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Different environmental gradients affect different measures of snake β -diversity in the Amazon rainforests

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Mechanisms generating and maintaining biodiversity at regional scales may be evaluated by quantifying β -diversity along environmental gradients. Differences in assemblages result in biotic complementarities and redundancies among sites, which may be quantified through multi-dimensional approaches incorporating taxonomic β -diversity (TBD), functional β -diversity (FBD) and phylogenetic β -diversity (PBD). Here we test the hypothesis that snake TBD, FBD and PBD are influenced by environmental gradients, independently of geographic distance. The gradients tested are expected to affect snake assemblages indirectly, such as clay content in the soil determining primary production and Height Above the Nearest Drainage (HAND) determining prey availability, or directly, such as percentage of tree cover determining availability of resting and nesting sites, and climate (temperature and precipitation) causing physiological filtering. We sampled snakes in 21 sampling plots, each covering 5 km², distributed over 880 km in the central-southern Amazon Basin. We used dissimilarities between sampling sites to quantify TBD, FBD and PBD, which were response variables in multiple-linear-regression and RDA models. We show that patterns of snake community composition based on TBD, FBD and PBD are associated with environmental heterogeneity in the Amazon. Despite positive correlations between all β -diversity measures, TBD responded to different environmental gradients compared to FBD and PBD. Our findings suggest that multi-dimensional approaches are more informative for ecological studies and conservation actions compared to a single diversity measure.

1 **Different environmental gradients affect different measures of snake β -diversity in the**
2 **Amazon rainforests**

3

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Abstract

Mechanisms generating and maintaining biodiversity at regional scales may be evaluated by quantifying β -diversity along environmental gradients. Differences in assemblages result in biotic complementarities and redundancies among sites, which may be quantified through multi-dimensional approaches incorporating taxonomic β -diversity (TBD), functional β -diversity (FBD) and phylogenetic β -diversity (PBD). Here we test the hypothesis that snake TBD, FBD and PBD are influenced by environmental gradients, independently of geographic distance. The gradients tested are expected to affect snake assemblages indirectly, such as clay content in the soil determining primary production and Height Above the Nearest Drainage (HAND) determining prey availability, or directly, such as percentage of tree cover determining availability of resting and nesting sites, and climate (temperature and precipitation) causing physiological filtering. We sampled snakes in 21 sampling plots, each covering 5 km², distributed over 880 km in the central-southern Amazon Basin. We used dissimilarities between sampling sites to quantify TBD, FBD and PBD, which were response variables in multiple-linear-regression and RDA models. We show that patterns of snake community composition based on TBD, FBD and PBD are associated with environmental heterogeneity in the Amazon. Despite positive correlations between all β -diversity measures, TBD responded to different environmental gradients compared to FBD and PBD. Our findings suggest that multi-dimensional approaches are more informative for ecological studies and conservation actions compared to a single diversity measure.

47 **Introduction**

48 Investigating how environmental gradients influence community structure is crucial to
49 understanding mechanisms and processes affecting biodiversity at different scales (*Keddy, 1992*).
50 Quantifying species-habitat associations across continuous landscapes helps disentangle the
51 mechanisms generating and maintaining patterns of regional and local biodiversity. This has
52 been widely demonstrated in the Amazon rainforests by estimates of assemblage β -diversity
53 associated with environmental gradients at mesoscales (e.g., *Drucker, Costa & Magnusson,*
54 *2008; Fraga, Lima & Magnusson, 2011; Bueno et al., 2012; Ribeiro-Jr, Lima & Magnusson,*
55 *2012; Rojas-Ahumada, Landeiro & Menin, 2012; Moulatlet et al., 2014; Menger et al., 2017*). In
56 general, levels of β -diversity across heterogeneous continuous landscapes has been estimated
57 through biotic complementarities and redundancies among sites. Most studies focused on
58 measures of β -diversity based on between-site dissimilarities in quantitative (based on abundance
59 data) and qualitative (presence/absence data) species composition. However, use of multiple
60 dimensions may be more informative, because different diversity measures often carry
61 complementary information (*Devictor et al., 2010; Weinstein et al., 2014*).

62 Numerous methods have been developed to quantify β -diversity, and each method
63 potentially gives different insights into the mechanisms driving biodiversity (*Dehling et al.,*
64 *2014*). Values of taxonomic β -diversity (TBD) may change across heterogeneous landscapes in
65 response to variation in availability of resources, because of selection for different physiological
66 characteristics, ecological plasticity, intra and interspecific interactions, and dispersal ability
67 (*Mariac et al., 2011; Hangartner, Laurila & Räsänen, 2012*). In general, patterns of community
68 assembly are caused by different portions of environmental gradients providing suitable

69 conditions to habitat-specialist species, while generalists cover larger portions of gradients (e.g.,
70 *Kinupp & Magnusson, 2005*).

71 Estimates of functional β -diversity (FBD) may change across heterogeneous landscapes
72 because function is mediated by phenotypes potentially affecting the species performance and
73 fitness, such as morphological, biochemical, behavioral and phenological traits (*Petchey &*
74 *Gaston, 2002*). Functional traits can be environmentally filtered when environmental
75 heterogeneity is sufficient to cause variation in local adaptation to different selection pressures
76 (*Weinstein et al., 2014*). Additionally, some traits such as foraging mode may determine the
77 ability of snakes to cross different habitat patches in Amazonia (*Fraga et al., 2017*). High levels
78 of FBD are often related to ecosystem dynamics, stability and productivity (*Tilman, 2001*).

79 Estimates of phylogenetic β -diversity (PBD) usually incorporate information on the
80 evolutionary history that is shared among species throughout assemblages (*Milcu et al., 2013*).
81 High values of PBD suggest convergent adaptation among historically isolated assemblages, but
82 recently connected (*Weinstein et al., 2014*), which is expected as a result from timescale
83 variation in stability and connectivity among habitat patches (*Morlon et al., 2011; Jetz & Fine,*
84 *2012*). In the Amazon rainforests, a combination between the Andean uplift and climate change
85 are though as major factors driving habitat evolution, and consequently driving species
86 diversification, dispersal and extinction (*Hoorn et al., 2010*). Alternatively, levels of PBD
87 positively related to FBD suggest assemblages evolutionary structured by niche conservatism
88 (*Wiens & Graham, 2005*).

89 Measures of β -diversity based on between-site differences in TBD, FBD and PBD are
90 more effective at identifying factors shaping community structure than measures of α -diversity,
91 such as number of species or functional groups at particular sites (*Cadotte et al., 2009; Flynn et*

92 *al.*, 2011). This is because mechanisms influencing community assembly act on biotic
93 complementarities and redundancies among sites, and not on the number of organism-units
94 within sites (*Diaz & Cabido, 2001; McGill et al., 2006*). In general, α -diversity measures fail to
95 capture the contribution of each species to the regional diversity, because different sites may
96 have equal values of diversity (e.g., number of species), even if the species found in each site are
97 taxonomically, functionally or phylogenetically distinct. Identifying mechanisms underpinning
98 β -diversity has clear implications for conservation management. These include identification of
99 unique characteristics in the regional diversity, which makes a site irreplaceable and therefore a
100 priority for conservation actions (*Pressey et al., 1993*). This approach has been used to test the
101 efficiency of protected areas in France (*Meynard et al., 2011*), the effects of forest modification
102 on birds and trees in South Africa (*Grass et al., 2015*), and the efficiency of environmental law
103 in Brazil (*Fraga, Lima & Magnusson, 2011; Bueno et al., 2012*).

104 Although much of the Amazon basin appears relatively homogeneous in satellite images,
105 ecological studies at mesoscales have shown that subtle changes along environmental gradients
106 influence patterns of co-occurrence of frogs (*Ribeiro-Jr, Lima & Magnusson, 2012; Rojas-*
107 *Ahumada, Landeiro & Menin, 2012*), understory birds (*Bueno et al., 2012; Menger et al., 2017*),
108 plants (*Costa, Magnusson & Luizão, 2005; Drucker, Costa & Magnusson, 2008*) and snakes
109 (*Fraga, Lima & Magnusson, 2011*). In this study, we sampled a continuous landscape across
110 about 880 km of rainforest, from central to southwest Amazonia. Most species of snakes
111 recorded are widely distributed throughout the Amazon basin and some occur in other
112 ecosystems in South America. However, species do not occupy all sites within their ranges, and
113 different assemblages could be expected even at scales of tens of kilometers (*Fraga, Lima &*
114 *Magnusson, 2011*). The wide distributions indicate that assemblage differences are more likely to

115 result from environmental effects than from historical contingencies, such as dispersal limitation
116 across geographic barriers.

117 In this study we examine the influence of environmental gradients on TBD, FBD and
118 PBD estimates for snake assemblages in the Amazon rainforests. Investigating multiple
119 assemblage dimensions in the same study system potentially allows accessing broad pictures of
120 factors causing and maintaining biodiversity. Snakes are useful organisms to test for
121 multidimensional changes in assemblages over landscapes in the Amazon because of the
122 exceptionally-high species diversity (e.g., *Bernarde et al., 2012*), great species-trait diversity
123 (e.g., body size and colors, reproductive and foraging modes), which implies large variation in
124 functional traits (e.g., *Martins & Oliveira, 1999*), and heterogeneous habitats that potentially
125 affect dispersal and gene flow (*Fraga et al., 2017*). In addition, snakes have been included in
126 estimates of global reptile decline (*Gibbons et al., 2000*), which highlights the importance of
127 assessing a broad picture of mechanisms generating diversity. This is particularly important in
128 the area we sampled, because it is under strong anthropogenic pressure due to rapid urban growth
129 (*Soares-Filho et al., 2006; Fraga et al., 2013a*), deforestation associated with paving the major
130 access road (*Fearnside & Graça, 2006; Soares-Filho et al., 2006*), and flooding by hydroelectric
131 power plants (*Fearnside, 2014*). Few studies have attempted to identify multiple factors driving
132 snake community assembly (e.g., *Fraga, Lima & Magnusson, 2011*). Furthermore, to our
133 knowledge, the standardized sampling effort used over such a large area in this study is
134 unprecedented.

135 We evaluate the effects of environmental gradients on snake assemblages and investigate
136 spatial structuring causing levels of TBD, FBD and PBD among sites. We test the general
137 hypothesis that patterns of community composition in taxonomic, functional and phylogenetic

138 spaces result from current environmental heterogeneity. Additionally, we hypothesize that
139 different β -diversity measures should respond to different environmental gradients, because they
140 carry complementary information on snake assemblages.

141

142 **Materials & Methods**

143 **Snake sampling.** We sampled snakes in 21 RAPELD sampling sites (*Magnusson et al.*,
144 *2005, 2013*), each of which has trails covering 5 km² (5 km separated by 1 km). RAPELD is a
145 Brazilian acronym to accommodate two study scales, rapid assessments (RAP) and long-term
146 ecological research (PELD – in Portuguese, *Pesquisas Ecológicas de Longa Duração*). RAPELD
147 sampling sites will be mentioned throughout the text as modules.

148 In each module, we sampled ten 250 m long by 10 m wide plots with center lines
149 following the altitudinal contours. The plots were distributed along two parallel 5-km long trails
150 (five plots per trail) with standardized distance of 1 km between neighboring plots. The modules
151 were distributed almost linearly over 880 km (Fig. 1) from central (Manaus, Amazonas) to
152 southwest Amazonia (Porto Velho, Rondônia). The study area includes Central Amazonia, to the
153 north of the Amazon River, the interfluvium between the middle regions of the Madeira and Purus
154 rivers, and the upper Madeira River, in southwestern Amazonia. Three modules were installed at
155 the Ducke Reserve, which is a 100-km² fragment of non-flooded primary rainforest, located on
156 the northern outskirts of Manaus. Eleven modules were installed along the federal highway BR-
157 319 that connects Manaus to western Brazil. The highway was largely abandoned in the 1980s,
158 and the modules were installed mainly to enable multi-taxa impact assessments of the effect of
159 the road on biodiversity. Along this road, modules were placed in areas covered by primary and
160 old-secondary rainforest, with patches of flooded forest and *campinarana* (forest on white sand).

161 The southern Madeira River region contains seven modules. The Madeira River was recently
162 dammed by two large hydroelectric power plants in the Porto Velho region, and the modules
163 were installed along the banks of the river for monitoring the effects of flooding on biodiversity.
164 The data used in this study were collected prior to flooding (see details below). The region is
165 covered by primary and secondary rainforest under increasing threat of human occupation.

166 We sampled snakes by nocturnal active visual search, with two observers per plot, and
167 standard searching time of 1 hour per plot. In the Amazon, nocturnal search simultaneously
168 allows finding foraging nocturnal species, and resting diurnal species (field observation). To
169 increase the sampling effort and accuracy in species detection, we undertook four non-
170 consecutive surveys of each plot between 2007 and 2014. We show below that temporal
171 variation (e.g., caused by seasonal environmental variables) in assemblage structure is unlikely,
172 because species composition did not differ among the surveys. Snakes were collected under
173 RAN-ICMBio / IBAMA (Ministry of Environment, Government of Brazil) permanent license nº
174 13777-2/2008 in the name of Albertina Pimentel Lima (coordinator of the sampling expeditions).
175 The license includes ethical approval of all the procedures used.

176 Detection probabilities of snakes are usually very low (*Steen, 2010; Fraga et al., 2014*),
177 and they may bias the results by generating statistical artifacts such as the arc effect (*Gauch,*
178 *1982*), mainly because no species occurrence is shared between sampling units. To avoid
179 statistical artifacts in this study, we used modules as sampling units rather than plots. This results
180 in loss of degrees of freedom, but it increases the predictive power of the analysis because the
181 sampling units usually shared more than one species. All the analyses in this study are based on
182 26 species (Table S1), belonging to four families (Boidae, Colubridae, Dipsadidae and
183 Viperidae).

184 **Taxonomic β -diversity (TBD).** We represented TBD as the scores from a PCoA
185 (Principal Coordinates Analysis) ordination of a matrix of Forbes' similarity index (*Forbes,*
186 *1907*) on species presence/absence data between modules. We transformed Forbes' similarities
187 in dissimilarities between modules by $1 - \text{Forbes}$. The Forbes index has been indicated as robust
188 in the case of incomplete sampling (*Alroy, 2015*), which is common in studies of snakes in the
189 Amazon due to the low detection probabilities of most species (*Fraga et al., 2014*). The PCoA
190 was undertaken in the vegan package (*Oksanen et al., 2015*) in R (*R Development Core Team,*
191 *2015*).

192 **Functional β -diversity (FBD).** We constructed a trait matrix using ten continuous and
193 discrete traits, measured or observed for adult individuals only. These were maximum total
194 length, tail length proportional to body length, diameter of the eye proportional to head length,
195 maximum size of offspring, discrete habitat (aquatic, arboreal, cryptozoic, fossorial, terrestrial),
196 period of activity (diurnal, nocturnal), foraging mode (ambush, active), diet (birds, bird eggs,
197 centipedes, earthworms, frogs, fish, lizards, mammals, snails, snakes, Squamata eggs, tadpoles),
198 defensive behavior (ball posture, bite, caudal autotomy, cloacal discharge, constriction, enlarged
199 head, flattened body, hidden head, inflated neck, liana imitation, shown mucosa, sound, strike,
200 tail shaking, tail sting, venom, vomit) and reproductive mode (oviparous, viviparous). All the
201 traits used have been described as ecologically relevant for snakes (literature compilation in
202 *Burbrink & Myers, 2015*). Further details on functional traits may be found in Table S2.

203 The continuous traits were measured, and we used average values per species (see
204 *Petchey & Gaston, 2006*). For the species for which we found less than five individuals, we
205 supplemented our data with published data (*Beebe, 1946; Belluomini & Hoge, 1958; Duellman,*
206 *1978; Cunha & Nascimento, 1983; Dixon & Soini, 1986; Michaud & Dixon, 1989; Cunha &*

207 *Nascimento, 1993; Starace, 1998; Martins & Oliveira, 1999; Fraga et al., 2013a*). We also
208 obtained most of the data for discrete traits per species from the literature, and they were
209 supplemented with field observations. The levels of most discrete traits are not mutually
210 exclusive (*e.g.* species which feed on a variety of prey), so we coded discrete traits into
211 independent binary traits as suggested by *Petchey & Gaston (2007)*.

212 We used the trait matrix to estimate FBD using the dFBD function in the FD R-package
213 (*Laliberté & Legendre, 2010; Laliberté, Legendre & Shipley, 2014*). This function calculates
214 Gower distances between species, which is an index thought to be more appropriate when
215 analyzing mixed continuous and discrete traits, although the results are often strongly correlated
216 with Euclidean distances (*Petchey & Gaston, 2007*). The dFBD function transforms the Gower
217 distance matrix by calculating square roots. This is important to avoid negative eigenvalues in
218 the PCoA calculated from the distance matrix, which should be set in Euclidean space to avoid
219 biased estimates of FD (*Laliberté & Legendre, 2010*). PCoA was used to obtain scores
220 representing four different functional indices (*Villéger, Mason & Mouillot, 2008*), which are
221 functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and
222 functional dispersion (FDis). In this study, we represented FBD using FDis, because this index
223 estimates functional β -diversity based on average distances to the centroid of multivariate
224 dispersion (*Anderson, 2006*). FDis has been described as a β -diversity index which is not
225 affected by species richness, it can handle any number and type of traits and it is little biased by
226 outliers (*Anderson, Ellingsen & McArdle, 2006*).

227 We visually controlled the robustness of the FBD estimate by constructing a functional
228 tree (Fig. S1) based on Gower pairwise distances between species, which was calculated in the
229 vegan R-package (*Oksanen et al., 2015*). We undertook a hierarchical cluster analysis on the

230 Gower dissimilarity matrix to build an UPGMA functional tree, using the hclust function
231 (argument average) in R.

232 **Phylogenetic β -diversity (PBD).** We estimated PBD based on a well-supported
233 phylogenetic hypothesis proposed by *Pyron, Burbink & Wiens (2013)*. Phylogeny of Squamata
234 reptiles was reconstructed by analyzing 12 concatenated genes (5 mtDNA and 7 nuclear) from
235 more than 4,000 species. Levels of clade support were estimated by non-parametric Shimodaira-
236 Hasegawa-Like implementation of the approximate likelihood-ratio test (further details in *Pyron,*
237 *Burbink & Wiens, 2013*). We used the ape R-package (*Paradis, 2012*) to obtain a subtree
238 composed of the species sampled in this study (Fig. S2).

239 We estimated PD using the phylosor function of the picante R-package (*Kembel et al.,*
240 *2010*), which estimates fractions of branch lengths in a phylogenetic tree that are shared among
241 communities (*Kembel et al., 2010*). The phylosor function returns a pairwise phylogenetic
242 similarity matrix, which was converted to a pairwise distance matrix (1-phylosor matrix) and
243 summarized by PCoA scores.

244 **Environmental gradients and inferential analysis.** We evaluated the influence of clay
245 content in the soil on the diversity measures because this gradient affects primary production,
246 which influences the overall trophic network (*Cintra et al., 2013*). Clay content was measured in
247 a pooled 5g sample derived from six subsamples per plot, and we used averages per module.
248 Technicians at the Laboratório Temático de Solos e Plantas (LTSP) of the Instituto Nacional de
249 Pesquisas da Amazônia (INPA, Manaus) conducted the physical analyses following standard
250 methods (*Embrapa, 2009*).

251 The Height Above the Nearest Drainage (HAND) algorithm estimates the depth to the
252 water table, which represents a gradient of relative water potential, in which higher values

253 indicate large gravitational potential and lower values may reflect soil waterlogging in the
254 absence of drainage. Here we tested the effects of HAND (log-normalized) on snake diversity
255 because vertical and horizontal distances from drainage are correlated in a micro-watershed scale
256 (*Schietti et al., 2013*), and horizontal distance from drainage was previously identified as an
257 important factor affecting snake assemblages through availability of physiological optimal or
258 prey availability at assemblage (*Fraga, Lima & Magnusson, 2011*) and population (*Fraga et al.,*
259 *2013b*) levels in Amazonia. We used percentage of tree cover (log-normalized) because this
260 gradient potentially filters species by their adaptability to variation in habitat openness,
261 considering the variation in factors such as availability of resting and nesting sites (*Burger &*
262 *Zappalorti, 1986*), availability of prey and protection from predators (*Webb & Shine, 1996*), and
263 light intensity (*Pringle, Webb & Shine, 2003*). The gradients HAND and tree cover were
264 obtained from raster surfaces downloaded from the public repository Ambdata (*Amaral et al.,*
265 *2013*; www.dpi.inpe.br/Ambdata).

266 We used temperature of the coldest month and precipitation of the wettest month because
267 climate is often considered as a primary factor determining distribution of biodiversity at
268 numerous spatial and temporal scales. Climate may limit species distribution through
269 physiological filtering, especially in ectothermic animals such as snakes (*Blain et al., 2009*).
270 Climate data were obtained from raster surfaces downloaded from the Worldclim database (*Fick*
271 *& Hijmans, 2017*). All raster surfaces used in this study have a resolution of 1 km, and values for
272 each gradient were extracted by the raster R-package (*Hijmans, 2015*) using geographic
273 coordinates per module.

274 Geographic distance has been found to be an important factor driving β -diversity for
275 several vertebrates, because potentially carries unmeasured environmental variation (*Qian &*

276 *Ricklefs, 2012*). Our study area covers about 4,400 km², and therefore we expect spatial
277 autocorrelation in the environmental data. To reduce the effects of geographic distance on the
278 environmental gradients we calculated Euclidean distances between centroid coordinates per
279 module, and reduced dimensionalities using the first axis from a PCoA. The coordinates were
280 used in linear regressions given by $gradient = a + b(\text{geographic distance})$. Residuals from these
281 models were used as independent variables in inferential models to quantify proportions of snake
282 diversity that are explained by environmental variation. We used this approach because multiple-
283 linear-regressions using raw environmental data as independent variables returned slight spatial
284 autocorrelation in the residuals for TBD (Moran's I = -0.272, P = 0.06), FBD (Moran's I = -
285 0.320, P = 0.02) and PBD (Moran's I = -0.261, P = 0.08), which was negatively significant (P <
286 0.05) in 20–30% of ten geographic distance classes (Fig. S3).

287 To test for the effects of gradients on the diversity measures we used multiple-linear-
288 regression models, that were built following the general formula $diversity\ measure = a + b_1(\text{clay}$
289 $\text{content residuals}) + b_2(\text{HAND residuals}) + b_3(\text{tree cover residuals}) + b_4(\text{temperature residuals})$
290 $+ b_5(\text{precipitation residuals})$. The gradients measured are given in different units, so we scaled
291 them using the scale function in R (*Becker, Chambers & Wilks, 1988*). The residuals
292 representing gradients showed little multicollinearity (≤ 0.7 in all cases). We have considered
293 significant relationships at $P \leq 0.05$ after Bonferroni correction. Additional information (e.g.,
294 amplitude and average values) on the gradients can be found in the Table S3.

295 Alternatively, we used redundancy analysis (RDA) to test the effects of environmental
296 gradients on raw distance matrices among sampling units, separately for each diversity measure.
297 This approach was useful to verify the robustness of the results obtained by the multiple linear
298 regressions, considering information loss by dimensionality compression through PCoA. We

299 constructed the models using taxonomic, functional and phylogenetic distance matrices as
300 dependent variables, and environmental gradients as independent variables, which is equivalent
301 to multiple-multivariate linear regression models (*Legendre, Fortin & Borcard, 2015*). We used
302 a permutation test of significance (5000 randomizations) to decide between accept or reject null
303 hypothesis.

304 We also compared the subsets of species that were found per plot in each of the four
305 surveys (2007–2014), to control any effect of temporal variation on the diversity measures. We
306 calculated Forbes pairwise dissimilarities among each survey on each plot, summarized the
307 resulting matrix using PCoA (axis 1), and tested differences among surveys using ANOVA. We
308 set a two-factors model – plot and survey – to decouple assemblage compositions between space
309 and time. We found that differences in assemblage composition are associated with plots ($P =$
310 0.03), and plots and surveys interacting with each other ($P = 0.01$), but not with surveys alone (P
311 $= 0.26$). This finding demonstrates that the patterns of spatial assemblage structure shown in this
312 study have no bias of assemblages changing over time.

313 To quantify relationships between different diversity measures we used matrix regression
314 with permutation test of significance (5000 randomizations). The models were set up with the
315 pairwise distance matrices used to summarize TBD, FBD and PBD.

316

317 **Results**

318 The first axis of PCoA ordination captured 59% of the original variance in the raw data
319 used to estimate TBD, and the second axis captured 39%. However, the variance captured by
320 axis 1 was not related to the environmental variation quantified by the gradients tested ($P > 0.25$
321 in all cases). Therefore, we used axis 2 to represent TBD. PCoA axis 1 captured 100% of the

322 variance for FBD and 30% for PBD and were used as univariate versions of the diversity
323 measures in the inferential models.

324 The multiple linear regression explained 61 percent (adjusted R^2) of the variance in TBD
325 ($F_{5,15} = 7.31$, $P = 0.001$, residual standard error = 0.29). This finding was particularly associated
326 to the effects of clay content ($P = 0.002$) and tree cover ($P = 0.034$) on β -diversity among the
327 sampling modules. HAND, temperature and precipitation were not related to TBD ($P > 0.45$ in
328 all cases). About 37 percent of the variance in FBD was explained by the multiple regression
329 ($F_{5,15} = 3.42$, $P = 0.02$, residual standard error = 0.45), which was mainly due to the effects of
330 HAND ($P = 0.023$) on dissimilarities between modules. Clay content, tree cover, temperature
331 and precipitation were not related to FBD ($P > 0.85$ in all cases). About 32 percent of the
332 variance in PBD was explained by the gradients ($F_{5,15} = 2.87$, $P = 0.05$, residual standard error =
333 0.11), but only HAND ($P = 0.034$) contributed to the model. The other gradients tested were not
334 related to PBD ($P = 1$ in all cases). All the multiple regression models returned residuals that did
335 not differ statistically from a normal distribution (Shapiro-Wilk $W > 0.92$, $P > 0.12$ in all cases).
336 A complete summary of the multiple-regression models can be found in Table 1 and the partial
337 regressions from each model are presented in Fig. 2.

338 The RDA models significantly captured 32% of the constrained variance to TBD ($F_{5-15} =$
339 1.42, $P = 0.05$), 43% to FBD ($F_{5-15} = 2.27$, $P = 0.04$) and 36% to PBD ($F_{5-15} = 1.71$, $P = 0.03$). In
340 general, the results were consistent with the multiple regressions (Table S4). However, tree cover
341 did not significantly explain TBD ($P = 0.24$).

342 All diversity measures were positively related to each other (Fig. 3). However, TBD was
343 more strongly related to PBD ($r^2 = 0.67$, $P < 0.0001$) compare to the relationships between TBD
344 and FBD ($r^2 = 0.13$, $P < 0.0001$), and between FBD and PBD ($r^2 = 0.23$, $P < 0.0001$).

345

346 **Discussion**

347 Our data indicate that environmental gradients affect snake co-occurrence in central-southern
348 Amazonia, which results in levels of β -diversity identified by taxonomic, functional and
349 phylogenetic dissimilarities among modules. These findings are consistent with temperate snake
350 assemblages, which may be structured by phylogenetic species variability and trait variability
351 (*Burbrink & Myers, 2015*). Furthermore, our data corroborate a previous study in Brazil, which
352 found variation in phylogenetic and phenotypic compositions of snake assemblages associated
353 with environmental gradients (*Cavalheri, Both & Martins, 2015*). However, the variation found
354 in that study was primarily due to differences between forested and open biomes, which is
355 expected to be pronounced. In this study, we show that variation in snake assemblages along
356 environmental gradients is consistent even within biomes, where structural differences between
357 sites are often subtle.

358 Environmental gradients affecting species composition have been found in many groups of
359 organisms in the Amazon, such as frogs (*Ribeiro-Jr, Lima & Magnusson, 2012, Rojas-Ahumada,*
360 *Landeiro & Menin, 2012*), understory birds (*Bueno et al., 2012; Menger et al., 2017*), plants
361 (*Drucker, Costa & Magnusson, 2008; Moulatlet et al., 2014*) and snakes (*Fraga, Lima &*
362 *Magnusson, 2011*). In general, it is expected that species occupy portions of gradients in a way to
363 optimize the balance between dispersal capacity, physiological needs and availability of
364 resources (*Laliberté, Legendre & Shipley, 2014*). However, our data indicate that TBD is
365 affected by different sets of environmental gradients compared to FBD or PBD, which suggests
366 that patterns of spatial structure in snake assemblages in the Amazon may not be characterized
367 by a single diversity measure. In fact, choosing environmental gradients as predictors in species-

368 habitat association models is not a trivial task, although it is an effective approach to evaluate
369 conservation issues such as environmental legislation (*Fraga et al., 2011; Bueno et al., 2012*).

370 We found that clay content in the soil predicted snake community assembly based on
371 taxonomic dissimilarities among modules. Associations between soil texture and patterns of
372 vertebrate community structure are often assumed as indirectly causal, because soil texture
373 affects many factors driving regional species occurrence, such as vegetation density (*Woinarski,*
374 *Fisher & Milne, 1999*) and distance from streams (*Bueno et al., 2012*). The environmental
375 heterogeneity in the Amazon rainforests include soil texture gradients from poorly-drained,
376 seasonally-flooded sandy soils (*Cintra et al., 2013*), in which plants find poor substrate for
377 rooting (*Quesada et al., 2012*), to well-drained soils that support older well-developed forests
378 (*Castilho et al., 2006; Emilio et al., 2013*). Therefore, variation in soil texture across landscapes
379 generates high β -diversity via suitability of the conditions for dispersal and colonization, which
380 has been found in plant (*Costa, Magnusson & Luizão, 2005; Costa et al., 2008*), invertebrate
381 (*Franklin, Magnusson & Luizão, 2005*) and vertebrate (*Woinarski, Fisher & Milne, 1999; Bueno*
382 *et al., 2012*; this study) assemblages.

383 We showed that HAND is related to snake assemblages based on functional traits and
384 phylogeny. Distance above the drainage has been identified as an important factor structuring
385 plant (*Drucker, Costa & Magnusson, 2008*) and animal (*Fraga, Lima & Magnusson, 2011;*
386 *Bueno et al., 2012; Rojas-Ahumada, Landeiro & Menin, 2012*) assemblages in the Amazon, and
387 riparian zones may be biologically distinct from adjacent areas (*Sabo et al., 2005*). Despite the
388 fact that most Amazonian snakes can cross different habitats, distance from drainage may
389 influences β -diversity (*Fraga, Lima & Magnusson, 2011*) and structures populations in terms of
390 variation in density and body size (*Fraga et al., 2013b*). In this study, we found that HAND

391 affects FBD mainly because lower distances from drainage favor assemblages composed by
392 arboreal (e.g., *Imantodes lentiferus*) and aquatic species (e.g., *Helicops angulatus*). Lower values
393 of HAND are often associated with seasonal surface waterlogging (*Schietti et al., 2013*), which
394 may complicate fossorial and terrestrial lifestyles. Therefore, variation in HAND across the
395 landscape generates regional dispersal corridors that may be more suitable for some species than
396 others, which could affect FBD and PBD.

397 We found inconsistency between the effects of tree cover on TBD estimated by multiple
398 regression and RDA. Different results may reflect different levels of statistical sensitivity of the
399 models to the data structure, or unidentified sampling bias. Therefore, we assume tree cover in
400 this study as a probable filter to snake regional co-occurrence. Variation in tree cover along
401 continuous landscapes generates mosaics of more and less suitable habitats for different subsets
402 of species, through factors that directly affects species biology. These include availability
403 (*Lindenmayer et al., 1991*) and non-random selection of nesting and resting sites (*Burger &*
404 *Zappalorti, 1986; Webb & Shine, 1996*), thermo-regulatory requirements, availability of prey,
405 scent chemical trails from potential prey (e.g., small mammals), protection from predators (*Webb*
406 *& Shine, 1996*), variation in light intensity, air and ground temperatures and wind speed (*Pringle,*
407 *Webb & Shine, 2003*). Furthermore, variation in tree cover at wider spatial scales (e.g., biomes)
408 may define regional subsets of species according to their morphological adaptation to use
409 different plant strata (*Cavalheri, Both & Martins, 2015*). This finding is relevant for
410 conservation, because maintenance of regional assemblages depends on protecting large areas,
411 which contain wide amplitudes of tree-cover gradients.

412 Changes in phylogenetic (PBD) composition among plots were proportional to changes in the
413 snake taxonomic identities (TBD). Spatial congruence between estimates of phylogenetic and

414 taxonomic β -diversity has been suggested as often higher compared to α -diversity measures
415 (*Devictor et al., 2010; Bernard-Verdier et al., 2013; Arnan, Cerdá & Retana, 2016*), especially
416 in cases of niche conservatism (*Wiens & Graham, 2005*). The tendency of species to retain
417 ancestral characteristics along generations results in local or regional assemblages structured by
418 environmental filtering, despite different environmental gradients may affect different diversity
419 measures (*Webb et al., 2002*). Additionally, the positive correlations between diversity measures
420 show that TBD and FBD efficiently captured a phylogenetic signal, which suggests assemblages
421 evolutionary structured by Brownian motion, in which species change mainly through genetic
422 drift and natural selection randomly directed (*Losos, 2008*). Concerning the positive relation
423 between FBD and PBD, we found that environmental gradients drive co-occurrence of species
424 that are simultaneously phylogenetically related and have similar ecological requirements
425 (*Keddy, 1992; Myers & Harms, 2009*), and one measure may be used as a proxy to the other.
426 Contrarily, TBD was not a good proxy for FBD, because large proportions of data were poorly
427 fitted between both diversity measures. Ultimately, combinations of TBD and FBD should be
428 part of studies on community ecology, because they give integrative approaches that reveal
429 taxonomic, ecological and evolutionary forces acting on community structuring, which is very
430 useful for conservation (*Devictor et al., 2010*).

431 From the point of view of conservation, the positive relationships between diversity measures
432 directs the focus of biodiversity monitoring programs and reserve planning to cover higher levels
433 of phylogenetic diversity, because this measure reflects the maintenance of ecosystem processes
434 operating over long timescales (*Cadotte, Carscadden & Mirotnick, 2011*). Functional diversity
435 is estimated based on sets of traits that reflect environmental tolerances and requirements, which
436 in turn determine where species can live (*Lavorel et al., 1997*) and interact with each other in

437 assemblages (*Davies et al., 2007*). Therefore, loss of evolutionarily distinct species may result in
438 irreversible loss of functions for ecosystems (*Bracken & Low, 2012*). However, at larger scales it
439 may be difficult to decide which diversity measure should be prioritized in conservation, and a
440 multi-dimensional approach may be more appropriate (*Devictor et al., 2010*), despite greater
441 difficulties of interpretation.

442 Our findings are unlikely to be biased by the spatial distribution of sampling units (see
443 *González-Caro et al., 2012*), because the RAPELD system provides regular distribution of plots
444 across the landscape regardless of logistical issues (*Magnusson et al., 2013*). However, snakes
445 usually have low detection probabilities (*Steen, 2010; Fraga et al., 2014*), which have been
446 estimated at less than 10 percent for multiple surveys of many Amazonian species in RAPELD
447 plots (*Fraga et al., 2014*). Low detection probabilities often cause false absences of species from
448 plots, and this may generate misinterpretation of how species respond to landscape change (*Gu*
449 *& Swihart, 2003*). We are unable to totally discount effects of low detectability on our results.
450 However, the strong relationships between diversity measures and environmental gradients
451 showed that a combination of high sampling effort, different methods used to quantify
452 biodiversity and the use of an appropriate multivariate distance measure may considerably
453 reduce the effect of false absences and return reliable results.

454

455 **Conclusions**

456 We used an unprecedented standardized sampling effort to show that environmental
457 heterogeneity is associated with β -diversity in Amazonian-forest snakes. Positive correlations
458 between β -diversity measures estimated show that PBD alone may be sufficient to investigate
459 spatial structure in Amazonian snake assemblages under taxonomic, functional and phylogenetic

460 perspectives. However, TBD response to different environmental gradients suggests that testing
461 the effects of a set of environmental gradients on at least two β -diversity measures can generate
462 deeper understanding of factors causing spatial community assembly. This finding highlights the
463 efficiency of using multi-dimensional approaches to quantify biodiversity in community-level
464 conservation status assessments and decision-making on natural resources management.

465

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470

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Table 1 (on next page)

Summary of statistical coefficients from multiple linear regressions testing the effects of environmental gradients on estimates of snake β -diversity in Brazilian Amazonia.

TBD = taxonomic β -diversity , FBD = functional β -diversity, PBD = phylogenetic β -diversity.
HAND = Height Above the Nearest Drainage. Bolded P-values are statistically significant after Bonferroni correction. R^2 values are adjusted to the number of sampling units. SE = standard error.

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	Coefficient	TBD	FBD	PBD
	<i>R</i> ²	0.612	0.377	0.319
	<i>P</i>	0.001	0.02	0.05
Clay content	SE	0.007	0.01	0.002
	<i>t</i>	-4.431	-0.499	1.233
	<i>P</i>	0.002	1	1
HAND	SE	0.08	0.127	0.033
	<i>t</i>	-0.045	3.325	3.142
	<i>P</i>	1	0.023	0.034
Tree cover	SE	0.16	0.247	0.064
	<i>t</i>	3.929	-1.435	0.661
	<i>P</i>	0.007	0.859	1
Temperature of the coldest month	SE	0.23	0.035	0.009
	<i>t</i>	-0.34	-0.044	-0.574
	<i>P</i>	1	1	1
Precipitation of the wettest month	SE	0.003	0.005	0.001
	<i>t</i>	-1.804	1.382	-0.589
	<i>P</i>	0.457	0.936	1

Figure 1

Map of the study area in Brazilian Amazonia showing plots where snake assemblages were sampled.

Black circles are 5 km² RAPELD sampling modules (see definition of RAPELD in the methods). The numbers can be used to check the species found in each module in Table S1. (A) Ducke Reserve, Manaus. (B) Federal highway BR-319, Purus-Madeira interfluve. (C) Upper Madeira River, Rondônia.

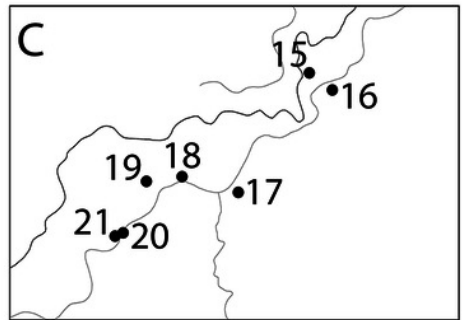
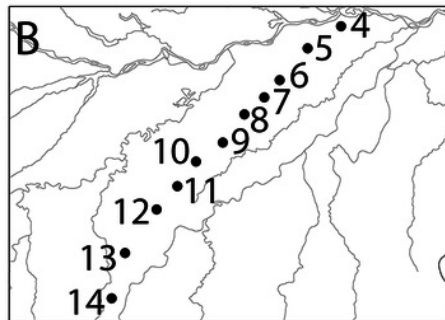
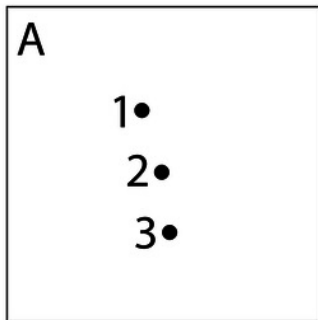
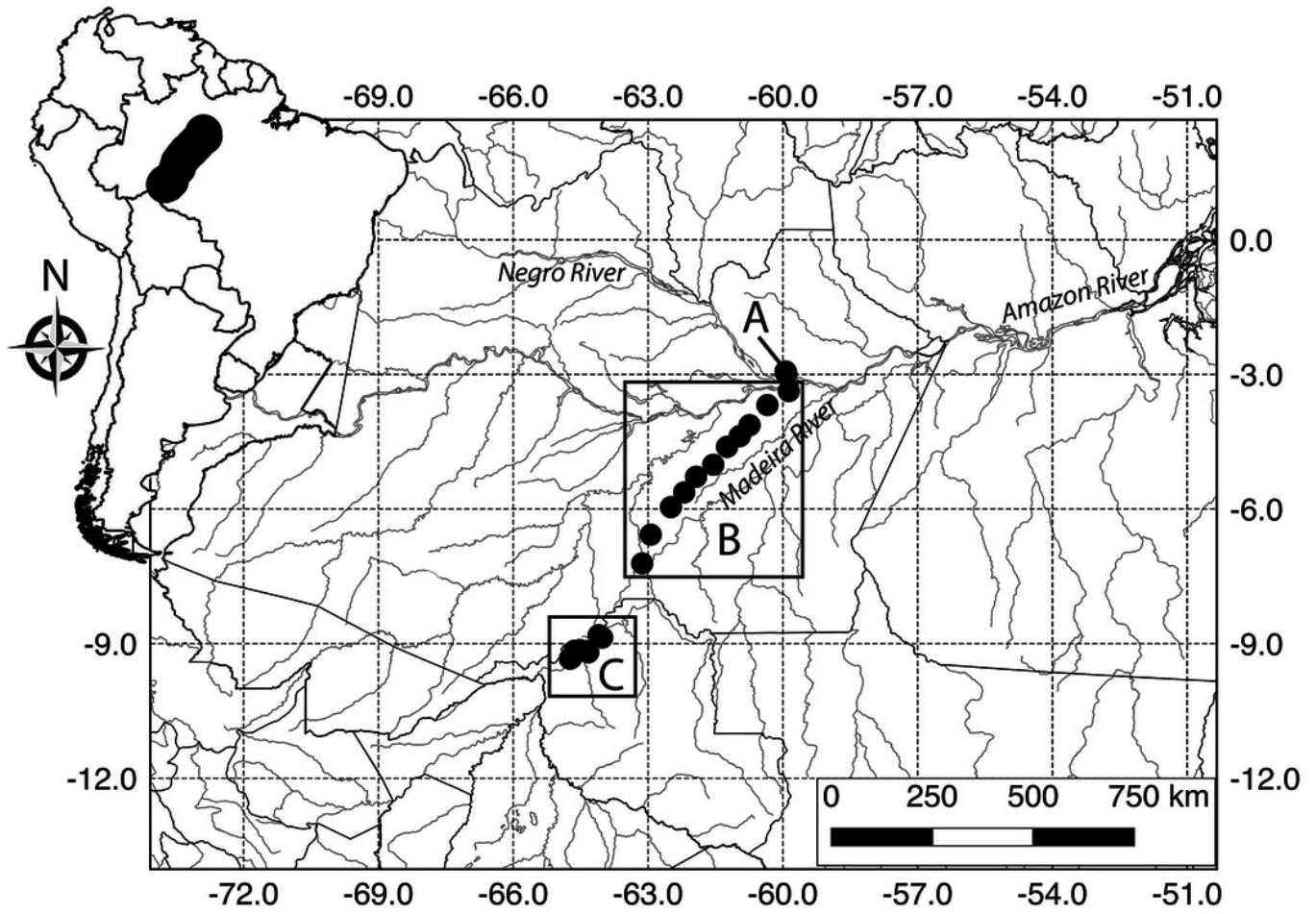


Figure 2

Relationships (partials from multiple linear regressions) between different measures of snake β -diversity and environmental gradients in central-southwestern Brazilian Amazonia.

(A) TBD = taxonomic β -diversity, (B) FBD = functional β -diversity, (C) PBD = phylogenetic β -diversity. HAND = Height Above the Nearest Drainage. Environmental gradients are shown as residuals from linear regressions used to reduce the effects of geographic distance on the environmental heterogeneity measured.

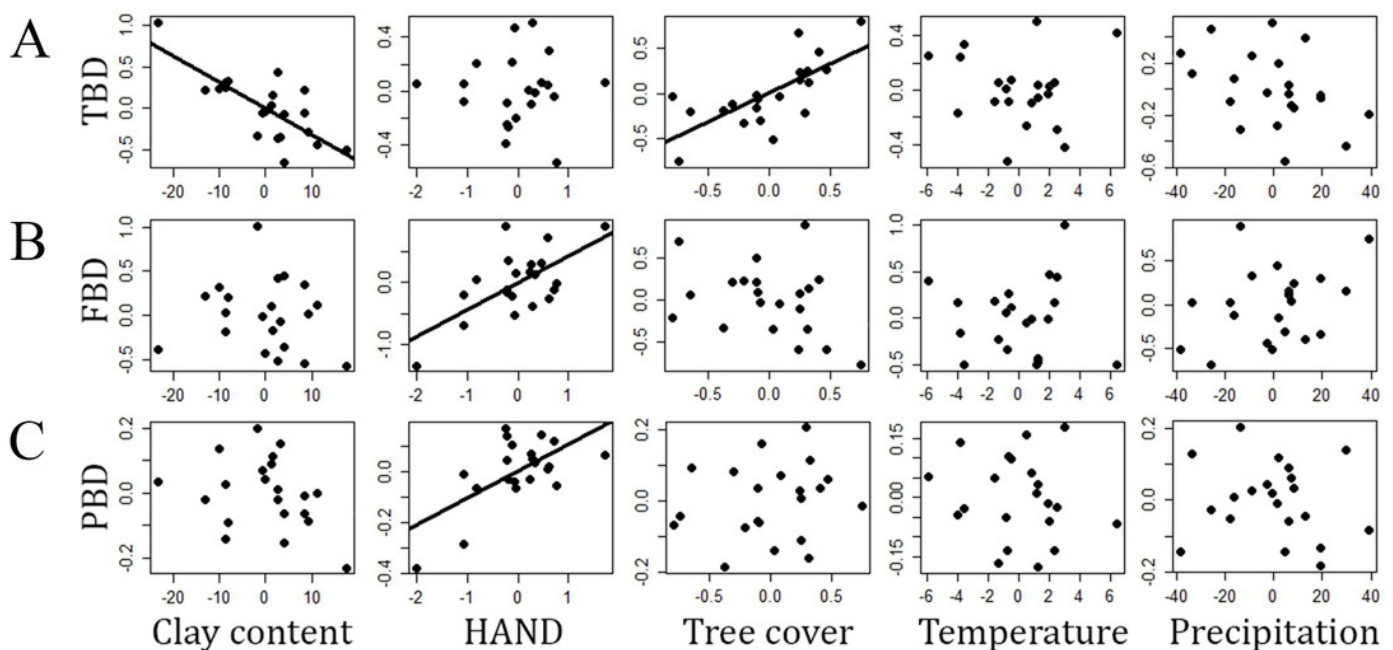


Figure 3

Relationships between dissimilarity matrices used to summarize different estimates of snake β -diversity in central-southwestern Brazilian Amazonia.

TBD = taxonomic β -diversity, FBD = functional β -diversity, PBD = phylogenetic β -diversity.

(A) Relationship between TBD and FBD. (B) Relationship between TBD and PBD. (C)

Relationship between FBD and PBD.

