

A compositional turnover zone of biogeographical magnitude within lowland Amazonia

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ABSTRACT

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

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

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

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

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

Keywords

Amazonia, dispersal barriers, edaphic heterogeneity, indicator species, Nauta/Içá Formation, parapatric speciation, Pebas/Solimões Formation, plant species turnover, soil cation concentration

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INTRODUCTION

Dispersal barriers are important for allopatric speciation, and thereby for the emergence of biogeographical regions and broad-scale species compositional differences. Amazonia is a vast area with an apparently uniform cover of tropical rain

forest, and explaining the origin of its extremely high species richness in the absence of obvious dispersal barriers has been a long-standing problem.

The oldest hypothesis is that the Amazon river itself acts as a dispersal barrier (Wallace, 1852). The distribution limits of many birds and primates indeed seem to follow major

rivers (Cracraft, 1985; Ayres & Clutton-Brock, 1992; Pomara *et al.*, 2014; Boubli *et al.*, 2015). More recently, soil properties have been suggested to restrict plant species composition and distributions in Amazonian forests (Gentry, 1981; Tuomisto *et al.*, 1995, 2003a,b; Phillips *et al.*, 2003; Salovaara *et al.*, 2004; Costa *et al.*, 2005; Ruokolainen *et al.*, 2007; Higgins *et al.*, 2011; Figueiredo *et al.*, 2014). However, this is controversial, as others have emphasized the ability of plants to grow across a wide range of soils (Duivenvoorden, 1995; Pitman *et al.*, 2001; ter Steege *et al.*, 2003).

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

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

Alternatively, the observed haplotype pattern might be related to habitat differentiation. A geological boundary between Miocene sediments of lacustrine or semimarine origin (the Solimões Formation) and younger fluvial sediments (the Içá Formation) crosses the Juruá river (Schobbenhaus *et al.*, 2004). This coincides with a boundary recognized between *floresta aberta* (open forest) and *floresta densa* (dense forest; IBGE 2004), which have been observed to differ in canopy tree composition elsewhere in Amazonia (Emilio *et al.*, 2010). However, the ecological or floristic significance of the Juruá boundary has not been investigated, although it may represent an edaphic limit between western and central Amazonia (Fittkau *et al.*, 1975; Sombroek, 2000; Higgins *et al.*, 2011).

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

It is an exciting thought that predictions about the biotic differentiation of forests in one part of Amazonia might be made on the basis of field studies carried out more than

1000 km away. To test the viability of such broad-scale predictions, we organized a 3-month expedition to the Juruá river. In addition to pteridophytes (ferns and lycophytes) and Melastomataceae, which were sampled in the Peruvian study, we included palms (Arecaceae) and Zingiberales to obtain data from structurally dissimilar and phylogenetically distant plant groups. Here, we document the floristic patterns of these four plant groups across the Solimões–Içá boundary, compare the patterns with those observed across the Pebas–Nauta boundary in Peru, and discuss the broader implications of these findings for Amazonian biogeography.

MATERIALS AND METHODS

Study area

The study was conducted in Brazilian Amazonia along the rivers Juruá and Tarauacá (Fig. 1). Average annual rainfall in the area (as reported for Eirunepé) is *c.* 2200 mm. Mean annual temperature is 27 °C, but temperatures as low as 15 °C can occur in June to August (Marengo *et al.*, 1997).

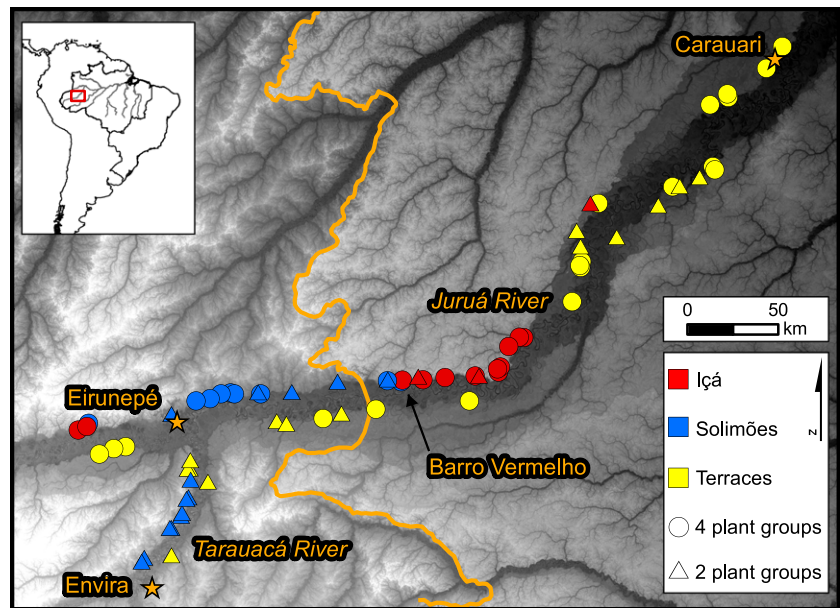
A geological boundary between the Solimões Formation in the west and the Içá Formation in the east runs north–south across the study area (Sombroek, 2000; Higgins *et al.*, 2011). Both formations consist of Quaternary sedimentary deposits and cover a large part of Western Amazonia. The Pebas/Solimões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

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

Sampling methods

Field sampling covered a 500-km stretch (air distance) along the Juruá and Tarauacá rivers. Sampling was planned with

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



the help of satellite imagery (Google Earth and the Landsat mosaic of Higgins *et al.*, 2011), SRTM elevation data and maps provided by Carlos C. Peres.

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

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

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

We inventoried four plant groups: pteridophytes (ferns and lycophytes), Melastomataceae, palms (*Arecaceae*) and *Zingiberales*. Pteridophytes and Melastomataceae were inventoried in all 71 transects, *Arecaceae* and *Zingiberales* in a subset of 39 transects. All individuals of each plant group were recorded and identified to species (or were given a field name, if the real species name was not known). To be included in the inventory, pteridophyte individuals needed at

least one green leaf (leafy stem in the case of lycophytes) exceeding 10 cm in length. Epiphytes and climbers were included if they had such leaves < 2 m above ground. For clonal species, each rooting stem was considered as an individual, even if connected to other rooting stems. All Melastomataceae individuals with post-cotyledon leaves were included. For the *Zingiberales*, a minimum height of 5 cm was applied, and in the case of clonal species, bunches of leaves separated by at least 20 cm were considered as separate individuals. All palm individuals higher than 5 cm were included, but palm seedlings that could not be identified to species level were excluded. Each ramet in a clonal or colonial species was counted as an individual.

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

Surface soil samples (top 5 cm of the mineral soil) were taken at three different points along each transect, usually at 50, 250 and 450 m. If needed, soil sample locations were modified to cover the extremes of the topographic gradient, or to avoid sampling in creeks or where the soil had been obviously disturbed. Each soil sample consisted of five subsamples collected within an area of *c.* 5 m by 5 m and mixed. Samples were stored in plastic bags and air-dried in the INPA soil laboratory after returning to Manaus. Laboratory analyses in the Agricultural Research Centre of Finland used standard methods (van Reeuwijk, 1993) for pH (in 1 M KCl), exchangeable bases (Ca, K, Mg and Na; extraction by

1 M ammonium acetate at pH 7), Al (extraction by 1 M ammonium acetate at pH 7) and LOI (loss-on-ignition at 420°). Total phosphorus was extracted following Quesada *et al.* (2010). Data analyses used the average value of each variable for each transect.

Data analyses

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

For the environmental data, separate distance matrices based on Euclidean distance were calculated for each soil variable. The concentrations of exchangeable cations and phosphorus were logarithmically transformed before calculating the distances to emphasize differences between small values – a unit change in nutrient concentration is physiologically most important when the nutrient is scarcest. Geographical distances were calculated using transect mid-point coordinates, and the distance values were logarithmically transformed.

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

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

Correlations between floristic dissimilarities and the environmental and geographical distances were calculated using simple and partial Mantel tests (Legendre & Legendre, 2012). Distance-based multivariate regression trees (De'Ath, 2002) were constructed to evaluate the predictability of floristic dissimilarities (presence–absence data only) on the basis of the quantitative edaphic variables. The method produces a

hierarchical classification of sites on the basis of their positions along one or more of the measured environmental gradients. In the first step, each environmental variable is divided at a point that minimizes the floristic differences among the sites in the same subgroup. The environmental variable that obtains the best cross-validation error criterion is then selected, and the process is repeated for each of the previously obtained subgroups until further divisions no longer meet the cross-validation criterion.

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

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

RESULTS

Landscape and soils

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

The ranges of the most important base cations (Ca, K and Mg) for the Solimões and Içá Formations did not overlap. The alluvial terraces were intermediate, with cation concentrations overlapping broadly with the Içá Formation. In the full data set of 71 transects, there was also overlap between the terraces and the Solimões Formation, due to three transects situated close to the limit between them. Similarly, soil phosphorus content did not overlap between the Solimões and Içá Formations, and alluvial terraces were intermediate.

The other soil variables overlapped between all terrain types, but Solimões Formation soils tended to have relatively high pH values and alluvial terraces relatively high aluminium concentration and LOI.

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

Floristic patterns

In the 39 transects, we recorded more than 112,000 plant individuals representing 458 species. Pteridophytes were most species-rich (154 species) and palms least (62 species), with Melastomataceae (128 species) and Zingiberales (114 species) intermediate. Pteridophytes were also the most abundant plant group (56,600 individuals), followed by palms (35,100), Zingiberales (13,500) and Melastomataceae (7500). The additional set of 32 transects only produced 18 pteridophyte and 18 Melastomataceae species that had not been present in the first 39 transects.

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

Ordination and classification of the 39-transect subset confirmed that the Solimões Formation sites were floristically

different from sites on alluvial terraces and the Içá Formation, independent of plant group and whether presence–absence or abundance data were used (Fig. 3). The three understorey plant groups (pteridophytes, Melastomataceae and Zingiberales), displayed a dichotomy with two well-separated groups, whereas palms showed more gradual turnover across the gradient.

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

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

Floristic patterns explained by environmental gradients

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

The binary dissimilarity matrix indicating whether two transects were on edaphically similar terrain types (Içá

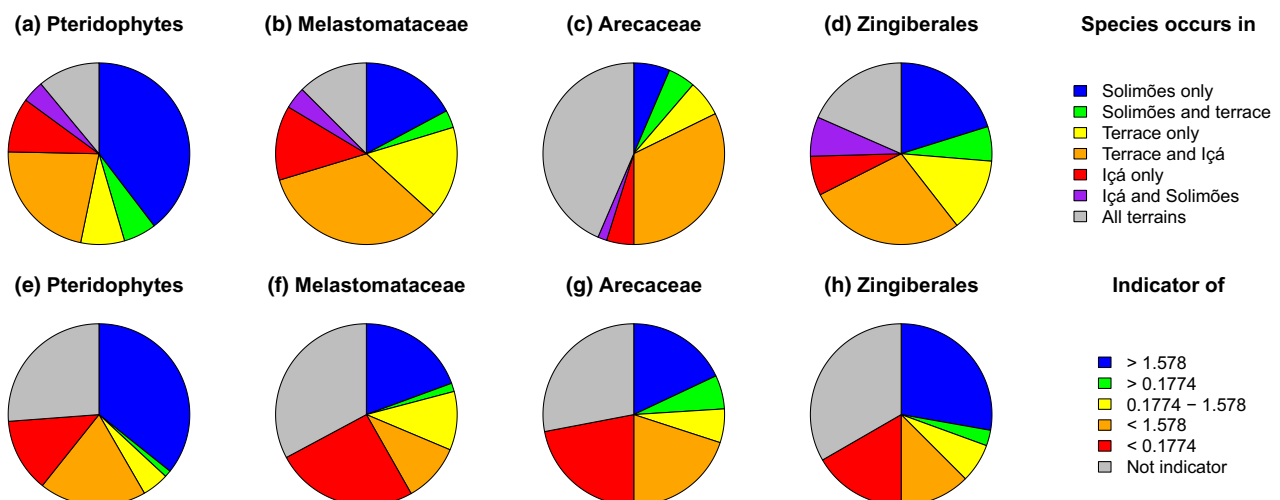


Figure 2 (a–d) Occurrence of plant species among three main terrain types along the Juruá river as observed in 39 transects (9 on the Solimões Formation, 19 on alluvial terraces and 11 on the Içá Formation). (e–h) Proportions of species with statistically significant indicator values for different parts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

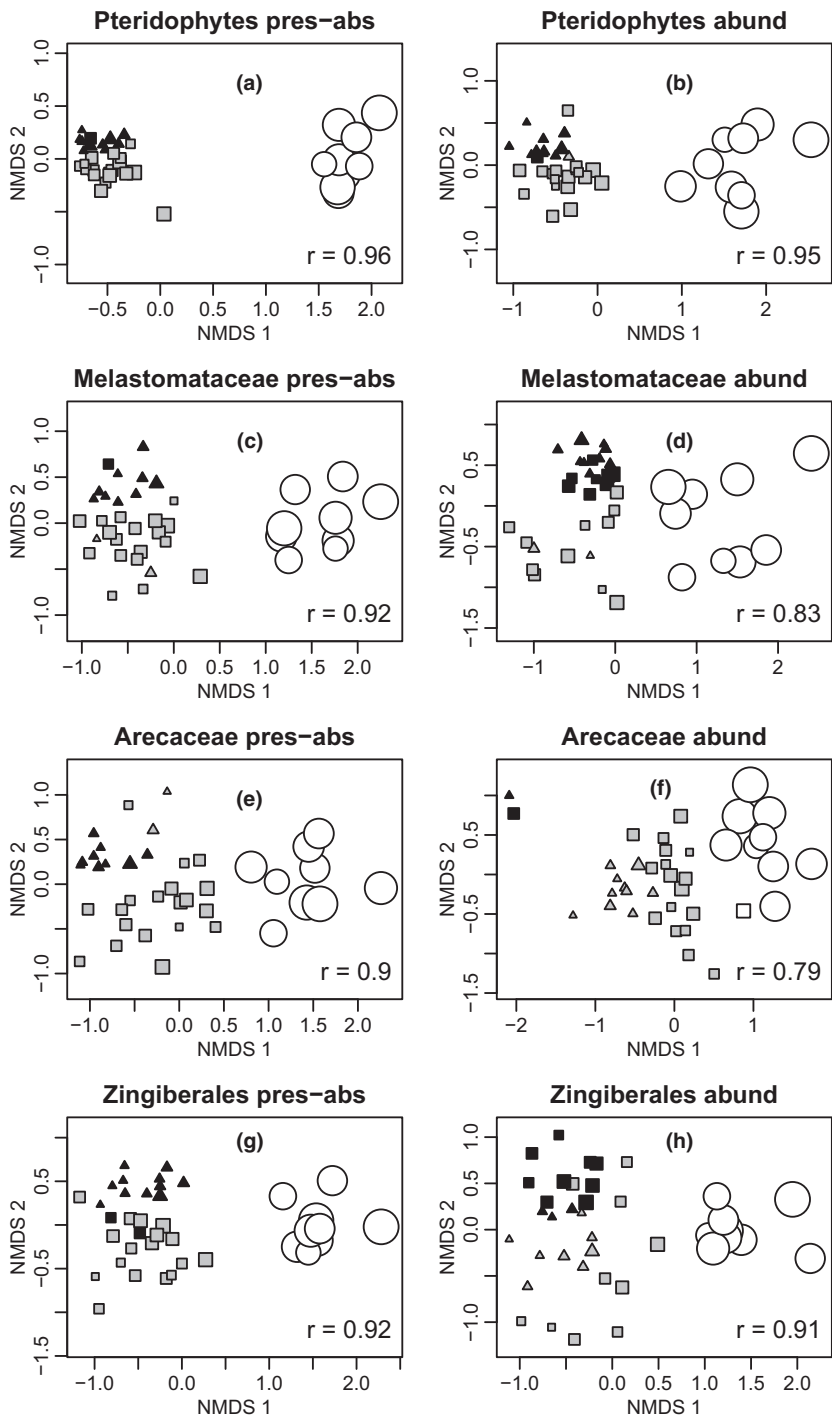


Figure 3 Floristic ordinations of 39 transects along the Juruá river based on four plant groups. Results are shown separately for presence–absence data (left) and abundance data (right). Correlation coefficients are between NMDS 1 and log-transformed sum of exchangeable bases (Ca, Mg, K, Na). Symbols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

Formation or alluvial terrace versus Solimões Formation) gave Mantel test results very similar to those obtained with soil calcium concentration (Table 1). Analyses based on whether the transects were on the same side of the east–west boundary also gave significant (but clearly lower) Mantel correlations. In contrast, whether transects were on the same or different sides of the Juruá river had little or no relationship with the degree of floristic dissimilarity between them.

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

Regression tree analyses clarified which combination of environmental variables explained species turnover best.

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

| | 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 | −0.01/0.05 | −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 |

With the 39-transect data, all plant groups gave the same three-cluster tree. The first division at sum of bases $1.578 \text{ cmol}(+) \text{ kg}^{-1}$ cleanly separated all Solimões Formation transects into one branch. The second division was at sum of bases $0.1774 \text{ cmol}(+) \text{ kg}^{-1}$, and all the transects below this limit were on the Içá Formation. The intermediate category contained some Içá Formation transects and all the terrace transects. The results only differed among plant groups in the proportion of variance explained by each variable. The first division explained a very high percentage of the variation in pteridophytes (81%) and at least half in the other plant groups (52–59%), but the second division explained less (3–8%).

In each plant group, 64–75% of the species were statistically significant indicators of at least one of the edaphic classes of the regression tree (Fig. 2e–h, see Appendix S2). Both pteridophytes and Zingiberales had many indicator species for the high-cation class, whereas Melastomataceae and palms had more equal numbers of indicator species along the gradient. Although a large proportion of palm species were observed in all terrain types, the high proportion of significant indicator species showed that their distributions were nevertheless concentrated to specific parts of the soil cation concentration gradient.

To test how consistent the indicator species were across geographical regions, we calculated indicator values for the pteridophyte and Melastomataceae species in the full 71-transect set using the same geological division that had been used along the Tigre river in Peru (Higgins *et al.*, 2011), that is, a simple dichotomy between the Solimões/Pebas Formation versus the Nauta/Içá Formation and alluvial terraces. In general, the results were very similar: no Melastomataceae and only two pteridophyte species were indicators of a different terrain type in the Juruá area than in the Tigre area (Fig. 4, see Appendix S2).

DISCUSSION

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

Like the Pebas–Nauta boundary, the Solimões–Içá boundary seems to be the result of surface erosion that started from the headwaters and proceeds gradually downwards (Higgins *et al.*, 2011). The process removes the relatively sandy (easily erodible) sediments of the Nauta/Içá Formation and exposes the lower lying clayey (denudation-resistant) sediments of the Pebas/Solimões Formation. Soil properties along the Juruá were similar to those on corresponding geological formations along the Tigre (Higgins *et al.*, 2011), although the cation concentrations on the Pebas/Solimões Formation were somewhat lower along the Juruá. This is consistent with the general trend in Amazonia of soils becoming poorer towards the east.

The ecological importance of the Solimões–Içá and *floresta aberta* – *floresta densa* boundaries was confirmed for all four plant groups. The 39-transect set was divided into the same two classes (Solimões Formation versus Içá Formation and alluvial terraces) with all plant groups whether unconstrained clustering or regression tree analysis was used. The second division of the regression tree was identical for all plant groups as well, but it did not exactly follow the geomorphological division to flat terraces versus hilly Içá Formation, consistent with these two terrain types overlapping in soil

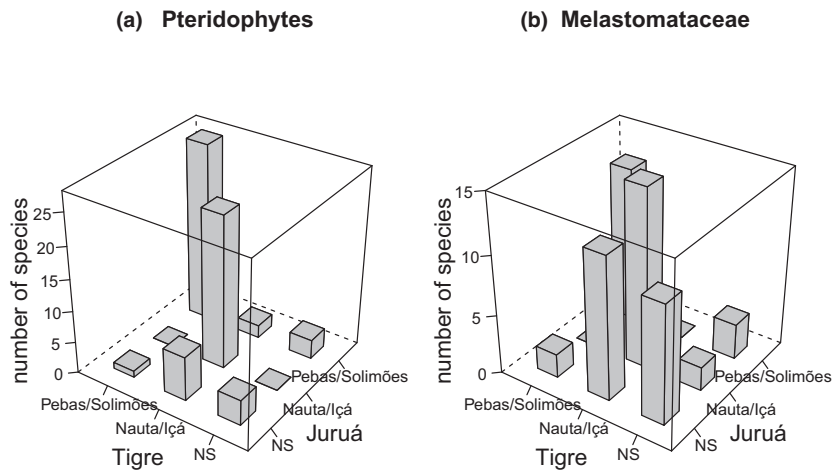


Figure 4 Consistency of species indicator status between our study area along the Juruá river (Brazil; the full 71-transect set) and in an earlier study along the Tigre river (Peru; Higgins *et al.*, 2011). Species tallied under each geological formation are the ones that obtained significant indicator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

properties. The separation between the Solimões transects and the terrace transects was less clear-cut in the full set of 71 transects both edaphically and floristically. This was partly due to the addition of terrace sites from the Tarauacá river. Terrace sediments reflect the average surface characteristics in the river's drainage area, and the Tarauacá drainage has a higher prevalence of the Solimões Formation than the Juruá drainage does.

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

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

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

A large proportion of the species in each plant group can be used as indicators of the edaphic conditions of the Solimões or Içá Formations. At least for pteridophytes and Melastomataceae, such results are transferable across regions: indicator species of one terrain type in the Tigre area in Peru were indicators of the corresponding terrain type also in the Juruá area in Brazil. Moreover, the same indicator patterns

have emerged in other parts of western and central Amazonia (Tuomisto & Poulsen, 1996; Tuomisto *et al.*, 2003b; Salovaara *et al.*, 2004; Suominen *et al.*, 2013; Zuquim *et al.*, 2014).

The dichotomy separating the Pebas/Solimões sites from the others was very sharp for the three understory plant groups, but more gradual for palms. Furthermore, few palm species were entirely excluded from either formation, but rather responded to the edaphic differences by (sometimes very large) changes in abundance. This suggests that palms are less specialized in their environmental requirements than the three smaller statured plant groups, which is consistent with the observation that several palm species are among the most abundant tree species in Amazonia (ter Steege *et al.*, 2013; Emilio *et al.*, 2014). Nevertheless, the abundance differences are so conspicuous that local people have traditionally used selected palm species to characterize forest types (Encarnación, 1985).

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

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

Because the forests on the two sides of the boundary are floristically different, any compositional or genetic differences in animals across the boundary may simply reflect habitat differences. Patton *et al.* (1994) reported that the headwaters clade and the river mouth clade of arboreal spiny rats overlapped at only one site, Barro Vermelho. This is consistent

with our data showing that both the Içá Formation and the Solimões Formation are present at this site (Fig. 1). The environmental heterogeneity hypothesis is also consistent with earlier studies on parasitic wasps and birds in Peruvian Amazonia, which have indicated floristic differences to be associated with animal species turnover (Sääksjärvi *et al.*, 2006; Pomara *et al.*, 2012).

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

The Solimões–Içá boundary is not static over time. If our hypothesis is correct, it has gradually migrated eastwards, and continues to do so. There are two main consequences of this kind of gradual replacement of one kind of surface by another. Firstly, plant populations that remain in the same place will experience a change in soil conditions and associated selection pressures over time. Secondly, the potential habitat area will increase for species associated with the Solimões Formation and decrease for species associated with the Içá Formation. A 1000-km-long boundary separating two environments as different as the ones described here must have been a significant factor in the origin and structuring of Amazonian biota. It forms a potential dispersal barrier for such plants (and possibly animals) that have preference for the edaphic conditions on one or other side of the boundary, and a frontier along which parapatric speciation may be taking place.

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SUPPORTING INFORMATION

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

Appendix S1 Soil properties and floristic ordinations of 71 transects.

Appendix S2 Plant species indicator values.

BIOSKETCH

All authors share an interest in the origin and spatial distribution of Amazonian biodiversity, with main interests in

different plant groups (pteridophytes: H.T. and G.M., Melastomataceae: K.R., palms: H.B., T.E. and D.P., Zingiberales: F.F.). H.T. leads the Amazon Research Team of the University of Turku (www.utu.fi/amazon) and H.B. the palm research group at the Aarhus University.

Author contributions: H.T. and K.R. conceived the idea and organized the field expedition; all authors participated in data collection; H.T. and G.M. analysed the data and led the writing.

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