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9 **Niche-based processes out-perform neutral processes when predicting distance decay**
10 **in co-dominance along the Amazon – Andes rainforest gradient**

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36

37 **ABSTRACT**

38 **Question:** Dispersal limitations (neutral hypothesis) and deterministic factors (niche
39 hypothesis) shape floristic gradients including between-site patterns of species' dominance (co-
40 dominance). Because their relative importance remains nonetheless poorly known, we ask how
41 their comparative contribution to co-dominance changes with elevation and geographical
42 extent.

43 **Location:** Madidi region, NW Bolivia.

44 **Methods:** We analysed floristic composition and environmental factors of 90 plots spanning
45 the gradient from Amazonian (<1000 m) to montane forests at three elevations (1200–1500,
46 2000–2300, and 2800–3200 m) and two geographical extents: local (plots <12 km apart) and
47 regional (38–120 km apart). We modelled distance decay within each elevational band with a
48 neutral model, using two parameters (speciation rate and dispersal distance). Subsequently, we
49 related the model's residuals to environmental differences using flexible machine learning
50 algorithms.

51 **Results:** We found that 5–44% of the variability in floristic differences along the gradient
52 studied can be explained by a neutral model of distance decay, while 18–50% can be explained
53 by environmental differences. Montane forests showed an overall gradient in floristic
54 composition that is congruent with an increase in elevation for both dispersal limitation and
55 environmental filtering. However, Amazonian forest was more niche-structured and more
56 dispersal-limited relatively to its elevation and topography.

57 **Conclusions:** Environmental differences explained floristic differences better than the neutral
58 model, even giving preferential attribution to the more parsimonious neutral processes.

59 **Keywords:** Amazon, Andes, Bolivia, species co-dominance, environmental determinism,
60 Madidi, Neutral Theory, niche partitioning, oligarchy hypothesis, species turnover, tropical
61 montane forests.

62 **Running title:** Distance decay & co-dominance Amazon-Andes forests

63

64 1 | INTRODUCTION

65 Communities differ from site to site in many aspects and at multiple scales, so understanding
66 this is a central goal of community ecology. Species' turnover, i.e. how species
67 presences/absences differ between sites, is a common measure of compositional change (e.g.
68 Tuomisto, 2010; Anderson et al., 2011). Another key aspect is how the relative abundances of
69 species vary from one site to another. For example, two communities may be made of the exact
70 same species, while their relative abundances could be dramatically different. The opposite can
71 be also true; two communities may share just a small fraction of species, but most of its
72 individuals belong to the same suite of dominant species. In the latter, both communities are
73 very similar in important ecological aspects, especially those affecting interactions between
74 individuals. The occurrence of such pattern in forests is known as “the oligarchy hypothesis”
75 (Pitman et al., 2001, 2013; Condit et al., 2002; Macía & Svenning, 2005; Arellano et al., 2015),
76 which states that tropical forest communities tend to be dominated by the same set of locally
77 abundant and geographically widespread species. There is ample empirical evidence supporting
78 this pattern (see Pitman, Silman, & Terborgh, 2013 and references therein) but the underlying
79 causes remain understudied.

80 Two hypotheses have been formulated to address the question of changes in plant
81 communities across space: the neutral hypothesis (Hubbell, 2001) and the niche hypothesis
82 (Gilbert & Lechowicz, 2004). The neutral hypothesis predicts differences between communities
83 should occur related to their spatial separation, based on neutral speciation and dispersal
84 limitation, irrespective of environmental conditions or of functional differences among species
85 (Chave & Leigh, 2002; Condit et al., 2002; Gilbert & Lechowicz, 2004). The niche hypothesis
86 states that, for a given spatial distance, two sites will show high (or low) floristic similarity
87 depending on their similar (or dissimilar) environmental conditions, a deterministic process

88 (Gilbert & Lechowicz, 2004). These two complementary hypotheses generate straightforward
89 qualitative predictions on co-dominance patterns, since species from two sites that are either
90 spatially close or environmentally similar should be similar in their relative abundances. How
91 the relative importance of these two hypotheses changes between different forest types and/or
92 different geographical extents remains unknown. From a neutral perspective, the greater
93 topographic variability and landscape fragmentation of montane regions should impose
94 stronger dispersal limitation (Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Brehm,
95 Colwell, & Kluge, 2007; Arellano et al., 2016b). From the niche perspective, increasing habitat
96 patchiness and variability, with locally abrupt changes in elevation, should also increase the
97 absolute importance of the niche hypothesis (Wiens, 2004; Brehm et al., 2007; Qian &
98 Ricklefs, 2012; Kozak & Wiens, 2010; Hutter, Guayasamin, & Wiens, 2013). Additionally,
99 geographical extent may determine the relative importance of the environment if niche plays a
100 disproportionately greater role at larger extents because longer and steeper environmental
101 gradients allow a more marked sorting of species by their different preferences (e.g. Kristiansen
102 et al., 2012; Pansonato, Costa, de Castilho, Carvalho, & Zuquim, 2013). In contrast, some
103 authors suggest that geographic distances shape regional floristic patterns, while environmental
104 differences operate mostly at local scales (Normand, Vormisto, Svenning, Grández, & Balslev,
105 2006). These differences remain unresolved.

106 In this study, we analysed data from four elevation bands along the eastern slopes of the
107 Bolivian Amazon-Andes transition (300 to 3200 m in elevation), each band containing a well-
108 defined forest type. Note that floristic changes across elevations are obvious due to the
109 magnitude of the elevational gradient in the area, so it would be trivial to perform any floristic
110 comparison between elevation bands. For that reason, our analyses were always confined to
111 within discrete elevation bands. We address the following questions.

112 (1) To what degree do neutral processes predict the pattern of distance decay in floristic
113 similarity?

114 (2) Is there any effect of elevation on the importance of the neutral processes?

115 (3) Do environmental factors explain differences in floristic composition beyond what
116 geographic distance does?

117 (4) Is the importance of these factors consistent across elevations and between local and
118 regional extents?

119 2 | METHODS

120 2.1 Floristic data

121 The study was conducted in the Madidi region, Bolivia, within or adjacent to the Madidi
122 National Park (Figure 1). Within an area of 100×120 km, we established 90 plots of 0.1 ha
123 (20×50 m) (Macía, 2008; Arellano & Macía, 2014). Plots were grouped into ten sites (6–10
124 plots/site) at four elevational bands, each hosting a different forest type: (1) Amazonian forest,
125 below 1000 m (36 plots in four sites); (2) lower montane forest, at 1200–1500 m (18 plots in
126 two sites); (3) intermediate montane forest, at 2000–2300 m (18 plots in two sites); and (4)
127 upper montane forest, at 2800–3200 m (18 plots in two sites). The minimum distance between
128 plots was 500 m in Amazonian forests and 250 m in the montane forests. All plots were located
129 in apparently mature rain forests without recent human disturbance.

130 We censused all tree stems with a diameter ≥ 2.5 cm at 130 cm of height. All individuals
131 were assigned to a morphospecies in the field, and > 6500 voucher specimens were collected
132 and deposited in the Herbario Nacional de Bolivia in La Paz (LPB). All individuals of the small
133 shrub *Psychotria carthagenensis* Jacq. from two plots were removed from analyses because
134 their extremely high density (mostly like by coppicing) would overestimate its co-dominance,
135 distorting the model. In all, less than 3% of total individuals were eliminated. The final dataset
136 contained 27,431 individual trees belonging to 1128 species, 374 genera and 109 families
137 (Appendix S1).

138 2.2 Environmental data

139 A composite sample of the uppermost soil layer (0–15 cm below the litter layer) was collected
140 for each plot by mixing soil from five subsamples within the plot. Soil samples were air-dried
141 and sieved (to < 2 mm). Soil pH was measured in a 1:2.5 suspension of soil in deionized water
142 by volume. Total C, N and S contents were determined by combustion (CHNS-932, LECO).
143 Plant-available macronutrients (Ca, Mg, K, P), micronutrients (Fe, Mn, Co, Ni, Cu, Zn) and Al
144 contents were determined by extraction with Mehlich 3 method (Mehlich, 1984), and analysed
145 through an inductively-coupled plasma spectrometer (ICP, Elan 6000 Perkin-Elmer).

146 Data for precipitation-based variables were obtained from the Tropical Rainfall Measuring
147 Mission database (Mulligan, 2006) and data for temperature-based variables from WorldClim
148 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005: <http://www.worldclim.org/bioclimate>). From
149 the ASTER Global Digital Elevation Map v. 2 (<http://asterweb.jpl.nasa.gov/gdem.asp>) we

150 estimated topographic variables for each plot: elevation, slope, eastness and northness (as
151 sin(aspect) and cosin (aspect), respectively).

152 **2.3 Measurement of co-dominance patterns**

153 We used the F index of co-dominance as a metric of compositional differences between two
154 communities. This index is the probability of finding two conspecifics of any species when
155 taking one individual from each of two different locations (i.e. samples), j and k :

$$156 \quad F_{jk} = \sum_{i=1}^S \frac{n_{ij}n_{ik}}{N_j N_k}$$

157 where n_{ij} is the abundance of species i in plot j , n_{ik} is the abundance of species i in plot k , N_j is
158 the number of individuals in plot j etc., and S is the total number of species. In a strict sense, F
159 does not capture species' turnover as much as patterns of species' co-dominance: its value is
160 large only when the two compared communities share the same suite of abundant species and
161 low if otherwise, regardless of species overlap.

162 **2.4 Implementation of Inference to the Best Explanation**

163 Similar analyses of the relative role of neutral and niche mechanisms have traditionally relied
164 on linear models, partitioning the variation in the response variable into (1) variation explained
165 exclusively by space (~dispersal, a neutral process), (2) variation exclusively explained by the
166 environment or environmental differences (~niche processes), (3) variation explained by both,
167 and (4) unexplained variation. We used an alternative approach to partitioning of variation
168 based on abductive reasoning. Abductive reasoning or Inference to the Best Explanation (IBE)
169 is one of the three forms of logical inference, along with deduction and induction (Lipton,
170 2004; Campos, 2011). Unlike traditional variation partitioning, IBE allows assessment of
171 different hypotheses, without making them compete directly, by ranking explanations from
172 more to less parsimonious and testing them sequentially. Firstly, raw data are analysed using a
173 model for the most parsimonious hypothesis. Subsequently, the second most parsimonious
174 hypothesis is tested on the residuals of the previous model, and so on. IBE favours simpler
175 models over complex ones. The main advantage of IBE is that one can formulate various
176 models of arbitrary shape and complexity.

177 During the modelling process, we assumed neutral processes to be the most parsimonious
178 explanation of patterns of distance decay on species' co-dominance. In Hubbell's (2006) words,
179 "*obtaining acceptable fits from neutral models shifts the burden of proof to those who would*

180 *assert that more complex theory is required to explain nature*". Consequently, preferential
181 attribution to neutral processes was based on considerations about parsimony alone and not on
182 any *a priori* expectation regarding the relative importance of the different processes despite
183 being the *a priori* expectation that niche processes are more important than neutral processes
184 (Pitman et al., 2001; Gravel, Canham, Beaudet, & Messier, 2006; Adler, HilleRisLambers, &
185 Levine., 2007). IBE thus functions as a stringent test on our prior hypotheses, more so than
186 favouring confirmatory bias.

187 **2.5 The most parsimonious hypothesis: co-dominance patterns expected by neutral** 188 **processes**

189 Early versions of the Neutral Theory (Hubbell, 1979, 1997) modelled composition of local
190 communities only in relation to the "omnipresent" source pool of species, disregarding the
191 greater connectedness between nearby communities. Chave & Leigh (2002) developed a
192 version of the neutral model for a very large forest where seeds disperse only a limited distance
193 from their parents, and modelled co-dominance as a function of the distance r between samples
194 j and k :

$$195 \quad F(r) \approx \frac{1}{2\rho\pi\sigma^2 + \ln\left(\frac{1}{\nu}\right)} 2K_0\left(\frac{r\sqrt{2\nu}}{\sigma}\right)$$

196 where K_0 is the zero-th order modified Bessel function of the second kind, ρ is the density of
197 individuals, ν is the speciation rate, and σ is the root-mean-square of the dispersal distance (the
198 mean distance between a seed and its parent tree). In this model, ρ is constant for a given forest
199 type, while ν and σ are the only free parameters. This model of decay has been successfully
200 applied to a variety of systems, including tropical forests (Chave & Leigh, 2002; Condit et al.,
201 2002; Gilbert & Lechowicz, 2004).

202 We fitted the neutral models of decay by minimizing the sum of the squared residuals
203 using method "nlminb" in function *optimx* ("optimx" package) in the R statistical program
204 (version 3.2.2). Estimates of both parameters (ν and σ) were obtained by jack-knife resampling
205 (i.e., fitting many models per forest type, leaving out one plot each time), so that the mean of
206 the resulting distribution represented the final estimation for both parameters, and the 0.025 and
207 0.0975 quantiles the corresponding 95% confidence intervals (CI). Estimated parameters of two
208 forest types are significantly different when their CI do not overlap.

209 2.6 Analysis of the residuals from the neutral model against environmental variables

210 To examine the relationship between the residuals of the neutral model (the variation of F
211 between communities unexplained by neutral processes) and environmental variables, we used
212 Random Forest models (Cutler et al., 2007), fitted with the “randomForest” R package. This
213 method combines many regression trees built from a bootstrap sample of response variables. In
214 comparison with linear methods, Random Forests are non-parametric; thus they allow for
215 complex interactions between variables while being less prone to over-fitting.

216 We conducted two Random Forest models for each forest type (elevational band), one at
217 the local scale (defined as pairs of plots <12 km apart in our dataset) and one at the regional
218 scale (pairs of plots 38–120 km apart). As predictor variables, we included the Euclidean
219 pairwise distances of the environmental variables between plots. A preliminary analysis
220 showed high correlation (Pearson's $|r| > 0.70$) between some variables. To avoid redundancy
221 we chose only one of the correlated variables as a surrogate for the rest (Appendix S2,
222 segregated by extent and forest type). The goodness-of-fit of each model was measured with
223 two metrics. First, the squared Pearson's r (r^2_{neutral} and r^2_{niche} , respectively) between
224 observations and expectations measures the ability of the predictors to explain the response
225 variable, directly included in the model (i.e. F in the case of the neutral model, but residual F
226 for Random Forest models). Second, the contributed r^2 ($\text{contr}r^2$) for each model measures the
227 ability of the predictors to explain the original response variable (F), as $\text{contr}r^2_{\text{neutral}} = r^2_{\text{neutral}}$ and
228 $\text{contr}r^2_{\text{niche}} = (1 - \text{contr}r^2_{\text{neutral}}) - r^2_{\text{niche}}$. These were used to estimate the relative importance of the
229 neutral and niche processes.

230 3 | RESULTS

231 3.1 Relationship between co-dominance (F index) and geographic distances

232 The magnitude of change in tree species' composition as a function of distance increased with
233 elevation (Figure 2). The predictive ability of the neutral model differed between forest types,
234 and was negligible in Amazonian forests and lower montane forests ($r^2_{\text{neutral}} = 7.7\%$ and 5.4% ,
235 respectively), but was moderate in the intermediate and upper montane forests ($r^2_{\text{neutral}} = 29.0\%$
236 and 44.3% , respectively). In all cases, the fit of the model was better at the local extent than at
237 the regional extent (Table 1). Dispersal potential (the distance parameter in the neutral model,
238 σ) in the montane forests decreased with elevation, being 81.9 m, 51.4 m and 33.8 m in lower,
239 intermediate and upper montane forests, respectively (Table 2). The dispersal potential found in

240 the Amazonian forest ($\sigma = 63.5$ m), however, was smaller than in the lower montane forest ($\sigma =$
241 81.9 m).

242 **3.2 Relationship between residual F index and environmental differences**

243 The variation in the residuals of the neutral model was relatively well explained by
244 environmental variables included in Random Forests models in all cases; r^2_{niche} ranged between
245 20.7% and 43.6% at the local extent, and between 22.5% and 50.5% at the regional extent (see
246 Table 1). Regardless of geographical extent, lowest and highest r^2_{niche} values were observed at
247 intermediate and upper forests, respectively (Table 1). The contributed r^2 from the niche
248 hypothesis ($\text{contr}r^2_{\text{niche}}$) was always greater than that from the neutral model ($\text{contr}r^2_{\text{neutral}}$)
249 regardless of either extent or forest type. Also, $\text{contr}r^2_{\text{niche}}$ was greater at the local than regional
250 extent among plots within elevation bands (Table 1). The relative weight of the niche variables
251 ($\text{contr}r^2_{\text{niche}}$) at both geographical extents was highest in upper montane forests followed by
252 Amazonian forests and lower montane forests, while it was lowest in intermediate montane
253 forests (Table 1).

254 The relative importance of individual environmental variables, measured as the increase of
255 node purity in the Random Forest models, varied greatly between forest types and spatial scales
256 (Figure 3; Appendix S3 contains the numerical results, with standard deviations). Climate
257 (including elevation) and topographic variables were only important in the Amazonian forest,
258 with the exceptions of precipitation of coldest quarter of the year (Bio19) and northness, which
259 were of moderate relevance in explaining the residual co-dominance in the upper montane
260 forest. Among soil properties, pH was the most important variable in every forest type. Overall,
261 environmental variables were more important locally than regionally in all forest types (Figure
262 3).

263 **5 | DISCUSSION**

264 Speciation and seed dispersal alone cannot explain variation in tree species' co-dominance in
265 our study area, despite the preferential, most parsimonious, attribution we gave to neutral
266 processes. This finding supports the idea that tropical forests, particularly at the regional extent,
267 are more similar in terms of co-dominance than anticipated under Hubbell's neutral models
268 (e.g. Terborgh, Foster; & Percy, 1995; Pitman et al., 1999; Pitman, Terborgh, Silma, & Núñez,
269 2001). Furthermore, our results suggest that the changes in co-dominance which the neutral
270 model could not explain were strongly correlated with environmental variables indicating that

271 environmental differences were, overall, more important than neutral processes for all four
272 forest types at both, local and regional extents.

273 **5.1 Dispersal in the Amazon-Andes transition**

274 We found that the distance decay pattern became steeper with elevation along the entire 300–
275 3000 m gradient. In the Andes, an elevation increase of 800 m resulted in 30–35% reduction in
276 dispersal potential (σ) within lower, intermediate and upper montane forests. This finding is
277 consistent with expected increases in frequency and effectiveness of dispersal barriers in
278 higher-elevation montane ecosystems (Ghalambor et al., 2006; Arellano et al., 2016b), a pattern
279 observed elsewhere (Condit et al., 2002; Bjorholm, Svenning, Skov, & Balsley, 2008).

280 However, we noted that among lower elevation forest types, dispersal potential was
281 unexpectedly lower in the rather flat Amazonian forest than in the moderately steep lower
282 montane forest. One possible explanation is that dispersal kernels at lower elevations are
283 limited by larger seed size rather than by topographic barriers, counteracting the greater
284 landscape connectivity. A study conducted by Hillyer & Silman (2010) in a neighbouring
285 region reported average seed masses of 0.35 g for Amazonian lowland species, while average
286 seed masses dropped to <0.15 g for species above 2000 m in the Andes. This is consistent with
287 the general correlation between temperature (and thus net primary productivity) and seed mass
288 observed at larger scales, including the Amazon (Malhado et al., 2015). We ran our dataset
289 against the Royal Botanic Gardens Kew (2017) Seed Information Database and verified that
290 our flora complies with the general pattern. Arguably, a greater prevalence of heavy-seeded
291 tree taxa (on average) in the Amazonian flora, with reduced seed rain ranges, may result in a
292 limited dispersal potential compared to lower montane forests.

293 **5.2 Niche processes affecting the distance decay in co-dominance**

294 The combination of comprehensive soil analyses and a highly flexible modelling approach
295 resulted in the high predictive power attributed to the niche hypothesis (as suggested by Jones
296 et al., 2008; Chang, Zelený, Li, Chiu, & Hsieh, 2013). Our results confirm that niche-based
297 processes are more important than neutral processes in structuring tropical plant communities
298 from local to regional scales, even within narrowly defined elevational bands. This finding is
299 consistent with the existing literature on drivers of compositional change, including both co-
300 dominance patterns (Pitman et al., 2001, 2013; Arellano et al., 2015) and patterns of beta
301 diversity (Phillips et al., 2003; Macía, Ruokolainen, Tuomisto, Quisbert, & Cala, 2007; Jones et
302 al., 2008; Myers et al., 2013).

303 Previous studies in the tropics have demonstrated the importance of temperature and
304 precipitation-based variables on floristic variations (e.g. Sesnie, Finegan, Gessler, & Ramos,
305 2009; Blach-Overgaard, Svenning, Dransfield, Greve, & Balslev, 2010). Our results not only
306 support the role of temperature and precipitation, but also highlight the role of climate
307 specialization in shaping patterns of species' local abundances, especially at elevations below
308 1500 m. At higher elevations, most climate variables were of lesser importance, as climate
309 generalists (i.e., species with abundances that barely change between different climates) make
310 up the bulk of high-elevation tropical plant communities (Stevens, 1992; Ghalambor et al.,
311 2006).

312 Soil differences were also important in determining levels of co-dominance that diverged
313 from those expected by neutral processes. In the studied area, pH was clearly the most
314 important soil variable. Similar correlations between soil acidity and composition have been
315 reported from other montane and lowland forests (Pyke, Condit, Aguilar, & Lao, 2001; Jones et
316 al., 2008; Homeier et al., 2010). Small variations in Al toxicity (closely related to soil acidity)
317 had a large effect on the floristic composition of Amazonian forests but, quite surprisingly, not
318 on any of the montane forests. Perhaps Al toxicity entirely bars particular species (e.g. Jones et
319 al., 2008; Andersen, Turner, & Dalling, 2010), while it does not substantially affect the
320 abundance of tolerant species. Amazonian forests may be more responsive (negatively) to Al
321 than any of the montane forest types, where 37–43% of individuals in the latter belonged to
322 families with many and/or taxa which are strong Al-hyperaccumulators (in comparison to 13%
323 in the Amazonian forest; Jansen, Broadley, Robbrecht, & Smets, 2002).

324 Variables associated with organic matter (C, C:N) are important in most tropical forests
325 (e.g. Andersen et al., 2010; Homeier et al., 2010; Duque et al., 2002; Phillips et al., 2003; Jones
326 et al., 2008), but in our study they were not so for Amazonian forest. By contrast, our results
327 for base cations (Mg, K, Ca) show that they are the most important in Amazonian forests, with
328 at least one of the cations being among the most relevant edaphic variables at either the local or
329 regional extent in all forest types. The association of floristic composition with these cations
330 has been widely reported in the Amazon (e.g., Tuomisto & Ruokolainen, 1994; Duque et al.,
331 2002; Phillips et al., 2003; Macía et al., 2007; Toledo et al., 2012), as well as in montane
332 forests at various elevations (Andersen et al., 2010; Homeier et al., 2010). Other potential
333 drivers of compositional changes, like P (e.g. Duque et al., 2002; Jones et al., 2008), Fe (e.g.
334 Macía et al., 2007) and some micronutrients, were rather poor predictors of co-dominance

335 patterns across all forest types.

336 **5.3 Changes with elevation and geographical extent**

337 Regarding the effect of the geographical extent (local and regional scales) on the importance of
338 the environment in determining floristic co-dominance patterns, we found that $\text{contr}r^2_{\text{niche}}$ was
339 greater in all forests at the regional extent. Similarly previous studies suggest that longer
340 environmental gradients result in more niche-structured communities (e.g. Kristiansen et al.,
341 2012; Pansonato et al., 2013), though others have found either the opposite pattern or no scale-
342 dependency (Arellano et al., 2016a). This may be related to the selection of different predictors
343 at different scales (e.g. large-scale studies frequently focus on climate, while small-scale
344 studies tend to incorporate more soil variables; Duque et al., 2002; Jones et al., 2008; Chang et
345 al., 2013).

346 We expected that more heterogeneous landscapes at higher elevations would result in a
347 greater accumulation of specialists (Kozak & Wiens, 2010; Qian & Ricklefs, 2012; Hutter et
348 al., 2013), and consequently a greater correlation between distance decay and niche differences,
349 which would shape a clear elevational trend in co-dominance. However, our results did not
350 support this expectation, perhaps due to the limited number of plots per forest type. At least for
351 the environmental variables and the spatial extents considered, we found that landscape
352 heterogeneity does not necessarily increase with elevation (as for Arellano et al., 2016b). It is
353 also possible that greater environmental heterogeneity was counterbalanced by an increase in
354 the dominance of generalist species (Stevens, 1992; Ghaleb et al., 2006), blurring the
355 gradient in the intensity of plant-environment associations with elevation.

356 Taken together, our results reinforce the idea that deterministic processes are more
357 important than neutral processes in driving floristic differentiation in tropical rain forests at
358 both local and regional extents (Pitman et al., 2001; Gravel et al., 2006; Adler et al., 2007).
359 Dispersal limitation was stronger in intermediate and upper montane forests than in any other
360 forest type, as was the importance of environment in driving co-dominance patterns. The
361 Amazonian forest was more niche-structured, while also being more dispersal-limited than the
362 lower montane forest, probably due to greater abundance of species with heavier, less
363 dispersible seeds.

364

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374 **Author contributions:** LNT and IGC conceived the hypotheses and designed the study. GA,
375 MJM and VC collected the data. LNT, GA and IP analysed the data. LNT, GA, IGC and IP
376 wrote the manuscript, MJM and VC discussed the results and contributed to the writing.

377 **Data accessibility:** Data are stored in the Tropicos® database hosted at the Missouri Botanical
378 Garden (<http://www.tropicos.org/PlotSearch.aspx?projectid=20>), as part of The Madidi Project
379 (www.mobot.org/madidi).

380

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552

553 **List of Appendices in Supporting Information**

554 **Appendix S1.** Number of plots, individuals and taxa, and environmental variables in our study
555 of Amazonian and Andean forest across ten sites in the Madidi region, northwestern Bolivia.

556 **Appendix S2.** Correlations between environmental distances for the four forest types studied in
557 the Madidi region, Bolivia, in an Excel file.

558 **Appendix S3.** Importance of variables in Random Forest models that predict residuals from a
559 neutral model of distance decay. The table provides the numerical results for Figure 3, with
560 standard deviations.

561

562 **Table 1.** Percentages of variance in F index of co-dominance between pairs of plots explained
563 by two models implemented consecutively. r^2_{neutral} refers to percentage of the variance
564 explained by spatial distance. r^2_{niche} refers to the percentage of the variance in co-dominance
565 explained by a Random Forest model based on environmental variables. $\text{contr}r^2_{\text{niche}}$ refers to the
566 explained variation in the residuals from the neutral model. The total explained variation is

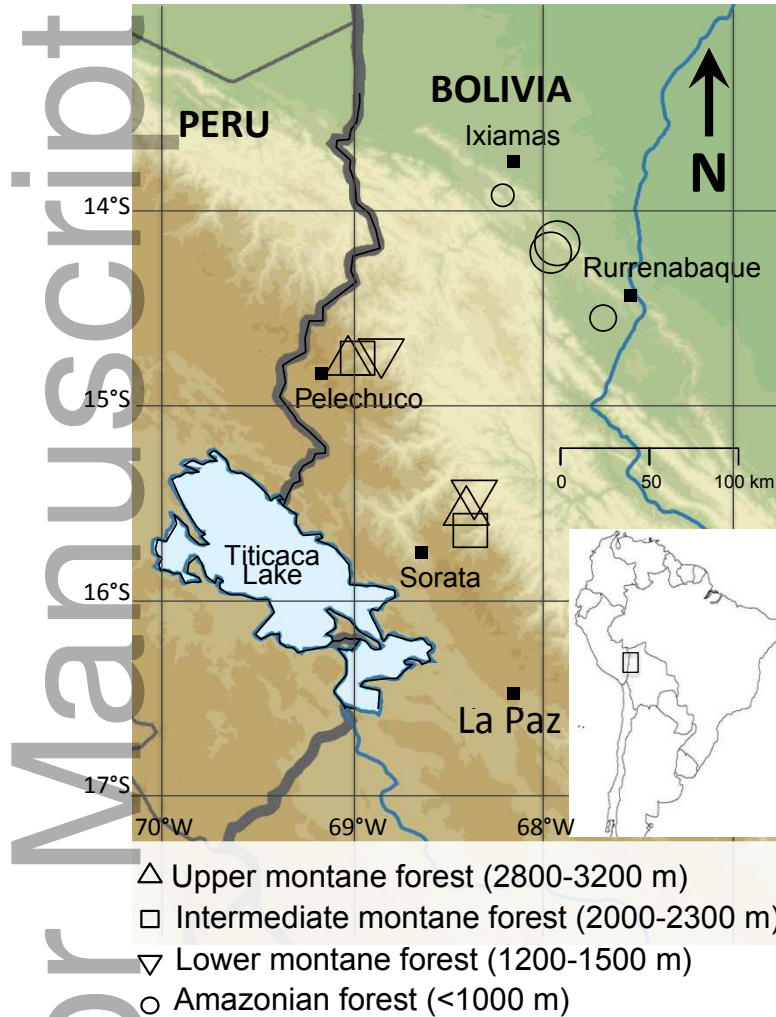
567 $r^2_{\text{neutral}} + \text{contr}r^2_{\text{niche}}$.

	Amazonian forest		Lower montane forest		Intermediate montane forest		Upper montane forest	
	(<1000 m elev.)		(1200–1500 m)		(2000–2300 m)		(2800–3200 m)	
	Local (<12 km)	Regional (>38 km)	Local (<12 km)	Regional (>38 km)	Local (<12 km)	Regional (>38 km)	Local (<12 km)	Regional (>38 km)
r^2_{neutral} (%)	16.1	0.2	14.2	3.5	11.0	5.3	17.1	1.6
r^2_{niche} (%)	36.5	34.5	33.3	32.6	20.7	22.5	43.6	50.5
$\text{contr}r^2_{\text{niche}}$ (%)	30.7	34.4	28.6	31.5	18.4	21.4	36.1	49.7
Total (r^2_{neutral} + $\text{contr}r^2_{\text{niche}}$) (%)	46.7	34.6	42.8	35.0	29.4	26.6	53.2	51.3

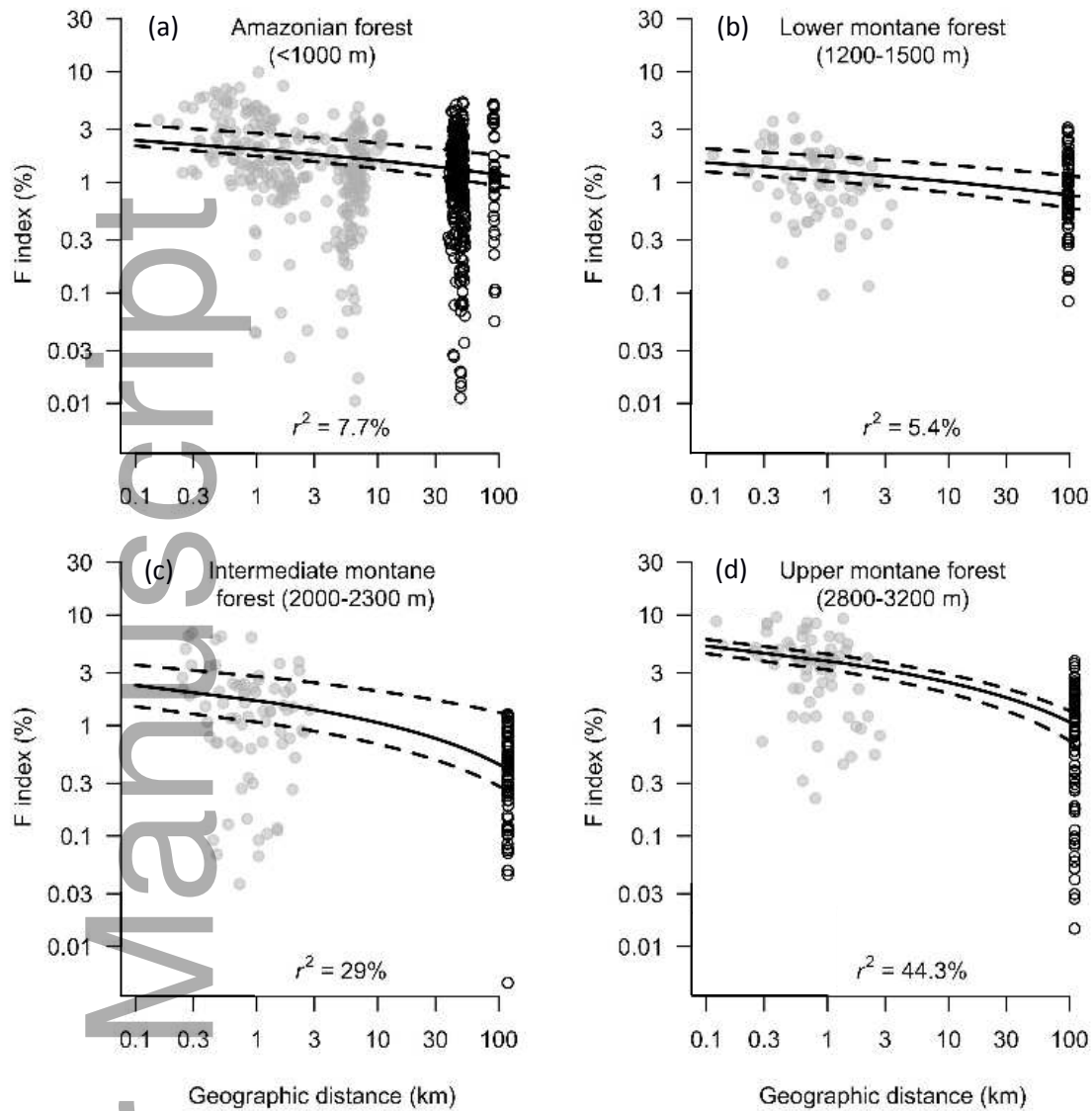
568

569 **Table 2.** Fitted parameters of the neutral model of distance decay in floristic similarity for
570 forest types at elevation bands in the Madidi National Park, Bolivia. Based on the 95%
571 confidence intervals we found some significant differences in dispersal potential σ , indicated by
572 superscripts.

Forest type	Parameter	Estimated	lower and upper boundaries of the 95% confidence interval	
Amazonian (<1000 m elev.)	Speciation rate (ν)	4.8e-13	3.66e-14	7.02e-12
	Dispersal (σ) (m)	63.5 ^b	56.1	64.0
Lower montane (1200–1500 m)	Speciation rate (ν)	2.9e-13	4.29e-15	2.29e-12
	Dispersal (σ) (m)	81.9 ^c	75.7	87.1
Intermediate montane (2000–2300 m)	Speciation rate (ν)	6.7e-09	3.83e-11	1.09e-08
	Dispersal (σ) (m)	51.4 ^b	47.0	64.3
Upper montane (2800–3200 m)	Speciation rate (ν)	2.2e-09	1.19e-09	6.29e-09



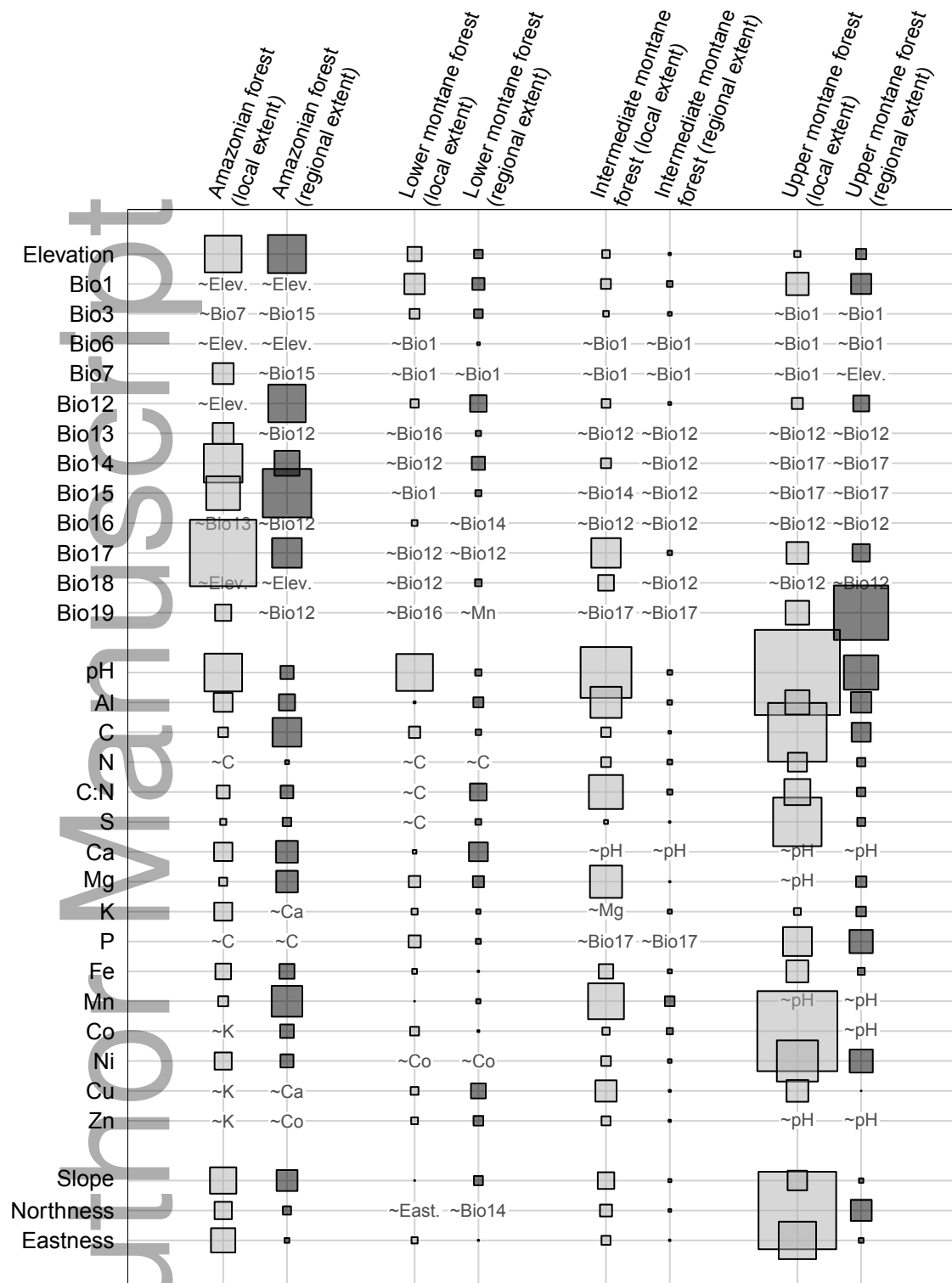
574 **Figure 1.** Study area in the Madidi National Park, Bolivia. The 90 plots are clustered among
 575 ten sites at four elevation bands: 36 were set among four Amazonian forest sites (<1000 m
 576 elevation); 18 plots among two lower montane forest sites (1200–1500 m); 18 plots among two
 577 intermediate montane forest sites (2000–2300 m); and 18 plots among two upper montane
 578 forest sites (2800–3200 m). Sites are represented by different symbols, their sizes proportional
 579 to the number of plots at each locality.



581

582 **Figure 2.** Distance decay by forest type. (a) Amazonian forest (<1000 m elevation), (b) lower
 583 montane forest (1200–1500 m), (c) intermediate montane forest (2000–2300 m) and (d) upper
 584 montane forest (2800–3200 m). Solid lines represent the fitted neutral model. Dashed lines
 585 represent 95% confidence intervals. These models are fitted to the entire collection of samples,
 586 although different symbols are used to highlight the two scales considered in the entire study.
 587 Solid gray and open black dots refer to local and regional extents, respectively.

588

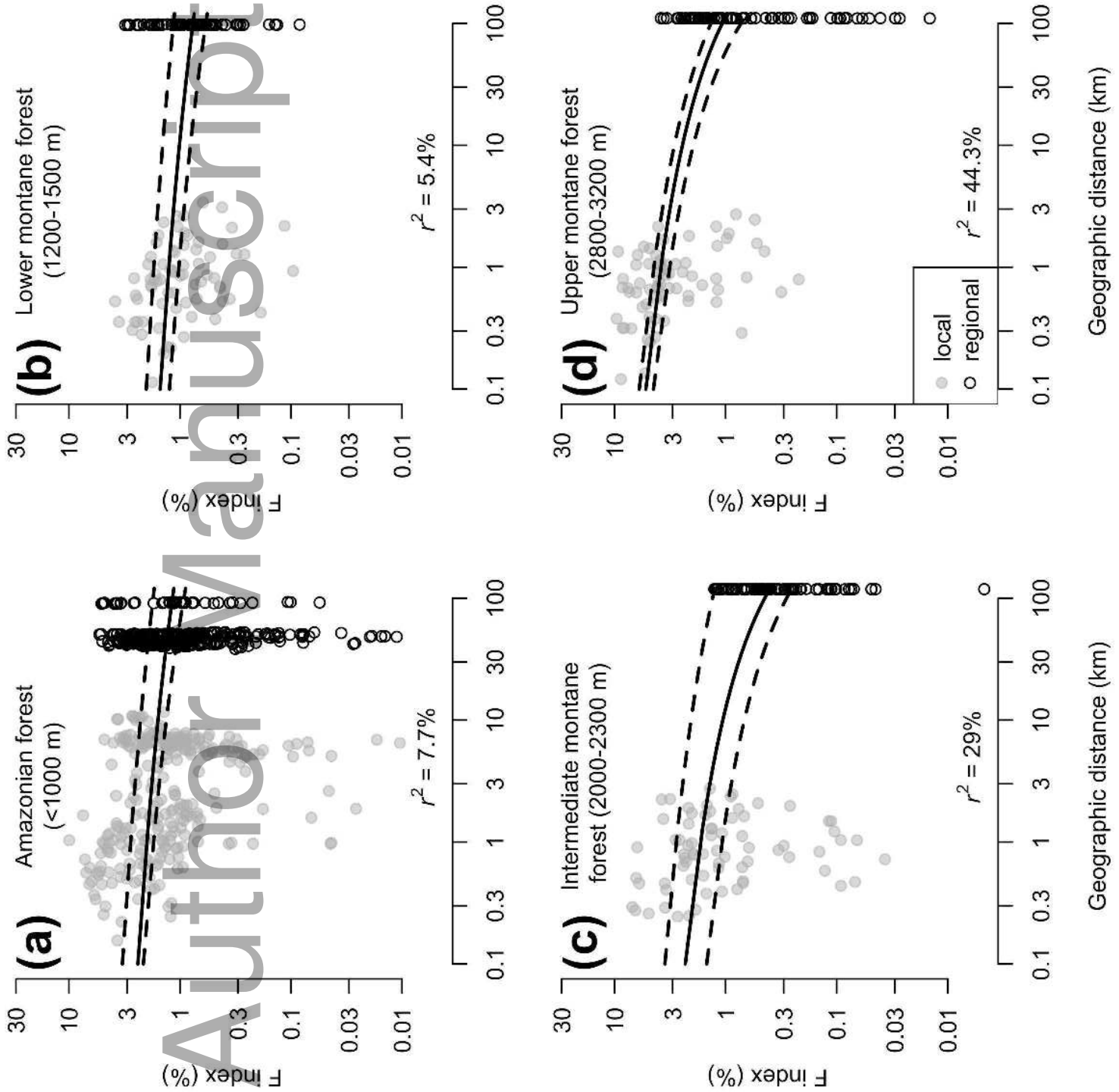


589
 590 **Figure 3.** Importance of variables in Random Forest models that predict residuals from a
 591 neutral model of distance decay in forests at four elevation bands (AF = Amazonian forest,
 592 <1000 m elevation; Lower montane forest, 1200–1500 m; Intermediate montane forest, 2000–
 593 2300 m; Upper montane forest, 2800–3200 m) and two extents (local and regional, <12 km and
 594 38–120 km apart, respectively) in Amazonian and montane forests in the Madidi region

595 (Bolivia). Importance of variable is displayed by a square size proportional to the increase in
596 node purity (INP) in the corresponding Random Forest model. Variables are grouped as
597 bioclimate (included elevation), soil chemistry, and topography. Variables excluded because
598 they were highly correlated ($|r| > 0.70$) with others are replaced with their best-correlated
599 variable, displayed as “~representative”. Appendix S3 contains the numerical results, with
600 standard deviations. Climatic variables are labeled according to WorldClim database (Hijmans
601 *et al.*, 2005) schema: Bio1 = annual mean temperature (all temperatures in $^{\circ}\text{C} \times 10$); Bio2 =
602 mean diurnal range (mean of monthly of (maximum temperature - minimum temperature));
603 Bio3 = isothermality ((Bio2/Bio7) $\times 100$); Bio4 = temperature seasonality (standard deviation \times
604 100); Bio5 = maximum temperature of warmest month; Bio6 = minimum temperature of
605 coldest month; Bio7 = temperature annual range (bio5-bio6); Bio8 = mean temperature of
606 wettest quarter; Bio9 = mean temperature of driest quarter; Bio10 = mean temperature of
607 warmest quarter; Bio11 = mean temperature of coldest quarter; Bio12 = annual precipitation
608 (all precipitations in mm); Bio13 = precipitation of wettest month; Bio14 = precipitation of
609 driest month; Bio15 = precipitation seasonality (coefficient of variation); Bio16 = precipitation
610 of wettest quarter; Bio17 = precipitation of driest quarter; Bio18 = precipitation of warmest
611 quarter; Bio19 = precipitation of coldest quarter.



- △ Upper montane forest (2800-3200 m)
- Intermediate montane forest (2000-2300 m)
- ▽ Lower montane forest (1200-1500 m)
- Amazonian forest (<1000 m)



Amazonian forest
(local extent)
Amazonian forest
(regional extent)

Lower montane forest
(local extent)
Lower montane forest
(regional extent)

Intermediate montane forest
(local extent)
Intermediate montane forest
(regional extent)

Upper montane forest
(local extent)
Upper montane forest
(regional extent)

Elevation
Bio1
Bio3
Bio6
Bio7
Bio12
Bio13
Bio14
Bio15
Bio16
Bio17
Bio18
Bio19
pH
Al
C
N
C:N
S
Ca
Mg
K
P
Fe
Mn
Co
Ni
Cu
Zn
Slope
Northness
Eastness

