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2

3 **On the floristic identity of Amazonian vegetation types**

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23 **ABSTRACT**

24 The Amazon forest is far from uniform, containing different forest types and even savannas,  
25 but quantitative analyses of this variation are lacking. Here, we applied ordination analyses  
26 to test the floristic differentiation amongst Amazonian vegetation types using data for  
27 virtually all known tree species occurring in the Amazon (8,224), distributed across 1,584  
28 sites. We also performed multiple regressions to assess the role of climate and substrate in  
29 shaping continental-scale patterns of community composition across Amazonia. We find that  
30 the traditional classification of Amazonian vegetation types is consistent with quantitative  
31 patterns of tree species composition, with high elevation and the extremes of substrate-related  
32 factors underpinning the floristic segregation of environmentally “marginal” vegetation types  
33 and *terra firme* forests (with climatic factors being relatively unimportant). These patterns  
34 hold at continental-scales, with sites of similar vegetation types showing higher similarity  
35 between them regardless of geographic distance, which contrasts with the idea of large-scale  
36 variation amongst geographic regions (e.g., between the Guiana Shield and southwestern  
37 Amazon) representing the dominant floristic pattern in the Amazon. In contrast to other  
38 tropical biomes in South America, including the *Mata Atlântica* (second largest rain forest  
39 biome in the neotropics), the main floristic units in the Amazon are not geographically  
40 separated, but are edaphically driven and spatially interdigitated across Amazonia. Two thirds  
41 of *terra firme* tree species are restricted to this vegetation type, whilst among marginal  
42 vegetation types, only white-sand forests (*campinaranas*) have a substantial proportion of  
43 restricted species, with other vegetation types sharing large numbers of species.

44

45 **Keywords:** community composition, edaphic conditions, environmentally marginal habitats,  
46 ordination analysis, environmental gradients, *terra firme* forests, tree species, white-sand  
47 forest.

48

49 **INTRODUCTION**

50

51 The Amazon forest, which spreads across the lowlands of the Amazon, Orinoco and other  
52 northern drainages of South America, is the world's largest continuous expanse of tropical  
53 rain forest, with an ever increasing number of described plant species (Cardoso *et al.*, 2017;  
54 ter Steege *et al.*, 2016). Since the first scientific exploration of the 18<sup>th</sup> and 19<sup>th</sup> centuries, it  
55 has been clear that the region is far from a continuous and undifferentiated rain forest, as  
56 there are striking contrasts among forest physiognomies and even patches of savanna  
57 vegetation.

58 Two main dichotomies in vegetation types have long been established, both using  
59 divisions based upon which environments are interpreted to be more marginal (Salovaara *et*  
60 *al.*, 2005). One contrasts upland, *terra firme* forests growing on flood-free interfluves  
61 (literally solid or firm ground; *tierra firme* in Spanish) with those growing on the seasonally  
62 inundated floodplains along wide and slow flowing, larger rivers (Luize *et al.*, 2018). The  
63 other dichotomy contrasts both *terra firme* and flooded forests with forest occurring on  
64 pockets of highly leached deposits of podzolized hypo-dystrophic white-sand (Adeney *et al.*,  
65 2016). But while the environmental differences between *terra firme*, flooded and white-sand  
66 forests are somewhat striking, the lines between these forests and the other vegetation types  
67 in the Amazon are not always sharp, contributing to some nomenclatural confusion (Phillips  
68 *et al.*, 2003).

69 There are several additional prominent vegetation types in the Amazon, growing on  
70 and around rock outcrops and coastal sands. In both edaphic situations, the vegetation shows  
71 a wide array of physiognomic expressions, including forests, dwarf-forests, scrublands and  
72 bushlands, often mixed in mosaics. Rock outcrops are particularly evident across the chain of

73 sandstone highlands of the Guiana Shield (often referred to as *tepuis*; Berry & Riina, 2005;  
74 Huber, 1997), and on the top of the numerous inselbergs of both the Brazilian and Guiana  
75 Shields (Gröger, 2000; Raghoenandan, 2000). Coastal vegetation mosaics include extensive  
76 tracts of mangrove forests that run almost uninterrupted from the Brazilian island of São Luís  
77 to the Orinoco Delta in Venezuela, and may penetrate inland as far as 40 km where they  
78 gradually blend with flooded forests (González, 2011; Nascimento *et al.*, 2013). Away from  
79 the mangroves, pockets of stabilized coastal sands bear a mosaic of vegetation types usually  
80 referred to as *restingas* and *matas de maré* in Brazil (Silva *et al.*, 2010).

81         Although virtually all the environmentally marginal vegetation types can include open  
82 physiognomies that may resemble savannas, the Amazon is also home to savannas *sensu*  
83 *stricto*, i.e. those associated with the existence of a dry season lasting for at least three  
84 months, and a flammable grass ground layer that may trigger fire outbreaks (Huber, 1997).  
85 Most of these savannas experience some form of waterlogging during the rainy season (see  
86 Pennington *et al.*, 2006).

87         From previous studies, we know that tree species distribution patterns do match some  
88 of these pre-defined vegetation types at local and regional scales (10 to 100,000 km<sup>2</sup>; e.g.,  
89 Draper *et al.*, 2018; Draper *et al.*, 2019; Duivenvoorden, 1995; Guitet *et al.*, 2015; Higgins *et*  
90 *al.*, 2011; Pitman *et al.*, 2008; Scudeller, 2018; Stropp *et al.*, 2011; ter Steege *et al.*, 2000)  
91 but, so far, this has not been scrutinized for the Amazon region as a whole and all its main  
92 vegetation types. A common conclusion stemming from the few Amazon-wide floristic  
93 studies is that distinct vegetation types in one region tend to resemble one another more  
94 closely than they do the same vegetation types in other regions (Silva-Souza & Souza, 2020;  
95 ter Steege *et al.*, 2006; Terborgh & Andresen, 1998). Such conclusions have led to a view of  
96 floristic regionalization that has neglected the different vegetation types of Amazonia. For  
97 example, there is a consistent west to east gradient in tree community composition, congruent

98 with an Amazon-wide variation in soil fertility and drought (soils in the eastern Amazon are  
99 poorer and climate is drier; ter Steege *et al.*, 2006). These continental-scale analyses have  
100 either been conducted at coarser taxonomic scales - at the family (Terborgh & Andresen,  
101 1998) and genus-level (ter Steege *et al.*, 2006) - or have lumped taxa from distinct vegetation  
102 types into large geographic ‘grid cells’ (e.g., 4° x 6° in ter Steege *et al.*, 2006; up to 20 km  
103 distance in Silva-Souza & Souza, 2020). Here, we bring together the most comprehensive,  
104 species-level dataset to date on the composition of tree communities across the entire  
105 Amazon basin, where individual communities have been assigned *a priori* to one of the  
106 predominant vegetation types in the Amazon.

107 Our objectives are three-fold. Firstly, we test the floristic differentiation of nine  
108 vegetation types, following the classification system proposed by Oliveira-Filho (2015). We  
109 predict that by using comprehensive, species-level tree community surveys, most (if not all)  
110 vegetation types will show an Amazon-wide compositional consistency.

111 Secondly, we test whether variation in edaphic and climatic conditions controls the  
112 floristic differentiation between *terra firme* forest and other vegetation types, with marginal  
113 vegetation types being placed in environments sometimes interpreted to be more stressful  
114 (Salovaara *et al.*, 2005). We predict that the floristic segregation of lowland vegetation types  
115 is primarily associated with edaphic factors (e.g., rockiness, sandiness, salinity, soil-  
116 waterlogging), with climate being only important in segregating highland vegetation types  
117 (e.g., montane forest, *tepui*) from all others.

118 Finally, to give context to our results and to explore the floristic distinctiveness of  
119 vegetation types, we also examine patterns of species shared amongst these vegetation types  
120 and the proportion of species restricted to individual vegetation types.

121

## 122 MATERIALS AND METHODS

123

## 124 **1. Study area**

125 The Amazon forest, as circumscribed here (see outline in Figure 1), includes most of the  
126 Amazon and Orinoco river basins (excluding the Andean headwaters of some rivers and the  
127 mid-Orinoco Llanos), and the North Atlantic coastal river basins between the states of Delta  
128 Amacuro, in Venezuela, and Maranhão, in Brazil. With regards to elevation, a maximum  
129 altitude of 1,100m was established on the Andean flanks to exclude the complex and  
130 extensive vegetation and environment gradients associated with the massive mountain chain.  
131 No altitudinal limit was established, however, for the highlands of the Guiana Shield, which  
132 are entirely embedded in the Amazon Province. This is a controversial issue in the sense that  
133 some authors consider the Guiana Highlands as a separate biogeographic province (e.g.,  
134 Cabrera & Willink, 1980; Cardoso *et al.*, 2017), supported by the high number of endemic  
135 species, many of which are restricted to particular *tepuis* or highlands (Berry & Riina, 2005).  
136 We based our decision on the following facts: (a) unlike the Andes, which make up a natural  
137 limit, the Guiana Highlands are encircled and pervaded by Amazonian lowlands; (b) the  
138 highest altitudes reached by the Guiana Highlands (2,500-3,000m) are modest compared to  
139 those of the Andes; and (c) *tepuis* and highlands also share a considerable number of species  
140 with lowland Amazonian vegetation types (Steyermark *et al.*, 1995-2005).

141

## 142 **2. Nomenclature**

143 The white-sand vegetation complex is particularly thorny when it comes to nomenclature.  
144 The main reason for this is the remarkable variation in physiognomy, which ranges from  
145 grass/shrublands to forests with slender-trunked trees and more open canopies compared to  
146 those of adjacent *terra firme* forests growing on more clayey soils (Adeney *et al.*, 2016).  
147 Throughout the Amazon, various local terms are also used to designate both the whole white-

148 sand complex and its physiognomic expressions, e.g. *bana*, *caatinga amazônica*, *campina*,  
149 *campinarana*, *varillal* and *chamizal* (Demarchi *et al.*, 2018; Fine *et al.*, 2010; García-  
150 Villacorta *et al.*, 2016; Stropp *et al.*, 2011). Following Daly *et al.* (2016), we here adopt  
151 *campinarana*, because of its official use in Brazil (IBGE, 2012) and because it embraces the  
152 whole array of physiognomies growing on podzolized sands liable to ground water saturation,  
153 but conveniently excludes white-sand floodplain forests, which we distinguish in this paper.

154 Nomenclature for vegetation occurring on seasonal floodplains is less complex. We use  
155 the prevailing nomenclature for two main seasonally flooded vegetation types in the Amazon,  
156 distinguishing *igapó* and *várzea* forests, depending on the types of rivers along which they  
157 occur (see Junk *et al.*, 2011; Kubitzki, 1987; Prance, 1979). *Várzea* forests are found along  
158 rivers carrying copious quantities of sediments (and nutrients), mostly brought from the  
159 Andes, with variation in the amount of clay resulting in waters that are many shades of  
160 brown. Confusingly, these rivers are often called white-water rivers (*rios de agua blanca*,  
161 *rios de água branca*). In contrast, *igapó* forests are found along rivers with small amounts of  
162 suspended mineral particles, which are called black or clear-water rivers (*rios de agua negra*  
163 *o clara*, *rios de água negra ou clara*). These rivers drain basins where white-sands or other  
164 highly leached soils prevail (e.g., flowing from the Brazilian and Guiana Shields) and can  
165 carry vast loads of humic acid colloids resulting from the arrested litter decay in these hypo-  
166 dystrophic soils. A similar process takes place in black-water oxbow lakes severed from  
167 white-water rivers as well as in narrower upstream floodplains throughout the basin. The  
168 dichotomy of *várzea* and *igapó* falls short when it comes to rivers with “mixed” waters, and  
169 rivers with temporal and spatial variations in suspended particles, of which the Casiquiare  
170 Channel in Venezuela is an example. In both *igapós* and *várzeas*, vegetation structure varies,  
171 from tall forests to floodplains with more open formations depending on local flooding  
172 dynamics and related processes of either erosion or sedimentation (Kalliola *et al.*, 1992;



173 Luize *et al.*, 2018; Salo *et al.*, 1986; Worbes *et al.*, 1992). The timing and duration of  
174 flooding in these forests can be variable, from once every few decades in rivers close to the  
175 Andes (e.g. on the Manu River in Peru, pers. comm. John Terborgh) to multiple months  
176 annually for the iconic *várzeas* and *igapós* along major rivers such as the Amazon and the  
177 Rio Negro.

178

### 179 **3. Dataset**

180 We extracted the dataset from the NeoTropTree (NTT) database  
181 (<http://www.neotropree.info/>), which consists of tree species checklists (trees defined here as  
182 freely standing woody plants >3 m in height) compiled for geo-referenced sites, from  
183 southern Florida (U.S.A.) and Mexico to Patagonia in Argentina and Chile. NTT currently  
184 holds 7,485 sites/checklists, 20,562 woody plant species and 1,206,314 occurrence records. A  
185 site/checklist in NTT is defined by a single vegetation type, following the classification  
186 system proposed by Oliveira-Filho (2015), contained in a circular area with a 10 km  
187 diameter. Where two or more vegetation types co-occur in the area, there can be multiple  
188 geographically overlapping sites in the NTT database.

189         The data were originally compiled from an extensive survey of published and  
190 unpublished (e.g. PhD theses) literature, particularly those on woody plant community  
191 surveys and floristic inventories. Additional occurrence records obtained from both major  
192 herbaria and taxonomic monographs have been added to the checklists when they were  
193 collected within the 10-km diameter of the original NTT site, and within the same vegetation  
194 type. NTT does not include sites with an indication of high anthropogenic disturbance nor  
195 those with low species richness, because this is often due to low sampling/collecting efforts,  
196 which results in poor descriptive power. Thus, secondary forests, which might be considered  
197 a distinct vegetation type, are not included in our study. Lowest species richness in the

198 Amazon dataset ranged from 20 species in savanna *s.s.* and *campinarana* to 100 in *terra*  
199 *firme* forest, while plot size (in floristic surveys derived from plot data) ranged from 1 to 5  
200 ha.

201 All species and their occurrence records were checked for taxonomic circumscriptions  
202 and geographical distributions as accepted by the teams of specialists responsible for the  
203 online projects *Flora do Brasil*, *Catalogue of the Vascular Plants of Ecuador*, *Peru Checklist*,  
204 *Bolivia Catalogue* (available at <http://floradobrasil.jbrj.gov.br/>,  
205 <http://www.tropicos.org/Project/CE/>, <http://www.tropicos.org/Project/PEC/>, and  
206 <http://www.tropicos.org/Project/BC/>, respectively) and published floras (Bernal *et al.*, 2016;  
207 Boggan *et al.*, 1997; Cardoso *et al.*, 2017; Steyermark *et al.*, 1995-2005). We eventually  
208 eliminated records for 111 species due to synonymy (59), invalid or dubious names (7),  
209 incorrect growth habit (15) and incorrect distribution (30).

210 The final dataset contained presence/absence data for 8,224 tree species across 1,584  
211 sites, with a total of 364,965 presences. Sites derived exclusively from herbarium data  
212 represented 41% of the full matrix (654 sites). The dataset also included 23 environmental  
213 variables (30 arc-sec resolution) for all its sites, derived from multiple sources. Procedures  
214 and protocols concerning variables' sources and extraction are thoroughly detailed at  
215 <http://www.neotroptree.info/>.

216 We adopted the vegetation descriptors provided by NTT and based on Oliveira-Filho  
217 (2015) to classify the sites into nine vegetation types: 776 *terra firme* forests, 171  
218 *campinaranas*, 291 *várzeas*, 176 *igapós*, 55 rock outcrops, 36 *tepui*s, 29 coastal mosaics, 28  
219 savannas *sensu stricto* (hereafter savanna *s.s.*) and 22 montane forests (Figure 1; Table S1).  
220 All sites classified as *tepui*s and montane forests occur above 1,100m of altitude (see Study  
221 Area), with *tepui*s differing from montane forests in their rocky soils and dwarfish  
222 physiognomy. The map in Figure 1 was designed using the packages *maptools* (Bivand &

223 Lewin-Koh, 2017) and raster (Hijmans, 2016) in R Statistical Environment (R Core Team,  
224 2018).

225         The NTT database also includes environmental variables for all its sites, derived from  
226 multiple sources (at a 30 arc-second resolution). Altitude at the NTT site centre was used as  
227 an integrative environmental variable. Variables representing average climate (mean annual  
228 precipitation and temperature) as well as climate extremes (e.g., precipitation in driest month)  
229 and seasonality (e.g., precipitation seasonality) were obtained from WorldClim 1.4 data  
230 layers (Hijmans *et al.*, 2005). Frost frequency (days) and cloud interception (mm) were  
231 obtained from interpolating known values as response variables (data obtained from 135 and  
232 57 Brazilian Meteorological Stations measuring frost frequency and cloud interception,  
233 respectively) with elevation, latitude and the WorldClim layers as predicting variables. Soil  
234 coarseness (% sand) and soil fertility (% base saturation) and surface rockiness (% exposed  
235 rock) were obtained from the Harmonized World Soil Database v 1.2 (available at  
236 [http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-](http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/)  
237 [database-v12/en/](http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/)) and ranked afterwards by mid-class percentage. The use of classes was  
238 adopted because high local soil heterogeneity can make raw figures unrepresentative. Soil  
239 Water Storage capacity (%) was obtained from the International Soil Moisture Network  
240 (available at [www.ipf.tuwien.ac.at/insitu/](http://www.ipf.tuwien.ac.at/insitu/)).

241

#### 242 **4. Analyses of community composition**

243 We first explored the patterns of floristic differentiation amongst previously defined  
244 vegetation types by performing non-metric multidimensional scaling (NMDS; McCune &  
245 Grace, 2002), and tested its overall significance by applying an analysis of similarities  
246 (ANOSIM; Clarke, 1993). Beforehand, we excluded 832 singletons (species found at a single  
247 site), as they commonly increase the noise in ordination analyses without contributing

248 information (Lepš & Šmilauer, 2003), and then computed pairwise compositional distances  
249 between all sites using Simpson distance as the dissimilarity metric (Simpson, 1960), which  
250 describes community turnover without the influence of richness gradients (Baselga, 2010).

251 We used the vegetation types confirmed in the ordination analysis to produce sets of  
252 diagnostic species based on their coefficient of fidelity (*phi*; Tichý and Chytrý, 2006). An  
253 advantage of this coefficient is that they can take negative values, which expresses the fact  
254 that a species tends to “avoid” a particular habitat and its environmental conditions (De  
255 Cáceres *et al.*, 2008; De Cáceres and Legendre, 2009). In this study, diagnostic species  
256 represent those statistically associated with one or more vegetation types so that their  
257 presence in species lists may be a strong indicator of the vegetation types themselves.  
258 Significance of *phi* was obtained via Monte Carlo permutations (999). Species’ *phi* for each  
259 vegetation type are provided as Supplementary Information (see Table S2).

260 We then used the major axes of compositional variation summarized by the ordination  
261 analysis to test whether the observed patterns of floristic differentiation in the Amazon are  
262 underpinned by increasingly stressful environmental conditions, segregating *terra firme*  
263 forests from environmentally marginal vegetation types. First, we selected a subset of  
264 significant environmental variables for each of the major NMDS axes through an AIC-based  
265 forward selection method for generalized linear models, and then performed an additional  
266 and progressive elimination of collinear variables based on their variance inflation factor  
267 (VIF), informed by their ecological relevance, until maintaining only those with  $VIF < 4$   
268 (Quinn & Keough, 2002). We tested the significance of the selected environmental variables  
269 by applying ANOVA permutation tests (999 permutations). We explored the results visually  
270 by fitting the values of the most important environmental variables in ordination space  
271 (NMDS). The variable selection, VIF and NMDS analyses were conducted using the *vegan*

272 (Oksanen *et al.*, 2016) and usdm (Naimi *et al.*, 2014) packages in the R Statistical  
273 Environment.

274 Finally, we used a chord diagram to assess the patterns of compositional overlap  
275 amongst Amazonian vegetation types. The chord diagram was designed using the D<sup>3</sup> Java  
276 Environment (Bostock *et al.*, 2011; custom codes available at <https://bl.ocks.org/nbremer>).

277

## 278 RESULTS

279

280 The distribution of the sites in ordination space yielded by NMDS (K = 2; stress = 0.17;  
281 Figure 2) largely segregated the previously defined Amazonian vegetation types (ANOSIM R  
282 = 0.85;  $P = 0.001$ ). We found a negligible decrease in stress values by adding a third NMDS  
283 axis, and a high correlation between the distances summarized by the first two axes and the  
284 full distance matrix (Pearson's  $r = 0.83$ ). Thus, we focused subsequent analyses on the two-  
285 dimensional ordination space, and the results are detailed below.

286 Axis 1 places both *terra firme* forests and *campinaranas* at intermediate scores, and is  
287 congruent with two gradients: the first towards seasonally flooded forests (*várzeas* and  
288 *igapós*), placed at one extreme, and the second towards montane forests and open formations  
289 (coastal mosaic, rock outcrops, savanna and *tepuis*), at the other extreme. Axis 2 segregated  
290 *várzeas*, *tepuis*, *terra firme* and montane forests at one extreme, and *igapós*, *campinaranas*,  
291 and the remaining open formations at the other. It is worth noting that *campinaranas* seem to  
292 be closer to savannas than to *terra firme* forests along this axis. In addition, the differentiation  
293 between *terra firme* forest, savanna and the coastal mosaic is more nuanced, and suggests a  
294 forest-to-savanna gradient. These patterns are robust to excluding sites (checklists) compiled  
295 exclusively from herbarium data (654 sites; Figure S1).

296           The furthest extremes of substrate-related variables lead to distinct, environmentally  
297 marginal vegetation types (Figure 2). The selected climatic and edaphic predictors account  
298 for 72% and 62% of the variation in community composition summarized by the first two  
299 NMDS axes, respectively (Table 1). An increase in sandiness was congruent with the floristic  
300 differentiation of *campinaranas* from all other vegetation types, while an increase in soil  
301 water storage capacity (a proxy of seasonal soil-waterlogging) was associated with the  
302 floristic differentiation between seasonally flooded forests (*várzeas* and *igapós*) and all other  
303 vegetation types. The somewhat nuanced differentiation between the two seasonally flooded  
304 vegetation types is congruent with decreasing soil fertility from *várzeas* to *igapós*.  
305 Precipitation seasonality was associated with the floristic differentiation of coastal mosaics  
306 and savanna from all other vegetation types, with the segregation between these two being  
307 associated with higher soil sandiness in coastal mosaics. High surface rockiness (a proxy of  
308 soil water deficit) was congruent with the floristic segregation of forests associated with  
309 *tepuis* and rock outcrops from all other vegetation types. *Tepuis* are also associated with  
310 higher cloud interception, thus reflecting lower water deficit when compared to rock  
311 outcrops. Finally, both *tepuis* and montane forests are found under lower mean annual  
312 temperature, with intermediate conditions of cloud interception segregating montane forests  
313 from *tepuis* (high cloud interception) and lowland *terra firme* forests (low cloud  
314 interception).

315           There are a considerable number of species restricted to *terra firme* forests in our  
316 dataset (4,424 species), which far surpasses the number of species *terra firme* shares with  
317 other vegetation types (2,032 species; Figure 3). There is also a high proportion of species in  
318 *campinaranas* that are restricted to that vegetation type (42%). In contrast, the other seven  
319 vegetation types have a low proportion of species restricted to them, ranging from 6% in  
320 coastal mosaics and savanna to 25% in *tepuis*. Species shared between *terra firme* forest (the

321 largest species pool) and other marginal vegetation types are high. Among marginal  
322 vegetation types, the number of species shared ranges from 18, between *igapó* and *tepui*, to  
323 655 shared between *igapó* and *várzeas* (Figure 3). These results indicate that, apart from *terra*  
324 *firme* forests, most of the tree flora of Amazonian vegetation types are shared among two or  
325 more vegetation types, with their community compositions, which are distinct (Figure 2),  
326 representing unique combinations of the Amazonian species pool.

327

## 328 **DISCUSSION**

329

### 330 **1. Continental-scale patterns**

331 The composition of the tree flora across the Amazon region shows variation congruent with  
332 traditional vegetation classifications. The most species rich and geographically widespread  
333 vegetation type is *terra firme* forest, while marginal vegetation types, such as *campinarana*,  
334 savannas, *igapó* or *várzea*, diverge in species composition along distinct environmental  
335 gradients. These marginal vegetation types house many tree species not found in *terra firme*  
336 forest, yet surprising numbers of them are shared amongst the different marginal vegetation  
337 types themselves, for example between *campinaranas* and rock outcrops.

338         The marginal vegetation types are placed at extreme values of the significant  
339 environmental gradients, potentially indicating eco-physiological stress, and our results  
340 highlighted that substrate, not climate, is the most important environmental driver controlling  
341 the major axes of composition in Amazonian tree communities. Different from other forest  
342 biomes in South America, where variation in temperature and water availability are clearly  
343 the most important factors controlling continental-scale patterns of tree community  
344 composition (e.g., in seasonally dry tropical forests (Neves et al., 2015), or in the *Mata*

345 *Atlântica* (Neves *et al.*, 2017)), climatic conditions are relatively unimportant in Amazonia  
346 (but see discussion for montane forests and *tepuis*).

347         Moreover, because these edaphic gradients are consistently important in segregating  
348 Amazonian vegetation types from local to continental scales, our results run counter to  
349 previous findings which have suggested that tree community composition in the Amazon is  
350 primarily driven by Amazon-wide gradients in environmental conditions (e.g., precipitation  
351 seasonality, soil fertility; Silva-Souza & Souza, 2020; ter Steege *et al.*, 2006). Previous  
352 Amazon-wide studies analyzed tree species composition data without separating or  
353 considering the different Amazonian vegetation types. If composition is summarized within  
354 geographic grid cells (e.g., ter Steege *et al.*, 2006; Silva-Souza & Souza, 2020), then a given  
355 grid cell may take on the compositional identity of the dominant vegetation type in the grid  
356 cell, and if there are geographic gradients in the prevalence of vegetation types, the  
357 geographic grid cell approach may lead to geographically-driven results, which mask  
358 vegetation heterogeneity within grid cells. Our approach ensured that every sample unit (i.e.  
359 site or community) represents only a single vegetation type, which is likely why we find a  
360 clearer signal for vegetation type than for geography in our results. That these vegetation  
361 types are floristically coherent across the Amazon basin also suggests that dispersal amongst  
362 areas of the same vegetation type is not particularly limited by geographic distance, in  
363 agreement with a recent study of several Amazonian tree genera (Dexter *et al.*, 2017).

364         Below we delve into the main floristic patterns observed in our results to discuss the  
365 compositional identity and environmental distinctiveness of Amazonian vegetation types.  
366 Because the dataset used in this study does not include sites with a high indication of  
367 anthropogenic disturbance, we stress that analyses including community inventories (e.g.,  
368 floristic checklists, plot data) from recently degraded areas, such as early-stage secondary  
369 forests, may reveal additional vegetation types.



370

371 **2. Forest types**

372 Flooded forests share a similar environmental condition driving their compositional  
373 distinction from *terra firme* forests: seasonal flooding, potentially combined with soil  
374 waterlogging during the low water season. This, however, does not lead to homogeneous  
375 stands of flooded forests throughout the Amazon and one of their main variations was  
376 captured here: the floristic, edaphic and distributional differentiation of *igapós* and *várzeas*.  
377 *Várzea* forests are more evenly distributed across major river basins in Amazonia, while most  
378 *igapó* forests are concentrated in the Rio Negro and upper Orinoco River Basins where the  
379 substrate is of highly leached and impoverished white-sands. Nonetheless, *igapó* forests are  
380 also found in other Amazonian regions under similar edaphic conditions (Montero *et al.*,  
381 2014; Wittman *et al.*, 2010). In addition, both types of flooded forests have species restricted  
382 to them in our dataset (160 species restricted to *várzeas*, and 168 to *igapós*), though the  
383 largest proportion of their species composition is either shared between them or with *terra*  
384 *firme* forests (Figure 3; Scudeller, 2018).

385 The tree flora of montane forests in Amazonia is compositionally coherent with the  
386 main floristic patterns described for Neotropical montane flora in general, such as the  
387 presence of some genera that are rare to absent in the lowland flora, including *Bonnetia*,  
388 *Brunellia*, *Drimys*, *Hedyosmum*, *Ilex*, *Laplacea*, *Meriania*, *Podocarpus*, *Symplocos* and  
389 *Weinmannia* (Webster, 1995). The overall lack of these taxa in lowland Amazonia is likely  
390 driven by temperature, an important environmental factor driving floristic differentiation  
391 between montane and *terra firme* forests in our dataset. Nonetheless, variation in temperature  
392 across the range and location of elevations sampled in our study is not large, thus explaining  
393 the high proportion of tree species shared between montane forests and other Amazonian  
394 habitats (88%), and supporting the claim that these forests should be treated as Amazonian

395 (contrasting with views in Cardoso *et al.*, 2017; Cabrera & Willink, 1980). *Igapó* forests, for  
396 instance, share a lower proportion of tree species with other Amazonian habitats (82%), yet  
397 *igapós* are consistently treated as Amazonian (Wittmann *et al.*, 2010). The fact is that many  
398 lowland *terra firme* species do extend their distribution towards high altitudes (1,100-  
399 3,000m), such as *Annona symphyocarpa*, *Coussapoa crassivenosa*, *Cyathea bipinnatifida*,  
400 *Cyathea macrosora*, *Elaeoluma nuda*, *Hieronyma oblonga*, *Miconia dodecandra*, *Miconia*  
401 *pseudocapsularis*, *Miconia punctata*, *Mollinedia ovata*, *Nectandra reticulata* and *Quiina*  
402 *cruegeriana*, to cite a few diagnostic species of both *terra firme* and montane forests (Table  
403 S2).

404         The scarcity of mineral nutrients in white-sand environments is probably the leading  
405 environmental distinction of *campinaranas*, and plant species are known to have acquired  
406 morphological, physiological and mutualistic traits to maximize both nutrient capture and  
407 retention (Adeney *et al.*, 2016). This specialized flora explains much of the differentiation of  
408 *campinaranas* from other vegetation types, which is evident in the high proportion of  
409 restricted species (42%; Figure 3). This is almost twice the proportion of 23% of endemics in  
410 western Amazonian *campinaranas* found by Garcia-Villacorta *et al.* (2016), but this is  
411 probably explained by the fact that those authors worked with the whole spectrum of growth  
412 habits, and not only trees, considered all available herbarium voucher data (not just those  
413 collected near NTT sites as done here) and concentrated their efforts only in western  
414 Amazonia.

415

### 416 **3. Open formations**

417 The coastal sand deposits along the Atlantic shores, covered by a mosaic of mangroves and  
418 sandy beaches, represent another Amazonian vegetation type associated with white-sand  
419 substrates. However, soils in these coastal mosaics are more fertile than in *campinaranas*, and

420 they are mostly found in the eastern Amazon, where precipitation seasonality is relatively  
421 more pronounced. Nonetheless, these white-sand, seasonally dry coastal environments are not  
422 too extensive (Cremers & Hoff, 2003; Silva *et al.*, 2010; González, 2011), nor do they seem  
423 to be restrictive floristically, as 94% of species in coastal mosaics are also found in other  
424 vegetation types. Accordingly, they have one of the lowest proportions of restricted tree  
425 species in Amazonian habitats – only 15 tree species are restricted to coastal sand deposits in  
426 this analysis, nine of which are typical of mangroves.

427         Water deficit intervals, mediated by climate, substrate or both, drives tree community  
428 differentiation in two other environments: savannas and rock outcrops. Most savannas are  
429 found where the dry season is longest in the Amazon, and where fire outbreaks may occur in  
430 the dry season. Interestingly, many of these savannas are hyper-seasonal (*sensu* Sarmiento,  
431 1983), in that they also face some form of water excess in the rainy season, mostly due to soil  
432 waterlogging either caused by poor drainage or floods, as in the Bolivian Llanos de Moxos  
433 and in the Brazilian estuarine island of Marajó. Nevertheless, there are also non-hyper-  
434 seasonal savannas, particularly on hills with shallow soils in the Brazilian state of Pará, where  
435 the flora shares a great number of species with that of the Cerrado savannas in Central Brazil  
436 (Devecchi, *et al.*, 2020). In fact, the tree flora of most Amazonian savannas does show some  
437 floristic affinity with the savannas of either the Brazilian Cerrados or the Venezuelan Llanos  
438 (Buzatti *et al.*, 2018; Ratter *et al.*, 2006; see also Devecchi, *et al.* 2020 for comparisons  
439 between all plant life-forms).

440         Rock outcrops are another common feature in the Amazon that may experience local  
441 water shortage, even in everwet areas, because rainwater is promptly drained from the  
442 substrate. Rock outcrops are particularly common across inselbergs on both the Guiana and  
443 Brazilian Crystalline Shields, where they host tree species not found elsewhere in the  
444 Amazon (Gröger, 2000; Raghoenandan, 2000). The xeric nature of rock outcrops is

445 confirmed by the disjunct occurrences of a considerable number of species that are also  
446 typical of seasonally dry deciduous forests outside of the Amazon, such as *Aspidosperma*  
447 *cuspa*, *Brasiliopuntia brasiliensis*, *Bursera simaruba*, *Cereus hexagonus*, *Guapira cuspidata*,  
448 *Senegalia riparia* and *Vachellia farnesiana*. Apart from rock outcrops, another substrate  
449 related to periods of water deficit in the Amazon is the hardened surface of some mudflats,  
450 such as those found on the Guyanese coastal plains and on the meanders of the Lower  
451 Amazon and mid-Marañon rivers. This condition probably explains the occurrence of a  
452 typical savanna vegetation and flora there, even under year-round ever-wet climates.

453         The *tepui*s are formed of the steep slopes and plateaus of the massive Paleozoic  
454 sandstones atop the Guiana Shield. Environmental factors along altitudinal gradients are  
455 hardly ever easily summarized by one variable, and include factors such as increasing cloud  
456 interception (an important factor in our models) and declining temperatures towards higher  
457 altitudes. Additional sources of environmental heterogeneity include slope, aspect, and  
458 surface rockiness, and there is usually a local combination of stressful factors at play. In  
459 general, scrubs and savannas prevail on the shallow soils and bare rocks at the summits of  
460 *tepui*s (Huber, 2005), where cloud interception is the major source of water, and are replaced  
461 by montane forests in colder environments with deeper soils.

462         It is important to bear in mind that, different from forest types, the open formations in  
463 our analyses do not represent a tree-dominated habitat. Therefore, our comparisons are based  
464 on the few tree species that occur in these plant communities, while herbs, forbs and shrubs  
465 are not included. If data for the whole plant community were available, we would expect  
466 even higher dissimilarities between these open habitats and other tree-dominated habitats,  
467 with increased number of endemic species in the former.

468

#### 469 **4. Conclusions**

470 Our findings show that the traditional classification of Amazonian vegetation formations is  
471 consistent with quantitative patterns of tree species distribution. We also demonstrate how the  
472 *terra firme* forest is the core vegetation type from which the eight marginal habitats  
473 differentiate floristically in a manner consistent with more extreme environmental conditions.  
474 These patterns, which have been previously described at a regional scale, are documented  
475 here for the first time across the entire Amazon Basin.

476 In addition, we show that a large proportion of tree species found in the eight marginal  
477 vegetation types are shared amongst each other and with *terra firme* forests. In fact, apart  
478 from *terra firme* forests and *campinaranas*, there is a small percentage of tree species  
479 restricted to a single vegetation type in the Amazon. Nonetheless, if future conservation  
480 strategies aim to protect the full set of tree species in the Amazon, they must consider the  
481 identity and distribution of the multiple vegetation types there, as well as their current status  
482 of conservation. Many of the localities in our analyses may have been impacted by the recent  
483 increase in deforestation and forest fires in the Amazon, especially those found across the  
484 south and eastern borders of the Brazilian Amazon – a region known as the “arc of  
485 deforestation” (Soares-Filho *et al.*, 2006).

486

487 **Table 1.** Significant climatic and edaphic predictors large-scale gradients of tree community  
 488 composition in the Amazon. Values under NMDS1 and NMDS2 represent the coefficients of  
 489 determination (adjusted  $R^2$ , and their respective  $P$ -values) of generalized linear models  
 490 (GLMs) between the first two axes of a Non-metric Multi-Dimensional Scaling and  
 491 environmental variables. Values in the last row represent coefficients of determination of  
 492 GLM-based multiple regressions between each NMDS axis and all significant variables. VIF  
 493 = variation inflation factor, as a measure of collinearity between all variables in the analyses  
 494 (variables were progressively eliminated until  $VIF < 4$ ).

	<b>NMDS1</b>	<b><i>P</i></b>	<b>NMDS2</b>	<b><i>P</i></b>	<b>VIF</b>
Cloud Interception	0.224	< 0.0001	0.059	< 0.0001	2.398
Mean Annual Temperature	0.228	< 0.0001	0.225	< 0.0001	2.812
Precipitation Seasonality	0.041	< 0.0001	-	-	1.046
Sandiness	0.051	< 0.0001	0.294	< 0.0001	1.990
Soil Fertility	-	-	0.207	< 0.0001	2.087
Soil Water Storage capacity	0.656	< 0.0001	0.013	< 0.0001	3.095
Surface Rockiness	0.327	< 0.0001	0.019	< 0.0001	2.534
<b>All variables</b>	0.723	< 0.0001	0.623	< 0.0001	-

495

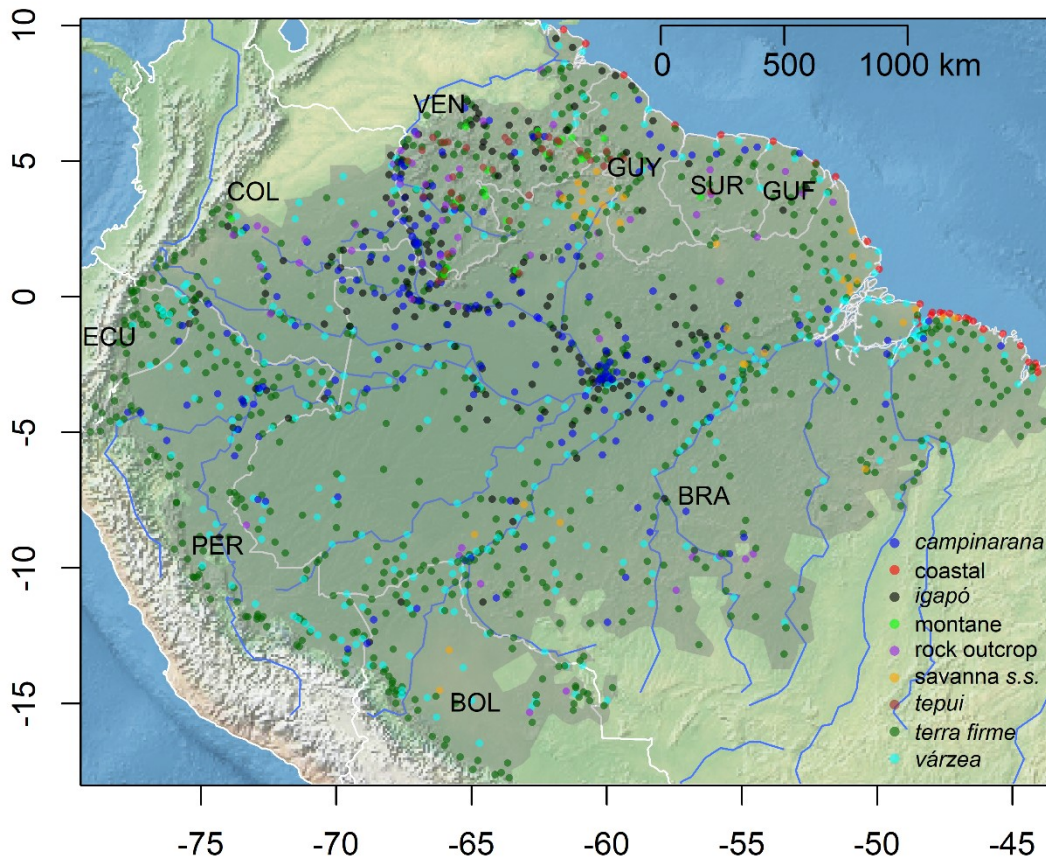
496 **FIGURE LEGENDS**

497 **Figure 1.** Distribution of the 1,584 Amazonian sites used in the analyses with their *a priori*  
498 classification into nine vegetation types. Blue and white contours illustrate major rivers and  
499 national borders, respectively. Our delimitation of the Amazon is outlined in a darker, gray-  
500 green colour.

501 **Figure 2.** Ordination of 1,584 tree communities in the Amazon inferred from non-metric  
502 multidimensional scaling of their species composition. Colors indicate the *a priori*  
503 classification into nine main vegetation types, and darker shades in each color indicate  
504 overlapping circles (i.e., two or more sites show high similarity in species composition).  
505 PrecSeas = precipitation seasonality; CloudIntcp = cloud interception; SoilFert = soil fertility;  
506 SWS = soil water storage capacity; TempAnn = mean annual temperature.

507 **Figure 3.** Overlap in tree species composition amongst Amazonian vegetation types. Values  
508 in white express the number of species that are shared amongst vegetation types or restricted  
509 to a given vegetation type, respectively. Chord width is proportional to the number of shared  
510 species.

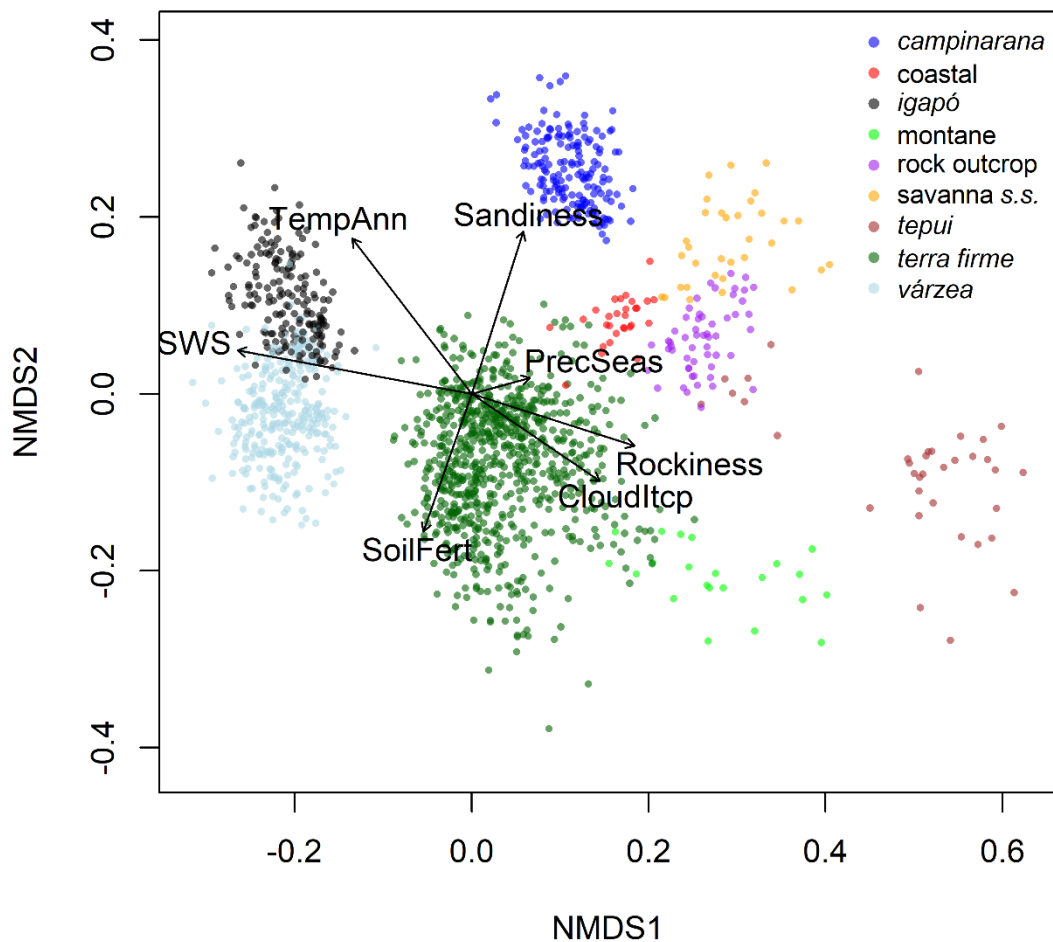
511



512

513 **Figure 1.** Distribution of the 1,584 Amazonian sites used in the analyses with their *a priori*  
 514 classification into nine vegetation types. Blue and white contours illustrate major rivers and  
 515 national borders, respectively. Our delimitation of the Amazon is outlined in a darker, gray-  
 516 green colour.





517

518 **Figure 2.** Ordination of 1,584 tree communities in the Amazon inferred from non-metric519 multidimensional scaling of their species composition. Colors indicate the *a priori*

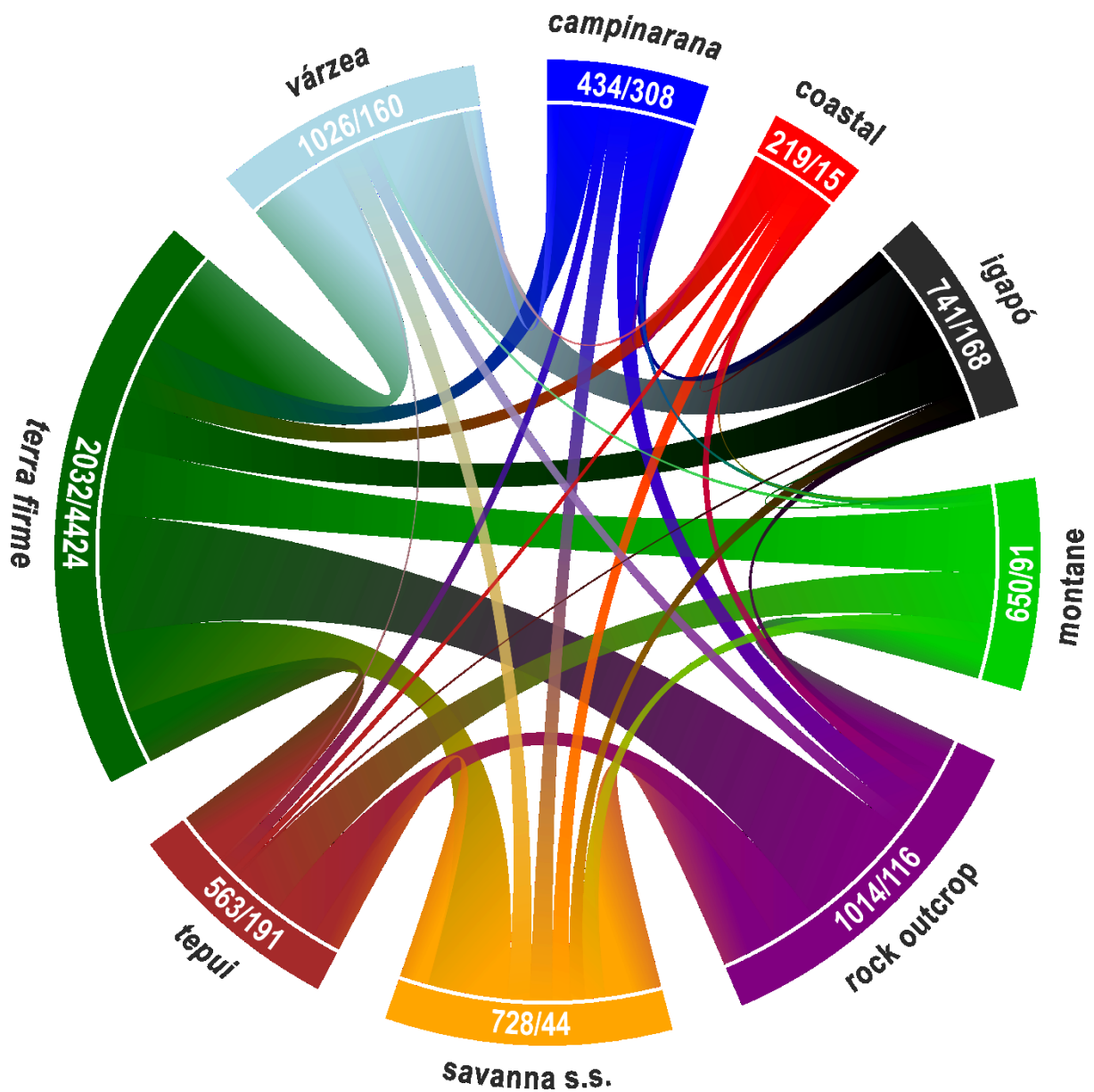
520 classification into nine main vegetation types, and darker shades in each color indicate

521 overlapping circles (i.e., two or more sites show high similarity in species composition).

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526 **Figure 3.** Overlap in tree species composition amongst Amazonian vegetation types. Values

527 in white express the number of species that are shared amongst vegetation types or restricted

528 to a given vegetation type, respectively. Chord width is proportional to the number of shared

529 species.

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541 manuscript; D.M.N. analysed the data; A.O.F. and D.M.N. led the writing with substantial  
542 input from R.T.P., K.G.D. and M.F.S. All authors commented on the manuscript and  
543 approved the final version.

544 **CONFLICT OF INTEREST**

545 The authors declare no conflict of interest.

546

547 **DATA AVAILABILITY STATEMENT**

548 Presence/absence data for the 8,224 tree species found across the 1,584 Amazonian  
549 communities were extracted from the NeoTropTree database (available at  
550 <http://www.neotropree.info/data>). Bioclimatic variables and altitude were obtained from  
551 WorldClim 1.4 data layers (available at: <http://www.worldclim.org/download>). Soil variables  
552 were obtained from the Harmonized World Soil Database v 1.2 (available at:  
553 [http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-](http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/)  
554 [database-v12/en/](http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/)). Soil Water Storage capacity was obtained from the International Soil  
555 Moisture Network (available at <https://ismn.geo.tuwien.ac.at/en/>).

556

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804 **SUPPLEMENTARY INFORMATION**

805 Additional supporting information may be found in the online version of this article:

806

807 **Table S1.** List of 1,584 tree communities used in this study with their respective metadata,  
808 including latitudes and longitudes, vegetation types, and sources.

809

810 **Table S2.** Diagnostic species of the nine main vegetation types of the Amazon Domain by  
811 applying the Tichý and Chytrý procedure to the species matrix.