Determinants of tree species turnover in a southern Amazonian rain forest

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Abstract

Questions: What is the relative importance of environmental variables and geographical distances to explain tree species turnover? Are these patterns consistent for different tree categories, i.e. all trees (DBH $\geq$ 2.5 cm), large trees (DBH $\geq$ 10 cm), small trees *sensu lato* (DBH < 10 cm) and small trees *sensu stricto* (strictly understorey species, DBH < 10 cm)?

Location: Department of Beni, Bolivia, southwestern Amazon.

Methods: A total of 55 0.1-ha plots were inventoried in old-growth *terra firme* forest in seven sites. Composite soil samples from each plot were analysed for physical and chemical properties. Environmental and geographical influences on tree species turnover were quantified with Mantel correlations and variation partitioning based on multiple regressions on distance matrices.

Results: Floristic differences between sites yielded significant correlations with both geographical distances and environmental variables (pH, Ca, Mg, exchangeable acidity, C:N ratio, sand content) for all tree categories. Phosphorus was correlated with floristic patterns only for small trees *sensu stricto*. Together, geographical distances and environmental variables explained 62% of the floristic variation for all trees. Environmental variables explained more variation for large trees than for small trees *sensu stricto*.

Conclusions: The results support the hypothesis that species distributions are driven by both geographical distances (as quantifiers of dispersal processes) and environmental variables (niche factors) in similar proportions. Spatial floristic patterns of large trees and small trees *sensu stricto* were in general terms congruent.

Introduction

In tropical rain forests, and particularly in the Amazon region, the relative importance of the factors influencing spatial patterns of plant communities remains largely debated. Two major views have been put forward: niche assembly models explain species distributions as a result of competition for resources (Tilman 1994; Tuomisto et al. 2003a; Chave 2008), whereas dispersal assembly models, derived as one aspect of neutral theory (Hubbell 2001), explain species distributions through dispersal limitation (Bell et al. 1993; Seidler & Plotkin 2006; Rosindell et al. 2011). Since explanations from the two models are not exclusive, there is a recent tendency to take into account

elements of both models to explain floristic spatial patterns (Barot 2004; Macía et al. 2007; Haegeman & Loreau 2010; Mutshinda & O'Hara 2010), which has been defined as the continuum hypothesis (Gravel et al. 2006). Inclusive explanations seem to account for differences found at different spatial scales. At medium and large scales, i.e. landscape and regional scales as defined by Poulsen et al. (2006), John et al. (2007) and Sesnie et al. (2009), environmental variables (resource-driven processes) seem to predominate in determining floristic patterns and species distributions (Duque et al. 2002; Phillips et al. 2003; Tuomisto et al. 2003a; Macía et al. 2007; Ruokolainen et al. 2007; Sesnie et al. 2009; Andersen et al. 2010; Slik et al. 2010). At small scales, i.e. plot size (<50 ha), floristic

patterns seem to be more influenced by geographical distances (as indicative of dispersal limitation) than by the environment (Condit et al. 2002; Bohlman et al. 2008; Legendre et al. 2009). However, this general tendency is debated, especially because environmental condition gradients tend to be spatially autocorrelated (Ruokolainen et al. 2007).

Floristic patterns and species distributions have been studied using many different proxies (see Tuomisto 2010a; b for a review), but here we focus on species turnover because it affords testing of neutral predictions (Tuomisto & Ruokolainen 2006, 2008; Baselga 2010). Species turnover quantifies the proportion of species composition that changes among compositional units (Tuomisto 2010b). Research on species turnover in tropical forests has yielded three significant insights. First, the determinants of species turnover seem to vary from one region to another (Chave 2008). Researchers have reported that geographical distances have more influence on floristic distances in Central America (Chust et al. 2006) than in the Amazon basin (Phillips et al. 2003; Macía et al. 2007) or in Borneo (Potts et al. 2002; Paoli et al. 2006). Second, in the few studies that have directly measured soil properties from inventory plots in the Amazon, edaphic conditions were crucial to explain species turnover (Duque et al. 2002; Phillips et al. 2003; Tuomisto et al. 2003b; Macía et al. 2007; Ruokolainen et al. 2007; Bohlman et al. 2008).

Third, the relative effects of geographical and environmental factors on floristic patterns may depend on the life-history traits of the species in question, especially on the life form and dispersal strategies. Some authors have suggested that understorey species distribution is more dependent on the environment than canopy species distribution (Duque et al. 2002; Kristiansen et al. 2012), although this apparent difference might largely be due to sampling (Jones et al. 2008a). Few studies have separately analysed floristic spatial patterns between different life forms. Some of them have studied only one or two plant groups, i.e. pteridophytes and Melastomataceae (Tuomisto et al. 2003b) or palms (Normand et al. 2006; Sesnie et al. 2009; Andersen et al. 2010). Of the few studies that analysed all woody plants, including canopy and understorey species, in one case the distinction was made only on the basis of diameter (Duque et al. 2002) and did not include a real distinction of understorey trees *sensu stricto* (Macía et al. 2007).

The objectives of this paper are (1) to assess the relative influence of environmental and geographical distances in explaining variation in tree species turnover; (2) to determine which of the studied environmental variables are the most relevant in explaining patterns of species turnover; and (3) to compare congruence in these floristic spatial patterns between large canopy trees and two groups of small understorey trees, segregated first according to diameter and second according to adult stature.

Methods

Study area

We conducted the study in the Tsimane' Indigenous Territory (Territorio Comunitario de Origen Tsimane'), located in the south of the department of Beni, in the Bolivian Amazon (Fig. 1). The Tsimane' are one of the largest indigenous groups in the Bolivian Amazon and inhabit a densely forested area (Reyes-García et al. 2010). The study area has a mean annual temperature of 25.8 °C (Navarro & Maldonado 2002), and a mean annual rainfall of 1743 mm (Godoy et al. 2008). The region shows a strong annual seasonality, with 4 mo with less than 100 mm of precipitation. Most soils are quaternary alluvial sediments of fluvial origin, particularly acrisols and ferralsols (Navarro & Maldonado 2002). The study area is covered with old-growth forest, which has been degraded by selective logging in many places (Gullison et al. 1996). Different
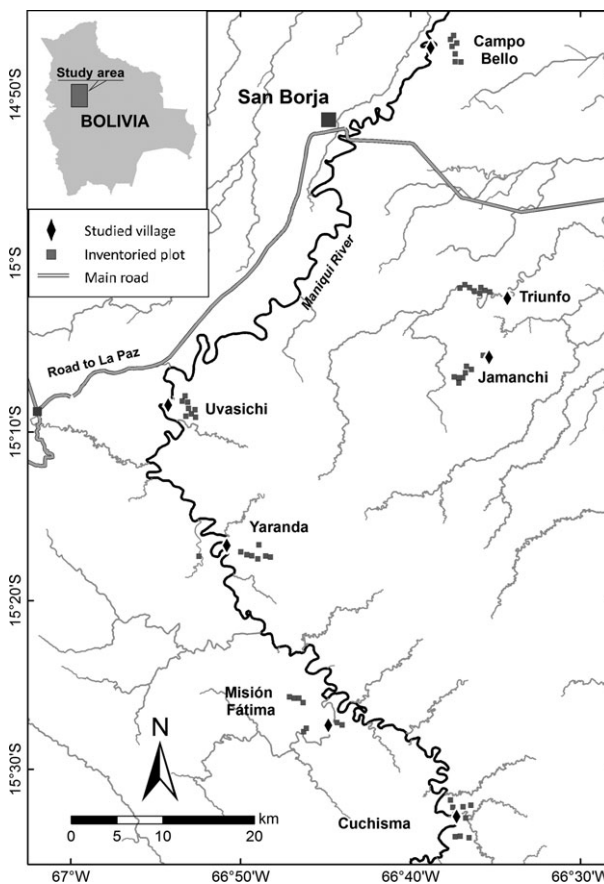

Fig. 1. Map of the sampling area showing the distribution of 55 0.1-ha plots in the Tsimane' territory, Bolivian Amazon.

broad forest types occur according to the flooding level history: most areas are never flooded and are covered with *terra firme* forests, but in some places seasonally or permanently flooded terrains present a range of *bajío* forests, with lower canopy height and tree diversity (Killeen et al. 1993; Macía 2008). In this study, we focus on lowland *terra firme* forests at elevations between 200 and 300 m a.s.l.

Floristic sampling

We inventoried 55 0.1-ha plots (50 m × 20 m) in *terra firme* forests within the territory of seven Tsimane' villages, between March and December 2009. The villages are settled along the Maniqui River in a north–south gradient or along logging roads (Fig. 1). We set up eight plots per village, except in one village where only seven plots were inventoried. The forest structure and topography in the studied area were generally homogeneous. We established plots in old-growth forests showing neither signs of recent human activity nor large canopy gaps, and at a minimal distance of 500 m from the closest house or agricultural field.

We measured all tree stems rooted within plots and with a diameter at breast height (DBH) ≥ 2.5 cm at 1.3 m above the ground. We measured multiple stems of the same tree separately but counting them as one individual. We collected voucher specimens for all individuals that we could not identify in the field. We sorted all vouchers to species or morphospecies level and identified them. Duplicates of the collections are deposited in LPB (Herbario Nacional de Bolivia, La Paz) and MA (Real Jardín Botánico, Madrid, Spain) herbaria, and unicates are kept in LPB. We included all morphospecies in the following analyses.

Environmental variables

We collected a composite superficial (0–15 cm) soil sample in each plot. Each composite soil sample was composed of five subsamples collected in the four corners and in the centre of each plot, and then mixed to obtain a unique sample for analysis. Soil samples were air-dried and transported to the Laboratory of Environmental Quality (Universidad Mayor de San Andrés, La Paz, Bolivia) for physico-chemical analyses. Samples were then sieved through a 2-mm sieve. Soil properties were determined following ISRIC protocols (van Reeuwijk 2002). Soil pH was measured in a 1:2.5 soil:1 M KCl suspension. Exchangeable bases (Ca, Mg, Na, K) were extracted with 1 M ammonium acetate solution, and exchangeable acidity was extracted with 1 M KCl solution. Exchangeable acidity contains the exchangeable fraction of aluminium. Total organic carbon and organic matter content

were determined following the Walkley and Black procedure (Walkley & Black 1974), total N following the semi-micro Kjeldahl procedure (Fawcett 1954), and available P with the Bray I method (colorimetry with blue ammonium molybdate; Murphy & Riley 1962). Texture was determined using the three-fraction method (van Reeuwijk 2002).

Data analysis

For all analyses, we subdivided the floristic data into four tree categories: (1) all trees (DBH ≥ 2.5 cm), (2) large trees (DBH ≥ 10 cm), (3) small trees *sensu lato* (*s.l.*, DBH < 10 cm), i.e. including juvenile stems of the large tree species, and (4) small trees *sensu stricto* (*s.s.*, DBH < 10 cm), i.e. excluding stems of the species that were included in the large trees category. We used this separation to allow comparison with other studies that have focused on canopy and understorey tree distributions (Duque et al. 2002; Macía et al. 2007).

We calculated three groups of distance matrices: (1) tree floristic distances, (2) environmental distances and (3) geographical distances. First, we calculated the Jaccard similarity index between plots for each of the tree categories and computed floristic distance matrices for each group as 1 – Jaccard index (Legendre & Legendre 1998). The Jaccard index is based on presence–absence data and quantifies the proportion of species shared by each pair of sites (Jaccard 1901; Tuomisto 2010c). Second, for all environmental variables, we calculated Euclidean distance matrices. Previously, we transformed exchangeable cation concentration values to their natural logarithms because plants are likely to be more responsive to differences in resources when resources are scarce (Jones et al. 2008a). Third, we calculated a geographical distances matrix as Euclidean distances. We applied a ln transformation to this matrix to make neutral hypotheses testable, as the theory predicts that floristic distance between two sites decreases approximately linearly along with the logarithm of geographical distance between these sites (Hubbell 2001; Tuomisto et al. 2003b).

To assess the role of the different environmental variables and geographical distances in explaining floristic patterns, we performed Mantel tests (r_M). Specifically, for each of the tree categories, we used Mantel tests to analyse correlations between (1) floristic and environmental distance matrices and (2) floristic and geographical distance matrices. We also performed a Mantel test between the floristic distance matrices of the two independent tree categories (large trees and small trees *s.s.*). To assess statistical significance at the $P < 0.001$ level, we ran 999 permutations in all cases. If floristic distances correlated significantly with environmental distances, we performed

partial Mantel tests, partialling out geographical distances, to verify whether the correlation remained significant after the effect of geographical distance had been taken into account. To visualize floristic patterns among the inventory sites, we performed non-metric multidimensional scaling (NMDS) ordinations.

To disentangle the relative contribution of environmental and geographical distances, i.e. to distinguish between pure environmental variation, spatial autocorrelation and their intercorrelation, we used variation partitioning analyses for each of the tree categories. Variation partitioning quantifies the statistical explanatory power of different groups of explanatory variables (Borcard et al. 1992; Tuomisto & Ruokolainen 2006). In our study, we based variation partitioning analyses on multiple regressions on distance matrices, a method similar to multiple regression analysis but that works on an unfolded distance matrix (Lichstein 2007; Goslee 2010; Smith & Lundholm 2010). For each of the four tree categories, we selected the significant environmental variables explaining the floristic patterns through a backward elimination procedure (removal criterion $P > 0.1$). We used three different models for variation partitioning. Model 1 includes matrices of environmental variables only, capturing environmental variation and environmental–geographical interactions. Model 2 includes ln-transformed geographical distances only, capturing geographical variation and environmental – geographical interactions. Model 3 includes environmental variables and ln-transformed geographical distances, capturing environmental variation, geographical variation and environmental–geographical interactions. The residuals of the most inclusive model (3) give the variation unexplained by environmental variables or geographical distances. We calculated the four fractions of variation in floristic distances by subtraction, using the R^2 of each regression (Legendre & Legendre 1998) as follows:

[a] = variation explained by environment = $R^2(3) - R^2(2)$;

[b] = variation explained by both environment and space = $R^2(1) + R^2(2) - R^2(3)$;

[c] = variation explained by geographical distance = $R^2(3) - R^2(1)$; and

[d] = variation unexplained = $1 - R^2(3)$.

As the fractions are subtractions, their significance could not be tested statistically (Legendre & Legendre 1998).

We ran all statistical analyses in R 2.11.1 using the 'vegan' package (R Foundation for Statistical Computing, Vienna, AT) for the Mantel and partial Mantel analyses, the 'ecodist' package for multiple regressions in variation partitioning, and the 'labdsv' package for NMDS ordination. The backward elimination procedure based

on distance matrices was performed using Permute! (http://www.bio.umontreal.ca/casgrain/en/labo/permute/index.html).

Results

Floristic variation

We measured and identified a total of 9082 tree individuals ≥ 2.5 cm DBH, representing 427 species and morphospecies in 55 0.1-ha *terra firme* plots (Table 1). We observed consistent differences in species richness and abundance in the four tree categories across the studied sites. We found the highest species richness in the Uvasichi plots and the lowest values in the Campo Bello plots, where the total richness accounted for only 36.5% of the total richness in Uvasichi. Large trees represented 36.4% of total individuals and 63.4% of total species (Table 1).

Juvenile individuals of canopy species represented most of the trees found in the understorey strata, and therefore the values of the group small trees *s.l.* were very close to those of the category all trees. Small trees *s.s.* were less diverse than the other tree categories, reaching an average of two to 13 species per plot, and representing 10.6% of total individuals and 34.0% of total species. The sum of large tree species and small tree species *s.s.* did not equal the total number of species because some individuals <10 cm DBH belonged to the large tree species category but never reached 10 cm DBH in our inventory. Specifically, there were 24 large tree species that never reached 10 cm DBH in our inventory and were therefore excluded from both categories.

In the NMDS ordinations, the position of plots showed a clear floristic separation between Campo Bello and the other sites for all floristic groups (Fig. 2). Triunfo and Jamanchi formed a consistent group that segregated from the other sites, but Cuchisama and Misión Fátima plots were widespread throughout the graphs. This pattern was relatively consistent among three of the floristic groups (Fig. 2a–c) but not for the group of small trees *s.s.* (Fig. 2d). The Mantel test between large trees and small trees *s.s.* was highly significant ($r_M = 0.46$, $P < 0.001$).

Environmental data and study sites

Soils showed clear differences between sites (Table 2). All soils were acidic with an average pH ranging from 3.86 to 5.11. We found the highest amount of all exchangeable cations (except Na) in Triunfo and the lowest in Misión Fátima. In contrast, Misión Fátima had the highest exchangeable acidity values and Triunfo the lowest. In all sites, Ca accounted for the largest part of the four principal exchangeable bases. The amount of available P was relatively homogenous among sites. For organic C, total

Table 1. Mean ± SD number of species and individuals per plot in four tree categories at eight study sites, as recorded in 55 0.1-ha plots in the lowland forests of the Tsimane' territory, Bolivian Amazon.

Study sites	Number of plots	All trees (DBH ≥ 2.5 cm)		Large trees (DBH ≥ 10 cm)		Small trees *sensu lato* (DBH < 10 cm)		Small trees *sensu stricto* (DBH < 10 cm)	
		Species	Individuals	Species	Individuals	Species	Individuals	Species	Individuals
Campo Bello	7	23 ± 3	89 ± 14	13 ± 3	50 ± 7	15 ± 3	38 ± 12	2 ± 1	8 ± 9
Cuchisama	8	47 ± 9	190 ± 40	24 ± 6	71 ± 9	36 ± 8	119 ± 36	6 ± 3	12 ± 11
Jamanchi	8	50 ± 5	153 ± 15	22 ± 2	51 ± 6	40 ± 5	103 ± 16	11 ± 3	21 ± 11
Misión Fátima	8	55 ± 7	188 ± 23	29 ± 6	64 ± 17	41 ± 6	124 ± 36	11 ± 3	23 ± 10
Triunfo	8	40 ± 6	158 ± 24	22 ± 3	57 ± 10	31 ± 4	101 ± 22	7 ± 2	14 ± 8
Uvasichi	8	63 ± 14	208 ± 41	28 ± 5	60 ± 10	50 ± 12	147 ± 38	13 ± 5	28 ± 15
Yaranda	8	50 ± 11	162 ± 19	25 ± 4	68 ± 10	37 ± 9	94 ± 23	10 ± 4	16 ± 8
Total	55	427	9082	258	3306	343	5770	145	964

N and organic matter, Triunfo had the highest values. Yet, we observed the highest value of the C:N ratio in Misión Fátima. Concerning soil textural properties, Misión Fátima had the highest sand proportion and the lowest proportion of silt and clay. In contrast, Triunfo showed the highest clay proportion and the lowest sand proportion.

Many environmental variables correlated with each other (Table 3). In particular, exchangeable cation amounts were correlated, with the exception of Na, which was not correlated with any other environmental variable. Calcium was also correlated with pH, whereas Ca, Mg and K were strongly correlated with the amount of sand and clay, but not with the amount of silt.

Determinants of floristic variation

All floristic groups showed strongly significant Mantel correlations for five environmental variables: two exchangeable cations (Ca, Mg), exchangeable acidity, C:N ratio and
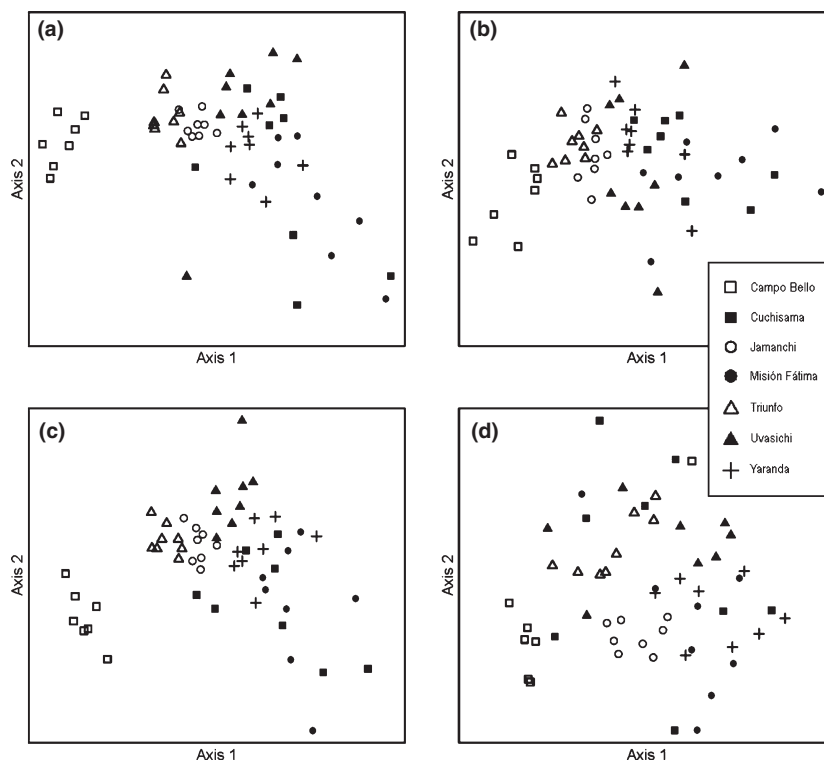

Fig. 2. Non-metric multidimensional scaling (NMDS) site scores for 55 0.1-h plots in lowland forest in the Tsimane' territory, Bolivian Amazon; (**a**) all trees (DBH ≥ 2.5 cm); (**b**) large trees (DBH ≥ 10 cm); (**c**) small trees *sensu lato* (DBH <10 cm); (**d**) small trees *sensu stricto* (DBH < 10 cm).

Table 2. Mean ± SD data for the environmental variables recorded in 55 0.1-ha plots at seven sites in the lowland forests of the Tsimane' territory, Bolivian Amazon.

Variable	Campo Bello	Cuchisama	Jamanchi	Misión Fátima	Triunfo	Uvasichi	Yaranda
pH (in KCl)	5.11 ± 0.96	4.21 ± 0.58	4.56 ± 0.47	3.86 ± 0.20	4.91 ± 0.39	4.61 ± 0.76	4.14 ± 0.55
Ca (cmol$_c$ kg^{-1})	6.04 ± 2.41	4.15 ± 4.51	4.65 ± 2.78	2.01 ± 2.54	9.83 ± 1.65	2.99 ± 1.62	3.08 ± 2.36
Mg (cmol$_c$ kg^{-1})	1.64 ± 0.57	0.85 ± 0.83	1.55 ± 0.96	0.71 ± 0.76	2.29 ± 0.46	0.97 ± 0.12	1.57 ± 1.15
Na (cmol$_c$ kg^{-1})	0.03 ± 0.01	0.05 ± 0.05	0.04 ± 0.01	0.03 ± 0.01	0.05 ± 0.01	0.03 ± 0.01	0.07 ± 0.08
K (cmol$_c$ kg^{-1})	0.20 ± 0.04	0.23 ± 0.18	0.15 ± 0.11	0.10 ± 0.06	0.30 ± 0.12	0.14 ± 0.05	0.19 ± 0.08
Exchangeable acidity (cmol$_c$ kg^{-1})	0.14 ± 0.19	1,20 ± 0.93	0.53 ± 0.64	2.25 ± 1,42	0.12 ± 0.09	0.38 ± 0.41	1.22 ± 1.05
Sum of Ca, Mg, Na, K	7.91 ± 2.47	5.28 ± 5.45	6.39 ± 3.78	2.86 ± 3.25	12.46 ± 2.04	4.13 ± 1.65	4.92 ± 3.00
Available P (mg kg^{-1})	5.46 ± 1.25	10.63 ± 5.90	3.53 ± 1.69	4.00 ± 1.40	7.33 ± 3.64	4.90 ± 1.95	4.65 ± 1.40
Total N (%)	0.11 ± 0.01	0.15 ± 0.05	0.10 ± 0.05	0.11 ± 0.04	0.22 ± 0.04	0.11 ± 0.03	0.15 ± 0.05
Organic C (%)	0.98 ± 0.18	1.47 ± 0.35	0.77 ± 0.30	1.13 ± 0.39	1.52 ± 0.44	1.16 ± 0.29	1.16 ± 0.39
Organic matter (%)	1.66 ± 0.30	2.55 ± 0.60	1.31 ± 0.49	1.69 ± 0.29	2.63 ± 0.74	1.99 ± 0.50	1.99 ± 0.68
C:N ratio	8.60 ± 0.87	10.08 ± 2.16	7.80 ± 0.99	11.35 ± 4.10	6.99 ± 1.07	10.78 ± 1.80	8.04 ± 2.22
Sand (%)	24.3 ± 9.9	43.4 ± 21.3	31.0 ± 13.7	49.8 ± 17.9	17.6 ± 8.7	43.1 ± 17.2	25.3 ± 18.5
Silt (%)	37.9 ± 7.4	21.4 ± 9.2	25.0 ± 9.9	18.5 ± 11.3	21.5 ± 13.9	20.9 ± 8.7	24.9 ± 10.1
Clay (%)	37.7 ± 13.0	35.4 ± 17.3	43.8 ± 20.5	31.8 ± 9.8	59.5 ± 13.6	36.0 ± 11.9	49.8 ± 20.4

sand content (Table 4). The correlations were significant although weak for exchangeable K.

Soil pH and silt content yielded significant Mantel correlations with all groups except large trees. The sum of exchangeable cations yielded significant correlations with all groups except small trees *s.s.* Nevertheless, we did not use this latter variable for further analyses because Ca and Mg contents accounted for most of the sum value, and significantly explained floristic patterns. Available P yielded a significant Mantel correlation only for small trees *s.s.* Soil Na content, total N, organic C, organic matter and clay amount showed no statistically significant Mantel correlations with any group of trees.

All tree groups showed strong statistically significant Mantel correlations with ln-geographical distances (Table 4). The five most important environmental variables remained significant when the effect of geographical distances was partialled out, and the correlations remained mostly unchanged, regardless of partialling out ln-geographical distances or not (except for pH and exchangeable acidity). Similarly, for small trees *s.s.*, the partial Mantel correlation for available P remained significant.

The step-wise selection procedure for environmental variables in multiple regression analyses showed that soil sand content and exchangeable acidity significantly explained the floristic patterns of all four tree groups (Table 5). However, Ca was most strongly significant ($P < 0.001$) in explaining the floristic patterns for all tree categories, with the exception of small trees *s.s.*, best explained by exchangeable Mg.

Variation partitioning analyses showed differences regarding the determinants of floristic patterns among tree groups, and geographical distances explained the main amount of variation for all groups. However, for large trees

a major amount of relative variation (36.2%) was explained by environmental variables with respect to the other tree groups. The group small trees *s.s.* showed reverse patterns, as environmental distances accounted for a small part (17.1%) of explained variation (Fig. 3B). For the four groups, the variation explained by both environmental variables and geographical distances was important (6.8–13.3% of total variation; Fig. 3A). A large part of the total variation remained unexplained (38.3% for all trees and 71.0% for small trees *s.s.*; Fig. 3A). The unexplained component increased as the sample size decreased: small trees *s.s.* had the smallest number of individuals and showed the highest unexplained variation.

Discussion

Determinants of species turnover: environmental vs geographical distances

Our results support the idea that environmental factors and geographical distances are both necessary to understand tree floristic patterns in southern Amazonian *terra firme* forests in several ways. First, the highest Mantel correlation coefficients are obtained for geographical distances, but the coefficients for two exchangeable cations (Ca and Mg) are comparable to those. Three other edaphic variables (exchangeable acidity, C:N ratio and sand content) also contribute to explain floristic patterns for all tree categories. Second, partial Mantel tests show that the contribution of edaphic variables remains significant and even in some cases increases when geographical distances are taken into account, suggesting that the contribution of edaphic variables to explain floristic patterns is not due to spatial autocorrelation. Third, in variation partitioning analyses for all tree categories, both geographical and environmental distances independently explain sizable

Table 3. Pearson correlation matrix of environmental variables recorded in 55 0.1-ha plots at seven sites in the lowland forests of the Tsimane' territory, Bolivian Amazon.

	pH	Ca	Mg	Na	K	Exchangeable acidity	Sum of Ca, Mg, Na, C	P	N	C	Organic matter	C:N	Sand	Silt
pH														
Ca	0.58***													
Mg	0.23	0.77***												
Na	−0.08	−0.03	−0.01											
K	0.26	0.76***	0.69***	0.03										
Exchangeable acidity	−0.63***	−0.58***	−0.41**	−0.03	−0.36**									
Sum of Ca, Mg, Na, C	0.42**	0.96***	0.85***	−0.03	0.78***	−0.36**								
P	0.09	0.31*	0.15	−0.03	0.39**	0.28*	0.28*							
N	0.22	0.70***	0.64***	0.06	0.72***	0.74***	0.74***	0.43**						
C	0.13	0.47***	0.37***	−0.05	0.54***	0.52***	0.52***	0.53***	0.75***					
Organic matter	0.19	0.53***	0.43**	−0.02	0.59***	0.55***	0.55***	0.60***	0.81***	0.95***				
C:N	−0.18	−0.45***	−0.51***	−0.16	−0.40**	−0.45***	−0.45***	0.01	−0.49***	0.14	−0.02			
Sand	−0.22	−0.67***	−0.79***	−0.05	−0.58***	0.26	−0.74***	−0.02	−0.60***	−0.34*	−0.37**	0.57***		
Silt	0.26	0.08	−0.03	0.01	−0.14	−0.11	0.03	−0.24	−0.09	−0.20	−0.16	−0.30*	−0.39**	
Clay	0.05	0.65***	0.85***	0.05	0.70***	−0.20	0.76***	0.17	0.68***	0.48***	0.49***	−0.41**	−0.80***	−0.23

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 4. Mantel correlations between floristic and environmental differences along with their partial Mantel correlations with the effect of geographical distances (GD) partialled out for significant variables, between 55 0.1-ha plots in lowland forests in the Tsimane' territory, Bolivian Amazon. Statistical significance was calculated with a Monte Carlo permutation test using 999 permutations.

Environmental variables	All trees (DBH $\geq$ 2.5 cm)	Large trees (DBH $\geq$ 10 cm)	Small trees *sensu lato* (DBH < 10 cm)	Small trees *sensu stricto* (DBH < 10 cm)
pH (in KCl)	0.22**	0.13	0.22**	0.18***
pH, GD partialled out	0.14*	0.05	0.14*	0.11*
Ca	0.53***	0.48***	0.46***	0.25***
Ca, GD partialled out	0.56***	0.47***	0.47***	0.19**
Mg	0.51***	0.47***	0.45***	0.25***
Mg, GD partialled out	0.54***	0.46***	0.46***	0.21**
Na	−0.01	0.02	0.01	0.04
K	0.15*	0.14*	0.12*	0.09*
K, GD partialled out	0.17*	0.14*	0.13*	0.08
Acidity	0.30***	0.22***	0.27***	0.25***
Acidity, GD partialled out	0.18***	0.11**	0.15**	0.15***
Sum of Ca, Mg, Na, K,	0.25***	0.18**	0.22***	0.14***
Sum, GD partialled out	0.17***	0.10*	0.13*	0.06
Available P	−0.06	−0.10	−0.05	0.16**
Available P, GD partialled out	−0.15	−0.17	−0.13	0.14*
Total N	−0.02	−0.06	−0.01	−0.01
Organic C	−0.11	−0.13	−0.11	−0.06
Organic matter	−0.12	−0.15	−0.12	−0.03
C:N ratio	0.25**	0.26**	0.24**	0.15**
C:N ratio, GD partialled out	0.29***	0.25**	0.23**	0.11*
Sand	0.32***	0.31***	0.29**	0.21***
Sand, GD partialled out	0.33***	0.30***	0.29***	0.18**
Silt	0.14*	0.07	0.14**	0.12**
Silt, GD partialled out	0.12*	0.03	0.12*	0.10*
Clay	0.06	0.02	0.05	0.06
Geographical distances	0.66***	0.53***	0.65***	0.49***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

parts of the total variation. Therefore, our results are consistent with other studies reporting significant contributions of both environmental and geographical factors on floristic patterns at comparable scales (Phillips et al. 2003; Tuomisto et al. 2003a; Vormisto et al. 2004; Macía et al. 2007; Duque et al. 2009; Sesnie et al. 2009; Andersen et al. 2010), further supporting the continuum hypothesis (Gravel et al. 2006).

Table 5. Multiple regression coefficients between floristic distance and environmental matrices.

	All trees (DBH ≥ 2.5 cm)	Large trees (DBH ≥ 10 cm)	Small trees *sensu lato* (DBH < 10 cm)	Small trees *sensu stricto* (DBH < 10 cm)
Ca	0.43***	0.40***	0.42***	n.s.
Sand	0.11*	0.12*	0.14*	0.12*
Acidity	0.17*	0.11*	0.15**	0.22***
Mg	n.s.	n.s.	n.s.	0.15*
K	n.s.	n.s.	−0.13*	n.s.
R^2	0.31***	0.25***	0.26***	0.12***

n.s. not significant coefficients. *P < 0.05; **P < 0.01; ***P < 0.001.

However, two biases challenge the interpretation of our results. First, the pure spatial fraction of explained variation is not necessarily due to seed dispersal, but may have an environmental component related to temporal variation (Jones et al. 2008b) that we did not capture, or to spatial autocorrelation of environmental variables not included here, mainly related to climate, such as rainfall. Second, the choice of the method used to model space might modify the relative contribution of geography and environment, although it has been suggested that the predictions of the neutral theory can only be tested using a distance approach (see Legendre et al. 2008 and Tuomisto & Ruokolainen 2008 for a debate between distance-based and canonical approaches; Stegen & Hurlbert 2011). Furthermore, a large part of the floristic variation remains unexplained in our models, suggesting either a bias due to sample size, or that other factors could be important to explain tree floristic patterns and that we did not take into account. Such factors include historical natural events and stochastic disturbance processes (Svenning et al. 2004; Svenning & Skov 2005; Cardinale et al. 2006; Hoorn et al. 2010), historical land use with varying degrees of intensity that may have influenced the distribution of some species (Heckenberger et al. 2003; Macía 2008) or other unmeasured environmental variables, such as rainfall, drainage, water availability in soils or depth of water table (Sollins 1998; Duque et al. 2002; Phillips et al. 2003; Tuomisto et al. 2003a; Brenes-Arguedas et al. 2011).

Environmental variables that contribute to explain floristic patterns

Differences in soil nutrient content and texture between plots explain a large part of the differences in floristic patterns in the study area. Consistent with other studies in the Amazon (Phillips et al. 2003; Macía et al. 2007; Ruokolainen et al. 2007) and throughout the humid tropics (e.g. Potts et al. 2002; Paoli et al. 2006), the strongest correlations with floristic patterns were for Ca and Mg, as well as exchangeable Al content. This is not surprising, since Ca and Mg are essential elements for cell processes (Honorio et al. 2009) and Al inhibits cellular growth and elongation (e.g. Kochian 1995).

Phosphorus is expected to be a limiting nutrient for plant growth in lowland tropical forests (Sollins 1998) but our results do not support this statement since available P was not significantly related to the floristic patterns, except for small trees *s.s.* This result is consistent with other studies finding no relation between P and
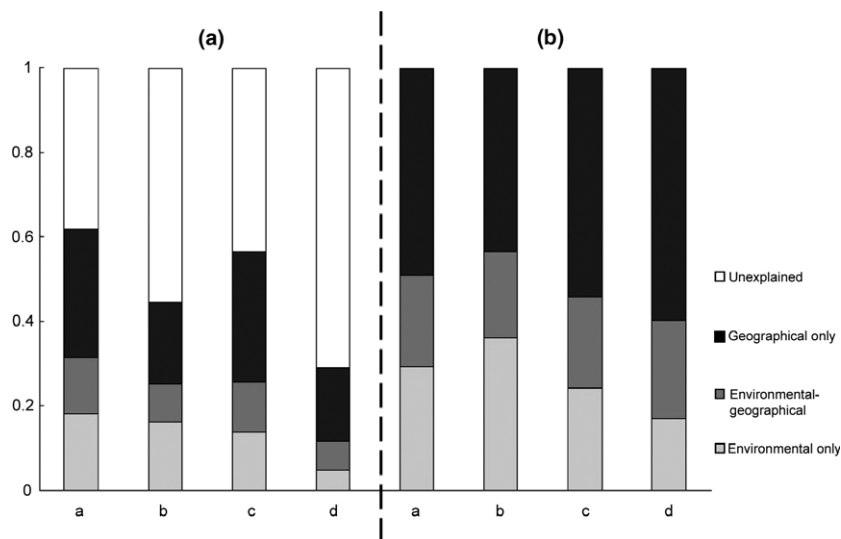

Fig. 3. Relative contribution of environmental variables, geographical distances, and the interaction of the two in explaining floristic patterns between 55 0.1-ha plots among four tree categories in lowland forest of the Tsimane' territory, Bolivian Amazon. A: Percentages of total variation. B: Percentages of explained variation only. Each bar represents a floristic group: **a** = All trees (DBH ≥ 2.5 cm); **b** = Large trees (DBH ≥ 10 cm); c = Small trees *s.l.* (DBH < 10 cm); d = Small trees *s.s.* (DBH < 10 cm).

floristic patterns in the Neotropics (Phillips et al. 2003; Poulsen et al. 2006; John et al. 2007; Macía et al. 2007), although in Asian Palaeotropics the opposite was found (Baillie et al. 1987; Paoli et al. 2006). Future studies are needed to clarify the significance of total and available P in plant–soil relationships.

Some studies have found N to be significant in explaining floristic patterns (Andersen et al. 2010 for understorey palms). However, in other studies N was relatively insignificant (e.g. Macía et al. 2007; Bohlman et al. 2008), probably because N is not limiting in lowland tropical rain forest soils (Sollins 1998; John et al. 2007). In our study, consistent with these results, total N had no influence on floristic patterns, although the C:N ratio was strongly related to it.

Studies that analysed pH found contrasting results regarding its influence on floristic patterns. Some authors found it significant (Baillie et al. 1987; Macía et al. 2007; Bohlman et al. 2008), while others were relatively insignificant (Tuomisto et al. 2003a). In our study, pH was significant to explain floristic patterns for all groups, except for large trees. It is possible that pH does not play an important role in the establishment of large tree species, whereas for small tree (understorey species) distribution, pH seems to be relevant. Bohlman et al. (2008) emphasized that the role of pH may be limited to some regions or taxa. Since pH was strongly correlated with Ca content, it is also possible that pH affects floristic patterns indirectly, modifying cation concentrations in soils (John et al. 2007).

Consistent with the results of earlier papers in the Neotropics (Poulsen et al. 2006; Bohlman et al. 2008; Sesnie et al. 2009), in our study sand content was important in explaining floristic patterns. Many studies have also found soil textural properties significantly associated to floristic patterns (Duque et al. 2002; Phillips et al. 2003; Tuomisto et al. 2003a).

At landscape and regional scales, many other studies in the Bolivian lowlands and elsewhere have found measured climatic variables such as rainfall amount and seasonality explain floristic patterns (e.g. Chust et al. 2006; Sesnie et al. 2009; Toledo et al. 2010). Since available meteorological data are very scarce in our study area, more efforts are needed in gathering such *in situ* climatic data.

Congruence between canopy and understorey tree species

Our results show a general congruence in floristic patterns between tree categories. This is highlighted by the significant Mantel correlation between large trees and small trees *s.s.*, suggesting that they are determined by common factors. We found that all trees and small trees *s.l.* categories show rather similar spatial patterns, which may be explained by the fact that most individuals of the category small trees *s.l.* are juveniles of canopy species. This finding implies that to show differences in understorey and canopy species turnover patterns, it is preferable to divide tree species according to their size at maturity rather than their diameter alone (Duque et al. 2002; but see Macía et al. 2007). However, we are confident that the cut-off used to determine tree categories (i.e. 10 cm DBH) might not be fully representative of all tropical forest strata.

Despite the general congruence observed, several differences were apparent in the floristic determinants of large trees and small trees *s.s.* First, the floristic patterns of large trees were explained more by environmental variables and those of small trees *s.s.* by geographical distances. Second, available P was significant only for small trees *s.s.* As P is principally present in the top 30 cm soil depth, it is possible that P acquisition is more efficient for understorey species than for canopy species (Liu et al. 2010), through differences in the root system or different seed sizes (e.g. Hanley et al. 2007). Third, the NMDS ordination for small trees *s.s.* shows a different spatial pattern than that for each of the other tree categories. Fourth, the R^2 in variables selection for small trees *s.s.* was the lowest, and the results were qualitatively different as different variables were selected. The differences observed between large trees and small trees *s.s.*, however, could, to a large extent, be due to sample size, since the density of small trees *s.s.* was much lower than the other categories (Jones et al. 2008a; see also Macía et al. 2007). Besides a probable sampling effect, our study is consistent with the results of Paoli et al. (2006), who found an increasing importance of niche processes when increasing tree diameter class, but not with those of Kristiansen et al. (2012) who found understorey palms of the Peruvian Amazon more strongly controlled by environmental conditions than canopy palms. One explanation for the significance of edaphic conditions on large trees is that geographical distances influence juvenile distribution through dispersal, and edaphic conditions subsequently modify species distributions through variation in growth and mortality rates (filtering effect; Metz 2012). Given the inconsistency of results within the Amazon, future research testing the influence of environmental factors on understorey vs large tree species is highly important, and should take into account species life-history traits and physiology, particularly their dispersal features and abilities to remove soil elements such as P.

Acknowledgements

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