



Universidad Autónoma  
de Madrid

**Biblos-e Archivo**  
Repositorio Institucional UAM

Repositorio Institucional de la Universidad Autónoma de Madrid  
<https://repositorio.uam.es>

Esta es la **versión de autor** del artículo publicado en:  
This is an **author produced version** of a paper published in:

Journal of Ecology 109.2 (2020): 888-899

DOI: <https://doi.org/10.1111/1365-2745.13514>

**Copyright:** © 2020 Wiley

El acceso a la versión del editor puede requerir la suscripción del recurso  
Access to the published version may require subscription

1 Title: Scale-dependent drivers of the phylogenetic structure and similarity of tree communities in  
2 northwestern Amazonia

3  
4 González-Caro. S.<sup>1</sup>, Duivenvoorden. J.F.<sup>2</sup>, Balslev, H.<sup>3</sup>, Cavelier. J.<sup>4</sup>, Grández. C.<sup>5</sup>, Macía. M.J.<sup>6,7</sup>,  
5 Romero-Saltos. H.<sup>8</sup>, Sánchez. M.<sup>1</sup>, Valencia. R.<sup>9</sup> and Duque. Á<sup>1\*</sup>.

6  
7  
8 <sup>1</sup>Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Medellín, Colombia;

9 <sup>2</sup>Institute for Biodiversity and Ecosystem Dynamics (IBED), Universiteit van Amsterdam,  
10 Amsterdam, The Netherlands;

11 <sup>3</sup>Aarhus University – Bioscience, Aarhus, Denmark;

12 <sup>4</sup>Global Environmental Facility (GEF), Washington, DC, USA;

13 <sup>5</sup>Universidad de la Amazonía Peruana, Iquitos, Perú;

14 <sup>6</sup>Departamento de Biología, Área de Botánica, Universidad Autónoma de Madrid,  
15 Madrid, Spain;

16 <sup>7</sup>Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad  
17 Autónoma de Madrid, Madrid, Spain;

18 <sup>8</sup>Escuela de Ciencias Biológicas e Ingeniería, Universidad Yachay Tech, Urcuquí, Ecuador;

19 <sup>9</sup>Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador

20  
21  
22 \* Corresponding author: Álvaro Duque; Departamento de Ciencias Forestales, Universidad  
23 Nacional de Colombia Sede Medellín. Carrera 65 No. 59A-110. Medellín, Colombia.

24 [ajduque@unal.edu.co](mailto:ajduque@unal.edu.co)/[ajduque09@gmail.com.co](mailto:ajduque09@gmail.com.co)

Abstract (350 words)

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 ( $\text{DBH} \geq 2.5 \text{ cm}$ ) 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.

Key words

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

## Introduction

The Amazon basin, which roughly harbors 15.000 tree species across ~6 million-km<sup>2</sup> (ter Steege et al., 2013), represents the largest and most diverse reserve of forests on earth. In Amazon forests, the complexity of tree communities emerges as the interplay of evolutionary and ecological processes that operate at different spatial scales (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Ricklefs, 2004). Overall, the interaction between evolutionary processes, such as speciation and extinction (Ricklefs, 2004), and ecological processes, such as habitat specialization and dispersal (Stropp et al., 2009), largely shapes both the phylogenetic structure and the distribution of tree communities across the region (Cavender-Bares et al., 2009; Fine & Kembel, 2011). For example, a dominant phylogenetic pattern of closely related species in a geographic region could be due to an extensive local in situ speciation followed by a subsequent limited dispersal. A pattern of co-occurring lineages geographically restricted would result in a phylogenetic differentiation or clustering (Fine, Zapata, & Daly, 2014). In contrast, if the distribution of lineages is strongly influenced by historical processes of dispersal, a homogeneous phylogenetic structure of tree communities would be expected. Under that scenario, the phylogenetic diversity of any internal region (or sub region) within the Amazon basin would be a random draw of the phylogenetic composition of the species pool of the entire region (Dexter et al., 2017).

In northwestern (NW) Amazon, where local tree species richness achieves values up to 640 species per hectare (Duque et al., 2017), different mechanisms have been invoked to explain the likely influence of evolutionary processes on determining the pattern of variation and complexity of tree species assemblages. The tendency of lineages to be confined to their ancestral niche, a pattern known as niche conservatism (Wiens & Graham, 2005), has been claimed to play an important role in differentiating tree phylogenetic communities restricted to white-sand formations from those occurring on either Tertiary or Quaternary deposits (Cárdenas, González-Caro, Duivenvoorden, Feeley, & Duque, 2017; Fine & Kembel, 2011; Honorio Coronado et al., 2015; Guevara et al., 2016). Thus, limited niche evolution in Guiana-shield formations may promote *in situ* radiations and a higher trend for lineages to remain in their original areas (Fortunel et al., 2016). In general, though, information on the phylogenetic structure of forests in NW Amazonian environments is scanty, some studies proposed NW Amazonian floodplains as phylogenetically specialized habitats that differentiate tree communities at intermediate spatial scales (Aldana,

Carlucci, Fine, & Stevenson, 2016). Others, however, described NW Amazonian floodplains as easy to be invaded by lineages that come from adjacent habitats with contrasting environmental features (Cárdenas et al., 2017; Pitman et al., 2014; Terborgh & Andresen, 1998). 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. Regarding the largest and most diverse terra firme forests on sedimentary Tertiary plains, the lack of stressful conditions along with the long time available for colonization and invasion might have induced high levels of evolutionary lability (Fortunel et al., 2016). Thus, forests on Tertiary sedimentary plains in NW Amazonia might be expected to show a high phylogenetic evenness and a low phylogenetic turnover ( $\beta$ -diversity) at both intermediate and large spatial scales. Combining information how abiotic factors characterize contrasting environments with the evolutionary history of the plant communities occurring there will help to identify the underlying mechanisms driving species assembly in Amazon forests (Fortunel et al., 2016; Terborgh & Andresen. 1998).

Virtually all phylogenetic patterns currently known from NW Amazonian forests are based on information from large canopy trees (diameter at breast height -DBH-  $\geq 10$  cm) (e.g. Cárdenas et al., 2017; Fine & Kembel, 2011; Honorio Coronado et al., 2015). The use of large canopy trees may overestimate the importance of dispersal (Dexter & Chave, 2016) but underestimate effects of habitat specialization regarding shrubs or small trees found in the forest understory ( Duque, Sánchez, Cavelier, & Duivenvoorden, 2002; Fortunel et al., 2016; Zhu, Comita, Hubbell, & Ma, 2015). Habitat specialization has primarily been associated with the nested variation of landscape units, geomorphology and soil types, and has shown to play a key role on determining the taxonomic composition of tree communities in Amazon forests (Baldeck et al., 2016; Duivenvoorden, 1995; Duque et al., 2002). Therefore, assessing the influence of environmental variation on shaping phylogenetic structure and phylogenetic  $\beta$ -diversity of tree and shrub communities at large and intermediate spatial scales (Swenson, Enquist, Thompson, & Zimmerman. 2007) will shed new insights on the extent to which the evolutionary history drives the origin and maintenance of the high diversity of Amazon forests.

In this study, using a set of 90 0.1-ha plots (DBH  $\geq 2.5$  cm) spread out across the main landscape units (terra firme, white sands floodplains, and swamps) in three subregions of NW Amazonia

(located in Colombia, Ecuador, and Peru; Fig. 1), we aim to assess the extent to which dispersal, flooding, and soil variation determine the phylogenetic structure of tree and shrub communities at intermediate and large (regional) scales. The main hypotheses evaluated are: i) at a large spatial scale, such as the whole of NW Amazonia, regional historical dispersal drives the phylogenetic assembly of tree communities (*sensu* Dexter et al., 2017). Under this assumption, we predict local phylogenetic communities to be a random draw of the regional species pool and a high phylogenetic similarity of communities occurring in different subregions or landscape units. Hence, we would not expect any phylogenetic pattern associated with either subregion or landscape. ii) Dispersal capability drives the phylogenetic structure increasing the geographic structure of Amazon tree lineages within subregions. Under the Terborgh and Andresen (1998) hypothesis, we assume that, independently of the habitat features (flooded or unflooded, but also regarding soils or landscape units), forest communities that are located more close to each other show an increased phylogenetic similarity. In our design, this would imply that two communities located in contrasting landscape units would be more similar in their phylogenetic composition than two communities located in one and the same landscape unit but in different subregions (Cárdenas et al., 2017; Terborgh & Andresen, 1998). iii) Abiotic environmental heterogeneity shapes the phylogenetic structure across NW Amazonian forests (Duque et al., 2002; Phillips et al., 2003; Tuomisto, Ruokolainen, & Yli-Halla, 2003). Under this scenario, there will be high phylogenetic clustering within habitats and low phylogenetic turnover between subregions. In other words, two communities located in different subregions but in the same landscape unit would be more similar in their phylogenetic composition than two communities located in same subregion but in different landscape units. iv) The inclusion of shrubs and juvenile trees ( $2.5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ), instead of only large trees ( $\text{DBH} \geq 10 \text{ cm}$ ), may increase the relative importance of environmental issues as drivers of both phylogenetic structure and turnover ( Duque, Sánchez, Cavelier, & Duivenvoorden, 2002; Fortunel et al., 2016; Zhu, Comita, Hubbell, & Ma, 2015).

## Materials and Methods

### *Study site*

The study was carried out in three different subregions in NW Amazonia: Metá-Chiribiquete (hereafter Metá), forming part of the middle Caquetá basin in Colombia; Yasuní in Ecuador; and Ampiyacu, which pertains to the Maynas Province in Peruvian Amazonia (Fig. 1). All areas are in

the Humid Tropical Forest life zone (bh-T) according to Holdridge et al. (1971). The average temperature is near 25°C. and annual precipitation varies around 3000 mm. All months show an average precipitation above 100 mm (Lips & Duivenvoorden, 2001).

#### *Vegetation sampling and identification of botanical vouchers*

A total of 90 0.1-ha plots were established: 40 in Metá-Chiribiquete (Duque et al., 2001; Duque, 2004) and 25 in both Yasuní (Romero-Saltos, Valencia, & Macía, 2001) and Ampiyacu (Grández et al., 2001). In order to establish the plots, starting locations and the direction of the tracks along which the forests were entered, were planned on the basis of the interpretation of aerial photographs or satellite images of Landsat TM (Tuomisto & Ruokolainen. 2001). During the walk through the forests, soils and terrain units were rapidly described, and forests were visually examined. In this way, sites with homogeneous soils and physiognomically uniform forest stands were identified. In these stands, rectangular plots (mostly 20 x 50 m) were delimited by compass, tape and stakes, working from a random starting point, with the restriction that the long side of the plot was parallel to the contour line. In each plot, all shrubs and trees with DBH  $\geq$  2.5 cm were numbered and measured with tape. Plots were located without bias with respect to floristic composition or forest structure (including aspects of tree density, thickness and height, and presence of lianas). They were made in forest that lacked signs of human intervention. The only exception to this were 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. Botanical identification took place at the herbaria COAH, QCA, QCNE, AMAZ, USM, MO, NY, and AAU (Holmgren et al., 1990). The nomenclature of families and genera followed Angiosperm Phylogeny Group version 4 (Stevens. 2001). Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics, were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens.

#### *Soil characterization*

In the central part of each plot, a soil augering was done to 120 cm depth. At each augering 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 content of Ca, Mg, K, Na, and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H<sub>2</sub>SO<sub>4</sub> (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of 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.

### *Species pool randomization and hypotheses testing*

We employed three different species pool randomizations, each one associated with one of the main hypotheses stated above, as follows: *i*) To address the first hypothesis, which assumes a high regional influence of historical dispersal (Dexter et al., 2017) at the Amazon scale, we applied a standardization procedure based on a null model that randomized the species composition of the entire dataset (90 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 independent-swap algorithm that retains the species richness within each plot and the relative frequency of species occurrences, but changes species co-occurrences [ref?]. 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). To address the second hypothesis associated to the effect of dispersal (Terborgh and Andersen hypothesis), we randomized the species presence-absence across all plots of each subregion maintaining species richness and frequency in each plot, applying the same standardization procedure described above. In this way the landscape effect within each subregion was ruled out in the null communities. Hereafter we will call this procedure as the Z2 species pool randomization. *iii*) To address the third hypothesis associated to the effect of habitat association (Duivenvoorden, 1995; 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 landscape unit (floodplains, terra firme, swamps, and white sands) 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 landscape units. Hereafter it will be called the Z3



species pool randomization. The use of standardized effect sizes aim to remove sampling effects associated with the size of the species pool (after Kraft et al., 2011).

#### *Phylogenetic structure*

We obtained a phylogenetic tree of the species list of 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 analyze the phylogenetic community structure (Webb, 2000; Webb, Ackerly, McPeck, & Donoghue, 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 Supplementary Information). These indexes were calculated using the package “picante” (Kembel et al., 2010) in R.

#### *Phylogenetic turnover*

We calculated the phylogenetic turnover (phylo  $\beta$ -diversity) 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 Supplementary Information). We standardized the phylo  $\beta$ -diversity according to each one of the species pool definitions (Z1, Z2, Z3). Positive values of the standardized effect sizes of phylo  $\beta$ -diversity represent greater divergence than expected by chance, while negative values represent greater similarity than

expected by chance. The PhyloSor index was calculated for all possible pairs of plots using the “PhyloMeasures” package (Tsirogianis & Sandel, 2015) in R.

#### *Environmental and spatial explanatory variables*

We used soil cation contents and flooding to characterize environmental variation. Flooding was defined as a presence/absence variable (dummy). Overall, swamps and floodplains are flooded (1), while terra firme and white sands do not (0). Flooding is considered as an environmental constraint for plant establishment due to the seasonal anoxia it creates mainly for the root component of shrubs and trees. We used principal component analysis (PCA) to reduce soil variation applying scaled variables (i.e., mean equal to zero and variance to one). The two main principal components that explain most of the total variance were used as explanatory variables. PCA allows interpreting soil variation in terms of a gradient of change across the whole region.

The spatial variation was assessed by principal coordinates of a neighbor matrices analysis (PCNM; Legendre & Legendre, 2012), which in the case of irregular sample designs represent a series of irregular wavelengths. The magnitude of the wavelengths is associated with the grain-size or spatial scale at which the hypothetical contagious processes, such as dispersal, acts. Then, we used a forward selection procedure to select the PCNM axes that were significantly associated with phylogenetic structure and turnover. The significant selected PCNM axes, employed as surrogate of biological spatially structured processes, hereafter used as a proxy of dispersal, were the PCNM1, PCNM2, PCNM3, PCNM4, and PCNM5 (Fig. S1).

#### *Environmental and spatial determinants of phylogenetic structure*

In order to test the effects of spatial and environmental variation on the phylogenetic structure across the plots, we used linear models to explain the variation of both the NRI and NTI (standardized under the three species pool randomizations) by the spatial (the five PCNMs) and environmental variables (the first two soil PCA axes and flooding). Stepwise selection was applied to independently select either the significant spatial or environmental variables.

#### *Environmental and spatial determinants of phylogenetic $\beta$ -diversity*

We used a non-metric multidimensional scaling ordination procedure on the observed and standardized effect sizes of phylo  $\beta$ -diversity to visualize differences among landscape units and subregions. To assess environmental and spatial effects on phylo  $\beta$ -diversity, we used a distance-based redundancy analysis (dbRDA) to partition the amount of variation of phylogenetic turnover 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 that were significant after the forward selection. The same procedure was applied for the soil PCA axes. In case of significance of both spatial and environmental variables, 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.

## Results

The 29,956 individuals used in the analyses belonged to 1726 (morpho) species, 592 genera, and 136 families (Table S1). The five families with the highest number of species were Fabaceae (201 species), Rubiaceae (126), Annonaceae (92), Lauraceae (88), and Melastomataceae (69). 39 families (28.6%) had only one species, and 14 families (10.2%) only two. The genera with the highest number of species were *Inga* (46), *Miconia* (40), *Pouteria* (31), *Protium* (30), and *Licania* (30). The most abundant species were *Oxandra polyantha* (1713 individuals), *Abarema adenophora* (1015), *Digomphia densicoma* (572), *Virola elongata* (357), and *Eschweilera coriacea* (353). We found an average species richness of  $105.8 \pm 46.02$  per each 0.1 ha plot and an average stem density of  $332.8 \pm 144.5$  individuals per plot. The total number of individuals and species richness per plot was not significantly correlated ( $r = 0.08$ ,  $p = 0.44$ ).

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 proportion of significant NRI and NTI values relative to the null expectation varied among landscape units and countries (Fig. 2). NRI was not significantly different from the null expectations for neither region, country or landscape unit ( $\text{NRI}_{Z1} = 0.35 \pm 0.86$ ;  $\text{NRI}_{Z2} = -0.19 \pm 0.91$ ;  $\text{NRI}_{Z3} = -0.27 \pm 0.88$ ). In contrast, NTI tended to be clustered ( $\text{NTI}_{Z1} = 1.36 \pm 0.81$ ;  $\text{NTI}_{Z2} = 1.01 \pm 0.91$ ;  $\text{NTI}_{Z3} = 1.07 \pm 0.90$ ). We found that the standardized NRI and NTI regressed significantly on the PCNM axes, but not on any of two soil PCA axes (Table 1). The standardized NRI obtained by employing the Z2 randomization differed between flooding regimens (Table 1). The analysis with only individuals with  $\text{DBH} \geq 10$  cm did not substantially change from those obtained with individuals of  $\text{DBH} \geq 2.5$  cm (Fig. S2).

The scores of the first two NMDS axes calculated on the basis of the PhyloSor index using each of the three species pool definitions (Z1, Z2, Z3; Fig.S3) were highly correlated (Fig. S4), suggesting that the principal patterns of phylogenetic turnover were independent from the species pool sizes. The mean standardized effect size of phylo  $\beta$ -diversity was negative for all randomization procedures ( $\text{PhyloSor}_{Z1} = -0.29 \pm 1.24$ ;  $\text{PhyloSor}_{Z2} = -1.40 \pm 3.13$ ;  $\text{PhyloSor}_{Z3} = -1.42 \pm 3.17$ ). The  $\text{PhyloSor}_{Z1}$  mean was distinctly higher than the  $\text{PhyloSor}$  means under the other two null models ([outcome test here?]). However, the  $\text{PhyloSor}_{Z1}$  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 reference (Z1), tends to drive the phylogenetic composition of plots to being random samples of the metacommunity.

Overall, local environmental variation in flooding and total bases in soils (PC1) along with the spatial location of the plots (PCNM 1 and PCNM2) explained most of the overall variation of the observed and standardized phylo  $\beta$ -diversity (Table 2). The effect of environmental and spatial variables on determining the phylogenetic compositional similarity increased after removing the sampling effects associated to the size of the regional species pool. These findings remained very similar when we used only trees with  $\text{DBH} \geq 10$  cm or excluded the white sands ( $\text{DBH} \geq 2.5$  cm) from the analyses (Table 3).

## Discussion

In NW Amazonian the phylogenetic patterns of shrub and tree communities observed in small plots related differently to spatial and environmental variables than the phylogenetic turnover rates (phylo  $\beta$ -diversity) between these plots. The standardized net relatedness index (NRI) reflected that the phylogeny of most plots was a random sample of the phylogeny of the entire region. The standardized nearest taxon index (NTI) of the plots was phylogenetically clustered. Both these indexes were primarily associated with spatial factors, and never with soil fertility. In contrast, the phylo  $\beta$ -diversity of shrub and tree communities was mainly associated with flooding and the variability of soil fertility. These results emphasize on the importance of quantifying abiotic factors across contrasting forest types (Fine et al., 2014; Fine, Daly, Villa-Muñoz, Mesones, & Cameron, 2005) as well as assessing the effect of the geographic spatial scale (Cavender-Bares, Keen, & Miles, 2006; Swenson, Enquist, Pither, Thompson, & Zimmerman, 2006; Swenson et al., 2007) to properly elucidate the mechanisms shaping the phylogenetic assembly and turnover of shrub and tree lineages in Amazonian forests.

### *Patterns and drivers of phylogenetic structure within small plots*

Independent of the randomizations applied to standardize the metrics, the NRI values of shrub and tree lineages at the plot level were mostly structured as random samples of the regional phylogeny (Fig. 1). White sand was the only habitat type in which no NRI value was different from random, a pattern already reported at the taxon level in Peru (Fine & Kembel, 2011). Nonetheless, our results contrast with several other studies that found white sand units as a habitat with a dominant trend to be composed by closely related lineages (Cárdenas et al., 2017; Guevara et al., 2016). These contrasting results may have two explanations: 1) in our study, white sands had the lowest sampling size (5 plots) and were sampled only in one of the three subregions (Metá-Chiribiquete), hampering the regional perspective for the whole of NW Amazonia (Guevara et al., 2016). 2) The inclusion of small individuals ( $2.5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ) might have yielded a high portion of transient juvenile individuals of species unable to reproduce and settle in this environment while still accounting for the observed random NRI patterns. However, when we ran the analysis with only individuals with  $\text{DBH} \geq 10 \text{ cm}$ , the observed patterns did not substantially change (Fig. S2; Table 3) from those obtained with individuals of  $\text{DBH} \geq 2.5 \text{ cm}$ . The dominantly random NRI values observed in the floodplain plots also contrast with the patterns of phylogenetic clustering

in flooded forests in the lowlands of northern Colombia (Aldana et al., 2016). In that study the authors associated the tolerance to flooding to the development of specific traits (Aldana et al. 2016). Therefore, the NRI supports shrub and tree communities in NW Amazonia as random samples of the whole pool phylogeny employed, as expected under the historical dispersal hypothesis (Dexter et al., 2017), and suggests that the evolutionary adaptations to flooding might have independently occurred multiple times on different clades along the evolutionary history of plant species.

Contrary to NRI, the NTI showed an important proportion (X% to Y%) of plots that were phylogenetically clustered (Fig. 1). For both landscape unit and country, the amount of plots with a clustered phylogenetic pattern at the tip of the phylogeny, as it is measured by NTI, increased with the size of the species pool. That said, when we applied the Z1 randomization procedure, the removal of the sampling effect from the whole phylogeny increased the capability of detection of closely related species coexisting in a particular site. The only case in which NTI patterns were associated with flooding was when we applied the Z2 randomization procedure, which employs the species pool of each subregion or country. However, spatial variables, although weakly correlated, remain as the only factors that significantly explained the pattern of variation of NTI. Our results shed limited support for dispersal limitation as a major source of phylogenetic clustering, and thus, as a overriding driver of parapatric speciation in NW Amazon forests (Fine & Kembel. 2011).

#### *Phylogenetic turnover between small plots*

The phylo  $\beta$ -diversity of shrubs and tree communities shows flooding as a major source of phylogenetic differentiation in Amazon forests at both regional (NW Amazonia) and subregional scales (country). Soil properties and spatially structured processes played a secondary but still important role as determinants of the phylogenetic turnover as well. These findings contradict the idea of Amazonian floodplains as an evolutionarily system easy to invade by lineages from adjacent habitats or landscape units (Cárdenas et al., 2017; Pitman et al., 2014; Terborgh & Andresen, 1998). In NW Amazonian, the need of species to establish and survive under the floods may have triggered the development of special traits, such as thick cuticle and thick outer epidermis wall to avoid fast rot when submerged (Parolin et al., 2004). However, the relative

importance of flooding increased with the decrease of the geographic area considered, and thus, with the decrease of the size of species pool. For example, the relative importance of flooding under the Z2 randomization method increased to 38.4% compared to 25.9% obtained under the Z1 procedure. This shift in almost 10 points in the relative importance of flooding was mirrored by an increase of spatial influence from 16.9% (Z2) to 24.1% (Z1). Therefore, our study highlights the importance of considering the influence of the geographic spatial scale and the likely negative correlation it has with the relative importance of environmental processes as determinants of the phylogenetic turnover of tree communities in Amazon forests.

The quantification of environmental variables at the plot level is a key issue to detect the influence they have on determining changes in the phylo  $\beta$ -diversity of tree communities in Amazon forests. The assumption of a nested structure of soil fertility in either geological or landscape units could bear the interpretation of the results in a wrong direction. For example, Cardenas et al. (2017) used geology to define the alluvial plains, which could hamper to exactly define forests currently submitted to flooding. In our study, the within landscape unit average of a key element for species distribution, such as P (Condit, Engelbrecht, Pino, Pérez, & Turner, 2013), was almost as high as that observed between landscape units within the same subregion. In the case of P, for instance, the concentration of this element in Peruvian terra firme forests ( $11.32 \pm 10.3$  ppm) two folded that reported in the same landscape unit in Colombia ( $5.2 \pm 1.5$  ppm). A similar pattern was found for C, N, and other key soil elements for plants (see Table S1). Such a high heterogeneity in soil cation concentrations should explain why environmental factors are as important both within countries and within landscapes, and call for caution for assuming homogeneous features in soil properties within a similar landscape unit at large geographical scales (Cárdenas et al., 2017; Fine & Kembel, 2011).

#### *Remarks on the size of DBH cut-off*

To our knowledge, this is the first time that a taxonomically standardized dataset that includes shrubs and small trees along with a standard quantification of soil properties and flooding, is employed to assess the influence of environmental factors on determining the phylo  $\beta$ -diversity of plant communities in NW Amazonia. However, contrary to our expectations, the inclusion of only individuals with  $DBH \geq 10$  cm had an almost negligible effect on the relative reduction of the

amount of variation explained by the variables employed to assess changes in the phylo  $\beta$ -diversity using individuals with  $\text{DBH} \geq 2.5$  cm. Although the net amount of explained variation got reduced, the proportional importance of either environmental or spatial variables remained very similar (Table S3). For example, under the Z1 randomization method, the total amount of variation of the phylogenetic turnover of tree communities explained by the dbRDA change from 56.7% employing all data ( $\text{DBH} \geq 2.5$  cm) to 50.4% employing only large trees ( $\text{DBH} \geq 10$  cm), of which 25.9% and 25.7%, respectively, were explained by the environment (Table 3). Therefore, the expected increase in the relative importance of environmental deterministic factors, such as flooding and soil fertility, on determining phylo  $\beta$ -diversity due to the inclusion of understory species (Duque et al., 2002; Swenson et al., 2007) was not supported by this study.

In NW Amazonia our NRI analysis supports the idea that local communities of shrubs and trees are random samples of the whole phylogeny, as claimed by Dexter et al. (2017). However, the high difference between observed and expected phylo  $\beta$ -diversity and the significant explanation of this deviation by several set of environmental and spatial factors do not support sampling effects (*sensu* Kraft et al., 2011) as the overriding cause of the phylogenetic turnover of tree communities in NW Amazonia. Our results emphasize that even if the local communities can be seen as random samples of the whole metacommunity, the overall distribution of lineages along the NW Amazonia region is not random and rather largely defined by aggregated communities due to environmental changes across regions and landscapes. Likewise, the use of an unpaired sample of white sands plots, which are expected to have a strong influence on driving  $\beta$ -diversity (Cárdenas et al., 2017; Fine et al., 2005), did not influence the claims of this study. The exclusion of the white sands from the analysis of phylogenetic  $\beta$ -diversity did not have a significant effect on the total variation explained by the explanatory factors. As shown in table 3, the observed total explained variation of the phylogenetic  $\beta$ -diversity (41.3%) did hardly change when the white sands were excluded (40.5%). This pattern remained after applying the standardization methods. For instance, for the Z1 randomization method, the overall explained variation changed from 56.7% when white sands were included to 54.2% when they were excluded, which supports the idea that the phylogenetic composition of white sands was built up by lineages spread out across different landscape units.



The historical assembly of Amazon tree communities is imprinted by the homogenizing effect of dispersal along evolutionary history, which results in a well representation of all lineages across the Amazon. However, the outcome of high dispersal would be a high gene flow among populations and therefore low speciation rates. Low speciation rates in Amazon forests appear as a difficult hypothesis to support in the largest and most diverse metacommunity on earth. Our findings propose a significant habitat filtering effect from flooding (e.g. Silva et al. 2019) and soil fertility, and in a lower degree by dispersal limitation, that increases the local phylogenetic clustering and the likelihood of a protracted speciation pattern (i.e. Hubbell. 2001). As shown by NTI, and the phylo  $\beta$ -diversity, habitat specialization, followed at a lower extent by dispersal limitation, should increase local diversity by triggering high speciation rates between contrasting adjacent units (Gentry, 1982).

In conclusion, the extent to which either environmental or spatial features shapes the phylogenetic structure and  $\beta$ -diversity of shrubs and tree communities in Amazon forests is scale dependent. Overall, our findings show that the relative importance of environmental features increase with the decrease of the spatial scale and the size of the species pool. The opposite could be claimed for spatial structured processes, such as dispersal limitation. However, our analysis at the NW Amazon scale shed support for the idea of Amazon forests as a large metacommunity (Dexter et al., 2017) in which historical dispersal has left its phylogenetic imprint on actual communities of shrubs and trees. The claimed effect of flooding suggests that drainage dynamics, which are difficult to reconstruct in the Amazon basin (Silva et al., 2019), have played a critical role separating lineages at the landscape scales. Soils fertility may have determined the isolation of populations that define species adaptation, which might reduce gene flow and increase speciation as well (Fine et al., 2014; Misiewicz & Fine. 2014). Thus, a model of historical isolation of populations reinforced by environmental constrains rather than by long geographic distances may have operated as a frequent driver of diversification in Amazon forests. Improving our understanding on the traits that define contrasting historical dispersal capability among lineages (Dexter & Chave. 2016) as well as the degree and causes of local habitat-specialization of shrubs and tree communities (Phillips et al., 2003; Zuleta et al., 2019) will surely help to identify opportunities to preserve and manage the actual diversity of Amazon forests.

489  
490  
491  
492  
493  
494  
495  
496  
497  
498  
499  
500  
501  
502  
503  
504  
505  
506  
507

Acknowledgements

SGC was supported by the Instituto de Ciencia, Tecnología e Innovación de Colombia - COLCIENCIAS grant (announcement 785). AD was funded by a NWO grant from The Netherlands (Budgetnr 8011) to visit the University of Amsterdam as invited researcher. Fieldwork, lab, and herbarium analyses were supported by the European Committee (ERB IC18 CT960038), WOTRO (WB 85-335), and Fundación Tropenbos Colombia.

Authors' contributions

SGC, AD, and JD conceived the idea and designed the methodology; AD, JD, HB, JC, CG, MM, MS, and RV collected the data; SGC analyzed the data; AD, SGC and JD 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.8w9gh> x3k9 (González-Caro et al., 2020)

508 References

- 509 Aldana. A. M., Carlucci. M. B., Fine. P. V. A., & Stevenson. P. R. (2016). Environmental  
 510 filtering of eudicot lineages underlies phylogenetic clustering in tropical South American  
 511 flooded forests. *Oecologia*. doi: 10.1007/s00442-016-3734-y
- 512 Anderson. M. J., Crist. T. O., Chase. J. M., Vellend. M., Inouye. B. D., Freestone. A. L., ...  
 513 Swenson. N. G. (2011). Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the  
 514 practicing ecologist. *Ecology Letters*. 14(1). 19–28. doi: 10.1111/j.1461-0248.2010.01552.x
- 515 Baker. T. R., Pennington. R. T., Magallon. S., Gloor. E., Laurance. W. F., Alexiades. M., ...  
 516 Phillips. O. L. (2014). Fast demographic traits promote high diversification rates of  
 517 Amazonian trees. *Ecology Letters*. 17(5). doi: 10.1111/ele.12252
- 518 Baldeck. C. A., Tupayachi. R., Sinca. F., Jaramillo. N., & Asner. G. P. (2016). Environmental  
 519 drivers of tree community turnover in western Amazonian forests. *Ecography*. 39(11). doi:  
 520 10.1111/ecog.01575
- 521 Bryant. J. a. Lamanna. C., Morlon. H., Kerkhoff. A. J., Enquist. B. J., & Green. J. L. (2008).  
 522 Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity.  
 523 *Proceedings of the National Academy of Sciences of the United States of America*. 105  
 524 Suppl. 11505–11511. doi: 10.1073/pnas.0801920105
- 525 Cárdenas. D., González-Caro. S., Duivenvoorden. J., Feeley. K., & Duque. Á. (2017).  
 526 Asymmetrical niche determinism across geological units shapes phylogenetic tree  
 527 communities in the Colombian Amazonia. *Perspectives in Plant Ecology. Evolution and*  
 528 *Systematics*. 28(June). 1–9.
- 529 Cavender-Bares. J., Keen. A., & Miles. B. (2006). Phylogenetic structure of Floridian plant  
 530 communities depends on taxonomic and spatial scale. *Ecology*. 87(7 Suppl). S109-22.  
 531 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/16922307>
- 532 Cavender-Bares. J., Kozak. K. H., Fine. P. V. A., & Kembel. S. W. (2009). The merging of  
 533 community ecology and phylogenetic biology. *Ecology Letters*. 12(7). 693–715. doi:  
 534 10.1111/j.1461-0248.2009.01314.x
- 535 Condit. R., Engelbrecht. B. M. J., Pino. D., Pérez. R., & Turner. B. L. (2013). Species  
 536 distributions in response to individual soil nutrients and seasonal drought across a  
 537 community of tropical trees. *Proceedings of the National Academy of Sciences of the United*  
 538 *States of America*. 110(13). 5064–5068. doi: 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. doi: 10.7717/peerj.2402
- Dexter. K. G., Lavin. M., Torke. B. M., Twyford. A. D., Kursar. T. A., Coley. P. D., ... Pennington. R. T. (2017). Dispersal assembly of rain forest tree communities across the Amazon basin. *Proceedings of the National Academy of Sciences*. 114(10). 2645–2650. doi: 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.
- Duivenvoorden. J. F., Balslev. H., Cavelier. J., Grandez. C., Tuomisto. H., & R. Valencia. R. (Eds.) (2001). Evaluación de recursos vegetales no maderables en la Amazonía noroccidental. IBED. Universiteit van Amsterdam.
- Duque. A., Muller-Landau. H. C., Valencia. R., Cardenas. D., Davies. S., de Oliveira. A., ... 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. doi: 10.1007/s10531-016-1265-9
- 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., 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.
- 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: Evaluación de recursos vegetales no maderables en la Amazonía noroccidental (J.F. Duivenvoorden. H. Balslev. J. Cavelier. C. Grandez. H. Tuomisto & R. Valencia. eds.). IBED. Universiteit van Amsterdam. pp. 99–129.
- 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. doi: 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

570       protieae (Burseraceae). *Evolution*. 68(7). 1988–2004. doi: 10.1111/evo.12414  
 571 Fine. P. V. a. Daly. D. C., Villa Muñoz. G., Mesones. I., & Cameron. K. M. (2005). The  
 572       contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in  
 573       the western Amazon. *Evolution; International Journal of Organic Evolution*. 59(7). 1464–  
 574       1478. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/16153032>  
 575 Fortunel. C., Paine. C. E., Fine. P. V. A., Mesones. I., Goret. J.-Y., Burban. B., ... Baraloto. C.  
 576       (2016). There's no place like home: seedling mortality contributes to the habitat  
 577       specialisation of tree species across Amazonia. *Ecology Letters*. 19(10). 1256–1266.  
 578 Gentry. A. H. (1982). *Patterns of neotropical plant species diversity*. Springer.  
 579 Grandez. C., García. A., Duque. A., & Duivenvoorden. J.F. (2001). La composición florística de  
 580       los bosques en las cuencas de los ríos Ampiyacu y Yaguasyacu (Amazonia peruana). In:  
 581       Evaluación de recursos vegetales no maderables en la Amazonía noroccidental (J.F.  
 582       Duivenvoorden. H. Balslev. J. Cavelier. C. Grandez. H. Tuomisto & R. Valencia. eds.).  
 583       IBED. Universiteit van Amsterdam. pp. 163–176.  
 584 Guevara. J. E., Damasco. G., Baraloto. C., Fine. P. V. A., Peñuela. M. C., Castilho. C., ... ter  
 585       Steege. H. (2016). Low Phylogenetic Beta Diversity and Geographic Neo-endemism in  
 586       Amazonian White-sand Forests. *Biotropica*. 48(1). 34–46. doi: 10.1111/btp.12298  
 587 Honorio Coronado. E. N., Dexter. K. G., Pennington. R. T., Chave. J., Lewis. S. L., Alexiades.  
 588       M. N., ... Phillips. O. L. (2015). Phylogenetic diversity of Amazonian tree communities.  
 589       *Diversity and Distributions*. 21(11). 1295–1307. doi: 10.1111/ddi.12357  
 590 Hoorn. C., Wesselingh. F. P., ter Steege. H., Bermudez. M. a. Mora. a. Sevink. J., ... Antonelli.  
 591       a. (2010). Amazonia through time: Andean uplift. climate change. landscape evolution. and  
 592       biodiversity. *Science (New York. N.Y.)*. 330(6006). 927–931. doi: 10.1126/science.1194585  
 593 Hubbell. S. P. (2001). *The unified neutral theory of biodiversity and biogeography* (Vol. 32).  
 594       Princeton University Press.  
 595 Kembel. S. W., Cowan. P. D., Helmus. M. R., Cornwell. W. K., Morlon. H., Ackerly. D. D., ...  
 596       Webb. C. O. (2010). Picante: R tools for integrating phylogenies and ecology.  
 597       *Bioinformatics*. 26. 1463–1464.  
 598 Kraft. N. J. B., Comita. L. S., Chase. J. M., Sanders. N. J., Swenson. N. G., Crist. T. O., ...  
 599       Myers. J. A. (2011). Disentangling the drivers of  $\beta$  diversity along latitudinal and  
 600       elevational gradients. *Science*. 333(6050). 1755–1758. doi: 10.1126/science.1208584

- Legendre. P., & Legendre. L. F. J. (2012). *Numerical ecology* (Vol. 24). Elsevier.
- Lips. J. M., & Duivenvoorden. J. F. (2001). Caracterización ambiental. In: Evaluación de recursos vegetales no maderables en la Amazonía noroccidental (J.F. Duivenvoorden. H. Balslev. J. Cavelier. C. Grandez. H. Tuomisto & R. Valencia. eds.). IBED. Universiteit van Amsterdam. pp. 19–45.
- Misiewicz. T. M., & Fine. P. V. A. (2014). Evidence for ecological divergence across a mosaic of soil types in an Amazonian tropical tree: *Protium subseratum* (Burseraceae). *Molecular Ecology*. 23(10). 2543–2558. doi: 10.1111/mec.12746
- Parolin. P. de. De Simone. O., Haase. K., Waldhoff. D., Rottenberger. S., Kuhn. U., ... others. (2004). Central Amazonian floodplain forests: tree adaptations in a pulsing system. *The Botanical Review*. 70(3). 357–380.
- Phillips. O. L., Núñez Vargas. P., Monteagudo. A. L., Cruz. A. P., Zans. M. E. C., Sánchez. W. G., ... Rose. S. (2003). Habitat association among Amazonian tree species: A landscape-scale approach. *Journal of Ecology*. 91(5). 757–775. doi: 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., ... Terborgh. J. W. (2014). Distribution and abundance of tree species in swamp forests of Amazonian Ecuador. *Ecography*. 37(9). 902–915. doi: 10.1111/ecog.00774
- Ricklefs. R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*. 7(1). 1–15. doi: 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. Amazonía ecuatoriana. In: Evaluación de recursos vegetales no maderables en la Amazonía noroccidental (J.F. Duivenvoorden. H. Balslev. J. Cavelier. C. Grandez. H. Tuomisto & R. Valencia. eds.). IBED. Universiteit van Amsterdam. pp. 131–162.
- Silva. S M; Peterson. A T ; Carneiro. L ; Burlamaqui. T C ; Ribas. C ; Sousa-Neves. T ; Miranda. L S ; Fernandes. A M ; Dhorta. F M ; Araujo-Silva. L E ; Batista. R ; Bandeira. C H ; Dantas. S M ; Ferreira. M ; Martins. D M ; Oliveira. J ; Rocha. T ; Sard. A. (2019). A dynamic continental moisture gradient drove Amazonian bird diversification. *Science Advances*.
- Stropp. J., Ter Steege. H., & Malhi. Y. (2009). Disentangling regional and local tree diversity in

the Amazon. *Ecography*. 32(1). 46–54. doi: 10.1111/j.1600-0587.2009.05811.x

Swenson. N. G., Enquist. B. J., Pither. J., Thompson. J., & Zimmerman. J. K. (2006). The problem and promise of scale dependency in community phylogenetics. *Ecology*. 87(10). 2418–2424. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/17089650>

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. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/17645023>

ter Steege. H., Pitman. N. C. a. Sabatier. D., Baraloto. C., Salomão. R. P., Guevara. J. E., ... Silman. M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science (New York. N.Y.)*. 342(6156). 1243092. doi: 10.1126/science.1243092

Terborgh. J., & Andresen. E. (1998). The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology*. 14(05). 645–664.

Tsirogiannis. C., & Sandel. B. (2015). PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography*.

Tuomisto. H., & Ruokolainen. K. (2001). Variación de los bosques naturales en las áreas piloto en lo largo de transectos y en imágenes de satélite. In: Evaluación de recursos vegetales no maderables en la Amazonía noroccidental (J.F. Duivenvoorden. H. Balslev. J. Cavelier. C. Grandez. H. Tuomisto & R. Valencia. eds.). IBED. Universiteit van Amsterdam. pp. 63–96.

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. doi: 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. doi: 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. doi: 10.1111/j.1471-8286.2004.00829.x

Wiens. J. J., & Graham. C. H. (2005). Niche conservatism: Integrating Evolution. Ecology. and Conservation Biology. *Annual Review of Ecology. Evolution. and Systematics*. 36(1). 519–539. doi: 10.1146/annurev.ecolsys.36.102803.095431

Williams-linera. G., Lodge. D. J., Guevara. R., Ruiz-sanchez. E., Oaxaca. U., Biology. M., &

Herbaria. J. (2016). *Phylogenetic diversity of macromycetes and woody plants along an elevational gradient in Eastern Mexico*. 0(0). 1–9.

Zhu. Y., Comita. L. S., Hubbell. S. P., & Ma. K. (2015). Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *Journal of Ecology*. 103(4). doi: 10.1111/1365-2745.12414



Table 1. Results of linear regression analyses of the standardized NRI and NTI retaining significant variables after forward selection. The full models included the first two axes of the soil PCA, the PCNM axes derived from the geographic coordinates, and flooding regime. Z1 = All data; Z2 = Restricted by subregion (effect of landscape unit removed within subregion); Z3 = Restricted by landscape unit (effect of subregion removed within landscape units). F = F-statistic of the each model and its p = p-value. R<sup>2</sup>: Total Explained variance of each model. Only the significant independent variables that remained after forward selection are listed.

Index	F	P	R <sup>2</sup>	Variable	Coefficient	SE	t	p
NRI Z1	2.712	0.005	0.156	(Intercept)	-0.35	0.08	-4.26	0.00
				PCNM4	2.26	0.79	2.88	0.00
NRI Z2	3.015	0.002	0.179	(Intercept)	0.14	0.16	0.87	0.39
				PCNM2	1.97	0.84	2.35	0.02
				PCNM4	1.79	0.87	2.06	0.04
				Flooding	-0.59	0.22	-2.74	0.01
NRI Z3	1.289	0.246	0.066	(Intercept)	-0.28	0.09	-3.12	0.00
				PCNM4	2.15	0.85	2.54	0.01
NTI Z1	1.794	0.069	0.142	(Intercept)	1.36	0.17	7.79	0.00
				PCNM3	2.09	0.87	2.40	0.02
NTI Z2	1.822	0.064	0.134	(Intercept)	1.03	0.18	5.80	0.00
				PCNM3	2.75	0.89	3.10	0.00
				PCNM4	2.10	0.91	2.30	0.02
NTI Z3	1.392	0.193	0.083	(Intercept)	1.07	0.09	11.74	0.00
				PCNM1	2.57	0.86	2.97	0.00

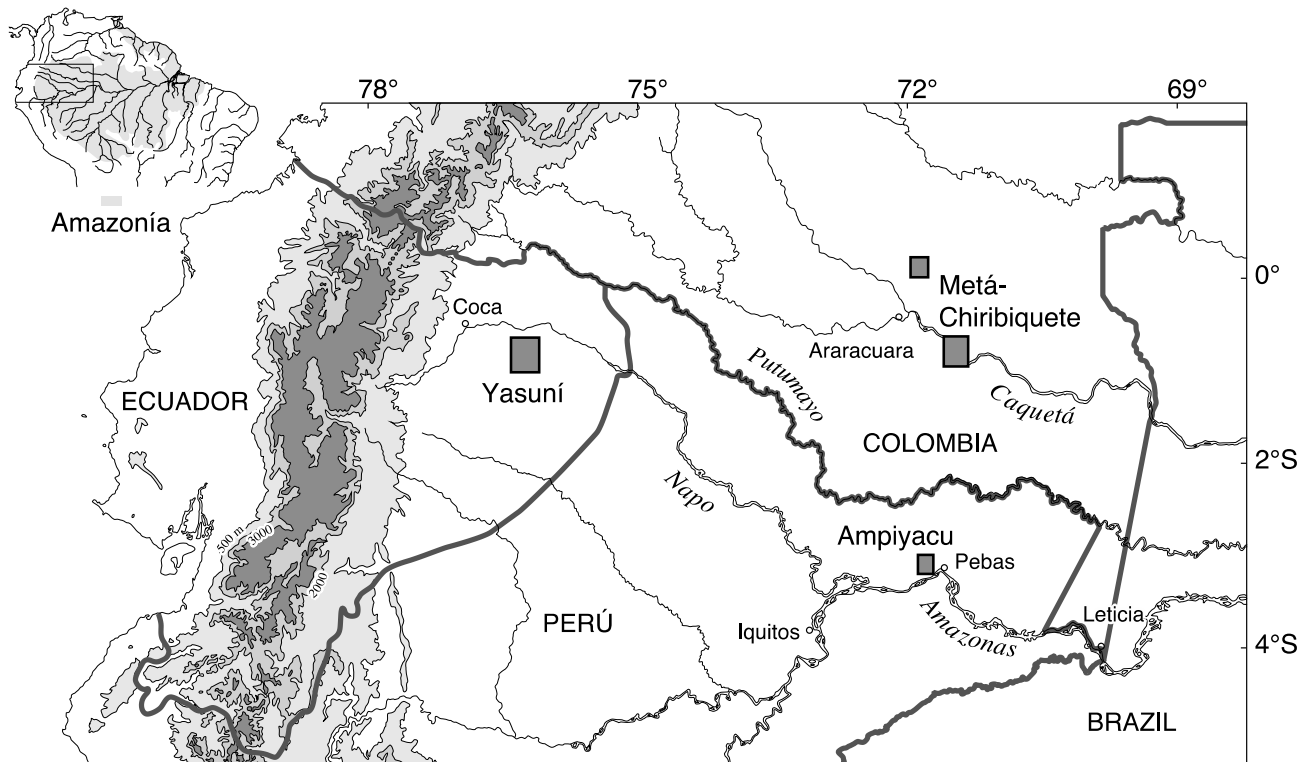
Table 2. Variation partitioning based on distance-based redundancy analysis (dbRDA) applied to the PhyloSor metric and their standardized values by the three species pool randomizations (Z1 = all data; Z2 = restricted by subregion 2; Z3 = restricted by landscape unit). In the upper panel we have the overall percentages of phylogenetic  $\beta$ -diversity explained by each set of variables associated to either the environmental or the spatial hypothesis. Env = pure environment; Space = pure spatial; Overlap = spatially structured environmental variation. In the lower panel we have the percentage of phylogenetic  $\beta$ -diversity explained by each one of the explanatory variables selected by the forward selection procedure. Flooding: Flooding regimen. PCA1 and PCA2: axis derived from the Principal Component Aanalysis applied to soil variables. PCNM1. PCNM2. PCNM3. PCNM4 and PCNM5 are the spatial variables selected from the principal coordinates on neighbor matrices analysis.

PhyloSor				
	Observed	Z1	Z2	Z3
Env	23.10	25.90	38.40	30.50
Space	15.10	24.10	16.90	19.30
Overlap	3.10	6.70	2.90	3.30
Total	41.30	56.70	58.20	53.10
Flooding	18.06	19.68	28.64	24.26
PCA1	5.68	10.10	7.45	6.75
PCA2	3.65	3.07	6.73	5.38
PCNM1	6.29	11.86	9.27	7.48
PCNM2	4.36	6.59	4.45	5.11
PCNM3	1.22	2.28	0.07	1.46
PCNM4	2.03	3.07	1.55	2.64
PCNM5	--	0.04	0.04	--

Table 3. Comparison of the dbRDA results employing the three different null models to estimate phylogenetic  $\beta$ -diversity on different datasets. All data: shrubs and trees sampled in our plots (DBH  $\geq$  2.5 cm; presented in Table 2). Only trees: trees with  $\geq$  DBH 10 cm. Excluding WS: removing White Sand plots to assess their influence in the reported effect of soil fertility.

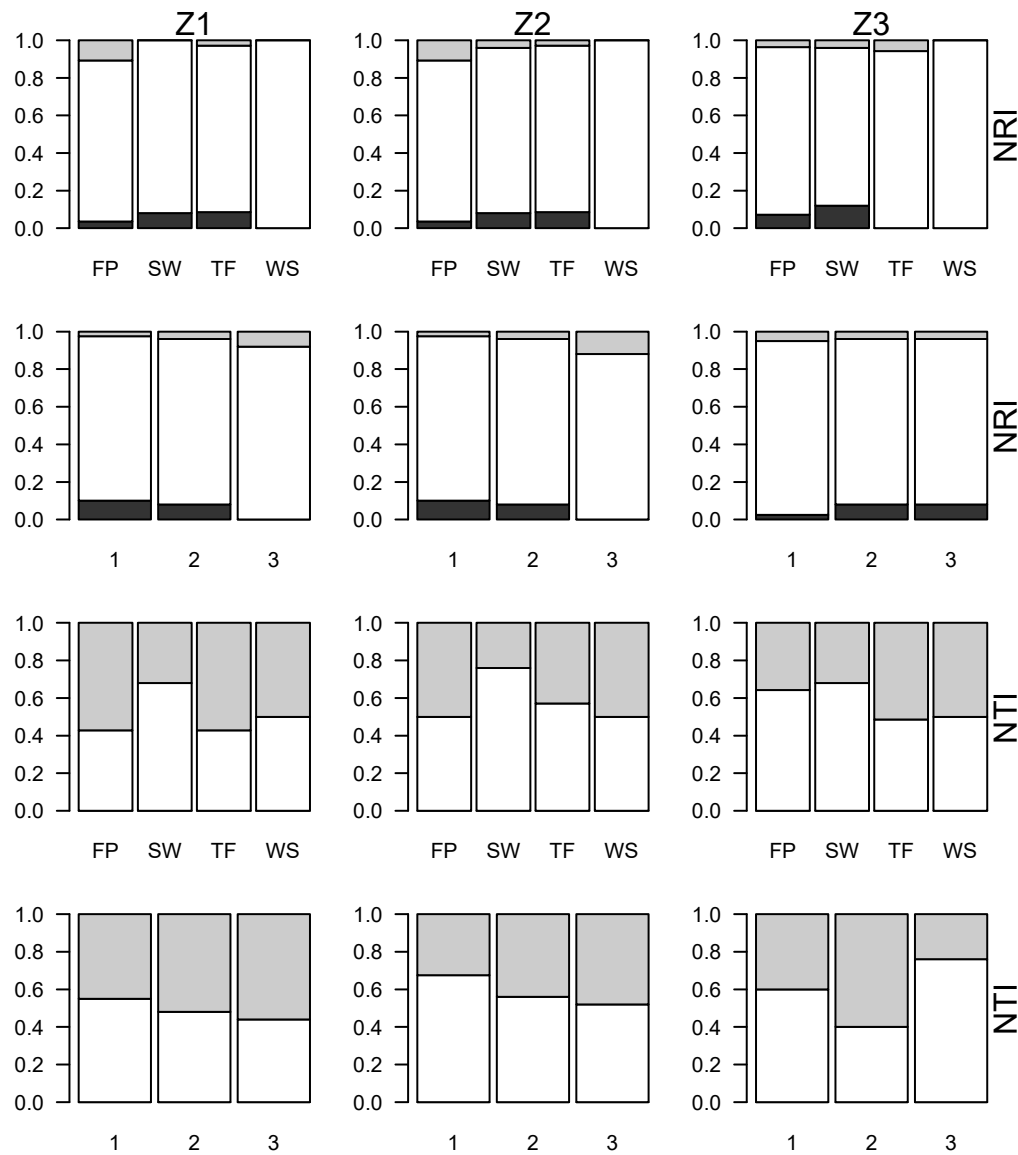
		Observed	Z1	Z2	Z3
Only trees	Total	34.44	50.42	45.37	45.29
	Env	20.04	25.72	30.47	27.27
	Space	11.42	18.82	11.67	15.24
	Overlap	2.98	5.88	3.23	2.78
Excluding WS	Total	41.00	54.00	56.00	51.00
	Env	21.00	20.00	36.00	29.00
	Space	15.00	19.00	18.00	20.00
	Overlap	5.00	4.00	2.00	2.00

702 Figure 1. Location of the three subregions of NW Amazonia recognized in this study. The  
 703 rectangles denote the area where the plots had been established.



704

705 Figure 2. Proportion of plots that showed significant clustering (underdispersion) or evenness  
 706 (overdispersion) in NRI and NTI values under the three species pool randomization models (Z1  
 707 = All data; Z2 = Restricted by subregion (effect of landscape unit removed within subregion); Z3  
 708 = Restricted by landscape unit (effect of subregion removed within landscape unit)). Light gray  
 709 represents the proportion of plots significantly clustered. Dark gray bar represents the proportion  
 710 of plots with a significant evenness pattern. White bars represent the plots with either NRI or  
 711 NTI values that were not significantly different from random. FP = Flood plain. SW = Swamp.  
 712 TF = Terra Firme. WS = White Sand. Metá-Chiribiquete = 1. Yasuní = 2. Ampiyacu = 3.



Supplementary Information

The scale-dependent nature of drivers of the phylogenetic structure and turnover of tree communities in Northwestern Amazonia

González-Caro. S.<sup>1</sup>, Duivenvoorden. J.F.<sup>2</sup>, Balslev, H. <sup>4</sup>, Cavelier. J. <sup>5</sup>, Grández. C. <sup>5</sup>, Macía. M.J.<sup>6</sup>, Romero-Saltos. H. <sup>7</sup>, Sánchez. M. <sup>1</sup>, Valencia. R. <sup>7</sup> and Duque. Á<sup>1\*</sup>.

Table S1. Summary of the plot inventory and soil data for subregion and landscape included in this study. FP: Flood Plain. SW: Swamp. TF: Terra Firme. WS: White Sand. Plots: Number of plots. Stems: Total number of Stems. S: Total Number of Species. G: Total Number of genera. F: Total number of families; Ind: Mean individual density per plot. SR: Mean species richness. Ca: Calcium. Mg: Magnesium. K: Potassium. Na: Sodium. P: Phosphorus. C: Carbon. N: Nitrogen. C:N: Ratio between Carbon and Nitrogen. Standard deviation in parenthesis. Lower case denoted significant differences among landscape units within each country. Upper case denoted significant differences among subregions.

	Metá-Chiribiquete					Yasuní				Ampiyacu			
	FP	SW	TF	WS	Total	FP	SW	TF	Total	FP	SW	TF	Total
Plots	11	5	19	5	40	8	7	10	25	9	10	6	25
Stems	3068	3147	7223	2543	15981	2229	842	3372	6443	2784	2912	1836	7532
S	472	205	1020	117	1349	490	231	673	886	492	347	501	814
G	252	128	373	78	462	251	151	319	361	240	180	230	325
F	85	49	105	36	120	75	58	86	91	79	61	75	88
Ind	278.90 <sup>a</sup> (66.86)	629.4 <sup>b</sup> (307.67)	380.15 <sup>c</sup> (65.18)	508.6 <sup>bc</sup> (218.87)	399.52 <sup>A</sup> (174.11)	278.62 <sup>ab</sup> (52.23)	120.28 <sup>a</sup> (31.78)	337.2 <sup>b</sup> (43.81)	257.72 <sup>B</sup> (100.27)	309.33 (63.80)	291.2 (77.92)	306 (21.39)	301.28 <sup>B</sup> (61.65)
SR	65.18 <sup>a</sup> (23.77)	60.8 <sup>a</sup> (17.54)	145.84 <sup>b</sup> (22.84)	32.8 <sup>a</sup> (15.15)	98.9 <sup>A</sup> (50.80)	109.87 <sup>a</sup> (38.01)	45.14 <sup>b</sup> (22.40)	156.2 <sup>c</sup> (14.13)	110.28 <sup>AB</sup> (52.32)	116.55 <sup>ab</sup> (13.28)	90.3 <sup>a</sup> (24.45)	143.83 <sup>b</sup> (12.98)	112.6 <sup>B</sup> (27.84)
Ca	77.3 <sup>a</sup> (95.75)	4.72 <sup>ab</sup> (1.8)	1.79 <sup>b</sup> (0.73)	1.42 <sup>ab</sup> (1.02)	22.88 (59.2)	42.01 (24.79)	66.51 (44.66)	19.73 (47.44)	39.96 (43.58)	25.64 (36.83)	47.82 (28.69)	2.54 (0.75)	28.97 (32.98)
Mg	169.38 <sup>a</sup> (164.66)	83.15 <sup>ab</sup> (34.81)	30.9 <sup>b</sup> (21.68)	1.41 <sup>b</sup> (0.7)	71.83 <sup>A</sup> (106.98)	222.95 (28.14)	157.87 (60.29)	162.05 (79.78)	180.36 <sup>B</sup> (66.47)	254.61 <sup>ab</sup> (121.99)	289.87 <sup>a</sup> (70.09)	127.01 <sup>b</sup> (40.15)	238.09 <sup>B</sup> (106.97)
K	233.51 <sup>a</sup> (157.78)	173.4 <sup>ab</sup> (77.9)	59.99 <sup>b</sup> (54.67)	1.09 <sup>b</sup> (0.49)	114.52 <sup>A</sup> (126.18)	222.95 (24.29)	164.07 (69.79)	155.5 (81.95)	179.48 <sup>A</sup> (69.62)	367.77 <sup>ab</sup> (119.72)	403.67 <sup>a</sup> (117.09)	211.51 <sup>b</sup> (71.77)	344.63 <sup>B</sup> (130.67)

Na	157.38 <sup>a</sup>	28.96 <sup>ab</sup>	14.54 <sup>b</sup>	1 <sup>b</sup>	53.93	132.02	106.45	80.77	104.36	158.38	93.28	25.57	100.47
	(190.93)	(12.67)	(14.62)	(1.39)	(116.95)	(41.03)	(123.11)	(68.27)	(80.72)	(160.74)	(76.94)	(4.96)	(116.27)
P	8.45 <sup>a</sup>	16.82 <sup>b</sup>	5.23 <sup>a</sup>	0.57 <sup>a</sup>	6.98 <sup>A</sup>	14.06 <sup>ab</sup>	23.58 <sup>a</sup>	9.85 <sup>b</sup>	15.04 <sup>B</sup>	11.65 <sup>a</sup>	21.98 <sup>b</sup>	11.32 <sup>a</sup>	15.7 <sup>B</sup>
	(4.52)	(8.19)	(1.5)	(0.28)	(5.74)	(3.79)	(9.85)	(2.41)	(7.96)	(3.74)	(11.88)	(10.3)	(10.35)
C	0.49 <sup>a</sup>	14.82 <sup>b</sup>	0.5 <sup>a</sup>	1.59 <sup>a</sup>	2.43	0.43 <sup>a</sup>	14.1 <sup>b</sup>	0.47 <sup>a</sup>	4.27	0.48	6.52	0.56	2.92
	(0.29)	(15.35)	(0.25)	(1.51)	(6.86)	(0.12)	(13.35)	(0.15)	(9.15)	(0.27)	(6.03)	(0.08)	(4.76)
N	0.04 <sup>a</sup>	0.99 <sup>b</sup>	0.05 <sup>a</sup>	0.03 <sup>b</sup>	0.16	0.07 <sup>a</sup>	0.74 <sup>b</sup>	0.07 <sup>a</sup>	0.26	0.05	0.34	0.06	0.17
	(0.02)	(0.7)	(0.02)	(0.01)	(0.39)	(0.02)	(0.67)	(0.02)	(0.46)	(0.02)	(0.28)	(0.01)	(0.22)
C:N	15.69	17.16	12.82	68.56	21.12	6.36	15.46	6.96	9.15	10.59	16.25	9.88	12.68
	(9.76)	(5.39)	(7.1)	(65.75)	(28.75)	(1.23)	(6.33)	(2.53)	(5.39)	(5.13)	(4.77)	(1.08)	(5.14)

---



Table S2. Loadings of the soil cations employed to assess the principal component analysis.

	Axis 1	Axis 2
Ca	0.43	0.03
Mg	0.51	0.09
K	0.46	0.08
Na	0.46	0.17
P	0.28	-0.44
C	0.05	-0.61
N	0.06	-0.60
C:N	-0.15	-0.09

Figure S1. Spatial variation of the principal coordinate neighbor axes estimated from the geographic coordinates of the plots used in this study.

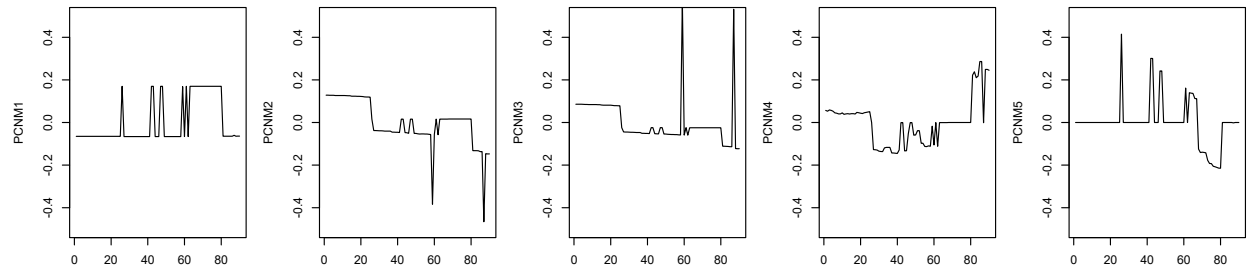


Figure S2. Proportion of NRI and NTI values calculated to tree communities composed of tree with DBH  $\geq 10$  cm that were significantly clustered or evenness under the three randomization models (Z1 = All data; Z2 = Restricted by subregion; Z3 = Restricted by landscape unit). Light gray represents the proportion of plots significantly clustered. Dark gray bar represents the proportion of plots with a significant evenness pattern. White bar represents the plots with either NRI or NTI values that were not significantly different from random. FP = Flood plain. SW = Swamp. TF = Terra Firme. WS = White Sand. Metá-Chiribique = 1. Yasuní = 2. Ampiyacu = 3.

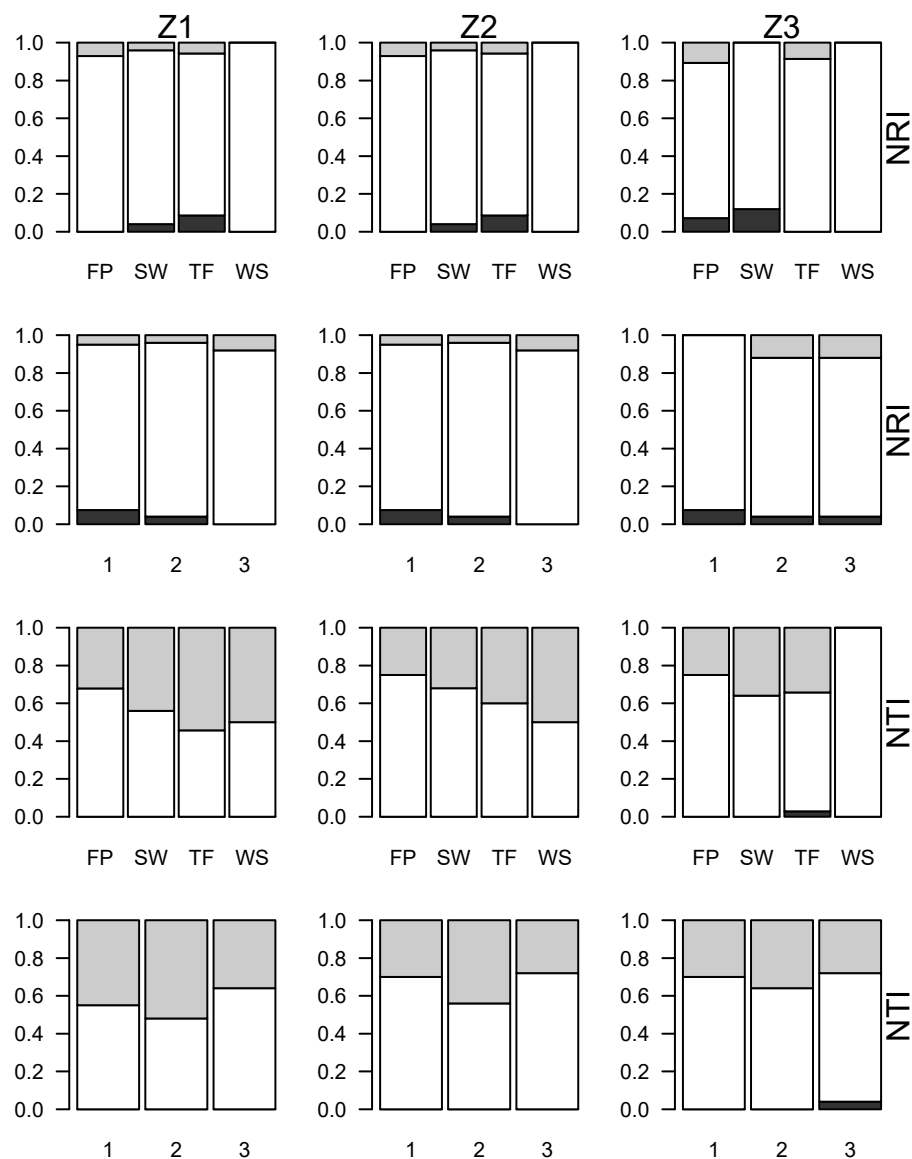


Figure S3. Non-metric multidimensional scaling ordination analysis of phylogenetic tree communities under different scenarios of species pools used in this study. Z1 = All data; Z2 = Restricted by subregion; Z3 = Restricted by landscape unit. Symbols denoted subregions: circle: Metá-Chiribiquete; triangle: Yasuní; square: Ampiyacu. Colors denoted landscape units: Flood plains: gray; Swamp: blue; Terra Firme: red; White Sand: green.

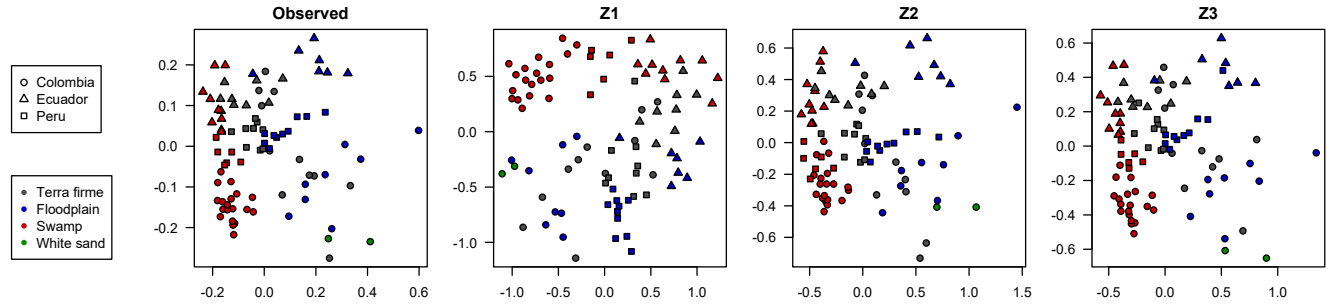


Figure S4. Pearson correlation coefficient between the the first and second axes of the non-metric multidimensional scaling ordination. Correlation values are assessed for standardized effect size of phylogenetic  $\beta$ -diversity among the three different species pools. The upper panel showed the Pearson correlation between each pair of axes. Species pool randomization used in this study are: Z1 = All data; Z2 = Restricted by subregion; Z3 = Restricted by landscape unit.

