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Importance of topography for tree species habitat distributions in a terra firme forest in the Colombian Amazon

Daniel Zuleta ⓘD · **Sabrina E. Russo · Andrés Barona · Juan S. Barreto-Silva ·
Dairon Cardenas · Nicolas Castaño · Stuart J. Davies · Matteo Detto · Sonia Sua ·
Benjamin L. Turner · Alvaro Duque**

Abstract

Aims To test the relative importance of topography versus soil chemistry in defining tree species-habitat associations in a terra firme Amazonian forest.

Method We evaluated habitat associations for 612 woody species using alternative habitat maps generated from topography and soil chemistry in the 25-ha Amacayacu Forest Dynamics Plot, Colombian Amazon. We assessed the ability of each habitat map to explain the community-level patterns of species-habitat associations using two methods of habitat randomization and different sample size thresholds (i.e., species' abundance).

Results The greatest proportion of species-habitat associations arose from topographically-defined habitats (55% to 63%) compared to soil chemistry-defined (19% to 40%) or topography plus soil chemistry-defined habitats (18% to 42%). Results were robust to the method of habitat randomization and to sample size threshold.

Conclusions Our results demonstrate that certain environmental factors may be more influential than others in defining forest-level patterns of community assembly and that comparison of the ability of different environmental variables to explain habitat associations is a crucial step in testing hypotheses about the mechanisms

D. Zuleta (✉) · A. Duque
Departamento de Ciencias Forestales, Universidad Nacional de Colombia Sede Medellín, MedellínStreet 59 A, N 63-20, Colombia
e-mail: dfzuleta@gmail.com

S. E. Russo
School of Biological Sciences, University of Nebraska, Lincoln, NE 68588-0118, USA

A. Barona · J. S. Barreto-Silva · D. Cardenas · N. Castaño · S. Sua
Herbario Amazónico Colombiano, Instituto Amazónico de Investigaciones Científicas Sinchi, Bogotá Street 20, N5–44, Colombia

S. J. Davies
Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Washington, DC, USA

M. Detto
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08540, USA

B. L. Turner
Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama

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underlying assembly. Our results point to topography-driven hydrological variation as a key factor structuring tree species distributions in what are commonly considered homogeneous Amazonian terra firme forests.

Introduction

Habitat filtering due to resource-based niche differentiation is hypothesized to contribute to the coexistence of large numbers of tree species in tropical forest communities (Ricklefs 1977; Tilman 1982). In Amazonian forests, variation in geology, soil fertility, and climate, as well as topography-driven heterogeneity in soil moisture and flooding frequency and severity have generated a mosaic of contrasting forest types across the Basin at both regional and local spatial scales (Sombroek 2000; Duque et al. 2002; Tuomisto et al. 2003b; ter Steege et al. 2006; Higgins et al. 2011; Quesada et al. 2011). Among forest types in the Amazon Basin, the distinction between flooded and non-flooded forests is a key determinant of species diversity and distribution. The terra firme forests (TFF), here defined as upland forests located on non-flooded areas with relatively well-drained soils (Duivenvoorden and Lips 1995), have been recognized as the terrestrial ecosystem that harbors the most tree species per unit area on Earth (ter Steege et al. 2003) and with a recent study reporting an average of 649 woody (trees and shrubs ≥1 cm dbh) species per hectare (Duque et al. 2017). Such high levels of diversity are thought to arise in part because coexistence of tree species is promoted by variation in their distributions along environmental gradients at regional scales in Amazonian TFF, a process mediated by habitat filtering (Phillips et al. 2003; Tuomisto et al. 2003a; Honorio et al. 2009). However, which environmental factors are the principle determinants of habitat filtering and their relative importance at local (ca. 1 km^2) versus larger scales are still debated. There are contrasting views about the degree to which topography and soil resources (Poulsen and Balslev 1991; Svenning 1999; John et al. 2007) or distance-dependent processes such as dispersal limitation (Hubbell 2001; Condit et al. 2002; Duque

et al. 2003; Valencia et al. 2004; Russo et al. 2007) shape species distributions at local scales. Quantifying how tropical woody species partition different types of environmental resources is therefore paramount to understanding the maintenance of species diversity in Amazonian TFFs.

There is ample evidence from a wide variety of tropical forests that many woody species segregate along environmental gradients, often defined by topography and soil characteristics (Clark et al. 1998; Harms et al. 2001; Phillips et al. 2003; Davies et al. 2005; Condit et al. 2013). In tropical forests, at spatial scales ≤1 km^2, many studies have defined tree species-habitat associations based only on topography (Svenning 1999; Duque et al. 2003; Valencia et al. 2004; Gunatilleke et al. 2006; Jucker et al. 2018). Yet, variation in soil properties may also influence the distribution of tree species (John et al. 2007). In fact, large numbers of tree species have been associated with both topography and soil characteristics in tropical forests, even at small spatial scales (Itoh et al. 2003; Davies et al. 2005). Even so, few studies, and none in Amazonian forests, have assessed the relative importance of topography versus soil characteristics in defining the tree species-habitat associations at spatial scales ≤1 km^2 (Davies et al. 2005; Dalling et al. 2012; Baldeck et al. 2013). Testing which sets of environmental variables explain tree species-habitat associations at the community level is important not only for understanding how niche specialization helps to maintain the high diversity of Amazonian TFFs, but also for linking tree species' distributions to demographic (Russo et al. 2005; Kenfack et al. 2014), functional, and physiological properties of species (Baltzer et al. 2005; Russo et al. 2010), which can be used to model the responses of Amazonian forests to the frequent and extreme climatic events predicted for the future (Duffy et al. 2015).

Analyses of tree species-habitat associations usually employ spatially explicit data on tree distributions and an independently derived habitat map to test if the observed relative density of a species in a given habitat is higher than that expected from random placement on null habitat maps obtained from simulations. Randomization methods overcome the limitation of spatial autocorrelation, which is known to induce statistical artifacts when assessing the association between different types of spatial processes (Clifford et al. 1989). The autocorrelation is present because trees are not independently distributed relative to conspecifics (Condit 1996)

due to spatially aggregated seed dispersal and recruitment (Condit et al. 1992; Schupp et al. 2002; Russo and Augspurger 2004) and because habitats are spatially structured. A crucial step in defining species-habitat associations is the prior definition of the habitat map. In some forests, at local scales, habitats have been defined in terms of variation in disturbance (Hogan et al. 2016), hydrology (e.g., swamps; Harms et al. 2001), soil properties (Davies et al. 2005), or topography (Chuyong et al. 2011). However, most studies do not apply a systematic approach to testing the relative importance of different kinds of environmental variation in defining the habitat associations of tree species, which limits our ability to test hypotheses about forest community assembly. In order to understand the mechanisms underlying habitat filtering and their physiological basis, the primary environmental factors to which trees respond should, ideally, be decoupled. However, many of these environmental factors can covary. For example, topography is a complex feature that can both integrate and define several variables to which trees respond, and so is sometimes found to covary with hydrology, soil texture, nutrient concentrations, and other soil properties (Daws et al. 2002; Costa et al. 2005; John et al. 2007; Quesada et al. 2009b). To the extent that different environmental factors display limited covariation, however, stronger comparative tests of the extent to which they define habitat associations of tree species can be achieved, making it possible to distinguish the principle axes explaining niche differentiation between species.

A first step in assessing the degree to which species respond to different environmental factors is to test the observed pattern of tree species distributions with respect to habitats against null expectations (Gotelli and Graves 1996). The most widely used method to simulate the null habitats is the torus translation (TT; Harms et al. 2001) and an alternative approach is the iterative amplitude adjusted Fourier transform (IAAFT; Venema et al. 2006). Ideally, ecological inferences about habitat associations of tree species should be robust to the statistical method used, but few studies have assessed whether different methods lead to the same conclusions about which environmental factors shape the species assemblages in tropical forests (but see Harms et al. 2001; Itoh et al. 2010).

In this study, we quantified tree species-habitat associations in the 25-ha terra firme Amacayacu Forest Dynamics Plot (AFDP), located in the Colombian Amazon. The spatial variation in, but weak correlation between, topography and soil chemistry in the AFDP provides an ideal setting for testing the relative influence of these environmental variables in shaping the compositional patterns of Amazonian TFFs. We evaluated the extent to which spatial variation in topography and soil chemistry jointly or independently explain patterns of tree species-habitat associations. Given that topography explains variation in forest composition at intermediate and regional scales (Duivenvoorden and Duque 2010), we predicted that it would also be an important driver of habitat association at smaller spatial scales within AFDP. However, we also predicted that tree species distributions would respond to variation in soil chemistry or potential toxins (i.e., exchangeable Al and Mn). We sought to disentangle the relative importance of these factors by generating contrasting habitat definitions using each set of variables jointly and independently in our analyses. We evaluated the robustness of our inferences by using both the TT and IAAFT analytical methods for testing habitat associations. Our findings point to a general framework for how tree species-habitat associations should be evaluated in forests worldwide.

Methods

Study area

This study was carried out in a highly-diverse Amazonian TFF in the southern part of the Colombian Amazon, hereafter named the Amacayacu Forest Dynamics Plot (AFDP). This plot is part of the Center for Tropical Forest Science - Forest Global Earth Observatory (CTFS-ForestGEO; Anderson-Teixeira et al. 2015), a global network that comprises >60 forest plots that were established following the same protocols (Condit 1998). The AFDP harbors around 1200 tree and shrub species in 25-ha (Duque et al. 2017) and is located in the Amacayacu National Natural Park (3°48′33.02" S and 70°16′04.29" W) on tertiary sediments of the Pebas formation (Hoorn 1994). The AFDP was established on a transitional area between low dissected tertiary plains and waterlogged soils on low terraces of the alluvial plain, which creates a depression that remains swampy in a small portion of the plot for a few months, but not in every year. The swampy area is seasonally flooded due to the interaction of poor drainage of soils in

the bottom part of internal valleys, the drainage of streamlets during the wet season, and the high seasonal level of the Amazon River's water table. The life zone of the AFDP corresponds to a Tropical wet forest (Holdridge 1978).

In the USDA Soil Taxonomy System (Soil Survey Staff 1999) the soils in the plot are Ultisols, including Paleaquults and Aquic, Oxyaquic, and Typic Paleudults (depending on landscape position), some of which contain plinthite (B.L. Turner and A. Duque, unpublished data). In general, soils in the Amacayacu Park have low fertility, pH and base saturation due to the dominance of minerals such as kaolinite and quartz, which are generally poor in nutrients (Chamorro 1989). Although the swampy area is not directly flooded by the Amazon River, it may influence the spatial variation within the plot in soil chemistry. The mean annual temperature is 25.8 °C, mean annual precipitation is 3216 mm with no months with less than 100 mm, and mean relative humidity is ca. 86% (climate statistics for the weather station at the airport at Leticia, 55.39 km away from the plot; Prieto 1994).

Plot census

We used spatially explicit data on tree species distributions from the AFDP establishment in 2007. During this census, all shrubs, trees, palms, and tree ferns with diameter at breast height (dbh) ≥1 cm were mapped, tagged, measured, and collected for species identification following the standardized methods for long-term tropical forest dynamics plots (Condit 1998; Anderson-Teixeira et al. 2015). Voucher specimens were deposited and identified in the Herbario Amazónico Colombiano (COAH) of the Instituto Amazónico de Investigaciones Científicas (SINCHI).

Topography and soil data

We divided the AFDP into 625 quadrats of 20×20 m and assigned to each quadrat values for three topographic and 12 soil chemical variables (Supplementary material, Fig. S1). We carried out a topographic survey estimating the elevation at the 5 m × 5 m scale, following the standard CTFS-ForestGEO protocol (Condit 1998). Based on this, the elevation, slope, and convexity were calculated at the 20 m scale using the convexity function available in the CTFS R Package (http://forestgeo.si.edu/). For each quadrat, elevation

was calculated as the mean elevation of the quadrat's four corners, and convexity as the mean elevation of the focal quadrat minus the mean elevation of its eight neighboring quadrats. For edge quadrats, convexity was defined internally as the elevation of the center point minus the mean elevation of the four corners. Each quadrat's slope was estimated by dividing each quadrat into four 10 m × 10 m sub-quadrats, calculating the slope from the elevations obtained from three randomly selected locations within each of the four sub-quadrats, and averaging the resulting slope values.

Soil cores were collected at 252 points in the plot during March 2011 using a protocol described previously (John et al. 2007; Baldeck et al. 2013). Samples were air dried (10 d, 22 °C) and sieved <2 mm to remove stones, debris, and soil fauna. Soil pH was determined in deionized water and 10 mM $CaCl_2$ in a 1:2 soil to solution ratio using a glass electrode. Concentrations of Al, Ca, Fe, K, Mg, Mn, and Na were determined by extraction in 0.1 M $BaCl_2$ (2 h, 1:30 soil to solution ratio), with detection by inductively-coupled plasma optical-emission spectrometry (ICP–OES) on an Optima 7300 DV (Perkin-Elmer Ltd., Shelton, CT) (Hendershot et al. 2008). Total exchangeable bases (TEB), exchangeable cation concentration (ECEC), and base saturation (BS) were calculated after kriging as follows: TEB was calculated as the sum of Ca, K, Mg, and Na; ECEC was calculated as the sum of the charge equivalents of Al, Ca, Fe, K, Mg, Mn, and Na; BS was calculated as (TEB ÷ ECEC) × 100. Extractable phosphate was determined by extraction in a solution containing 30 mM NH_4F and 25 mM HCl (Bray-1) with phosphate detection by automated molybdate colorimetry on a Lachat Quikchem 8500 (Hach Ltd., Loveland, CO). Soil nutrients were block kriged according to the procedure described by John et al. (2007). This involved interpolation of measured values incorporating spatial variation in variogram models, yielding estimates of nutrient concentrations in each quadrat.

Role of topography vs. soils in explaining tree species-habitat associations

To evaluate the role of topography and soil chemistry in explaining tree species-habitat association patterns, we assessed the extent to which the abundance and distribution of tree species were associated with alternative habitat maps generated from three different sets of environmental variables quantified at the 20 m × 20 m

quadrat scale: topography, soil, and topography plus soil (all). Figure 1 illustrates our overall approach to defining the tree species-habitat associations in the AFDP.

Based on each independent set of environmental variables (Fig. 1a), habitat maps were defined by cluster analyses, so that, for a given habitat map, every 20 × 20 m quadrat in the plot is ultimately assigned to a habitat. Since there is a wide variety of clustering methods and criteria to classify and decide the optimal

number of clusters (e.g., Fraley and Raftery 2007; Legendre and Legendre 2012), determining how finely divided habitats should be is not straightforward, and there is no definitive approach. A simple and widely used method is to generate a dendrogram using hierarchical clustering of the set of environmental variables (Reynolds et al. 2006; Altman and Krzywinski 2017). We used Ward's minimum variance method of hierarchical clustering and made selective cuts across the
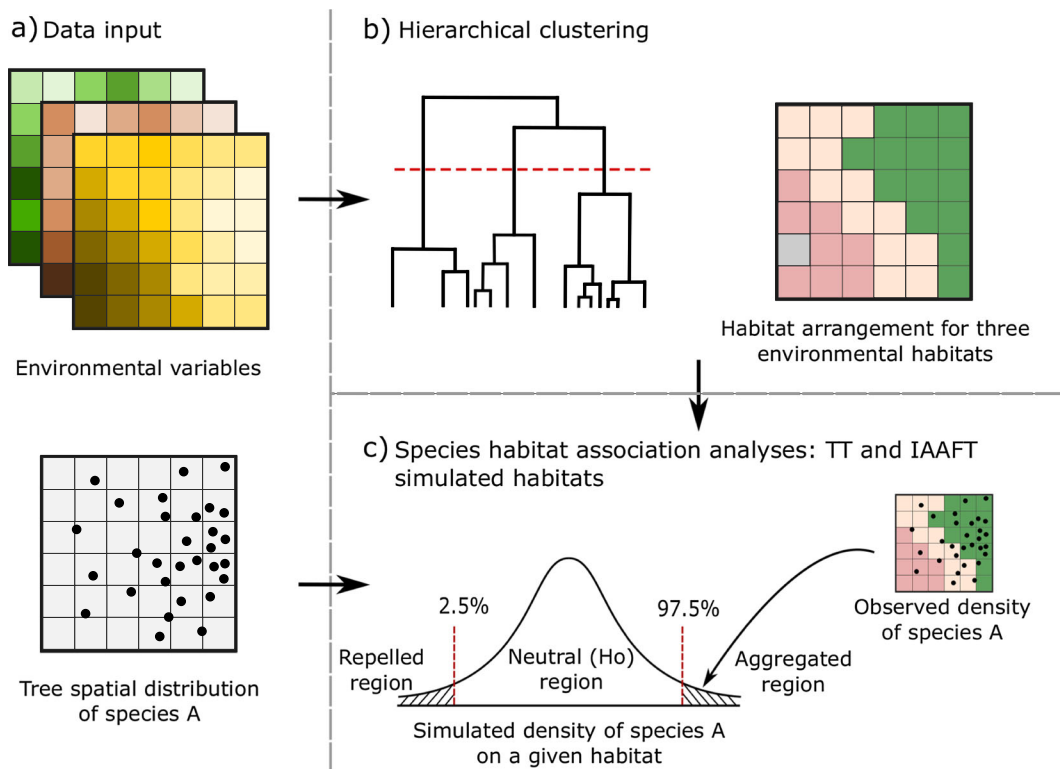

Fig. 1 Analytical procedure to evaluate tree species-habitat association in Forest Dynamics Plots. To exemplify, the general procedure is shown assessing association of species "A" on green habitat. **a** Data input consists of the environmental variables quantified at the 20 m × 20 m quadrat scale and spatially explicit tree distribution of each species in the plot, showing an example for one species. **b** Hierarchical clustering is employed to generate a dendrogram from the set of environmental variables and a selective cut (red dashed line) is used to define habitats. In this example, there are three habitats. Based on the range of environmental variables, each quadrat in the plot is then classified as belonging to a particular habitat, producing a habitat map in which quadrats belonging to the same habitat are here represented by same color. **c** The observed relative tree density of each species on each habitat is calculated relative to the species' overall tree density and is compared with a distribution of null relative tree densities representing what would arise under the hypothesis of spatially

random distribution of the species with respect to habitats. The null distribution is generated by maintaining the tree species distribution, but rearranging the habitats using the torus translation approach (TT; Harms et al. 2001) or randomizing the habitats to maintain their spatial structure using the iterative amplitude adjusted Fourier transform (IAAFT; Schreiber and Schmitz 2000) and recalculating the relative tree density for each habitat rearrangement. A species is significantly positively (i.e., aggregated) or negatively (i.e., repelled) with a given habitat if the observed relative density from the true habitat map of a species is greater (or less) than at least 97.5% (or 2.5%) of the simulated relative densities (i.e., $\alpha = 0.05$). In the example, the observed relative density of species "A" on the green habitat is greater than that estimated from simulated maps more than 97.5% of the time. Hence, species "A" is significantly positively or aggregated on this habitat. The procedure is repeated for each of the sufficiently abundant species in the community and for each habitat

dendrograms to build up maps with three and four habitats (Fig. 1b), which produced a total of six alternative habitat maps (two from each of the three sets of environmental variables). This approach to defining habitats does not use information on the actual distributions of the tree species, and therefore could be viewed as a purely statistical rather than an ecological description (Altman and Krzywinski 2017). However, in order to test hypotheses about the importance of alternative environmental factors for determining tree species distributions, habitats should be defined a priori, independently of the trees. We initially constructed habitat maps by grouping all soil chemistry versus all topographic variables. However, in doing so, some variables with reduced effects on plant distribution (e.g., Na) could obscure the effects of variables that were more influential. We evaluated this possibility by testing species distributions with habitat maps constructed using each soil and topographic variable separately. The inferences we made about the relative importance of topography versus soil properties for habitat filtering when using habitats defined by single variables were similar to those obtained when habitats were defined by grouping all topographic or all soil variables as a set (see *Results*). We therefore present only the results obtained when the variables were grouped.

We performed species-habitat association tests for each of 612 species (including 98 unidentified morphospecies) with 25 or more stems (dbh ≥ 1 cm) in the AFDP. While this is a conservative threshold commonly employed to differentiate rare from abundant species (Hubbell and Foster 1986; Pitman et al. 1999), it could affect statistical power to detect habitat associations. We therefore repeated the habitat association tests using different abundance thresholds for each habitat map (species with 50, 75, 100 or more stems). For each of the six different habitat maps, we calculated the observed tree density of each species on each habitat relative to its overall tree density. We generated null distributions of the relative tree densities of each species on each habitat expected under a hypothesis of random distribution of tree individuals with respect to habitats. Then, we tested whether the observed species relative density on a habitat was different from that expected from the null distribution (Fig. 1c). Species with observed relative densities on a given habitat less than or equal to the 2.5 percentile of the null distribution were considered significantly negatively associated (i.e., repelled). Species with observed relative densities on a given habitat greater than or equal to the 97.5 percentile of the null distribution were considered significantly positively associated (i.e., aggregated). Species were considered as neutrally distributed on a habitat when the observed relative density fell between these percentiles in the null distribution.

For each of the six habitat maps, we evaluated the sensitivity of the species-habitat associations to the habitat randomization procedure using two methods to calculate confidence intervals for the null hypothesis of no association between species and habitats. The first method employed was the torus translation procedure (TT), which generates simulated maps by applying a random toroidal rotation and reflection of the true habitat map wrapping around the edges of the plot each 20 m increments (see Harms et al. 2001 for details). The second method employs the iterative amplitude adjusted Fourier transform (IAAFT) to randomize the map of habitats in a way that preserves both the frequency and the spatial structure (i.e., the autocorrelation function) of the habitats as in the original map (Schreiber and Schmitz 2000; Venema et al. 2006). IAAFT is a method to generate surrogate fields that test for non-linearity in time series (Schreiber and Schmitz 2000), and it has been applied to randomize scattered cloud fields (Venema et al. 2006), digital elevation models (Detto et al. 2013), and in other ecological applications (e.g. Deblauwe et al. 2012). The TT analysis was conducted using R version 3.4.2 (R Core Team 2017), while the IAAFT was performed using a Matlab function (Venema et al. 2006).

The main difference between the IAAFT and TT is that IAAFT does not alter the habitat structure by wrapping strips of quadrats around the edges and causing artificial landscape fragmentation. IAAFT tests the association by creating alternative habitat maps with statistical properties similar to the original map, but with different location of the habitats. In addition, the IAAFT generates 1000 random maps, while the simulated maps obtained from the TT method depends on the plot dimensions and three further translations of the true map. In our case, the AFDP has 25-ha, with a 25 (N-S) × 25 (E-W) grid of 625 20 m × 20 m quadrats, which produces 625 unique-torus translated maps. Three further maps are generated from each translation: 180° rotation, mirror image, and 180° rotation of the mirror image (sensu Harms et al. 2001), for a total of 2499 ((25 × 25) × 4–1) unique torus-translated maps different than the real map.

We tested the relative importance of topography versus soil chemistry in defining tree species-habitat associations for explaining tree species distributions using the six habitat maps. Our goal was to select the habitat map that would reflect the actual species-habitat associations of the tree community and indicate the importance of those environmental variables in determining species distributions. We accounted for the number of species positively and negatively associated with at least one habitat type within each of the six alternative habitat maps. We then compared these quantities among the habitat maps based on the results from the two methods of habitat randomization and different species abundance thresholds. The habitat map with the greatest number of habitat associations should reflect the most important combination of environmental factors explaining tree species distributions. Our rationale was that most tree species are not habitat generalists (Harms et al. 2001; Phillips et al. 2003; Davies et al. 2005; Chuyong et al. 2011), so we consider more cases of significant habitat association as indicating a better habitat definition. Habitat maps generating larger proportions of neutrally distributed or generalist species would indicate that the habitats were not well defined.

Beta diversity map and community composition differences

To visually interpret the species turnover between any two quadrats in the AFDP, we generated a map of community composition variation for the 612 species analyzed in this study. We used Nonmetric Multidimensional Scaling (NMDS) with Bray-Curtis dissimilarity and three ordination axes (Oksanen et al. 2016) to quantify spatial variation in species composition among the 20 m × 20 m quadrats. We translated each quadrat from the three-dimensional ordination space (Thessler et al. 2005) into a four-dimensional color palette of green, yellow, black, blue, using the function "colors2d" of the software package "matthewkling" (https://github.com/matthewkling).

Results

Environmental habitats

All environmental variables that we used to define habitats varied across the AFDP (Table 1). In general, the

correlation between topography and soil chemistry was low (Fig. S2). Only the effective cation exchange capacity, Al, and Mg content correlated with topographic variables (Pearson's $r > 0.40$ and $p < 0.05$; Fig. S2). The definition of habitats and their spatial arrangement changed depending on the set of variables employed (Fig. 2). The inclusion of only topographic variables produced maps in which quadrats of the same habitat were more contiguous (Fig. 2a, d), whereas the inclusion of variables related to soil chemistry produced a more fragmented (patchy) arrangement of habitats in the AFDP (Fig. 2b-f). Regardless of the number of groups or the set of variables used, topographic and soil chemical variables showed significant differences between habitats in all cases (Table S1).

Importance of topography vs. soil chemistry for tree species-habitat associations

We evaluated habitat associations for a total of 106,545 trees representing 612 species and 88 families in the AFDP. The total number of significant positive and negative associations varied strongly among habitat maps (Table 2). There were more species aggregated or repelled on one or more of the habitats defined by topography alone than those defined by soil or by topography plus soil variables (Table 2). The highest number of habitat associations arose for three and four topographic habitats using the IAAFT method (353 and 386 out of 612 species, respectively; Table 2). Similarly, using only topographic variables to define habitats yielded the greatest number of significant positive and negative associations out of the potential species-habitat combinations, regardless of the analytical method, the number of habitats, or the species abundance threshold employed (Fig. 3). The total number of significantly associated species was slightly greater for four than three habitats for both TT and IAAFT methods (Table 2). The TT and the IAAFT habitat randomization methods were consistent in that both pointed to the greater importance of topography, as opposed to soil chemistry, in determining the amount of habitat-associated species (Table 2; Fig. 3). However, the IAAFT method reported more species associated with one or more habitats than the TT method (Table 2). In all cases, the results were robust to the sample size threshold employed (Fig.3; Fig. S3).

Table 1 Summary statistics for environmental variables kriged at the 20 m × 20 m quadrat scale in the Amacayacu Forest Dynamics Plot

Environmental measure	Mean	SD	Minimum	Maximum
Topographic				
Mean elevation (m a.s.l.)	93.6	4.3	88.8	108.1
Convexity (dimensionless)	0.0	0.6	−1.6	2.4
Slope (°)	5.6	4.0	0.2	16.6
Soil chemistry				
Phosphorus (P)	8.9	2.2	2.4	17.8
pH	3.9	0.1	3.7	4.2
Aluminium (Al)	599.1	108.5	306.4	994.0
Calcium (Ca)	145.0	72.3	46.5	503.4
Iron (Fe)	6.9	2.5	2.2	19.9
Potassium (K)	46.1	5.7	31.8	72.4
Magnesium (Mg)	41.3	8.5	23.7	90.8
Manganese (Mn)	45.0	15.2	12.8	101.6
Sodium (Na)	3.9	1.3	0.6	10.1
Total exchangeable bases (TEB)	1.2	0.5	0.5	3.7
Effective cation exchange capacity (ECEC)	8.3	1.2	4.2	12.4
Base saturation (BS)	15.3	6.0	6.8	45.0
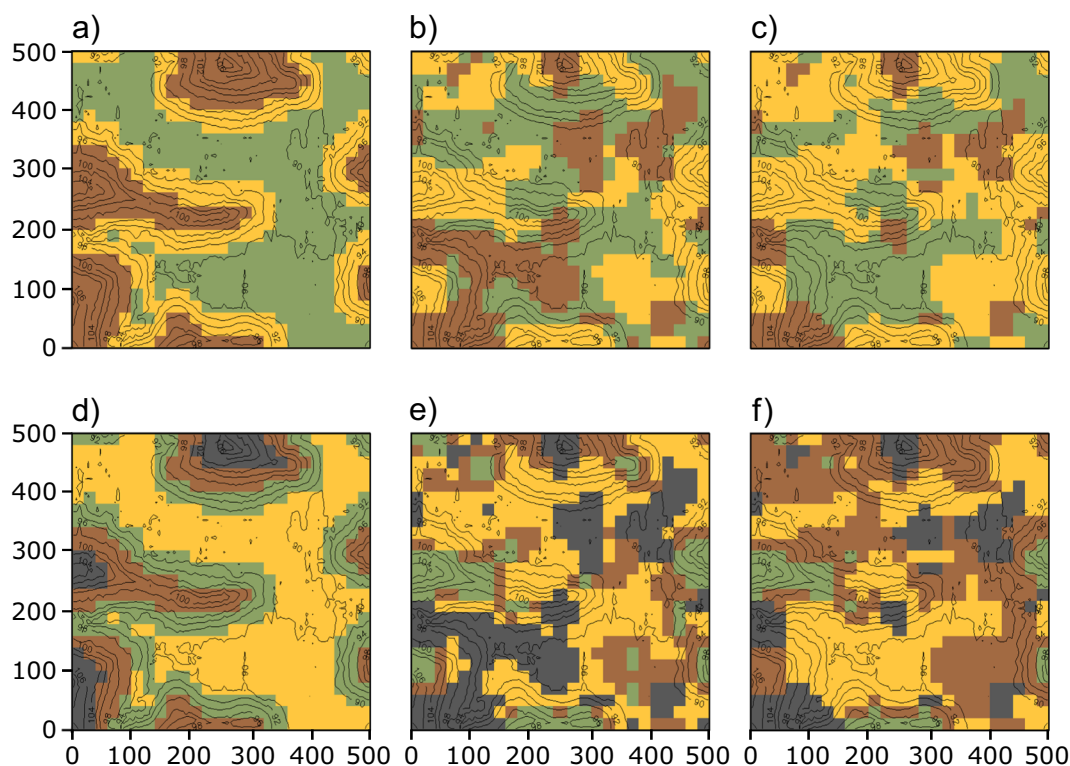
Fig. 2 The six habitat maps generated from topographic (**a**, **d**), soil (**b**, **e**), and topographic plus soil (**c**, **f**) sets of environmental variables at the 20 m × 20 m quadrat scale in the Amacayacu Forest Dynamics Plot, Colombia, that were tested in this study. Selective cuts in hierarchical clustering analysis were employed to define three (**a**, **b**, **c**) and four (**d**, **e**, **f**) habitats within each habitat map. Definition of habitats in terms of their variables (mean ± sd) can be found in the supplementary material (Table S1). North is oriented towards the top of the figure

Table 2 Number of tree species positively and negatively associated with three (H3: h1-h3) and four (H4: h1-h4) habitats defined from topographic, soil, and topographic plus soil (all) sets of environmental variables using two methods of habitat randomization, the torus translation (TT) and the iterative amplitude adjusted Fourier transform (IAAFT) in the Amacayacu Forest Dynamics Plot, Colombia

Number of habitats	Habitat association	Topography		Soil		All	
		TT	IAAFT	TT	IAAFT	TT	IAAFT
H3	h1+	68	72	46	60	32	40
	h2+	60	63	27	53	22	38
	h3+	130	140	12	15	15	25
	Total+	258	275	85	128	69	103
	h1-	73	81	29	43	18	24
	h2-	79	77	28	50	28	48
	h3-	176	181	13	15	20	28
	Total-	328	339	70	108	66	100
	Total associations	339	353	122	176	111	154
	Neutral	273	259	490	436	501	458
H4	h1+	32	34	46	56	32	39
	h2+	56	63	20	39	9	29
	h3+	60	59	35	58	30	62
	h4+	130	138	12	13	15	26
	Total+	278	294	113	166	86	156
	h1-	71	71	29	45	18	22
	h2-	72	78	23	42	23	37
	h3-	79	79	36	66	71	91
	h4-	176	182	13	21	20	25
	Total-	398	410	101	174	132	175
	Total associations	368	386	174	246	185	256
	Neutral	244	226	438	366	427	356

A total of 612 species with at least 25 stems in the first census of the plot in 2007 were tested for habitat associations. For each habitat (h), positive and negative associations are denoted by "+" and "-" symbols, respectively. "Total associations" refers to the total number of species that were significantly positively or negatively associated with one or more habitats of each habitat map. "Neutral" refers to the number of species that were not positively nor negatively habitat associated i.e., generalists. Note that the total number of associations is not the total sum of positive and negative associations because a species can be positively or negatively associated with one or more habitats

Community composition differences

The importance of topography in defining tree species habitat associations was also evident from the spatial variation in species composition, which, although calculated independently from the topographic habitat maps, showed striking similarity to them (compare topographic habitats in Figs. 2a, d; and the beta diversity map in Fig. 4h). While many species showed strong patterns of aggregation and repulsion to different habitats (Figs. 4a-g), there was still floristic variation that was not captured by the available data on topography or soil properties. Specifically, there was substantial floristic variation evident in the valleys, as evidenced by the variation from dark blue to green on the beta diversity map (Fig. 4h). Indeed, based on visual inspection, there are 11 species with tree aggregations in the valley of the southeast portion of the plot, an area that is not defined as its own habitat based on available environmental data (e.g., *Virola loretensis*, Fig. 4g).

Discussion

Patterns of forest diversity strongly depend on how tree species are distributed with respect to the environment. In the AFDP, a large fraction of tree species distributions were influenced by edaphic conditions. This is
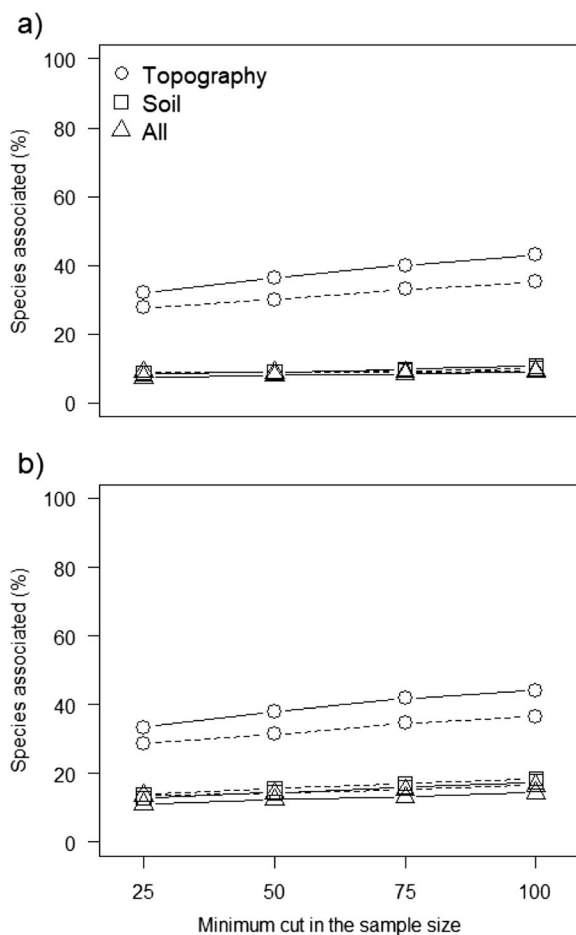
a)

b)

Fig. 3 Percent of positive and negative associations related to the potential species-habitat combinations on the three (H3: solid lines) and four (H4: dashed lines) topographic, soil, and topographic plus soil (all) habitat maps for different minimum cuts in the sample size, i.e., species with a minimum of 25, 50, 75, or 100 stems in the Amacayacu Forest Dynamics Plot. Species-habitat combinations are calculated as the number of species multiplied by the number of habitats for each habitat map and species abundance threshold. Results are shown for two methods of habitat randomization: the torus translation (TT, **a**) and the iterative amplitude adjusted Fourier transform (IAAFT, **b**)

consistent with findings for other Amazonian TFFs at intermediate and regional scales (Phillips et al. 2003; Tuomisto et al. 2003a; Honorio et al. 2009), and for other non-Amazonian tropical forests at local spatial scales in Panamá (e.g., Harms et al. 2001; Condit et al. 2013), Sri Lanka (Gunatilleke et al. 2006), Malaysia (Davies et al. 2005) and Cameroon (Chuyong et al. 2011). Our results therefore indicate that fine-scale niche-based processes (Ricklefs 1977; Tilman 1982) are important mechanisms structuring tree communities in Amazonian TFFs, which have been considered to be

fairly homogeneous (Pitman et al. 2001). Revealing the particular environmental factors that most strongly structure forest diversity is important for understanding community assembly processes, and it is evident from our findings that testing how well alternative environmental variables explain tree species distributions is a crucial step. Only when the key environmental factors important for structuring forest diversity are identified can more informed experimental studies be designed to test hypotheses about the underlying mechanisms that dictate the species-habitat association patterns in tropical forests.

Relative importance of topography and soil chemistry in determining tree species-habitat associations

While many studies have used topography alone (Svenning 1999; Duque et al. 2003; Valencia et al. 2004; Gunatilleke et al. 2006; Jucker et al. 2018) or in combination with soil variables (Davies et al. 2005) to quantify the habitat associations of tree species, few have tested whether topography or soil variables better explain tree species distributions (Itoh et al. 2003; Dalling et al. 2012). We showed that a greater fraction of tree species have distributions correlated with the topographic than with the soil chemical variables analyzed in this study. We are aware that individual species vary in their responses to different environmental factors (i.e., soil chemistry could be more important than topography for certain species), but in this study, we focus on the community-wide consistency among species in their responses to different types of environmental variation, which suggests what is the most important environmental factor structuring diversity at a forest-wide scale. Interestingly, combining topography and soil chemistry in the AFDP resulted in fewer species-habitat associations than employing them separately, which further indicates that, unlike many other forests, these sets of environmental variables do not covary in this plot (Fig. S2) and makes the AFDP the ideal setting to test the relative influence of these environmental factors in shaping tree species distributions in Amazon terra firme forests. Likewise, our results indicate that the addition of further environmental variables (soil chemical to topographic) in defining habitats may not necessarily always yield better inferences because doing so can obscure the particular gradients to which trees may be responding.
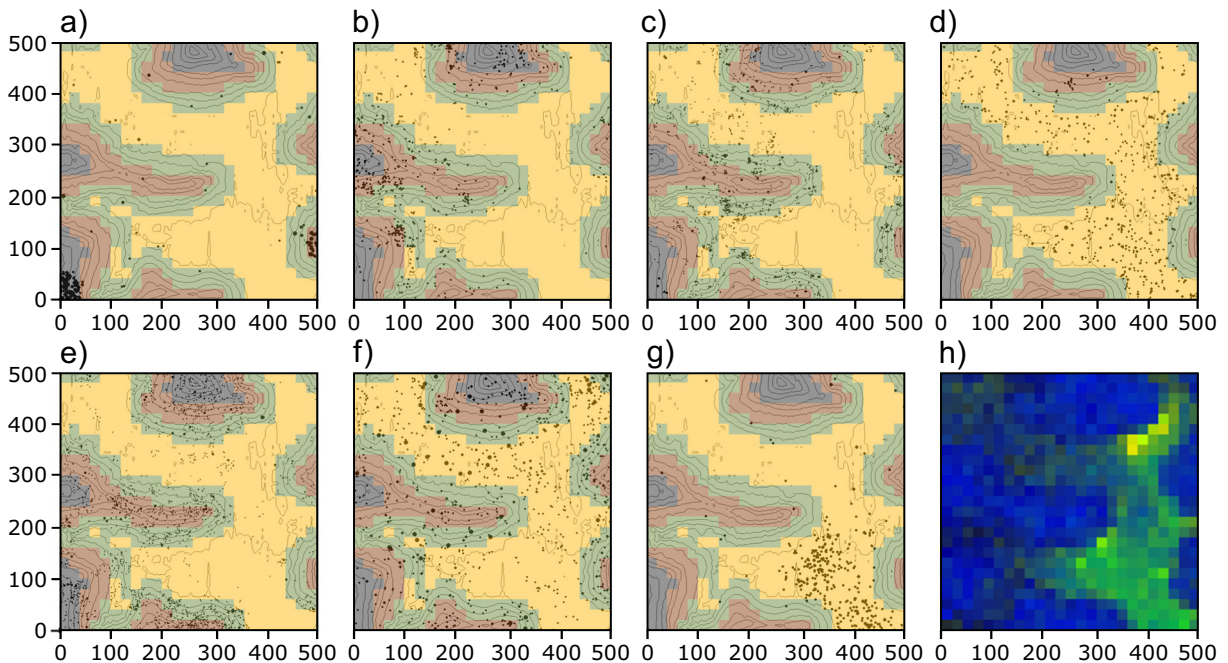
Fig. 4 Distribution maps of the stems of seven tree species exemplifying contrasting habitat associations overlain on the habitat map constructed for four topographic habitats (**a-g**) and of compositional variation of the tree community (**h**) in the Amacayacu Forest Dynamics Plot. For (a-g), colors indicate habitats, with grey for ridge tops, red for ridges, green for slopes, and orange for valleys (h1, h2, h3 and h4 respectively in Tables 2, and S1). First row: a species positively aggregated on ridge tops (**a**, *Chimarrhis glabriflora*), ridges (**b**, *Siparuna guianensis*), slopes (**b**, *Warszewiczia coccinea*) and valleys (**c**, *Zygia latifolia*). Second row: a species aggregated on ridges and slopes and neutrally distributed on ridge tops and valleys (**e**, *Rinorea lindeniana*), a species that is neutrally distributed across all habitats i.e., generalist (**f**, *Virola pavonis*), a species aggregated on valleys that is especially clustered on the quadrats on the southeast of the plot (**g**, *Virola loretensis*), and the community composition beta diversity map (**h**, sensu Thessler et al. 2005) for the 612 species with 25 or more stems in the plot. In (**a-g**), each dot depicts a stem and its size is scaled to the diameter at the breast height. In (**h**), quadrats with more similar colors depict more similar tree species composition (see methods). North is oriented towards the top of the figure

Baldeck et al. (2013) reported that for six of the eight tropical forests tested, adding soil variables to topography doubled the proportion of variation in compositional structure explained by habitat filtering and that soil resources were as important as topography in explaining the variation in species composition in these forests. To compare our individual species-based study with those at the community level, in a *post-hoc* analysis, we reproduced Baldeck's analysis for the 612 species employed in this study. We found that topography explained more of the community compositional variation than soils (10% and 7%, respectively) and that the variation explained by soil properties after accounting for topography was much lower than that explained by the topographic variation alone (3% versus 10%, respectively). Recent analysis in the Wanang FDP in Papua New Guinea has also shown reduced importance of soil nutrients relative to topography for forest community compositional variation mainly due to of the importance of natural disturbances such as landslides in determining tree species distributions (Vincent et al. 2018).

Why does topography seem to be more important than soil chemistry in constraining species distributions in the AFDP?

Factors such as the lithostratigraphy of the outcropping geological units and the variation in the density of streamlets could lead to dissected topographies and to contrasting soil properties in Amazonian forests (Duivenvoorden and Duque 2010), which in turn creates spatial variation in soil physical properties (e.g., drainage) and soil water distribution (Daws et al. 2002; Allié et al. 2015) and seems to define hydrological niches in the AFDP. Our study indicates that water availability controlled by the drainage network (i.e., hydrological

niches) is likely to be a key determinant of tree species distribution in the Amazonian TFFs. In fact, it has been shown that hydrological niches influence the species distribution (Schietti et al. 2014), functional traits (Cosme et al. 2017) and drought tolerance strategies (Brum et al. 2018; Oliveira et al. 2018) of Amazonian trees. However, variation in soil drainage had not been reported to play a key role in determining species distribution at the local spatial scales that we show here (< 1 km^2). Differential responses of trees to past drought events across topographic habitats in the AFDP support this inference (Zuleta et al. 2017) and such drought-related mortality is likely to have shaped forest composition in relation to physiographic characteristics, as observed in other Amazonian and neotropical forests (Engelbrecht et al. 2007; Cosme et al. 2017; Oliveira et al. 2018; Zhang et al. 2018). Other factors such as the occasional flooding during extreme rain events in the southeast part of the valleys of the AFDP may also have influenced the greater role played by topography on the species distribution patterns in this forest because the flooding can act as a filter for waterlogging tolerant species. Although this can be supported from the aggregation of some species in this part of the plot, more comprehensive data on the flooding process and the species physiology is needed to test it.

A likely cause of the relatively low power of soil chemistry to differentiate habitats for tree species as well as of the incongruence between soils and topography is that the AFDP is located on a single parent material (i.e., the Pebas formation; Hoorn 1994), which is expected to homogenize soil formation and edaphic properties (Brady and Weil 2002). Nonetheless, soil variables differed significantly among habitats defined based on topography, soil chemistry, or both together (Table S1), implying that such statistical differences alone are not sufficient to define the habitats important for tree species. Another potential cause of the low power of soils in determining species-habitat associations at the community level could be the inclusion of all of the soil variables together. However, we ruled out this possibility because even when analyses were performed using single soil variables or excluding cations that are not strongly associated with tree growth (e.g., Na), single soil variables did not explain the tree distributions as well as the topographic variables.

In general, soils in the AFDP are relatively infertile. Except for P, soil nutrient concentration of Ca, Fe, K, Mg, and Mn are much lower in Amacayacu than in

Yasuní, the 50-ha plot located in the northwestern Amazonia. Comparing soil variation (standard deviations) in the AFDP with three other tropical FDPs (Barro Colorado Island, La Planada, and Yasuní), we found that variation in Mg was higher in these plots (Table 1 in John et al. 2007) than in the AFDP (Table 1). On the contrary, variation in Ca, K, and P was much higher in the AFDP than in La Planada and Yasuní. In Amazonian forests, the influence of the soil chemical component on forest composition (Tuomisto et al. 2003a; ter Steege et al. 2006; Higgins et al. 2011), structure (Laurance et al. 1999; de Castilho et al. 2006; Quesada et al. 2012), dynamics (Phillips et al. 2004; Quesada and Lloyd 2016), and functioning (Quesada et al. 2009a; Lloyd et al. 2015), has widely been recognized at regional scales. Yet, at smaller spatial scales in the Amazon, contrary to other tropical forests (Davies et al. 2005), soil chemistry has a lower discriminative power than topography in defining the tree community composition in the AFDP.

Inference robustness to the habitat randomization method

The predominant effect of topography over soil in defining species-habitat associations in the AFDP was independent of the randomization method (TT and IAAFT) employed. However, we found subtle differences in the species-habitat associations reported by both randomization methods. For instance, regarding the three habitats defined from topographic variables, TT reported eight positively associated species not defined when employing the IAAFT randomization method (hereafter referred to as unique TT-specialists), whereas 23 positively associated species were reported by the IAAFT (Table S2). Since both methods attempt to disassociate the clumped spatial patterns due to seed dispersal limitation from that due to habitat association, it seems that the degree of clustering of TT- and IAAFT-specialist species could define differences in the capability to detect habitat associations by both methods. To test this idea, we calculated the relative conspecific Omega (Ω) neighbourhood density index (sensu Condit et al. 2000) for the specialist species exclusive from each method at five spatial scales (10, 20, 30, 40, and 50 m). After the 20 m spatial scale, we found that the proportion of species spatially aggregated ($\Omega \geq 1$) was slightly higher for unique TT-specialist species (range from 25% to 50%) than for unique IAAFT-

specialist species (range from 9% to 17%) (Table S2). More non-aggregated tree species ($\Omega < 1$) reported as unique IAAFT- but not TT-specialists may indicate constraints of the TT method to effectively control the non-independent distribution of trees with respect to conspecifics (Law et al. 2009). This might be due to the fact that the TT provides inflated type I error rates in case of highly aggregated species patterns because it alters the structure of the habitats by placing strips of quadrats to the opposite side of the plot when they are beyond the border in each translation (Harms et al. 2001). However, the IAAFT method could underestimate the spatial autocorrelation function at small scales (Deblauwe et al. 2012). The loss of spatial autocorrelation also induces inflated type I error rates because of the incapability of the null model to account for the presences in highly spatially autocorrelated cases. Certainly, choosing the most appropriate null models is not straightforward, but convergent results from the use of alternative habitat randomization methods help us to ensure robustness on the identification of significant species-habitat associations.

Additional factors influencing the observed species-habitat association patterns

The proportion of species neutrally distributed across all habitats of the six soil-topographic habitat maps employed in our study (Table 2), could either show the wide tolerance of these species to the array of environmental variables evaluated in the AFDP, be the result of randomness and dispersal limitation (Hubbell et al. 1999; Hubbell 2001; Condit et al. 2002), or be overestimated because they respond to unpredictable or unmeasured environmental variation (e.g., light). On one hand, in the Yasuní terra firme FDP in the Ecuadorian Amazon, Valencia et al. (2004) reported subtle differences in the tree species composition along a ridge-valley catena, supporting a greater role of short-distance dispersal and recruitment on structuring tree communities. However, some topographically defined habitat association signals were consistent between the Yasuní and the Amacayacu FDPs. For example, *Rinorea lindeniana*, a dominant shrub of the Violaceae family, was strongly associated with the ridge-slope habitats of both plots (Fig. 4 in Valencia et al. 2004 and Fig. 4e in this study). Comparative analyses of species-habitat association between the three large existing plots available in Amazonian TFFs (Anderson-Teixeira et al.

2015; Duque et al. 2017) will surely shed new insights onto the extent at which different species assembly mechanisms operate to maintain the high diversity recorded at local scales in the Amazonian TFFs (ter Steege et al. 2003; Duque et al. 2017).

On the other hand, even despite our extensive topography and soils data, we still observed unexplained variation in the composition of the tree community in the valley habitat ($p < 0.05$ for pairwise dissimilarity index). It is important to note that no habitat map that we evaluated was able to capture this floristic variation, which may have been caused by an unmeasured environmental factor. Given our comprehensive environmental data and the mortality responses of trees in this forest to drought (Zuleta et al. 2017), what seems more likely, is that these tree species are highly sensitive to microtopographic variation that remained unresolved even with elevation data collected at the 5 m × 5 m scale. Whether topography, soil chemistry, or some other factor (e.g., mycorrhizal associations; Peay et al. 2015) is the strongest driver of tree species distributions undoubtedly varies across forest systems. Therefore, evaluating the relative importance of these factors for forest community assembly, requires robust tests of alternative hypotheses about them, including consideration of spatial scale (Chase 2014), relevant environmental and biological variables, and the robustness of inferences to different analytical methods, as we have done here.

Conclusion

For this Amazonian TFF in Colombia, we found that hydrological variation related to topography to be more important than soil chemical variation in structuring tree species distributions, suggesting that responses to water availability may be an important process of niche assembly in this forest. Although many studies use data on mapped tree populations and spatial environmental variation to make inferences about how diversity is structured in species-rich tropical forests, they generally focus on a single type of environmental factor. However, our results show that in order to make robust inferences about the importance of environmental heterogeneity in structuring diversity, studies of habitat association must test alternative habitat maps with as comprehensive data as possible. The fact that even our extensive topographic and soil chemical data could not explain a substantial proportion of the floristic variation indicates that tree

responses are complex and that many interacting factors determine their distributions. While conclusions derived from one forest cannot, therefore, be generalized to others, avoiding arbitrary definitions of habitats is paramount not only to improve our understanding on the mechanisms contributing to the maintenance of diversity in tropical forests, but also on the mechanisms shaping tropical forest communities in the face of the extreme climatic events.

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