1   **Running header:** Morphological structure of ant assemblages

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3   **Morphological structure of ant assemblages in tropical and temperate forests**

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26 **Abstract**

27 Morphological variation in co-occurring species often is used to infer species assembly rules and

28 other processes structuring ecological assemblages. We compared the morphological structure of

29 ant assemblages in two biogeographic regions along two extensive latitudinal gradients to examine

30 common patterns and unique characteristics of trait distribution. We sampled ant assemblages along

31 extensive latitudinal gradients in Tropical Atlantic Forest in eastern Brazil and temperate forests in

32 the eastern United States. We quantified 14 morphological traits related to the ecology and life

33 history of each of 599 ant species and defined the morphological space occupied by different ant

34 assemblages. Null models were used to test whether tropical and temperate ant assemblages differed

35 from random expectation in morphological structure. Correlations between traits and climate were

36 used to infer associations between habitat characteristics and morphological space occupied by ant

37 assemblages. Tropical ant assemblages had higher morphological diversity and variation in the

38 space of occupied morphospace, whereas temperate assemblages had higher variance in size.

39 Although tropical ant assemblages had smaller morphological distances among species, species

40 packing (i.e., mean nearest-neighbor distance) did not differ between regions. Null model analysis

41 revealed scant evidence of habitat filtering or niche differentiation within assemblages. Different

42 traits had different means, variances, skewness, and kurtosis values along each environmental

43 gradient. Mean trait values within assemblages were associated mainly with region and correlated

44 with temperature but trait variances had more complex responses to climate, including interactions

45 between temperature and precipitation in the models. The higher functional diversity in tropical ant

46 assemblages occurs by expansion of the morphospace rather than through an increase in species

47 packing. Different traits vary independently along environmental gradients. Analysis of individual

48 traits together with categorization of the moments of trait distributions (statistical central

49 tendencies) provide new directions for quantifying morphological diversity in ant assemblages.

50 **Keywords**

51   Ants, Brazilian Atlantic forest, Eastern United States, environmental gradients, Formicidae,

52   functional traits, morphology, traits.

53

54   **Introduction**

55   Contemporary community ecology is strongly focused on functional traits, what constrains

56   them, and their relationship with environmental variables and community structure (Cadotte et al.

57   2013, Winemiller et al. 2015). An increasing number of studies suggest that examining functional

58   traits of individual organisms may help to construct a mechanistic and predictive framework for the

59   study of species distribution and co-occurrence (Cadotte et al. 2013). Trait diversity, which is

60   closely related to functional diversity, increasingly has been used as a measure of phenotypic

61   diversity in species assemblages (McGill et al. 2015). However, few studies have evaluated how

62   morphological diversity is distributed along extensive latitudinal or environmental gradients,

63   particularly in highly diverse invertebrate assemblages (Arnan et al. 2014, Yates et al. 2014, Silva

64   and Brandão 2014). Without such analyses, it remains difficult to identify or test mechanistic

65   hypotheses regarding the geographic distribution of biodiversity in light of the distribution of

66   organismal functions (Swenson et al. 2012). A better understanding of the relationships between

67   traits and geographic or environmental variables also is critical for improving predictions of

68   functional and composition responses to ongoing global climatic change (Fortunel et al. 2014).

69   The morphospace of an assemblage can be defined as the distribution of morphological trait

70   values within it (Ricklefs and Travis 1980). Quantifying the volume, overlap, and packing of

71   morphological trait space generally improves our understanding of how different ecological

72   processes structure morphological diversity and ecological strategies (Mouillot et al. 2005,

73   Lamanna et al. 2014). For example, studies of morphological variation have revealed several

74   interesting patterns in the occupation of niche space (Stevens et al. 2006, Inward et al. 2011,

75   Ricklefs, 2012), morphological disparity between assemblages (how the variety of body plans

76 within a taxon fills a morphospace) (McClain et al. 2004), responses of assemblage structure to

77 habitat complexity (Willis et al. 2005, Montaña and Winemiller, 2010), and convergent or divergent

78 patterns of morphology among continents (Ricklefs and Travis 1980, Winemiller 1991, Inward et al.

79 2011, Ricklefs 2012, Montaña et al. 2014). Morphological data also have been used to test the

80 relative importance of environmental filtering and limiting similarity in structuring species

81 assemblages (e.g., Cadotte et al. 2013, 2015).

82 The trait approach may be particularly useful for interpreting patterns of diversity of taxa

83 such as arthropods that are hyperdiverse, relatively small in size, and poorly studied. For many

84 arthropod groups, morphology of functionally important traits is the most easily obtainable,

85 repeatable, and accurately measurable dimension associated with ecological diversity (Pie and

86 Traniello 2007, Yates et al. 2014). Among the arthropods, ants are an ideal taxonomic group for

87 investigating relationships between morphology, traits, and assemblage structure because they (i)

88 are abundant, comprising the dominant fraction of animal biomass in most terrestrial ecosystems

89 (Wilson and Hölldobler, 2005), (ii) perform a range of important ecosystems functions (Del Toro et

90 al. 2012), (iii) exhibit a very large morphological diversity at very small scales (Silva and Brandão

91 2010), and (iv) vary in composition along environmental gradients (Gotelli and Ellison 2002). In

92 addition, many studies have shown that ant species have specific traits that are correlated with

93 environmental conditions (Wiescher et al. 2012), macro- or microhabitat structure (Kaspari and

94 Weiser 1999, Farji-Brener et al. 2004, Gibb and Parr 2010, Yates et al. 2014) and resource

95 exploitation (Retana et al. 2015). Finally, recent research with stable isotopes has identified

96 evidence of a relationship between ant morphology and their trophic position within food webs

97 (Gibb and Cunningham 2013, Gibb et al. 2015b).

98 Here, we present the first broad-scale description of the morphological differentiation of

99 functional traits between temperate and tropical ant assemblages. We used three approaches to

100 quantify morphological differentiation. First, we used diversity metrics to estimate the amount of

101 morphological space occupied by temperate and tropical ant assemblages. Second, we combined

102 multivariate statistics and null model analyses to ask whether morphological differentiation within

103 assemblages was greater than expected, given their regional species pools. Third, we contrasted the

104 moments of trait distributions between the two regions.

105   We combined these analytical approaches to test the following predictions: 1) Because of

106 higher species diversity in the tropics and many more specialized predators, tropical and temperate-

107 zone ant assemblages differ in morphological diversity and structure; 2) Because temperate forests

108 experience harsher and more variable climates throughout the year, temperate ant assemblages

109 should have a stronger imprint of habitat filtering (morphological clustering); and 3) Ecological

110 traits of ant assemblages are correlated with climate. Our data base of functional traits is one of the

111 largest compiled to date for ants and includes a large number of species-specific morphological

112 traits from different assemblages across two extensive environmental gradients. We identified both

113 similarities and differences in morphological structure of ant assemblages in tropical and temperate

114 ant faunas and illustrate that analysis of individual traits can reveal unexpected patterns in

115 relationships between traits, environmental gradients, and changes in land-use.

116

117 **Material and Methods**

118 **Data Analysis**

119 **Ant assemblages**

120   We used data from two previous studies in which ants were sampled systematically along

121 two latitudinal gradients (Fig. 1). For the temperate-zone forests, Del Toro (2013) sampled ground-

122 nesting ants at 67 sites spanning ten degrees of latitude and seven North American Level II

123 ecoregions in the eastern United States. In the Neotropics, we focused on leaf-litter ant communities

124 distributed throughout the Atlantic Forests of eastern Brazil. Leaf-litter ants are the most diverse ant

125 fauna in the world in terms of phenotypic and functional diversity (Silva and Brandão 2010). The

126   Atlantic Forest of eastern Brazil is the second largest tropical forest and spans the largest latitudinal

127   gradient of all tropical forests in the Neotropics. All statistics analyses were carried out in the R v.

128   3.2.1 statistical environment (R Core Team 2015). The data and R code are archived online in the

129   Harvard Forest Archives http://harvard-forest.fas.harvard.edu/data-archive.

130   **Morphological data**

131   Our study draws on morphological data for 599 species of ants, 508 species from the

132   Brazilian Atlantic Forest and 91 from temperate eastern North American forests. We examined

133   fourteen characters that represent various aspects of ant ecology (Table 1; see Silva and Brandão

134   2010 for morphometric definition of each trait). These variables characterize morphological

135   structures related to diet, habitat, and foraging strategies and are good proxy measures for ant

136   species ecology (Silva and Brandão 2010, Arnan et al. 2014, Yates et al. 2014, Gibb et al. 2015b).

137   Measurements of pinned specimens (± 0.01 mm) were made using an ocular micrometer

138   attached to a Leica MZ75 stereomicroscope. We used the highest magnification that allowed the

139   trait measured to be fitted within the range of the ocular micrometer. We measured fourteen

140   morphological traits of between 1 and 25 (6 ± 4.7) individuals and of 1 to 11 (3 ± 1.4) individuals

141   from the temperate and tropical datasets, respectively. A minimum of six individuals of each species

142   were measured whenever possible. We used Weber's length (Table 1) as the descriptor of body size

143   and used the other traits (head, mesosoma, metasoma, and body appendages) to describe the shape

144   of each ant. For polymorphic or dimorphic species only measurements of minor-caste workers were

145   included in the analyses.

146   We used log-transformed mean trait values for all analyses, as is routinely done for trait-

147   based studies of continuous morphological characters (Trisos et al. 2014). Morphological traits were

148   strongly and positively correlated (r = 0.65 − 0.96), largely because of their association with overall

149   body size as well as phylogenetic correlations. To prevent these correlations from biasing analyses

150   toward detecting only processes associated with body size, we used ordination techniques (based on

151   principal component analysis) to derive independent trait axes.

Statistical analyses

Principal component analysis

First we compared ant morphological diversity between the two biogeographic faunas (temperate in the Nearctic region and tropical in the Neotropical region), based on a principal component analysis calculated from the correlation matrix of the 14 log-transformed variables measured for all 599 ant species.

Morphological diversity metrics based on multiple traits

We used two standard metrics to quantify morphological diversity: functional diversity (FD: Petchey and Gaston 2002) and convex hull volume (CHV: Cornwell et al. 2006). Morphological diversity is a measure of how dispersed a set of species is in the trait space (Petchey and Gaston, 2002), while CHV is the smallest convex set in trait space enclosing all species trait values within a community (Cornwell et al. 2006). We selected FD and CHV because they are widely used with presence/absence data and have been shown to have a relatively high power to detect trait clustering (CHV) and overdispersion (FD) in community assembly simulations (Mouchet et al. 2010, Aiba et al. 2013). We calculated FD and CHV using three derived trait principal axes that were centered and relative to the species pool (i.e., the full data set of trait values for each region; see also Villéger et al. 2008). Because they test concurrently for habitat filtering and niche differentiation, both FD and CHV are considered to be multiple-niche-axis metrics (Trisos et al. 2014).

We also estimated mean morphological diversity (MPD) and mean nearest-neighbor distance (MNND), both of which have been used commonly as measures of community relatedness and have been the subject of previous power analyses (Kraft et al. 2007, Trisos et al. 2014) (Table 2). MPD is the mean of pairwise distances between co-occurring species and is most sensitive to tree-wide patterns of morphological clustering and evenness (Trisos et al. 2014). Mean pairwise-distance measures the volume of all species in a community within the morphological space (Webb 2000).

176 MNND is the mean of the morphological distances separating each species from its closest co-

177 occurring relative and is most sensitive to patterns of morphological clustering or evenness at the

178 tips from a cluster dendrogram of morphological similarity (Kraft et al. 2007); MNND measures

179 how clumped species are in morphological space (Webb 2000).

180   Further, we analyzed each derived trait axis individually using metrics to test for both

181 assembly patterns (clustering and overdispersion) and metrics used to test for only one assembly

182 pattern (Table 2). We focused on three multi-pattern metrics (Trisos et al. 2014): (1) FD applied to a

183 single trait axis; (2) variance in species values within an assemblage along a single trait axis; and

184 (3) range in species trait values within an assemblage. Variance and range have also been used as

185 measures of trait clustering (Stubbs and Wilson 2004, Kraft et al. 2008, Kraft and Ackerly 2010).

186 We also used one single pattern metric, SD of MNND (the standard deviation of the distances

187 between neighboring species along a single trait axis). This latter index quantifies evenness of

188 species dispersion or packing in morphological space, and is used only to detect the regular spacing

189 in species trait values predicted by competitive exclusion (Kraft and Ackerly 2010). We calculated

190 these metrics using two derived trait principal axes that were centered and relative to the species

191 pool (i.e., the data set of trait values for each regional species pools separately).

192   We tested differences in morphological diversity between tropical and temperate ant

193 assemblages using linear mixed effect models (LMEs) with a random intercept and random slope

194 terms. We compared models with the same random effect structure but different fixed structure (i.e.,

195 morphological diversity ~ observed species richness or morphological diversity ~ observed species

196 richness + region); the random structure was observed species given region. The LMEs allow us to

197 compare morphological diversity between regions accounting for species richness differences in the

198 ant assemblages. We used the *lmer* function in nlme version 3.1-128 (Pinheiro et al. 2016) to build

199 the models.

200 ***Morphological diversity metrics based on single traits***

201   We also selected eight "priority" ant traits to calculate community metrics of spacing of trait

202   values (range, variance, SD, mean, kurtosis and skewness), to explore deterministic process in the

203   communities. For example, if habitat filtering occurred at the sampling scale, the range of observed

204   trait values would be smaller than that expected under a null model. Whereas the range is useful to

205   detect effects of a habitat filter, it does have the statistical downside of being susceptible to extreme

206   observations that could be due to mass effects (Shmida and Wilson 1985). For this reason, it is

207   important to present results for both range and variance of the traits (Cornwell and Ackerly 2009).

208   Note that habitat filtering may reduce variance but it may also be affected by niche differentiation.

209   Habitat filtering restricts the range of trait values and the limits of similarity affect spacing

210   (Cornwell and Ackerly 2009); both of these processes are likely to affect the variance of trait values

211   among species within a community. Habitat filtering may shift the mean of the trait distribution

212   relative to a null expectation (but also can occur without this effect; Kraft et al. 2008). Likewise, if

213   niche differentiation is occurring, the kurtosis of the distribution of trait values, will be smaller than

214   expected from a null model (Stubbs and Wilson 2004, Cornwell and Ackerly 2009).

215   We calculated the variance, SD, range, mean, skewness, and kurtosis for the eight selected

216   ant traits (HL, SL, EL, MW, DEM, FL, ID, PeH) based on presence-absence of species at a site

217   because we were interested in quantity changes that arise from a replacement of species with

218   different traits, which reflects among-species variation within communities (Cadotte et al. 2010).

219   ***Null models***

220   We used null models to generate expected values of community structure given the observed

221   number of species present at each site. We used null models to help identify patterns in the

222   assemblages rather than to identify specific ecological processes, including those that alter

223   dispersion of a trait (or traits) within a species assemblage as a filter (biotic or abiotic). In the null

224   models, both number of species and occurrence of species in the assemblages were maintained. Null

225   model simulations were conducted in R using functions from Swenson (2014) modified for our

226   datasets. A measure of structure for a particular assemblage was considered significant if it fell

227   outside the extremes of the distribution of random structures generated from the null model (Table

228   2).

229   We defined different species pools to assemble the null communities, constraining which

230   species could disperse to a given location in the tropical and temperate regions. For the tropical data

231   set, we used the Atlantic Forest regions defined by Silva and Brandão (2014) and for the temperate

232   data set we used the five different EPA Level II ecoregions (Del Toro 2013). The following regions

233   were used in the analysis: temperate data set: (1) Appalachian Forests (18 sites and 63 species), (2)

234   Atlantic Highlands (22 sites and 65 species), (3) Mixed Wood Plains (13 sites and 53 species), (4)

235   Southeastern Coastal Plains (7 sites and 54 species), (7) Southeastern US Plains (7 sites and 44

236   species); tropical data set: (1) high southeastern-south areas (8 sites, 262 species), (2) low

237   southeastern-south areas (6 sites, 229 species), (3) intermediate latitude areas (4 sites, 239 species),

238   and (4) north Atlantic Forest areas northeastern (8 sites, 233 species).

239   ***Environmental gradients and morphological traits***

240   Geographic distributions of ants are affected by a number of environmental characteristics;

241   temperature and precipitation are usually the strongest direct and indirect correlates (Dunn et al.

242   2009, Jenkins et al. 2011, Gibb et al. 2015a) as they possibly affect the amount and distribution of

243   available resources. We therefore tested the hypothesis that aspects of temperature variability and

244   precipitation were important predictors of ant morphological structure. We obtained for each site

245   estimates of precipitation and minimum temperature values based on data from WorldClim climate

246   data layers (Hijmans et al. 2005). Annual precipitation (bioclimatic variable 12) is defined as the

247   sum of all the monthly precipitation estimates; minimum temperature of coldest month (bioclimatic

248   variable 6) is defined as the lowest temperature of any weekly minimum temperature.

249   First, we used Pearson's correlation coefficients to examine the relationships between means

250   of trait values and the two climatic variables. Then, we tested the relationship between the eight

251 selected traits and the two climatic variables. Relationships between trait means and variances in

252 assemblages and climatic variables can be complex, and may exhibit interactions between drivers

253 and non-linear responses (Símová et al. 2015). We examined these complex relationships using

254 multiple regression in which the eight trait values entered as response variables, while all the

255 environmental variables (linear and quadratic terms) and their interaction terms entered the model

256 as driver variables. Because there is a low overlap in climate between tropical and temperate zones,

257 observed relationships could arise solely because of mean trait differences between zones, and

258 without any actual relationship between traits and climate within each zone. Thus, we included

259 region as a term in the model. We used stepwise selection by AIC in the *MASS* package (Venables

260 and Ripley 2002) to determine the best of the multiple regression models. We used a Type III

261 ANOVA to test for the presence of a main effect after model selection using the *anova* function in

262 the *car* package (Fox and Weisberg 2011), as this approach does not depend on the order of

263 explanatory variables in the model.

264 **Results**

265 **The morphospace of temperate and tropical assemblages**

266 The first principal component based on the total dataset represented a general size axis

267 accounting for 79% of the total variance, followed by component 2 (9%, eye size and petiole

268 height) and component 3 (3%, distance of eyes to the mandibles and mandible width) (Fig. 2,

269 Supplementary material Appendix 1, Table A1).

270 **Trait analyses**

271 All results of trait analyses were based on constrained species pools to quantify trait

272 diversity in the ant assemblages. However, unconstrained analyses produced similar results.

273 Tropical assemblages had higher morphological diversity and morphological volume than temperate

274 assemblages (Fig. 3a-b); however, conditional on species richness, MPD and MNND values were

275 not higher in tropical forests than temperate forests (Fig. 3c-d; Supplementary material Appendix 1,

276 Table A2; Appendix 2, Figs. A1-A2). Temperate assemblages had larger variance in size (PC1)

277 whereas tropical assemblages had larger range values. Functional diversity metric (FD) from PC1

278 axis had higher values in tropical assemblages. SD of MNND suggested higher species packing in

279 tropical assemblages as calculated from PC1 axis (Fig. 4a-d). However, the differences in trait

280 diversity values in tropical assemblages as calculated from PC1 axis were not higher than temperate

281 forests given their species richness (Supplementary material Appendix 1, Table A2).

282 **Single trait analysis**

283   The moments of trait distributions indicated clear trait differences between temperate and

284 tropical assemblages. The community mean of traits was strongly different between regions;

285 temperate assemblages had larger values of traits and tropical assemblages higher density of small

286 values (Fig. 5). Further, tropical assemblages had higher asymmetry in mean trait values. On the

287 other hand, the distribution of mean traits calculated from species pools had large overlap between

288 regions (Supplementary material Appendix 2, Fig. A3).

289   Neotropical assemblages had higher right-skewed trait distribution suggesting that most co-

290 occurring species tended to have similar trait values (as also suggested by MNND and SD of

291 MNND) (Supplementary material Appendix 2, Fig. A4). Distance of the eye to the mandibles had

292 larger overlap in skewness distribution at the assemblage level. However, the distribution of

293 community variance was relatively similar between regions, except for the variance of the distance

294 of the eye to the mandibles in the temperate region (Supplementary material Appendix 2, Fig. A5).

295   Kurtosis had strong differences between regions. In general, temperate assemblages had

296 smaller values, suggesting more platykurtic distribution and indicating an increase in the average

297 trait dissimilarity between co-occurring species (Supplementary material Appendix 2, Fig. A6).

298 Finally, we did not find clear differences in trait ranges; scape length, eye length and the distance of

299 the eye to the mandibles had large overlaps in range of values (Supplementary material Appendix 2,

300 Fig. A7).

Null model analysis

301

302   Overall, we found weak evidence of habitat filtering or niche differentiation at the

303 assemblage scale. Non-random values in the morphological metrics were rarely observed. The

304 proportion of temperate assemblages in which we detected significant values in the metrics ranged

305 from less than 1 to 16% and was rarely observed in the Neotropical region. Habitat filtering was

306 detected more commonly in the temperate assemblages, especially for the moments of trait

307 distributions for eight selected ant traits (Supplementary material Appendix 1, Table A3). This

308 pattern also was detected for single trait analysis (PC1 or PC2), although significant results

309 decreased when PC2 was considered (probably because PC2 had a very low contribution to the

310 variance in the morphospace). Significant lower morphological diversity than expected was

311 detected mainly in temperate assemblages (Supplementary material Appendix 1, Table A3, for

312 multiple trait metrics). Null models testing using constrained species pools yielded similar deviation

313 from the null expectation, consistent with the results of unconstrained analysis (Supplementary

314 material Appendix 1, Table A4).

315 **The relationship between assemblage trait variation and climate**

316   Mean trait values of all 599 measured ant species were characterized by high correlations,

317 which influenced the relationship between trait means and climate variables. Trait means of HL, SL,

318 EL, PeH, DEM, and FL all were best explained by the region term in the model, without climate

319 relationships; tropical assemblages were characterized by lower mean trait values than temperate

320 assemblages. By the other hand, MW and ID means were best explained by the quadratic term of

321 temperature and region; the relationship was concave and trait means values decreased with

322 increasing temperature (Supplementary material Appendix 1, Table A5). The relationship between

323 trait variances and climate were more variable, suggesting that variation in variances in trait values

324 was driven by region and multiple environmental factors. Trait variances of EL, PeH, MW, and the

325 DEM were all best explained by region, without climate relationships; temperate assemblages had

326 larger variance in traits than tropical assemblages. Variance in HL and FL were best explained by

327 the quadratic term of temperature and region; the relationship was concave and variance values

328 decreased with increasing temperature. The quadratic term of precipitation, region and the

329 interaction term between temperature and precipitation were the best predictors of variance in SL.

330 Finally, ID had no relationship with region or climate (Supplementary material Appendix 1, Table

331 A5).

Discussion

333 We found strong differences in morphological space occupied by ant communities in

334 temperate and tropical regions. As expected, ant communities in tropical areas showed higher

335 morphological diversity; however, temperate ant communities showed higher variance in size. We

336 found evidence that tropical assemblages harbor higher levels of morphological diversity that the

337 temperate-zone ants. In general, more diverse niches and fewer gaps within the total niche space are

338 expected in diverse tropical communities than in those from similar habitats containing fewer

339 species at higher latitudes (Winemiller et al. 2015).

340 Although there was an overall higher diversity of traits in the tropics, we unexpectedly did

341 not find more tightly packed species in the tropics within the trait space. Such species packing could

342 result from a lack of biotic interactions (or Connell's "ghost of competition past"), low population

343 sizes reducing the encounter rate of species, or finer partitioning of local scale environmental

344 gradients (Swenson and Weiser 2014). It is interesting that different results (higher functional

345 diversity and species packing) were found in comparisons of plant functional diversity between

346 North and South America (Swenson et al. 2012). Recent studies on phylogenetic structure of

347 arboreal (Blaimer et al. 2015) and leaf-litter ant communities (Donoso 2014) also have suggested

348 that habitat filtering structures the communities in humid forests, selecting for related species with

349 similar ecological traits and leading to a clustered pattern. By contrast, in temperate forests of North

350 America and Europa, Machac et al. (2011) found evidence either for overdispersion or random

351 structure at lower elevation and clustering at high elevation sites.

352 Because temperate-zone ant communities showed similar species packing (quantified as the

353 mean nearest neighbor distance in multivariate trait space), we hypothesize that the higher

354 morphospace volume and functional diversity in tropical communities occurs via an increase in the

355 morphological volume. This also suggests that as species are added to assemblages they tend to

356 expand the volume to a greater degree than they pack the functional volume.

357 *Null models and morphological structure*

358 There was little evidence within either temperate or Neotropical ant assemblages of habitat

359 filtering or niche differentiation patterns based on our null models, although as expected, habitat

360 filtering was detected more commonly in the temperate-zone ant assemblages. In abiotically harsh

361 environments assemblages should contain a non-random subset of species that are more

362 functionally similar than expected (Swenson et al. 2012). The absence of both clustering and

363 overdispersion in traits has been reported fairly widely in plants and for some animal communities

364 at local scales, and is typically interpreted as evidence for a neutral model of community assembly

365 (Trisos et al. 2014). The use of multiple niche axis metrics, as mean pairwise morphological

366 distances (a measure of overall dispersion of morphology for each local assemblage), detected that

367 16% of temperate assemblages had lower than expected functional diversity given their observed

368 species richness. In fact, niche filtering rather than niche partitioning appears to structure ant

369 assemblages in temperate forests in the south-eastern United States (Fowler et al. 2014). It is

370 relatively well known that processes that shape ant communities depend on spatial scale and likely

371 vary among ecosystems (Nipperess and Beattie 2004, Gotelli and Ellison 2002, Sanders et al. 2007,

372 Fowler et al. 2014).

373 We found weak patterns of niche differentiation in the tropical dataset. Community ecology

374 studies generally predict that niche differentiation will be a dominant influence on community

375 assembly in the tropics (Algar et al. 2011, Winemiller et al. 2015). Our null model analysis may be

376   potentially biased because the analyzed scale may be inadequate to detect niche differentiation

377   evidences. However, similar analyses for the tropical data set by Silva and Brandão (2014) using a

378   smaller number of traits and constrained pool null models also did not find strong evidences of

379   under- or overdispersion in the leaf-litter ant fauna, but suggested shifts in the morphospace

380   structure along the latitudinal gradient. In this case, co-occurrence analysis at sample point scale (1

381   m^2) or constrained by guilds can be particularly informative (Silva and Brandão 2014) because

382   patterns of morphological structure should be more probable within, rather than across feeding

383   guilds.

384   The prediction that under more harsh climatic conditions the North America assemblages

385   should be constrained more often by habitat filtering also was supported only weakly by

386   examination of a single niche axis. Our result appear to contradict recent studies on habitat filtering

387   that found strong significant evidence for convergence in ant communities traits in North America

388   (e.g., Fowler et al. 2014). In conclusion, we did not find strong pattern of non-random convergence

389   or divergence in traits when comparing to the species pool of temperate or tropical regions. Rather,

390   the link between ecological assembly processes and trait patterns might be complex and weak

391   (Gerhold et al. 2015).

392   *Single trait analysis*

393   The use of selected single traits to compare trait distribution between assemblages was

394   useful in describing differences between regions. We suggest that focused analysis of single traits

395   may be an important approach to compare and describe the distribution of ant functional diversity.

396   Trait-based metrics combine multiple traits into a single analysis (e.g., functional diversity) and

397   because different traits are often associated with different niche axes, these metrics may have the

398   advantage of providing an integrated overview of community structure (Trisos et al. 2014).

399   However, if different assembly processes act on separate traits or exert combined effects, a potential

400   drawback is that multiple-traits may combine signals of contrasting assembly processes (Swenson

401 and Enquist 2009, Trisos et al. 2014).

402   The moments of trait distributions showed marked differences between temperate and

403 tropical assemblages. For example, the distribution in size of ant attributes was strongly right

404 skewed, indicating higher density of smallest ants in tropical sites. The bulk of leaf-litter ant species

405 is composed by very small species, spanning diverse trophic groups (generalist and specialist

406 predators, omnivorous species, from small to medium size; Silva and Brandão 2010, Donoso,

407 2014).

408   Single trait analyses revealed not only differences between ant morphology in tropical and

409 temperate assemblages, but also different within-region responses of traits in variance, kurtosis,

410 skewness and range. Although there was a high correlation between traits, the analysis of the

411 moments of trait distributions suggested that all selected traits can be important to detect differences

412 in morphological structure. In particular, both variance and kurtosis in the distance of the eye to the

413 mandible insertion showed it to be the strongest difference comparing assemblages and we suggest

414 that it may be an important attribute to trait-based analysis of ant communities. Eye morphology

415 seems to be particularly important in trait-based studies; eye relative size in ants is related to period

416 of activity (Yilmaz et al. 2014), degree of predatory behavior (Fowler et al. 1991), determines the

417 ability to see laterally, and influences the success of species travelling through complex habitats

418 (e.g., leaf-litter habitat) (Gibb and Parr 2013).

419   The trait distributions in skewness or kurtosis also suggest that in Neotropical ant

420 assemblages most co-occurring species tend to have similar traits, whereas in temperate

421 assemblages there tends to be on average higher trait dissimilarity between co-occurring species. In

422 fact, the results of multiple trait analysis suggest that temperate communities have higher trait

423 dissimilarity than tropical communities. Of course, tropical species exhibit an extraordinary variety

424 of adaptations molded by their interactions with resources, competitors, and antagonists (Ricklefs

425 2012). In sum, our results suggest that the larger tropical species pools occupy a morphological

426   space distinct from that of temperate species but not a more tightly packed morphospace.

427   In general, we can confidently describe that leaf-litter ant fauna in the Neotropics as

428   composed by more specialist taxa (Delabie et al. 2000) and that the epigaeic temperate-zone ant

429   fauna includes predominantly opportunistic and omnivorous feeders species (Ellison et al. 2013).

430   The range distribution of a petiole measure, as such petiole height, showed strong difference

431   between tropical and temperate ant assemblages. Ant petiole measures may be used to describe

432   morphological groups of species, especially for predator species (Silva and Brandão 2014). We

433   suggest that petiole measures also should be considered to understand how ant traits respond to

434   environment, especially in the tropics where predators are often an important component of

435   communities.

436   Taken together, the results of single trait analysis suggest that choosing traits that can be

437   used to test hypotheses can be important for detecting differences in morphological structure of ant

438   communities, especially when considering effects of disturbance and climatic change on

439   assemblage structure. Our results also support a recent trend in community ecology that proposes

440   not only the integration of data sets but also their subdivision into niche axes before analysis

441   (Spasojevic and Suding 2012, Trisos et al. 2014, Winemiller et al. 2015).

442   *Ant traits and habitat characteristics*

443   Ant traits have been shown to respond to habitat characteristics such as structural

444   complexity (Farji-Brener et al. 2004, Gibb and Parr 2010, Yates et al. 2014). For example, leg

445   length decreases with habitat complexity (Farji-Brener et al. 2004, Sarty et al. 2006, Gibb and Parr

446   2010). Gibb and Parr (2013) extended analysis testing morphological trait responses to habitat

447   complexity in sites on three continents, finding predictive responses of sensory morphology of ant

448   assemblages to habitat complexity. Eye position has been suggested as a key response variable to

449   predatory behavior (Silva and Brandão 2014) and habitat complexity (Gibb and Parr 2013). Clear

450   differences between macrohabitats in in ant's scape length, eye size, leg length, and body size have

451 been described (Yates et al. 2014, Schofield et al. 2016); further, ant morphology may respond to

452 competition (Nipperess and Beattie 2004).

453   Temperature and precipitation are considered drivers of ant species richness patterns at

454 global scale (Dunn et al. 2009, Jenkins et al. 2011, Gibb et al. 2015a) and recent studies also suggest

455 a strong relationship between temperature and ant functional responses (Diamond et al. 2012,

456 Stuble et al. 2013). Ant functional diversity decreased with reduced temperature in a high elevation

457 gradient (Raymond et al. 2013) and climate seasonality played an important role in shaping the

458 occurrence of functional species traits in Mediterranean ant communities (Arnan et al. 2014). Our

459 analysis suggests that trait mean values all were correlated with region; size also decreased with

460 increasing temperature for some traits. Our environmental model largely reflects the smaller ants in

461 tropical assemblages. On the other hand, the environmental model for trait variances largely reflects

462 the higher variance in ant traits in temperate assemblages. However, the response of trait variances

463 was more complex and the explained variance by models was lowest compared to the trait mean

464 model. For example, head length, and femur length correlated negatively with temperature.

465 Interactions between temperature and precipitation were detected for trait related to food search (as

466 scape length), suggesting that relationships between climate and traits varies for ants among

467 regions.

468 *Concluding remarks*

469   The human-induced extinction of species in the Anthropocene (Dirzo et al. 2014) with

470 ongoing biotic impoverishment may alter key ecosystem processes with important consequences for

471 ecosystem services needed by the humanity (Mouillot et al. 2014). Our results indicate that ant traits

472 respond to environmental gradients and single trait analysis may be an important approach to

473 analyze the loss of particular functions delivered by ants. This approach may guide future studies on

474 ant responses to habitat modification and climate change. Although many aspects of the

475 morphological structure in ant communities are as yet unexplored (including the relationship

476　between morphology and the variety of resources), our results underline the importance of

477　morphological analyses in arthropod communities and point out to the need for more through

478　characterization of morphological space for modeling the impacts of habitat disturbance and climate

479　change on morphological diversity.

480　**Acknowledgments**

484

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656

657   **Table 1.** The fourteen ant traits used in this study, the code given to each trait and a description of
658   the functional significance of traits.

659

Morphological trait	Code	Functional significance
Head Length	HL	Indicative of diet; longer heads may accommodate larger mandibular muscles that allow capture or larger or fiercer prey (Fowler et al. 1991).
Head Width	HW	Size of spaces through which ant can pass (Sarty et al. 2006); wider heads may accommodate larger mandibular muscles that allow capture of larger or fiercer prey
Mandible Width	MW	May indicate feeding behavior; wider mandibles may cut and masticate larger food resources; further may keep, transport and hold larger preys (Fowler et al. 1991).
Mandible Length	ML	Longer mandibles permit attack larger prey; narrow, sublinear to linear and long mandibles describe species with trap-jaw mandibles employed for hunting.
Clypeus Length	CL	Clypeus length is related to sugar feeding in ants (Eisner 1957).
Scape Length	SL	Sensory morphology, related to an ant's ability to navigate, sense and move through its surroundings (Yates et al. 2014).
Eye Length	EL	Eye size indicates feeding behavior (Yates et al. 2014); hypogaeic predatory ants have smaller eyes, whereas epigaeic predatory ants have greater eyes.
Interocular Distance	ID	Eye position; eyes set farther apart may be important in more complex habitats (Gibb and Parr 2013). Also indicates feeding behavior; hypogaeic predatory ants have eyes set very close to the mandible; epigaeic predatory ants or generalist species have eye set away from the mandibles.
Distance of the eye to the mandible insertion	DEM	
Pronotum Width	PW	Size of spaces through which ant can pass (Sarty et al. 2006); narrow pronotum may permit access to resources in small cavities; also, it is a proxy for size in ants.
Weber's Length	WL	Proxy for body size in ants; strongly correlated with many physiological, ecological, and life-history traits, including as resource use (Arnan et al. 2014).
Femur length	FL	Longer legs enable species to discover food resources more quickly (Gibb and Parr 2013); there appears to be some advantage to shorter-legged species in more complex habitats (Farji-Brener et al. 2004).
Petiole Length	PeL	The dimensions of petiole (length, height and width) are related to trophic position and predator behavior (Silva and Brandão 2010).
Petiole Height	PeH	

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662 **Table 2.** List of selected morphological metrics, hypothesis tested, predictions, and description of the biological significance.

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	Hypothesis	Expected (values)	Expected (p-value)	Description
Multiple-traits metrics				
FD	Habitat filtering and niche differentiation	Lower or higher than the null model	≤ 0.025 or ≥ 0.975	Small values means similar co-occurring species or low FD; high values means dissimilar co-occurring species or high FD (Kraft et al. 2007, Mouchet et al. 2010, Swenson 2014).
CHV	Habitat filtering and niche differentiation	Lower or higher than the null model	≤ 0.025 or ≥ 0.975	
MPD	Habitat filtering and niche differentiation	Lower or higher than the null model	≤ 0.025 or ≥ 0.975	
MNND	Niche differentiation	Higher than the null model	≥ 0.950	If specie's traits reflect partitioning, we would then expect a non-random, even spacing of trait values within communities; in general, decrease with increasing species richness (Kraft et al. 2007, Swenson 2014).
Single-axis PCA metrics				
FD	Overdispersion or clustering	Lower or higher than the null model	≤ 0.025 or ≥ 0.975	Small values means similar co-occurring species or low FD; high values means dissimilar co-occurring species or high FD.
Variance	Overdispersion or clustering	Lower or higher than the null model	≤ 0.025 or ≥ 0.975	Trait variance within an assemblage lower than expected from regional species pool reflects a decrease in the available niche space (Stubbs and Wilson 2004, Kraft and Ackerly 2010).
Range	Overdispersion or clustering	Lower or higher than the null model	≤ 0.025 or ≥ 0.975	Assembly processes can restrict the range of trait values at a given community; another processes (e.g. limit of similarity) can influence the spacing of trait values within the restricted range (Stubbs and Wilson 2004, Kraft and Ackerly 2010).
SD of MNND	Niche differentiation	Higher than the null model	≥ 0.950	Similar to MNND, used to detect only the regular spacing in species trait values (Kraft and Ackerly 2010, Trisos et al. 2014).
Moments of the trait distributions for communities				
Variance	Habitat filtering	Lower than the null model	≤ 0.050	Assembly processes can restrict the variance of trait

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				values at a given community (Swenson 2014).
SD	Habitat filtering	Lower values than the null model	≤ 0.050	Higher standard deviation values are indicative of more functional diversity in a community; co-occurrence of functionally similar species will be reflected by a lower standard deviation (Swenson 2014).
Range	Habitat filtering	Lower than the null model	≤ 0.050	Assembly processes can restrict the range of trait values at a given community (Kraft and Ackerly 2010, Swenson 2014).
Skewness	Habitat filtering	Higher values than the null model	≥ 0.950	Higher values indicate that most co-occurring species tend to have similar traits values (Swenson 2014).
Mean	Habitat filtering	Just "change"	≤ 0.025 or ≥ 0.975	Shifts in site mean trait values indicate environmental filtering, whereby convergent trait values are expected for co-occurring species due to environmental trait selection; habitat filtering affect mean trait values through differences in species composition, species abundance, and phenotypic plasticity (Swenson 2014).
Kurtosis	Niche differentiation	Lower values than the null model	≤ 0.050	Lower values (platykurtic distribution) may indicate an increase in the average trait dissimilarity between co-occurring species; a process that spreads species trait values in communities, result in lower values than expected distribution within communities (Swenson 2014).

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667 **Figure 1.** Study sites along two latitudinal gradients in temperate forests and in the South American

668 Atlantic Forest (A), and frequency distributions of mean annual temperature in the regions (B).

669 **Figure 2.** The morphological distribution on one size and one shape principal component axis for

670 tropical (light gray dots) and temperate-zone forest (black dots) ants morphospace (N= 599).

671 **Figure 3.** Four measures of distance between species (multiple-axis metrics) in the morphospace

672 plotted as functions of the number of species in the ant assemblages in the temperate and tropical

673 regions: (a) Morphological Diversity (FD), (b) convex hull volume (CHV), (c) mean morphological

674 distance (MPD), and (d) mean nearest morphological distance (MNND). Each metrics was calculated

675 using species scores on the first three principal component axes, derived from constrained species pools

676 for each region separately; each species is a composite of fourteen traits.

677 **Figure 4.** Four measures of distance between species (single-axis metrics) in the morphospace plotted

678 as functions of the number of species in the ant assemblages in the temperate and tropical regions. (a)

679 Variance, (b) Range, (c) standard deviation of MNND (SD of MNND), and (d) Functional Diversity

680 (FD). Each metrics was calculated using PC 1 axis, derived from constrained species pools for each

681 region separately; each species is a composite of fourteen traits.

682 **Figure 5.** Frequency distributions of trait means at assemblage scale in the temperate and tropical
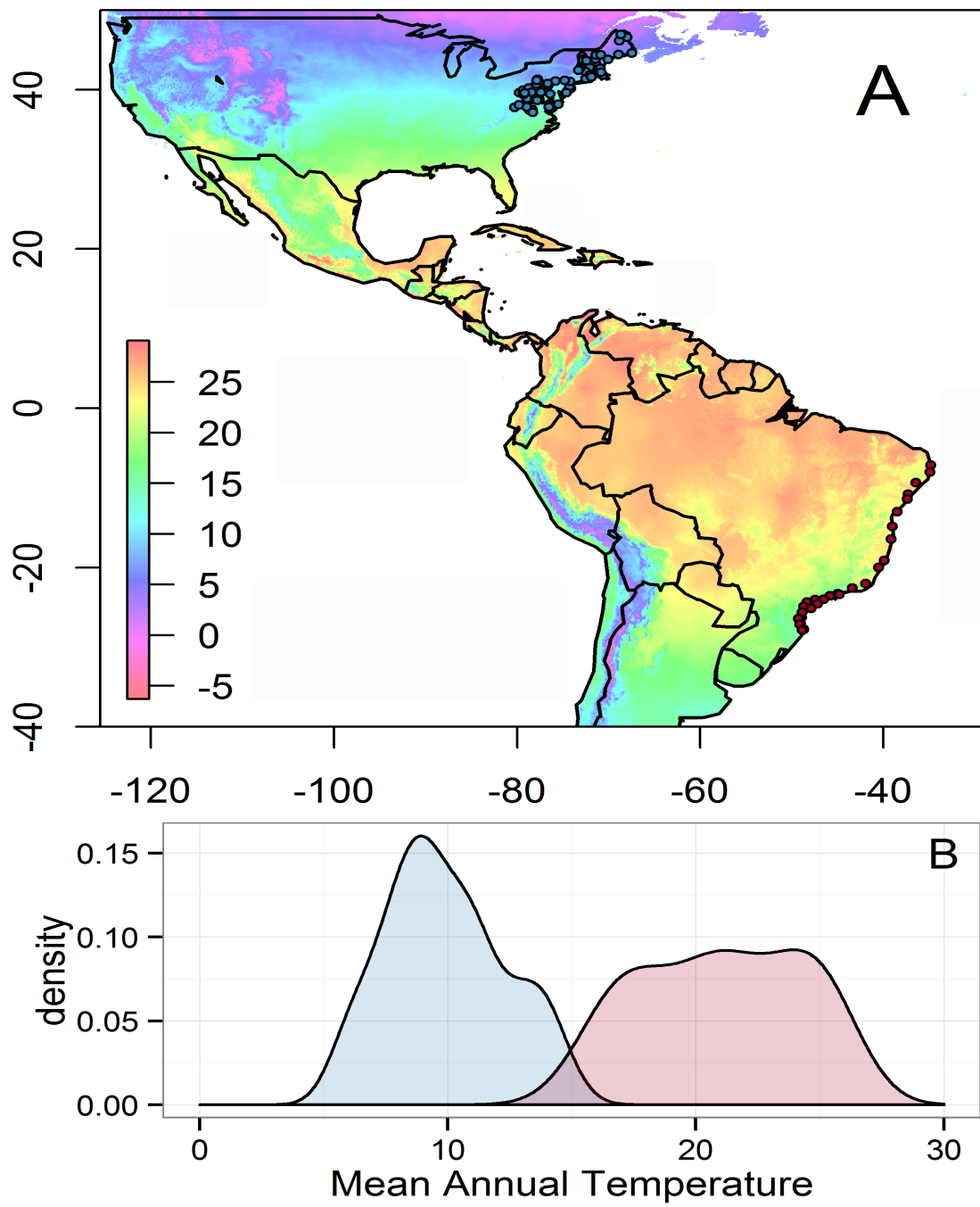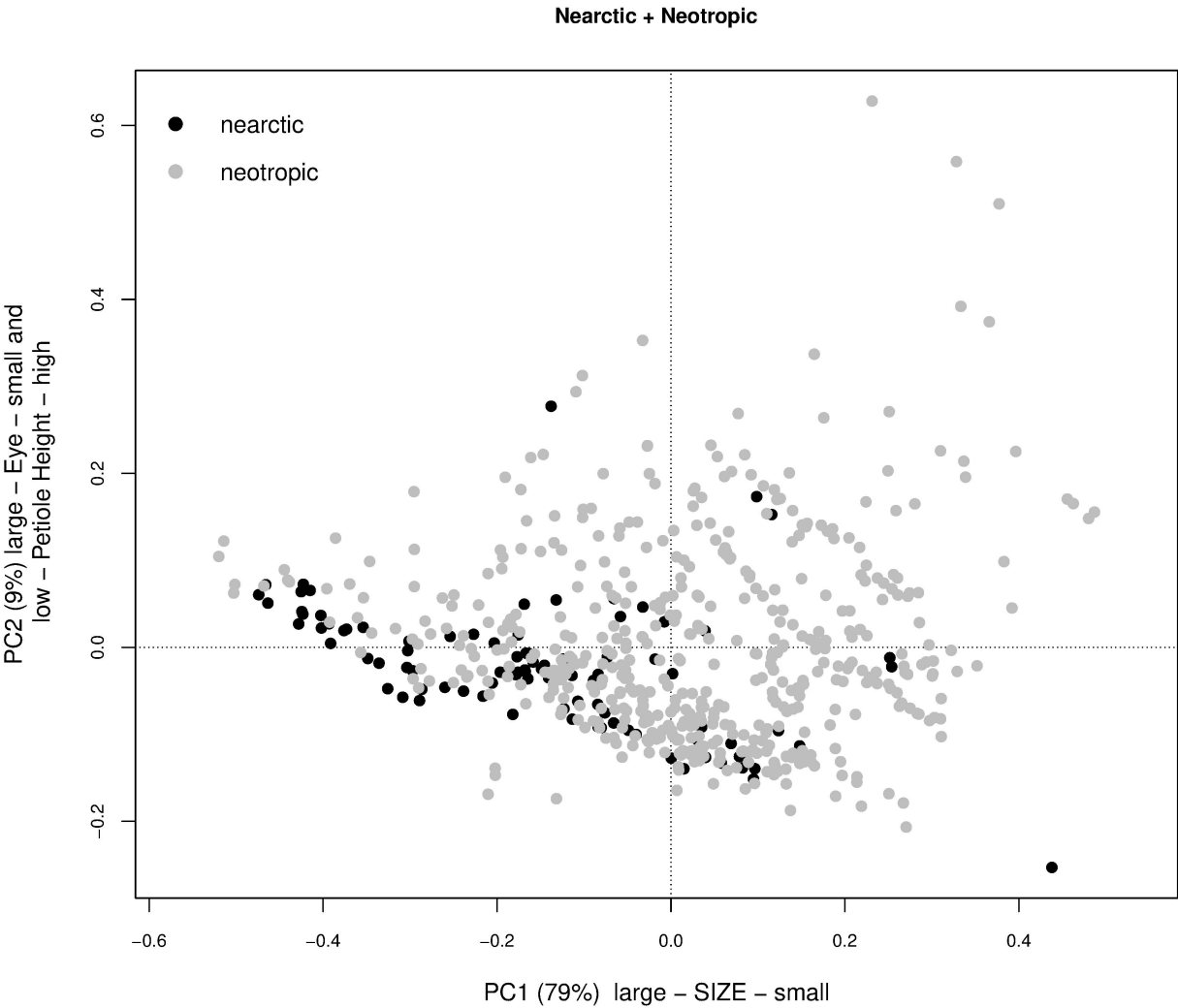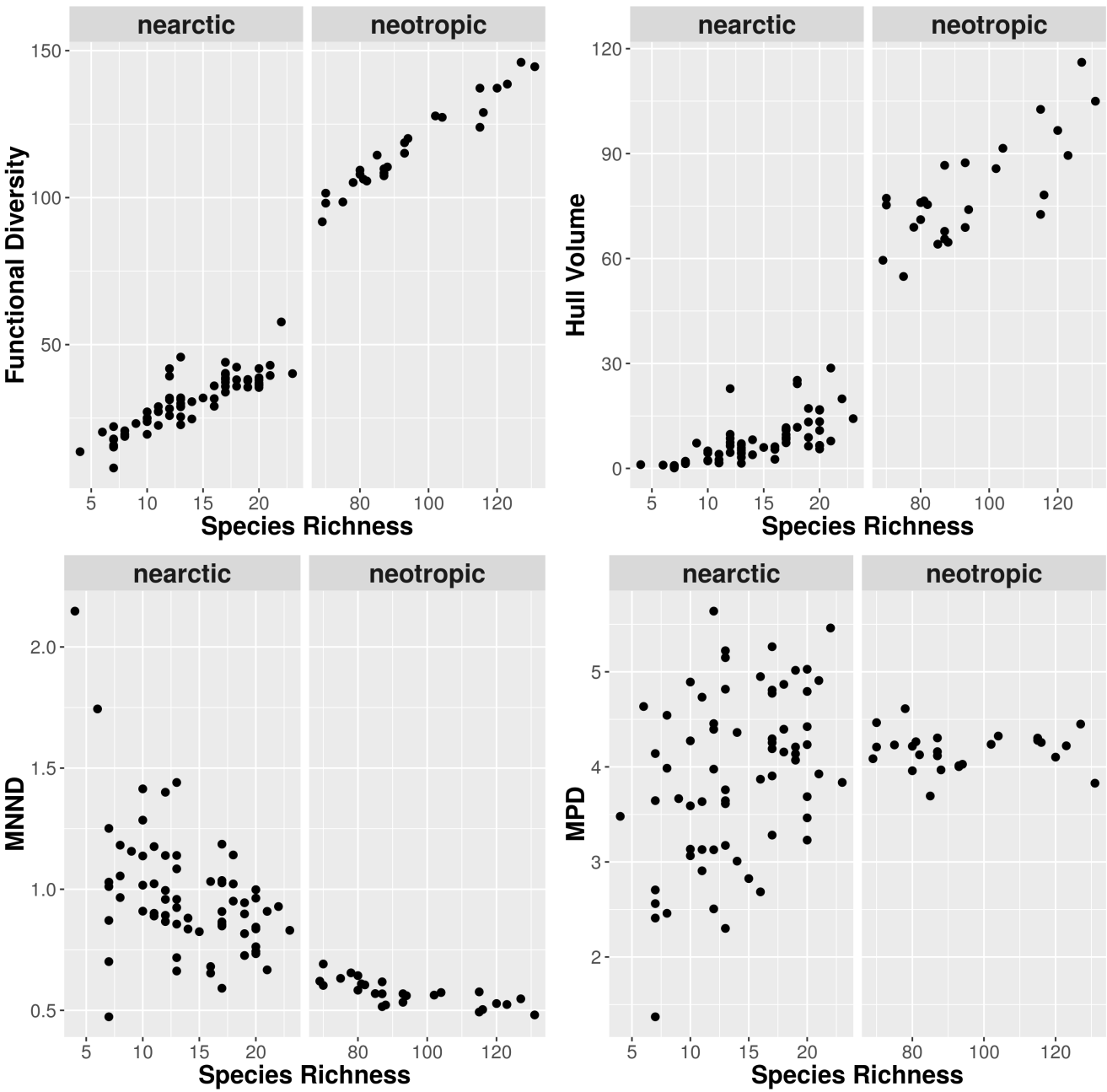
683 regions.

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Fig. 1

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Fig. 2

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Nearctic + Neotropic

693 **Fig. 3**

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699 **Fig. 5**

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Trait means