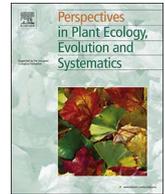


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Asymmetrical niche determinism across geological units shapes phylogenetic tree communities in the Colombian Amazonia



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ABSTRACT

We evaluate the role of differences in substrate age and environmental conditions, as represented by different geological units, in determining the phylogenetic structure and distribution of tree communities in the northwest Amazon. We used 412 0.1-ha plots distributed across the three main geological units (craton, tertiary and alluvial) in the Colombian Amazon, to answer the following research questions: i) To what extent do environmental filtering and dispersal limitation determine the phylogenetic composition of tree communities across geological units in the Colombian Amazon? and ii) Are there differences between geological units in the extent to which niche conservatism shapes the phylogenetic structure of indicator species (i.e., strong habitat-specialists) in tree communities? The results of our study give support for both environmental filtering and dispersal being important drivers of the phylogenetic structure and turnover of tree communities. Nonetheless, the extent to which geology explained the phylogenetic turnover of tree communities was surpassed by the geographic distance between plots, which was used to account for effects of dispersal limitation. This finding suggests that most of the lineages have had sufficient time to migrate and establish into adjacent geological units, contradicting claims that geological conditions are the dominant factors determining the distribution of tree communities across northwestern Amazonia. However, in the craton unit, indicator species were more closely related than expected by chance, while in the alluvial and tertiary units, observed relationships were not statistically different from null expectations. These results indicate that environmental filtering is asymmetrical among geological units, with the craton environment being the most restrictive. In contrast, the alluvial unit may be relatively easy to colonize and hence ecological strategies may be more labile through evolutionary history.

1. Introduction

The Amazon basin harbors one of the most diverse tree communities on Earth (Slik et al., 2015; Duque et al., 2017). Such a high diversity has been attributed to a complex geological history resulting from the Andean uplift and involving different tectonic movements, changes in the direction of rivers, and processes of sedimentation (Hooen et al., 2010). Therefore, Amazon forests have evolved on highly variable geological conditions that change in terms of age (2.5–65 my), soil fertility, and patterns of drainage from the eastern white-sand Guiana shield dominated systems (hereafter craton unit) to the western Andean foothills (ter Steege et al., 2006). The extent to which these geological differentiations can be translated into evolutionary processes that determine the floristic differences in the Amazon forests has been intensively

debated (Fine and Kembel., 2011; Dexter et al., 2012, 2017; Guevara et al., 2016). Although different mechanisms, such as environmental filtering or dispersal ability, have been suggested as being important historical drivers of the current biota in Amazon forests, the relative importance that each plays in structuring the phylogenetic structure of tree communities remains controversial (Fine and Kembel, 2011; Fortunel et al., 2016; Dexter et al., 2017).

Under the environmental filtering view of Amazonian diversity, we expect abrupt changes in tree community composition across different geological units (Higgins et al., 2011; ter Steege et al., 2006). A comparison of functional traits between contrasting geological units, such as the white-sands in French Guiana and the tertiary terra firme forests in Peru, indicates strong habitat filtering as the main driver of the tree community composition in these areas (Fortunel et al., 2014). These

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findings suggest that dispersal plays a weak role in shaping the species composition of tree communities across geological units, and that environmental conditions primarily determine the capability of tree species to establish and reproduce in specific environments (Fortunel et al., 2016). In cases such as this, we can expect a high phylogenetic turnover between geological units controlled by plant-habitat specialization due to a constrained evolution of the species' niches through time (niche conservatism *sensu* Wiens and Graham, 2005). High niche conservatism between geographically separate geological units may influence allopatric speciation (Wiens and Harrison, 2004; Guevara et al., 2016), which will produce a pattern of geographically structured phylogenies with a high abundance of closely related species associated with each environmental unit.

In contrast, under a dispersal-mediated view of Amazonian diversity, we assume that species movement has been a primary determinant of floristic composition and diversity independent of the geological features. In other words, according to this viewpoint, species distributions in the Amazon basin have historically been determined by the species' differential dispersal abilities and with only a relatively weak influence of geographical barriers (Dexter et al., 2012, 2017; Smith et al., 2014). If there is effective establishment of propagules of clades with origins in different geological units through time, the ecological traits associated to each geological unit (*sensu* Fortunel et al., 2014) should be labile through evolutionary history. If this is true, ecological speciation may have been an important driver of Amazon diversification (Misiewicz and Fine, 2014). Based on this scenario of evolutionary convergence, we will expect that the local coexistence of tree species will be geographically structured by distantly related species (Dexter et al., 2017), which may also be widespread across geological units (Pitman et al., 1999). We also expect larger (Wang et al., 2013), older geological units to support more diverse communities due to greater likelihood and time to accumulate species (Fine and Ree, 2006). This idea of Amazon forests structured by geological units floristically differentiated just by the capability of species to migrate and colonize new areas in geographical space (Hubbell, 2001) has received recent support at evolutionary timescales as well (Dexter et al., 2017).

In the Amazon, the oldest geological craton units with precambrian origin are derived from the Guiana shield; however, we know that there are fewer species, genera, and families in these units than in the younger tertiary sedimentary terra firme and the quaternary floodplains (Duivenvoorden, 1995; Duque et al., 2002), contradicting the expectation of the time-integrated species-area effect (Fine and Ree, 2006). This phenomenon, named by Hoorn et al. (2010) as the craton paradox, is by itself a strong argument supporting niche conservatism and environmental filtering as important mechanisms that shape the phylogenetic structure of tree communities in the Amazon basin (Fine and Kembel, 2011; Guevara et al., 2016; but see Dexter et al., 2017). The low-nutrient content, seasonal anoxia, and bad drainage of soils in white-sand systems (Lips and Duivenvoorden, 1996) may increase the level of environmental stress, and thus promote the development of convergent adaptive strategies. Likewise, in Amazon floodplains, the reported dominant pattern of phylogenetic clustering for tree communities (Aldana et al., 2016; Umaña et al., 2012), gives additional support to the assumption of environmental filtering as one of the most important mechanisms determining the phylogenetic structure of tree communities across geologic units in the Amazon basin (Fine et al., 2005; Fortunel et al., 2016). Therefore, comparative regional assessments of the phylogenetic structure and turnover of tree communities that include the most contrasting geological units, such as craton, tertiary sedimentary plains, and quaternary floodplains, are needed to help unravel the role played by asymmetric environmental filtering across geologic units in determining the distribution of tree communities in the Amazon. This prediction implies that the degree of niche conservatism will change between different evolutionary and ecological scales, and as so, between geological units.

Here, we aim to evaluate the role of differences in substrate age and environmental conditions, as represented by the main geological units, in determining the phylogenetic structure and distribution of tree communities in the Colombian Amazon. The Colombian Amazon has a strong longitudinal gradient of geological formations and substrates, which varies from the western Andean mountains to the eastern craton dominated formations, crossing through tertiary sedimentary plains and floodplains. The overall geological variation in the Colombian Amazon reflects the variation found throughout the Amazon basin, allowing us to use it as a benchmark to assess the extent to which environmental filtering determines the evolution and distribution of Amazon tree communities more generally. It is important to note that the use of phylogenetic indices to infer the main structuring mechanisms of plant communities has previously been criticized (Cavender-Bares et al., 2009). In particular, it has been argued that using assemblages of either distantly or closely related species to disentangle the roles played by competition vs. habitat filtering is "out of date" in modern species coexistence theory (Mayfield and Levine, 2010). According to this argument, more fundamental problems can arise when we assume that increasing phylogenetic differences favor species coexistence. To bypass some of these concerns, we employ phylogenetic turnover and structure, focusing on the main theoretical frame introduced above, to assess the extent to which dispersal (represented by geographical distances) and environmental filtering (represented by geological units) determine tree community composition in the Colombian Amazon, but avoiding any reference to competition. In other words, we assume that environmental filtering is due to a combination of both species' strict abiotic habitat requirements and competitive exclusion based on species' differential competitive abilities in different settings (Mayfield and Levine, 2010).

The main research questions and associated hypotheses addressed in this study are:

- i) To what extent do environmental filtering and dispersal limitation determine the phylogenetic composition of tree communities across geological units in the Colombian Amazon? We expect a high correlation of phylogenetic turnover with geology as well as a high phylogenetic clustering of indicator species in each geological unit, which would support environmental filtering as the main factor shaping the evolution of tree communities in the Amazon forests.
- ii) Are there differences between geological units in the extent to which niche conservatism shapes the phylogenetic structure of indicator species (i.e., strong habitat specialists) in tree communities? We hypothesize that niche conservatism increases with the age of the geological unit. In geological units with greater environmental stress, such as craton and floodplains, we expect the associated species to have evolved similar ecological traits that allow them to be abundant and widely distributed within each geological unit. In other words, the indicator species associated to each geological unit will be phylogenetically clustered if ecological advantages (traits) evolved in a conserved fashion.

2. Methods

2.1. Study region

The Colombian Amazon covers an area of roughly 483,119 km², which represents 41% of the country's continental territory, and 8.7% of the Amazon basin (Fig. 1). Although the Colombian Amazon includes the largest deforestation hotspot in the country, the natural forests are still well preserved in more than 70% of the region. The Colombian Amazon has the lowest population density (1.5 people km⁻²), and harbors the highest portion of indigenous communities of the whole country. To date, 84% of the region's territory is consolidated into protected areas including Indigenous Reserves and National Parks.

The Colombian Amazonia can be divided into three main geological

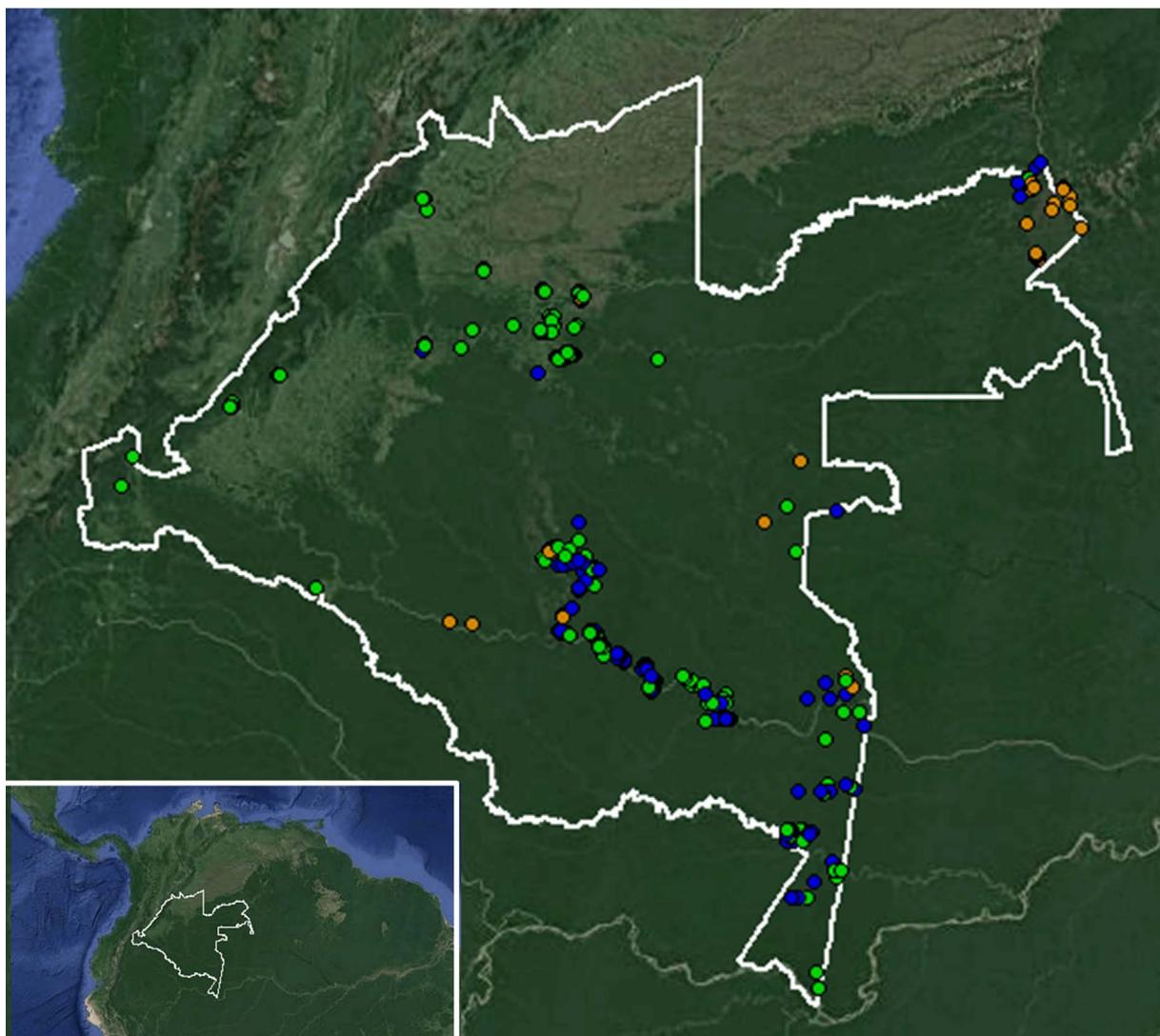


Fig. 1. Map showing the location of study plots. Red points indicate craton plots, blue points indicate alluvial plots and green points indicate Tertiary plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

units (PRORADAM, 1979; Botero, 1999) according to substrate age and origin: 1) The Amazonian craton, which is the oldest geological formation with its origins in the precambrian age (> 600 Ma). The craton unit is structured by Precambrian rock formations of the Guiana Shield that primarily emerged in the North-East part of the region (Hoorn et al., 2010). 2) The Amazon tertiary basin infills, which were mainly deposited during the Miocene and are part of the northern extension of the Solimões intracratonic basin (Hoorn, 1994; Hoorn et al., 2010). The depositional process of the area filled in by sediments from the Guiana shield gave origin to the sand units informally known as Mariñame and Apaporis (Hoorn et al., 2010). On the contrary, the depositional process of clay sediments with Andean origin created the Pebas formation (Hoorn, 1994), which was part of the mega-wetland that covered the Amazon during the Late Miocene (Hoorn, 2006). Although there are clear differences in the soils derived from either the sand or clay sediments in terms of structure and fertility (Lips and Duivenvoorden, 1996), here we include both as the tertiary unit but split them as needed into Tertiary-Shield or Tertiary-Pebas geological units, respectively. Any white-sand systems enclosed within these tertiary systems were treated as cratonic due to the parental material they are located on (Duivenvoorden et al., 1995). 3) Alluvial formations, which were all considered with Quaternary origin mostly due to the observation from the field to be located on floodplains. Although in the alluvial

formations there could be fluvial terraces that stem from Pliocene, Pleistocene or Holocene, they are assumed to be never flooded and therefore not included within our Alluvial definition of a Quaternary origin. Likewise, the alluvial formations can be described and differentiated in terms of their geologic origin as well, but in this study, all alluvial formations were treated as a single geologic unit framed by the rivers' flood plains.

2.2. Plot inventory data

Between 1990 and 2010, we conducted floristic surveys of 412 0.1-ha plots across the Colombian Amazon region (Fig. 1). To establish the plots, the direction of the trails along which the forests were entered was planned a priori on the basis of the interpretation of aerial photographs and satellite images (e.g. Duivenvoorden and Lips, 1993). Forests were visually examined to identify terrain units that were more or less homogeneous. In these units, rectangular plots (20-m wide x 50-m long or 10-m wide x 100 m long) were located and delimited by compass, tape, and stakes. All of the plots were mapped by GPS and were established in mature forests that did not show obvious signs of recent human intervention. In each plot, all trees and palms with a DBH (Diameter at Breast Height) ≥ 10 cm were recorded and collected. Each plot was assigned to one of the three main geological units (craton,

tertiary, or alluvial); when needed, we also divided the tertiary geological unit into Tertiary-Sand or Tertiary-Pebas as explained above.

The identification of the botanical collections was performed at the COAH, COL, MO, and AAU herbaria. Within families or groups of closely allied families, specimens that could not be identified at the species level because of a lack of sufficient diagnostic characteristics were clustered into morphospecies on the basis of simultaneous morphological comparisons with all other specimens. Hereafter, the term species refers to both morphospecies and botanical species.

2.3. Phylogenetic similarity

We built a hypothesized phylogenetic tree for all tree species found in our Colombian Amazon plot dataset using phylomatic version 3.0 (Webb and Donoghue, 2005) (Newick file in Appendix S1). We included unidentified species as genus or family level polytomies depending on botanical identification. Our phylogenetic tree was made up of 1693 tips and 422 nodes (24% of the evolutionary relationships were resolved). The largest proportion of polytomies is distributed within genera and deep phylogenetic relationships can be considered relatively well-resolved. Thus, our phylogenetic analyses are primarily focused at the genus level, minimizing analytic problems with plot comparisons associated with the level of resolution of tree species identification.

We used the PhyloSorensen index to build a matrix of phylogenetic similarities between plots based on species' presence-absence data. The PhyloSorensen index sums branch length of shared clades between sites (Bryant et al., 2008) relative to the sum of branch lengths of both sites:

$PhyloSorensen_{ij} = \frac{BL_{ij}}{0.5(BL_i + BL_j)}$ where BL_{ij} is the sum of branch length shared between plots i and j , and BL_i and BL_j are the sum of branch length of unique tips within plots i and j , respectively. Thus, if shared and unique branch length is balanced, the index takes a value near to 1. In contrast, if unique branch length exceeds shared branch length the index is close to 0. This metric was estimated using the *phylosor.query* function available in the *PhyloMeasures* (Tsirogianis and Sandel, 2015) package for R.

2.4. Statistical analyses

To define the compositional pattern of phylogenetic variation across the geological units, we used the hierarchical Wards clustering method (Cayuela et al., 2006) built from the phylogenetic similarity matrix of the plots. To find the cutoff point that maximizes the phylogenetic compositional differences between groups of plots, we used an iterative method based on the R-statistic obtained from an analysis of similarities (ANOSIM) (Legendre and Legendre, 2012). The ANOSIM method evaluates whether differences within groups are comparable with differences between groups. The method employed here systematically assessed the increment in the R-statistics of ANOSIM in relation to the increment in the length and number of branches in the Ward's clustering dendrogram until the R-value asymptoted. Furthermore, we used a chi-squared test to evaluate the congruence between Ward's dendrogram-based clusters and geological units. The chi-squared test allows us to evaluate if proportions are distributed randomly or the dendrogram clustering is constrained to specific geological units. The chi-squared test was performed on a contingency table that uses the geological units and dendrogram groups as categorical variables and the estimated number of plots for each combination.

We used the Mantel test (Legendre and Legendre, 2012) to evaluate the influence of geology in determining the phylogenetic turnover of trees in the Colombian Amazon. To run the Mantel test, the PhyloSorensen distance matrix was converted into a distance by applying 1–similarity. This analysis allows us to assess the influence of geology on the phylogenetic tree turnover to understand the expected deterministic effects of environment (e.g. geology) on the pattern of tree distributions. For the Mantel analysis, we used the PhyloSorensen distance

between plots and a presence-absence matrix of geological units. The presence-absence distance matrix of geology includes 0 when two plots were located on the same geological unit and 1 otherwise.

Likewise, we used the Mantel test to evaluate the influence of geographical distances between plots (straight line distances in km) in determining the phylogenetic turnover of trees in the Colombian Amazon. In this study, we used the geographic distances to account for the hypothesized effect of spatially structured biological processes, such as dispersal limitation (Condit et al., 2002). For this analysis, we used the PhyloSorensen similarity between plots and the log-transformed geographic distance between plots (Fine and Kembel, 2011). The distance-decay approach (Nekola and White, 1999; Tuomisto et al., 2003) was then applied to visualize the relationship between the phylogenetic similarities and the log-transformed spatial distances. The approximately linear distance-decay along the logarithm of geographical distance can be used as an explicit prediction (and test) of Hubbell's neutral theory (Morlon et al., 2010). Finally, we used the partial Mantel test to assess the effect from either geology or geographical space after controlling for the effect of the other. Mantel and partial Mantel tests were performed using the library *vegan* (Oksanen et al., 2013) for R.

2.5. Indicator species and phylogenetic clustering

In order to explore species associations with geological units, we used the indicator value index (INDVAL) proposed by Dufrene and Legendre (1997). This method incorporates the relative abundance and relative frequency of individual species across habitats (e.g. geological units) to test the degree of habitat associations based on a null model assuming a random distribution of each species among habitat types. The significance is based on the distribution of the observed value relative to 1000 iterations of the random model. We used 0.01 as the confidence limit to define indicator species. Based on the set of indicator species of particular conditions that prevailed in site groups (Legendre and Legendre, 2012), we evaluated the role of niche conservatism for geological unit.

We expected that high niche conservatism along evolutionary history results in high habitat specialization and potentially habitat dominance. Taking into account the assumptions stated in the introduction section, phylogenetic niche conservatism can be used to predict phylogenetic clustering of co-occurring species under particular habitat conditions (Wiens and Graham, 2005). To assess niche conservatism, we conducted the following analysis: first, we calculated a phylogenetic mean pairwise distance (MPD) between indicator species within each geological unit. Next, we randomly chose the same number of species from a regional species pool that did not include the subset of indicator species and calculated their MPD. This procedure was repeated 1000 times and the standardized observed values were used to build the expected distribution. Standardized values were calculated as the observed value minus the mean random value divided by the standard deviation of the random distribution. We then multiplied these standardized values by -1 to obtain a Net Relatedness Index (NRI), a common phylogenetic community structure metric (Webb, 2000). Negative values of NRI indicate phylogenetic overdispersion and positive values indicate phylogenetic clustering. Significance was determined by ranking the observed value on the null distribution divided by the number of replicates. This procedure was run in the library *picante* (Kembel et al., 2010) for R.

Phylogenetic clustering/overdispersion patterns are dependent on null model and species pool definition (Lessard et al., 2012). Therefore, in order to test phylogenetic dispersion of indicator species within each geological unit, we used three different species pool definitions. Our first species pool definition included all of the species present in our dataset after having removed the species indicator set. Phylogenetic clustering could indicate habitat filtering of conserved traits imposed by geological units. The second species pool was made up of all species present within each geological unit. This species pool definition allows

us to evaluate if indicator species of a particular geological unit are more clustered than expected by chance in relation to other species that occur within that particular unit. Within geological units, phylogenetic clustering of indicator species may indicate conservatism of evolutionary advantages (i.e. defense to herbivory) that should facilitate ecological specialization through environmental filtering. On the contrary, phylogenetic overdispersion of indicator species within geological units may indicate converging ecological traits on the phylogeny along the evolutionary history. Finally, we used a species pool including all indicator species with the aim of evaluating whether ecologically indicator species in a particular geological unit are phylogenetically clustered in regards to all indicator species found across geological units.

3. Results

Across all 412 inventory plots, we tallied 27,192 individual trees belonging to 1683 species from 84 plant families. Overall, 84.9% of individuals were identified to the species level, 9.1% to the genus level and 2.1% to the family level. The remaining 3.9% of individuals that were not identified at least to the family level were removed from the community matrix and all subsequent analyses.

In all plots, there are 358 singleton species (21.2%) and 206 doubletons (12.24%). In contrast, *Oenocarpus bataua* was the most abundant species with 703 individuals, followed by *Oxandra polyantha* (583 individuals), *Euterpe precatoria* (543 individuals), *Socratea exorrhiza* (459 individuals) and *Micrandra sprucei* (427 individuals). The five most diverse families were Fabaceae (249 species), Annonaceae (100 species), Lauraceae (96 species), Rubiaceae (95 species) and Chrysobalanaceae (75 species). On average, there were 29.4 species (range = 1–67) per plot and 66 individuals (range = 10–284) per plot. Across geological units, the number of individuals was significantly higher in the alluvial formation than in the tertiary, while species richness was significantly higher in the tertiary than in the craton and alluvial geological formations (Table 1). There were no differences in the mean phylogenetic distance between geological units (Table 1).

Based on the ANOSIM R-statistic, we differentiated seven phylogenetic groups primarily associated with geology (Fig. 2). The plots located on the craton unit were divided into two main groups, one of them located in the middle of the tertiary forests. The chi-squared test showed a significant correlation between geological units and phylogenetic clustering ($X^2 = 10.21$; $p < 0.001$), which suggests that the phylogenetic composition of each plot was strongly associated with a specific geological unit. However, none of the clusters was made up exclusively of plots from only one geologic unit.

When the entire dataset derived from plots located in all geological

units was analyzed, the phylogenetic composition was significantly correlated with geology (Mantel $r = -0.16$). Furthermore, the correlation between phylogenetic composition and geology decreased (Mantel $r = -0.09$) when we split the tertiary unit into Tertiary-Shield and Tertiary-Pebas. When the alluvial formation was excluded, the Mantel correlation increased from -0.16 to -0.29 (Table 2), suggesting that phylogenetic similarity varies strongly between pairs of alluvial plots across the whole Colombian Amazon. Likewise, when the entire dataset was considered, phylogenetic composition had a stronger correlation with the spatial configuration of the plots (Mantel $r = -0.25$) than with geology; the Mantel correlation increased again from -0.25 to -0.39 (Table 2) when the alluvial plots were removed (Table 2). When the effect of either geology or geographical distance was accounted for, the correlation between phylogenetic similarity of tree communities and the remaining explanatory factor (geographic distance or geology, respectively) were in all cases still significant (Table 2). However, the stronger correlation observed with geographic distances than with geology suggests an active effect of plot distance that tended to increase with plot proximity up to an average distance of 20 km between plots (Fig. 3).

According to the indicator value index (*INDVAL*), there were 241 indicator species in the three geological units (Table 3) that represent 14% of all species registered in the plots. Of these indicator species, 127 were found in the craton, 66 in the tertiary, and 48 in the alluvial unit (represent 25.6%, 5.0%, and 4.5% of the total of species found in each unit, respectively). In all cases analyzed, the craton indicator species were phylogenetically clustered. In contrast, indicator species from tertiary and alluvial units showed a clear, but statistically insignificant, trend towards phylogenetic overdispersion (Table 4).

4. Discussion

The results of our study give support for both environmental filtering and dispersal as being important drivers of the phylogenetic turnover and structure of tree communities in the Amazon basin. However, our first hypothesis about the expected dominant role of plant-habitat specialization being the most important mechanism determining tree phylogenetic assemblages in the main geological units was partially rejected. The extent to which the geographic distance between plots explained the phylogenetic turnover of tree communities, used to account for dispersal limitation (Eiserhardt et al., 2013; Morlon et al., 2011), surpassed that of geology. Dispersal limitation appears to actively drive phylogenetic turnover at distances equal to or lower than approximately 20 km; beyond this distance, abiotic filters have a significant complementary effect. This finding suggests that most of the lineages have had sufficient time to migrate and establish into adjacent geological units (Pitman et al., 1999; Dexter et al., 2017), contradicting the claims that geological conditions are the dominant factors determining the distribution of tree communities across north-western Amazonia (Higgins et al., 2011; Pitman et al., 2008).

The strong influence of spatial distance in determining the phylogenetic similarity between tree communities illustrates the fundamental role that dispersal has had in shaping the evolutionary patterns of tree communities in the Colombian Amazon (Dexter and Chave, 2016; Dexter et al., 2017; Fine and Kembel, 2011). This result is contrary to expectations based on the age of the geological formation and the strong role of the transition between Guiana to Andean systems (Hoorn et al., 2010). This finding suggests that niche conservatism is weak in Amazon Trees – at least at the community level. Weak niche conservatism among geological units could be expected if the meta-community of any local community is composed by the complete regional species pool (Dexter et al., 2017), which may make the development of specific traits labile through time (Silvertown et al., 2006). However, our study is mostly focused on large trees, which may mask the stronger abiotic filtering effects of habitat specialization in earlier developmental stages of trees as seedlings (Fortunel et al.,

Table 1

Summary of the 412 plots. Total species and individual counts include identified and unidentified morphospecies. Parenthetical values indicate standard deviations. Letters show distinct groups based on Tukey honest significant difference. The mean phylogenetic similarity is based on the assessment of the mean Phylosorensen index estimated for all species present in each plot.

	Craton	Tertiary	Alluvial	Total
Number of plots	69	201	142	412
Number of individuals	4997	12419	9776	27192
Number of species	495	1312	1060	1683
Number of families	52	76	72	84
Mean species per plot	23.27 ^C (7.2)	32.97 ^A (11.8)	27.23 ^B (12.7)	29.37 (12.1)
Mean stems per plot	75.57 ^{AB} (25.7)	73.94 ^B (19.4)	82.41 ^A (43.9)	66 (31.1)
Mean PhyloSorensen	0.39 (0.10)	0.38 (0.07)	0.35 (0.08)	0.36 (0.07)
Number of indicator species	127	66	48	241

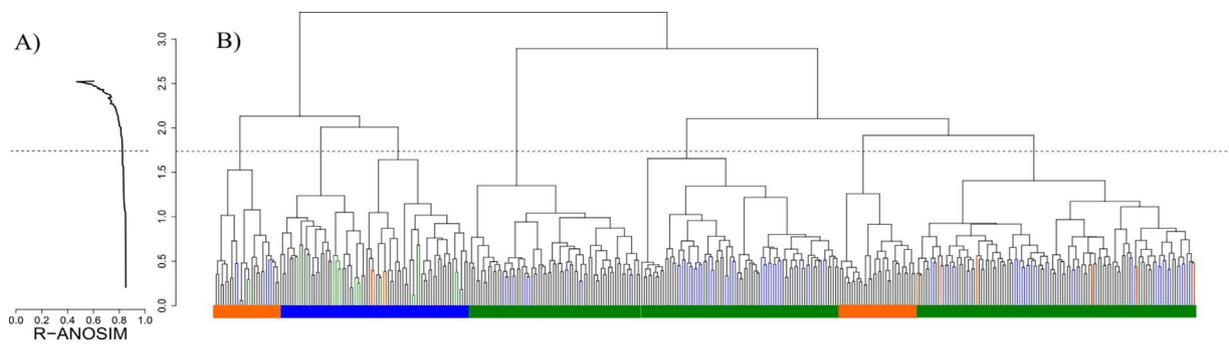


Fig. 2. A) Analysis of similarity (ANOSIM) showing the trend of the correlation value (R). B) Dendrogram based on phylogenetic similarities between plots. Dotted line indicates significant groups based on a maximization of ANOSIM R statistics. Groups are colored according to the main geological unit associated with each group. Non-conforming geological units are indicated by coloring the terminal branches of the dendrogram. Red: craton plots; blue: alluvial plots; and green: Tertiary plots.

Table 2

Mantel and Partial mantel tests results from phylogenetic similarity related with geological and spatial (log-transformed) distances. Analyses were run while including and excluding alluvial plots.

	Variable	R	p
Including Alluvial plots	geo	-0.16	0.001
	spa	-0.25	0.001
	geo, spa	-0.15	0.001
Excluding Alluvial plots	spa, geo	-0.23	0.001
	geo	-0.29	0.001
	spa	-0.39	0.001
	geo, spa	-0.17	0.001
	spa, geo	-0.33	0.001

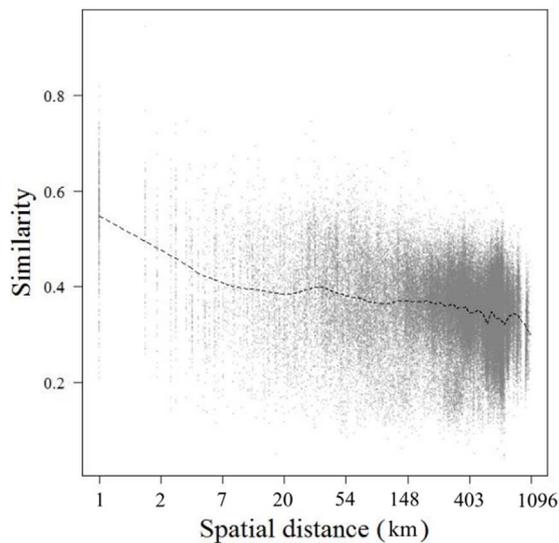


Fig. 3. Observed relationship between the phylogenetic similarity and geographic distance (log transformed) for pairwise combinations of plots.

2016). Therefore, we cannot completely rule out the role played by environmental filtering as a more active complementary mechanism of dispersal in shaping the phylogenetic structure and turnover of Amazon tree communities.

The smaller but significant role played by geology in determining the phylogenetic structure of Amazon tree communities may in large part be attributable to physiological filters imposed on plant species by the stressful environmental conditions mostly derived from the seasonal low availability of oxygen in soils and very low nutrient contents, typical of the craton unit (Duijvenvoorden et al., 1995; Fortunel et al., 2016). For example, based on the total number of species found in each geological unit, we found a larger portion of indicator species in the craton (25.6%) than in the tertiary (5%) and alluvial (4.5%) geological

units. The significant phylogenetic clustering found in the craton unit confirms and emphasizes the role played by niche conservatism in shaping the evolutionary development of specific traits, such as herbivore defenses (Fine et al., 2005), that enable some particular species to succeed in this geological unit. The significant trend of phylogenetic clustering for indicator species in the craton unit persisted independently of the species pool definition employed (regional, habitat or only indicator species). Furthermore, the separation of the plots located on the craton into two different groups according to the cluster (Fig. 1) suggests an apparently slow evolution of the species' niches and supports niche conservatism, likely due to a strong influence of an allopatric process of speciation as a main driver of diversification in the white-sand formations (Guevara et al., 2016).

Our results about the influence of niche conservatism in the craton unit defined from the coexistence of closely related species differed of recent results obtained from better-resolved phylogenies of some specific genera (Dexter et al., 2017). Dexter et al. (2017) found a lack of geographic phylogenetic structure in the *Inga*, *Swartzia*, *Protieae*, and *Gutteria* lineages across different regions of the Amazon. However, in French Guyana and the Atlantic coastal rainforest of Brazil where soil characteristics, such as low fertility due to leaching, are similar to those found in our craton unit, some of these taxa were phylogenetically clustered. A tendency to find geographical phylogenetic structure associated to systems with very low nutrient contents or drainage anomalies gives support to our claims of higher environmental filtering in the craton unit than in the other environments due to resource limitation. Although the use of phylogenetic clustering of only indicator species to infer environmental filtering as the main mechanism determining the composition of tree communities in the craton is debatable (Cavender-Bares et al., 2009; Mayfield and Levine, 2010), the evidence from other studies showing a trend towards geographic phylogenetic structuring in white sands (Guevara et al., 2015) support our findings. Nonetheless, we acknowledge the need of additional experimental and observational studies based on well-resolved phylogenies to more conclusively test the idea that the craton unit operates as a dissimilar environment and drives closely related species to similar stabilizing niche differences, thereby promoting species coexistence.

In contrast to the craton and contrary to expectations, the alluvial geological unit was the most widespread geological formation across the phylogenetic clusters defined here. This suggests that flooding may not be a strict factor in restricting the colonization of species from across diverse lineages. Overall, tree communities in flooded plots tended to be more phylogenetically similar to nearby unflooded forests than to more distant flooded plots. In other words, although we cannot deny the physiological stresses imposed by flooding, floodplains may be defined as successional forests where the bulk of the tree community composition is mostly composed of species that disperse in from the locally and regionally adjacent tertiary sedimentary plains (Terborgh and Andresen, 1998; Pitman et al., 2014). Thus, the alluvial formation appears to be a geologic unit that is evolutionarily “easy” to colonize,

Table 3

Ten most important indicator species per geological unit analyzed. The indicator value is the index from Legendre and Borcard analysis (see Methods). Relative abundance is the proportion of individuals of each species in the associated geological unit. N is the total number of individuals per species.

Geological unit	Indicator species	Family	Indicator value	Relative Abundance	N	
Craton	<i>Clathrotropis glaucophylla</i>	Fabaceae	0.318	0.95	108	
	<i>Leopoldinia piassaba</i>	Arecaceae	0.297	0.89	230	
	<i>Macrolobium limbatum</i>	Fabaceae	0.215	0.78	67	
	<i>Caraipa longipedicellata</i>	Calophyllaceae	0.209	0.76	142	
	<i>Protium divaricatum</i>	Burseraceae	0.207	0.95	69	
	<i>Eperua purpurea</i>	Fabaceae	0.202	1	97	
	<i>Micrandra sprucei</i>	Euphorbiaceae	0.201	0.99	427	
	<i>Protium paniculatum</i>	Burseraceae	0.196	0.9	50	
	<i>Mouriri grandiflora</i>	Melastomataceae	0.181	0.96	36	
	<i>Glandonia williamsii</i>	Malpighiaceae	0.171	0.98	32	
	Tertiary	<i>Socratea exorrhiza</i>	Arecaceae	0.315	0.76	448
		<i>Pseudolmedia laevis</i>	Moraceae	0.271	0.72	297
		<i>Micropholis guyanensis</i>	Sapotaceae	0.17	0.53	175
		<i>Iryanthera ulei</i>	Myristicaceae	0.163	0.55	263
		<i>Crepidosperrum rhoifolium</i>	Burseraceae	0.158	0.8	80
		<i>Dendropanax arboreus</i>	Araliaceae	0.117	0.72	66
<i>Pseudolmedia laevigata</i>		Moraceae	0.112	0.62	127	
<i>Perebea xanthochyma</i>		Moraceae	0.112	0.62	99	
<i>Protium sagotianum</i>		Burseraceae	0.104	0.74	57	
<i>Protium apiculatum</i>		Burseraceae	0.097	0.8	51	
Alluvial		<i>Euterpe precatoria</i>	Arecaceae	0.225	0.59	535
		<i>Mauritia flexuosa</i>	Arecaceae	0.146	0.8	374
		<i>Oxandra polyantha</i>	Annonaceae	0.112	0.99	583
		<i>Vatairea guianensis</i>	Fabaceae	0.105	0.83	44
		<i>Licania longistyla</i>	Chrysobalanaceae	0.094	0.95	36
		<i>Virola surinamensis</i>	Myristicaceae	0.079	0.93	64
	<i>Oxandra mediocris</i>	Annonaceae	0.073	0.74	46	
	<i>Gustavia pulchra</i>	Lecythidaceae	0.07	1	50	
	<i>Couratari oligantha</i>	Lecythidaceae	0.067	0.96	42	
	<i>Zygia inaequalis</i>	Fabaceae	0.066	0.72	37	

Table 4

Test of the degree of habitat association based on a null model of the net relatedness index (NRI) from indicator species for each geological unit assuming a random distribution of each species among habitat types. The significance is based on the distribution of the observed value relative to 1000 iterations of the random model. We used 0.01 as the confidence limit to define indicator species. The NRI was estimated for three different species pool definition: 1: All species reported in our dataset. 2: All species in each geological unit. 3: All indicator species. *: $p < 0.1$; **: $p < 0.05$.

	1	2	3
Craton	1.54*	1.60**	1.56**
Tertiary	-0.76	-0.81	-0.77
Alluvial	-0.91	-0.98	-0.91

which explains the phylogenetic overdispersion found for the alluvial indicator species. Although previous studies reported a trend of phylogenetic clustering in flooded forests (Umaña et al., 2012; Gonzalez-Caro et al., 2014; Aldana et al., 2016), its ecological interpretation, in both this and former studies, need to be treated with caution due to statistical insignificance of the results. However, in this study, we find that the indicator species reported in the alluvial unit belonged to the Arecaceae family, which agrees with previous reports made for this geologic unit in Amazon forests (Duque et al., 2002, ter Steege et al., 2013). In contrast, in other studies (i.e. Aldana et al., 2016), Fabaceae, a lineage well represented in most of the Amazon geologic units, was one of the indicator and dominant families in the alluvial formation. Historical-biogeographic differences between geographic regions that determine the floristic composition could explain the differences in the underlying processes that drive the tree phylogenetic structure of tropical forests in this particular ecosystem.

The indicator species showed contrasting patterns between geological units in terms of abundance and phylogenetic origin. The craton units are largely dominated by species from the Eudicot clade, particularly from the Rosid families. For example, *Micrandra sprucei* is the most abundant species and is recognized as being hyperdominant on

podzolised soils of the white-sand formations (ter Steege et al., 2013). In addition, Fabaceae is within this clade and is the most representative taxa of our craton units. Species of this family are recognized for their mutualism with *Rhizobium* species that increase their ability to uptake nutrients under poor soil conditions (Adams et al., 2016). The high number of Fabaceae indicator species may therefore support the increased importance of environmental filtering as a main driver of tree diversity in the craton unit (Fortunel et al., 2014). Alluvial units are dominated by the three major angiosperm clades: Magnoliids, Eudicots and Monocots. The most abundant species in all Amazonia (ter Steege et al., 2013), *Euterpe precatoria*, and other palms such as *Mauritia flexuosa*, were likewise the most representative species in this geological unit. Some Magnoliid species from Annonaceae such as *Oxandra polyantha*, which was dominant in our study, has also been reported as dominant in black-water flooded forests (ter Steege et al., 2013). As stated before, this phylogenetic overdispersion of indicator species could be the result of a weak evolutionary restriction of flooding conditions and water stress for species establishment into these forests (Pitman et al., 2014). The co-occurrence of distantly related species inhabiting floodplains emphasizes the need for understanding the wide range of ecological tolerances that species have developed to tolerate flooding and the mechanisms that allow such a high diversity of trees in this geologic unit (Parolin et al., 2004). In the tertiary unit, the most dominant species, such as *Socratea exorrhiza* (Monocot) and *Pseudolmedia laevis* (Eudicot), correspond to different angiosperm clades in a similar way as in the alluvial units. In summary, the phylogenetic structure of indicator species suggest that evolutionary and ecological mechanisms differ between the three geological units, but with a marked difference between craton and the other two units. Therefore, we find support for our second hypothesis about an asymmetric effect of niche conservatism between geological units that differentially shapes the evolution of tree communities in the Colombian Amazon.

The asymmetric effect of phylogenetic clustering between geologic units proposes that the movement of propagules from tertiary and

alluvial to craton may have been less frequent than between them through time. For example, Misiewicz and Fine (2014) showed that the white-sand – terra firme transition influences the genetic structure and morphological traits of *Protium subseratum* populations, suggesting that divergent natural selection affects immigration between soil types. In contrast, Dexter et al. (2012) showed that the terra firme – alluvial transition does not affect the genetic population structure of eight *Inga* species, which is line with our results. In this context, craton units may have operated as a historical source of species to tertiary and alluvial plots rather than vice-versa, a pattern that may have had consequences on the species diversification of Amazon tree communities. Dexter and Chave (2016) showed that genus range size and species richness are negatively related, indicating that species formation may depend upon range fragmentation and slow secondary contact, both processes directly related to dispersal limitation. In addition, they suggest that dispersal-related traits such as tree height are important drivers of the genus – species richness relationship found in different geological units in Amazon forests, indicating that intrinsic factors such as dispersal ability may be one of the most important drivers of tree diversification in the Amazon basin (Claramunt et al., 2012; Dexter and Chave, 2016; Dexter et al., 2017), as it is proposed in this study.

To conclude, our study suggests that from an evolutionary perspective, both dispersal and environmental filtering interact to shape the assembly of Amazon tree communities. The extent at which these two processes determine the phylogenetic structure of Amazon tree communities is asymmetrical between geological units. In the craton unit, environmental filtering appears as the dominant force due to the more restrictive conditions that may constrain seedling establishment (Fortunel et al., 2016). In the craton unit, the environmental restrictions have diminished the evolutionary opportunity of ecological success, resulting in a dominance of closely related species, a mechanism widely known as niche conservatism. The restrictions imposed by the craton for species establishment is directly associated with the magnitude and significance of statistical tests of beta diversity when this geologic unit is included. In contrast, in the younger and more diverse tertiary and alluvial units, a very active exchange of propagules is driving compositional patterns in these two geological units. In particular, our findings support the idea that alluvial units may have largely been colonized by habitat generalist species with few species specifically restricted to it (Pitman et al., 2014). This result suggests that there is a wide range of ecological strategies that enable species to inhabit floodplains, and that these strategies may have evolved in a convergent fashion across the angiosperm phylogeny. However, the lower amount of specialized species in floodplains may be more important in those areas subjected to more intensive and frequent inundations. This combination of contrasting mechanisms of speciation that has acted at a differential extent on the main geological units, and so along the evolutionary history of the Amazon basin, have left their fingerprint on the biogeographic patterns of the Amazon basin.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2017.06.001>.

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