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6 **Phylogenetic diversity of Amazonian tree communities**

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88 Understanding the distribution of phylogenetic diversity is critical to conservation
89 prioritization and determining the origins of high species richness. We calculated the
90 phylogenetic diversity (PD) present in 283 ~1 ha forest inventory plots from across
91 Amazonia. We show that PD has a non-random spatial distribution. PD, measured as the sum
92 of phylogenetic branch length in plots (*PD sensu stricto*, PDss), was highest in tree
93 communities of central and western Amazonia. Because PDss is strongly correlated with
94 species richness (SR), this is unsurprising. However, western Amazonian communities have
95 higher PDss than predicted by SR alone, while central communities have lower than expected
96 PDss. The Brazilian and Guiana Shields, while species poor and thus having low PDss, also
97 have PDss greater than predicted by SR. We suggest that the excess PD in western Amazonia
98 may be due to an easy-to-colonize environment (fertile, aseasonal), while the high values in
99 the Shields may be due to their great age. Meanwhile, some particularly stressful
100 environments (white-sand and seasonally dry tropical forests) have lower than expected
101 PDss, perhaps because the adaptations required in such environments present difficult to
102 surmount evolutionary barriers. Conservation planning in Amazonia should consider PD and
103 SR in future assessments.

104

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106 species richness, white-sand forest

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111 **1. Introduction**

112 A central task of biology is to quantify biodiversity and how it varies geographically [1].

113 Elucidating and understanding the dominant patterns of diversity is particularly important

114 within the tropics, because of their high species richness and the pressing need to develop and

115 apply effective conservation strategies in the face of massive habitat alteration. While the

116 species diversity of specific areas can be measured using different indices (e.g. species

117 richness, Shannon-Wiener Index, Fisher's alpha), these ecological metrics may fail to account

118 for the evolutionary, or lineage, diversity of communities. As a result, some authors have

119 advocated developing and implementing metrics, such as phylogenetic diversity, that quantify

120 the lineage diversity of communities [2, 3].

121 Phylogenetic diversity (PD) is generally estimated as the total branch length of a phylogeny

122 representing species in a community [2]. This metric tends to be correlated with species

123 richness (SR; the total number of species in a community), and thus SR can sometimes be

124 used as a proxy for PD [4, 5]. However, some areas contain significantly greater or less PD

125 than expected given their SR [6, 7], a pattern that could add complementary information

126 about the evolutionary history and conservation significance of a site [8]. Some researchers

127 have advocated other metrics that show less dependence on species richness, such as the

128 mean phylogenetic distance between species in a community, as alternative metrics to
129 represent the evolutionary diversity in communities [9-11]. The availability of different PD
130 metrics, in conjunction with the recent developments of standardized floristic sampling across
131 Amazonia [12, 13] and of a robust angiosperm phylogeny [14], now make it possible to
132 examine how PD and its covariance with species richness vary at large spatial scales across
133 the world's most species-rich tropical forest [see also 15]. By examining the PD of tree
134 communities throughout Amazonia, we aim to provide insights into its biogeographical
135 history and inform conservation prioritization.

136 Previous research [16] has shown tree species diversity in 1 ha plots across the Amazon to be
137 highest in the western and central portions and lowest in the Guianan and Brazilian shields.
138 Assuming that PD is correlated with SR, we would therefore expect that PD will be greatest
139 in the western and central Amazon. However, numerous factors may drive spatial variation in
140 PD and whether communities show greater or less PD than expected given their SR. For
141 example, based on variation in substrate age, one might hypothesize that tree communities on
142 the Guiana and Brazilian Shields, which overlay sediments of Pre-Cambrian origin [17],
143 would have had the opportunity to accumulate lineage diversity over many millions years,
144 and thus might have higher PD than expected given their low SR. In contrast, tree
145 communities of western Amazonia overlying Pliocene and Pleistocene sediments from the
146 Andes [17, 18] might be expected to show lower than expected PD because of the dominance
147 of recent evolutionary radiations within certain clades [19, 20]. The branches leading to
148 recently derived species should be short in comparison to the deep branches separating
149 species from older diversification events [21]. Gentry [22] suggested that the Andean
150 orogeny could have promoted high recent species diversification on the western Amazon
151 fringe through repeated creation of new habitats and large-scale rearrangement of complex,
152 dissected landscapes [see also 18]. Recent phylogenetic evidence has supported this notion,

153 showing that radiations of some diverse Andean and pre-Andean genera apparently coincide
154 with the uplift of the Andes [19, 20, 23].

155 Soil fertility and seasonality also vary across Amazonia. Overall, the relatively young soils of
156 western Amazonia are fertile in comparison with the highly weathered soils of central and
157 eastern Amazonia and the Guianan and Brazilian Shields, while the poorest soils are found
158 beneath white-sand forests that occur sporadically in small to large patches throughout the
159 northern part of the basin [17]. In addition, the dry season varies from being essentially
160 absent in the northwest to lasting 5-6 months in the southeast and some northern areas [24],
161 where moist forests give way to savannas and seasonally dry tropical forest (SDTF). Some of
162 these environmental conditions may represent stressful ecophysiological barriers that few
163 lineages have been able to overcome [25, 26]. Thus an alternative hypothesis to the one
164 above, based on substrate age, is that tree communities in areas of the Amazon with more
165 potential ecophysiological barriers to entry (i.e. white-sand forests in north-western
166 Amazonia and the Guiana Shield, savannas in south-western Amazonia, SDTF in the
167 northern Andes and south-western Amazonia) will show the greatest negative deviation from
168 expected PD given their SR [27].

169 We used a network of 283 forest inventory plots [RAINFOR; 28] to quantify the PD of tree
170 communities and examine its spatial variation across Amazonia. We rarefied all plots to the
171 same number of trees, and then calculated (i) the total phylogenetic branch length of all
172 species occurring in each plot, PD *sensu stricto* [PD_{ss}; 2], (ii) the deviation from expected
173 PD given SR [PD_{res}; 6], and (iii) the mean pairwise phylogenetic distance among co-
174 occurring species [MPD_t; 11, 29]. We first tested the assumption that PD_{ss} largely depends
175 on SR. We then tested the hypothesis, based on substrate age, that tree communities in the
176 Guiana and Brazilian Shields will show the greatest PD_{res}, while those in the western

177 Amazon will show the lowest PDres. While our sample sizes in savanna, SDTF, and white-
178 sand forests are limited, we conducted a preliminary test of the hypothesis that tree
179 communities in these stressful environments will show the lowest PDres. As MPDt is
180 putatively independent of SR, we expected it to show the same patterns as PDres.

181

182 **2. Methods**

183 **(a) Tree community plot data**

184 In this study, we used a total of 283 inventory plots of the RAINFOR forest plot network
185 [Date of extraction: 28/01/2013; 30; see supplementary material, Table S1]. Plots are
186 generally one hectare in size (mean \pm SD = 1.1 \pm 0.6 ha) and sample all trees \geq 10 cm
187 diameter at breast height (DBH). We restricted analyses to old-growth forest plots. Each plot
188 was treated as a community and classified into three main biomes (Figure 1): tropical moist
189 forest, TMF (n = 267 plots), SDTF (n = 11), and savannas, S (n = 5). Fourteen plots were
190 from the northern Andes (Colombia and Venezuela), outside the Amazon basin, but were
191 included because of their close phylogeographical connection to Amazonia.

192 The 267 tropical moist forest plots were further classified by the maximum age of the
193 underlying geological formation. The Guiana and Brazilian Shields represent the oldest
194 geological formations in Amazonia (TMF.o: > 500 Ma), followed by formations of central
195 and eastern Amazonia (TMF.i: 20-100 Ma) located between the Shields, while areas near to
196 the Andes (western Amazonia and northern Andes) are dominated by younger sediments
197 [TMF.y: < 20 Ma; 17] deposited mainly during the Pliocene and the Pleistocene [18] (Figure
198 1). All TMF plots were also classified by forest types: flooded forest (affected by the flooding
199 of rivers or with a shallow water table), montane forest (at 1650 - 3000 m a.s.l.), terra firme

200 forest (in the interfluvial plain on clayed or brown-sand soils), and white-sand forest (on
201 white-sand soils). Note that, in our data set, not all of the forest types are represented for each
202 of the geological formations (e.g. there were no communities of white-sand forests sampled
203 overlaying the geological formations of intermediate age).

204 In total, the dataset included 183,908 individual trees sampled in Bolivia, Brazil, Colombia,
205 Ecuador, French Guiana, Guyana, Peru, Surinam, and Venezuela. To ensure a standardized
206 nomenclature across plots based on the APG-III classification [14], the Taxonomic Name
207 Resolution Service version 3.0 was used (<http://tnrs.iplantcollaborative.org>; accessed on
208 01/03/2013). Tree ferns and gymnosperms only occur in significant numbers in montane
209 plots, and they are exceedingly rare in lowland forest, which is the focus of this study. These
210 very rare species represent 0.018 % of all individual trees in our lowland plots and are
211 essentially stochastically sampled in any given 1 ha plot (they were found in a total of 11
212 plots). Given this stochasticity and the strong effect of tree ferns and gymnosperms on
213 phylogenetic diversity metrics (they are subtended by very long phylogenetic branches; [15,
214 31, 32]), we excluded them from phylogenetic diversity calculations. We also excluded all
215 individuals not identified to species (13.6 %), while testing for the effect of doing so in the
216 analyses (see below). The final dataset contained a total of 157,340 individuals, belonging to
217 3,868 species, 732 genera and 126 families of angiosperms.

218 **(b) Phylogenetic tree and diversity metrics**

219 A phylogenetic tree of the whole species pool (see supplementary material, Figure S1) was
220 generated using Phylomatic in PHYLOCOM version 4.2 [33]. This tool provides a
221 phylogenetic hypothesis for the relationships among taxa by matching the list of species with
222 up-to-date family and genus names, and tip labels of a provided megatree [34]. In this case,
223 the topology of R20120829.new provided at <http://phylodiversity.net/phyloomatic/> was used.

224 An ultrametric phylogeny including branch length in millions of years (Ma) was obtained
225 using `bladj` in PHYLOCOM. This command fixes the root node (angiosperms, 179 Ma) and
226 other nodes to specified ages based on Wikström *et al.* [35]. Inconsistencies in syntax
227 between internal node labels of the phylogeny and the ages file were modified manually to
228 ensure a better performance of the node calibration using `bladj` [36].

229 Three metrics were used to evaluate the evolutionary history present in communities, (i)
230 phylogenetic diversity *sensu stricto* [PD_{ss}; 2], that is the total phylogenetic branch length of
231 all species occurring in a given community, (ii) deviation from expected PD_{ss} given species
232 richness (SR), that is a measure of the residuals from the relationship between PD_{ss} and SR
233 [PD_{res}; 6], and (iii) mean pairwise phylogenetic distance among co-occurring species [MPD_t;
234 11, 29]. While other phylogenetic diversity metrics exist [e.g. 9, 10], these were chosen
235 because of their simplicity and history of use in the literature [e.g. 6, 37, 38].

236 (c) Data assessment and analysis

237 To minimize the effects of sampling effort (i.e. plot size) and variation in tree density, we
238 used a rarefaction procedure that standardized all plots to 249 individuals, which was the
239 lowest observed number of individuals amongst all plots. Values for PD_{ss}, PD_{res}, and MPD_t
240 for each rarefacted community were calculated using the package PICANTE [39] in the R
241 Statistical Software version 2.15.1. SR was calculated as the total number of taxa in each
242 rarefacted community. Each taxon was classified into one of the three major angiosperm
243 clades (Magnoliids including Chloranthales, Monocots, and Eudicots) and the percentages of
244 species and individuals in each clade were estimated. The mean of the phylogenetic diversity
245 metrics, SR, and the proportion of major clades across 100 rarefactions were used for further
246 analyses.

247 The relationship between the phylogenetic diversity metrics measured as PDss and MPDt
248 were assessed against SR and the proportion of major clades. The level of significance of the
249 deviations from the relationship of PDss on SR was tested for different biomes using a *t* test.
250 The values of all three phylogenetic diversity metrics were compared among the different
251 biomes using F-tests and Tukey tests. We also assessed the correlation of the phylogenetic
252 diversity metrics with the latitude and longitude of plots.

253 We assessed if there was any bias to the phylogenetic diversity metrics with respect to
254 unidentified individuals by examining the correlation between percentage of unidentified
255 individuals in plots and the PD metrics. Finally, we also re-analysed a subset of the data (*n* =
256 117 plots with large sample size) rarefying the plots to 500 individuals per sampling unit, to
257 test the effect of sample size in the rarefaction procedure on estimating phylogenetic
258 diversity.

259

260 **3. Results**

261 **(a) Species richness and major angiosperm clades**

262 Terra firme moist forests of intermediate and young geological formations have the highest
263 species richness (SR), with an average of 88 and 72 species respectively (for 249 rarefacted
264 individuals; Table 1). Flooded moist forest communities in western and central Amazonia
265 had greater SR than flooded and terra firme forests on the Guiana and Brazilian Shields,
266 while the lowest SR was found in white-sand forests of the Guiana Shield and Andean
267 montane forests (Table 1). SDTF and savannas show intermediate values of SR, resembling
268 values of forest types on old geological formations.

269 On average, 85.8 % of species per plot belong to Eudicots, 11.1 % to Magnoliids, and 3.1 %
 270 to Monocots. These values were similar when comparing percentages of individuals, except
 271 for Monocots, which tend to be more abundant in the western Amazon (Table 1). Early
 272 diverging clades such as Magnoliids and Monocots tend to have a higher percentage of
 273 species and individuals on young geological formations than on intermediate and old
 274 formations, while Eudicots show the opposite pattern (Table 1). SDTF shows the lowest
 275 percentage of Magnoliid and Monocot species, and the greatest of Eudicots, but the
 276 abundance of these clades in savannas is more similar to the values typical of the moist forest
 277 plots.

278 **(b) Phylogenetic diversity metrics**

279 Species richness strongly positively correlates with PDss ($r = 0.98, p < 0.001$; Figure 2a),
 280 following a power relationship ($\log(\text{PD}) \sim \log(\text{SR}) \approx \text{PD} = 230.6 \times \text{SR}^{0.7}$), which was a
 281 better fit than a linear relationship ($\text{PD} \sim \text{SR} \approx \text{PD} = 1160.0 + 37.1 \times \text{SR}$; $r = 0.92, p < 0.001$).
 282 We used the residuals of the power relationship as our measure of PDres ($= \text{PD}_{\text{observed}} -$
 283 $\text{PD}_{\text{expected}}$). A much weaker correlation was observed between species richness and MPDt ($r =$
 284 $0.38, p < 0.001$; see supplementary material, Figure S2). In contrast, the percentage of species
 285 in Magnoliids + Monocots (i.e. = 1- Eudicots) correlates strongly with MPDt ($r = 0.88, p <$
 286 0.001 ; Figure 2b), which is driven mostly by variation in the relative abundance of
 287 Magnoliids ($r = 0.88, p < 0.001$) rather than Monocots ($r = 0.27, p < 0.001$). The correlation
 288 of the percentage of species in major clades with PDss was mostly weaker ($r_{1\text{-Eudicots}} = 0.52,$
 289 $r_{\text{Magnoliids}} = 0.48, r_{\text{Monocots}} = 0.26, \text{ all } p < 0.001$; see supplementary material, Figure S2).

290 **(c) Spatial patterns**

291 Our PD metrics show non-random spatial distributions across Amazonia (Figure 3). MPDt
 292 shows a strong longitudinal gradient, increasing from east to west ($r_{\text{Longitude}} = -0.45, p <$

293 0.001), while PD_{ss} ($r_{\text{Latitude}} = 0.14, p < 0.05$; $r_{\text{Longitude}} = -0.16, p < 0.05$) and PD_{res} ($r_{\text{Latitude}} = -$
294 $0.15, p < 0.01$; $r_{\text{Longitude}} = -0.14, p < 0.05$) show weaker, but still significant correlations with
295 both latitude and longitude. PD_{ss} was greatest in communities on young and intermediate
296 aged geological formations (Figure 3a), while PD_{res} was greatest in communities on young
297 and old geological formations (Figure 3b). MPD_t was greatest in young geological
298 formations (Figure 3c). These spatial patterns are conserved among forest types of the moist
299 forest biome (Table 1). For all metrics, PD values of savannas were similar to moist forest
300 communities, while SDTF consistently showed low phylogenetic diversity (Figure 3d-f).
301 PD_{ss} shows no relationship with the percentage of unidentified individuals excluded per plot
302 ($r^2 = 0.002, p = 0.20$), while PD_{res} ($r^2 = 0.02, p < 0.05$) and MPD_t ($r^2 = 0.02, p < 0.05$) show
303 weak relationships (see also supplementary material, Figure S3). In addition, for plots with
304 sufficient sample size to assess, we found a strong 1:1 relationship between phylogenetic
305 diversity metrics (PD_{res} and MPD_t) calculated with rarefactions of 500 versus 249
306 individuals (see supplementary material, Figure S4).

307

308 4. Discussion

309 Our results illustrate the non-random spatial distribution of phylogenetic diversity of tree
310 communities across Amazonia. Consistent with previous studies (in savannas of North
311 America [40] and in the Cape flora of South Africa [6]), phylogenetic diversity *sensu stricto*
312 (PD_{ss}) in the Amazon shows a strong correlation with species richness (SR). Thus,
313 communities of the most species-rich areas, central and western Amazonia [16], show the
314 greatest PD_{ss} (Figure 3a). Interestingly, once the relationship between PD_{ss} and SR is taken
315 into account, we found that western and central Amazonia show strikingly different patterns.
316 Western Amazonian tree communities show significantly greater PD_{ss} than expected given

317 their SR (i.e. strong positive PDres), while central Amazonian tree communities show
318 significant negative PDres (Figure 3b). Among moist forests, communities of the Brazilian
319 and Guianan Shields have the lowest values of PDss, but high PDres, on par with that found
320 in western Amazonia. Among the drier biomes found on the edges of Amazonia, savannas
321 have moderate PDss and high values of PDres, while seasonally dry tropical forests (SDTFs)
322 have consistently low PDss and PDres (Figure 3d,e).

323 We found that the mean pairwise phylogenetic distance among co-occurring species (MPDt)
324 does not correlate well with species richness, suggesting that it could be a better metric of
325 phylogenetic diversity than PDss. However, we found that MPDt values depend primarily on
326 how evenly taxa are distributed amongst the three major angiosperm clades (Magnoliids
327 including Chloranthales, Monocots, and Eudicots), which is shown by the strong positive
328 correlation between the MPDt values and the proportion of taxa in plots that are Magnoliids
329 and Monocots (the two rarer clades; see Figure 2b). Thus, areas that have many Magnoliids
330 and Monocots present (in our case western Amazonia), perhaps due simply to environmental
331 conditions favourable to these early divergent taxa, show the greatest MPDt values. While it
332 is important to have a measure of how evenly distributed taxa are across the major clades of a
333 phylogeny, it is uncertain if MPDt is a useful metric upon which to make conservation
334 decisions.

335 **(a) Has the greatest phylogenetic diversity been accumulated in communities overlaying**
336 **old geological formations?**

337 Communities on old geological substrates in the Brazilian and Guianan Shields and
338 communities on young geological substrates showed equally high PDres (Figure 3e; TMF.o
339 and TMF.y). Thus, the prediction that PDres would be positively correlated with substrate
340 age was rejected. Nevertheless, we suggest that the high PDres found in the Guiana and

341 Brazilian Shields may be explained by their long-term geological history. Recent
342 phylogenetic studies have shown that some of the most diverse and characteristic clades of
343 the Shields are very old (e.g. *Licania*, ca. 46 Ma, [41]; *Pouteria*, ca. 60 Ma, Richardson, pers.
344 comm.), and it seems diversity has been accumulating in these regions for many millions of
345 years.

346 Rather, to understand the rejection of the hypothesis that geologically older substrates show
347 the greatest PDres, we need to consider why tree communities of western Amazonia show
348 such high PDres. That communities of western Amazonia show high PDss is unsurprising, as
349 we have shown PDss to be strongly correlated with SR, and SR is substantially higher in the
350 western Amazon [16]. However, much of this diversity is due to recently-radiated species-
351 rich genera [22] such as *Inga* [19] and *Guatteria* [20], and short branches do not greatly
352 increase phylogenetic diversity [21]. Another exceptional aspect of western Amazonian tree
353 communities that must be considered is that they are occupied by lineages from the entirety
354 of the angiosperm phylogeny. We propose that the fertile and aseasonal environments in the
355 west may be easier for various lineages with diverse evolutionary backgrounds to invade.
356 Moreover, the ability of diverse lineages to establish in the western Amazon may also be
357 related to the high rates of disturbance and turnover in the region [42]. Finally, the complex
358 geological configuration of western Amazonia [18, 43] may also contribute to high PDres by
359 creating an environment suitable to maintaining high phylogenetic diversity.

360 **(b) Do areas with more potential ecophysiological barriers show the lowest PD in their**
361 **tree communities?**

362 We expected that more extreme ecological conditions in seasonality and soil fertility may
363 represent potential evolutionary barriers that few lineages have been able to overcome [25-
364 27]. Both savannas and SDTF have a stressful dry season, but they show contrasting

365 phylogenetic diversity patterns. While phylogenetic diversity metrics of savannas were
366 similar to those of nearby communities in tropical moist forest, SDTF has consistently low
367 phylogenetic diversity by all metrics (Figure 3d-f). Savannas and tropical moist forest
368 communities may share similar lineages across the angiosperm phylogeny, a pattern that
369 supports previous studies that suggested that savannas in south-western Amazonia are formed
370 by the colonisations of lineages from nearby biomes that managed to adapt to fire around 4-
371 10 Ma [44, 45]. Conversely, the low phylogenetic diversity values shown for SDTF
372 communities suggest that fewer clades have succeeded in colonizing SDTF, and that
373 consequently, SDTF is occupied principally by close relatives. However, our conclusions
374 must be taken as preliminary given the low sample size and limited geographic extent of our
375 savanna and SDTF plots.

376 Previous studies have indicated a strong habitat specialization in white-sand communities as
377 indicated by the high number of individuals that belong to white-sand specialist species [46],
378 and by the distinct herbivore and ecophysiological defences that these species have evolved
379 to live in such poor-fertile soils [47]. Therefore, we also expected that white-sand forests
380 would have a high frequency of closely related species and low phylogenetic diversity. Our
381 results showed that only white-sand communities of the Guiana Shield have low PDres
382 values (comparable to SDTF; Table 1). In contrast, higher values of PDres were found in the
383 small patches of white-sand forests of north-western Amazonia, which may indicate a higher
384 influence by the regional pool (i.e. species present in the surrounding terra firme forest) than
385 in the larger, more contiguous white-sand patches of the Guiana Shield.

386

387 **5. Conclusions**

388 Our study has revealed a non-random spatial distribution of phylogenetic diversity across
389 Amazonia, with some areas holding significantly more, or less, phylogenetic diversity than
390 expected from their species richness alone. These results indicate that species richness may
391 not give sufficient information to establish conservation priorities for evolutionary diversity
392 in Amazonia. Other metrics, in particular PDres, should be considered [6, 8]. For example,
393 the PDres differs between forests of central and western Amazonia, both of which have
394 communities that are exceptionally species rich. Communities of central Amazonia are
395 occupied by phylogenetically close relatives, while more distantly related taxa occur in
396 western Amazonian forests. Moreover, the Brazilian and Guiana Shields, while species poor,
397 also have great PDres. We suggest that the high PDres of the Shields is due to the
398 accumulation of many lineages over their long history, while the high PDres of the western
399 Amazon is due to the easy-to-colonize fertile and aseasonal environments present there. In
400 addition, specific habitats elsewhere in the Amazon basin (e.g. white-sand and seasonally dry
401 tropical forests) may require adaptations that are more difficult to evolve, and thus are
402 dominated by close relatives from fewer lineages. If we are to preserve the full spectrum of
403 lineage diversity and the evolutionary processes that led to the exceptional biodiversity of
404 Amazonian communities, regional conservation planning may need to incorporate
405 phylogenetic information in order to explicitly account for the deviation of phylogenetic
406 diversity from expectations based on species richness.

407

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429

430 **Data accessibility:** Dataset of the RAINFOR forest plot network is available at

431 <https://www.forestplots.net/>

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579 **Table and figure captions**

580 Table 1. Community composition and diversity across forest types, showing proportional
581 representation of major clades and mean values of species richness (SR) and phylogenetic
582 diversity (Phylogenetic diversity *sensu stricto* (PD_{ss}), deviations from expected PD_{ss}
583 accounting for species richness (PD_{res}), and mean pairwise phylogenetic distance among co-
584 occurring species (MPD_t) are given in millions of years (Ma)).

585 Figure 1. Location of 283 permanent RAINFOR plots indicating geological formations and
586 biomes in South America. Geographical regions used in the text are indicated in bold.

587 Figure 2. Relationship between (a) phylogenetic diversity *sensu stricto* and species richness,
588 and between (b) mean pairwise phylogenetic distance among co-occurring species and the
589 proportion of species of Magnoliids and Monocots (= 1 - Eudicots). Tropical moist forest
590 biome is classified based on maximum age of geological formations [young: < 20 Ma;
591 intermediate: 20-100 Ma, old: > 500 Ma; 17].

592 Figure 3. (a-c) Variation in the spatial distribution and (d-f) among biomes of phylogenetic
593 diversity in South America. Phylogenetic diversity *sensu stricto* (PD_{ss}), deviations from
594 expected PD_{ss} accounting for species richness (PD_{res}), and mean pairwise phylogenetic
595 distance among co-occurring species (MPD_t) are provided in different columns. Maps show
596 mean values of PD for tree inventories in one-degree grid. Tropical moist forest biome is
597 classified based on maximum age of geological formations [TMF.y: < 20 Ma; TMF.i: 20-100
598 Ma, TMF.o: > 500 Ma; 17]. Savanna and seasonally dry tropical forest are indicated as S and
599 SDTF, respectively. Letters in boxplots indicate significant difference among mean values
600 (Tukey's HSD; $p < 0.05$). Asterisks indicate the level of significance of PD_{res} (t test; * $p <$
601 0.05, ** $p < 0.01$, *** $p < 0.001$), i.e. communities with higher or lower PD_{ss} values than
602 expected by their species richness.

603 Table 1

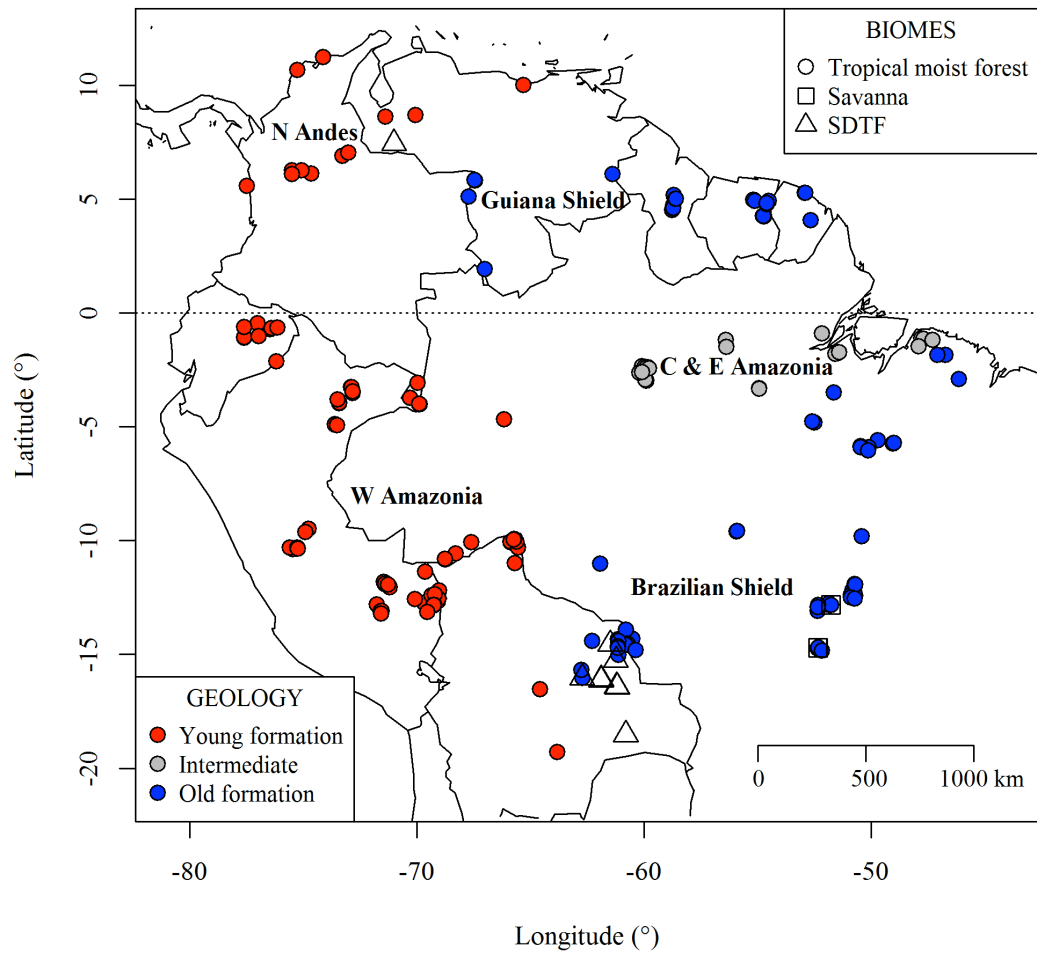
Biome (max. geological age)	Forest type	N° of plots	Sample area (ha)	Indiv. ID to spp (%)*	Species & individuals (mean, %)						Mean diversity values			
					Magnoliids		Monocots		Eudicots		SR	PDss (Ma)	PDres (Ma)	MPDt (Ma)
					spp	ind	spp	ind	spp	ind				
Tropical moist forest (< 20 Ma)	Flooded	12	17	86	16	15	6	18	78	67	72	3,963	83	260
	Montane	16	16	80	12	10	1	1	87	89	29	2,180	78	255
	Terra firme	88	97	85	14	14	5	14	81	72	77	4,101	55	256
	White sand	4	4	83	10	5	5	5	85	91	42	2,839	192	254
Tropical moist forest (20 - 100 Ma)	Flooded	2	2	73	9	5	0	0	90	95	72	3,478	-409	242
	Terra firme	39	54	85	12	9	1	2	87	89	88	4,200	-255	248
Tropical moist forest (> 500 Ma)	Flooded	17	16	89	5	4	2	4	93	92	34	2,368	61	238
	Terra firme	85	94	87	10	10	3	6	87	85	56	3,310	54	247
	White sand	4	4	87	7	1	0	0	93	99	22	1,608	-178	233
Savanna	Savanna	5	4	100	5	4	2	2	93	94	47	3,105	189	239
SDTF	Dry forest	11	12	96	2	1	3	3	95	96	35	2,214	-183	223
TOTAL		283	320	86	11	10	3	8	86	82	63	3,510	3	249

* The mean proportion of individuals identified to species.

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607 Figure 1



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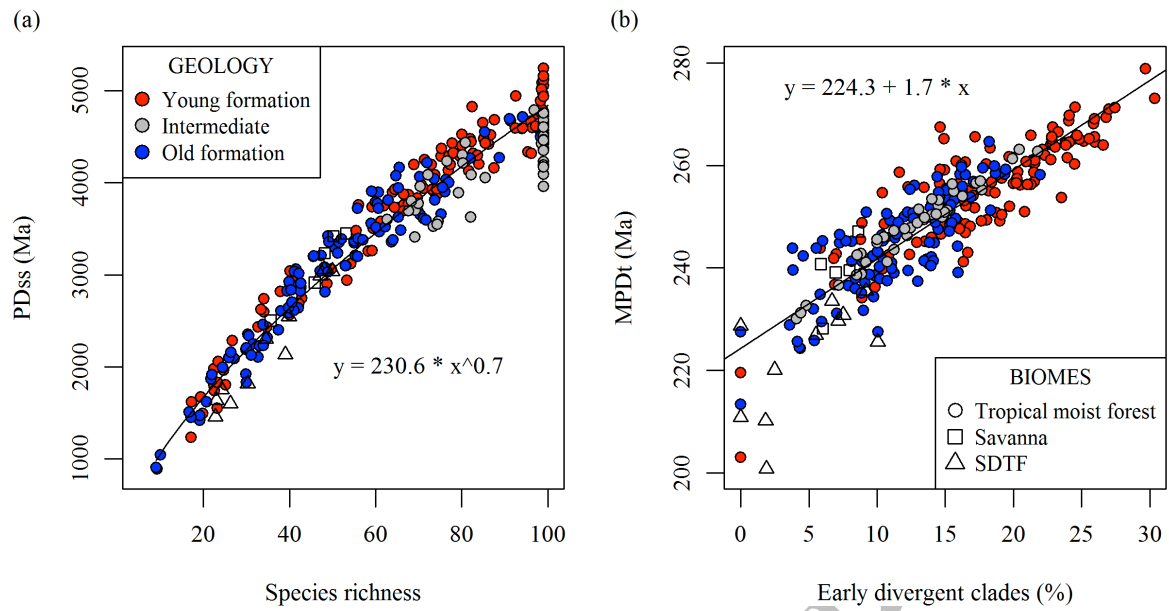
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616 Figure 2



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