

# Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae?

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**Abstract:** Studies in western Amazonian forests have found that similarities in soil cation concentration and texture explain floristic similarities between sites, when these are measured using trees, pteridophytes or Melastomataceae. However, it is not known to what extent the three plant groups react to the same soil characteristics, because tree studies have almost always been conducted in different areas than studies on the understorey plant groups. We made inventories in 23 sites representing non-inundated rain forests on clayey to loamy soil in three regions of western Amazonia. Significant Mantel correlations between the floristic patterns of trees and pteridophytes were found in all three regions when floristic differences were measured with species presence–absence data. When species abundance data were used, and when the floristic patterns of trees and Melastomataceae were compared, significant correlations were found in one or two regions. Mantel correlations between plant groups were highest in the two regions where the observed variation in soil characteristics was largest. In all regions, the same soil variables emerged with significant Mantel correlations with trees, pteridophytes and Melastomataceae. Soil calcium and magnesium were most frequently retained in the models of multiple regression on distance matrices. On average, soil differences explained 50% of the variation in floristic differences (range = 14–84%), and geographical distances explained 16% (range = 0–64%). Our results demonstrate that beta diversities of the three plant groups are highly correlated, and that much of this congruence is explained by similar reactions to soil variation. These results support the idea that pteridophytes, and to a lesser degree Melastomataceae, can be used as indicators of general floristic and edaphic patterns in Amazonian rain forests. Since understorey plants are much quicker to inventory than trees, this would make it possible to recognize and map floristic patterns over huge areas of lowland Amazonia within a reasonable time.

**Key Words:** Amazonia, beta diversity, indicator species, Melastomataceae, pteridophytes, soil, trees, tropical rain forest, vegetation inventory

## INTRODUCTION

Vegetation maps are used as sources of habitat information in ecological research and conservation planning. The Natura programme of the European Union and the Gap Analysis of the USA aim at guaranteeing that conservation area networks include all recognized habitat types and preserve sufficient habitat for all species. Whether an approach based on this concept of complementarity (Ferrier 2002) is feasible in tropical

forests depends on two fundamental questions. First, are the patterns in species composition and beta-diversity (difference in species composition among sites; Vellend 2001) consistent between plant groups and predictable from external environmental factors? Second, is it possible in practice to define, recognize and map sufficiently detailed habitat types over large enough areas?

In the case of Amazonian lowland rain forests, both questions are still unresolved. In vegetation maps (Huber & Alarcón 1988, IBGE 2004), huge areas of non-inundated terrain with non-podzolized soils (tierra firme) appear uniform. Some researchers maintain that the forests are much more heterogeneous than these maps suggest, and that plant species composition varies widely between sites in response to environmental

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and particularly edaphic variability (Gentry 1988, Ruokolainen *et al.* 1997, Tuomisto & Poulsen 1996, Tuomisto *et al.* 1995, 2003a; Young & León 1989). Others have emphasized the relative homogeneity of the forests, maintaining either that they are dominated over large areas by an oligarchy of generalist tree species (Macía & Svenning 2005, Pitman *et al.* 2001, Terborgh *et al.* 2002), or that species abundances fluctuate randomly in space and time (Condit *et al.* 2002; the neutral model of Hubbell 2001).

Several recent studies have found that both environmental differences and geographical distances are important in explaining the variation in beta diversity (Duque *et al.* 2002, Phillips *et al.* 2003a, Tuomisto *et al.* 2003b, c; Vormisto *et al.* 2004). This gives support to both the environmental control model and the neutral model. Despite focusing on plants of different life-forms (trees, palms, shrubs or herbs), all these studies found variation in soil characteristics to be relevant when explaining variation in beta diversity even when all sites were a priori thought to represent the same forest type. This indicates that the structural forest classifications need to be refined with floristic inventories to yield realistic estimates of beta diversity.

If plant community composition is at least partly deterministic, and different plant groups react to a common set of edaphic variables, then inventorying just a small part of the flora (indicator species or indicator plant groups; Ruokolainen *et al.* 1997) should give an indication of the overall floristic patterns of the forest. One consequence of such determinism would also be that species with known ecological preferences could be used to assess local edaphic conditions. In temperate and boreal areas, there is a long history of such a practice (Cajander 1926, Ellenberg 1988, Gégout *et al.* 2003, Wilson *et al.* 2001). The floristic pattern revealed by indicator groups can also work as a basis for optimizing complementarity when planning conservation area networks (Faith & Walker 1996, Ferrier 2002).

In Amazonian forests, inventorying and identifying all plants is a daunting task. Most floristic inventories have been facilitated by excluding epiphytes, lianas, understorey plants and tree saplings, and instead concentrating on trees exceeding a predefined stem diameter, but it has also been suggested that easily spotted understorey plants could be used as indicators of general floristic and edaphic patterns (Ruokolainen *et al.* 1997). Higgins & Ruokolainen (2004) found that concentrating sampling efforts on a preselected taxon (genus or family) is more efficient in representing the floristic patterns of the full dataset than concentrating on a preselected size class. However, some studies have suggested that plants from different vegetation layers yield different classifications of field sites (McCune & Allen 1985, Oliver *et al.* 1998, Sagers & Lyon 1997, Webb *et al.* 1967).

Four earlier studies (Ruokolainen & Tuomisto 1998, Ruokolainen *et al.* 1997, Tuomisto *et al.* 1995, Vormisto *et al.* 2000) have reported high congruence between the floristic patterns (as measured with floristic distance matrices) of trees, Melastomataceae and pteridophytes. However, all these studies were conducted in a region famous for its heterogeneous soils, including white sands (Loreto department in northern Peru; Gentry 1988). In Colombian Amazonia, variation in tree species abundances was found to be related to variables derived from the abundances of pteridophytes and Melastomataceae (Duque *et al.* 2005), but differences in analysis methods prevent direct comparison between the Colombian and Peruvian results. Therefore, it is not clear how general the congruence between plant groups is across regions.

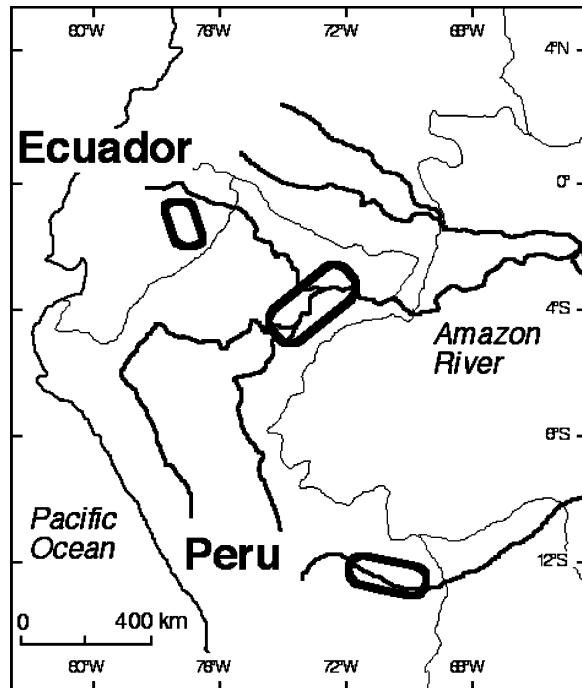
The aim of the present paper is to test the reliability of indicator plant groups in inferring floristic and edaphic patterns in Amazonian rain forests using a larger data set than has been available before. To this effect, we first analyse to what degree different plant groups (trees, pteridophytes and Melastomataceae) produce congruent floristic patterns in Amazonian tierra firme forests of three separate regions. Then we analyse to what degree this congruence may be explained by edaphic differences and geographical distances.

## MATERIAL AND METHODS

### Study sites

Field work was conducted in three regions of western Amazonian lowlands (Figure 1, Table 1): the departments of Madre de Dios (200–300 m elevation) and Loreto (100–200 m) in Peru, and the Yasuní National Park in Ecuador (200–300 m). The climate is clearly seasonal with a mean annual precipitation of 2300 mm in the Madre de Dios region (Pitman *et al.* 2001) and aseasonal with a mean annual precipitation of about 3000 mm in the Loreto and Yasuní regions (Lips & Duivenvoorden 2001).

Seven sites were inventoried in Madre de Dios and Yasuní, and nine in Loreto. All sites were situated in old-growth closed-canopy tierra firme forest. The soils at all sites were clayey to loamy. Although forests on white-sand soils were found in Loreto, these were excluded from the present study because they can easily be recognized in the field by their physiognomy, and their floristic distinctness is already widely acknowledged. The Loreto sites have been used earlier in somewhat similar but less-comprehensive analyses than those of the present paper (Ruokolainen & Tuomisto 1998, Ruokolainen *et al.* 1997, Tuomisto *et al.* 1995).



**Figure 1.** Map of the study area. Circled areas indicate the approximate locations of the three study regions: Yasuní (in Ecuador), Loreto (northern Peru) and Madre de Dios (southern Peru).

### Floristic inventories

Three plant groups were inventoried at each site: trees, Melastomataceae and pteridophytes. Tree plots were placed such that recent tree-fall gaps were avoided. In Madre de Dios, trees  $\geq 10$  cm diameter at breast height (dbh) were inventoried in square 100 m  $\times$  100-m plots (1 ha) except in one case where the plot covered only 0.865 ha (Pitman *et al.* 2001). In Loreto, four 20 m  $\times$  20-m plots were established per site (totalling 0.16 ha),

and local topographic variability was included by placing two plots on hill tops and two in valley bottoms (Ruokolainen & Tuomisto 1998, Ruokolainen *et al.* 1997). In Yasuní, usually one (but sometimes two) 20 m  $\times$  50-m (0.1 ha) plot was established per site (Romero-Saltos *et al.* 2001). All tree individuals  $\geq 2.5$  cm dbh were inventoried in both Loreto and Yasuní.

Voucher specimens were collected of all tree individuals that could not be confidently identified to a species that had already been collected. The vouchers were identified to species, or if an applicable species name could not be found, assigned to morphospecies that were thought to correspond to biological species. Vouchers collected in the same region were cross-checked to get consistent identifications among sites. Duplicates of the vouchers collected in Madre de Dios are deposited in CUZ and DUKE, those collected in Loreto are in AMAZ, TUR and USM, and those collected in Yasuní are in AAU, MA, QCA and QCNE (herbarium acronyms according to Holmgren *et al.* 1990).

Melastomataceae and pteridophytes were inventoried at all sites using 5 m  $\times$  500-m line transects (Tuomisto *et al.* 2003a, c). In Madre de Dios, all transects shared a strip of 5 m  $\times$  100-m with their corresponding tree plot. In Loreto, the original transect line was usually 1300 m long, but only the first 500 m are used here. In one site, all four tree plots shared a strip of 5 m  $\times$  20-m with the transect, in most sites two tree plots did, and in two sites, one did. Each transect in Yasuní overlapped with a strip of 5 m  $\times$  50-m of the corresponding tree plot, except in three sites, where the transect extended between two tree plots.

All terrestrial Melastomataceae individuals with post-cotyledon leaves were recorded. All pteridophyte individuals with at least one green leaf longer than 10 cm were recorded, including epiphytes and climbers if they had such leaves less than 2 m above ground. Each rooting stem of vegetatively spreading species was counted as one individual. Voucher specimens were collected for each

**Table 1.** Results of floristic inventories made in three regions in lowland western Amazonia. Floristic similarity between sites is calculated both with the Steinhaus index (Steinh.) (abundance data) and with the Sørensen index (Søren.) (presence-absence data).

Plant group	Area (ha) sampled per site (per region)	Total number of species	Mean number of species per site (range)	Total number of individuals	Mean number of individuals per site (range)	Similarity between sites (mean $\pm$ SD)	
						Steinh.	Søren.
<b>Madre de Dios</b>							
Trees	1.0 <sup>1</sup> (6.875)	479	159 (134–183)	3886	555 (498–609)	0.31 $\pm$ 0.09	0.40 $\pm$ 0.06
Pteridophytes	0.25 (1.75)	105	35 (23–53)	13539	1934 (668–4488)	0.21 $\pm$ 0.18	0.35 $\pm$ 0.17
Melastomataceae	0.25 (1.75)	58	14 (5–27)	789	113 (9–374)	0.11 $\pm$ 0.12	0.21 $\pm$ 0.14
<b>Loreto</b>							
Trees	0.16 (1.44)	1158	228 (201–271)	3884	432 (354–543)	0.18 $\pm$ 0.07	0.21 $\pm$ 0.07
Pterid.	0.25 (2.25)	101	33 (22–41)	16901	1878 (916–4178)	0.17 $\pm$ 0.14	0.44 $\pm$ 0.12
Melast.	0.25 (2.25)	96	27 (15–38)	3356	373 (130–984)	0.18 $\pm$ 0.17	0.30 $\pm$ 0.18
<b>Yasuní</b>							
Trees	0.1 (1.0)	655	152 (130–179)	3097	310 (240–380)	0.25 $\pm$ 0.05	0.31 $\pm$ 0.05
Pterid.	0.25 (1.75)	111	55 (43–64)	17468	2495 (1094–4842)	0.33 $\pm$ 0.11	0.63 $\pm$ 0.10
Melast.	0.25 (1.75)	87	36 (26–46)	1770	253 (168–342)	0.32 $\pm$ 0.13	0.53 $\pm$ 0.09

<sup>1</sup>At one site the plot was 0.875 ha.

species in each region and for individuals that could not be confidently identified to an already vouchered species. Duplicates of the vouchers collected in Madre de Dios are deposited in CUZ, TUR and USM, those collected in Loreto are in AMAZ, TUR and USM, and those collected in Yasuní are in TUR, QCA and QCNE.

### Soil sampling

Surface soil samples (top 5 cm of the mineral soil) were collected from at least three points along each transect: near the beginning, middle and end. If the terrain was hilly, two samples were taken in hill tops, and one in a valley bottom. Each soil sample consisted of five pooled subsamples collected within an area of about 5 m × 5-m.

The soil samples were analysed for pH, exchangeable bases (Ca, K, Mg, Na, each separately), exchangeable aluminium, and loss on ignition at 420 °C (LOI, a proxy for the content of organic matter). The analyses followed standard procedures (Ruokolainen & Tuomisto 1998, van Reeuwijk 1993). The soil samples from Madre de Dios and Yasuní were analysed in the laboratory of the MTT Agrifood Research Finland. The samples from Loreto were analysed either in MTT, the International Soil Reference and Information Centre (ISRIC, The Netherlands) or the Geological Survey of Finland (GSF).

Soil texture was characterized by the percentage of the sand fraction of soil weight (particles 0.063–2 mm in diameter). All samples of Loreto and four of Yasuní were analysed by sieving after pretreatment with H<sub>2</sub>O<sub>2</sub> and citrate-dithionite-bicarbonate (MTT and ISRIC) or after ultrasonic dispersion (GSF). All samples from Madre de Dios and three from Yasuní were analysed in the laboratory of the Department of Geology, University of Turku, using a laser grain analyser after the same pretreatment as in GSF.

### Computing of distance matrices

Since tree taxonomy had not been harmonized among regions, distance matrices were computed independently for each of the three regions, and all analyses were run for each region separately. Floristic distance matrices were computed separately for trees, pteridophytes and Melastomataceae. The Sørensen index and the mathematically similar Steinhaus index were used for presence–absence and abundance data, respectively (Legendre & Legendre 1998). These similarities were converted to distances by subtracting them from one.

Separate distance matrices were computed for all trees, common trees and rare trees. Common trees were defined in two alternative ways: (1) the most common 150 species or (2) the most common 20% of the species in each regional data set. All other species were considered rare.

The primary measure of commonness was the number of stems, and the secondary measure was the number of plots in which the species was recorded. All species with the same abundance and the same frequency were allocated to the same commonness category, so the number of common species deviated slightly from the nominal limit in each region.

Three of the Yasuní sites possessed two paired tree plots. The tree distance matrices were initially computed using all plots separately. Afterwards, the matrix was trimmed to the correct number of sites by using the mean of the two resemblance values computed between a site with paired plots and another site. The alternative of averaging tree abundances before computing the distance values would have artificially decreased the distance values involving the paired plots, as the distance measures used here are sensitive to sample size (Wolda 1981).

Soil differences between plots were expressed in Euclidean distances computed separately for each soil variable. The concentrations of elements (Al, Ca, K, Mg and Na) were transformed to their natural logarithms before calculating the Euclidean distances in order to give more weight to a unit difference in concentration when the overall concentration was low than when it was high.

Geographical distances between sites were computed from latitude and longitude that were obtained either in the field with a hand-held GPS or estimated from a rectified satellite image. The geographical distances were transformed to their natural logarithms before analysis. All resemblance matrices were computed using the program Le Proiciel R (available at <http://www.bio.umontreal.ca/legendre/indexEnglish.html>).

### Mantel tests and ordinations

If environmental factors control species composition, floristic similarity should decrease monotonically with increasing environmental difference between sites, and floristic similarities of different plant groups should be correlated. If random dispersal and local extinctions are the main structuring forces, floristic similarity should decrease approximately linearly with increasing logarithm of geographical distance (Hubbell 2001, fig. 7.9) but should not be correlated with edaphic differences, and the floristic similarities of different plant groups should not be correlated beyond the geographical distance effect.

Mantel test of matrix correspondence was used to test whether distance matrices were correlated (Legendre & Legendre 1998). The standardized form of the Mantel statistic was used ( $r_M$ , similar to the Pearson correlation coefficient) and the statistical significance of each correlation was estimated by 999 permutations.

Mantel tests were run to quantify the correlations between plant groups, between each plant group and

environmental distances, and between plant groups and log-transformed geographical distances. Partial Mantel tests were run to verify whether the floristic distance matrices remained correlated after the effect of geographical distances had been taken into account. In order to visualize the floristic patterns among the inventory sites, we ran Principal Coordinates Analysis (PCoA) using the floristic distance matrices of each plant group separately. Both Mantel tests and ordinations were run using the program Le Proiciel R.

It has been suggested that regions extending over thousands of square kilometres may be dominated by a set of ecologically generalist tree species (Macía & Svenning 2005, Pitman *et al.* 2001, Terborgh *et al.* 2002) that may be more indifferent to edaphic effects than rare tree species (Phillips *et al.* 2003a, Pitman *et al.* 2001), so we ran all analyses separately for common and rare trees.

### Multiple regressions on distance matrices

The relative contributions of soil differences and geographical distances to explaining the variation in each floristic distance matrix were quantified using multiple regression on distance matrices (Legendre *et al.* 1994) following the variation partitioning approach of Duivenvoorden *et al.* (2002). Separate analyses were run with three combinations of independent matrices. (1) Eight edaphic variables. Each cation was used as a separate distance matrix, and variables that did not have a statistically significant ( $P < 0.1$  after Bonferroni correction) contribution to explaining the variation in the floristic distance matrix were excluded by backward elimination. If only one environmental variable remained, the variable that had shown the highest Mantel correlation with the floristic distance matrix was used. (2) Log-transformed geographical distances (only retained for further analyses if  $P < 0.1$ ). (3) All independent variables retained in the first or second model.

The resulting percentages of explained variation in floristic distances,  $R^2(1)$  through  $R^2(3)$ , were used to compute the fractions *a* through *d* as follows: *a* = variation explained by edaphic differences alone =  $R^2(3) - R^2(2)$ ;

*b* = variation explained by edaphic and geographical distances jointly =  $R^2(3) - R^2(2) - R^2(1)$ ; *c* = variation explained by geographical distances alone =  $R^2(3) - R^2(1)$ ; and *d* = variation explained by neither edaphic nor geographical distances (unexplained) =  $100\% - R^2(3)$ . With increasing correlation between the environmental and geographical distances, it becomes increasingly difficult to separate between their effects, which leads to a larger *b* fraction and smaller *a* and *c* fractions.

The program Permute! was used to run multiple regression on distance matrices (available at <http://www.bio.umontreal.ca/legendre/indexEnglish.html>).

## RESULTS

### Floristic inventories

We inventoried 23 sites, including a total of 10 867 individuals of trees, 47 908 of pteridophytes, and 5915 of Melastomataceae (Table 1). Tree species outnumbered pteridophyte and Melastomataceae species by an average of 7-fold and 10-fold, respectively. There were obvious differences between regions in the number of species encountered. For trees this is partly due to differences in sampling methods. Each site contained, on average, 150–230 tree species, 33–55 pteridophyte species and 14–36 Melastomataceae species.

Compared with the huge differences among plant groups in the numbers of individuals and species, the differences in mean similarities between sites within a region were small. Generally, floristic similarity was higher between sites in Yasuní than in the other regions (Table 1), but again caution is needed: the relatively high similarity values for trees in Madre de Dios may be due to sampling differences.

### Soils

Soil analyses revealed marked differences in soil characteristics both among regions and among sites within regions (Table 2). All sites had acid soils: only three

**Table 2.** Results of chemical and physical analyses of soils within three regions in lowland western Amazonia. Cation concentrations are given in  $\text{cmol}(+) \text{kg}^{-1}$ , LOI (loss on ignition) and sand content in %.

	Madre de Dios		Loreto		Yasuní	
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
Al	1.69 $\pm$ 1.46	0.30–4.75	5.67 $\pm$ 2.36	2.80–9.00	9.91 $\pm$ 3.71	3.77–14.37
Ca	4.52 $\pm$ 5.39	0.05–11.68	1.22 $\pm$ 2.08	0.02–6.17	3.52 $\pm$ 2.41	1.54–8.68
K	0.23 $\pm$ 0.11	0.12–0.38	0.12 $\pm$ 0.06	0.05–0.21	0.21 $\pm$ 0.04	0.16–0.25
Mg	0.92 $\pm$ 0.98	0.08–2.44	0.27 $\pm$ 0.36	0.05–1.15	1.25 $\pm$ 0.41	0.97–2.14
Na	0.02 $\pm$ 0.01	0.01–0.03	0.02 $\pm$ 0.01	0.01–0.05	0.04 $\pm$ 0.01	0.02–0.06
pH	4.09 $\pm$ 0.65	3.52–5.11	3.82 $\pm$ 0.14	3.58–3.98	3.59 $\pm$ 0.16	3.39–3.86
LOI	4.0 $\pm$ 0.8	3.0–4.9	6.2 $\pm$ 1.2	4.6–8.1	8.6 $\pm$ 1.5	6.9–11.5
Sand	52 $\pm$ 29	19–90	70 $\pm$ 23	33–97	82 $\pm$ 11	59–91

**Table 3.** Mantel correlations between floristic differences based on three different plant groups in three western Amazonian regions. Partial Mantel tests, where the effect of geographical distances has been removed before computing the correlation between the two floristic distance matrices, are shown in parenthesis. Sørensen index uses species presence–absence data, Steinhaus index abundance data. Statistical significances were obtained by a Monte Carlo permutation test using 999 permutations: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ . The probability of obtaining a significant correlation coefficient by chance at the  $P < 0.05$  level is 1 out of 20 tests, i.e. clearly lower than found here.

	Trees – pteridophytes	Trees – Melastomataceae	Pteridophytes – Melastomataceae
Madre de Dios			
Sørensen	0.72** (0.56*)	0.49* (0.24)	0.59** (0.46*)
Steinhaus	0.47* (–0.01)	0.07 (–0.17)	0.62** (0.61**)
Loreto			
Sørensen	0.82*** (0.81***)	0.86*** (0.85***)	0.86*** (0.85***)
Steinhaus	0.77*** (0.76***)	0.78*** (0.77***)	0.74*** (0.73***)
Yasuní			
Sørensen	0.54* (0.55*)	0.32 (0.21)	0.62* (0.62*)
Steinhaus	0.28 (0.24)	0.21 (0.07)	0.47 (0.45)

sites in Madre de Dios had soil pH higher than 4. Mean soil aluminium concentration was highest in Yasuní and lowest in Madre de Dios, whereas the concentrations of exchangeable bases were highest in Madre de Dios and lowest in Loreto.

Sites in Yasuní had more similar soils than sites in the two other regions, but on average, the finest-textured soils were found in Yasuní and the coarsest in Madre de Dios. In Loreto and Madre de Dios, among-site variation in soil Ca and Mg concentrations ranged over two orders of magnitude with standard deviations larger than the mean. In Yasuní, soil Ca and Mg concentrations varied within one order of magnitude with standard deviations clearly smaller than the mean (Table 2).

### Congruence between plant groups

Floristic patterns of all three plant groups, when measured with presence–absence data (Sørensen index), were found to be significantly correlated in all regions, with one exception (trees – Melastomes in Yasuní; Table 3). The highest Mantel correlation coefficients were obtained in Loreto ( $r_M \geq 0.82$  for all plant group pairs), and the lowest in Yasuní ( $r_M \leq 0.62$ ).

Floristic patterns of pteridophytes were always correlated with those of trees and Melastomataceae, even when the effect of geographical distances was removed through a partial Mantel test. Taking the geographical distances into account made almost no difference in Loreto and Yasuní. Floristic patterns of Melastomataceae correlated with those of trees in two regions (Madre de Dios and Loreto), but only the Loreto correlation was independent of geographical distances.

The correlation coefficients were generally lower when abundance data were used (Steinhaus index), and the incidence of non-significant correlations was higher than with presence–absence data (Table 3). Nevertheless, the floristic patterns based on abundance data of all three

plant groups were correlated in Loreto, and these correlations were independent of geographical distances. The floristic patterns of pteridophytes were correlated with those of trees and Melastomataceae also in Madre de Dios, but only the latter correlation was independent of geographical distances. In Yasuní, none of the correlations was statistically significant.

The rare and common trees produced very similar Mantel test results in Madre de Dios and Loreto, but not in Yasuní where weaker correlations were obtained with rare trees than with common trees (Table 4). The correlations of both tree categories with pteridophytes were stronger than their correlations with Melastomataceae in Madre de Dios and Yasuní, but about the same in Loreto. The floristic patterns of common and rare trees were correlated with each other. These correlations were very similar to the correlations that both groups of trees showed with pteridophytes (Table 4), and were lower than or similar to the correlations that all trees showed with pteridophytes (compare Tables 3 and 4). The results were qualitatively similar when common trees were defined as the top 150 species or the top 20% of species, so for the other analyses we report only the results for the top 150 species.

### Congruence between floristic, environmental and geographic patterns

Mantel test results between floristic and edaphic differences varied among soil variables, among regions and, to a lesser degree, among plant groups (Table 5). Calcium, magnesium and the sum of cations yielded high and statistically significant Mantel correlations with most floristic distance matrices in Madre de Dios and Loreto. The correlations involving pH or geographical distances were mostly significant in Madre de Dios but mostly not significant in the other regions, whereas a high incidence of significant correlations involving Al, K or

**Table 4.** Mantel correlations between floristic differences based on different plant groups in three western Amazonian regions. The Sørensen index (presence–absence data) was used in all cases. Statistical significances were obtained by a Monte Carlo permutation test using 999 permutations: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ ; \* $P < 0.05$ . The probability of obtaining a significant correlation coefficient by chance at the  $P < 0.05$  level is 1 out of 20 tests, i.e. clearly lower than found here.

Tree group	Mantel correlation with		
	Rare trees	Pteridophytes	Melastomataceae
<b>Madre de Dios</b>			
Common trees (147 spp.)	0.63*	0.65*	0.43*
Common trees (20%)	0.68*	0.64*	0.32
Rare trees (332 spp.)	–	0.64**	0.44*
Rare trees (80%)	–	0.65**	0.52*
<b>Loreto</b>			
Common trees (157 spp.)	0.84***	0.79***	0.83***
Common trees (20%)	0.83***	0.80***	0.84***
Rare trees (1001 spp.)	–	0.82***	0.85***
Rare trees (80%)	–	0.81***	0.84***
<b>Yasuní</b>			
Common trees (152 spp.)	0.36*	0.49*	0.37
Common trees (20%)	0.39*	0.54*	0.36
Rare trees (503 spp.)	–	0.27	0.16
Rare trees (80%)	–	0.22	0.34

sand content was typical of Loreto. In Yasuní, only Mantel correlations involving sand, pH and Mg ever reached statistical significance. Loss on ignition did not correlate significantly with any of the floristic differences in any region, and Na only did once in Madre de Dios.

Although the Mantel test results obtained with the three plant groups and the two floristic distance measures were far from identical, they usually gave the same idea of which edaphic variables were important for explaining the variation in floristic differences in each region. Table 5 shows 27 cases where floristic variation is related to edaphic variation (nine edaphic variables in three regions). If the division between common and rare trees is ignored for the moment, in 24 of the 27 cases either all six floristic distance matrices agreed on whether the Mantel correlation with a given edaphic distance matrix was significant or not, or just one of them gave a different result. Considering the common and rare trees separately brings this congruence between plant groups down to 20 out of 27 cases, but there is no tendency in whether it is the rare or the common trees that yield higher Mantel correlations.

Within each region, the same edaphic variables tended to yield high Mantel correlation with all floristic distance matrices. The highest correlations were obtained with Ca and Mg concentration in Madre de Dios and Ca concentration and sum of cations in Loreto. In Yasuní, soil sand content yielded the highest correlations in most cases, and the differences were very small when pH or Al concentration yielded higher Mantel correlations. Rare trees in Yasuní deviated from the general pattern, as they yielded the highest Mantel correlations with LOI.

The ordinations obtained with the three plant groups were congruent in all three regions (Figure 2). In Madre

de Dios, the sample plots in the western part of the study area, where soil cation concentrations were highest, were floristically more similar to each other than to the plots further to the east. In Loreto, the floristic ordinations separated between the sample plots with high soil cation concentration and those with low soil cation concentration, even though the poor-soil sites were spread over long geographical distances. In Yasuní, the ordinations based on trees and pteridophytes showed that the site with the highest soil cation concentration (Tiputini 8) was floristically different from the other sites, irrespective of geographical distance. For the Melastomataceae, geographical proximity seemed to be more important, as Tiputini 8 appeared floristically rather similar to the plot that was geographically closest to it but with poorer soils (Tiputini 9).

The amount of variation in floristic distances that could be explained in the variation partitioning models differed markedly among the three regions (Figure 3). The proportion of explained variation was generally highest in Madre de Dios (50–86%, mean = 71%), next highest in Loreto (30–57%, mean = 47%) and lowest in Yasuní (14–74%, mean = 41%). The explained variation in Sørensen distances was usually higher than that explained in Steinhaus distances of the same plant group.

Edaphic difference always contributed to explaining floristic differences (statistically significant multiple regression result, and a non-zero  $a$  fraction), no matter which region and which plant group was analysed. In contrast, geographical distances made a statistically significant contribution in less than two-thirds of the analyses, and the  $c$  fraction was in most cases smaller than the  $a$  fraction. A spatial structure in both the edaphic and the floristic data was most evident in Madre de Dios, where

**Table 5.** Mantel correlations between floristic differences and either edaphic or geographical distances in three regions of lowland western Amazonia. Three different plant groups were analysed separately using either the Steinhaus index (St; abundance data) or the Sørensen index (So; presence–absence data). LOI = loss on ignition. Edaphic differences were based on the Euclidean distance. The highest correlation coefficient of an edaphic variable for each region is shown in bold. Statistical significance of each correlation coefficient was assessed with a Monte Carlo permutation test using 999 permutations. \*\*\*P < 0.001, \*\*P < 0.01, \*P < 0.05, °P < 0.1 (the last probability level is indicated to facilitate comparison with Fig. 3). The probability of obtaining a significant correlation coefficient by chance at the P < 0.05 level is 1 out of 20 tests, i.e. clearly lower than found here.

Soil variable	All trees		Common trees		Rare trees		Pteridophytes		Melastomataceae	
	St	So	St	So	St	So	St	So	St	So
<b>Madre de Dios</b>										
Al	−0.01	0.30°	−0.03	0.31*	−0.01	0.03	0.32°	0.34°	0.47***	0.66***
Ca	<b>0.53*</b>	<b>0.74*</b>	<b>0.52*</b>	<b>0.72*</b>	<b>0.50*</b>	<b>0.48*</b>	<b>0.80**</b>	<b>0.88**</b>	0.58**	0.58*
K	0.01	0.28°	0.00	0.35°	0.10	0.00	0.49°	0.41°	0.50*	0.34°
Mg	0.32	0.55*	0.30	0.54*	0.32°	0.29°	0.70**	0.79**	<b>0.66**</b>	<b>0.67**</b>
Na	0.02	0.25	0.01	0.32°	0.13	0.03	0.56*	0.45°	0.43°	0.30°
Sum cations	0.40°	0.66*	0.39°	0.65*	0.42*	0.39°	0.77**	0.81**	0.63**	0.60**
LOI	0.26	0.06	0.25	−0.03	0.27	0.23	0.09	0.17	−0.08	0.00
pH	0.20	0.45*	0.18	0.41*	0.26	0.28	0.60*	0.71*	0.48**	0.53**
Sand	0.04	0.10	0.03	0.07	0.14	0.11	0.07	0.00	0.10	0.05
Geographical distance	0.76**	0.79**	0.72*	0.70*	0.81***	0.80***	0.62*	0.54**	0.24	0.45*
<b>Loreto</b>										
Al	0.42*	0.43*	0.42*	0.46*	0.46*	0.43*	0.34*	0.39*	0.25°	0.38*
Ca	0.63**	0.65***	0.62**	0.65**	<b>0.58**</b>	<b>0.59**</b>	<b>0.52**</b>	<b>0.70**</b>	0.44*	<b>0.68**</b>
K	0.61**	0.63**	0.60*	0.62*	0.60**	0.57**	0.50**	0.41*	0.36*	0.50*
Mg	0.49*	0.51**	0.48*	0.50**	0.41*	0.40*	0.33*	0.31°	0.27°	0.35*
Na	0.04	0.07	−0.01	0.04	0.13	0.12	−0.07	0.13	−0.17	0.01
Sum cations	<b>0.64**</b>	<b>0.66**</b>	<b>0.63**</b>	<b>0.66**</b>	0.55**	0.56**	0.49**	0.61**	<b>0.45*</b>	0.60**
LOI	0.25°	0.26°	0.23°	0.26°	0.25°	0.21°	0.24°	0.08	0.10	0.09
pH	0.24°	0.28°	0.20°	0.27°	0.32*	0.31*	0.36*	0.13	0.14	0.18
Sand	0.39*	0.40*	0.41*	0.41*	0.43*	0.41*	0.28*	0.52**	0.24°	0.48*
Geographical distance	0.21	0.20	0.18	0.15	0.39*	0.34*	0.23°	0.31*	0.21°	0.28*
<b>Yasuní</b>										
Al	0.35	<b>0.47°</b>	0.27	0.31	0.27°	0.26°	0.03	0.56	0.39°	0.16
Ca	0.10	0.20	0.04	0.09	0.22	0.18	0.19	0.56	0.30	0.24
K	0.00	0.08	−0.01	0.07	0.18	0.18	−0.26	−0.19	−0.09	−0.25
Mg	0.35	0.42°	0.30	0.32	0.22	0.19	0.22	0.73*	0.33°	0.26
Na	−0.22	−0.11	−0.23	−0.04	0.22	0.25°	0.02	0.02	0.02	0.20
Sum cations	0.17	0.26	0.12	0.15	0.21	0.17	0.22	0.61	0.30	0.24
LOI	0.18	0.26	0.13	0.28	<b>0.28°</b>	<b>0.28°</b>	−0.23	−0.10	−0.11	−0.11
pH	<b>0.38°</b>	0.44*	<b>0.35°</b>	0.38°	0.26	0.24	0.11	0.29	0.05	−0.01
Sand	<b>0.38</b>	0.46°	0.33	<b>0.39</b>	0.22	0.20	<b>0.38°</b>	<b>0.80*</b>	<b>0.40*</b>	<b>0.37</b>
Geographical distance	0.50*	0.49*	0.51*	0.57**	0.16	0.13	0.14	0.13	0.30	0.31

fraction *b* (jointly explained by edaphic and geographical distances) was usually large (Figure 3).

At least one of the exchangeable bases Ca, K and Mg (most commonly Ca) was retained in all the multiple regression models in Madre de Dios and Loreto, and in four of the ten models in Yasuní. In addition, Al was often retained in Madre de Dios, LOI in Loreto and sand in Yasuní (Figure 3).

In Madre de Dios and Loreto, the total proportion of explained variation in floristic differences was relatively similar for common and rare trees. However, the unique contribution of edaphic differences was clearly larger for common trees than for rare trees, whereas the unique contribution of geographical distances was larger for rare trees than for common trees. In Yasuní, the proportion of

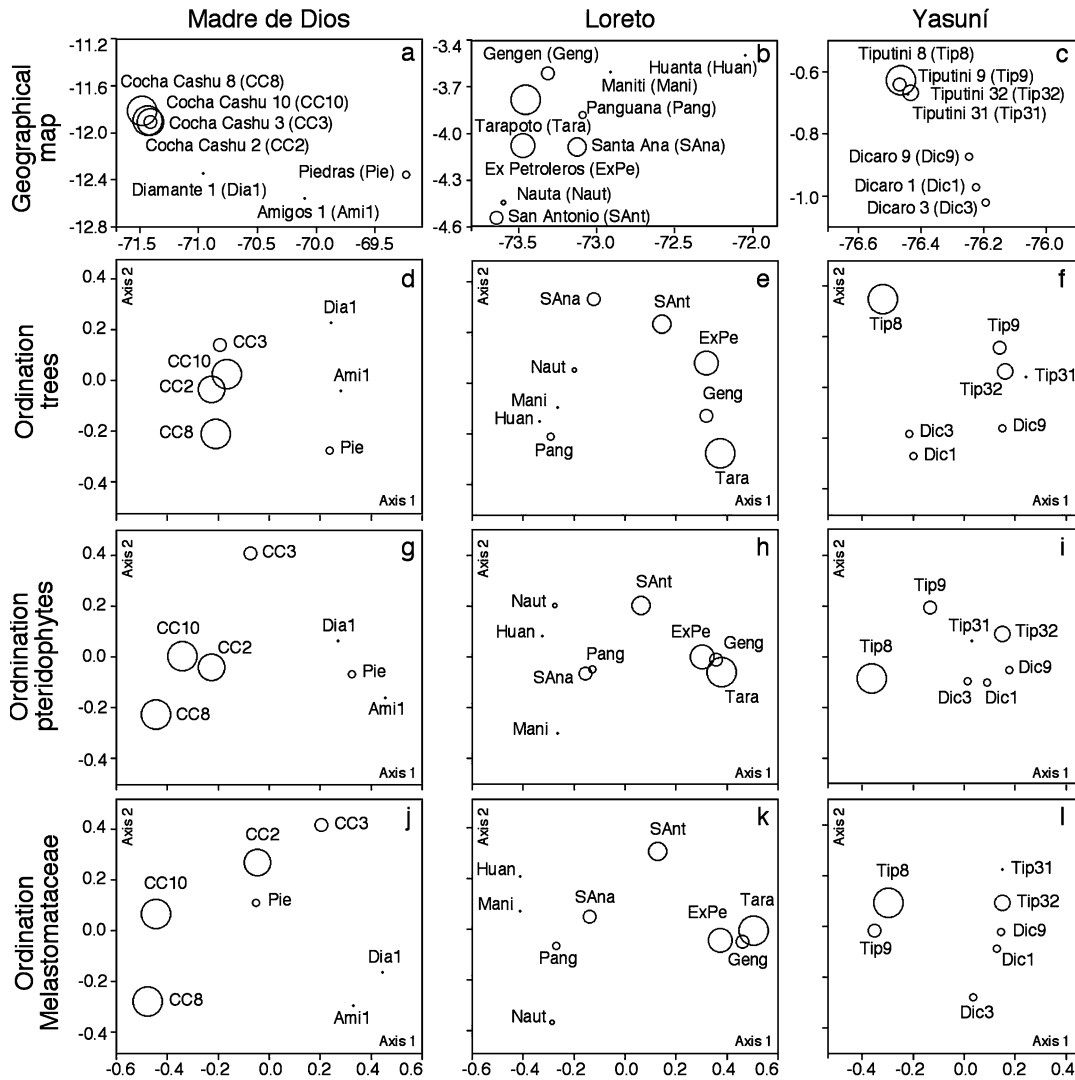
explained variation was clearly higher for common trees than for rare trees (Figure 3).

## DISCUSSION

### Determinants of floristic patterns

The Mantel correlations between pteridophytes and all trees varied between 0.54 and 0.82 (presence–absence data), which means that 29–67% of the variation in the beta diversity of trees can be modelled with a simple linear function of the beta diversity of pteridophytes. In the multiple regression models, 22–80% of the variation in the beta diversity of all trees was explained by edaphic





**Figure 2.** Geographical locations of the study sites within each of three study regions (a, Madre de Dios; b, Loreto; c, Yasuní; latitude and longitude indicated in degrees), and floristic ordinations (Principal Coordinates analysis based on the Sørensen index) as obtained for each of three plant groups separately (d–f, trees; g–i, pteridophytes; j–l, Melastomataceae). The diameter of the circles is proportional to the mean concentration of exchangeable bases (Ca + K + Mg + Na) in the corresponding site relative to that in the other sites in the same region. The cumulative eigenvalues of the first two axes in the ordinations were 41–76%. For the location of the three regions, see Figure 1.

differences, 0–64% by geographical distances, and 49–86% by the two combined. These can be considered high percentages, given that all study sites represented structurally similar forests that are generally thought to belong to the same forest type.

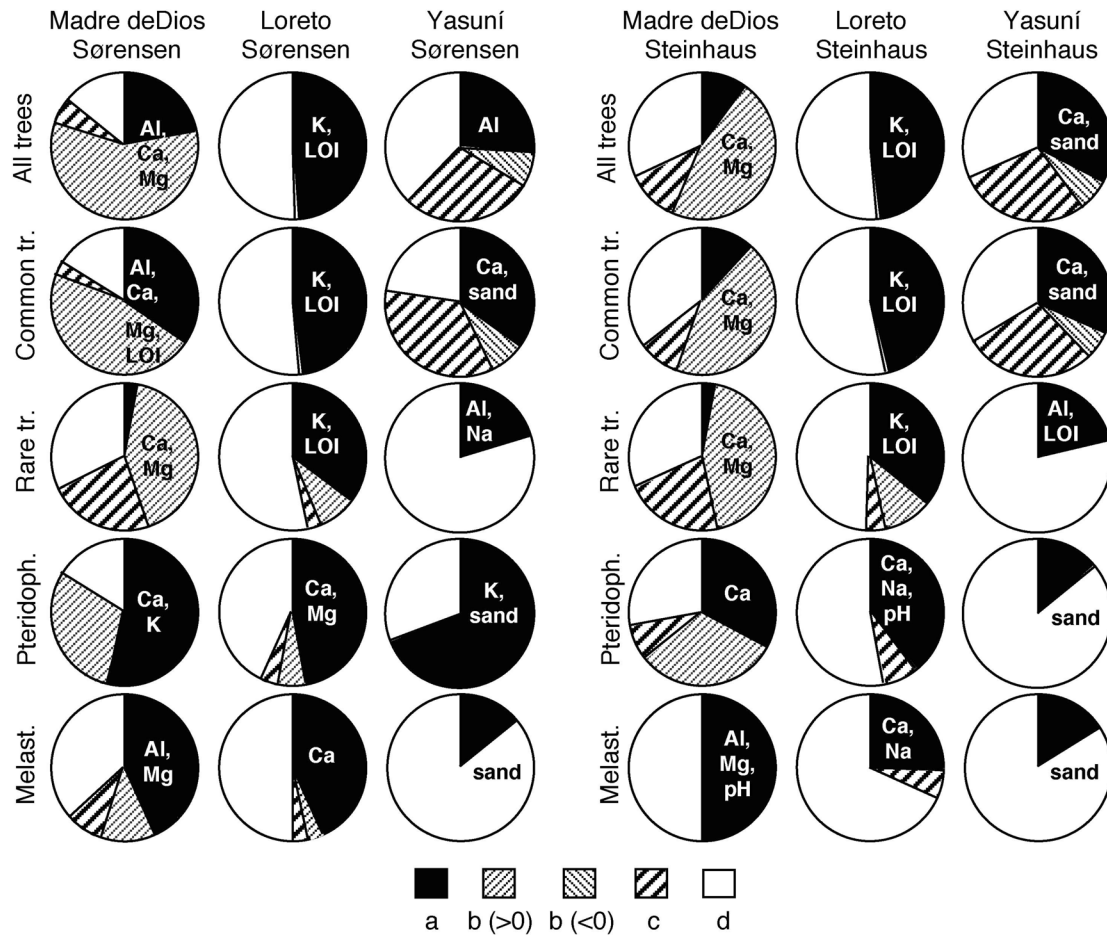
The floristic predictability that these results imply seems to arise from similar responses of the different plant groups to edaphic variability; usually the same edaphic factors emerged with high Mantel correlation coefficients no matter which of the three plant groups was analysed.

The relationships between plant groups and environmental properties become noisier as the length of the observed environmental gradient decreases (Ruokolainen *et al.* 1997). This probably explains the observed differences among our study regions. Soil properties

varied least in Yasuní and most in Loreto. Accordingly, the floristic differences among sites were smaller, the Mantel correlations between plant groups lower, and the role of edaphic differences in explaining floristic patterns smaller in Yasuní than in Madre de Dios and especially Loreto.

Geographical distances were most important in Madre de Dios, where the edaphic characteristics themselves were spatially autocorrelated. In Loreto and Yasuní, where geographical proximity was a less reliable predictor of edaphic similarity, geographical distances contributed less to explaining floristic differences.

We found that soil differences played a more important role than geographical distances in explaining floristic patterns, which agrees with several recent studies (Phillips *et al.* 2003a, Potts *et al.* 2002, Tuomisto *et al.*



**Figure 3.** Results of variation partitioning of floristic differences (as based on multiple regression on distance matrices) in three regions of lowland western Amazonia. Trees (tr.), Pteridophytes (Pteridoph.) and Melastomataceae (Melast.) were analysed separately using either the Sørensen index (presence-absence data, left) or the Steinhaus index (abundance data, right). Edaphic differences were based on the Euclidean distance. The soil variables retained in a backward elimination procedure, and hence included in the final analysis, are shown in each case (LOI = loss on ignition). Proportions of variation explained: a = uniquely explained by the edaphic differences; b = jointly explained by the edaphic and geographical distances; c = uniquely explained by the geographical distances; d = unexplained. Since fraction b is obtained by subtraction, it may be either positive or negative.

2003a, b, c). However, Vormisto *et al.* (2004) found that geographical distances were more important, which might be due to differences among the focal plant groups or the studied geographical regions, or the fact that Vormisto *et al.* had not measured all the soil variables that were found significant in the other studies.

On average, the variation in floristic differences of all trees was explainable to a higher degree (62%) than that of either pteridophytes (57%) or Melastomataceae (37%). This suggests, in accordance with Svenning *et al.* (2004), that beta diversity of trees is no less dependent on spatial and edaphic factors than beta diversity of the smaller-statured plant groups. The differences between plant groups may even reflect the relatively small number of sites in our study: in a larger data set, little difference was found between Melastomataceae and pteridophytes (Tuomisto *et al.* 2003c).

The Mantel tests and multiple regression analyses showed that the within-region floristic differences of common trees were at least as well explainable by edaphic differences as the floristic patterns of rare trees. This agrees with Phillips *et al.* (2003a) in that even if common trees are competitively superior and able to dominate the forest in some circumstances (Pitman *et al.* 2001), they are not indifferent to environmental heterogeneity.

#### Are these results reliable?

Our data set has five evident sources of error, which all bias the results towards underestimating the correspondence between edaphic and floristic patterns. (1) The tree plots overlapped only partly with the line transects data. (2) Many environmental variables known to affect plant

growth were not measured (e.g. light availability, soil drainage and soil nitrogen). (3) Only three soil samples were taken at each site, only the surface soil was sampled, and all samples were taken on a single occasion. (4) Standard laboratory protocols may not give an optimal representation of soil properties at the root surface. (5) The soil samples from Loreto were analysed in three different laboratories, which led to measurement error.

A larger data set might have yielded stronger relationships between the floristic and edaphic patterns, as small data sets are error-prone and only very clear patterns can yield statistically significant results. In a 27-site study in Yasuní, we covered the local soil gradient better than in this study and indeed found stronger relationships between Melastomataceae, pteridophytes and soils (Tuomisto *et al.* 2003a).

The Mantel correlations between plant groups may be affected by the number of species per group. For the very species-rich trees, the plots are too small to contain a representative sample of the local flora, but species-poor groups may reflect the edaphic patterns incompletely (Higgins & Ruokolainen 2004). This may partly explain why beta diversity of trees was more closely correlated with beta diversity of pteridophytes than that of Melastomataceae in Madre de Dios and Yasuní, where pteridophytes were clearly more species-rich than Melastomataceae. It is actually surprising that Melastomataceae can give a fair idea of the floristic patterns of trees in Madre de Dios, where the average site has only 14 Melastomataceae species but 159 tree species. This result can hardly be explained unless the same external factors control species distributions in both plant groups.

Despite differences among the three regions in the tree plot area and diameter class limits, the total number of stems sampled per region and the average number of stems per site were rather similar. Because increasing the number of stems in diameter-class inventories seems to yield better representation of general floristic patterns whatever the size of the stems (Higgins & Ruokolainen 2004), we consider the tree plots comparable for the purposes of the present study. If plant size is negatively correlated with the degree of ecological specialization (cf. Duque *et al.* 2002, Ruokolainen & Vormisto 2000, Ruokolainen *et al.* 2002), the correlation coefficients obtained for trees may be biased downwards in Madre de Dios, where only large trees were sampled, but even there the proportion of variation explainable with edaphic differences was comparable for the three plant groups.

In general, the floristic patterns of trees, pteridophytes and Melastomataceae were more strongly correlated when presence–absence than abundance data were used. This difference is probably due to sampling error: reliable measurement of the abundance of a species at a site necessitates inventorying a larger surface area than reliable estimation of whether the species is present.

## Practical implications

Our results are in agreement with the suggestion that edaphic heterogeneity plays an important role in promoting beta diversity in Amazonian tierra firme forests, and that floristic patterns are sufficiently strongly linked to edaphic patterns to be considered both predictable and relatively stable in time. Consequently, classifying these forests to edaphically defined site types, which also reflect floristic variation, appears both realistic and useful.

The information on habitat heterogeneity within tierra firme forests needs to become more detailed to allow evaluating how well existing protected area networks achieve complementarity, and where areas representing habitats not yet included in protected areas are situated. Such information also helps in evaluating to where results from field studies can be extended, as interpolation within the same forest type is less risky than extrapolation to a different type. Because inventories including all plant species are laborious, it will be a great advantage if reliable maps on floristic patterns can be based on surrogates, such as easily observable indicator plant groups in combination with environmental and remotely sensed data (Faith & Walker 1996, Ferrier 2002, Salovaara *et al.* 2005, Thessler *et al.* 2005, Tuomisto *et al.* 1995, 2003a, b). Mapping floristic patterns in Amazonian tierra firme forests over hundreds of thousands of square kilometres is hardly realistic if ground-truthing is based on inventories of trees or all plants. In our experience, both field inventories and species identifications of pteridophytes and Melastomataceae are at least an order of magnitude faster than those of trees (see also Higgins & Ruokolainen 2004, Phillips *et al.* 2003b). The congruence among plant groups in our study was far from perfect, but when the tree data were divided into two subsets (common trees and rare trees), the Mantel correlations between these were similar to the correlations between either tree subset and pteridophytes. This indicates that pteridophytes provide as accurate a picture of floristic patterns in trees as do subsets of the trees themselves. We find that these results warrant recommending the use of indicator groups for general habitat mapping and analyses of heterogeneity and distinctiveness, as promoted by Faith & Walker (1996) and Ferrier (2002).

The indicator groups obviously cannot provide direct information on non-inventoried taxa. So even if the modelling of beta diversity and consequent habitat mapping were based on indicator species, inventories of trees and other plants should still be conducted at a subset of the field sites both to obtain direct data on their distributions, and to verify to what degree they conform with the floristic patterns of the indicators. The indicator groups can help in stratifying the sampling for these more time-consuming studies, which in turn can

be used iteratively to refine the initial models (Ferrier 2002).

It can be argued that forest types could be separated on the basis of soil data, and indicator species would hence not be needed (Duque *et al.* 2005). However, soil mapping at a sufficient spatial resolution would necessitate collecting and analysing very large numbers of soil samples. The number and cost of soil samples increase in direct proportion to the size of the area of interest, and the data would only be available after laboratory analyses. In contrast, a list of indicator species occurring at a site can be obtained quite rapidly, and is immediately available for use. Indicator plant groups may also help in weighting the importance of environmental variables, indicate effects of such environmental variables that are difficult or impossible to measure from soil samples, and reveal biogeographical differences in regional species pools which are indispensable for conservation purposes (cf. Faith & Walker 1996, Ferrier 2002, Tuomisto *et al.* 2003c).

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## LITERATURE CITED

- CAJANDER, A. K. 1926. The theory of forest types. *Acta Forestalia Fennica* 29:1–108.
- CONDIT, R., PITMAN, N., LEIGH, E. G. Jr, CHAVE, J., TERBORGH, J., FOSTER, R. B., NÚÑEZ, V., P., AGUILAR, S., VALENCIA, R., VILLA, G., MULLER-LANDAU, H., LOSOS, E. & HUBBELL, S. P. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.
- DUIVENVOORDEN, J. F., SVENNING, J.-C. & WRIGHT, S. J. 2002. Beta diversity in tropical forests. *Science* 295:636–637.
- DUQUE, A., SÁNCHEZ, M., CAVELIER, J. & DUIVENVOORDEN, J. F. 2002. Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology* 18:499–525.
- DUQUE, A. J., DUIVENVOORDEN, J. F., CAVELIER, J., SÁNCHEZ, M., POLANÍA, C. & LEÓN, A. 2005. Ferns and Melastomataceae as indicators of vascular plant composition in rain forests of Colombian Amazonia. *Plant Ecology* 178:1–13.
- ELLENBERG, H. 1988. *Vegetation ecology of Central Europe*. Cambridge University Press, Cambridge. 753 pp.
- FAITH, D. P. & WALKER, P. A. 1996. How do indicator groups provide information about the relative biodiversity of different sets of areas?: On hotspots, complementarity and pattern-based approaches. *Biodiversity Letters* 3:18–25.
- FERRIER, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology* 51:331–363.
- GÉGOUT, J.-C., HERVÉ, J.-C., HOULLIER, F. & PIERRAT, J.-C. 2003. Prediction of forest soil nutrient status using vegetation. *Journal of Vegetation Science* 14:55–62.
- GENTRY, A. H. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Science of USA* 85:156–159.
- HIGGINS, M. & RUOKOLAINEN, K. 2004. Rapid tropical forest inventory: a comparison of techniques using inventory data from western Amazonia. *Conservation Biology* 18:799–811.
- HOLMGREN, P. K., HOLMGREN, N. H. & BARNETT, L. C. 1990. *Index herbariorum*. New York Botanical Garden, New York. 693 pp.
- HUBBELL, S. P. 2001. *The Unified Neutral Theory of biodiversity and biogeography*. Princeton University Press, Princeton. 448 pp.
- HUBER, O. & ALARCÓN, C. 1988. Mapa de vegetación de Venezuela. Ministerio del ambiente y de los recursos naturales renovables, Caracas.
- IBGE 2004. Mapa de vegetação do Brasil. Third edition. Ministério do planejamento, orçamento e gestão. <http://www.ibge.gov.br/>
- LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical ecology*. Elsevier, Amsterdam. 870 pp.
- LEGENDRE, P., LAPOINTE, F.-J. & CASGRAIN, P. 1994. Modeling brain evolution from behaviour: a permutational regression approach. *Evolution* 48:1487–1499.
- LIPS, J. & DUIVENVOORDEN, J. F. 2001. Caracterización ambiental. Pp. 19–45 in Duivenvoorden, J. F., Balslev, H., Cavelier, J., Grandez, C., Tuomisto, H. & Valencia, R. (eds). *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental*. IBED, Universiteit van Amsterdam, Amsterdam.
- MACÍA, M. J. & SVENNING, J.-C. 2005. Oligarchic dominance in western Amazonian plant communities. *Journal of Tropical Ecology* 21:613–626.
- MCCUNE, B. & ALLEN, T. F. H. 1985. Will similar forest develop on similar sites? *Canadian Journal of Botany* 63:367–376.
- OLIVER, I., BEATTIE, A. J. & YORK, A. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in eastern Australia. *Conservation Biology* 12:822–835.
- PHILLIPS, O. L., NÚÑEZ VÁRGAS, P., LORENZO MONTEAGUDO, A., PEÑA CRUZ, A., CHUSPE ZANS, M.-E., GALIANO SÁNCHEZ, W., YLI-HALLA, M. & ROSE, S. 2003a. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* 91:757–775.
- PHILLIPS, O. L., VÁSQUEZ MARTÍNEZ, R., NÚÑEZ VÁRGAS, P., LORENZO MONTEAGUDO, A., CHUSPE ZANS, M.-E., GALIANO

- SÁNCHEZ, W., PEÑA CRUZ, A., TIMANÁ, M., YLI-HALLA, M. & ROSE, S. 2003b. Efficient plot-based floristic assessment of tropical forests. *Journal of Tropical Ecology* 19:629–645.
- PITMAN, N. C. A., TERBORGH, J., SILMAN, M. R., NÚÑEZ, V. P., NEILL, D. A., CERÓN, C. E., PALACIOS, W. A. & AULESTIA, M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82:2101–2117.
- POTTS, M. D., ASHTON, P. S., KAUFMAN, L. S. & PLOTKIN, J. B. 2002. Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83:2782–2797.
- ROMERO-SALTOS, H., VALENCIA, R. & MACÍA, M. J. 2001. Patrones de diversidad, distribución y rareza de plantas leñosas en el Parque Nacional Yasuní y la Reserva Étnica Huaorani, Amazonía ecuatoriana. Pp. 131–162 in Duivenvoorden, J. F., Balslev, H., Cavelier, J., Grandez, C., Tuomisto, H. & Valencia, R. (eds). *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental*. IBED, Universiteit van Amsterdam, Amsterdam.
- RUOKOLAINEN, K. & TUOMISTO, H. 1998. Vegetación natural de la zona de Iquitos. Pp. 253–365 in Kalliola, R. & Flores, S. (eds). *Geoecología y desarrollo amazónico: estudio integrado en la zona de Iquitos, Perú*. Annales Universitatis Turkuensis Ser A II 114.
- RUOKOLAINEN, K. & VORMISTO, J. 2000. The most widespread Amazonian palms tend to be tall and habitat generalists. *Basic and Applied Ecology* 1:97–108.
- RUOKOLAINEN, K., LINNA, A. & TUOMISTO, H. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographic patterns in Amazonian rain forests. *Journal of Tropical Ecology* 13:243–256.
- RUOKOLAINEN, K., TUOMISTO, H., VORMISTO, J. & PITMAN, N. 2002. Potential effects of two biases on estimating Amazonian plant distributions. *Journal of Tropical Ecology* 18:935–942.
- SAGERS, C. L. & LYON, J. 1997. Gradient analysis in a riparian landscape: contrasts among forest layers. *Forest Ecology and Management* 96:13–26.
- SALOVAARA, K., THESSLER, S., MALIK, R. N. & TUOMISTO, H. 2005. Classification of Amazonian primary rain forest vegetation using Landsat ETM+ satellite imagery. *Remote Sensing of Environment* 97:39–51.
- SVENNING, J.-C., KINNER, D. A., STALLARD, R. F., ENGELBRECHT, B. M. J. & WRIGHT, S. J. 2004. Ecological determinism in plant community structure. *Ecology* 85:2526–2538.
- TERBORGH, J. N., PITMAN, N., SILMAN, M., SCHICHTER, H. & NÚÑEZ, V., P. 2002. Maintenance of tree diversity in tropical forests. Pp. 1–17 in Levey, D. J., Silva, W. & Galetti, M. (eds). *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, Wallingford.
- THESSLER, S., RUOKOLAINEN, K., TUOMISTO, H. & TOMPPONEN, E. 2005. Mapping gradual landscape-scale floristic changes in Amazonian primary rain forests by combining ordination and remote sensing. *Global Ecology and Biogeography* 14:315–325.
- TUOMISTO, H. & POULSEN, A. 1996. Influence of edaphic specialization on pteridophyte distribution in neotropical rain forests. *Journal of Biogeography* 23:283–293.
- TUOMISTO, H., RUOKOLAINEN, K., KALLIOLA, R., LINNA, A., DANJOY, W. & RODRIGUES, Z. 1995. Dissecting Amazonian biodiversity. *Science* 269:63–66.
- TUOMISTO, H., POULSEN, A. D., RUOKOLAINEN, K., MORAN, R. C., QUINTANA, C., CELI, J. & CAÑAS, G. 2003a. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications* 13:352–371.
- TUOMISTO, H., RUOKOLAINEN, K., AGUILAR, M. & SARMIENTO, A. 2003b. Floristic patterns along a 43-km-long transect in an Amazonian rain forest. *Journal of Ecology* 91:743–756.
- TUOMISTO, H., RUOKOLAINEN, K. & YLI-HALLA, M. 2003c. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299:241–244.
- VAN REEUWIJK, L. P. 1993. *Procedures for soil analysis*. (Fourth edition). ISRIC Technical Paper 9. Wageningen, The Netherlands. 95 pp.
- VELLEND, M. 2001. Do commonly used indices of  $\beta$ -diversity measure species turnover? *Journal of Vegetation Science* 12:545–552.
- VORMISTO, J., PHILLIPS, O., RUOKOLAINEN, K., TUOMISTO, H. & VÁSQUEZ, R. 2000. A comparison of small-scale distribution patterns of four plant groups in an Amazonian rainforest. *Ecography* 23:349–359.
- VORMISTO, J., SVENNING, J.-C., HALL, P. & BALSLEV, B. 2004. Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazon basin. *Journal of Ecology* 92:577–588.
- WEBB, L. J., TRACEY, J. G., WILLIAMS, W. T. & LANCE, G. N. 1967. Studies in the numerical analysis of complex rain-forest communities II. The problem of species-sampling. *Journal of Ecology* 55:525–538.
- WILSON, S. M., PYATT, D. G., MALCOLM, D. C. & CONNOLLY, T. 2001. The use of ground vegetation and humus type as indicators of soil nutrient regime for an ecological site classification of British forests. *Forest Ecology and Management* 140:101–116.
- WOLDA, H. 1981. Similarity indices, sample size, and diversity. *Oecologia* 50:296–302.
- YOUNG, K. R. & LEÓN, B. 1989. Pteridophyte species diversity in the central Peruvian Amazon: importance of edaphic specialization. *Brittonia* 41:388–395.

