

Scale-dependent drivers of the phylogenetic structure and similarity of tree communities in northwestern Amazonia

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Abstract

1. The extent to which historical dispersal, environmental features and geographical barriers shape the phylogenetic structure and turnover of tree communities in northwestern Amazonia at multiple spatial scales remains poorly understood.
2. We used 85 floristically standardized 0.1-ha plots (DBH \geq 2.5 cm) distributed in three subregions of northwestern (NW) Amazonia across three main habitat types (floodplain, swamp and terra firme forests) to hypothesize that (a) historical dispersal overcome geographical barriers, which meant low local phylogenetic relatedness and low phylogenetic turnover. (b) Geographical barriers triggered dispersal limitation, causing high local and subregional phylogenetic clustering and high regional phylogenetic turnover. (c) Edaphic properties and flooding were negatively associated with stem size and determined the tree phylogenetic structure and turnover at local and regional scales in Amazon forests.
3. We found that the extent to which environmental or evolutionary features shaped the phylogenetic structure and phylogenetic similarity of tree communities in NW Amazonia was scale dependent. Specifically, we show that the relative importance of environmental factors increases as spatial scale and species pool decreases. Furthermore, we find that these results are generally robust for both adult and juvenile trees.
4. *Synthesis.* Our analysis at the regional (NW Amazon) scale lends support to the idea of Amazonian forests as a large meta-community primarily structured by historical dispersal at large spatial scales with an increasing importance of environmental factors at finer spatial scales. The convergence of ancestral lineages across habitat types may have been due to the relatively recent formation of geographical barriers that promoted local isolation and allopatric speciation.

KEYWORDS

Amazon meta-community, flooding, historical dispersal, null models, soil heterogeneity, spatial scale

1 | INTRODUCTION

The complexity of tree communities results from the dynamic interplay of evolutionary and ecological processes that operate at different spatial scales (Cavender-Bares et al., 2009; Ricklefs, 2004). In forests, the interaction between speciation and extinction (Ricklefs, 2004), as well as between habitat specialization and biotic interactions (Stropp et al., 2009), largely shapes the phylogenetic structure and distribution of tree communities at both local and regional scales (Cavender-Bares et al., 2009; Fine & Kembel, 2011). Nonetheless, the capability of lineages to disperse across large geographical areas (Dexter & Chave, 2016) plays a key role connecting distantly separated areas, and thus, adding new species into local communities (Cavender-Bares et al., 2009). The extent to which dispersal can shape tree phylogenetic communities largely depends on the frequency and age of geographical barriers across the region, which can constrain species distributions across different regions and habitats. Overall, the trade-off between lineage age and the time of formation of physical barriers (e.g. big rivers) often shapes lineage distributions across geographical space (Ruokolainen et al., 2019). For lineages that originated before the presence of geographical barriers, dispersal may be paramount determining the phylogenetic structure of the whole meta-community at large spatial scales (Dexter et al., 2017). On contrary, geographical barriers may constrain the spatial distribution of young lineages (i.e. those younger than emergence of geographical barriers), increasing the co-occurrence of closely related species within subregions separated by older geographical barriers (Ruokolainen et al., 2019).

The Amazon basin, which roughly harbours 15,000 tree species across ~6 million km² (ter Steege et al., 2020), is covered by the largest and most diverse reserve of forests on Earth. Particularly in northwestern (NW) Amazonia, where local tree species richness achieves mean values up to 640 woody species per hectare (Duque et al., 2017), the interaction between dispersal and geographical barriers has direct consequences on how speciation and local selection shape the phylogenetic structure of plant communities (Fine & Kembel, 2011). On the one hand, if the distribution of lineages is strongly influenced by historical dispersal, a homogeneous phylogenetic structure of tree communities would be expected. Under that scenario, the phylogenetic diversity of any local community would be a random draw of the phylogenetic composition of the species pool of the meta-community (Dexter et al., 2017). On the other hand, a dominant pattern of local phylogenetic clustering across regions separated by geographical barriers, such as big rivers, could be due to an extensive in situ speciation and high habitat specialization. This pattern would also lead to high turnover of lineages among regions separated by big rivers across the Amazon (Fine et al., 2014).

The influence of habitat heterogeneity and associated environmental constraints imposed by the endogenous properties of the main habitat types of Amazon forests, such as floodplains, swamps and terra firme (Duivenvoorden, 1995), may also act as local barriers to species distributions. In NW Amazonia, some studies have proposed that floodplains represent phylogenetically specialized habitats that differentiate tree communities at intermediate spatial scales (Aldana et al., 2016). Others, however, described NW Amazonian floodplains as habitats that can easily be invaded by lineages that come from adjacent habitats with contrasting environmental features (Cárdenas et al., 2017; Pitman et al., 2014; Terborgh & Andresen, 1998). Specifically, Terborgh and Andresen (1998) suggested that flooded and unflooded forests within a region would resemble each other more than either flooded or unflooded forests located in distant regions (i.e. dispersal overrides environmental filtering). In swamps, where few species dominate, poor soil drainage and anoxia have been shown to operate as important selection factors that make this habitat type more difficult to invade (ter Steege et al., 2019). The environmental filter associated to swamps proposes that closely related species could tend to coexist more often than expected by chance, which supposes high levels of phylogenetic turnover at both intermediate and large spatial scales. Regarding the largest and most diverse terra firme forests, which are located on sedimentary Tertiary plains, the lack of harsh conditions such as flooding along with an older age of this geological formation, should have facilitated the colonization of lineages with different evolutionary histories (Dexter et al., 2017). Therefore, assuming dispersal across NW Amazon as a frequent historical process, the terra firme forests might be expected to have a high representation of the main phylogenetic lineages at local scales. High phylogenetic diversity at a local scale will, in turn, increase phylogenetic evenness at the deepest level of the phylogeny, but will decrease phylogenetic turnover (β -diversity) at both subregional (i.e. country) and regional (i.e. NW Amazon) spatial scales. Improving our understanding on the concurrent effect of the spatial scale and the evolutionary history will help identifying the main drivers of tree community assembly in Amazonian forests (Cárdenas et al., 2017; Fine & Baraloto, 2016; Fine & Kembel, 2011).

Virtually, all phylogenetic patterns currently known from NW Amazonian forests are based on information from large canopy trees (diameter at breast height [DBH] ≥ 10 cm; e.g. Cárdenas et al., 2017; Fine & Kembel, 2011; Honorio Coronado et al., 2015). The inclusion of only canopy trees rules out more than a half of the total number of species expected in a plot (Duque et al., 2017). The main evolutionary features of typical understory lineages (e.g. Rubiaceae, Melastomataceae and Piperaceae), usually differ from those of dominant canopy lineages (e.g. Fabaceae, Lecythidaceae, Sapotaceae and Myristicaceae). Overall, small plant size in wet tropical forests has been associated with an increase in both habitat specialization

(Duque et al., 2002; Fortunel et al., 2016; Macía, 2011) and dispersal limitation (Dexter & Chave, 2016). Hence, including small-statured lineages in plot analyses can be expected to increase phylogenetic turnover at intermediate and large spatial scales, compared to analyses only based on large canopy trees. Assessing the extent to which distinct evolutionary and ecological processes shapes the phylogenetic structure and phylogenetic β -diversity of plant communities in relation to plant size at different spatial scales (e.g. Swenson et al., 2007) will significantly contribute to our understanding of the main determinants of the diversification and maintenance of the high diversity of Amazonian forests.

In this study, we aimed to assess the extent to which historical dispersal, flooding, geographical barriers and soil fertility variation determine the phylogenetic structure of tree communities at intermediate and large scales. For this purpose, we used 85 0.1-ha plots (trees and shrubs with DBH \geq 2.5 cm) covering three of the main habitat types (terra firme, floodplains and swamps) in three subregions of NW Amazonia (located in Colombia, Ecuador and Peru). The main hypotheses evaluated were as follows: (H1) Historical dispersal overcome geographical barriers and played a key role on structuring the phylogenetic assembly of tree communities in NW Amazonia (sensu Dexter et al., 2017). Under this assumption, local phylogenetic community structure of tree communities will be a random draw of the regional species pool, and thus, we expect a low phylogenetic β -diversity regardless of spatial scale and stem size of the included lineages. (H2) Geographical barriers have caused an evolutionary separation of ancestral communities imposing limitations to the dispersal of lineages across the region. A separation of subregions by geographical barriers proposes an increase in phylogenetic similarity between forest communities located closer geographically (the

Terborgh and Andresen hypothesis), particularly if smaller-statured lineages are incorporated (Dexter & Chave, 2016). If this process is frequent along evolutionary time, this would imply that two communities located in contrasting habitat types but in the same subregion, would be more similar in their phylogenetic composition than two communities located in the same habitat type but in different subregions (Cárdenas et al., 2017; Terborgh & Andresen, 1998). (H3) Abiotic environmental heterogeneity shapes the phylogenetic structure across NW Amazonian forests (Fine & Kembel, 2011). Under this scenario, we expect a high phylogenetic clustering in habitats prone to strong environmental filtering (i.e. flooded forests), especially if small-statured lineages are included (Comita et al., 2007; Duque et al., 2002; Fortunel et al., 2016). Two communities located in different subregions but in the same habitat would be more similar in phylogenetic composition than two communities in one subregion but in different habitats.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in three different subregions in NW Amazonia: Metá-Chiribiquete (hereafter Metá), forming part of the middle Caquetá basin in Colombia; Yasuní, part of the Napo basin in Ecuador and Ampiyacu, in the Maynas Province of Perú (Figure 1). The average temperature in all areas is around 25°C and annual precipitation varies around 3,000 mm (based on worldclim database; Hijmans et al., 2005). All months show an average precipitation above 100 mm (Lips & Duivenvoorden, 2001).

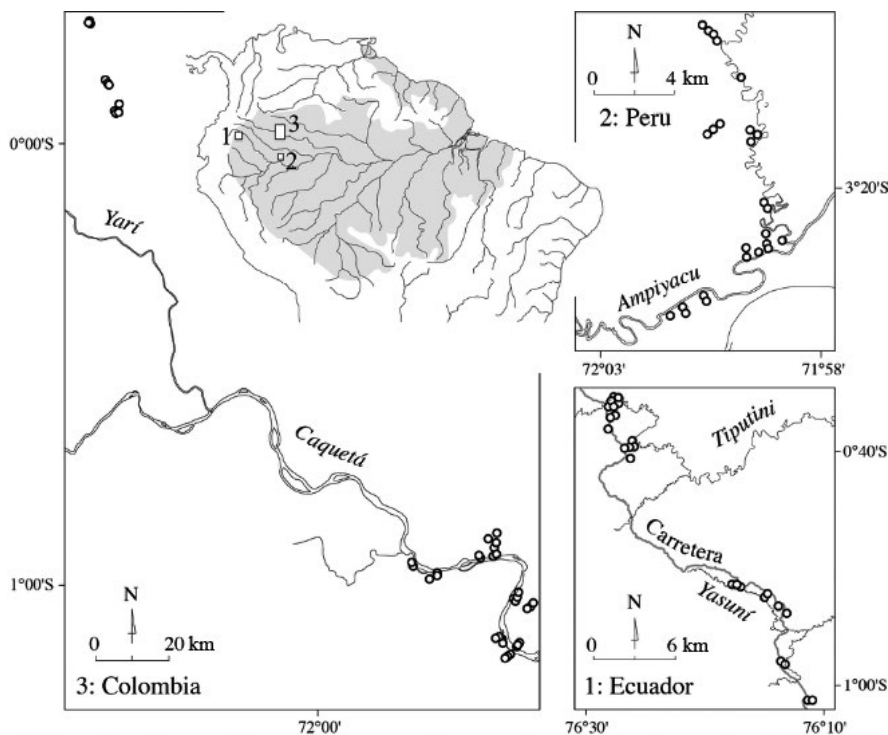


FIGURE 1 Location of the three subregions of NW Amazonia recognized in this study. The rectangles denote the area where the plots were established

2.2 | Vegetation sampling and identification of botanical vouchers

A total of 85 0.1-ha plots were established: 35 in Metá-Chiribiquete (Duque, 2004; Duque et al., 2001) and 25 in both Yasuní (Romero-Saltos et al., 2001) and Ampiyacu (Grandez et al., 2001; Figure 1). Plots were rectangular (20 × 50 m) and delimited by compass, tape and stakes from a random starting point respect to topographic conditions (i.e. elevation and slope), with the restriction that the long side of the plot was parallel to the contour line. The plots were located in areas with relatively homogeneous soils and physiognomically uniform forest stands. In each plot, all shrubs, treelets and trees with DBH ≥ 2.5 cm were numbered and measured with tape. Plots were located in forest that lacked signs of human intervention, except in some swamp plots in the floodplain of the Ampiyacu River in Peru, where few palms had been cut recently to harvest fruits from *Mauritia flexuosa* L.f. Plots were established at a minimum between-plot distance of 500 m and were mapped with GPS.

In each plot, at least one botanical collection of each morpho-species was collected. The nomenclature of families and genera followed Angiosperm Phylogeny Group version 4 (Chase et al., 2016). Within families or groups of closely allied families, specimens that could not be identified to species because of lack of sufficient diagnostic characteristics were treated as morpho-species on the basis of simultaneous morphological comparisons with all other specimens in herbarium. Hereafter, we will mostly refer as to species for both morpho-species and species. Botanical identification took place at the herbaria COAH, QCA, QCNE, AMAZ, US MO, NY and AAU. Vouchers of around 90% of the species and morpho-species described by each independent group were pooled together and compared in MO and AAU between 2000 and 2002.

2.3 | Habitat type definition

Floodplain forests were those located in areas flooded by river water in times of high river water levels. Because river water levels vary in a 'seasonal' way (depending on local and regional rainfall), these forests can be seen as seasonally flooded forests. If not flooded by river water, soils in floodplain forests were well drained. Swamp forests are forests on soils that were permanently inundated due to poor drainage. These swamp forests could be located in or outside areas subjected to flooding by river water. Terra firme forests occurred in areas not affected by flooding by river water, where soil drainage conditions were good (see Lips & Duivenvoorden, 2001 for additional details).

2.4 | Soil characterization

In the centre of each plot, using a soil auger, a soil sample was taken at a depth of 65–75 cm. For analyses, soil samples were dried at temperatures below 40°C, crumbled and passed through a 2-mm sieve. Total contents of Ca, Mg, K, Na and P were determined by means

of atomic emission spectrometry of a subsample of 100–200 mg from the sieved fraction, previously digested in a solution of 48% HF and 2M H₂SO₄ (following Lim & Jackson, 1983). Total content of C and N was determined for the sieved fraction using a Carlo Erba 1106 elemental analyser. Soil analyses were done at the soil laboratory of the Institute for Biodiversity and Ecosystem Dynamics of the Universiteit van Amsterdam (for more details, see Lips & Duivenvoorden, 2001).

2.5 | Species pool randomization and hypotheses testing

We used three different species pool, each one associated with one of the main hypotheses stated above, as follows: (a) To address the first hypothesis (*H1*; Dexter et al., 2017), which assumes that historical dispersal overrides geographical barriers (e.g. big rivers) at the entire NW Amazon scale, we applied a standardization procedure based on a null model that randomized the species composition of the entire dataset (85 0.1-ha plots). Hereafter, we will refer to this procedure as the *Z1* species pool randomization. To draw a null distribution based on 999 replicates, we used an algorithm that retains the species richness within each plot and the relative frequency of species occurrences, and randomize species identity for each community (Kembel et al., 2010). The standardization of the metrics employed to assess phylogenetic structure and turnover (see below) was obtained by subtracting the mean of the null model from the observed value, divided by the standard deviation (Webb, 2000). (b) To address the second hypothesis associated to the effect of geographical barriers as a cause of dispersal limitation (*H2*; Terborgh & Andresen, 1998), we randomized the species presence–absence across all plots of each subregion (i.e. countries) maintaining species richness and frequency in each plot, applying the same standardization procedure described above. In this way, the habitat effect within each subregion was ruled out in the null communities. Hereafter, we will call this procedure the *Z2* species pool randomization model. (c) To address the third hypothesis associated to the effect of habitat filtering (*H3*; Duque et al., 2002; Phillips et al., 2003; Tuomisto et al., 2003), we randomized the species presence–absence among plots located in one and the same habitat type (terra firme, floodplains and swamps) across all three subregions, applying the same standardization procedure described above. Hence, in this null model, the effect of spatial distance between subregions was ruled out within the habitat types. Hereafter, it will be called the *Z3* species pool randomization.

2.6 | Growth form and life stage development

To assess the effect of plant size, which is associated with growth form (shrub or tree) and the stage of development (juvenile or adult), on determining changes in the magnitude of the responses to either environmental or spatial factors, we divided the dataset in four categories

according to a size cut-off threshold, as follows: (a) all individuals: includes all trees (juvenile and adults; DBH \geq 2.5 cm) and shrubs in each plot. Shrub species were classified based on the BIEN database (Engemann et al., 2016). (b) Only trees (excluding shrubs). (c) Adult trees (DBH \geq 10.0 cm). (d) Juvenile trees (DBH < 10.0 cm). Although only shrubs were also separated as an independent category, the high abundance of zeros and presence of unique species in many plots impeded the capacity to a comprehensive analysis of this growth form.

2.7 | Local phylogenetic structure of communities

Using all species and morpho-species (hereafter species) that could be assigned to at least family taxonomically, we obtained a phylogenetic tree for our entire dataset based on the *Phylomatic* repository using the R20120803 backbone phylogenetic tree (Webb & Donoghue, 2005). We calculated the net relatedness index (NRI) and the nearest taxon index (NTI) to analyse the local phylogenetic community structure (Webb, 2000; Webb et al., 2002). The NRI is a standardized average mean phylogenetic distance between all pairs of coexisting species in a site. The NTI is a normalized measure of the average phylogenetic distance between each species and its mean nearest taxon distance. NTI tends to quantify the degree of clustering among terminal taxa, whereas NRI signals clustering at deeper levels in the phylogeny.

We further standardized the NTI and NRI values of each plot by subtracting the mean value of the null communities from the observed plot value and dividing the resulting difference by the standard deviation of the plot values drawn from the null model, following each one of the three species pool definitions (Z1, Z2 and Z3). The standardized values were then multiplied by -1 so that negative values indicated phylogenetic over-dispersion (i.e. more distantly related species than expected under the null model), and positive values phylogenetic clustering (i.e. more closely related species than expected under the null model; see Methods in the Supporting Information). These indexes were calculated using the *PICANTE* package (Kembel et al., 2010) in R.

2.8 | Phylogenetic similarity among communities

We calculated the phylogenetic similarity using the PhyloSorensen index (hereafter PhyloSor). This index estimates the length of the branches on the phylogenetic tree of shared lineages between two samples relative to the sum of the lengths of lineages not shared between the samples (Bryant et al., 2008; see Methods in the Supporting Information). We standardized the phylogenetic similarity according to each one of the species pool definitions (Z1, Z2 and Z3). Positive values of the standardized effect sizes of phylogenetic similarity represent greater divergence than expected by chance, whereas negative values represent greater similarity than expected by chance. The PhyloSor index was calculated for all possible pairs of plots using the *PHYLOMEASURES* package (Tsirogiannis & Sandel, 2015) in R.

2.9 | Environmental and spatial explanatory variables of phylogenetic turnover

To characterize environmental variation, we applied soil cation contents and a binary anoxia factor. The latter factor was built up by an amalgamation of the flooding and swamp effect (anoxia level 1) and a terra firme effect (anoxia level 0). Flooding and swamp effects are considered as an environmental constraint for plant establishment due to the anoxia it creates mainly for the root component of trees. In addition, we used principal component analysis (PCA; Legendre & Legendre, 2012) to reduce soil variation on the seven continuous variables measured in soil samples (C, N, P, Ca, Mg, K and Na). These variables were scaled (i.e. mean equal to zero and variance to one) previous to the PCA because their units have different magnitudes. The two main principal components that explain most of the total variance were used as explanatory variables. PCA allowed interpreting soil variation in terms of a gradient of change across the whole region. This analysis was made using *STATS* package in R (R Core Team, 2018).

The spatial variation was assessed by principal coordinates of a neighbour matrices analysis (PCNM; Legendre & Legendre, 2012). PCNM analysis was run using a threshold value or truncated Euclidean distance among the geographical coordinates of the plots, which returns an independent set of orthogonal axes that represent the spatial configuration of plots relative to themselves. As recommended, we only selected PCNM axes with positive eigenvalues that represent spatial associations among plots. The PCNM was run using the default option of the *pcnm* function in the *VEGAN* package (Oksanen et al., 2019) in R. In the case of irregular sample designs, the PCNM represent a series of irregular wavelengths. The magnitude of the wavelengths is associated with the grain-size or spatial scale at which the hypothetical or surrogate processes, such as geographical barriers or dispersal, acts. We then used a forward selection procedure to select the PCNM axes that were significantly associated with phylogenetic turnover. The selected PCNM axes, employed as surrogate of spatially structured processes at different scales, were PCNM1, PCNM2, PCNM3, PCNM4 and PCNM5 (Figure S1). Large-scale processes, such as historical dispersal or geographical barriers, can be associated to the first two PCNM axes. On contrary, the effect of dispersal limitation tends to be better described by intermediate to small wavelengths, such as PCNM 3, 4 and 5.

2.10 | Environmental and spatial determinants of phylogenetic similarity

We used a non-metric multidimensional scaling (NMDS) ordination procedure on the observed and standardized effect sizes of phylogenetic similarity to visualize differences among habitat types and subregions. To assess environmental and spatial effects on phylogenetic similarity, we used a distance-based redundancy analysis (dbRDA; Legendre & Legendre, 2012) to partition the

amount of variation of phylogenetic similarity explained by each set of explanatory variables. The dbRDA is a method to carry out constrained ordinations using non-Euclidean distance measures. In the dbRDA, the standardized PhyloSor matrix was internally transformed to principal coordinates, which were then used in a redundancy analysis (RDA). Prior to the analysis, the standardized PhyloSor values were converted to positive distances by scaling them between 0 and 1. Then, we ran dbRDA with only the spatial variables and applied a forward selection procedure to identify significant PCNM axis. The same procedure was applied for the soil PCA axes and anoxia. Finally, we ran a dbRDA including significant variables from both spatial and environmental variables, and we carried out a variation partitioning to evaluate the relative importance of each set of explanatory factors (Legendre & Legendre, 2012). For all models, we reported our results in terms of the adjusted R^2 values. The analyses were run using the *VEGAN* package (Oksanen et al., 2019) in R.

3 | RESULTS

3.1 | Structural patterns

The 30,150 individuals used in the analyses belonged to 2,266 morpho-species (1,859 fully identified), 592 genera and 136 families. In total, 29,376 individuals were classified as trees (2,127 morphospecies) and 774 were shrubs (139 morphospecies). Plot species richness averaged 106 ± 46 (1 SD) and average stem density was 333 ± 145 individuals per plot (Table S1).

The proportion of significant NRI and NTI values relative to the null expectation varied among habitat types and subregions (Figure 2). NRI was not significantly different from the null expectations for the entire region, subregion or habitat type ($NRI_{Z1} = 0.35 \pm 0.86$; $NRI_{Z2} = -0.19 \pm 0.91$; $NRI_{Z3} = -0.27 \pm 0.88$). In contrast, around 40% of the NTI values were significantly clustered at each scale ($NTI_{Z1} = 1.36 \pm 0.81$; $NTI_{Z2} = 1.01 \pm 0.91$; $NTI_{Z3} = 1.07 \pm 0.90$). NRI and

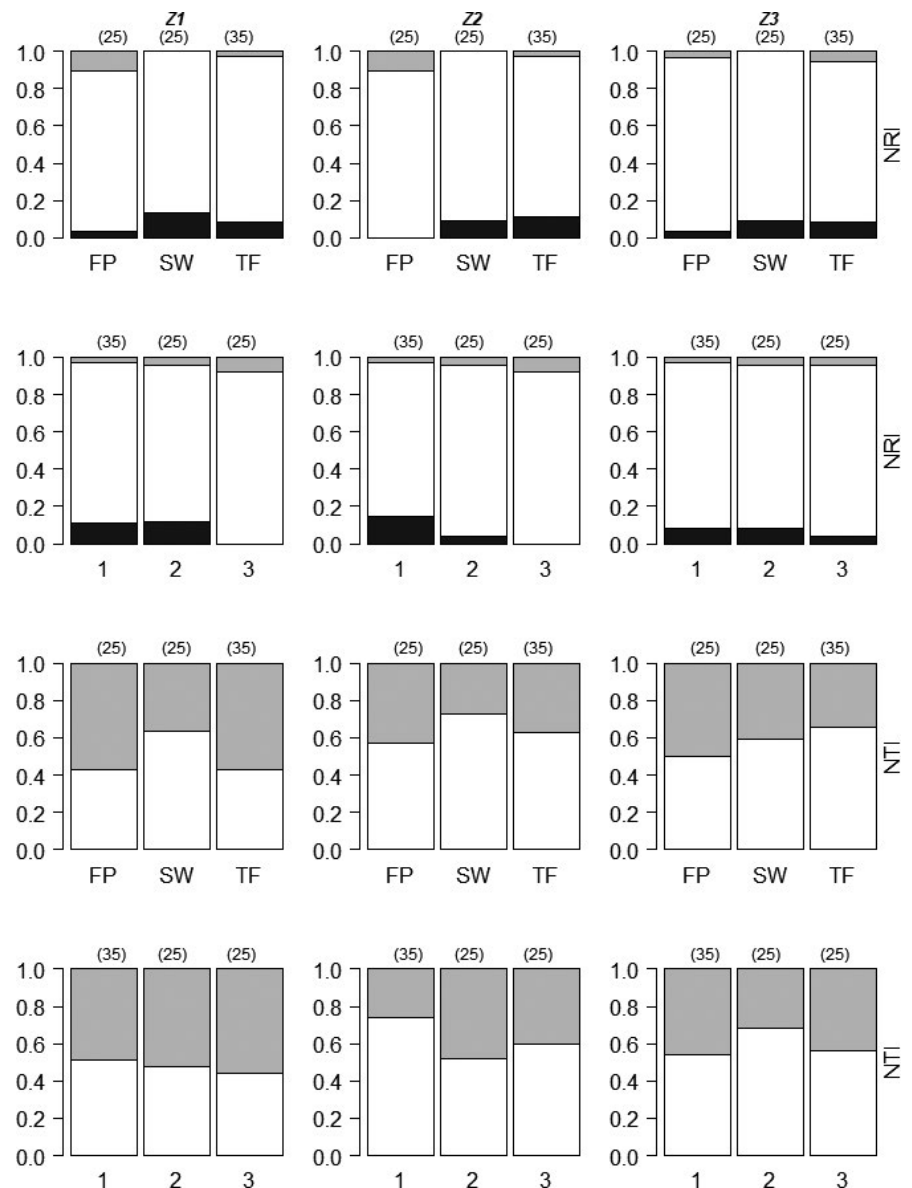


FIGURE 2 Proportion of plots that showed significant clustering (underdispersion) or evenness (overdispersion) in NRI and NTI values considering all individuals ($DBH \geq 2.5$ cm) under the three species pool randomization models (Z1 = All data; Z2 = Restricted by subregion (effect of habitat type removed within subregion); Z3 = Restricted by habitat type (effect of subregion removed within habitat type). Light grey represents the proportion of plots significantly clustered. Dark grey bar represents the proportion of plots with a significant evenness pattern. White bars represent the plots with either NRI or NTI values that were not significantly different from random. FP = Flood plain; SW = Swamp; TF = Terra Firme; Metá-Chiribiquete = 1; Yasuní = 2; Ampiyacu = 3

NTI patterns were not significantly different across life stage of development (Figure 2; Figures S2 and S3).

3.2 | Pattern and drivers of phylogenetic turnover

The first PCA axis of the soil variables explained 42% and was positively correlated to total bases (Ca, Mg, K and Na). The second PCA axis explained 31% and was negatively correlated to C, N and P concentrations (Table S2). PCNM1 was highly correlated with longitude ($r = 0.98$, $p < 0.001$). PCNM2 and PCNM3 were correlated to latitude ($r = 0.80$, $p < 0.001$; $r = -0.47$, $p < 0.001$, respectively), while the others two PCNM axes represented smaller scales of spatial variability.

The scores of the first two NMDS axes (calculated on the basis of the PhyloSor index for all individuals using each of the three species pool definitions [Z1, Z2 and Z3; Figure 3; Figures S4 and S5]) were highly correlated (Figure S6), suggesting that the principal patterns of phylogenetic similarity were independent from the species pool sizes. The mean standardized effect size of phylogenetic similarity was negative for all randomization procedures ($\text{PhyloSor}_{Z1} = -0.24 \pm 1.24$; $\text{PhyloSor}_{Z2} = -1.40 \pm 3.13$; $\text{PhyloSor}_{Z3} = -1.42 \pm 3.17$). The PhyloSor_{Z1} mean was distinctly higher than PhyloSor_{Z2} and PhyloSor_{Z3} ($F = 284.9$,

$p < 0.001$; Figure S7). Overall, the PhyloSor_{Z1} means were lower in absolute values (closer to zero), which indicate a lower phylogenetic similarity between the plots if tested against null model Z1 than that compared to the other two null models (Z2 and Z3). In other words, using the whole of NW Amazonia as a reference (Z1) tends to drive the phylogenetic composition of plots to being random samples of the meta-community.

Under the Z1 species pool definition, both anoxia and large-scale spatial processes (captured by PCNM1 and PCNM2) explained most of the overall variation of the standardized phylogenetic similarity for the four developmental stage categories. Under the Z2 and Z3 species pool definition, however, environmental factors, such as anoxia and PCA1 soils, became more important than spatially structured processes as drivers of the changes in the standardized phylogenetic similarity (Table 1). The total explained variation was always higher under the Z1 species pool definition, and lower for adult trees ($\text{DBH} \geq 10$ cm) independent of the species pool definition applied. When we analysed juvenile and adult trees, under the Z2 and Z3 species pool definition, the spatially structured processes were negligible in the former but more important in the later. Furthermore, the inclusion of shrubs as an independent category of juvenile trees had a negligible effect in the RDA analysis (Table 1).

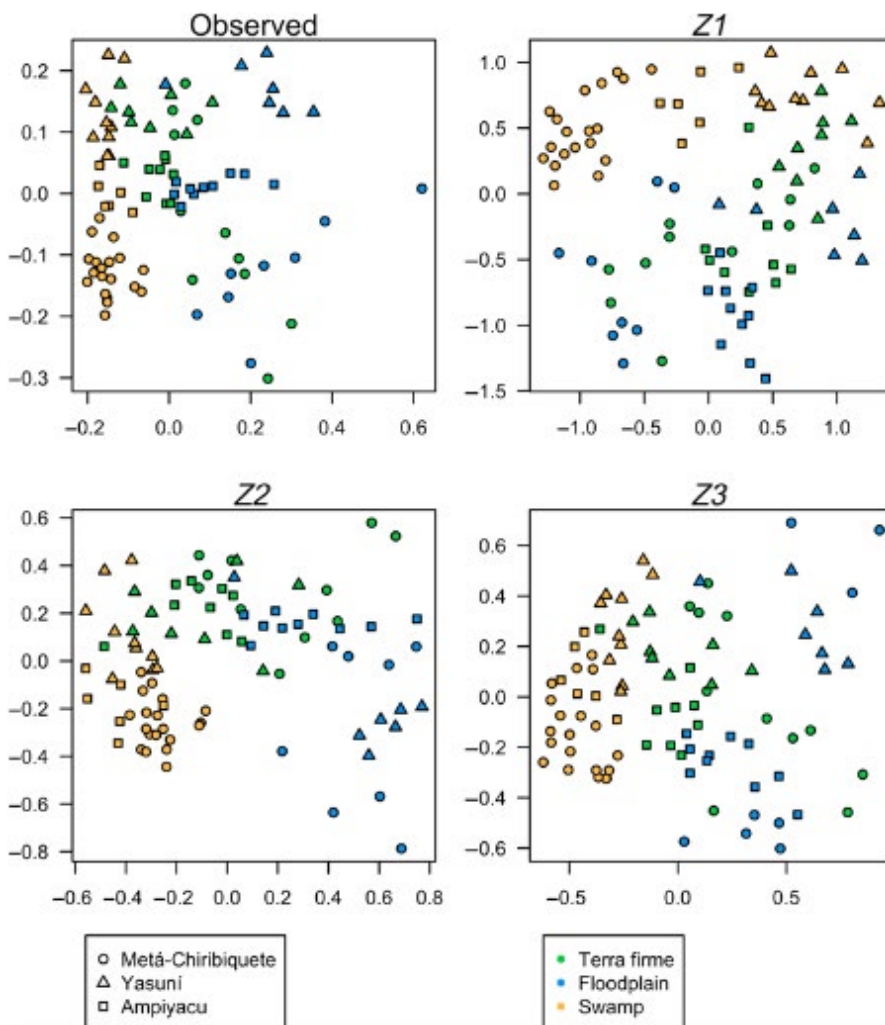


FIGURE 3 Non-metric multidimensional scaling ordination analysis of phylogenetic similarity tree communities including all individuals under different scenarios of species pools used in this study. Z1 = All data; Z2 = Restricted by subregion; Z3 = Restricted by habitat type. Symbols denoted subregions: circle = Metá-Chiribiquete; triangle = Yasuní; square = Ampiyacu. Colours denoted habitat types: Flood plains: orange; Swamp: blue; Terra Firme: green

TABLE 1 Variation partitioning based on distance-based redundancy analysis (dbRDA) applied to the PhyloSor metric and their standardized values by the three species pool randomizations (Z1 = all data; Z2 = restricted by subregion; Z3 = restricted by habitat type) and four community definitions (all individuals of trees and shrubs, only trees, adult trees and juvenile trees). In the left panel, we have the overall percentages of phylogenetic β -diversity explained by each set of variables associated to either the environmental or the spatial hypothesis. Env = pure environment; Spa = pure spatial; Over = spatially structured environmental variation. In the right panel, we have the percentage of phylogenetic β -diversity explained by each one of the explanatory variables selected by the forward selection procedure. Anoxia: Flooding regimen. PCA1 and PCA2: axis derived from the Principal Component Analysis applied to soil variables. PCNM1, PCNM2, PCNM3, PCNM4 and PCNM5 are the spatial variables selected from the principal coordinates on neighbour matrices analysis

Community	Null model	Env	Over	Spa	Total	Anoxia	PCA1	PCA2	PCNM1	PCNM2	PCNM3	PCNM4	PCNM5
Trees & shrubs	Z1	22.51	6.18	27.74	56.43	21.49	2.84	–	16.69	6.89	3.69	3.41	1.43
	Z2	38.08	2.55	5.28	45.92	29.59	5.55	2.09	1.79	2.37	–	2.76	1.77
	Z3	36.33	2.40	5.77	44.46	25.83	5.43	1.79	4.08	2.70	1.26	3.67	1.65
Only trees	Z1	23.58	6.44	28.61	58.64	23.05	3.11	–	17.50	7.31	4.06	3.62	0.00
	Z2	38.80	2.58	5.34	46.73	30.22	5.47	1.95	2.07	2.45	–	2.76	1.81
	Z3	36.64	2.31	5.69	44.66	26.07	4.74	1.55	3.76	2.42	1.25	3.31	1.56
Large trees (>10 cm DBH)	Z1	24.12	5.85	22.44	52.31	24.14	2.02	–	15.61	5.09	2.98	2.47	–
	Z2	30.62	1.62	1.23	33.47	25.98	2.96	1.69	1.33	–	–	1.51	–
	Z3	33.96	2.37	–1.39	34.95	25.11	3.02	1.56	1.94	1.13	–	2.19	–
Small trees (<10 cm DBH)	Z1	22.72	6.08	27.77	56.57	21.46	2.91	–	15.43	7.22	4.29	3.51	1.74
	Z2	31.49	2.47	10.84	44.82	28.18	2.03	–	7.08	5.60	–	2.81	2.12
	Z3	31.63	1.90	10.51	44.06	25.30	–	–	6.71	4.41	–	3.76	1.79

4 | DISCUSSION

4.1 | Patterns of local phylogenetic structure in NW Amazonia

Our findings identify an important pattern of scale dependency in the local phylogenetic structure in the tree communities of NW Amazonia. We found striking differences in the patterns obtained from NRI and NTI, which measures deep and tip phylogenetic levels, respectively. Since NRI emphasize patterns at deep levels of the phylogeny, the random NRI patterns we observed at the plot scale indicate high lability in ancestral traits in the NW Amazon region across habitat types. Therefore, at least at the deepest part of the phylogeny, we found support to our first hypothesis (*H1*), that is, that local samples represent random draws from the regional phylogeny (Dexter et al., 2017). Contrary to NRI, NTI results showed an important proportion (3%–41%) of plots were phylogenetically clustered at both the subregion and habitat type level. At both of these smaller spatial scales, the number of plots with a clustered phylogenetic tip-level pattern increased along with the size of the species pool (Figure 2). In other words, when we applied the Z1 randomization procedure, the removal of the sampling effect from the whole phylogeny at the scale of the entire NW Amazonia increased the capability to detect closely related species coexisting in a particular site. Thus, the NTI clustering trend suggests more recent events, such as the relatively recent change in the channel location of big and medium size rivers (Ruokolainen et al., 2019), have acted as effective geographical barriers and constrained plant dispersal. These findings also suggest that small peripheral populations isolated by distance could act as an important source of speciation (Hubbell, 2001; Rosindell et al., 2010). Taken together, our results indicate that at local scales, particular lineages are overrepresented in term of species and individuals, probably as a result of selective pressures or competitive dominance. However, across habitats and at larger spatial scales, this pattern dissolves as other lineages with origin in different habitat types (e.g. terra firme) are also represented (Cárdenas et al., 2017; Fine & Baraloto, 2016).

4.2 | Phylogenetic similarity across NW Amazonia

The phylogenetic similarity of tree communities in NW Amazonia was primarily accounted for by anoxia and large-scale spatially structured processes, respectively. The separation of the individuals inhabiting the forest understory in different growth forms, such as juvenile trees and shrubs, did not substantially changed the relative importance of either environmental or spatial factors as drivers of the phylogenetic similarity pattern of tree communities (Table 1). However, both the spatial scale (randomization method applied) and the stage of development of plant communities led the substantial differences in the extent to which either environment or dispersal shaped the phylogenetic assembly of tree lineages. Our results are similar to other studies

that assessed the effect of habitat heterogeneity and spatial distance on the phylogenetic structure of Amazon tree communities (Fine & Kembel, 2011). However, to our knowledge, this is the first study that evaluates the effect of the stage of development on the phylogenetic structure of Amazon tree communities.

At the spatial scale of the entire NW Amazonia (Z1), the importance of anoxia and large-scale spatially processes were almost the same, which rejects our expectations (*H2*) of an overwhelming influence of dispersal rather than environmental constraints on determining the phylogenetic similarity of tree lineages (sensu Terborgh & Andresen, 1998). These findings contradict the idea of Amazonian floodplains as an forest type that is easy to invade by lineages from adjacent habitat types (Cárdenas et al., 2017; Pitman et al., 2014; Terborgh & Andresen, 1998). The need of species to establish and survive in conditions of severe soil anoxia may have triggered the development of particular traits, such as a thick cuticle and thick outer epidermal walls to avoid fast rot when submerged (Parolin et al., 2004). However, in NW Amazonia, the highly dynamic geological history has promoted historical and continuous river readjustments and formation of terrestrial mosaics (Hoorn et al., 2010) that seemed to have been overcome by some lineages but not for others, explaining the paired relative importance of both anoxia and historical dispersal at a regional scale.

The reduction of the species pool size (Z2 and Z3 species pool definitions) drove the relative importance of spatial processes to almost negligible values and pointed to anoxia as the overriding factor structuring the phylogenetic similarity patterns of tree communities at both the country and habitat type level (Table 1). These findings support our third hypothesis (*H3*), which suggest the effect of environmental filtering as the overriding mechanism that structures Amazon tree communities, but only when the overall size of the regional species pool is reduced (e.g. intermediate scales; Duque et al., 2002; Phillips et al., 2003). Although more subtly, soil fertility also increased in relative importance in shaping phylogenetic similarity among communities when the species pool size was reduced (Table 1). Therefore, at more local and intermediate (i.e. sub-region) scales, soil conditions also played a small but significant role on differentiating tree lineage assembly across NW Amazon (Phillips et al., 2003).

Under the Z2 and Z3 species pool definition, the inclusion of small trees (i.e. shrubs and juveniles) had a significant effect on determining the relative important of spatial processes on shaping the phylogenetic similarity of either adult or small trees. However, contrary to our expectations, environmental variation had a stronger effect on phylogenetic differentiation on adult than small trees. Although under the Z2 and Z3 species pool definition the total amount of explained variation of adult trees decreased, the proportional importance of the spatial variables became almost negligible (Table 1). Therefore, environmental filtering, primarily due to the limited tolerance to flooding in the earlier developmental stages of tree species and the local adaptation to soil conditions, played a key role on shaping the phylogenetic assembly of adult trees across NW Amazonia. When small trees were

included (under Z2 and Z3), the relative importance of the spatial variables almost four-folded that of adult trees (Table 1). This finding suggests that dispersal limitation of small trees, probably many small-statured lineages (e.g. Rubiaceae), is also driving community assembly at local to intermediate scales (Dexter & Chave, 2016). Then, comparisons of lineages of different plant size can inform about the effect of dispersal on community assembly and diversification of Amazon tree lineages (Dexter & Chave, 2016).

Our results also highlight that phylogenetic differentiation within habitat types is significantly affected by variation in soil fertility throughout NW Amazonia (Tuomisto et al., 2003). For example, the within habitat type average of key elements for species distributions, such as P (Condit et al., 2013), was almost as high as that observed between habitat types within the same subregion. In the case of P in particular, the concentration of this element in Peruvian terra firme forests (11.32 ± 10.3 ppm) was twofold higher than that in the same habitat type in Colombia (5.2 ± 1.5 ppm). A similar pattern was found for C, N and other key soil elements (see Table S1). Such a high heterogeneity in soil cation concentrations support a need of including soils fertility as an explanatory variable in the models that aim to explain an understand the evolutionary patterns of tree species in Amazon forests. Therefore, we call for caution for assuming homogeneous features in soil properties within a similar habitat type at large geographical scales (Cárdenas et al., 2017; Fine & Kembel, 2011). Likewise, understanding the trade-off between soils fertility and biotic interactions at finer spatial scales should help to unravel the mechanisms that structure the evolutionary history and distribution of tree lineages in tropical forests (Baldeck et al., 2016).

In conclusion, the extent to which either environmental or spatial features shapes the local phylogenetic structure and phylogenetic similarity of tree communities in Amazon forests is scale dependent. Overall, the relative importance of environmental factors increases with both decreases in spatial scale and the size of the species pool. We emphasize on the need of additional studies that focus on the trade-off between biotic interactions and soil fertility at finer spatial scales than those employed here. In the face of global environmental changes, understanding how evolutionary history can shape the phylogenetic structure and turnover of Amazonian plant communities will identify opportunities to preserve this highly diverse but threatened ecosystem.

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AUTHORS' CONTRIBUTIONS

S.G.-C., Á.D. and J.F.D. conceived the idea and designed the methodology; Á.D., J.F.D., H.B., J.C., C.G., M.J.M., M.S., H.R.-S. and R.V. collected the data; S.G.-C. analysed the data; Á.D., S.G.-C. and J.F.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.8w9ghx3k9> (González-Caro et al., 2020)

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REFERENCES

- Aldana, A. M., Carlucci, M. B., Fine, P. V. A., & Stevenson, P. R. (2016). Environmental filtering of eudicot lineages underlies phylogenetic clustering in tropical South American flooded forests. *Oecologia*, 183(2), 327–335. <https://doi.org/10.1007/s00442-016-3734-y>
- Baldeck, C. A., Kembel, S. W., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Madawala, S., Gunatilleke, N., Gunatilleke, S., Bunyavejchewin, S., Kiratiprayoon, S., Yaacob, A., Supardi, M. N. N., Valencia, R., Navarrete, H., Davies, S. J., Chuyong, G. B., Kenfack, D., Thomas, D. W., & Dalling, J. W. (2016). Phylogenetic turnover along local environmental gradients in tropical forest communities. *Oecologia*, 182(2), 547–557. <https://doi.org/10.1007/s00442-016-3686-2>
- Bryant, J. A., Lamanna, C., Morlon, H., Kerkhoff, A. J., Enquist, B. J., & Green, J. L. (2008). Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 105(Suppl), 11505–11511. <https://doi.org/10.1073/pnas.0801920105>
- Cárdenas, D., González-Caro, S., Duivenvoorden, J., Feeley, K., & Duque, Á. (2017). Asymmetrical niche determinism across geological units shapes phylogenetic tree communities in the Colombian Amazonia. *Perspectives in Plant Ecology, Evolution and Systematics*, 28(June), 1–9. <https://doi.org/10.1016/j.ppees.2017.06.001>
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7), 693–715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>
- Chase, M. W., Christenhusz, M. J. M., Fay, M. F., Byng, J. W., Judd, W. S., Soltis, D. E., Mabberley, D. J., Sennikov, A. N., & Soltis, P. S., & Stevens, P. F. (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181(1), 1–20.
- Comita, L. S., Condit, R., & Hubbell, S. P. (2007). Developmental changes in habitat associations of tropical trees. *Journal of Ecology*, 95(3), 482–492.
- Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, 110(13), 5064–5068. <https://doi.org/10.1073/pnas.1218042110>
- Dexter, K., & Chave, J. (2016). Evolutionary patterns of range size, abundance and species richness in Amazonian angiosperm trees. *PeerJ*, 4, e2402. <https://doi.org/10.7717/peerj.2402>
- Dexter, K. G., Lavin, M., Torke, B. M., Twyford, A. D., Kursar, T. A., Coley, P. D., Drake, C., Hollands, R., & Pennington, R. T. (2017). Dispersal assembly of rain forest tree communities across the Amazon basin.

- Proceedings of the National Academy of Sciences of the United States of America*, 114(10), 2645–2650. <https://doi.org/10.1073/pnas.1613655114>
- Duivenvoorden, J. F. (1995). Tree species composition and rain forest-environment relationships in the middle Caquetá area, Colombia, NW Amazonia. *Vegetatio*, 120(2), 91–113.
- Duque, A. J. (2004). *Plant diversity scaled by growth forms along spatial and environmental gradients: A study in the rain forests of NW Amazonia* (PhD dissertation). University of Amsterdam.
- Duque, A., Muller-Landau, H. C., Valencia, R., Cardenas, D., Davies, S., de Oliveira, A., Pérez, Á. J., Romero-Saltos, H., & Vicentini, A. (2017). Insights into regional patterns of Amazonian forest structure, diversity, and dominance from three large terra-firme forest dynamics plots. *Biodiversity and Conservation*, 26(3), 669–686. <https://doi.org/10.1007/s10531-016-1265-9>
- Duque, A., Sánchez, M., Cavelier, J., & Duivenvoorden, J. F. (2002). Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology*, 18(04), 499–525. <https://doi.org/10.1017/S0266467402002341>
- Duque, A., Sánchez, M., Cavelier, J., Duivenvoorden, J. F., Miraña, P., Miraña, J., & Matapí, A. (2001). Relación bosque-ambiente en el Medio Caquetá, Amazonia colombiana. In J. F. Duivenvoorden, H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto, & R. Valencia (Eds.), *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental* (pp. 99–129). IBED, Universiteit van Amsterdam.
- Engemann, K., Sandel, B., Boyle, B., Enquist, B. J., Jørgensen, P. M., Kattge, J., McGill, B. J., Morueta-Holme, N., Peet, R. K., Spencer, N. J., Violle, C., Wiser, S. K., & Svenning, J.-C. (2016). A plant growth form dataset for the New World. *Ecology*, 97(11), 3243. <https://doi.org/10.1002/ecy.1569>
- Fine, P. V. A., & Baraloto, C. (2016). Habitat endemism in white-sand forests: Insights into the mechanisms of lineage diversification and community assembly of the neotropical flora. *Biotropica*, 48(1), 24–33. <https://doi.org/10.1111/btp.12301>
- Fine, P. V. A., & Kembel, S. W. (2011). Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. *Ecography*, 34(4), 552–565. <https://doi.org/10.1111/j.1600-0587.2010.06548.x>
- Fine, P. V. A., Zapata, F., & Daly, D. C. (2014). Investigating processes of neotropical rain forest tree diversification by examining the evolution and historical biogeography of the proteiae (Burseraeae). *Evolution*, 68(7), 1988–2004. <https://doi.org/10.1111/evo.12414>
- Fortunel, C., Paine, C. E. T., Fine, P. V. A., Mesones, I., Goret, J.-Y., Burban, B., Cazal, J., & Baraloto, C. (2016). There's no place like home: Seedling mortality contributes to the habitat specialisation of tree species across Amazonia. *Ecology Letters*, 19(10), 1256–1266. <https://doi.org/10.1111/ele.12661>
- González-Caro, S., Duivenvoorden, J. F., Balslev, H., Cavelier, J., Grández, C., Macía, M. J., Romero-Saltos, H., Sánchez, M., Valencia, R., & Duque, Á. (2020). Data from: Scale-dependent drivers of the phylogenetic structure and similarity of tree communities in northwestern Amazonia. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.8w9ghx3k9>
- Grandez, C., García, A., Duque, A., & Duivenvoorden, J. F. (2001). La composición florística de los bosques en las cuencas de los ríos Ampiyacu y Yaguasyacu (Amazonia peruana). In J. F. Duivenvoorden, H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto, & R. Valencia (Eds.), *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental* (pp. 163–176). IBED, Universiteit van Amsterdam.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 25(15), 1965–1978.
- Honorio Coronado, E. N., Dexter, K. G., Pennington, R. T., Chave, J., Lewis, S. L., Alexiades, M. N., Alvarez, E., Alves de Oliveira, A., Amaral, I. L., Araujo-Murakami, A., Arets, E. J. M. M., Aymard, G. A., Baraloto, C., Bonal, D., Brienen, R., Cerón, C., Cornejo Valverde, F., Di Fiore, A., Farfan-Rios, W., ... Phillips, O. L. (2015). Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions*, 21(11), 1295–1307. <https://doi.org/10.1111/ddi.12357>
- Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer, A., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., & Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science (New York, NY)*, 330(6006), 927–931. <https://doi.org/10.1126/science.1194585>
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography* (Vol. 32). Princeton University Press.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Legendre, P., & Legendre, L. F. J. (2012). *Numerical ecology* (Vol. 24). Elsevier.
- Lim, C. H., & Jackson, M. L. (1983). Dissolution for total elemental analysis. *Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties*, 9, 1–12.
- Lips, J. M., & Duivenvoorden, J. F. (2001). Caracterización ambiental. In J. F. Duivenvoorden, H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto, & R. Valencia (Eds.), *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental* (pp. 19–45). IBED, Universiteit van Amsterdam.
- Macía, M. J. (2011). Spatial distribution and floristic composition of trees and lianas in different forest types of an Amazonian rainforest. *Plant Ecology*, 212(7), 1159–1177. <https://doi.org/10.1007/s11258-011-9895-1>
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., & Legendre, P. (2019). *Vegan: Community ecology package*. R package version 2–5.
- Parolin, P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M. T. F., & Junk, W. J. (2004). Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *The Botanical Review*, 70(3), 357–380. [https://doi.org/10.1663/0006-8101\(2004\)070\[0357:CAFFTA\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2004)070[0357:CAFFTA]2.0.CO;2)
- Phillips, O. L., Vargas, P. N., Monteagudo, A. L., Cruz, A. P., Zans, M.-E., Sánchez, W. G., Yli-Halla, M., & Rose, S. (2003). Habitat association among Amazonian tree species: A landscape-scale approach. *Journal of Ecology*, 91(5), 757–775. <https://doi.org/10.1046/j.1365-2745.2003.00815.x>
- Pitman, N. C. A., Andino, J. E. G., Aulestia, M., Cerón, C. E., Neill, D. A., Palacios, W., Rivas-Torres, G., Silman, M. R., & Terborgh, J. W. (2014). Distribution and abundance of tree species in swamp forests of Amazonian Ecuador. *Ecography*, 37(9), 902–915. <https://doi.org/10.1111/ecog.00774>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7(1), 1–15. <https://doi.org/10.1046/j.1461-0248.2003.00554.x>
- Romero-Saltos, H., Valencia, R., & Macía, M. (2001). Patrones de diversidad, distribución y rareza de plantas leñosas en el Parque Nacional Yasuní y la Reserva Étnica Huaorani, Amazonia ecuatoriana. In J. F. Duivenvoorden, H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto, & R. Valencia (Eds.) *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental* (pp. 131–162). IBED, Universiteit van Amsterdam.
- Rosindell, J., Cornell, S. J., Hubbell, S. P., & Etienne, R. S. (2010). Protracted speciation revitalizes the neutral theory of biodiversity. *Ecology Letters*, 13(6), 716–727. <https://doi.org/10.1111/j.1461-0248.2010.01463.x>

- Ruokolainen, K., Moulatlet, G. M., Zuquim, G., Hoorn, C., & Tuomisto, H. (2019). Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis. *Frontiers of Biogeography*, 11(3), 1–10. <https://doi.org/10.21425/F5FBG45046>
- Stropp, J., Ter Steege, H., & Malhi, Y. (2009). Disentangling regional and local tree diversity in the Amazon. *Ecography*, 32(1), 46–54. <https://doi.org/10.1111/j.1600-0587.2009.05811.x>
- Swenson, N. G., Enquist, B. J., Thompson, J., & Zimmerman, J. K. (2007). The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, 88(7), 1770–1780. <https://doi.org/10.1890/06-1499.1>
- ter Steege, H., Henkel, T. W., Helal, N., Marimon, B. S., Marimon-Junior, B. H., Huth, A., Groeneveld, J., Sabatier, D., Coelho, L. D. S., Filho, D. D. A. L., Salomão, R. P., Amaral, I. L., Matos, F. D. D. A., Castilho, C. V., Phillips, O. L., Guevara, J. E., Carim, M. D. J. V., Cárdenas López, D., Magnusson, W. E., ... Melgaço, K. (2019). Rarity of monodominance in hyperdiverse Amazonian forests. *Scientific Reports*, 9(1), 1–15. <https://doi.org/10.1038/s41598-019-50323-9>
- ter Steege, H., Prado, P. I., Lima, R. A. F. D., Pos, E., de Souza Coelho, L., de Andrade Lima Filho, D., Salomão, R. P., Amaral, I. L., de Almeida Matos, F. D., Castilho, C. V., Phillips, O. L., Guevara, J. E., de Jesus Veiga Carim, M., Cárdenas López, D., Magnusson, W. E., Wittmann, F., Martins, M. P., Sabatier, D., Irume, M. V., ... Pickavance, G. (2020). Biased-corrected richness estimates for the Amazonian tree flora. *Scientific Reports*, 10(1), 1–13. <https://doi.org/10.1038/s41598-020-66686-3>
- Terborgh, J., & Andresen, E. (1998). The composition of Amazonian forests: Patterns at local and regional scales. *Journal of Tropical Ecology*, 14(05), 645–664. <https://doi.org/10.1017/S0266467498000455>
- Tsirogianis, C., & Sandel, B. (2015). PhyloMeasures: A package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography*, 39(7), 709–714.
- Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299(5604), 241–244.
- Webb, C. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, 156(2), 145–155. <https://doi.org/10.1086/303378>
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33(1), 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Webb, C. O., & Donoghue, M. J. (2005). Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes*, 5(1), 181–183. <https://doi.org/10.1111/j.1471-8286.2004.00829.x>

SUPPORTING INFORMATION

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