Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest

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The congruence in floristic patterns between different life-forms of woody plants remains poorly understood in tropical rain forests. We explored whether the floristic patterns of woody plants, divided into small trees 2.5–10 cm dbh, large trees ≥10 cm dbh, and lianas ≥2.5 cm dbh were associated with each other or with patterns in soil properties, elevation, and geographical distances between sample plots. We also tested whether ecological amplitudes in relation to environmental variables differed among the plant groups. Trees and lianas were inventoried in 44 0.1-ha plots, distributed among three lowland and two submontane sites in the Madidi National Park, Bolivia. Soil samples were analysed for physico-chemical properties. Floristic differences between sites (as measured with each plant group separately) yielded significant Mantel correlations with each other, and with pH, Ca, Mg, elevation and geographical distance. Mantel correlations with edaphic distances were higher for large trees than small trees, but for Mantel correlations with geographical distance the situation was reversed. Environmental and geographical distances explained 31% of the variation in floristic differences for large trees, 22% for small trees, and 10% for lianas. The ecological amplitudes of lianas were wider than those of all trees for pH, Mg and elevation. The amplitudes of the two size classes of trees did not differ. In principal coordinates ordination, the three plant groups produced similar overall floristic patterns that were explainable by environmental factors.

Recent studies have sought to identify whether variation in plant species abundances, community composition and beta diversity in a given area can be explained by deterministic factors (soil or other environmental characteristics) or random effects (birth and death dynamics, dispersal limitation; Ruokolainen et al. 1997, 2007, Hubbell 2001, Duivenvoorden et al. 2002, Duque et al. 2002, Potts et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a, b, c, Vormisto et al. 2004). When support for environmental determinism is found in one plant group, two logical questions follow. First, which are the environmental variables that best explain the observed patterns in the focal plant group? Second, are the most important environmental variables generally relevant for all plants,

or do different plant life-forms react to environmental variation in dissimilar ways?

In a review on the importance of soils in tropical forests, Sollins (1998) suggested that relevant soil characteristics can be ranked in order of decreasing importance as follows: phosphorus availability, aluminium toxicity, drainage, water-holding capacity, and availability of base cations (K, Ca, and Mg), micronutrients (e.g. Zn) and nitrogen. More recent studies have more or less been in agreement with this ranking, except in relation to phosphorus and base cations. Two extensive studies reported magnesium to be more important than phosphorus in explaining the variation in floristic differences among 105 tree plots in Borneo (Potts et al. 2002) and 88 tree plots in Amazonian Peru

(Phillips et al. 2003). Similarly, a study on pteridophytes and Melastomataceae in Amazonian Ecuador (Tuomisto et al. 2003a) found that floristic differences between sites were correlated with differences in soil base cation content but not with differences in soil phosphorus content. On the other hand, a recent paper from Borneo found phosphorus to be the most important soil variable in a study on Dipterocarpaceae trees (Paoli et al. 2006). More observations are clearly needed on the relationships between plants on the one hand and phosphorus and other soil variables on the other.

If species distributions of different life-forms are largely controlled by the same external factors, congruent floristic patterns are expected among life-forms. Webb et al. (1967) were apparently the first to study this postulate, and they found that the variation in species composition in ground herbs, epiphytes and lianas had relatively little congruence with that in trees and shrubs. Similarly, Pérez-Salicrup et al. (2001) observed no correlation between floristic differences of trees and those of lianas. On the other hand, different taxonomically defined sets of rain forest plants, including both trees and smaller plants (herbs and shrubs), have been found to show similar floristic patterns in various studies (Tuomisto et al. 1995, 2003a, b, c, Ruokolainen et al. 1997, 2007, Ruokolainen and Tuomisto 1998, Vormisto et al. 2000, Higgins and Ruokolainen 2004, Duque et al. 2005).

It has been suggested that large plants have, on average, broader ecological amplitudes than small plants both in the tropics and elsewhere (Eriksson and Jakobsson 1998, Ruokolainen and Vormisto 2000, Lavergne et al. 2003), but to our knowledge this suggestion has not been tested for tropical rain forest plants with explicit soil data. A consequence of this phenomenon would be that large plants should show weaker relationships with environmental variables than small plants. Duque et al. (2002) indeed reported that differences in soil properties yielded higher Mantel correlations with understorey trees than canopy trees.

Lianas have received much less attention than trees in studies on tropical rain forests, despite their high species richness (Gentry 1991) and their importance to both rain forest dynamics (Phillips et al. 2002, 2005, Schnitzer 2005) and local human economies (Phillips 1991, Paz y Miño et al. 1995). Some studies have shown that the abundance of lianas increases with forest disturbance and the availability of light (Putz 1984, DeWalt et al. 2000, Schnitzer et al. 2000, Nabe-Nielsen 2001, Laurance et al. 2001, Pérez-Salicrup et al. 2001, Ibarra-Manríquez and Martínez-Ramos 2002). Lianas have been suggested to be less abundant and/or to have lower biomass on nutrient-poor soils than on more fertile soils (Proctor et al. 1983, Putz and Chai 1987, Gentry 1991, Laurance et al. 2001, DeWalt

et al. 2006), but this pattern is not always clear (Balfour and Bond 1983, DeWalt and Chave 2004). DeWalt et al. (2006) also reported that liana species composition in Bornean rain forests changed along a strong edaphic gradient but, to our knowledge, no attempt has yet been made to study the distribution of liana species in relation to explicitly measured soil chemical characteristics.

In the present paper, our aim is to document floristic patterns of both trees and lianas in Bolivian Amazonia. We are especially interested in whether the lack of congruence between the floristic patterns in these plant groups observed earlier (Webb et al. 1967, Pérez-Salicrup et al. 2001) also holds in our study area, which is close to the southern limit of the Amazon basin and contains an elevational gradient from the lowlands to submontane areas. More specifically, our research questions are: 1) are floristic patterns of large trees (≥ 10 cm dbh), small trees (2.5–10 cm dbh), and lianas (≥ 2.5 cm dbh) congruent with each other? 2) Are the floristic patterns congruent with patterns in environmental variables? 3) If so, which are the most important environmental variables for the different life-forms? 4) Are ecological amplitudes in relation to the environmental variables similar among the life-forms?

Methods

Study area

The study area is located in the Madidi National Park in Departamento La Paz, Abel Iturralde province in Amazonian Bolivia (Fig. 1). The Madidi region contains the last eastern foothills of the Andes and has a heterogeneous and steep topography, which makes the area difficult to access. The mean annual precipitation is 2335 mm and the mean temperature 26.1°C (Navarro et al. 2004). The area experiences a dry period between May and August (3–4 months), during which the rainfall is on average 81 mm/month and the periodic Patagonian winds may drop the temperature to as low as 4.5°C (Macía and Svenning 2005).

The vegetation in the study area is closed-canopy old-growth tropical rain forest. More than 90% of the area is non-inundated and well-drained terrain (tierra firme), and <10% is flooded seasonally or sporadically by streams and rivers (Macía unpubl.). Satellite images and field work indicated that permanently water-logged swamp forests do not occur in the study area. A preliminary description of vegetation types and checklist of the vascular plants for the Madidi region can be found in Fuentes (2005) and Jørgensen et al. (2005).
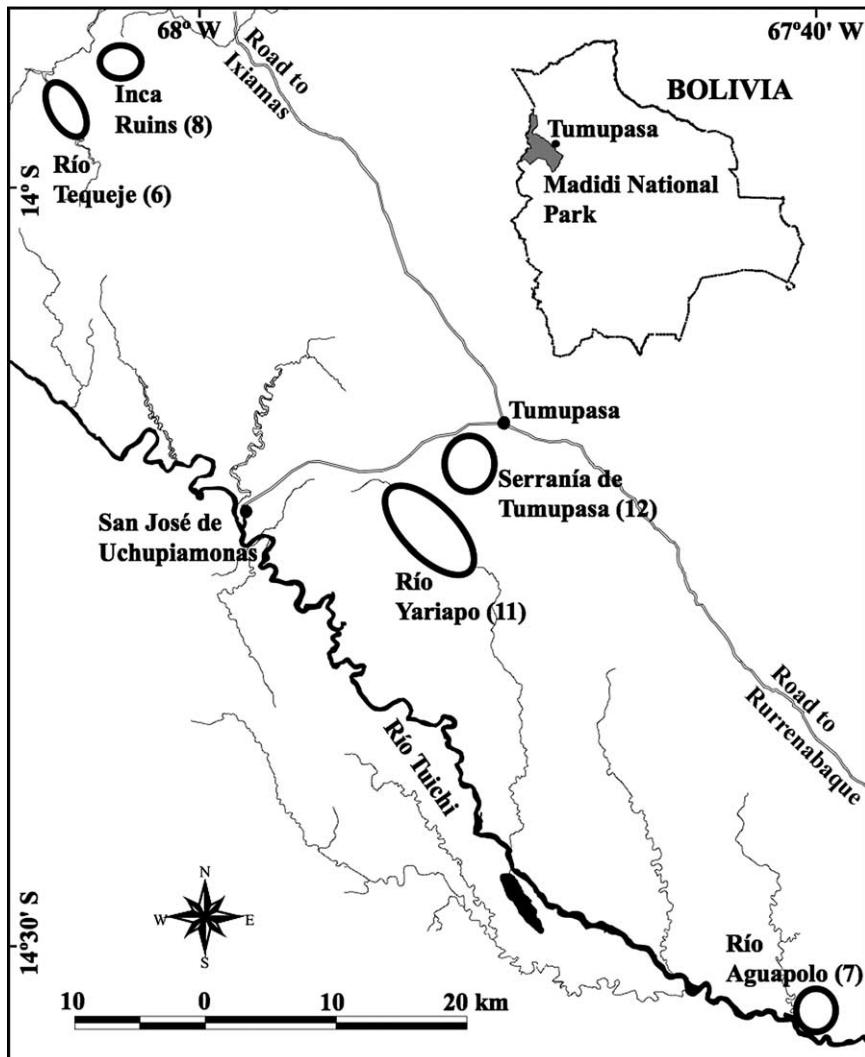
Fig. 1. Map of the study area showing the five study sites in the Madidi National Park, Bolivian Amazonia. Number of plots in each site is given in parentheses.

Floristic data collection

Fieldwork was carried out between 2001 and 2002 in five different sites along a north-south gradient (Fig. 1). Three sites were in the lowlands (260–610 m elevation) in the vicinities of Aguapolo, Tequeje and Yariapo rivers. Two sites were submontane (735–1070 m elevation), one in the Serranía de Tumupasa and the other in the proximity of an Inca fort ruins, ca 15 km south of Ixiamas village. The Ruins site was the only one with known human disturbance albeit >300 yr ago (Armentia 1897, Renard-Casevitz et al. 1988). The forest at the Ruins site was structurally indistinguishable from mature forest, but floristically it differed from the other inventoried sites (Macía and Svenning 2005).

Fourty-four 0.1-ha (50×20 m) plots were inventoried: 24 plots were established in the lowland sites (6–11 plots per site) and 20 plots in the submontane sites (8–12 plots per site; Table 1). Plot locations were selected to sample closed-canopy forests devoid of big canopy gaps, signs of recent human disturbance or obvious heterogeneity in physiognomy or soils. Plots within the same site were at least 500 m apart. More detailed habitat description, geographical coordinates and elevations of all plots are listed by Macía and Svenning (2005).

All woody plant stems ≥2.5 cm dbh (measured at 1.30 m perpendicularly above ground, also for lianas) and independently rooted in the ground within a plot were measured and given a field name. Multiple stems of trees and lianas were measured separately, but all

Table 1. Number of species (Spp.) and individuals (Ind.) in different woody plant life-forms and size classes at five study sites, as recorded in 44 0.1-ha plots in lowland and submontane forests in the Madidi National Park, Bolivian Amazonia. Mean ±standard deviation values per plot are given in parentheses; n =number of plots. The numbers of individuals of small trees and large trees add to less than the number of individuals of all trees, because any species that reached ≥10 cm dbh anywhere in the data set were excluded from the small trees category.

Life-form		Total (n =44)	Lowlands (n =24)			Submontane (n =20)	
			Aguapolo (n =7)	Tequeje (n =6)	Yariapo (n =11)	Ruins (n =8)	Tumupasa (n =12)
Woody plants	Spp.	861 (84±17)	280 (86±11)	305 (102±21)	327 (76±16)	307 (80±13)	405 (83±17)
(dbh ≥2.5 cm)	Ind.	12 709 (289±77)	1924 (275±41)	2055 (342±52)	2596 (236±42)	2806 (351±101)	3328 (277±73)
All trees	Spp.	674 (73±14)	219 (73±9)	247 (87±16)	256 (66±14)	255 (70±12)	331 (74±14)
(dbh ≥2.5 cm)	Ind.	11 600 (264±70)	1715 (245±33)	1863 (310±43)	2341 (213±39)	2576 (322±93)	3105 (259±66)
Large trees	Spp.	403 (33±8)	119 (34±4)	124 (36±6)	133 (29±7)	143 (35±5)	198 (34±11)
(dbh ≥10 cm)	Ind.	3219 (73±17)	423 (60±8)	482 (80±9)	742 (67±15)	739 (92±18)	833 (69±16)
Small trees	Spp.	271 (16±6)	63 (16±5)	87 (21±9)	82 (13±4)	71 (15±4)	101 (15±5)
(dbh <10 cm)	Ind.	1675 (38±20)	344 (49±14)	194 (32±18)	343 (31±19)	381 (48±28)	413 (34±19)
All lianas	Spp.	207 (11±5)	65 (14±3)	61 (15±6)	72 (10±4)	58 (11±4)	76 (9±4)
(dbh ≥2.5 cm)	Ind.	1109 (25±17)	209 (30±13)	192 (32±21)	255 (23±16)	230 (29±26)	223 (19±11)

stems rooting in the same place were counted as one individual for the purposes of the present paper. Voucher specimens were collected to represent each field name and when there was any uncertainty of the identity of a stem. The sterile vouchers were identified by matching them to already identified material in LPB, MA, MO, NY, and USZ (herbarium acronyms according to Holmgren et al. 1990). Duplicates of the specimens were distributed to taxonomic specialists who agreed to identify them (see Acknowledgements). A full set of duplicates is deposited in LPB and MA, and a nearly complete set in MO. Unicates are kept in LPB.

All analyses in the present paper are based on species-level identifications with all subspecific taxa lumped under the parent species. Morphospecies that could not be identified to a named species (25% of all species) are treated in the same way as identified species. Woody hemi-epiphytes were too rare for meaningful analyses and were therefore excluded.

Soil samples

One superficial soil sample (top 0–15 cm of the A horizon, i.e. below the organic matter layer) was collected at the centre of each plot. Chemical and textural soil properties were analysed at Univ. Autónoma de Madrid. Soil samples were air-dried and sifted through a 2 mm sieve. Soil pH was measured in a 1:2.5 soil:1M KCl suspension. Exchangeable cations (Ca, Mg, Na, K) were extracted with 1M ammonium acetate solution and cation exchange capacity was determined at pH 7 (van Reeuwijk 1995). The total organic carbon content was determined by the Walkley and Black method (Walkley and Black 1974), and total nitrogen by semi-micro Kjeldahl method, employing digestion and distillation units (Jackson 1964). The concentration of total phosphorus was determined colorimetrically in filtered samples by the molybdenum-blue method (Murphy and Riley 1962). Total concentrations of other elements (Fe, Mn, Zn, Cu) were obtained after acid digestion (HF-HNO$_3$-HClO$_4$) of soil samples (van Reeuwijk 1995). The concentration of different elements were determined by atomic absorption spectrophotometry using a Perkin-Elmer 3103 analyser. Particle size distribution was analysed using the hydrometer method (Day 1965) following H$_2$O$_2$ oxidation of organic matter and dispersion with hexametaphosphate.

Data analyses

Floristic patterns
The analyses were run separately for 1) all woody plants (trees and lianas ≥2.5 cm dbh); 2) all trees (≥2.5 cm dbh); 3) large trees (≥10 cm dbh); 4) small trees (species with all individuals between 2.5 and 10 cm dbh); and 5) all lianas (≥2.5 cm dbh). The large and small tree categories shared no species because if a species was represented in the large trees category, any juvenile individuals of it were discarded from the small trees category.

Most of the analyses use distance matrices that are based on either species composition, environmental characteristics or geographical position. Between-plot floristic distance is here defined as the proportion of non-shared species out of the total species list of the two plots to be compared (which equals one minus Jaccard index, Legendre and Legendre 1998).

Between-plot differences in environmental characteristics were expressed using Euclidean distance. Separate Euclidean distance matrices were computed for each soil variable. The concentrations of exchangeable bases (Ca, Mg, K, Na) were transformed to their natural logarithms before calculating the Euclidean distances in order to give a unit difference in concentration more weight when the element had a low concentration than when it had a high concentration. A combined Euclidean distance matrix was computed using just those soil variables that yielded significant Mantel correlations with the floristic distance matrices (see below). In this case, the variables were standardized to zero mean and unit variance before computing the distances in order to give each variable equal weight.

Geographical distances between plots were computed from the latitude-longitude information of the plots. Coordinates were obtained in the field with a hand-held GPS unit. The geographical distances were transformed to the natural logarithms to evaluate neutral theory's proposition (Hubbell 2001, Fig. 7.10) that floristic similarity decreases approximately linearly with increasing logarithm of geographical distance.

Our research questions about floristic patterns (congruence between plant groups, congruence between plants and environmental variables) can be statistically tested by analysing whether the corresponding distance matrices are positively correlated. If a congruence between trees and lianas is not explainable with the measured environmental variables, either we failed to measure the relevant environmental variables, or the floristic patterns are less related to soil properties than to biological and/or historical features, such as dispersal limitation.

The Mantel test of matrix correspondence was used to test for the correlation between distance matrices. The standardised form of the Mantel statistic (r_M) was used, which is mathematically similar to the Pearson correlation coefficient between the cell values of the two distance matrices (Legendre and Legendre 1998). An estimate of the statistical significance of the correlation coefficient is obtained by permutation; 999 permutations were used in all cases, which allows testing of the statistical significance at the $p < 0.001$ level for each correlation.

Mantel tests were run to quantify the correlations between plant groups, between each plant group and environmental distances, and between plant groups and geographical distances. When two floristic distance matrices were found to correlate with geographical distances, a partial Mantel test was also run to analyse whether the floristic distance matrices remained correlated after the effect of geographical distances had been taken into account. Partial Mantel tests between floristic and soil distance matrices were also run with the effect of elevation partialled out, to separate between the potential effects of elevation (as a surrogate of climate) and soil variables.

Because the edaphic, elevational and geographical distance matrices may be intercorrelated, their unique and shared contributions to explaining the variation in each of the floristic distance matrices were examined by variation partitioning based on multiple regression on distance matrices (Legendre et al. 1994, Legendre and Legendre 1998, Duivenvoorden et al. 2002, Tuomisto et al. 2003c). Multiple regression on distance matrices is conceptually similar to traditional linear multiple regression, except that the dependent and independent variables are distance matrices rather than the original variables on which the distance matrices are based.

In the present case, variation partitioning was run with three groups of explanatory variables. Consequently, the variation in the dependent floristic distance matrix was divided into eight fractions: a) uniquely explained by edaphic differences; b) uniquely explained by elevation differences; c) coexplained by edaphic and elevation differences; d) uniquely explained by geographical distances; e) coexplained by edaphic differences and geographical distances; f) coexplained by elevation differences and geographical distances; g) coexplained by all three groups of variables; h) unexplained.

The proportion of variation in each of these eight fractions were calculated from the proportions of explained variation (R^2) in seven multiple regression models, where either one, two or all three groups of explanatory variables were included. Model I initially included all edaphic variables, but backward elimination was applied so variables that did not have a statistically significant ($p < 0.05$ after Bonferroni correction) contribution to explaining the variation in the floristic distance matrix were eliminated (if only one edaphic variable remained, the variable that had shown the highest Mantel correlation with the floristic distance matrix was used). The R^2 of model I equals the sum of the fractions a, c, e, and g. Model II included elevation difference, if this was statistically significant at $p < 0.05$, and this model's $R^2 = b + c + f + g$. Model III included log-transformed geographical distance, if this was statistically significant at $p < 0.05$, and this model's $R^2 = d + e + f + g$. Model IV included all variables retained in the models I and II, with model's $R^2 = a + b + c + e + f + g$. Model V included all variables retained in models I and III, with model's $R^2 = a + c + d + e + f + g$. Model VI included all variables retained in models II and III, with model's $R^2 = b + c + d + e + f + g$. Finally, model VII included all variables retained in models I–III, with model's $R^2 = a + b + c + d + e + f + g$.

In order to visualise the floristic patterns among the inventory plots, we ran Principal coordinates analysis (PCoA) using the different floristic distance matrices.

In the resulting ordination diagrams, plots that are displayed close to each other are floristically relatively similar, while plots displayed far apart are floristically more different.

All multivariate analyses were done using the programs Le Progiciel R and Permute! (available on-line at <http://www.bio.umontreal.ca/legendre/index English.html>).

Comparisons between ecological amplitudes of trees and lianas

A straightforward measure of ecological amplitude is the range of values (absolute difference between the highest and lowest value) of a given environmental variable in the plots where a species has been observed. Specialist species will occur in plots that are relatively similar, whereas a generalist will occur in plots spanning a wide range of environmental conditions.

The observed environmental range does not only depend on the degree of specialisation of the species but also on its frequency (the number of 0.1-ha plots in which it was observed). A species that has only been observed in a few plots is likely to show a narrower range than a more frequent species, even if both have exactly the same ecological amplitude. Therefore, the comparisons of ecological amplitudes between two plant groups were performed taking into account frequencies as follows. First, for each frequency class (e.g. species observed in exactly two plots) separately, the median range of species along the environmental variable of interest was computed so that all species of both plant groups with that frequency were combined. Thereafter, for each plant group separately it was determined how many species had ranges above the overall median in each of the frequency classes. For the number of liana species above the median (L_g) of e.g. the frequency class of two, we can write L_{g2}, in which the subscript number indicates the frequency class. For trees, the corresponding notation is T_{g2}. Next we summed the numbers of above-median species per plant group – for lianas $L_{g2} + L_{g3} + \ldots + L_{gn} = L_g$ and for trees $T_{g2} + T_{g3} + \ldots + T_{gn} = T_g$. One should note that species that had been observed in only one plot were excluded, and only frequencies that included species of both plant groups under comparison were considered. The test statistic (K) was formed by calculating the absolute difference between the plant groups in the proportions of above-median species, as indicated by the formula:

$$K = \left| \frac{L_g}{L_s} - \frac{T_g}{T_s} \right|$$

in which L_s and T_s indicate the total included number of liana and tree species, respectively.

The statistical significance of K was estimated using Monte Carlo permutations, where everything else was kept fixed but the labels indicating plant group membership were permuted within each frequency class. After each permutation, the test statistic was recalculated. Any test statistic equal to or larger than the original was taken as evidence in favour of the null hypothesis that the amplitudes of the species in the two plant groups being compared do not differ. The randomisation procedure was repeated 999 times to test for statistical significance at the $p < 0.001$ level.

These analyses were run separately for each of those environmental variables that had been found important in the other analyses. The randomisation procedure was carried out with a macro made in Excel for MacOS X.

Results

Inventory data

A total of 12 709 individuals and 861 species of woody plants ≥ 2.5 cm dbh were found in the 44 inventoried 0.1-ha plots, with an average of 289 individuals (range = 154–503) and 84 species (range = 52–135) per plot (Table 1). On average, submontane plots had 307 individuals and 82 species, whereas lowland plots had 274 individuals and 85 species. Thirty-seven percent of the species were found in both lowland and submontane sites.

Free-standing trees ≥ 2.5 cm dbh constituted 91% of all individuals (mean = 264 individuals per plot) and 78% of all species (mean = 73 species per plot), whereas lianas had 9% of individuals (mean = 25 per plot) and 24% of species (mean = 11 per plot; Table 1). Large trees had more individuals per site than the other life forms, by about a factor of two when compared to small trees and a factor of three when compared to lianas. The percentages of tree and liana species add to >100% because the categorisation to life-forms was done on a per-individual basis, and some liana species grow as free-standing trees in their juvenile stage or rarely viceversa (a total of 19 species and 26 stems). The submontane Ruins site had the lowest observed liana species richness.

Environmental variation

Soils were generally acidic, with mean pH per site ranging between 3.08 and 5.32, but there were large differences among plots within sites, and some plots had neutral soils (Table 2). The concentration of exchangeable bases (Ca, Mg, Na, K) in the soil varied considerably among sites, with the highest values found in Tumupasa and the lowest in Ruins. The sum of

exchangeable bases was mainly determined by calcium, which accounted for 52–94% (mean = 72%) of it, and consequently also had a great contribution to the value of cation exchange capacity. Also magnesium concentrations were much higher than sodium and potassium concentrations in all sites. Soil contents of carbon, nitrogen and iron were, on average, higher in the submontane sites than in the lowland sites, but with big differences among plots. Soil phosphorus content ranged from 33 to 1302 mg kg^{-1} in the individual plots, but was, on average, rather similar in all sites except in Tumupasa, where average phosphorus content was higher than elsewhere. Similarly, the sites differed little in textural properties although there was variation among plots, and the dominant component was sand (>57%) in all sites. Seasonally flooded forests were only found in the lowland sites.

Many of the environmental variables were correlated with each other (Table 3). In particular, soil exchangeable calcium and magnesium concentrations were correlated both with each other and with soil pH and soil contents of potassium and zinc. Some differences were observed between the lowland and submontane plots: soil exchangeable calcium and magnesium concentrations were significantly correlated with soil texture and soil carbon and iron content in the lowland plots but not in the submontane plots, whereas with phosphorus the opposite was true. Elevation was correlated with soil exchangeable cation concentrations in the lowland plots but with soil nitrogen content in the submontane plots.

Floristic, environmental and geographical patterns

Floristic patterns of large trees and small trees were significantly correlated with each other ($r_M = 0.47$, p < 0.001). When the effect of either geographical or elevation distances was partialled out, the congruence among these two tree categories grew weaker but remained significant (partial $r_M = 0.37$ and 0.42, respectively, p < 0.001 in both cases). The floristic patterns of lianas were most correlated with all trees ($r_M = 0.40$, partial $r_M = 0.34$ with either geographical or elevation difference partialled out, p < 0.001 in all cases) and almost as correlated with large trees ($r_M = 0.37$, partial $r_M = 0.32$ with either geographical or elevation difference partialled out, p < 0.001 in all cases). The floristic patterns of lianas and small trees were less correlated ($r_M = 0.21$, partial $r_M = 0.16$ with elevation difference partialled out, partial $r_M = 0.14$ with geographical distance partialled out; p < 0.001 in the two first cases, p = 0.002 in the latter).

The Mantel test results differed between environmental variables. All plant groups had statistically significant Mantel correlations with five environmental variables: soil pH, soil Ca content, soil Mg content, soil content of exchangeable bases, and elevation (Table 4). In addition, soil C content yielded significant Mantel correlations with all plant groups except large trees, and soil N content, soil Fe content and soil cation exchange capacity yielded significant Mantel correlations with all plant groups except small trees. Below, we focus on

Table 2. Mean environmental variables recorded in 44 0.1-ha plots distributed over five sites in lowland and submontane areas in the Madidi National Park, Amazonian Bolivia. Ranges are given in parentheses; n = number of plots.

Variable	Lowlands			Submontane	
	Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa
pH (KCl)	4.14 (3.64–4.77)	4.40 (3.59–5.50)	5.01 (3.48–6.73)	3.08 (2.33–3.68)	5.32 (3.31–7.40)
Ca (cmol$_c$ kg^{-1})	3.58 (2.17–7.71)	6.32 (1.14–16.9)	9.65 (5.12–15.8)	1.86 (1.38–3.16)	23.3 (2.87–55.1)
Mg (cmol$_c$ kg^{-1})	1.17 (0.66–1.78)	1.49 (0.56–2.97)	2.08 (1.28–2.75)	1.00 (0.55–1.94)	3.19 (1.13–6.06)
Na (cmol$_c$ kg^{-1})	0.21 (0.09–0.32)	0.27 (0.18–0.37)	0.71 (0.37–1.39)	0.19 (0.10–0.27)	0.40 (0.13–0.72)
K (cmol$_c$ kg^{-1})	0.15 (0.09–0.20)	0.24 (0.09–0.50)	0.15 (0.09–0.24)	0.21 (0.09–0.35)	0.53 (0.25–1.09)
Sum of Ca, Mg, Na, K	5.11 (3.42–10.0)	8.32 (1.97–20.7)	12.6 (7.21–19.2)	3.26 (2.24–5.45)	27.2 (4.25–62.7)
Cation exchange capacity	6.96 (3.89–15.4)	11.6 (2.92–27.2)	12.0 (5.37–17.3)	19.6 (2.86–34.3)	25.7 (11.9–61.1)
C (%)	0.75 (0.12–1.62)	2.47 (0.19–8.41)	1.50 (0.29–2.47)	4.67 (0.06–10.5)	6.68 (1.94–16.5)
N (%)	0.26 (0.13–0.48)	0.31 (0.22–0.59)	0.17 (0.06–0.23)	0.79 (0.08–1.70)	0.44 (0.19–0.81)
Total P (mg kg^{-1})	419 (107–1302)	491 (170–1250)	466 (202–592)	470 (33–768)	789 (362–1024)
Fe (%)	0.81 (0.39–1.46)	1.22 (0.14–1.99)	1.24 (0.84–2.00)	2.25 (0.16–4.21)	2.13 (0.51–3.44)
Mn (mg kg^{-1})	406 (190–600)	583 (200–750)	537 (287–1150)	564 (160–1300)	949 (300–3150)
Zn (mg kg^{-1})	8 (1–26)	24 (1–48)	34 (19–53)	28 (1–79)	67 (14–120)
Cu (mg kg^{-1})	11 (7–20)	14 (10–18)	18 (7–92)	18 (7–33)	16 (5–23)
Sand (%)	67.3 (45.0–76.8)	63.8 (48.2–81.4)	57.3 (45.0–75.9)	64.5 (51.4–81.4)	64.4 (49.6–78.6)
Silt (%)	21.1 (11.2–33.2)	21.4 (7.5–30.0)	25.6 (10.5–31.4)	19.0 (10.7–26.4)	22.2 (11.9–30.4)
Clay (%)	11.6 (7.7–21.8)	14.8 (11.1–22.2)	17.1 (13.6–23.6)	16.5 (7.9–25.4)	13.4 (9.0–24.5)
Elevation (m)	330 (260–420)	480 (425–550)	530 (460–610)	915 (735–1045)	880 (800–1070)
Tierra firme (n)	4	5	6	8	12
Floodplain (n)	3	1	5	0	0

Table 3. Pearson correlations between environmental variables in the Madidi National Park, Amazonian Bolivia. Below the diagonal are shown the values for the lowland sites (24 plots) and above the diagonal for the submontane sites (20 plots). Sum =sum of exchangeable cations concentrations (Ca, Mg, Na, K); CEC =cation exchange capacity; Elev. = elevation. The measurement units are as in Table 2. *p <0.05; **p <0.01; ***p <0.001. At the p <0.05 level, one test out of 20 is expected to give a significant result by chance, which is considerably less than found here.

	pH	Ca	Mg	Na	K	Sum	CEC	C	N	P	Fe	Mn	Zn	Cu	Sand	Silt	Clay	Elev.
pH		0.86***	0.65**	0.41	0.67**	0.86***	0.38	0.07	−0.46*	0.52*	0.11	0.15	0.50*	0.10	−0.14	0.24	−0.06	−0.42
Ca	0.75***		0.65**	0.65**	0.80***	1.00***	0.67**	0.07	−0.17	0.46*	0.12	0.03	0.45*	0.22	−0.18	0.28	−0.05	−0.18
Mg	0.44*	0.82***		0.10	0.83***	0.70***	0.48*	0.08	−0.30	0.59**	0.29	0.07	0.77***	0.24	−0.08	0.22	−0.14	−0.29
Na	0.32	0.51*	0.59**		0.36	0.62**	0.52*	−0.09	0.27	0.36	0.14	0.38	0.02	0.27	−0.27	0.41	−0.05	0.22
K	0.17	0.47*	0.50*	−0.07		0.83***	0.69***	0.18	−0.18	0.56*	0.22	0.08	0.64**	0.20	−0.24	0.35	−0.03	−0.10
Sum	0.72***	0.99***	0.87***	0.57**	0.48*		0.67**	0.08	−0.19	0.49*	0.14	0.04	0.49*	0.23	−0.18	0.28	−0.05	−0.19
CEC	0.49*	0.82***	0.72***	0.12	0.61**	0.74***		0.03	0.39	0.38	0.17	−0.12	0.23	0.31	−0.34	0.39	0.08	0.32
C	0.37	0.73***	0.70***	0.29	0.50*	0.74***	0.67***		−0.10	−0.08	0.26	−0.24	0.17	0.28	0.05	−0.24	0.20	−0.24
N	0.06	0.28	0.18	−0.36	0.54**	0.25	0.54**	0.37		0.10	0.29	0.03	−0.14	0.34	−0.36	0.15	0.41	0.66**
P	−0.04	0.15	0.20	−0.06	0.16	0.15	0.24	0.09	0.10		0.65**	0.61**	0.79***	0.58**	−0.64	0.66**	0.25	0.04
Fe	0.45*	0.68***	0.73***	0.21	0.68***	0.70***	0.70***	0.59**	0.28	0.35		0.24	0.69***	0.83***	−0.62**	0.31	0.64**	0.08
Mn	0.05	0.33	0.47*	0.00	0.32	0.34	0.52**	0.38	0.35	0.19	0.52		0.27	0.16	−0.33	0.41	0.04	0.14
Zn	0.48*	0.80***	0.85***	0.43*	0.54**	0.82***	0.75***	0.62**	0.16	0.35	0.86***	0.58**		0.55*	−0.49*	0.37	0.35	−0.26
Cu	0.24	0.28	0.14	0.01	0.00	0.26	0.26	−0.07	0.05	−0.02	0.09	−0.09	0.14		−0.56**	0.40	0.44	0.07
Sand	−0.08	−0.53**	−0.67***	−0.44*	−0.29	−0.57**	−0.59**	−0.49*	−0.15	−0.29	−0.54**	−0.49*	−0.64***	−0.01		−0.79***	−0.68***	−0.29
Silt	0.03	0.48*	0.60**	0.37	0.30	0.51*	0.52**	0.44*	0.25	0.36	0.53**	0.45*	0.60**	0.01	−0.94***		0.10	0.22
Clay	0.15	0.47*	0.60**	0.42*	0.19	0.50*	0.53**	0.45*	−0.06	0.09	0.39	0.42*	0.51*	0.01	−0.81***	0.57**		0.22
Elev.	0.39	0.57**	0.52**	0.46*	0.07	0.59**	0.41*	0.59**	−0.17	0.19	0.37	0.26	0.57**	−0.01	−0.32	0.18	0.49*	

Table 4. Mantel correlations between floristic and environmental differences between 44 0.1-ha plots in lowland and submontane forests in the Madidi National Park, Bolivian Amazonia. The results for the seven most significant environmental variables are shown at top, along with their partial Mantel correlations, with the effect of geographical distances (GD) and elevation (Elev.) partialled out, are shown. The results for the less significant environmental variables are shown after those of geographical distance, and these environmental variables were not used in further analyses. Floristic differences were based on the Jaccard index and environmental differences on Euclidean distance; geographical distances were ln-transformed. Statistical significance was calculated with a Monte Carlo permutation test using 999 permutations. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. At the $p < 0.05$ level, one test out of 20 is expected to give a significant result by chance, which is considerably less than found here.

Environmental variables	Woody plants (dbh $\geq$2.5 cm)	All trees (dbh $\geq$2.5 cm)	Large trees (dbh $\geq$10 cm)	Small trees (dbh <10 cm)	All lianas (dbh $\geq$2.5 cm)
pH	0.41***	0.42***	0.37***	0.23***	0.20***
pH; GD partialled out	0.38***	0.38***	0.33***	0.17***	0.17**
pH; Elev. partialled out	0.43***	0.43***	0.37***	0.22***	0.19***
Ca	0.42***	0.42***	0.37***	0.26***	0.21***
Ca; GD partialled out	0.33***	0.33***	0.29***	0.14**	0.15**
Ca; Elev. partialled out	0.42***	0.42***	0.36***	0.24***	0.19**
Mg	0.38***	0.38***	0.33***	0.22***	0.21***
Mg; GD partialled out	0.31***	0.30***	0.27***	0.13*	0.17**
Mg; Elev. partialled out	0.38***	0.37***	0.32***	0.21***	0.20**
C	0.14*	0.14*	0.10	0.09*	0.11*
C; GD partialled out	0.15*	0.15*	0.10	0.08	0.11*
C; Elev. partialled out	0.07	0.07	0.04	0.04	0.07
N	0.36***	0.36***	0.33***	0.008	0.18**
N; GD partialled out	0.35***	0.35***	0.32**	−0.04	0.16**
N; Elev. partialled out	0.24**	0.24**	0.24**	−0.09	0.11
Fe	0.18**	0.18**	0.21**	0.04	0.14**
Fe; GD partialled out	0.16*	0.16*	0.19**	0.01	0.12**
Fe; Elev. partialled out	0.08	0.08	0.13*	−0.02	0.08
pH, Ca, Mg, C, N, Fe	0.49***	0.49***	0.45***	0.19***	0.27***
pH, Ca, Mg, C, N, Fe; GD partialled out	0.45***	0.44***	0.40***	0.10*	0.23**
pH, Ca, Mg, C, N, Fe; Elev. partialled out	0.42***	0.42***	0.38***	0.12*	0.22**
Elev.	0.41***	0.41***	0.34***	0.24***	0.22***
Elev.; GD partialled out	0.28***	0.28***	0.24***	0.10	0.16***
GD	0.48***	0.47***	0.36***	0.42***	0.21***
GD; Elev. partialled out	0.38***	0.38***	0.26***	0.37***	0.14**
Na	0.06	0.06	0.06	0.05	0.08*
K	0.05	0.05	0.08	0.09*	0.04
Sum of Ca, Mg, Na, K	0.41***	0.41***	0.36***	0.25***	0.19***
Cation exchange capacity	0.17**	0.17**	0.17**	0.06	0.10*
P	0.12	0.12	0.12*	0.14**	0.08
Mn	0.05	0.05	0.10	0.03	−0.04
Zn	0.08	0.08	0.09	0.13*	0.10*
Cu	−0.06	−0.05	−0.07	0.02	−0.07
Sand	−0.03	−0.03	−0.03	0.01	0.03
Silt	−0.01	−0.01	0.02	0.02	0.06
Clay	0.02	0.02	0.02	0.004	−0.03
Tierra firme	0.05	0.05	−0.01	0.05	−0.06

these variables. Although soil cation exchange capacity, sum of bases and the combination of six edaphic variables also yielded highly significant Mantel correlations, they were excluded from further analyses because they are either derived from the other variables, highly determined by Ca and Mg, or both (Table 2). Soil content of Na, K, P and Zn yielded statistically significant Mantel correlations with one or two plant groups, but the other environmental variables, including soil texture and flooding, never did.

All plant groups yielded statistically significant Mantel correlations with logarithmically transformed geographical distances. When the effect of geographical distances was partialled out from the plant-environment correlations involving the seven most important environmental variables, the correlation coefficients decreased but the significant ones remained significant in all cases except when small trees were correlated with soil C content and elevation (Table 4). When the effect of elevation, the only non-edaphic environmental variable, was partialled out from the significant plant-soil correlations, the correlation coefficients became lower in all cases but lost statistical significance only in analyses involving C and Fe, and in one case of lianas involving N (Table 4).

The highest Mantel correlations with environmental variables were found for all woody plants, all trees and large trees. Small trees and lianas yielded lower Mantel correlations (Table 4).

All multiple regression models included difference in soil pH and elevation. In most cases, difference in soil Mg content was also included, but this was replaced by difference in soil N content for small trees (Table 5). Geographical distance was included in all models except that for lianas. The proportion of variation in floristic distances that could be explained by the regression models was highest for all woody plants and all trees (43%) and lowest for lianas (10%).

In the variation partitioning analyses, the unique contribution of edaphic differences to explaining the variation in floristic differences was invariably higher than that of elevation differences, and also higher than that of geographical distances except with small trees (Table 6). The unique contribution of elevation differences was invariably low, but the fractions where elevation co-contributed with edaphic and/or geographical differences varied from 5 to 17% of the variation in floristic distances.

The visualisation of floristic patterns in all trees through Principal coordinates analysis (Fig. 2) showed that the high-elevation, high-nitrogen and low-pH Ruins site was distinct from all the lowland sites. The other submontane site, Tumupasa, was floristically in between these two extremes (assuming there is an arch which is a typical feature in this ordination method, Legendre and Legendre 1998). Plots in the Ruins site that were floristically most similar to Tumupasa had higher pH than other Ruins plots, and plots in Tumupasa that were floristically most similar to the lowland sites had higher pH and lower N than other Tumupasa plots. The same edaphically and altitudinally interpretable pattern appears to be present in the ordinations of large and small trees, albeit not as clearly. The ordination based on lianas does not resemble the ordination for trees, but even there, the main gradients related to elevation, soil pH and soil N content are visible. The Pearson correlations of the first two ordination axes with the seven most significant

environmental variables (insets in Fig. 2a, c, e, g) also show similar general trends. Two groups of arrows are visible in the insets: one consisting of pH, Ca and Mg, and the other consisting of C, Fe, N and elevation.

Ecological amplitudes

Lianas were found to have larger proportions of wide-amplitude species than all trees (≥ 2.5 cm) along the gradients of elevation, soil pH, and soil Mg content. Over 60% of liana species had wider than median amplitudes along these gradients, and the differences between life-forms were statistically significant (Fig. 3A). The same pattern existed also when lianas were compared to small trees, but in the case of soil Mg content the difference was not statistically significant (Fig. 3C). When lianas were compared to large trees, lianas showed a higher proportion of wide-amplitude species along six of the seven environmental variables but none of these differences was statistically significant (Fig. 3B). Finally, large tree species had more wide-amplitude species than small trees along the gradients of elevation, soil pH, soil Ca and soil C content, but the difference was statistically significant only in the last case (Fig. 3D).

Discussion

Congruence among plant groups

Correlated floristic patterns between lianas and different-sized trees suggest that common ecological or historical factors determine their distributions. The dynamics of random mortality and spatially limited dispersal as depicted by the neutral theory of Hubbell (2001) can be one such factor, as the logarithm of geographical distance between study plots significantly contributed to explaining the variation in floristic distances of all the studied plant groups. However, in most cases the contribution of environmental distances to floristic patterns was even larger. Other recent analyses using large data sets in the tropics have also

Table 5. Results of multiple regression on distance matrices where floristic differences among 44 0.1-ha plots in Bolivian Amazonia are explained by environmental and geographical distances. Originally, each multiple regression model included eight independent variables, the distance matrices based on the seven most significant environmental variables from Table 4 and geographical distance. Only the independent variables that were retained in the final model after backward elimination (partial regression coefficients) are shown. Significance levels were based on 999 permutations. **$p < 0.01$; ***$p < 0.001$; n.s. =not significant.

Life-form	pH	Mg (cmol$_c$ kg^{-1})	N (%)	Elevation (m)	Geographical distance	R^2
Woody plants (dbh ≥ 2.5 cm)	0.28***	0.20***	n.s.	0.27***	0.27***	0.43***
All trees (dbh ≥ 2.5 cm)	0.29***	0.19***	n.s.	0.27***	0.27***	0.43***
Large trees (dbh ≥ 10 cm)	0.27***	0.18**	n.s.	0.24***	0.17**	0.31***
Small trees (dbh <10 cm)	0.19**	n.s.	−0.13**	0.15**	0.34***	0.22***
All lianas (dbh ≥ 2.5 cm)	0.14**	0.15**	n.s.	0.20***	n.s.	0.10***

Table 6. Percentages of relative importance for different factors in explaining variation in floristic distances (by using multiple regression on distance matrices) among 44 plots of 0.1 ha in Amazonian Bolivia. For each woody plant life-forms and size classes, analysis were run separately using the Jaccard index. Environmental differences were based on the Euclidean distance. The soil variables retained in a backward elimination procedure (p <0.1 after Bonferroni correction) were used in the permutation analysis. All analysis retained pH, Mg and N, with the exception of small trees (dbh <10 cm) that only retained the first two variables.

Explanatory variables	Woody plants (dbh ≥2.5 cm)	All trees (dbh ≥2.5 cm)	Large trees (dbh ≥10 cm)	Small trees (dbh <10 cm)	Lianas (dbh ≥2.5 cm)
Soil variables	17	17	13	2	4
Elevation	3	3	0	0	2
Geographical distances (GD)	9	8	3	8	1
Soil variables+elevation	3	3	5	1	1
Soil variables+GD	3	3	3	5	1
Elevation+GD	4	4	3	5	0
Soil variables+elevation+GD	7	7	4	0	2
Unexplained	54	55	69	79	89

found that both environmental and geographical factors are important, both for trees (Pyke et al. 2001, Potts et al. 2002, Phillips et al. 2003) and for other plant groups (Tuomisto et al. 2003b, c, Vormisto et al. 2004).

Compared with earlier studies, the observed Mantel correlations between the plant groups were low (Ruokolainen et al. 1997, 2007, Tuomisto et al. 2003a), which means that the floristic distances of each plant group varied relatively independently of each other. The question is, to what degree this is due to sampling error caused by small sample plots size, and to what degree it indicates true ecological differences in how the species in the different plant groups respond to their environment. Sampling error is probably an important source of variation in our data, because the average liana species was represented by only 5.5 individuals in the entire data set, the average small tree species by 7 individuals, and the average large tree species by 8 individuals. Therefore, the absence of a species from a plot does not necessarily mean that the species does not occur in the area the plot supposedly represents, which diminishes our ability to recognise shared patterns among plant groups (Kessler and Bach 1999, Higgins and Ruokolainen 2004).

Several lines of evidence suggest that small trees, large trees and lianas are probably responding to the environment in similar ways. First, the Mantel test results were qualitatively similar for all plant groups: mostly the same set of environmental variables emerged with statistically significant Mantel correlations in each case. Second, almost the same environmental variables were retained after backward elimination in the multiple regression models for all plant groups. Third, the distribution of the explained variation among the different fractions of the variation partitioning was similar among the plant groups.

The proportion of explained variation in the multiple regression models and variation partitioning were not particularly high for any of the plant groups, but

it is noteworthy that these proportions were always higher for those plant groups that included most individuals, especially all woody plants and all trees which combined several size classes. When subsets of data are combined for analysis, an increase in the proportion of explained variation is only expected when the subsets respond similarly to the explanatory variables, but taken separately are more noisy than the combined data. Consequently, we believe that the common response of the separate plant groups to environmental variables is stronger than suggested by the sheer values of Mantel correlation coefficients or proportions of explained variation in multiple regression tests. This interpretation is also consistent with the ordination diagrams, where a common general pattern becomes less apparent for plant groups that contained fewer individuals.

Our results contrast those of earlier studies (Webb et al. 1967, Pérez-Salicrup et al. 2001) that did not find any congruence between the floristic patterns of trees and lianas. The differences in results may partly be due to the different statistical method used by Webb et al. (1967) and the relatively small sample size of Pérez-Salicrup et al. (2001), so further investigation is still needed. The degree of congruence also depends on the length of the environmental and/or spatial gradient over which the patterns are compared (Ruokolainen et al. 1997). DeWalt et al. (2006) observed that, in general, liana species composition varied among ecologically distinct forest types as expected on the basis of their soils and tree species composition.

A clear difference between the life-forms in our study was that patterns in the measured environmental variables were able to explain the floristic patterns of large trees to a higher degree than those of lianas and small trees. In other words, environmental control of species turnover appeared to be stronger for large trees. This is in contrast to the results of Duque et al. (2002), who reported that floristic patterns of small trees were explained by environmental differences better than
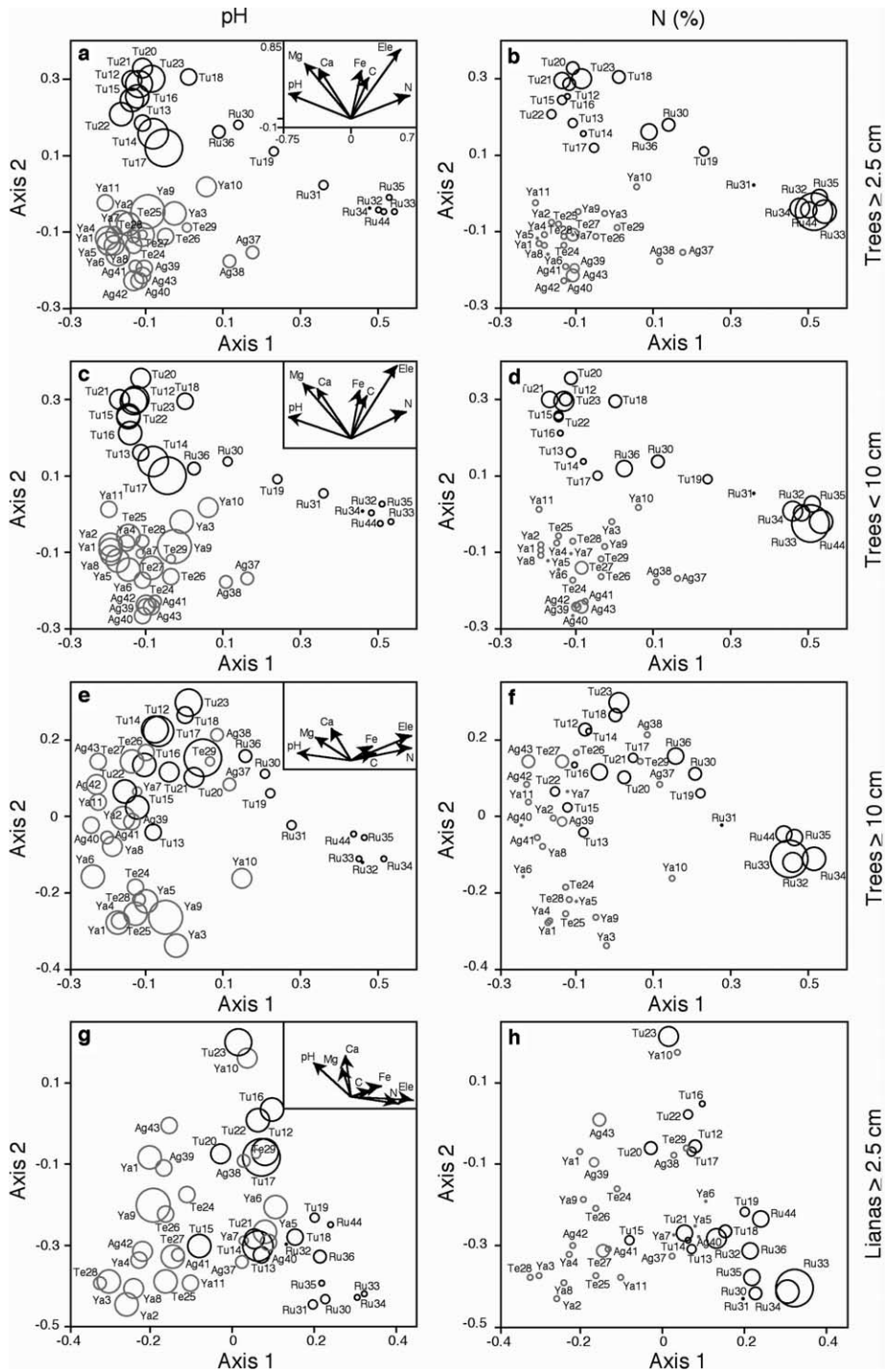
Fig. 2. Floristic ordination diagrams (principal coordinates analysis) obtained for each of the four life-forms separately (a–b, all trees ≥2.5 cm dbh; c–d, large trees ≥10 cm dbh; e–f, small trees <10 cm dbh; g–h, all lianas ≥2.5 cm dbh) for the 44 inventoried 0.1-ha plots in Bolivian Amazon. Similarity matrices for floristic composition were based on Jaccard index, and for environmental variables were calculated with Euclidean distance. The proportional size of the circles represents the values of pH (in panels a, c, e, g) and N (b, d, f, h) in each plot. Black circles corresponds to submontane plots and grey circles to lowland plots. Arrows in the insets of panels a, c, e, and g indicate the correlation of each of the seven environmental variables to the first two ordination axes.
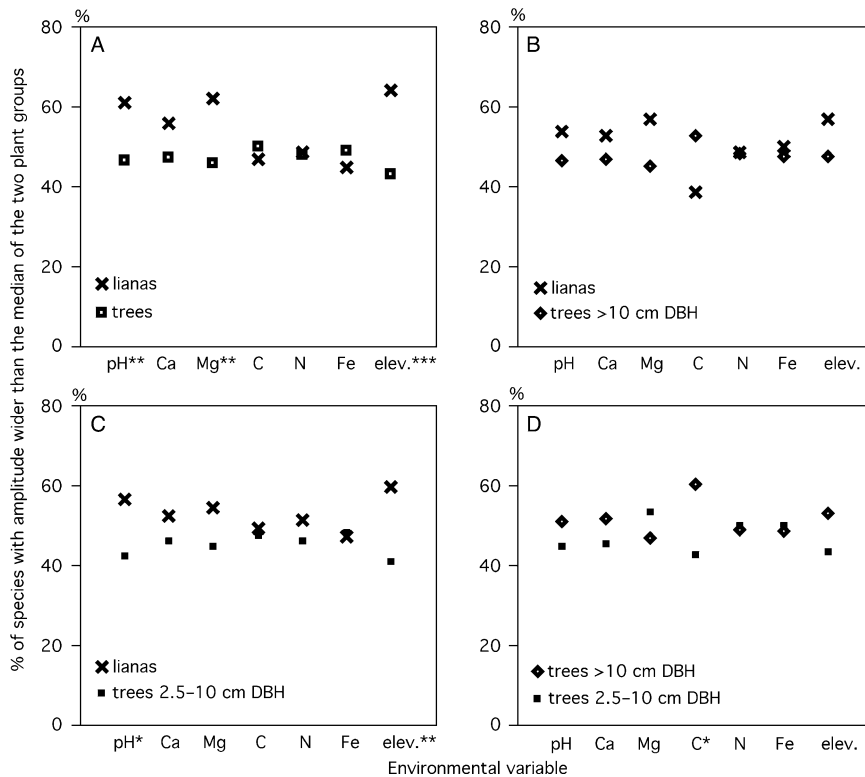
Fig. 3. Percentages of species of lianas and different tree-groups (A, lianas vs all trees; B, lianas vs large trees; C, lianas vs small trees; D, large trees vs small trees) with ecological amplitudes wider than the median amplitude of both life-forms combined for plots of 0.1-ha in the Madidi National Park, Amazonian Bolivia. Values do not sum to 100 because they are differences from mean amplitude and do not include species with amplitudes exactly on the median value. The probability of obtaining the observed difference in percentages between life-forms by chance for each environmental variable is shown, controlling for the frequency of the species in 44 plots as determined by 999 permutations: *p < 0.05; **p < 0.01; ***p < 0.001.

those of large trees. However, in our study the difference is probably a sampling artefact, because small trees were represented by fewer stems than large trees, and there was no difference in their amplitudes along the seven most important environmental gradients.

In contrast, an ecological explanation appears likely for the difference between lianas and trees in the amount of explained variation of floristic distances. Lianas were observed to have wider ecological amplitudes than trees along those three environmental gradients (elevation, soil pH and soil Mg content) that were in most cases retained in the final multiple regression models. This suggests that lianas can be considered ecologically more generalist than trees along these soil gradients. Whether lianas are more generalist along other environmental gradients is unclear. For example, we did not measure light intensity, which has been related to liana abundance in several earlier studies (Putz 1984, DeWalt et al. 2000, Laurance et al. 2001, Ibarra-Manríquez and Martínez-Ramos 2002). According to Brown (1984), a species that is a generalist in respect to some habitat features may tend to be a

generalist towards other features as well, but narrow specialisation to many habitat features may be counter-productive, because this would reduce the area of suitable habitat so much that the species might not be able to maintain viable populations. The latter line of argumentation would lead to the proposition that if lianas are more specialised in relation to light environment than trees are, then they might have evolved to be less specialised in relation to edaphic factors.

One possible mechanism explaining the apparently smaller sensitivity of lianas to soil variation is that their more extensive root systems enable them to exploit a greater range of soil conditions (Schnitzer 2005). Dispersal ability may also contribute to our observation that lianas occupy wider ecological amplitudes than trees. If lianas disperse their seeds over longer distances than trees, and if the variation in environmental characteristics is spatially autocorrelated, then there could be more lianas than trees growing in habitats where they cannot maintain viable populations (mass effect of Shmida and Wilson 1985, sink populations of

Pulliam 1988). Unfortunately, our data do not allow to separate between these possibilities. Experiments or detailed and extensive field measurements of growth and reproduction would be needed to solve the question.

If one plant group shows the same pattern of species turn-over among sites as the rest of the flora, then significant savings of time and money can be achieved if that group only is used for field documentation of general floristic patterns (Ruokolainen et al. 1997, 2007, Kessler and Bach 1999, Higgins and Ruokolainen 2004). From this point of view, our results are somewhat ambiguous: in very general terms, the results obtained with small and large trees and lianas were congruent, but they differed in the details. Earlier studies involving pteridophytes and Melastomataceae have documented higher degrees of congruence among plant groups (Ruokolainen et al. 1997, 2007), but whether this is due to differences between the geographical areas involved or differences among the plant groups is not known at present.

Relative importance of environmental variables

Patterns in soil variables may be noisy due to the use of single cores rather than composite soil samples, as the latter would give more reliable mean estimates of local soil properties. Nevertheless, significant correlations between base cation contents, particularly Ca and Mg, are consistent with several studies from both the New and Old World tropics (Austin et al. 1972, Baillie et al. 1987, Johnston 1992, Ruokolainen and Tuomisto 1998, Potts et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a, Duque et al. 2005, Ruokolainen et al. 2007). The fact that base cations have been linked with floristic composition in these studies is not surprising given that they are important plant nutrients, and different species can be postulated to have adapted to different availabilities of these nutrients. Calcium and magnesium also influence the functioning of mycorrhiza (Baillie et al. 1987, Jarstfer et al. 1998).

However, not all of the important plant nutrients that were analysed from our soil samples yielded high Mantel correlations with the studied plant groups. Notably, our results contrast the expectation that phosphorus would be one of the most significant soil factors for explaining floristic patterns in tropical rain forests (Sollins 1998). Earlier studies have yielded conflicting results, with some finding phosphorus to be relatively insignificant (Potts et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a) and others finding it more important than base cations (Newbery et al. 1986, Paoli et al. 2006). Lack of variation in phosphorus contents could be an explanation for its limited importance, but this does not seem to be an explanation

in our study, as phosphorus content varied about as much as the contents of base cations (roughly 50-fold in our data). However, these phosphorus contents are relatively high by tropical rain forest standards, and therefore phosphorus may not be a limiting factor in our study area. The analysis of extractable P instead of total P might be more appropriate for detecting plant-soil associations (Paoli et al. 2006), and it is also possible that temporal variation in phosphorus content in the soil or technical difficulties in measuring its availability to plants affect the results (Newbery et al. 1988, Sollins 1998). Further studies are needed to clarify these questions.

Nitrogen is another nutrient for which analytical considerations are necessary. Nitrate and ammonium ions are the main sources of nitrogen for plants, but both are easily volatile. Our soil samples were stored at ambient temperature until analysis, so the nitrogen concentrations may have been altered from what was actually available for plants in the field.

Several studies, including the present one, have found soil pH important for plant species distributions (Newbery et al. 1986, Baillie et al. 1987, Johnston 1992, Phillips et al. 2003), but others have found it insignificant (Gartlan et al. 1986, Tuomisto et al. 2003a, c). A problem with pH is its rather wide temporal variation, which may blur existing patterns (Sollins 1998). Many earlier studies have found soil texture important (Gartlan et al. 1986, Newbery et al. 1986, Phillips et al. 2003, Tuomisto et al. 2003a, c), but this was not the case in our study area, probably because soil texture was rather homogeneous.

The dichotomy of floodplain and tierra firme forests was not important for floristic patterns in our study, which is contrary to numerous earlier studies (Gartlan et al. 1986, Balslev et al. 1987, Kahn and de Granville 1992, Duivenvoorden 1995, Romero-Saltos et al. 2001, Ibarra-Manríquez and Martínez-Ramos 2002, Duque et al. 2002). This is most probably because the rather steep topography in our study area causes floods to remain sporadic and of short duration compared to those further downstream, where forests may be inundated for several months at a time.

It has been known for a long time that the structure and floristic composition of vegetation change along elevational gradients. Elevation is a typical indirect environmental gradient (Austin and Smith 1989), meaning that elevational patterns are actually due to either direct environmental gradients (such as temperature) or resource gradients (such as soil nutrient content) that happen to be correlated with elevation. Several studies have reported that chemical and textural soil properties vary with elevation (Grubb et al. 1963, Gentry 1988, Grubb 1989, Ashton 2003). For this reason we examined the partial Mantel correlations between floristic and edaphic distance matrices after

controlling for the effect of elevation. The results in most cases showed that our edaphic and elevational distances covaried very little, with the exception of soil nitrogen and iron content. Elevation was included in all the multiple regression models, and therefore one can argue that some unmeasured but elevationally structured environmental variables, such as temperature or precipitation, were actually significantly controlling plant species distributions in our data. However, this interpretation does not gain support from the variation partitioning results, where the unique contribution of elevation difference was small.

Although soils, climate and elevation are fundamentally interlinked, and it is difficult to separate their independent causal effects on species distributions, soils alone explained a significant amount of the variance in plant species distributions in our data set.

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