identify and
201 categorized microhabitat heterogeneity within the grid, we performed two independent
202 Hierarchical Cluster Analysis (HCA) in JMP® (ver. 9, SAS Institute Inc., Cary, NC,
203 1989-2007) for each season. These analyses enabled us to cluster the sample stations
204 with similar characteristics according to the sampled variables for both seasons. We
205 used Ward's method (1963) where the distance between two clusters is the ANOVA'
206 sum of squares between them, added up over all variables. Visual inspection of the
207 dendrogram and no drastic changes in the variance scree plot gave us three general
208 groups of stations for both seasons, which we interpreted as distinct microhabitat types
209 (M1-3). We further statistically validated such microhabitats carrying out independent
210 Discriminant Analyses for both seasons (DA, Addinsoft SARL's XLSTAT 2013; $F =$
211 9.99 dry; $F = 9.64$, rains; Wilk's Lambda = 0.0001 in both) (Fig. A.1). These analyses
212 allow us to know what type of microhabitat corresponded to each sampling station.
213 Thus, we constructed two different maps, assigning to each sampling station a color
214 mark that represented the three different microhabitats for both seasons (M1: red, M2:
215 green, M3: blue) (Fig. 2, Fig. A.1). To create typologies that describe at a fine scale the
216 behavior of each one of the 23 variables within three microhabitats for both seasons, we
217 built a plot whereas "Y" axis comprises of the 23 standardized variables and in the "X"
218 axis corresponds to the three microhabitats constructed with the same 23 variables (Fig.
219 A.1).

220 Due to not all 23 variables did not reveal a normal distribution, we applied two
221 different tests to analyze the distribution changes on each microhabitat variable between
222 the rainy and dry seasons. First, distribution normality was checked for every variable
223 with Kolmogorov-Smirnov tests (Zar 1999). Thus, we used Student's t-parametric tests
224 for variables normally distributed and non-parametric Wilcoxon test for non-normal

225 variables (Table 2). To know whether the number of stations structuring each type of
226 microhabitat changed between seasons (seasonal microhabitat heterogeneity), we used a
227 contingency table and χ^2 test. All these analyses were performed with XLSTAT 13
228 (Addinsoft SARL). To examine the association between changes in spatial
229 heterogeneity of microhabitats and dispersion patterns of *Peromyscus*, along with the
230 entire grid, we conducted a Contingency Tables Analysis. Then, for visualizing
231 associations between the *Peromyscus* and microhabitats, we performed a
232 Correspondence Analysis with the constructed Contingency Tables for both seasons,
233 including the abundance of each species in the three microhabitats (Table A.2).

234

235 *Spatial analysis*

236

237 To map variations in point density captures of small mammals, and to find density
238 gradients across the plot area, we used the Kernel function (PAST, ver. 3.14, Hammer *et al.*
239 *al.* 2001). To test the ecological dispersion patterns of both species within the plot (*i. e.*,
240 clustering or overdispersion) for both seasons, we used a “Nearest Neighbor Analysis”
241 (Clark and Evans, 1954) using the PAST software (ver. 3.14, Hammer *et al.* 2001). We
242 applied the Wrap-around edge effect adjustment which is only appropriate for
243 rectangular domains as our plot sampling (Hammer *et al.* 2001). In general, the
244 “Nearest Neighbor Analysis” compares the mean distance of each main individual from
245 its nearest neighbor of the same species with the mean distance expected for a set of
246 points randomly dispersed at the same density (Vázquez and Álvarez-Castañeda 2011).
247 The ratio of the observed mean distance to the expected distance (R) indicates how the
248 observed distribution deviates from random. Clustered points give $R < 1$, Poisson
249 patterns give $R \sim 1$, while overdispersed points give $R > 1$.

250 To assess whether both species were associated or disassociated, we compared
251 dispersion patterns between the two mice, using Ripley's K bivariate function (Ripley
252 1977), since the method considers all distances among individuals located under a
253 Cartesian scheme (X, Y) in a quadrat plot (Ripley 1976, Dale 1999, Zavala-Hurtado *et*
254 *al.* 2000). We used PASSaGE (*ver.* 2, Rosenberg and Anderson 2011) to carry out
255 Ripley's bivariate K analysis. We used the option to test the associations conditional on
256 current locations hypothesis in PASSaGE. In this test, the point locations remain fixed,
257 and only the types are randomized (the two *Peromyscus*). The number of each type
258 remains fixed, but the association of each type with a specific, fixed location is
259 randomized. In this case, one is not testing whether the points are themselves random or
260 clustered, but rather whether the association of type A with type B (*P. difficilis* vs. *P.*
261 *melanotis*) is what one would expect given the locations of the points as fixed
262 (Rosenberg and Anderson 2011). We assigned coordinates to each sampling stations
263 considering 5 m distance between them. Therefore, because each sampling station had a
264 Cartesian coordinate system, we used as data input each station where we capture mice.
265 Thereby, our null hypothesis involved independence between our two species *P.*
266 *difficilis* and *P. melanotis* (Ripley 1976, Diggle 1983, Dale 1999), since we were
267 interested in whether points of a specific type (*P. difficilis*) were associated, or
268 disassociated, with points of the other specific type (*P. melanotis*). In other words,
269 Ripley's $K_{12}(d)$ allowed us to assess spatial attraction or repulsion between the two
270 species, among the stations of the plot. To evaluate the statistical significance of $K_{12}(d)$,
271 we estimated 95% confidence envelopes (95% CI), using a Monte Carlo procedure,
272 based on 1000 stochastic relocation simulations of the sampling stations in the plot
273 (Upton and Fingleton 1985; Bailey and Gatrell 1995; Zavala-Hurtado *et al.* 2000).
274 When $L(d)$ was positive and took values over the upper limit of the confidence region,

275 we inferred dissociation or repulsion between the *Peromyscus* at the corresponding (d)
276 scale; whereas a significant negative deviation indicated us a pattern of association or
277 attraction between the two mice (Dale 1999). If $L(d)$ remains within the limits of the
278 95% CI for a given value of d , the null hypothesis of independence between the two
279 contrasts cannot be rejected (Dale 1999). The height of the $L(d)$ function (peak height)
280 indicates the intensity of the association or repulsion. Control for edge effect was
281 carried out for analysis by rescaling the counts based overlap with the study boundary
282 setting the options area/volume which has been recommended for quadrats plots
283 (Rosenberg and Anderson 2011).

284

285 *Prediction of microhabitat elements affecting the use of space by each species*

286

287 The next step was to assess which specific environmental variables best explained the
288 frequency of both species within the plot at each season. For this, we performed
289 Generalized Linear Models (GLMs), using JMP® (ver. 9, SAS Institute Inc., 1989-
290 2007, Cary, NC.). First, we conducted a Principal Component Analysis (PCA) on the
291 means of the 23 variables to obtain functions summarizing the most significant variance
292 at each season. Because in both seasons the three first functions summarized a good
293 portion of the variance (38.61 for the dry season and 45.92 for rains), we used these
294 functions to construct the GLMs. Therefore, we assessed different models using the PCs
295 as effect variables to explain the frequency of the individuals of both species for both
296 seasons. Then, to visualize the fit of the model, the predicted values from the GLMs
297 were plotting against the Principal Components of the best model chosen. For each
298 species, the response variable in the models was the capture frequency at each trapping
299 station of the grid, and we assumed a Poisson distribution with a log link function.

300

301

Results

302 *Frequency of captures*

303

304 The total number of individuals captured from both species during the dry season was
305 111, while for the rainy season was 168. For *P. difficilis* the total number of frequency
306 capture in the dry season was 64. For *P. melanotis* during the dry season, we captured 47
307 individuals. On the other hand, during the rainy season, the frequency of capture of *P.*
308 *difficilis* was 87. While the total captures for *P. melanotis* were 81 (Table A.2).

309

310 *The Behavior of 23 variables of microhabitat between seasons*

311

312 When considering the mean value over all stations, 16 out of the 23 environmental
313 variables showed a significant difference between the two seasons (Table 2, Fig. 3, Fig.
314 A.1). The main changes were observed for variables related to herbaceous vegetation,
315 according to plant coverage at different heights, and vegetation species richness (VR).
316 As expected in overall, woody life forms were more stable between seasons (Table 2,
317 Fig. 3, Fig. A.1). Components of microhabitat showing no statistical change between
318 seasons were frequency of herbaceous plants at 10 cm (FH11), the frequency of both 35
319 cm (FW23) and 50 cm (FW24) woody plants, as well as coverage of logs (CLO), rocks
320 (RC), and bare soil (BS). Therefore, space configuration given by these structural
321 features remained stable in both seasons (Fig. 3).

322

323

324

325 *Microhabitat heterogeneity*

326

327 The dendrogram from cluster analysis revealed three different classes of microhabitats
328 (M1, M2, and M3) within the sampling plot in each season (Fig. A.1). M1 included
329 more sampling stations during the dry season, while M2 covered the majority of
330 sampling stations during the rainy season (Fig. 2, Fig. A.1, Table A.1). Indeed, Fisher's
331 exact test of Contingency Tables Analysis revealed significant changes in the number of
332 sampling stations ($p = 0.004$) from dry to rains. The main changes occurred between
333 M1 ($\chi^2 = 2.123, p < 0.05$) and M2 ($\chi^2 = 3.348, p < 0.05$), especially in the latter, since it
334 augmented 24 sampling stations from the dry season to the rainy season (Fig. 2, Table
335 A.1). Conversely, the number of sampling stations remained quite stable in M3 ($\chi^2 =$
336 0.011) throughout the study (Fig. 2, Fig. A.1, Table A.1).

337 Discriminant analyses validated heterogeneity of the three microhabitats (Fig. 2)
338 within and between pluvial seasons. the percentage of variance associated to each
339 discriminant function was clearer during the rainy season (dry season: F1 = 58.67 %, F2
340 = 42.32 %; rainy season: F1 = 72.581 %, F2 = 27.419 %) (Fig. 2, Fig. A.1).

341 Discriminant functions explained variation due to woody plants in the understory in the
342 dry season, while herbaceous vegetation together with decayed matter and logs became
343 more relevant at rains (Table A.3). Wilk's Lambda showed that at least the mean of one
344 microhabitat differed statistically from the others either in the dry and rainy season ($p =$
345 0.0001; $p = 0.0001$, respectively) (Fig. A.1). These results corroborated spatial and
346 temporal heterogeneity drawn from cluster analysis of individual station features in the
347 grid plot. During the dry season, 93.33 % of individual sampling stations remained
348 correctly classified, and 94.17 % of them during the rainy season (Fig. 2).

349

350 *Description of microhabitats within the plot*

351

352 *Microhabitat 1.* M1 (Fig. 2, Fig. A.1) was characterized by low amounts, or absence, of
353 vegetation cover at different heights (VC) and by a low frequency of herbaceous and
354 woody plants (FH and FW, respectively). In contrast, organic matter on the ground
355 (OM) was the most frequent component. This microhabitat was also distinctive for
356 having extensive coverage of logs (CLO) on the ground and for being the microhabitat
357 with the significant presence of burrows (BW).

358 *Microhabitat 2.* M2 (Fig. 2, Fig. A.1) was the largest area covered by herbaceous life
359 forms at different heights; vegetation species richness (VR) and the total number of
360 herbaceous plants (TH) also remained very high. Woody life forms at 25 cm (FW22)
361 were present but at low frequencies, while FW24 and FW25 remained at higher
362 frequencies. Coverage on the ground of small logs or dead wood (CLO), of rocks (RC),
363 and organic matter (OM) were shallow during the study. Bare soil surface (BS)
364 increased to higher amounts during the dry season, while it decreased during the rainy
365 season. There were no burrows (BW) in this microhabitat.

366 *Microhabitat 3.* In M3 (Fig. 2, Fig. A.1), VC25, VC35, VC50, and VC100 showed high
367 values, while vegetation species richness (VR) averaged the highest compared to other
368 microhabitats. The total number of woody plants (TW) and frequency of woody plants
369 at different heights (FW21-25) remained very high, while the total number of
370 herbaceous plants (TH) was low. Vegetation coverage at 10 cm (VC10), rocks (RC),
371 logs (CLO), and bare soil surface (BS) were low during the dry season; however, VC10
372 increased in the rainy season. Conversely, OM was present in the dry season but
373 decreased in the rainy season. The number of burrows (BW) remained quite scarce.

374

375 *Association between the microhabitats and species*

376

377 Kernel Graphs (Fig. 4) indicated that the two species used space distinctive since they
378 were differentially scattered along the plot. *Peromyscus difficilis* was more abundant
379 during the dry season, occupying a large portion of the plot. Instead, *P. melanotis*
380 increased its distribution during the rains when it seemed to displace *P. difficilis* into
381 other sampling stations (Fig. 4). Distribution rearrangements between seasons implied
382 that one species occupied some stations more frequently than the other, and vice versa
383 (Fig. 4). Indeed, the two χ^2 tests yielded statistical abundance differences in each species
384 at both microhabitats and seasons (Table A.2: dry season; R^2 (U) = 0.09, $n = 111$, $df = 2$,
385 Likelihood Ratio $\chi^2 = 15.07$, $p = 0.00005$; rainy season; R^2 (U) = 0.02, $n = 168$, $df = 2$,
386 Likelihood Ratio $\chi^2 = 6.40$, $p = 0.0406$).

387 During the dry season (Fig. 5 and Table A.2), *Peromyscus difficilis* was highly
388 related to M2 (80 % captured mice) and also related to M1 (64 % captured mice);
389 conversely, *P. melanotis* was captured more frequently in M3 (66 % captured mice).
390 Spatial use of microhabitats changed for both species in the rains (Fig. 5 and Table
391 A.2), showing a microhabitat partition again, though less visible: in the Correspondence
392 Analysis, 61 % of mice caught in M1 were *P. difficilis*. This species was also related to
393 M3, while 60% of mice caught of *P. melanotis* were captured in M2.

394

395 *Spatial Patterns*

396

397 The Nearest Neighbor Analysis revealed that in both seasons both species showed a
398 significant clustered pattern within the plot (Table 3). In the dry season, the mean
399 distance between individuals of *P. difficilis* displayed to be more clustered than the

400 individuals of *P. melanotis*. However, the mean distance between individuals of *P.*
401 *difficilis* increases in the rainy season, while individuals of *P. melanotis* showed a
402 reduction in their area occupied (Table 3).

403 On the other hand, during the dry season, Ripley's bivariate K showed a
404 statistically significant pattern of repulsion for both *Peromyscus* in almost all analyzed
405 distances of the entire plot, excused at 2 m where it shows an attraction pattern (Fig.
406 6a). Such repulsion pattern turned over in almost all distances during the rainy season
407 (Fig. 6b), since the two species became more associated, sharing microhabitats in
408 almost all capture stations. However, during the rainy season, significant statistical
409 peaks of repulsion reappeared between the species at distances of five, ten, and 14 m
410 (Fig. 6b). Analyses also revealed the intensity of these patterns; *e.g.*, the likelihood for
411 finding individuals of *P. difficilis* and *P. melanotis* together at the same capture station
412 was very low during the dry season (Fig. 6a), while this probability increased in the
413 rainy season (Fig. 6b).

414

415 *Structural components of microhabitats affecting the distribution of small mammals*

416

417 Criteria for the selecting models that most explained the frequency of mice for each
418 species at each season in the sampling stations included: model significance of $p <$
419 0.05; lowest Akaike Information Criterion (AIC), *i. e.*, a measure of goodness-of-fit
420 penalized by the number of variables (Posada and Buckley 2004); Pearson goodness-of-
421 fit ($p < 0.05$) and its deviation (Deviance; $p < 0.05$); as well as the biological and
422 ecological meaning of results. Therefore, during the dry season, PC1 and PC3 predicted
423 the frequency of *P. difficilis* according to the best Generalized Linear Model for this
424 season (AICc 212.55) (Table 5, Fig. 5c). Environmental variables with higher scores in

425 the PC1 ($p = 0.0186$) were the total number of herbaceous plants (TH), vegetation
426 species richness (VR), and vegetation cover at 10 cm (VC10). In PC3 ($p = 0.0001$),
427 characterizing variables were the number of logs on the ground (CLO), as well as the
428 presence of burrows (BW) (Table 4, 5, Fig. 5c). These five variables were also the main
429 elements characterizing M2 (PC1) and M1 (PC3), the two habitats where the frequency
430 of capture of *P. difficilis* was the higher. As for *P. melanotis* (Fig. 5c), the frequency of
431 capture of *P. melanotis* was positively related to PC2 (AICc = 204.47, $p = 0.0001$).
432 Here, among the four variables with higher scores, were the total number of woody
433 vegetation (TW) and frequency of woody life forms characterizing 10 cm height
434 (FW21), the two main elements at M3 for the dry season (Table 4, 5, Fig. 5c).

435 During the rainy season, a similar pattern of microhabitat partition occurred
436 between the two species. The best GLM model for *P. difficilis* in this season (Table 4, 5,
437 Fig. 5c) was mainly associated with the total number of woody plants (TW),
438 herbaceous forms at 50 cm (FH14), woody forms at 10 and 100 cm (FW21, FW25,
439 respectively) and with the number of logs on the ground (CLO), in PC2; and with the
440 number of logs on the ground (CLO), and organic matter (OM) in PC3 (AICc = 286.76,
441 $p = 0.0001$) (Table 4, 5). The latterly involved variables with a high presence at M1
442 (PC3) and M3 (PC2) during the wet season, where *P. difficilis* was more frequently
443 captured. On the other hand, *P. melanotis* (Fig. 5c) was only associated with PC1 (AICc
444 = 241.01, $p = 0.0343$). The primary variables characterizing this component were the
445 number of total herbaceous plants (TH), vegetation species richness (VR), and the plant
446 cover at almost all analyzed heights (VC10-100 cm) (Table 4).

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Discussion

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452 Our results of Contingency Tables Analysis, Correspondence Analysis, and GLMs
453 models showed that the two syntopic species of *Peromyscus* switched and split
454 resources in space, as environmental conditions changed. Also, our findings on
455 microhabitat relations of rodents in a patch of a mid-latitude temperate forest, concur
456 with the habitat heterogeneity coexistence hypothesis (Cramer and Willig 2002;
457 Valladares *et al.* 2015). We found that both *Peromyscus* were sensitive to slight changes
458 in microhabitat structure and that the three microhabitats provided different resources
459 for each one. Our results also suggest that coexistence between these syntopic
460 *Peromyscus* is facilitated by temporal differences in space structure, and probably also
461 by changes on the availability of both food and shelter that go with it (Pianka 1973;
462 Schoener 1974). For instance, *P. difficilis* was more related to M1 and M2 by the dry
463 season, while *P. melanotis* was highly related to M3. Conversely, *P. difficilis* was more
464 related to M1 and frequently captured to M3 by the rainy season, while *P. melanotis*
465 was highly related to M2. Partition in space use has already been documented for
466 coexisting species of *Peromyscus* within a community; *i.e.*, extensive studies of niche
467 partitioning by *Peromyscus leucopus* and *P. maniculatus* (Kaufman and Kaufman
468 1989). Moreover, several studies have demonstrated variation in spatial resource use by
469 congeneric species (Barry *et al.* 1990; Dooley and Dueser 1996; Kalcounis-Rüppell and
470 Millar 2002).

471 In our study, *P. difficilis* remained related to M1 in both seasons, especially to
472 the former during the wet season. The number of fallen logs was very high at M1. Such
473 microhabitat represents small patches of food for small mammals, offering invertebrates
474 (Bellows *et al.* 2001), refuges and shelters (Bowman *et al.* 2001). In this microhabitat,

475 individuals of *P. difficilis* can also use the long and big fallen logs as pathways for quick
476 and straight locomotion inside the forest (Bellows *et al.* 2001; Dewalt *et al.* 2003).
477 Indeed, fallen logs promote structural complexity of forests and may enhance positive
478 interaction among species of small mammals (Bowman and Facelli 2013). GLM's
479 analyses showed that PC1 and PC3 explained the abundance of *P. difficilis* during the
480 dry season and by PC2 and PC3 in the rainy season. In the dry season, variables
481 contributing most to PCA ordination in PC1 and PC3 were the total number of
482 herbaceous vegetation (TH), vegetation species richness (VR), vegetation coverage at
483 10 cm (VC10), herbaceous forms at 10 cm (FH11) and the number of logs on the
484 ground (CLO), as well as burrows (BW). While in the dry season, PC2 and PC3
485 represented woody vegetation (TW), the number of logs on the ground, herbaceous
486 forms at 50 cm (FH14), woody forms at 25 and 100 cm (FW21 and FW25, respectively)
487 and organic matter (OM). Bellows *et al.* (2001) found a similar result in a high latitude
488 temperate forest (Virginia, USA), where distribution of a small mammal, generalist
489 species was associated with the diameter of fallen logs, the frequency of shrubs, and
490 degree of canopy closure. Association between rodents and fallen logs was also
491 documented for *Nectomys squamipes* that builds up its nests inside decomposed, fallen
492 logs (Briani *et al.* 2004); this has also been recorded for other rodent species in several
493 biomes with different vegetation types (*e. g.*, *Rattus rattus*, *Nesomys audeberti* in
494 Lehtonen *et al.* 2001; *Oligoryzomys nigripes* in Dalmagro and Vieira 2005). In contrast,
495 *P. melanotis* showed a close relation with only one PC over each pluvial season. During
496 the dry season, the frequency of this species was only related to PC2, which represented
497 the total number of woody vegetation (TW) and FW21. Then by the rainy season, the
498 species became only related to PC1, which accounted for understory dominated by
499 herbaceous life forms (TH). Relationships between frequency of rodents and habitats

500 with increased understory density have been interpreted as a protection against aerial
501 predators (Dalmagro and Vieira 2005) or as a preference for more complex habitats that
502 enable for vertical stratifications and, thus for extended coexistence inside fragments
503 (Grelle 2003; Johnson 2007).

504 Intrinsic factors as sex and mating system must also be related to the coexistence
505 of both *Peromyscus*. For instance, the Nearest Neighbor Analysis revealed that in both
506 seasons both species showed a significant clustered pattern within the plot. However,
507 the mean distance between individuals of *P. difficilis* displayed to be more clustered
508 than the individuals of *P. melanotis*, especially during the dry season. Indeed, the mean
509 distance between individuals of *P. difficilis* increases in the rainy season, while
510 individuals of *P. melanotis* showed a reduction in their area occupied. These patterns
511 are related with the breeding season of both species. Our data (not published) revealed
512 that during the dry and rainy seasons were captured individuals of *P. difficilis* with signs
513 of reproductive activity, especially during the dry season (males: inguinal vs. scrotal
514 testicles, females: alopecia, the presence of milk, the appearance of the vagina,
515 gestation). While for *P. melanotis* the primary breeding season occurs during the rains.
516 Individuals need different resources requirements to fulfill the breeding season and this
517 impact on its dispersion and coexistence. We believe that *P. melanotis* may be moving
518 to other areas with more beneficial conditions (*i. e.* more availability of resources).
519 Thus, the coexistence between both *Peromyscus* may occur because the geographic
520 segregation of *P. melanotis* to search for better environmental conditions to survive.
521 Indeed, in this study, we define to *P. melanotis* as an opportunistic species throughout
522 the study area because the capture frequencies of the individuals only increased (as we
523 pointed out early) when the environmental conditions became more beneficial for the
524 survival of these. That is, throughout the time of capture except for the rainy season, its

525 frequency of capture remained at low levels compared to those of *P. difficilis* (resident
526 species), increasing drastically in the rainy season when there is greater accessibility for
527 the use of resources and competition between the two species decreases. Therefore, *P.*
528 *melanotis* may be coming back to the area during the rainy season to carry out the
529 breeding season. However, Chupp (2002) showed an opportunistic habitat use by small-
530 sized *Peromyscus leucopus*, which he related to predation risk. Further studies about the
531 geographic segregation and the influence of predation on the opportunistic behavior of
532 *P. melanotis* are needed. Also, the increase in the number of captures of both species
533 from the dry to the rains could be leaded for the breeding season and resources
534 availability. One possible consequence of such intrinsic and extrinsic operating factors
535 is that *P. difficilis* remained more abundant and always present at the microhabitats with
536 more stable elements in the study area (our unpublished data), while *P. melanotis* only
537 increased its abundance during the rainy season, when environmental conditions
538 became more benign, and plant cover became denser. Since rains promote an increase
539 of primary productivity, allowing more resource availability (mainly food) and
540 enhancing microhabitat carrying capacity, such habitat changes facilitate coexistence
541 between both *Peromyscus*, and with other small land mammals in the area (Castro-
542 Campillo *et al.* 2008, 2012). Ripley's bivariate K supported and shed light into such
543 outcome since the species showed repulsion between them in almost all analyzed
544 distances during the dry season; *i.e.*, due to resources availability are more scarce during
545 this season, is not so common that a mixed pair of mice used the same microhabitat.
546 Moreover, as in this season is the primary breeding season of *P. difficilis* is probably
547 that territoriality behavior can occur. Conversely, the intensity of such repulsion
548 decreased substantially during the rainy season; indeed, at some analyzed distances, the
549 two deer mice showed an association pattern. Holding our results that the increase of

550 resources available during the rainy season can allow that the species can share the
551 habitat. Thus, our results indicate that in these two syntopic *Peromyscus*, both
552 microhabitat use and spatial organization are seasonally variable (Brown and Zeng
553 1989; Cramer and Willig 2002). It is important to point out that during both seasons
554 Ripley's bivariate K indicated an interesting attraction pattern between 2 and 3 m. This
555 patterns could be due to sampling design. Ergo we set only one Sherman trap in each
556 sampling station for two days, therefore if one individual of *P. difficilis* was captured in
557 the first day and then one individual of *P. melanotis* was captured in the same station
558 where we captured the *P. difficilis*, the analysis counts this pattern as an association
559 because they were trapped in the same station at a very short distance.

560 Also, the partition of space by this syntopic deer mice must be facilitated by
561 their respective locomotive habits as semiarboreal (*P. difficilis*) and cursorial (*P.*
562 *melanotis*). The long tail of *P. difficilis* must enable it to rush and climb along shrubs or
563 trees (Álvarez-Castañeda 2005), thus easing its preference for habitats where it can
564 escape from predators. In fact, adult color coat changed in *P. difficilis* between pluvial
565 seasons, becoming more similar to ground litter; *e. g.*, in this resident deer mouse, color
566 phenotype plasticity must be a cryptic response elicited against predators. On the other
567 hand, a smaller sized body, together with a shorter tail and narrower soles (Fernandez *et*
568 *al.* 2010), should enable the cursorial *P. melanotis* to occupy such zones as M2 and M3,
569 where predators cannot easily spot it through a dense vegetation cover, so it can scape
570 very quickly. Indeed, high shrubs cover provide both protection from predators and
571 food sources, since seeds may be concentrated under shrub canopies (Thompson 1982;
572 Mohammadi 2010). In fact, rodents usually avoid foraging in unsheltered microhabitats
573 and forest edges where they are more likely to be spotted by avian (Kotler *et al.* 1991)
574 and other vertebrate predators (Morris and Davidson 2000; Mohammadi 2010).

575 Finally, we want to highlight and recommend our sampling of environmental
576 features and quantitative analyses, especially for Ripley's bivariate K, as neither one has
577 been extensively used in studies focusing on the spatial dynamics of dispersion in small
578 rodents, despite its important advantages. The methodological approach used here,
579 together with the gathered evidence became relevant for providing us with necessary
580 information about the ability of this two *Peromyscus* to split resources in a mid-latitude
581 temperate forest at the edge of a megalopolis, which continuous growth produces
582 fragmentation and patching of natural microhabitats. Therefore, our local scope was
583 explicitly designed at this initial point, to focus on small-sized rodents with low vagility.
584 Besides, we successfully aimed to reconstruct vegetation structure, to provide us with
585 clues as to how to eventually manage such perturbed ecosystems for conservation
586 purposes. We also think that our methodology can be helpful in other scenarios for
587 understanding small rodents, such as ethological dynamics, activity patterns, and
588 reproductive systems at either or both intra or interpopulation levels.

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Figure legends

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792 **Fig. 1.** Sampling plot design. a) Total plot area was 2475 m²; each intersection (n = 120)
793 was an independent sampling station for capturing mice. An influence area of 2.5 m²
794 around each station was constructed for sampling 24 microhabitat environmental
795 variables. b) Close up to the influence area showing the eight transects used for drawing
796 environmental variables; note subdivisions into three subtransects.

797 **Fig. 2.** Map of the distribution of the microhabitats (M1 = red, M2 = green, M3 = blue)
798 in the study quadrant for dry (A) and rainfall (B). The bar graph below shows the change
799 in the number of sampling stations between dry and rainy seasons. ** $p = 0.001$

800 **Fig. 3.** Box-plots are showing the seasonal heterogeneity of the 23 variables sampled in
801 the study plot between dry and rainy seasons. Overall, vegetation variables show an
802 increase in the rainy season, while the organic matter (OM) decrease. Structural elements
803 as logs on the ground do not show differentiation between seasons. Some variables were
804 not present in high quantities along the study plot. Therefore we were unable to build the
805 box-plot. The red cross represents the mean of each variable.

806 **Fig. 4.** Spatial analysis with Kernel density points showing capture frequencies for *P.*
807 *difficilis* at dry (a) and rainy (b) seasons, and for *P. melanotis* at dry (c) and rainy (d).
808 Dots depict actual capture points, while hot spots color indicates higher density.

809 **Fig. 5.** Correspondence analysis from contingency tables of frequency capture data for
810 each deer mouse (*P. difficilis* and *P. melanotis*) in each microhabitat (M1-3), during the
811 dry (a) and rainy (b) seasons, respectively. Axis c1 and c2 indicate the coordinates
812 resulted from the ordination of each variable from the analysis. Figure c shows the plots
813 for the GLMs models, the response variable for each graph are the predicted values of the
814 model to that principal component (the model effect). All of the PCs fitted in the model

815 show a positive relationship, indicating that the probability of capture frequency of the
816 individuals of two mice, increases with the presence of that variables. Therefore, the
817 figure also shows in the “X” axis in parenthesis the variables with the higher loading
818 scores in the ordination of this PCs.

819 **Fig. 6.** Ripley's bivariate K Analysis for interactions between the two *Peromyscus*. (a)
820 Repulsion pattern between both species in all analyzed distances during the dry season.
821 (b) Attraction from 6 - 12 m, and repulsion at 5, 10, and 14 m during the rainy season.
822 Black solid line represent the Ripley's K bivariate pattern; red dashed lines represent the
823 95% CI; blue solid line shows the null hypothesis.

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844 **Fig. 1**

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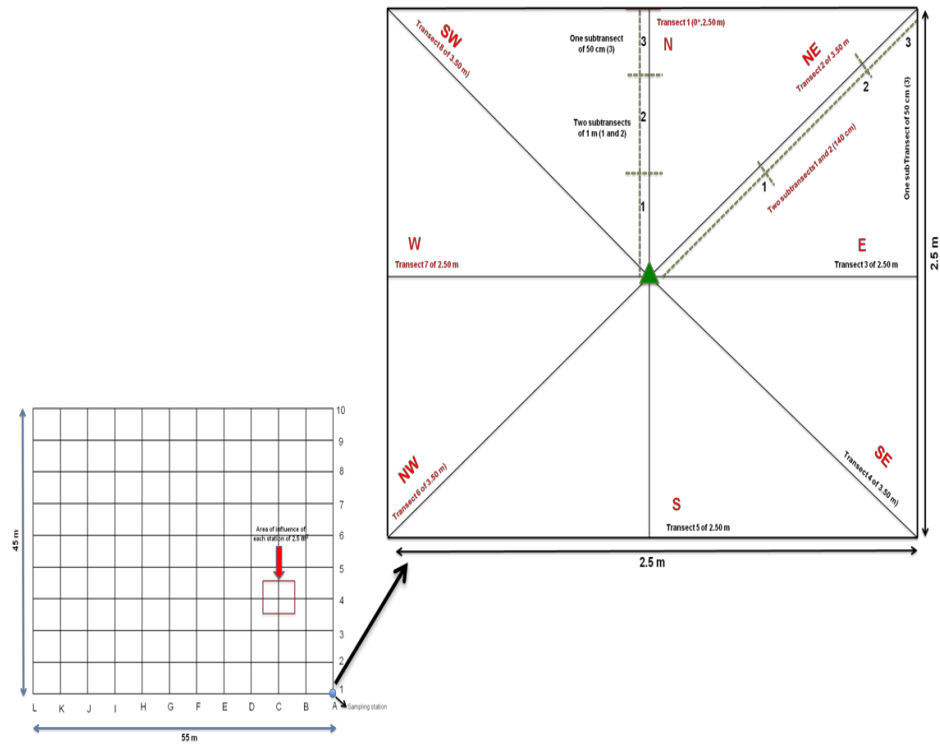
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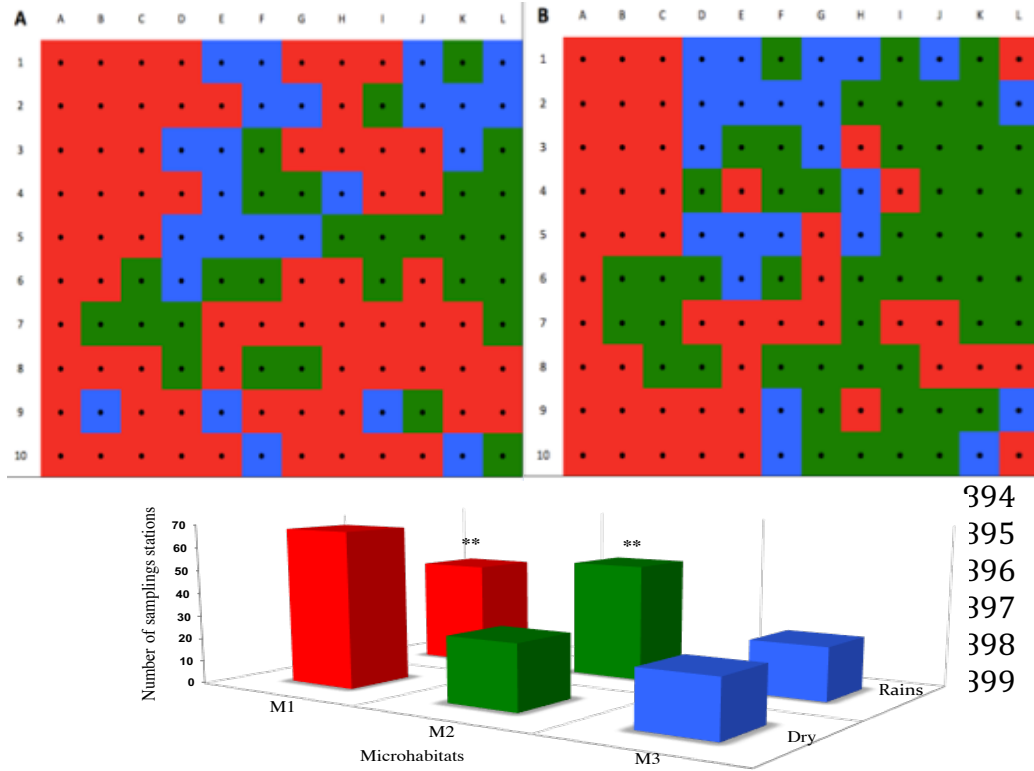
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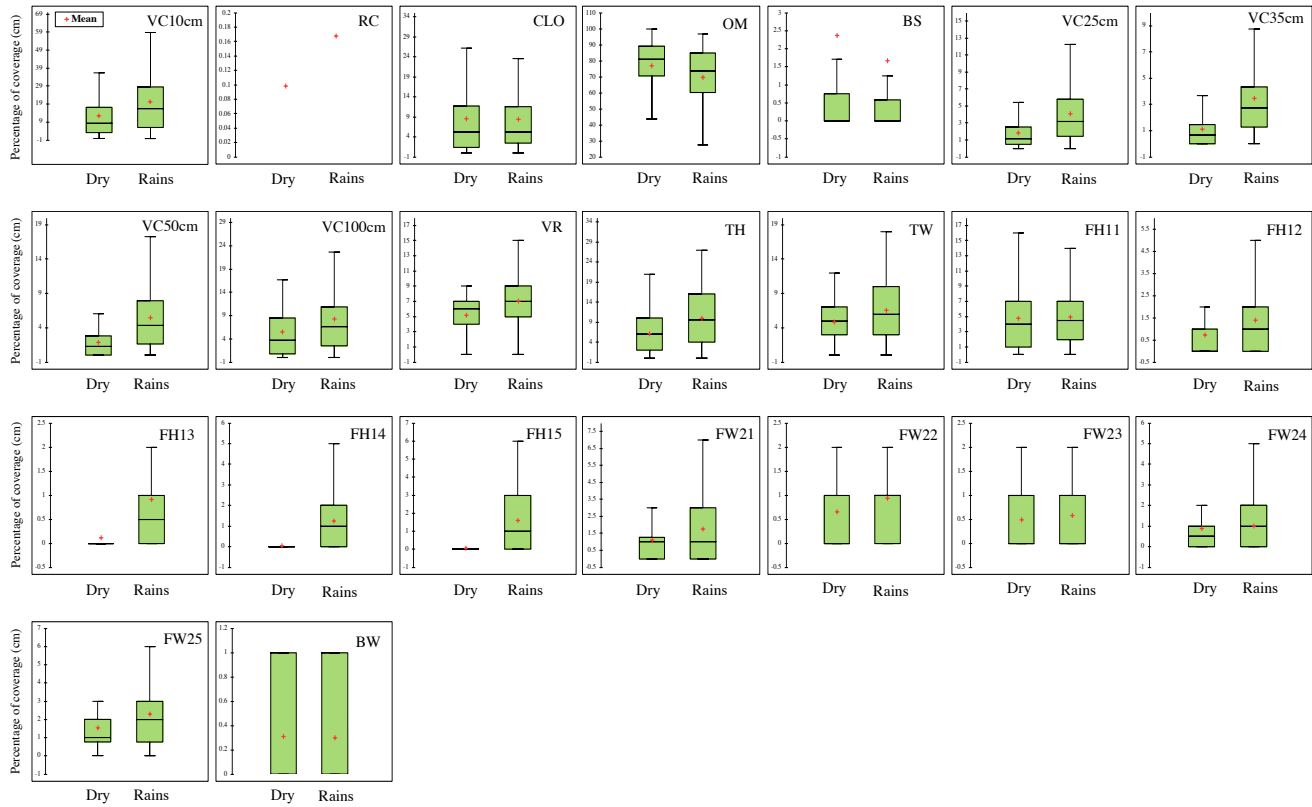
Fig. 2



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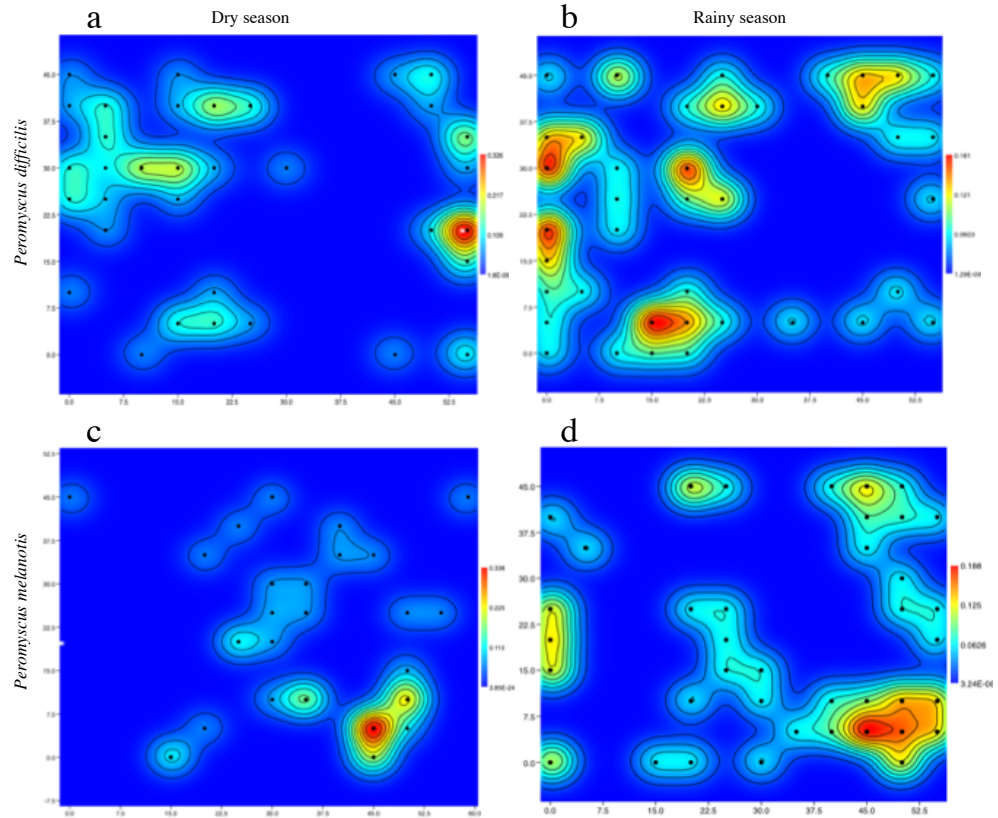
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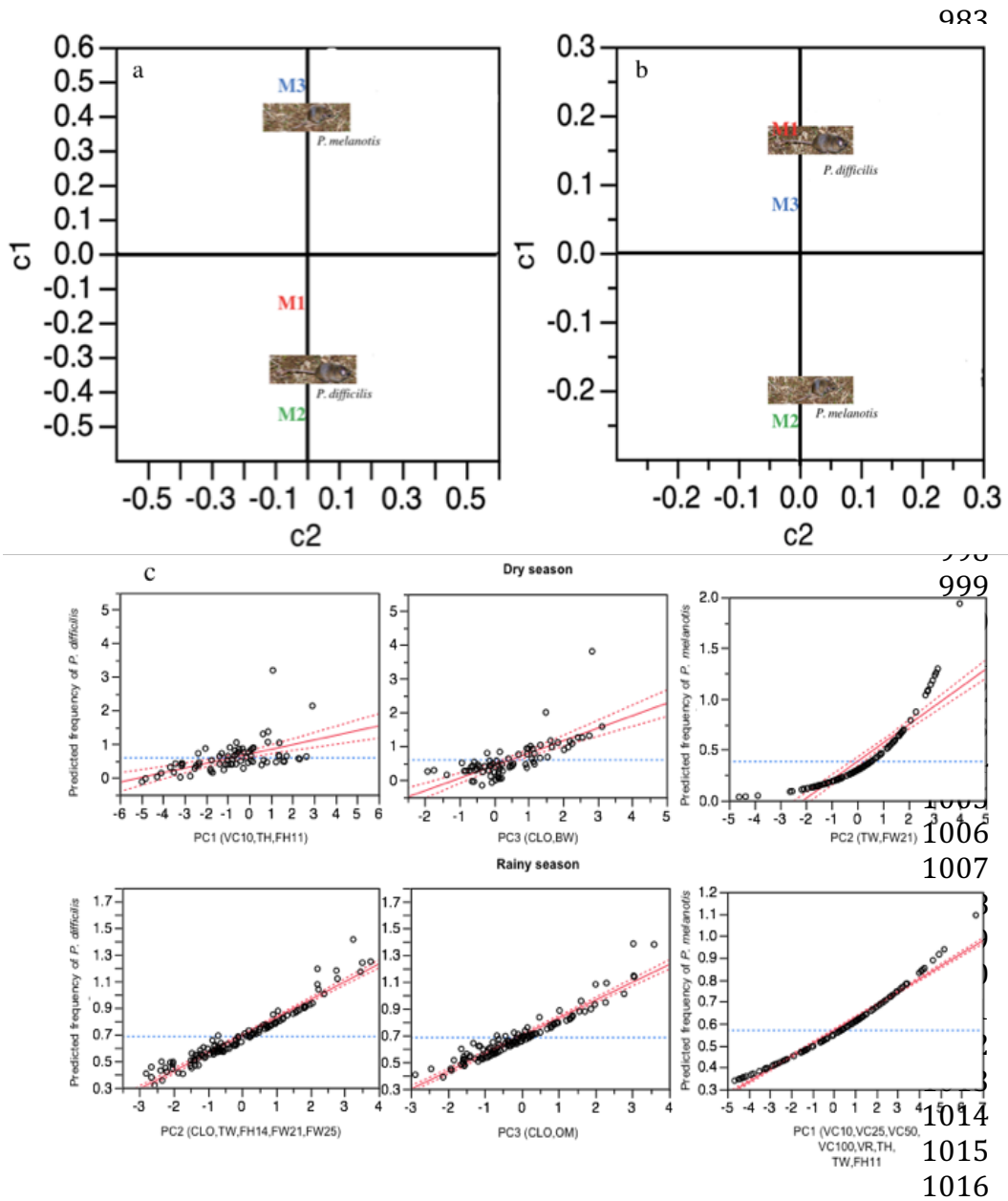
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Fig. 4



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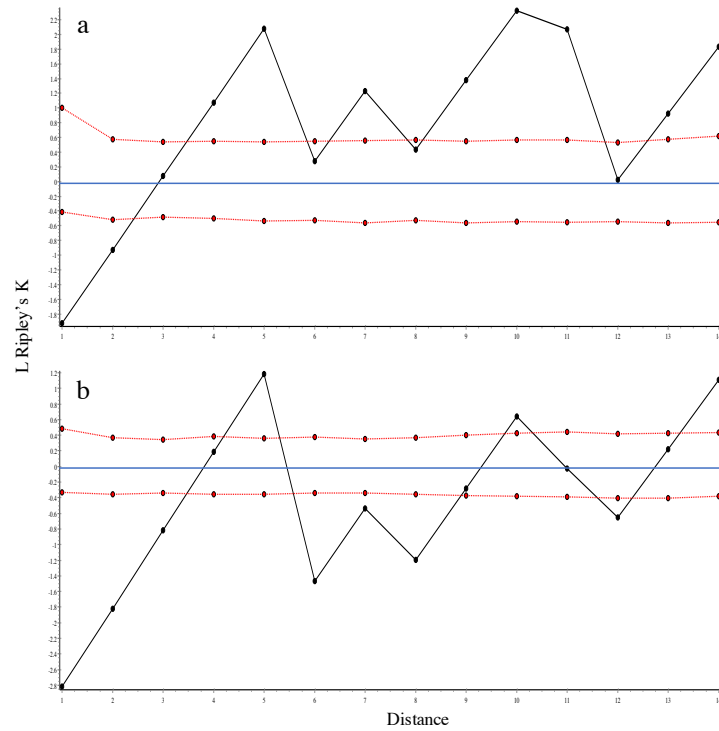


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1029 **Fig. 6**

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1076 **Table 1.** Environmental variables used to measure the horizontal and vertical structure of microhabitat
 1077 at each sampling station, showing its ecological interpretation (kind or resource type) for both species
 1078 of *Peromyscus*.

Variable code	Predation		Resources				
	Diminished risk	Refuges	Breeding Space	Food	Temporal food and refuges	Permanent	Resting places
	Vegetation Cover (cm)						
VC10	X			X	X		X
VC25	X		X	X	X		X
VC35	X		X	X	X		X
VC50	X		X	X	X		X
VC100	X		X	X	X		X
	Frequency of Herbaceous Plants (cm)*						
FH11	X		X	X	X		X
FH12	X		X	X	X		X
FH13	X		X	X	X		X
FH14	X		X	X	X		X
FH15	X		X	X	X		X
	Frequency of Woody Plants (cm)*						
FW21	X	X	X	X	X	X	X
FW22	X	X	X	X	X	X	X
FW23	X	X	X	X	X	X	X
FW24	X	X	X	X	X	X	X
FW25	X	X	X	X	X	X	X
	Species Vegetation Richness						
VR	X	X	X	X	X	X	X
	Total of Herbaceous Plants						
TH	X		X	X	X		X
	Total of Woody Plants						
TW	X	X	X	X	X	X	X
	Rocks						
RC	X	X	X			X	X
	Organic Matter (litter, twigs, small trunks)						
OM				X	X		
	Bare Soil						
BS					X		
	Coverage of Logs (stumps, fallen trunks)						
CLO	X	X	X			X	X
	Numbers of Burrows						
BW	X	X	X			X	X

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1080 * = Frequencies of plant types (FH, FW) involve the same heights as in VC.

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1085 **Table 2.** Normality (**NOR**) tests for 22 variables (**VAR**) of microhabitat, and
 1086 comparisons^{abc} (**COM**) for average values between the dry (**DRY**) and rainy (**RAINS**)
 1087 seasons, respectively. Variable names in Table 1.
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VAR	NOR		COM	VAR	NOR		COM	VAR	NOR		COM
	DRY	RAINS			DRY	RAINS			DRY	RAINS	
BS	0.0001	0.0001	<i>1.0</i>	VC100	0.002	0.003	0.0001	TW	<i>0.143</i>	<i>0.08</i>	0.0004
CLO	0.0001	0.0001	<i>0.972</i>	VR	0.006	<i>0.082</i>	0.0001	FW21	0.0001	0.0001	0.004
OM	0.010	0.034	0.0001	TH	0.0001	<i>0.072</i>	0.0001	FW22	0.0001	0.0001	0.026
RC	0.0001	0.0001	<i>0.432</i>	FH11	0.015	0.028	<i>0.658</i>	FW23	0.0001	0.0001	<i>0.875</i>
VC10	0.002	0.041	0.0001	FH12	0.0001	0.0001	0.001	FW24	0.0001	0.0001	<i>0.378</i>
VC25	0.009	0.003	0.0001	FH13	0.0001	0.0001	0.0001	FW25	0.0001	0.001	0.0001
VC35	0.0001	0.002	0.0001	FH14	0.0001	0.0001	0.0001	BW	0.0001	0.0001	1
VC50	0.0001	0.019	0.0001	FH15	0.0001	0.0001	0.0001				

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1090 Parametric: ^aKolmogorov-Smirnov; ^bStudent for two samples; non-parametric: ^cWilcoxon). The *p*-values in italics do
 1091 not reject normality (*p* = 0.05), or do not indicate significant differences between pluvial seasons.

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1107 **Table 3.** Nearest Neighbor Analysis for both species of *Peromyscus*, it shows the mean
 1108 distance in which individuals from both *Peromyscus* are segregated. R-value indicates
 1109 how the observed distribution deviates from random. Clustered points give $R < 1$, Poisson
 1110 patterns give $R \sim 1$, while overdispersed points give $R > 1$.

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	Dry season		Rain season	
	<i>P. difficilis</i>	<i>P. melanotis</i>	<i>P. difficilis</i>	<i>P. melanotis</i>
Points	57	39	58	52
Mean distance	1.40	2.39	1.67	2.09
<i>R</i>	0.42	0.77	0.55	0.64
<i>P</i> value	1.1263×10^{-16}	0.006	8.6577×10^{-11}	8.7708×10^{-7}
Point pattern	Clustering	Clustering	Clustering	Clustering

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1132 **Table 4.** Principal components used as effect model in the GLMs analysis for both

1133 seasons. Red colors represent the variables that have the major eigenfactors to the

1134 ordination of the components.

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Variables	Dry season			Rainy season		
	PC1	PC2	PC3	PC1	PC2	PC3
VC10	0.713	-0.388	-0.134	0.659	-0.179	-0.374
RC	-0.145	-0.055	-0.110	0.014	0.062	0.034
CLO	0.030	0.118	0.828	-0.153	0.411	-0.583
OM	-0.604	0.303	-0.487	-0.499	-0.122	0.775
BS	0.130	-0.187	0.112	-0.028	0.154	-0.328
VC25	0.415	0.280	0.034	0.658	-0.061	0.237
VC32	0.287	0.184	0.052	0.580	-0.003	-0.126
VC50	0.523	0.107	0.078	0.669	-0.173	-0.030
VC100	0.335	0.408	0.052	0.656	-0.053	0.107
VR	0.762	0.251	-0.269	0.776	0.380	0.058
TH	0.837	-0.430	-0.131	0.874	-0.319	-0.076
TW	0.520	0.684	-0.168	0.615	0.711	0.270
FH11	0.784	-0.394	-0.214	0.678	0.007	-0.228
FH12	0.573	-0.345	0.176	0.548	-0.278	0.256
FH13	0.247	0.073	0.113	0.463	-0.260	0.067
FH14	0.149	-0.186	-0.023	0.580	-0.530	-0.043
FH14	0.080	0.117	-0.236	0.481	-0.267	-0.019
FW21	0.127	0.510	-0.394	0.342	0.603	0.311
FW22	0.015	0.064	-0.105	0.266	0.212	0.416
FW23	0.199	0.256	-0.228	0.196	0.366	-0.241
FW24	0.424	0.359	0.195	0.337	0.165	0.159
FW25	0.515	0.366	0.380	0.494	0.469	0.026
BW	-0.105	0.249	0.557	-0.170	0.332	-0.218

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1157 **Table 5.** Generalized Linear Models constructed with the Principal Components and the
 1158 frequency of *P. difficilis* and *P. melanotis* for both seasons. The partition of resources by
 1159 both species is observed at both seasons of the year. Different main components within
 1160 each season explain the frequency of capture of each of the species. Also, the table is
 1161 related to what type of microhabitat the new variables belong to (M1-M3). The goodness
 1162 of fit tests are shown; Pearson and Deviance.

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<i>P. difficilis</i>						
Dry season						
Term	Estimate	Std Error	L-R χ^2	P value	Pearson	Deviance
Intercept	-0.97	0.15	55.73	0.0001	$\chi^2 = 155.80$ ($p = 0.0096$)	$\chi^2 = 123.56$ ($p = 0.3210$)
PC1 = M2	0.11	0.05	5.53	0.0186	AICc = 212.55	
PC3 = M1	0.45	0.06	44.73	0.0001		
Rainy season						
Term	Estimate	Std Error	L-R χ^2	P value	Pearson	Deviance
Intercept	-0.40	0.11	14.37	0.0002	$\chi^2 = 168.56$ ($p = 0.0008$)	$\chi^2 = 156.43$ ($p = 0.0062$)
PC2 = M3	0.23	0.06	10.92	0.0009	AICc = 286.76	
PC3 = M1	0.26	0.07	10.95	0.0009		
<i>P. melanotis</i>						
Dry season						
Term	Estimate	Std Error	L-R χ^2	P value	Pearson	Deviance
Intercept	-1.21	0.18	74.28	0.0001	$\chi^2 = 237.65$ ($p = 0.0001$)	$\chi^2 = 138.70$ ($p = 0.0935$)
PC2 = M3	0.46	0.09	23.34	0.0001	AICc = 204.47	
Rainy season						
Term	Estimate	Std Error	L-R χ^2	P value	Pearson	Deviance
Intercept	0.60	0.12	28.15	0.0001	$\chi^2 = 132.71$ ($p = 0.13$)	$\chi^2 = 132.72$ ($p = 0.13$)
PC1 = M2	0.10	0.04	4.47	0.0343	AICc = 241.01	

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