

1 **Original Article**

2 **A COMPOSITIONAL TURNOVER ZONE OF BIOGEOGRAPHICAL**
3 **MAGNITUDE WITHIN LOWLAND AMAZONIA**

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14 **Short running head:** Biogeographical turnover zone within lowland Amazonia

15 Word count: 7576

16 Figures and tables will take 2-3 pages

17

18 **ABSTRACT**

19 **Aim** To assess the relative roles of geologically defined terrain types (environmental
20 heterogeneity) and a major river (physical dispersal barrier) as predictors of ecological
21 structuring and biogeographical differentiation within Amazonian forests.

22 **Location** Western Brazilian Amazonia, where the Juruá river and its terraces cross a 1000-
23 km-long boundary between two geological formations (the Solimões and Içá Formations).

24 **Methods** We sampled a 500-km stretch of the Juruá with 71 transects (5 m by 500 m) that
25 spanned both the river and the geological boundary. All transects were inventoried for
26 pteridophytes (ferns and lycophytes) and Melastomataceae, and a subset of 39 transects also
27 for palms and Zingiberales. Three surface soil samples were collected from each transect.
28 The data were analysed using ordinations, regression trees, indicator species analyses and
29 Mantel tests.

30 **Results** All plant groups showed congruent species turnover between geologically defined
31 terrain types, but little evidence of isolation by the river or geographical distance. Soil cation
32 concentration differed between the Solimões Formation and other terrain types and emerged
33 as the main explanatory factor for species turnover. A large proportion of the plant species
34 were significant indicators for specific parts of the soil cation concentration gradient, and
35 these edaphic associations were congruent with those found in other parts of Amazonia.
36 Pteridophytes had a larger proportion of species in the cation-rich soils than the other plant
37 groups did, and palms had a higher proportion of generalists.

38 **Main conclusions** The geological boundary between the Solimões and Içá formations is
39 confirmed as significant floristic turnover zone. Since it runs in a north-south orientation for
40 more than 1000 km, the edaphic differences associated with this boundary have wide-ranging
41 implications for speciation and biogeographical patterns in Amazonia.

42 **Keywords:** Amazonia; dispersal barriers; edaphic heterogeneity; Nauta/Içá Formation;
43 indicator species; parapatric speciation; soil cation concentration; Pebas/Solimões Formation;
44 plant species turnover

45 **INTRODUCTION**

46 Dispersal barriers are important for allopatric speciation, and thereby for the emergence of
47 biogeographical regions and broad-scale species compositional differences. Amazonia is a
48 vast area with an apparently uniform cover of tropical rain forest, and explaining the origin of
49 its extremely high species richness in the absence of obvious dispersal barriers has been a
50 long-standing problem.

51 The oldest hypothesis is that the Amazon river itself acts as a dispersal barrier (Wallace
52 1852). The distribution limits of many birds and primates indeed seem to follow major rivers
53 (Cracraft 1985; Ayres & Clutton-Brock 1992; Pomara *et al.* 2014; Boubli *et al.* 2015). More
54 recently, soil properties have been suggested to restrict plant species composition and
55 distributions in Amazonian forests (Gentry 1981, Tuomisto *et al.* 1995, 2003a; b; Phillips *et*
56 *al.* 2003; Salovaara *et al.* 2004; Costa *et al.* 2005; Ruokolainen *et al.* 2007; Higgins *et al.*
57 2011; Figueiredo *et al.* 2014). However, this is controversial, as others have emphasised the

58 ability of plants to grow across a wide range of soils (Duivenvoorden 1995; Pitman *et al.*
59 2001; ter Steege *et al.* 2003).

60 Western Amazonian soils are largely derived from either fluvial deposits of varying ages and
61 origins (Salo *et al.* 1986; Räsänen *et al.* 1987, 1992), or from Miocene sediments deposited in
62 a large lacustrine environment with a marine connection (the Pebas system; Hoorn 1993;
63 Räsänen *et al.* 1995; Hoorn *et al.* 2010). Such differences in geological history are reflected
64 in soil properties, so understanding soil heterogeneity and its relationships with local species
65 composition provides a link between local community processes and broader biogeographical
66 phenomena (Tuomisto & Poulsen 1996; Phillips *et al.* 2003; Salovaara *et al.* 2004; Tuomisto
67 2007; Hoorn *et al.* 2010; Higgins *et al.* 2011; Kristiansen *et al.* 2012).

68 The river barrier hypothesis has been tested for the genetic differentiation of non-volant
69 mammals along the Juruá river (Patton *et al.* 1994, 1996, 2000; da Silva & Patton 1998). No
70 differentiation across the river was found, but communities differed between the lower and
71 upper reaches. Da Silva and Patton (1998) tentatively related this to the Iquitos Arch – a
72 geological subsurface feature that crosses the middle Juruá almost perpendicularly.

73 Alternatively, the observed haplotype pattern might be related to habitat differentiation. A
74 geological boundary between Miocene sediments of lacustrine or semimarine origin (the
75 Solimões Formation) and younger fluvial sediments (the Içá Formation) crosses the Juruá
76 river (Schobbenhaus *et al.* 2004). This coincides with a boundary recognised between
77 *floresta aberta* (open forest) and *floresta densa* (dense forest; IBGE 2004), which have been
78 observed to differ in canopy tree composition elsewhere in Amazonia (Emilio *et al.* 2010).
79 However, the ecological or floristic significance of the Juruá boundary has not been

80 investigated, even though it may represent an edaphic limit between western and central
81 Amazonia (Fittkau *et al.* 1975; Sombroek 2000; Higgins *et al.* 2011).

82 On the basis of studies across a boundary along the Tigre river in northern Peru, we predicted
83 specific soil and floristic properties for the two sides of the Juruá boundary (Higgins *et al.*
84 2011). Both boundaries showed similar characteristics in Landsat satellite images and SRTM
85 elevation data, and correspond to the limit between the Solimões Formation and the Içá
86 Formation (known in Peru as the Pebas Formation and the Nauta Formation, respectively).

87 It is an exciting thought that predictions about the biotic differentiation of forests in one part
88 of Amazonia might be made on the basis of field studies carried out more than 1000 km
89 away. To test the viability of such broad-scale predictions, we organised a 3-month
90 expedition to the Juruá river. In addition to pteridophytes (ferns and lycophytes) and
91 Melastomataceae, which were sampled in the Peruvian study, we included palms (Arecaceae)
92 and Zingiberales to obtain data from structurally dissimilar and phylogenetically distant plant
93 groups. Here we document the floristic patterns of these four plant groups across the
94 Solimões–Içá boundary, compare the patterns with those observed across the Pebas–Nauta
95 boundary in Peru, and discuss the broader implications of these findings for Amazonian
96 biogeography.

97 **MATERIAL AND METHODS**

98 **Study area**

99 The study was conducted in Brazilian Amazonia along the rivers Juruá and Tarauacá (Fig. 1).
100 Average annual rainfall in the area (as reported for Eirunepé) is about 2200 mm. Mean

101 annual temperature is 27°C, but temperatures as low as 15°C can occur in June to August
102 (Marengo *et al.* 1997).

103 A geological boundary between the Solimões Formation in the west and the Içá Formation in
104 the east runs north-south across the study area (Sombroek 2000; Higgins *et al.* 2011). Both
105 formations consist of Quaternary sedimentary deposits and cover a large part of Western
106 Amazonia. The Pebas/Solimões Formation consists of cation-rich clay sediments deposited
107 under semi-marine or lacustrine conditions during the Miocene (Hoorn 1993; Räsänen *et al.*
108 1995; Gross *et al.* 2011; Hoorn & Wesselingh 2011). The Nauta/Içá Formation consists of
109 more coarse-grained and less cation-rich fluvial or deltaic sediments deposited during the
110 Pliocene to Pleistocene after the uplift of the Andes had drained the Pebas wetlands (Rossetti
111 *et al.* 2005; Rebata H. *et al.* 2006; Hoorn & Wesselingh 2011). The Nauta/Içá Formation may
112 have initially covered the Pebas/Solimões sediments, which have subsequently been exposed
113 by rainwater denudation. The erosion front appears to have advanced from west to east
114 roughly perpendicularly to the rivers, but islands of the Nauta/Içá Formation remain in the
115 landscape dominated by the Pebas/Solimões Formation (Higgins *et al.* 2011). The
116 Pebas/Solimões Formation typically has a gently undulating topography, whereas areas
117 covered by the Nauta/Içá Formation are steeply hilly.

118 Both Juruá and Tarauacá are meandering, dynamic white-water rivers with alluvial terraces
119 that run adjacent to their current floodplains but are not currently influenced by floods. The
120 terraces are younger than the Nauta/Içá Formation and topographically flat. Alluvial terraces
121 have been mapped as Acrisols, the Solimões Formation as Acrisols or Cambisols, and the Içá
122 Formation as Plinthosols (Dijkshoorn *et al.* 2005).

123 **Sampling methods**

124 Field sampling covered a 500-km stretch (air distance) along the Juruá and Tarauacá rivers.
125 Sampling was planned with the help of satellite imagery (Google Earth and the Landsat
126 mosaic of Higgins *et al.* 2011), SRTM elevation data and maps provided by Carlos C. Peres.

127 Our main aim was to sample the Pebas/Solimões and Nauta/Içá Formations as well as
128 possible, given accessibility constraints. Alluvial terraces were included in the sampling to
129 obtain a more comprehensive view of the compositional variability within the *terra firme*
130 forests. Each sampled site was classified into one of three terrain types (Solimões Formation,
131 Içá Formation or alluvial terrace) on the basis of topography (undulating, hilly or flat,
132 respectively) and satellite imagery (high near infrared reflectance over the Solimões
133 Formation).

134 The floodplain of the Juruá river is up to 20 km wide, so sampling was restricted to places
135 where *terra firme* forest was accessible directly from the river, or a creek made it possible to
136 traverse the flooded forest in a small boat and return the same day. The desired sampling
137 locality within the forest was found using satellite images, local field guides, compasses and
138 hand-held GPS receivers. In total, we made inventories at 71 sites.

139 Floristic inventories followed the sampling methods described in Tuomisto *et al.* (2003a).
140 Each site was represented by a transect of 5 m by 500 m, oriented across the main slope to
141 include a representative sample of the local topographical variation. Transects were
142 georeferenced through GPS coordinates at approximately 100-m intervals.

143 We inventoried four plant groups: pteridophytes (ferns and lycophytes), Melastomataceae,
144 palms (Arecaceae) and Zingiberales. Pteridophytes and Melastomataceae were inventoried in
145 all 71 transects, Arecaceae and Zingiberales in a subset of 39 transects. All individuals of
146 each plant group were recorded and identified to species (or were given a field name, if the
147 real species name was not known). To be included in the inventory, pteridophyte individuals
148 needed at least one green leaf (leafy stem in the case of lycophytes) exceeding 10 cm in
149 length. Epiphytes and climbers were included if they had such leaves less than 2 m above
150 ground. For clonal species, each rooting stem was considered as an individual, even if
151 connected to other rooting stems. All Melastomataceae individuals with post-cotyledon
152 leaves were included. For the Zingiberales, a minimum height of 5 cm was applied, and in the
153 case of clonal species, bunches of leaves separated by at least 20 cm were considered as
154 separate individuals. All palm individuals higher than 5 cm were included, but palm seedlings
155 that could not be identified to species level were excluded. Each ramet in a clonal or colonial
156 species was counted as an individual.

157 All species of all plant groups were documented by one or more voucher specimens.
158 Additional specimens were collected of individuals that could not be assigned with certainty
159 to a species with a recent voucher. A complete set of pteridophyte and Melastomataceae
160 specimens was deposited in SP (herbarium acronyms according to Thiers continuously
161 updated), with duplicates in TUR and INPA. Zingiberales were deposited in INPA and
162 privately with Fernando O.G. Figueiredo, and palm specimens in INPA and AAU. The INPA
163 sets have fertile specimens only.

164 Surface soil samples (top 5 cm of the mineral soil) were taken at three different points along
165 each transect, usually at 50 m, 250 m and 450 m. If needed, soil sample locations were

166 modified to cover the extremes of the topographic gradient, or to avoid sampling in creeks or
167 where the soil had been obviously disturbed. Each soil sample consisted of five subsamples
168 collected within an area of about 5 m by 5 m and mixed. Samples were stored in plastic bags
169 and air dried in the INPA soil laboratory after returning to Manaus. Laboratory analyses in
170 the Agricultural Research Centre of Finland used standard methods (van Reeuwijk 1993) for
171 pH (in 1 M KCl), exchangeable bases (Ca, K, Mg and Na; extraction by 1 M ammonium
172 acetate at pH 7), Al (extraction by 1 M ammonium acetate at pH 7) and LOI (loss on ignition
173 at 420°). Total phosphorus was extracted following Quesada *et al.* (2010). Data analyses used
174 the average value of each variable for each transect.

175 **Data analyses**

176 Most data analyses were based on dissimilarity matrices. For the floristic data, these were
177 calculated separately for each plant group using the Bray-Curtis index. Both presence-
178 absence data and relative abundance data (number of individuals of a species divided by the
179 site total) were used in parallel. For pteridophytes and Melastomataceae, two separate sets of
180 dissimilarity matrices were constructed, one based on all 71 transects and the other based on
181 the same 39 transects for which Arecaceae and Zingiberales data were available.

182 For the environmental data, separate distance matrices based on Euclidean distance were
183 calculated for each soil variable. The concentrations of exchangeable cations and phosphorus
184 were logarithmically transformed before calculating the distances to emphasise differences
185 between small values — a unit change in nutrient concentration is physiologically most
186 important when the nutrient is scarcest. Geographical distances were calculated using transect
187 midpoint coordinates, and the distance values were logarithmically transformed.

188 Three binary dissimilarity matrices based on categorical variables were calculated, indicating
189 whether the transects were: 1) on edaphically similar terrain types (Içá Formation or alluvial
190 terraces vs. Solimões Formation); 2) on the same side of the east-west boundary delimited by
191 Higgins *et al.* (2011); and 3) on the same side of the Juruá river. The third matrix provided a
192 direct test of the river barrier hypothesis, and the first matrix of the geological control
193 hypothesis. The second matrix simplified the geological information to a spatial dichotomy
194 that ignored the islands of Içá Formation west of the boundary and the islands of Solimões
195 Formation east of the boundary, helping to clarify to what degree species turnover patterns
196 might relate to geological vs. spatial factors.

197 The main floristic patterns were illustrated with ordination diagrams based on non-metric
198 multidimensional scaling (NMDS) optimised for two dimensions. Weak treatment of ties was
199 used to allow recovery of long gradients and avoid an arch effect (De'Ath 1999). Hierarchical
200 agglomerative clustering using Ward's minimum variance method (Legendre & Legendre
201 2012) was used to classify the transects.

202 Correlations between floristic dissimilarities and the environmental and geographical
203 distances were calculated using simple and partial Mantel tests (Legendre & Legendre 2012).
204 Distance-based multivariate regression trees (De'Ath 2002) were constructed to evaluate the
205 predictability of floristic dissimilarities (presence-absence data only) on the basis of the
206 quantitative edaphic variables. The method produces a hierarchical classification of sites on
207 the basis of their positions along one or more of the measured environmental gradients. In the
208 first step, each environmental variable is divided at a point that minimizes the floristic
209 differences among the sites in the same subgroup. The environmental variable that obtains
210 the best cross-validation error criterion is then selected, and the process is repeated for each

211 of the previously obtained subgroups until further divisions no longer meet the cross-
212 validation criterion.

213 To assess the relevance of the environmental site classification obtained from the regression
214 tree for the individual plant species, we ran indicator species analyses (Dufrêne & Legendre
215 1997). Indicator values (*indval.g* of De Cáceres *et al.* 2015) were calculated for each of the
216 final classes separately and for all ecologically meaningful class combinations. The indicator
217 value of a species for a class (or class combination) ranges [0,1] and combines a measure of
218 affinity (proportion of a species' occurrences that are within the class) with a measure of
219 fidelity (proportion of sites in the class that contain the species). Statistical significance of the
220 indicator value is assessed through permutation. We restricted indicator species analysis to
221 species occurring in at least three transects.

222 All data analyses were carried out using the R statistical program. The package *vegan*
223 (Oksanen *et al.* 2015) was used to construct the distance matrices (function *vegdist*) and to
224 run NMDS (function *monoMDS*) and Mantel tests (function *mantel*). Hierarchical clustering
225 analyses were run with function *agnes* of package *cluster* (Maechler *et al.* 2015), distance-
226 based multivariate regression trees with function *mvpert* of package *mvpert* (Therneau *et al.*
227 2013) and indicator species analyses with function *multipatt* of package *indicspecies* (De
228 Cáceres *et al.* 2015).

229 **RESULTS**

230 **Landscape and soils**

231 Classification of the study area into three terrain types (Solimões Formation, Içá Formation
232 and alluvial terraces) was based on a preliminary interpretation of satellite imagery and
233 SRTM data prior to fieldwork. Laboratory analyses revealed that Solimões Formation soils
234 averaged an order of magnitude higher concentrations of exchangeable bases than soils in the
235 other terrain types, with an even greater difference for calcium (Table S1.1 in Appendix S1 of
236 Supporting Information).

237 The ranges of the most important base cations (Ca, K and Mg) for the Solimões and Içá
238 Formations did not overlap. The alluvial terraces were intermediate, with cation
239 concentrations overlapping broadly with the Içá Formation. In the full dataset of 71 transects
240 there was also overlap between the terraces and the Solimões Formation, due to three
241 transects situated close to the limit between them. Similarly, soil phosphorus content did not
242 overlap between the Solimões and Içá Formations, and alluvial terraces were intermediate.
243 The other soil variables overlapped between all terrain types, but Solimões Formation soils
244 tended to have relatively high pH values and alluvial terraces relatively high aluminium
245 concentration and LOI.

246 The subset of 39 transects, which was sampled for all four plant groups, was a representative
247 sample of the full set of 71 transects, with similar means and ranges for most soil variables
248 (Table S1.1). However, the full dataset showed a more continuous gradient of soil properties
249 between alluvial terraces and the Solimões Formation because many of the additional
250 transects were intermediate.

251

252 **Floristic patterns**

253 In the 39 transects, we recorded more than 112,000 plant individuals representing 458
254 species. Pteridophytes were most species-rich (154 species) and palms least (62 species),
255 with Melastomataceae (128 species) and Zingiberales (114 species) intermediate.

256 Pteridophytes were also the most abundant plant group (56,600 individuals), followed by
257 palms (35,100), Zingiberales (13,500) and Melastomataceae (7,500). The additional set of 32
258 transects only produced 18 pteridophyte and 18 Melastomataceae species that had not been
259 present in the first 39 transects.

260 There were clear differences among the plant groups in how their species were distributed
261 across the landscape (Fig. 2A–D). Palms had a large proportion of generalist species that
262 occurred on all three terrain types, and pteridophytes had a large proportion of specialist
263 species that were only observed on the Solimões Formation. Melastomataceae and
264 Zingiberales were more evenly distributed, with a large proportion of species occurring on
265 both the Içá Formation and alluvial terraces.

266 Ordination and classification of the 39-transect subset confirmed that the Solimões Formation
267 sites were floristically different from sites on alluvial terraces and the Içá Formation,
268 independent of plant group and whether presence-absence or abundance data were used (Fig.
269 3). The three understorey plant groups (pteridophytes, Melastomataceae and Zingiberales),
270 displayed a dichotomy with two well-separated groups, but palms showed more gradual
271 turnover across the gradient.

272 The alluvial terraces and Içá Formation were only partly distinct floristically, which is
273 consistent with their wide overlap in soil properties (Table S1.1). Interestingly, the pre-
274 defined landscape types separated from each other more clearly with presence-absence than
275 abundance data (Fig. 3).

276 Results of the ordination analyses with all 71 transects paralleled those of the 39-transect
277 subset (Fig. S1.1 in Appendix 1 of Supporting Information). The gap between the Solimões
278 and Içá Formation transects was bridged more completely by the alluvial terrace transects
279 than in the 39-transect subset, the extra sampling having introduced overlap in cation
280 concentration between the alluvial terraces and Solimões Formation.

281 **Floristic patterns explained by environmental gradients**

282 Mantel tests confirmed a strong correlation between species turnover and difference in soil
283 properties for all plant groups (Table 1). All measured soil variables except LOI yielded
284 statistically significant Mantel test results, and correlations were especially high for variables
285 involving the concentration of one or more soil cations. Correlations with geographical
286 distances were also statistically significant, but partialling out the effect of geographical
287 distances had very little effect on the correlations between species turnover and edaphic
288 differences.

289 The binary dissimilarity matrix indicating whether two transects were on edaphically similar
290 terrain types (Içá Formation or alluvial terrace vs. Solimões Formation) gave Mantel test
291 results very similar to those obtained with soil calcium concentration (Table 1). Analyses
292 based on whether the transects were on the same side of the east-west boundary also gave
293 significant (but clearly lower) Mantel correlations. In contrast, whether transects were on the

294 same or different sides of the Juruá river had little or no relationship with the degree of
295 floristic dissimilarity between them.

296 All correlations were higher for presence-absence data than for abundance data. For example,
297 with sum of bases the correlations ranged 0.75–0.91 for presence-absence data and 0.53–0.78
298 for abundance data. When the Mantel tests were repeated for pteridophytes and
299 Melastomataceae using the entire dataset, the results remained essentially the same (Table 1).

300 Regression tree analyses clarified which combination of environmental variables explained
301 species turnover best. With the 39-transect data, all plant groups gave the same three-cluster
302 tree. The first division at sum of bases 1.578 cmol(+)/kg cleanly separated all Solimões
303 Formation transects into one branch. The second division was at sum of bases 0.1774
304 cmol(+)/kg, and all the transects below this limit were on the Içá Formation. The intermediate
305 category contained some Içá Formation transects and all the terrace transects. The results
306 only differed among plant groups in the proportion of variance explained by each variable.
307 The first division explained a very high percentage of the variation in pteridophytes (81%)
308 and at least half in the other plant groups (52–59%), but the second division explained less
309 (3–8%).

310 In each plant group, 64–75% of the species were statistically significant indicators of at least
311 one of the edaphic classes of the regression tree (Fig. 2E–H, Appendix 2). Both pteridophytes
312 and Zingiberales had many indicator species for the high-cation class, whereas
313 Melastomataceae and palms had more equal numbers of indicator species along the gradient.
314 Even though a large proportion of palm species were observed in all terrain types, the high

315 proportion of significant indicator species showed that their distributions were nevertheless
316 concentrated to specific parts of the soil cation concentration gradient.

317 To test how consistent the indicator species were across geographical regions, we calculated
318 indicator values for the pteridophyte and Melastomataceae species in the full 71-transect set
319 using the same geological division that had been used along the Tigre river in Peru (Higgins
320 *et al.* 2011), i.e. a simple dichotomy between the Solimões/Pebas Formation vs. the Nauta/Içá
321 Formation and alluvial terraces. In general, the results were very similar: no Melastomataceae
322 and only two pteridophyte species were indicators of a different terrain type in the Juruá area
323 than in the Tigre area (Fig. 4, Appendix 2).

324 **DISCUSSION**

325 Our results confirmed that the boundary between the Solimões and Içá Formations across the
326 middle Juruá river in western Brazil is floristically and edaphically very similar to the
327 boundary between the Pebas and Nauta Formations across the Tigre river in northern Peru
328 (Higgins *et al.* 2011). Just like the Peruvian boundary, the Brazilian one is visible in Landsat
329 and SRTM imagery, and corresponds to a significant floristic turnover zone. Given that the
330 Brazilian boundary is over 1000 km long, it is of high relevance to Amazonian biogeography.

331 Like the Pebas–Nauta boundary, the Solimões–Içá boundary seems to be the result of surface
332 erosion that started from the headwaters and proceeds gradually downwards (Higgins *et al.*
333 2011). The process removes the relatively sandy (easily erodible) sediments of the Nauta/Içá
334 Formation and exposes the lower-lying clayey (denudation-resistant) sediments of the
335 Pebas/Solimões Formation. Soil properties along the Juruá were similar to those on

336 corresponding geological formations along the Tigre (Higgins *et al.* 2011), although the
337 cation concentrations on the Pebas/Solimões Formation were somewhat lower along the
338 Juruá. This is consistent with the general trend in Amazonia of soils becoming poorer
339 towards the east.

340 The ecological importance of the Solimões–Içá and *floresta aberta* – *floresta densa*
341 boundaries was confirmed for all four plant groups. The 39-transect set was divided into the
342 same two classes (Solimões Formation vs. Içá Formation and alluvial terraces) with all plant
343 groups whether unconstrained clustering or regression tree analysis was used. The second
344 division of the regression tree was identical for all plant groups as well, but it did not exactly
345 follow the geomorphological division to flat terraces vs. hilly Içá Formation, consistent with
346 these two terrain types overlapping in soil properties. The separation between the Solimões
347 transects and the terrace transects was less clear-cut in the full set of 71 transects both
348 edaphically and floristically. This was partly due to the addition of terrace sites from the
349 Tarauacá river. Terrace sediments reflect the average surface characteristics in the river's
350 drainage area, and the Tarauacá drainage has a higher prevalence of the Solimões Formation
351 than the Juruá drainage does.

352 Although geological formations can be useful as indicators of broad-scale habitat patterns,
353 plant responses to them depend on the properties of the corresponding soils. In agreement
354 with earlier studies, compositional turnover was most strongly related to differences in soil
355 cation concentration, especially Ca and Mg. The floristic composition changed predictably
356 according to the soil properties even when small patches of one kind of soil occurred in a
357 matrix of the other. This was especially evident in the western part of the study area, where
358 remnants of the Içá Formation exist in a matrix of the Solimões Formation.

359 According to published soil data (Dijkshoorn *et al.* 2005), Içá Formation corresponds to
360 Plinthosols but both alluvial terraces and large parts of the Solimões Formation to Acrisols.
361 This contrasts our observations of high edaphic and floristic similarity between alluvial
362 terraces and the Içá Formation.

363 Although a soil cation concentration gradient is obvious in the ordination diagrams, not all of
364 the plant compositional variation seen in them is readily explained by measured soil
365 properties. Given the weak correlations between geographical and floristic distances, it is
366 unlikely that simple dispersal limitation is a decisive factor in structuring these forests. The
367 possible importance of unmeasured environmental variables and historical idiosyncracies
368 remains open.

369 A large proportion of the species in each plant group can be used as indicators of the edaphic
370 conditions of the Solimões or Içá Formations. For pteridophytes and Melastomataceae, such
371 results are transferable across regions: indicator species of one terrain type in the Tigre area
372 in Peru were indicators of the corresponding terrain type also in the Juruá area in Brazil.
373 Moreover, the same indicator patterns have emerged in other parts of western and central
374 Amazonia (Tuomisto & Poulsen 1996; Tuomisto *et al.* 2003b; Salovaara *et al.* 2004;
375 Suominen *et al.* 2013; Zuquim *et al.* 2014).

376 The dichotomy separating the Pebas/Solimões sites from the others was very sharp for the
377 three understorey plant groups, but more gradual for palms. Furthermore, few palm species
378 were entirely excluded from either formation, but rather responded to the edaphic differences
379 by (sometimes very large) changes in abundance. This suggests that palms are less
380 specialised in their environmental requirements than the three smaller-statured plant groups,

381 which is consistent with the observation that several palm species are among the most
382 abundant tree species in Amazonia (ter Steege *et al.* 2013; Emilio *et al.* 2014). Nevertheless,
383 the abundance differences are so conspicuous that local people have traditionally used
384 selected palm species to characterise forest types (Encarnación 1985).

385 The Solimões–Içá boundary was so clear that it must also affect plant groups we did not
386 inventory. Indeed, edaphic differences of the magnitude observed across this boundary have
387 been associated with significant species turnover of canopy trees elsewhere in Amazonia
388 (Phillips *et al.* 2003; ter Steege *et al.* 2006; Ruokolainen *et al.* 2007; Higgins *et al.* 2011).

389 There was no indication that the Juruá river limits plant species distributions. Earlier studies
390 on mtDNA haplotypes of non-volant vertebrates did not find a river barrier effect either
391 (Patton *et al.* 1994, 2000; da Silva & Patton 1998; Gascon *et al.* 2000). However, there was a
392 difference in mammalian haplotypes between sampling localities separated by the Solimões–
393 Içá boundary. This division was originally interpreted as a lingering effect of past isolation by
394 the Iquitos Arch, but our results suggest a more proximate cause.

395 Because the forests on the two sides of the boundary are floristically different, any
396 compositional or genetic differences in animals across the boundary may simply reflect
397 habitat differences. Patton *et al.* (1994) reported that the headwaters clade and the river
398 mouth clade of arboreal spiny rats overlapped at only one site, Barro Vermelho. This is
399 consistent with our data showing that both the Içá Formation and the Solimões Formation are
400 present at this site (Fig. 1). The environmental heterogeneity hypothesis is also consistent
401 with earlier studies on parasitic wasps and birds in Peruvian Amazonia, which have indicated

402 floristic differences to be associated with animal species turnover (Sääksjärvi *et al.* 2006;
403 Pomara *et al.* 2012).

404 Habitat differences can promote genetic and species compositional differentiation in two
405 ways. Firstly, existing species (and haplotypes) can simply be sorted through community
406 assembly processes, such that only those members of the regional species (or haplotype) pool
407 that are sufficiently well adapted to the conditions prevailing on one or the other side of the
408 boundary are able to persist there. Secondly, the boundary may trigger parapatric
409 differentiation (and ultimately speciation), as natural selection improves adaptations to the
410 conditions prevailing on each side of the boundary separately, with a concurrent decrease in
411 the ability to grow on the other side of the boundary. The relative importance of these
412 processes is probably related to the spatial and temporal scales involved. If environmental
413 patchiness has a small grain, gene flow across the boundary will be frequent and community
414 assembly processes may prevail. In coarse grained environments, the ecological
415 differentiation and isolation by distance can reinforce each other, causing accelerated
416 evolution. Indeed, parapatric speciation along environmental gradients has been suggested to
417 be common in Amazonia (Gentry 1981; Brown Jr 1987; Fine *et al.* 2005, 2013; Tuomisto
418 2006, 2007). The increasing availability of phylogenies and species distribution data allows
419 clarification of the degree to which sister species are ecologically vs. geographically
420 separated, which is one step towards assessing the likelihood of sympatric or parapatric
421 speciation (Papadopoulos *et al.* 2011).

422 The Solimões–Içá boundary is not static over time. If our hypothesis is correct, it has
423 gradually migrated eastwards, and continues to do so. There are two main consequences of
424 this kind of gradual replacement of one kind of surface by another. Firstly, plant populations

425 that remain in the same place will experience a change in soil conditions and associated
426 selection pressures over time. Secondly, the potential habitat area will increase for species
427 associated with the Solimões Formation and decrease for species associated with the Içá
428 Formation. A 1000-km-long boundary separating two environments as different as the ones
429 described here must have been a significant factor in the origin and structuring of Amazonian
430 biota. It forms a potential dispersal barrier for such plants (and possibly animals) that have
431 preference for the edaphic conditions on one or other side of the boundary, and a frontier
432 along which parapatric speciation may be taking place.

433 **ACKNOWLEDGEMENTS**

434 We thank Peterson Campos and Deborah Castro for their participation in data collecting, and
435 numerous local field assistants, in particular José Francisco Gomes da Cruz, for their
436 practical help in the field. We are grateful for the crew of the expedition ship “Guiado por
437 Deus” for their dedication and good humor during the three months of the expedition: José
438 Rodrigues da Silva Filho, Radisvom Teixeira de Lima and Perla Maciel da Silva. We are
439 grateful to Carlos C. Peres who helped us in finding the ship and its crew. Ethan
440 Householder, Hans ter Steege, Richard Ladle and an anonymous reviewer gave useful
441 comments on the manuscript. Research permits were granted by CNPq (Processo n°
442 001693/2011-5), CEUC/SDS (Autorização n° 047/2011) and SISBIO (Autorização n° 27998-
443 3). Funding from the Academy of Finland (grants to H.T.), Danish National Research
444 Council (grant #10-083348 to H.B.) and CNPq (fellowship to T.E.) is gratefully
445 acknowledged.

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665

666 SUPPORTING INFORMATION

667 Additional Supporting Information may be found in the online version of this article:

668 Appendix S1. Table of soil properties (Table S1.1) and figure of floristic ordinations based
 669 on 71 transects inventoried for pteridophytes and Melastomataceae (Fig. S1.1) along the
 670 Juruá river in western Brazil.

671 Appendix S2. Table of indicator species values of pteridophytes, Melastomataceae, palms
 672 and Zingiberales for soil cation concentration classes along the Juruá river in western Brazil.

673 BIOSKETCH

674 All authors share an interest in the origin and spatial distribution of Amazonian biodiversity,
 675 with main interests in different plant groups (pteridophytes: H.T. and G.M.,
 676 Melastomataceae: K.R., palms: H.B., T.E. and D.P., Zingiberales: F.F.). H.T. leads the

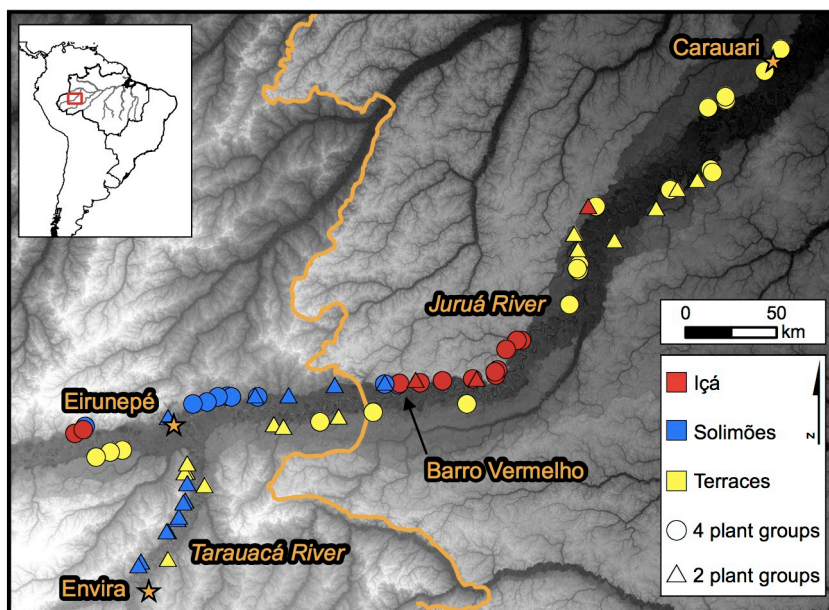
677 Amazon Research Team of the University of Turku (www.utu.fi/amazon) and H.B. the palm
678 research group at the Aarhus University. Author contributions: H.T. and K.R. conceived the
679 idea and organised the field expedition; all authors participated in data collection; H.T. and
680 G.M. analysed the data and led the writing.

681 Editor: Mark Bush

682

683 **FIGURES**

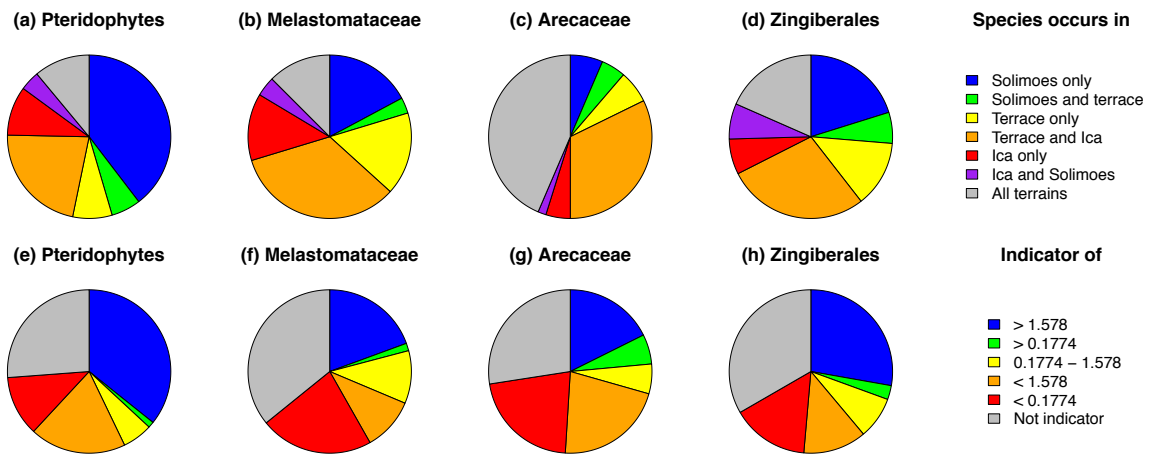
684 Fig. 1. The study area in the western part of Brazilian Amazonia. Background map is based
 685 on SRTM elevation data and the orange line is the boundary identified by Higgins *et al.*
 686 (2011). Each symbol corresponds to one transect of 5 m by 500 m that was inventoried for
 687 either two plant groups (pteridophytes and Melastomataceae) or four plant groups (adding
 688 Arecaceae and Zingiberales). Note that there is a Solimões Formation transect almost hidden
 689 by the Içá Formation transect at Barro Vermelho.



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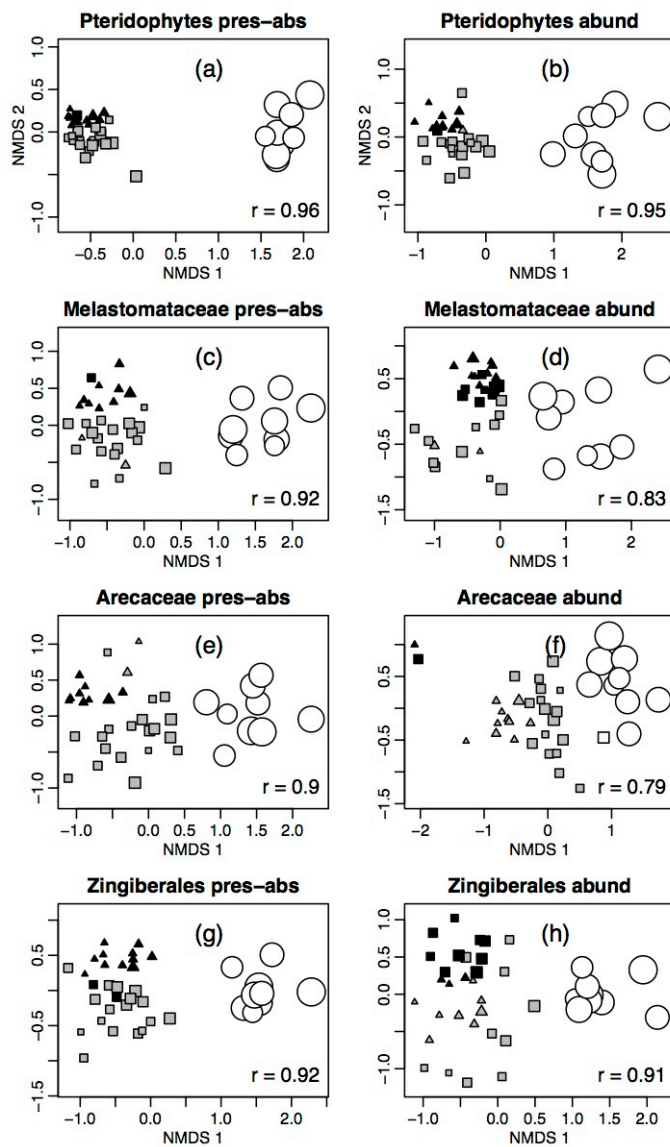
692 Fig. 2. A–D. Occurrence of plant species among three main terrain types along the Juruá river
 693 as observed in 39 transects (9 on the Solimões Formation, 19 on alluvial terraces and 11 on
 694 the Içá Formation). E–H. Proportions of species with statistically significant indicator values
 695 for different parts of the soil cation concentration gradient (units given in $\text{cmol}(+)/\text{kg}$).



696

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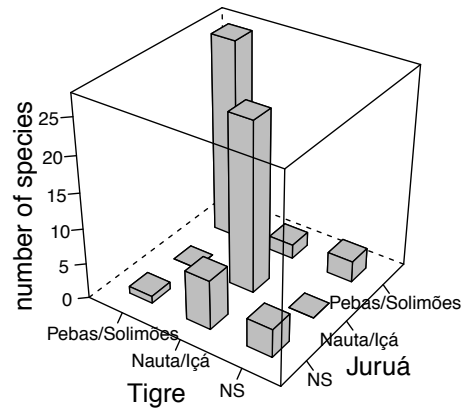
698 Fig. 3. Floristic ordinations of 39 transects along the Juruá river based on four plant groups.
699 Results are shown separately for presence-absence data (left) and abundance data (right).
700 Correlation coefficients are between NMDS 1 and log-transformed sum of exchangeable
701 bases. Symbols indicate the terrain type of each transect (triangles – Içá Formation; squares –
702 alluvial terrace; circles – Solimões Formation) and symbol sizes are proportional to the
703 concentration of exchangeable bases (Ca, Mg, K, Na) in the soil. Gray shades indicate the
704 first three classes obtained in an agglomerative classification of the floristic data based on
705 Ward's method.



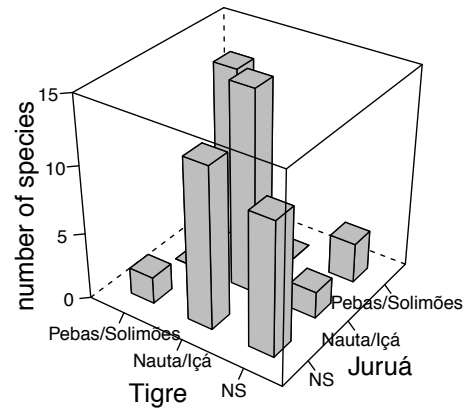
706

707 Fig 4. Consistency of species indicator status between our study area along the Juruá river
 708 (Brazil; the full 71-transect set) and in an earlier study along the Tigre river (Peru; Higgins *et*
 709 *al.* 2011). Species tallied under each geological formation are the ones that obtained
 710 significant indicator values for that formation (with alluvial terraces combined with the Içá
 711 Formation).

(a) Pteridophytes



(b) Melastomataceae



712

713

714 **TABLES**

715 Table 1. Pearson correlation coefficients between floristic dissimilarities and distance
 716 matrices based on either environmental variables or geographical coordinates. In each cell,
 717 the first value was obtained with species presence-absence data and the second with
 718 abundance data. The statistically significant correlation coefficients (simple Mantel test,
 719 $P < 0.05$) are shown in bold; all correlation coefficients > 0.25 were significant at $P < 0.001$.
 720 Partial Mantel tests were also run to partial out the effect of log-transformed geographical
 721 distances before calculating the correlation between environmental and floristic distances, but
 722 the results were almost identical to those of simple Mantel tests and are not shown.

723

	Pteridoph.	Melast.	Palms	Zingib.	Pteridoph.	Melast.
Transects	39	39	39	39	71	71
log(Ca)	0.93 / 0.78	0.81 / 0.54	0.73 / 0.51	0.80 / 0.64	0.90 / 0.77	0.75 / 0.48
log(K)	0.30 / 0.31	0.29 / 0.20	0.39 / 0.35	0.31 / 0.26	0.34 / 0.31	0.33 / 0.16
log(Mg)	0.88 / 0.75	0.78 / 0.50	0.75 / 0.56	0.77 / 0.63	0.82 / 0.69	0.70 / 0.44
log(Na)	0.43 / 0.35	0.41 / 0.24	0.43 / 0.36	0.41 / 0.35	0.24 / 0.18	0.23 / 0.15

log(Sum of bases)	0.91 / 0.78	0.80 / 0.53	0.75 / 0.54	0.79 / 0.65	0.85 / 0.72	0.72 / 0.46
log(P)	0.52 / 0.50	0.46 / 0.41	0.51 / 0.40	0.46 / 0.36	0.52 / 0.48	0.45 / 0.32
Al	0.02 / 0.09	0.06 / 0.05	0.04 / 0.02	0.09 / 0.14	0.12 / 0.14	0.15 / 0.11
pH	0.39 / 0.34	0.40 / 0.32	0.41 / 0.25	0.37 / 0.38	0.36 / 0.29	0.38 / 0.28
LOI	-0.09 / 0.03	-0.02 / 0.04	-0.01 / -0.01 / 0.01	-0.01 / 0.05	-0.05 / 0.01	-0.01 / 0.02
Geol. formation	0.93 / 0.78	0.82 / 0.56	0.70 / 0.50	0.79 / 0.65	0.84 / 0.67	0.69 / 0.42
E-W boundary	0.40 / 0.32	0.44 / 0.30	0.44 / 0.21	0.44 / 0.37	0.38 / 0.28	0.36 / 0.19
River bank	-0.10 / -0.06	-0.04 / 0.01	-0.09 / -0.03	0.00 / 0.06	0.02 / 0.03	0.08 / 0.08
log(Geod.)	0.19 / 0.25	0.33 / 0.35	0.30 / 0.25	0.37 / 0.33	0.25 / 0.24	0.30 / 0.28

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SUPPORTING INFORMATION

728

729 **A COMPOSITIONAL TURNOVER ZONE OF BIOGEOGRAPHICAL**730 **MAGNITUDE WITHIN LOWLAND AMAZONIA**

731 Hanna Tuomisto, Gabriel Moulatlet, Henrik Balslev, Thaise Emilio, Fernando O. G

732 Figueiredo, Dennis Pedersen, Kalle Ruokolainen

733

734

735 **APPENDIX S1** Table of soil properties (Table S1.1) and figure of floristic ordinations based

736 on 71 transects inventoried for pteridophytes and Melastomataceae (Fig. S1.1) along the

737 Juruá river in western Brazil.

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740

741 Table S1.1. Results of chemical analyses of surface soil samples and topographic information
 742 for transects representing three geomorphologically different types of terrain along the Juruá
 743 and Tarauacá rivers in Brazilian Amazonia. Means (and ranges in parentheses) are given
 744 separately for the full set of 71 transects (for which floristic data on pteridophytes and
 745 Melastomataceae are available) and a subset of 39 transects (for which also data on palms
 746 and Zingiberales are available). LOI = loss on ignition.

Soil variable	Number of transects	Içá Formation	Alluvial Terraces	Solimões Formation
Ca [cmol(+)/kg]	71	0.02 (0.01–0.04)	0.07 (0.02–0.93)	5.3 (0.10–23.99)
Ca [cmol(+)/kg]	39	0.02 (0.01–0.04)	0.04 (0.02–0.12)	5.71 (1.51–10.80)
K [cmol(+)/kg]	71	0.06 (0.04–0.09)	0.14 (0.05–0.24)	0.21 (0.11–0.42)
K [cmol(+)/kg]	39	0.07 (0.04–0.09)	0.15 (0.07–0.22)	0.22 (0.15–0.32)
Mg [cmol(+)/kg]	71	0.06 (0.04–0.12)	0.18 (0.06–0.45)	1.40 (0.18–3.19)
Mg [cmol(+)/kg]	39	0.06 (0.04–0.12)	0.17 (0.08–0.27)	1.64 (0.88–2.74)
Na [cmol(+)/kg]	71	0.01 (0.00–0.01)	0.01 (0.00–0.03)	0.02 (0.00–0.04)
Na [cmol(+)/kg]	39	0.01 (0.01–0.01)	0.02 (0.01–0.02)	0.02 (0.01–0.04)
Sum of bases	71	0.15 (0.11–0.26)	0.41 (0.14–1.57)	6.93 (0.41–27.64)

[cmol(+)/kg]				
Sum of bases [cmol(+)/kg]	39	0.16 (0.12–0.26)	0.37 (0.18–0.60)	7.59 (2.56–13.89)
P (g/kg)	71	0.12 (0.06–0.18)	0.19 (0.10–0.41)	0.30 (0.20–0.44)
P (g/kg)	39	0.13 (0.06–0.18)	0.18 (0.12–0.27)	0.31 (0.24–0.38)
Al [cmol(+)/kg]	71	3.16 (2.13–4.66)	6.13 (2.97–11.44)	4.04 (0.01–9.09)
Al [cmol(+)/kg]	39	3.32 (2.14–4.66)	6.02 (3.54–10.65)	3.92 (1.05–6.38)
pH	71	3.78 (3.66–4.00)	3.70 (3.44–4.01)	4.01 (3.72–5.15)
pH	39	3.75 (3.66–3.89)	3.70 (3.44–4.01)	3.91 (3.74–4.10)
LOI (%)	71	4.46 (3.16–5.88)	6.11 (3.93–8.52)	5.15 (3.63–6.66)
LOI (%)	39	4.52 (3.16–5.88)	6.11 (3.93–7.92)	5.25 (3.97–6.12)
Elevation difference (m)	71	28.4 (17.7–40.6)	6.7 (0–21.7)	16.9 (7.5–29.3)
Elevation difference (m)	39	30.5 (19.0–40.6)	8.7 (2.7–21.7)	17.7 (13.3–20.3)

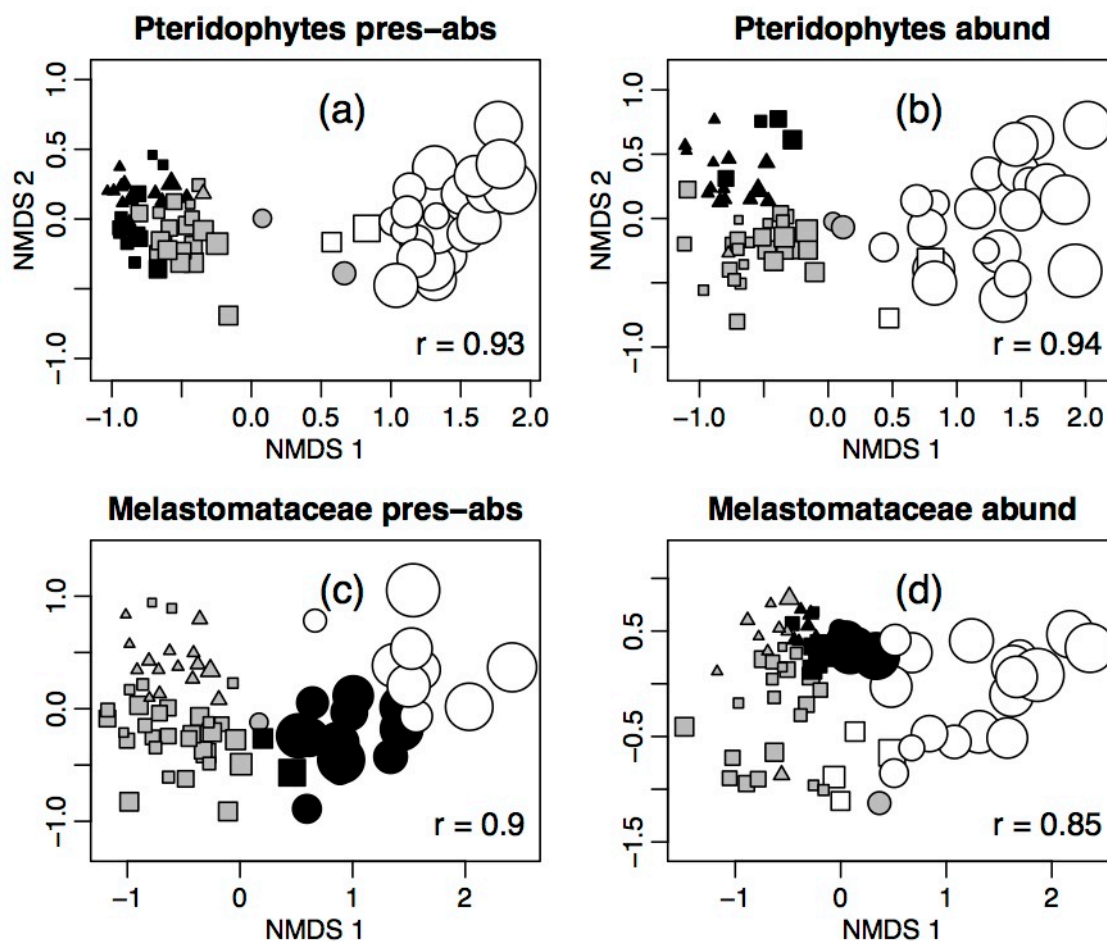
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751 Fig. S1.1. Ordination of 71 transects along the Juruá and Tarauacá rivers on the basis of their
 752 pteridophyte and Melastomataceae species composition. Results are shown separately for
 753 presence-absence data (left) and abundance data (right). Correlation coefficients are between
 754 NMDS 1 and log-transformed sum of bases. Symbols indicate the terrain type of each
 755 transect (triangles - Içá Formation; squares - alluvial terrace; circles - Solimões Formation).
 756 Colours indicate the first three classes obtained in an agglomerative classification based on
 757 Ward's method.



758

759 **APPENDIX S2** List of plant species with statistically significant indicator values for transect classes defined using the cation concentration threshold values that were obtained from regression tree analysis. Data from 39 transects (5 m by 500 m each) along the middle Juruá river in western Brazilian Amazonia. Soil cation concentration limit between classes 1 (lowest cation concentration) and 2 is 0.1774 and that between the classes 2 and 3 (highest cation concentration) is 1.578 cmol(+)/kg. Pteridophyte and Melastomataceae species that were significant indicators for the same terrain types here and in an earlier study in northern Peru (Higgins *et al.* 2011) are shown in bold.

Plant group	Species	1	1+2	2	2+3	3
Pteridophytes	<i>Adiantum cajennense</i> Willd. ex Klotzsch				0.75	
Pteridophytes	<i>Adiantum humile</i> Kunze					0.94
Pteridophytes	<i>Adiantum paraense</i> Hieron. or <i>A. tuomistoanum</i> J.Prado		0.97	0.83		
Pteridophytes	<i>Adiantum petiolatum</i> Desv.					0.81
Pteridophytes	<i>Adiantum pulverulentum</i> L.					0.94
Pteridophytes	<i>Adiantum terminatum</i> Kunze ex Miq.		0.92	0.8		
Pteridophytes	<i>Adiantum tomentosum</i> Kl.	0.85	1			
Pteridophytes	<i>Anetium citrifolium</i> (L.) Splitgb.					0.86
Pteridophytes	<i>Asplenium auritum</i> Sw.					0.67
Pteridophytes	<i>Asplenium pearcei</i> Baker					0.88
Pteridophytes	<i>Asplenium serratum</i> L.		0.99	0.92		
Pteridophytes	<i>Asplenium stuebelianum</i> Hieron.					0.82
Pteridophytes	<i>Bolbitis lindigii</i> (Mett.) C.Chr.					0.82
Pteridophytes	<i>Bolbitis nicotianifolia</i> (Sw.) Alston					0.94
Pteridophytes	<i>Campyloneurum aphanophlebium</i> (Kunze) Moore					0.82
Pteridophytes	<i>Campyloneurum fuscocosquamatum</i> Lellinger					0.92
Pteridophytes	<i>Cnemidaria ewanii</i> (Alston) Tryon	0.79				
Pteridophytes	<i>Ctenitis refulgens</i> (Mett.) Vareschi					0.67
Pteridophytes	<i>Cyathea bradei</i> (Windish) Lellinger			0.49		
Pteridophytes	<i>Cyathea lasiosora</i> (Mett. ex Kuhn) Domin	0.78	0.84			

Pteridophytes	<i>Cyathea pungens</i> (Willd.) Domin								0.79
Pteridophytes	<i>Cyathea traillii</i> (Baker) Domin	0.81							
Pteridophytes	<i>Cyclodium meniscioides</i> (Willd.) Presl	0.92	0.84						
Pteridophytes	<i>Cyclodium trianae</i> (Mett.) A.R. Smith								0.58
Pteridophytes	Danaea subgen. Arthrodanaea					0.67			
Pteridophytes	<i>Danaea lepreurii</i> Kunze	0.86	0.84						
Pteridophytes	<i>Danaea nigrescens</i> Jenman								1
Pteridophytes	<i>Didymochlaena truncatula</i> (Sw.) J. Smith								0.94
Pteridophytes	<i>Diplazium grandifolium</i> (Sw.) Sw. var. <i>andicola</i> Stolze								0.67
Pteridophytes	<i>Lindsaea falcata</i> Dryand. or <i>Lindsaea</i> sp. 8	0.95	0.71						
Pteridophytes	<i>Lindsaea lancea</i> (L.) Bedd. var. <i>lancea</i>		0.97	0.87					
Pteridophytes	<i>Lindsaea phassa</i> K.U. Kramer								0.75
Pteridophytes	<i>Lindsaea</i> sp. 5					0.53			
Pteridophytes	<i>Lindsaea</i> sp. 9					0.53			
Pteridophytes	<i>Lindsaea ulei</i> Hieron.					0.49			
Pteridophytes	<i>Lomagramma guianensis</i> (Aubl.) Ching						0.8	0.84	
Pteridophytes	<i>Lomariopsis japurensis</i> (Martius) J. Smith								1
Pteridophytes	<i>Lomariopsis nigropaleata</i> Holttum		0.88	0.86					
Pteridophytes	<i>Metaxya parkeri</i> (Hook. & Grev.) J.Sm.		0.71						
Pteridophytes	<i>Metaxya rostrata</i> (HBK.) Presl	0.77							
Pteridophytes	<i>Microgramma megalophylla</i> (Desv.) Sota	0.54							
Pteridophytes	<i>Polybotrya caudata</i> Kze.								0.94
Pteridophytes	<i>Polybotrya crassirhizoma</i> Lellinger								0.88
Pteridophytes	<i>Polybotrya pubens</i> Mart.		0.93	0.79					
Pteridophytes	<i>Pteris altissima</i> Poiret								0.67
Pteridophytes	<i>Saccoloma inaequale</i> (Kunze) Mettenius		0.92						
Pteridophytes	<i>Salpichlaena volubilis</i> (Kaulf.) J. Smith	0.89	0.68						

Pteridophytes	<i>Schizaea elegans</i> (Vahl.) Sw.	0.8				
Pteridophytes	<i>Selaginella exaltata</i> (Kunze) Spring					0.67
Pteridophytes	<i>Selaginella haematodes</i> (Kunze) Spring					0.82
Pteridophytes	<i>Selaginella lechleri</i> Hieron.	0.75				
Pteridophytes	<i>Selaginella parkeri</i> (Hook. & Grev.) Spring	0.79	0.84			
Pteridophytes	<i>Thelypteris abrupta</i> (Desv.) Proctor					0.94
Pteridophytes	<i>Thelypteris bifurcata</i> (Rosenst.) Tryon					1
Pteridophytes	<i>Thelypteris opulenta</i> (Kaulf.) Fosberg					0.67
Pteridophytes	<i>Thelypteris pennellii</i> A.R.Sm.					0.75
Pteridophytes	<i>Trichomanes diversifrons</i> (Bory) Mett. ex Sadeb.					0.88
Pteridophytes	<i>Trichomanes elegans</i> Rich.	0.8	0.84			
Pteridophytes	<i>Trichomanes hostmannianum</i> (Kl.) Kunze			0.58		
Pteridophytes	<i>Trichomanes pinnatum</i> Hedwig	0.83	0.97			
Pteridophytes	<i>Trichomanes</i> sp. 1		0.89	0.79		
Pteridophytes	<i>Trichomanes</i> sp. 4			0.93		
Pteridophytes	<i>Trichomanes trollii</i> Bergdolt	0.92	0.84			
Pteridophytes	<i>Triplophyllum dicksonioides</i> (Fée) Holttum or <i>T. funestum</i> (Kunze) Holttum or <i>T. sp. 3</i>		0.98	0.87		
Melastomataceae	<i>Adelobotrys boissieriana</i> Cogn.			0.65		
Melastomataceae	<i>Clidemia allardii</i> Wurdack	0.87				
Melastomataceae	<i>Clidemia dimorphica</i> Macbr.					0.88
Melastomataceae	<i>Clidemia heterophylla</i> (Desr.) Gleason					0.74
Melastomataceae	<i>Clidemia septuplinervia</i> Cogn.					0.88
Melastomataceae	<i>Leandra</i> sp. 20	0.5				
Melastomataceae	<i>Leandra candelabrum</i> (Macbr.) Wurdack	0.71	0.75			
Melastomataceae	<i>Leandra longicoma</i> Cogn.					0.86
Melastomataceae	<i>Maieta guianensis</i> Aubl.	0.87	0.87			
Melastomataceae	<i>Maieta poeppigii</i> Mart. ex Cogn.	0.71				

Melastomataceae	<i>Miconia aureoides</i> Cogn.						0.67
Melastomataceae	<i>Miconia barbinervis</i> (Benth.) Tr.			0.71			
Melastomataceae	<i>Miconia brachybotrya</i> Tr.						0.75
Melastomataceae	<i>Miconia carassana</i> Cogn.	0.61					
Melastomataceae	<i>Miconia dichrophylla</i> Macbr.				0.79	0.8	
Melastomataceae	<i>Miconia duckei</i> Cogn.	0.52					
Melastomataceae	<i>Miconia fosteri</i> Wurdack				0.53		
Melastomataceae	<i>Miconia grandifolia</i> Ule						0.65
Melastomataceae	<i>Miconia klugii</i> Gleason			0.95	0.85		
Melastomataceae	<i>Miconia napoana</i> Wurdack						0.88
Melastomataceae	<i>Miconia prasina</i> (Sw.) DC.			0.82	0.8		
Melastomataceae	<i>Miconia rimachii</i> Wurdack				0.68		
Melastomataceae	<i>Miconia schunkei</i> Wurdack						
Melastomataceae	<i>Miconia serrulata</i> (DC.) Naud.						0.87
Melastomataceae	<i>Miconia spennerostachya</i> Naud.						0.82
Melastomataceae	<i>Miconia tetrasperma</i> Gleason					0.72	
Melastomataceae	<i>Miconia tomentosa</i> (L. C. Rich.) D. Don			0.86	0.87		
Melastomataceae	<i>Miconia traillii</i> Cogn.	0.84		0.8			
Melastomataceae	<i>Miconia zubenatana</i> Macbr.						0.67
Melastomataceae	<i>Ossaea bullifera</i> (Pilger) Gleason	0.97		0.71			
Melastomataceae	<i>Tococa</i> sp. 9	0.82					
Melastomataceae	<i>Tococa ulei</i> Pilger	0.81		0.8			
Areaceae	<i>Alphanes horrida</i> (Jacq.) Burret				0.49		
Areaceae	<i>Astrocaryum aculeatum</i> G.Mey.			0.8			
Areaceae	<i>Astrocaryum chambira</i> Burret						0.78
Areaceae	<i>Astrocaryum gynacanthum</i> Mart.			0.98	0.88		
Areaceae	<i>Astrocaryum ulei</i> Burret					0.88	

Arecaceae	<i>Attalea butyracea</i> (Mutis ex L.f.) Wess.Boer								0.65
Arecaceae	<i>Attalea insignis</i> (Mart.) Drude							0.84	0.78
Arecaceae	<i>Attalea maripa</i> (Aubl.) Mart.			0.9	0.9				
Arecaceae	<i>Attalea microcarpa</i> Mart.		0.72	0.8					
Arecaceae	<i>Attalea phalerata</i> Mart. ex Spreng.								0.75
Arecaceae	<i>Bactris acanthocarpa</i> Mart.		0.88	0.77					
Arecaceae	<i>Bactris balanophora</i> Spruce		0.67						
Arecaceae	<i>Bactris bifida</i> Mart.				0.69				
Arecaceae	<i>Bactris concinna</i> Mart.						0.77	0.95	
Arecaceae	<i>Bactris corossilla</i> H.Karst.		0.75						
Arecaceae	<i>Bactris elegans</i> Schaedtler		0.77	0.68					
Arecaceae	<i>Bactris halmooerei</i> A.J.Hend.		0.66						
Arecaceae	<i>Bactris hirta</i> Mart.			0.91	0.76				
Arecaceae	<i>Bactris killipii</i> Burret		0.97	0.75					
Arecaceae	<i>Bactris maraja</i> Mart.			0.98	0.91				
Arecaceae	<i>Bactris oligocarpa</i> Barb.Rodr.				0.64				
Arecaceae	<i>Bactris simplicifrons</i> Mart.			0.9	0.76				
Arecaceae	<i>Bactris sphaerocarpa</i> Trail		0.79						
Arecaceae	<i>Bactris syagroides</i> Barb.Rodr. & Trail		0.6						
Arecaceae	<i>Chamaedorea pinnatifrons</i> (Jacq.) Oerst.								1
Arecaceae	<i>Desmoncus mitis</i> Mart.								0.87
Arecaceae	<i>Desmoncus polyacanthos</i> Mart.			0.71					
Arecaceae	<i>Euterpe precataria</i> Mart.						0.82	0.89	
Arecaceae	<i>Geonoma brongniartii</i> Mart.								0.83
Arecaceae	<i>Geonoma maxima</i> (Poit.) Kunth			0.96	0.82				
Arecaceae	<i>Geonoma stricta</i> (Poit.) Kunth			0.91	0.85				
Arecaceae	<i>Hyospathe elegans</i> Mart.		0.9						

Areaceae	<i>Iriartea deltoidea</i> Ruiz & Pav.				0.86	0.88
Areaceae	<i>Iriartella setigera</i> (Mart.) H. Wendl.	0.86	0.82			
Areaceae	<i>Oenocarpus bacaba</i> Mart.	0.77				
Areaceae	<i>Oenocarpus bataua</i> Mart.	0.89	0.97			
Areaceae	<i>Phytalephas macrocarpa</i> Ruiz & Pav.					0.88
Zingiberales	<i>Goepertia</i> sp. 25					0.67
Zingiberales	<i>Goepertia</i> sp. 26	0.56				
Zingiberales	<i>Goepertia</i> sp. 36	0.88				
Zingiberales	<i>Goepertia</i> sp. 38					0.67
Zingiberales	<i>Goepertia</i> sp. 4	0.88				
Zingiberales	<i>Goepertia curaraya</i> (H. Kenn.) Borchs. & S. Suárez					0.86
Zingiberales	<i>Goepertia fragilis</i> (Gleason) Borchs. & S. Suárez			0.58		
Zingiberales	<i>Goepertia fucata</i> (H. Kenn.) Borchs. & S. Suárez					0.65
Zingiberales	<i>Goepertia loeseneri</i> (J.F. Macbr.) Borchs. & S. Suárez					0.74
Zingiberales	<i>Goepertia micans</i> (L. Mathieu) Borchs. & S. Suárez		0.85	0.8		
Zingiberales	<i>Goepertia microcephala</i> (Poepp. & Endl.) Borchs. & S. Suárez					1
Zingiberales	<i>Goepertia neblinensis</i> (H. Kenn.) Borchs. & S. Suárez	0.55				
Zingiberales	<i>Goepertia straminea</i> (Petersen) Borchs. & S. Suárez	0.87	0.82			
Zingiberales	<i>Goepertia variegata</i> (K. Koch) Borchs. & S. Suárez					0.82
Zingiberales	<i>Goepertia zingiberina</i> (Körn.) Borchs. & S. Suárez	0.9	0.75			
Zingiberales	<i>Chamaecostus</i> sp. 1 C.D. Specht & D.W. Stev.					0.75
Zingiberales	<i>Chamaecostus</i> sp. 2 C.D. Specht & D.W. Stev.	0.57				
Zingiberales	<i>Costus</i> sp. 4					0.87
Zingiberales	<i>Costus amazonicus</i> (Loes.) J.F. Macbr.					0.72
Zingiberales	<i>Costus lasius</i> Loes.		0.88	0.81		
Zingiberales	<i>Costus scaber</i> Ruiz & Pav.					0.97
Zingiberales	<i>Heliconia subulata</i> Ruiz & Pav.			0.58		

Zingiberales	<i>Heliconia brachyantha</i> L. Andersson				0.49		
Zingiberales	<i>Heliconia juruana</i> Loes.						0.82
Zingiberales	<i>Heliconia lourteigiae</i> Emygdio & E. Santos					0.84	
Zingiberales	<i>Heliconia spathocircinata</i> Aristeg.						1
Zingiberales	<i>Heliconia stricta</i> Huber						0.94
Zingiberales	<i>Heliconia tenebrosa</i> J.F. Macbr.			0.87	0.86		
Zingiberales	<i>Heliconia velutina</i> L. Andersson			0.77	0.68		
Zingiberales	<i>Hylaeantha unilateralis</i> (Poepp. & Endl.) A.M.E. Jonker & Jonker						0.88
Zingiberales	<i>Ischnosiphon</i> sp. 1			0.81	0.75		
Zingiberales	<i>Ischnosiphon</i> sp. 10						0.85
Zingiberales	<i>Ischnosiphon</i> sp. 2			0.68	0.78		
Zingiberales	<i>Ischnosiphon</i> sp. 8						0.85
Zingiberales	<i>Ischnosiphon arouma</i> (Aubl.) Körn.				0.82	0.8	
Zingiberales	<i>Ischnosiphon killipii</i> J.F. Macbr.		0.67				
Zingiberales	<i>Ischnosiphon lasiocoleus</i> Schum. ex Loes.		0.59				
Zingiberales	<i>Ischnosiphon longiflorus</i> K. Schum.		0.85	0.98			
Zingiberales	<i>Monotagma</i> sp. 5		0.68				
Zingiberales	<i>Monophyllanthe aracuarensis</i> S. Suárez, Galeano & H. Kenn.			0.8			
Zingiberales	<i>Monotagma exile</i> Hagberg & R. Erikss.		0.66				
Zingiberales	<i>Monotagma laxum</i> (Poepp. & Endl.) Schum.		0.73				
Zingiberales	<i>Monotagma tomentosum</i> K. Schum. ex Loes.			0.71			
Zingiberales	<i>Phenakospermum guyannensis</i> (Rich.) Endl.		0.8	0.9			
Zingiberales	<i>Renealmia</i> sp. 4						0.88
Zingiberales	<i>Renealmia breviscapa</i> Poepp. & Endl.						0.78
Zingiberales	<i>Renealmia cernua</i> (Sw. ex Roem. & Schult.) J.F. Macbr.						0.75
Zingiberales	<i>Renealmia monosperma</i> Miq.					0.66	