Environmental heterogeneity and the diversity of pteridophytes and Melastomataceae in western Amazonia

HANNA TUOMISTO AND KALLE RUOKOLAINEN

TUOMISTO, H. & RUOKOLAINEN, K. 2005. Environmental heterogeneity and the diversity of pteridophytes and Melastomataceae in western Amazonia. *Biol. Skr.* **55**: 37-56. ISSN 0366-3612. ISBN 87-7304-304-4.

We studied species richness and diversity of terrestrial and low-epiphytic pteridophytes and Melastomataceae in lowland rain forests in western Amazonia. Our objective was to analyse 1) how alpha-diversity is related to ecological gradients, and 2) whether alpha-diversity of one of these plant groups can be used as an indicator of alpha-diversity of the other. We made field inventories in Colombia, Ecuador, northern Peru, and southern Peru, using several transects that represented both inundated and non-inundated (*terra firme*) forests in each area. The total area sampled exceeded 79 ha for pteridophytes and 102 ha for Melastomataceae. The total number of species observed was 323 for pteridophytes and 297 for Melastomataceae. Transects of 0.25 ha (500 m by 5 m) contained, on average, 34 species of pteridophytes and 22 species of Melastomataceae. Both plant groups had lower within-transect species richness and diversity (Shannon's H) in inundated than in non-inundated forests, but along soil gradients within the two major landscape types, the trends were different. In terra firme forest, for example, pteridophyte species richness increased linearly with the logarithm of soil cation content, whereas Melastomataceae species richness showed a tendency to peak at intermediate cation contents. Both species richness and diversity were correlated between the two plant groups. However, correlation coefficients were relatively low, especially when compared to correlations that have been reported previously when between-site similarities in species composition were analysed for the same plant groups. We conclude that it is less realiable to use indicator plant groups for predicting patterns in alpha-diversity than for predicting patterns in beta-diversity.

Hanna Tuomisto, Department of Biology, University of Turku, FI-20014 Turku, Finland. E-mail: hanna.tuomisto@utu.fi

Kalle Ruokolainen, Department of Biology, University of Turku, FI-20014 Turku, Finland. E-mail: kalle.ruokolainen@utu.fi

Introduction

Early interest in species diversity gradients was largely focussed on trends in gamma diversity at continental to global scales, and on differences in regional species richness relative to such environmental variables as potential or actual evapotranspiration (*e.g.*, Currie 1991 and references cited therein). More recently, trends in alpha-diversity (local species richness) along different ecological gradients have attracted attention. Especially disturbance,

herbivory and productivity are being used to explain variation between sites in local plant species richness (reviewed in Givnish 1999; Waide *et al.* 1999; Pausas & Austin 2001; Wright 2002).

With increasing attention to biodiversity conservation, alpha-diversity (local or within-sample diversity) has gained status as one of the criteria that can be used in selection of nature reserves (Flather *et al.* 1997). Consequently, hope emerged that an easy-to-obtain general measure of alpha-diversity could be developed. This would save researchers and conservation planners the effort of measuring the species richness of all plant and animal groups separately, which would be an unmanageably big task especially in the tropics. However, predicting alpha-diversity has proven a difficult business, and reliable indicators of alpha-diversity have been hard to find. One approach has been to look for such plant or animal groups whose species richness could serve as an indicator of the species richness in other plant or animal groups. The success of this approach has been limited, as it has usually been found that the species richness of different groups of organisms are correlated weakly or not at all (Prendergast *et al.* 1993; Lawton *et al.* 1998; Tuomisto *et al.* 2002).

Another approach has been to model species richness as a function of physical environmental conditions, such as temperature, rainfall, or soil fertility, which would be easier to measure than species richness itself. This approach faces the problem that the alpha-diversities of different plant or animal groups may show different trends along the environmental gradients, or they may show no systematic trends at all. For example, contrasting models on the response functions of alpha-diversity along fertility gradients have been proposed, including bimodal (Austin & Smith 1989), unimodal (Tilman 1988; Vandermeulen *et al.* 2001) and monotonic (Abrams 1995). Givnish (1999) suggested that forests on fertile soils should have more tree species than forests on infertile soils, because soil infertility promotes chemical defenses that reduce the effect of pathogens. On the other hand, if plant-plant interactions were the only ones operating in the forest, maximum diversity would be expected at intermediate soil fertility.

Field studies of plant alpha-diversity along soil fertility gradients in tropical rain forests have also yielded contradicting results: some have found increasing alpha-diversity with increasing soil fertility (Gentry 1988; Duivenvoorden 1994, 1996; Tuomisto & Poulsen 1996; Tuomisto *et al.* 2002) others the opposite (Huston 1980), and some have documented a diversity peak at intermediate soil fertility (Ashton 1992; Rosenzweig & Abramsky 1993) or no relationship at all (Clinebell *et al.* 1995). These discrepancies may be due to, for example, different ranges in the environmental gradients covered in each study, confounding environmental factors, different behavior of the different plant groups studied, or inherent differences between geographical areas. In any case, much more understanding of the distribution of alpha-diversity is needed before environmental variables can be used as a surrogate for measuring alpha-diversity.

Here, we investigate patterns in plant alpha-diversity of two independent plant groups in western Amazonian rain forests. Our aim is to understand the correlations between them, and to study how their alpha-diversities are related to environmental (especially edaphic) gradients. In addition, we attempt to estimate the level of environmental heterogeneity within each sample for the simple reason that environmentally more heterogeneous samples probably contain more species than more homogeneous ones. Our data come from pteridophyte and Melastomataceae inventories in four different parts of western Amazonia. We also estimate regional (gamma-diversity) and

Fig. 1. Map of western South America with the four study regions indicated.

between-sample (beta-diversity) diversities within the four study areas to see if they affect local species diversity, as has been suggested by several authors (Ricklefs 1987; Shmida & Wilson 1985; Ricklefs & Schluter 1993).

Material and methods

We surveyed lowland rain forests in Colombia, Ecuador, northern Peru, and southern Peru (Fig. 1). All areas are within the range 100-400 m above sea level, and have flat, gently undulating or hilly topography with hills rarely exceeding 60 m in height. Climate in the three northern areas is tropical and almost aseasonal with about 3000 mm of rain annually. Southern Peru has a more seasonal climate and a total annual precipitation of about 2000 mm (Hoffmann 1975; Gentry 1990; Marengo 1998; Lips & Duivenvoorden 2001). Two plant groups were inventoried in the same sites: pteridophytes (ferns and fern allies) and the Melastomataceae (a family of shrubs, small trees and vines).

To estimate the sizes of the regional species pools (gamma-diversity) of these plant groups for each of the four regions, we used both literature data (Tryon & Stolze 1989-1994; Brako & Zarucchi 1993; Jørgensen & León-Yánez 1999) and all inventory data we have collected ourselves. The latter is the same data set that was used in Ruokolainen *et al.* (2002), and it includes about 200 sites inventoried using sampling units of different sizes and shapes. The sampling units consisted of either 1) several square plots (20 m by 20 m or 25 m by 25 m in size), 2) a 5-m-wide line transect of 500 m or 1300 m in length, or 3) a 2-m-wide line transect of 9.7 km to 43 km in length. In each transect, all species of pteridophytes and Melastomataceae were inventoried, with the exception of pteridophytes with all leaves shorter than 10 cm, and epiphytes and climbers with the lowermost green leaves more than 2 m above ground. These conditions were set in order to speed up the field work, as searching for tiny juveniles and climbing trees to collect canopy epiphytes are very time-consuming excercises. Each of the methods has been explained in more detail elsewhere (Tuomisto & Ruokolainen 1994; Ruokolainen *et al.* 1997; Ruokolainen & Tuomisto 1998; Tuomisto *et al.* 2003a, b). The total area sampled in the four regions exceeded 79 ha for pteridophytes and 102 ha for Melastomataceae.

Our principal interest here is in local species diversity, and we have chosen to operate simultanously with two different alpha-diversity measures: the number of species in a fixed surface area (species richness) and Shannon's index of diversity (H).

$$H = -\sum p_i \ln p_i \qquad (1)$$

where p_i is the proportion of individuals belonging to the ith species in the sample (Magurran 1988). Local species richness and diversity were quantified in a subset of the data described above, namely 160 line transects of 0.25 ha each (5 m x 500 m). The transect inventories included non-inundated forests on clayey, loamy and sandy soils, as well as seasonally inundated and swamp forests. This is the same dataset that was used in Tuomisto *et al.* (2003c), except that we excluded three transects that included both non-inundated and seasonally inundated parts. The transects were allocated to two categories: non-inundated *terra firme* forests (124 sites) and inundated forests (36 sites, including both seasonally inundated floodplain forests and permanently waterlogged swamp forests).

Within each of the four study regions, we estimated species turnover or beta-diversity by calculating the Jaccard similarity index between all pairs of transects, and subtracting its values from 1. The Jaccard index is computed by dividing the number of shared species with the total number of species in two transects (Legendre & Legendre 1998), so after its 1-complement is taken, high index values indicate high species turnover. The Jaccard index was computed separately for pteridophytes and Melastomataceae and expressed in percentages (original index value x 100%).

Several (usually three) surface soil samples were taken along each transect. Each sample was a composite of five subsamples collected within 5 m from each other and mixed. Most soil samples were analysed in MTT Agrifood Research Finland, although some samples were analysed in the Geological Survey of Finland or the International Soil Reference and Information Centre (Wageningen, the Netherlands) using standard methods (van Reeuwijk 1993). More detailed descriptions of soil sampling and analyses are given by Ruokolainen and Tuomisto (1998) and Tuomisto *et al.* (2003a).

Here we analyse response functions of species richness and diversity along three edaphic gradients: soil cation content (Ca+K+Mg+Na, expressed in cmol(+)/kg), soil Al content, and soil pH. These soil properties are generally considered to correlate with soil fertility. Before analysis, cation and Al contents were log-transformed, because a given difference in element concentration is ecologically more important at low than at high concentrations. Since pH already is a logarithm, it was not transformed. Both first-order and second-order polynomial regressions were fitted to test for linear and unimodal relationships, respectively. We considered the values of the coefficients of determination of the regressions and their probabilities of error as criteria when evaluating whether diversity had a monotonic, unimodal or no relationship with each soil characteristic.

We measured the topographic profiles of the transects using a Suunto clinometer. The elevational range within each transect was used as a measure of topographic variability. As other measures of within-transect variability, we used standard deviations of the three chemical soil characteristics. Since a logical hypothesis is that alpha-diversity increases with site heterogeneity, we tested for linear and logarithmic regressions, but not for unimodal ones.

To test how similar the patterns in alpha-diversity were between pteridophytes and Melastomataceae, we computed linear Pearson's correlation coefficients for their species richness and diversity values. A correlation between the alpha-diversities of the two plant groups may result if both respond similarly to some of the environmental gradients. To investigate whether this was the case, we also computed a partial correlation coefficient between the alpha-diversities of pteridophytes and Melastomataceae. This was done so that first the alpha-diversity of each plant group was regressed on an environmental characteristic,

using either the linear or the quadratic regression function obtained earlier (but so that the same form was always used for both plant groups). Thereafter, the residuals of these regressions were extracted and the correlation coefficient computed between them. The amount of difference between the simple and partial correlation coefficient provides an esti-

Table 1. Inventory details for four geographical regions studied for pteridophytes and Melastomataceae in western Amazonia. Only the 0.25-ha transects were used in the numerical analyses, but the total area surveyed was used to obtain the total number of species found in inventories for each region. When available, regional species counts from floras or checklists are provided for comparison.

	Total area surveyed (ha)		Number of 0.25-ha transects	Total number of species found in inventories		Total number of species reported in literature	
	Pter.	Mel.	(non-inundated)	Pter.	Mel.	Pter.	Mel.
Colombia	14.74	24.97	17 (13)	127	133		
Ecuador	15.94	17.84	53 (43)	197	120	317	162
Northern Peru	37.00	47.46	43 (33)	195	188	243	236
Southern Peru	12.00	12.00	47 (35)	173	109	155	69
Total	79.68	102.27	160 (124)	323	297		

Table 2. Relationship of species richness and diversity of pteridophytes and Melastomataceae with some edaphic gradients and within-transect variability in edaphic factors in 124 *terra firme* transects in western Amazonia. The coefficients of determination (R-squares) of linear, second-order polynomial and/or logarithmic regressions are given. P values are those of the highest-order term in the regression. Statistically significant values are emphasized in bold. SD = standard deviation.

	Species richness (number of species)				Species diversity (Shannon's H)			
	Linear fit		Polynomial fit		Linear fit		Polynomial fit	
Edaphic gradient	Pterid.	Mel.	Pterid.	Mel.	Pterid.	Mel.	Pterid.	Mel.
log(Ca+K+Mg+Na)	**0.41** (<0.0001)	0.01 (0.4167)	**0.48** (<0.0001)	**0.04** (0.0319)	**0.19** (<0.0001)	**0.06** (0.0063)	0.20 (0.3022)	**0.14** (0.0025)
log(Al)	**0.23** (<0.0001)	**0.42** (<0.0001)	**0.27** (0.0166)	**0.45** (0.0104)	**0.05** (0.0128)	**0.50** (<0.0001)	0.05 (0.9461)	0.50 (0.2848)
pH	0.00 (0.4829)	**0.10** (0.0004)	**0.05** (0.0229)	**0.16** (0.0049)	0.01 (0.2564)	**0.17** (<0.0001)	**0.07** (0.0069)	**0.24** (0.0019)
Source of variation	Linear fit		Logarithmic fit		Linear fit		Logarithmic fit	
Elevation difference	**0.15** (<0.0001)	0.00 (0.8885)	**0.20** (<0.0001)	0.03 (0.0751)	**0.12** (0.0002)	0.00 (0.7533)	**0.11** (0.0003)	**0.05** (0.0135)
SD of log (Ca +K+Mg+Na)	**0.26** (<0.0001)	0.02 (0.1477)	**0.21** (<0.0001)	0.02 (0.1534)	**0.07** (0.0028)	**0.04** (0.0239)	**0.08** (0.0019)	0.03 (0.0602)
SD of log(Al)	0.01 (0.2065)	**0.04** (0.0269)	0.02 (0.1307)	**0.04** (0.0288)	**0.08** (0.0024)	0.00 (0.5386)	**0.08** (0.0022)	0.00 (0.8458)
SD of pH	0.00 (0.4847)	**0.05** (0.0125)	**0.03** (0.0464)	**0.03** (0.0478)	0.00 (0.5303)	0.03 (0.0796)	0.02 (0.1265)	0.02 (0.1185)

Table 3. Relationship of species richness and diversity of pteridophytes and Melastomataceae with some edaphic gradients and within-transect variability in edaphic factors in 36 seasonally inundated and swamp forest transects in western Amazonia. The coefficients of determination (R-squares) of linear, second-order polynomial and/or logarithmic regressions are given. P values are those of the highest-order term in the regression. Statistically significant values are emphasized in bold. SD = standard deviation.

	Species richness (number of species)				Species diversity (Shannon's H)			
	Linear fit		Polynomial fit		Linear fit		Polynomial fit	
Edaphic gradient	Pterid.	Mel.	Pterid.	Mel.	Pterid.	Mel.	Pterid.	Mel.
log(Ca+K+Mg+Na)	0.05 (0.1978)	**0.13** (0.0310)	0.07 (0.4233)	**0.27** (0.0187)	0.01 (0.6158)	0.09 (0.0793)	0.06 (0.1824)	**0.34** (0.0013)
log(Al)	0.02 (0.4371)	**0.36** (0.0001)	0.11 (0.0737)	0.39 (0.1643)	0.01 (0.5899)	**0.28** (0.0009)	**0.19** (0.0099)	**0.40** (0.0160)
pH	0.00 (0.8682)	**0.40** (<0.0001)	0.00 (0.8578)	0.45 (0.0797)	**0.12** (0.0360)	**0.40** (<0.0001)	0.17 (0.2050)	0.41 (0.4959)
Source of variation	Linear fit		Logarithmic fit		Linear fit		Logarithmic fit	
Elevation difference	0.00 (0.6852)	0.06 (0.1630)	0.01 (0.5528)	**0.15** (0.0182)	0.04 (0.2161)	0.10 (0.0627)	0.08 (0.0982)	**0.24** (0.0027)
SD of log(Ca+K+Mg+Na)	0.00 (0.9789)	0.02 (0.3620)	0.01 (0.5166)	0.03 (0.2882)	0.00 (0.8433)	0.09 (0.0793)	0.01 (0.6303)	0.08 (0.1016)
SD of log(Al)	0.01 (0.5704)	0.04 (0.2234)	0.01 (0.5181)	0.06 (0.1387)	0.08 (0.0991)	**0.12** (0.0376)	0.06 (0.1339)	**0.16** (0.0141)
SD of pH	0.03 (0.3216)	0.04 (0.2527)	0.00 (0.8398)	0.05 (0.1799)	0.00 (0.8572)	0.07 (0.1067)	0.00 (0.6845)	0.08 (0.0853)

mate of the importance of the environmental variable for the congruence in pteridophyte and Melastomataceae diversities.

Results

In total, we found 323 species of pteridophytes and 297 species of Melastomataceae (Table 1). Each region had more than 100 species of both plant groups, and usually there were more pteridophyte species than Melastomataceae species. The exception was Colombia, where Melastomataceae were slightly more speciose. The gamma-diversity estimates obtained from the literature were sometimes higher, sometimes lower than those based on field inventories (Table 1).

Each 0.25-ha transect contained, on average, 34 species of pteridophytes and 22 species of Melastomataceae (Fig. 2A, B). Species richness per transect varied between 4 and 76 species for pteridophytes, and between 2 and 46 species for Melastomataceae. Diversity (Shannon's H) varied between 0.19 and 3.38 (mean = 2.24) for pteridophytes, and between 0.14 and 3.35 (mean = 2.28) for Melastomataceae (Fig. 2C, D). The frequency distributions of the number of species per transect were close to normal, but the distributions of the values of Shannon's H were skewed to the left for both plant groups.

Both pteridophytes and Melastomataceae showed lower within-transect species richness in inundated than in non-inundated forests.

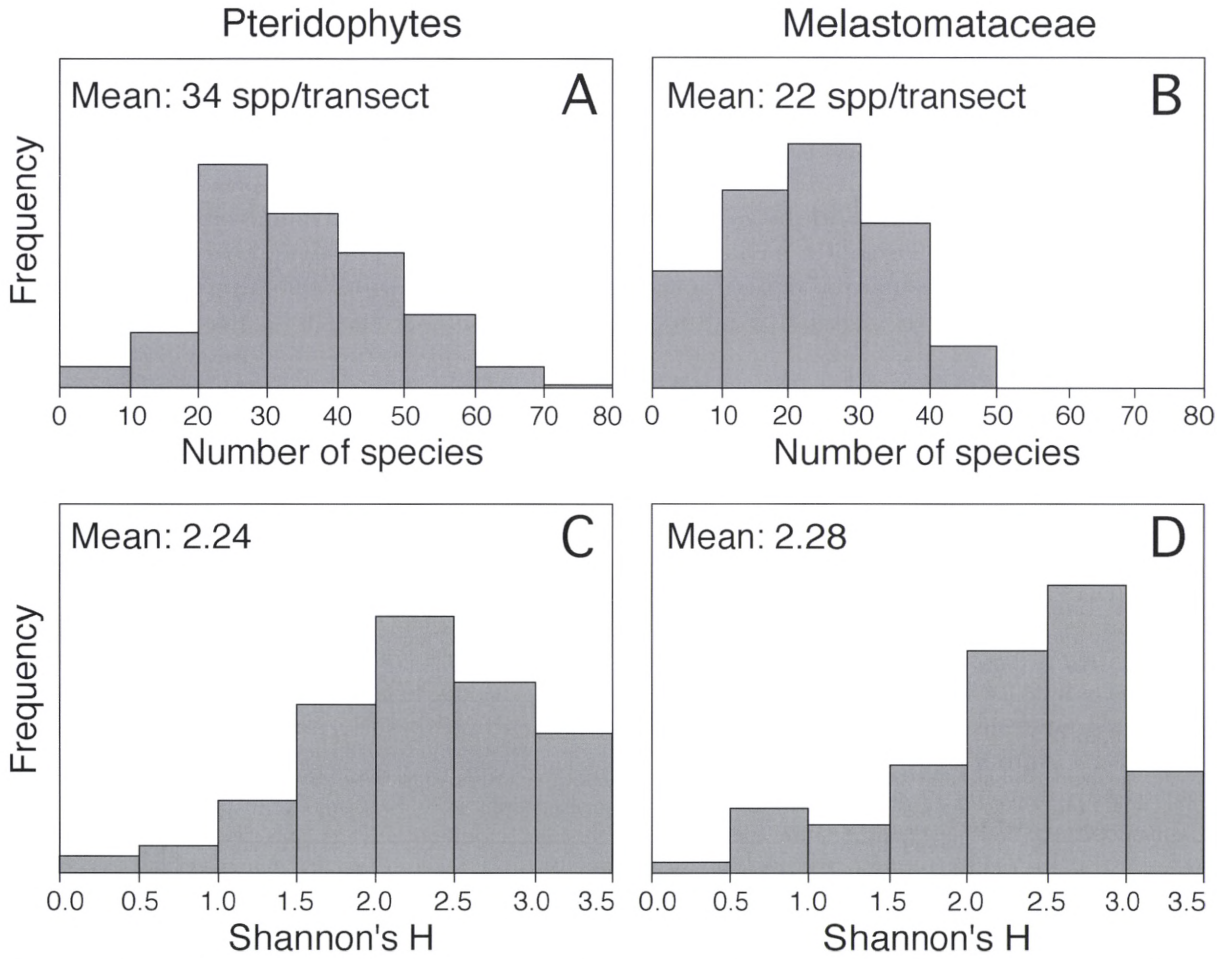

Fig. 2. Frequency histograms of the distribution of species richness (A, B) and Shannon's H diversity index (C, D) of pteridophytes (A, C) and Melastomatacese (B, D) in 160 transects (5 m by 500 m) in western Amazonia.

For pteridophytes, the mean number of species was 22 in inundated areas and 37 in non-inundated areas. For Melastomataceae, the mean number of species was 11 in inundated areas and 26 in non-inundated areas. Diversity (Shannon's H) was also lower in inundated than in non-inundated areas (means 1.62 vs. 2.42 for pteridophytes, 1.46 vs. 2.52 for Melastomataceae).

There were some regional differences in within-transect species richness. Transects in Ecuador showed generally high species richness for both plant groups. There was little difference between transects in the other three regions in pteridophyte species richness, but southern Peruvian transects showed clearly lower Melastomataceae species richness than transects in the other regions. The same tendency was observed in diversity, but differences between regions were smaller (*e.g.*, Fig. 3).

The relationships between species richness or diversity and the different environmental

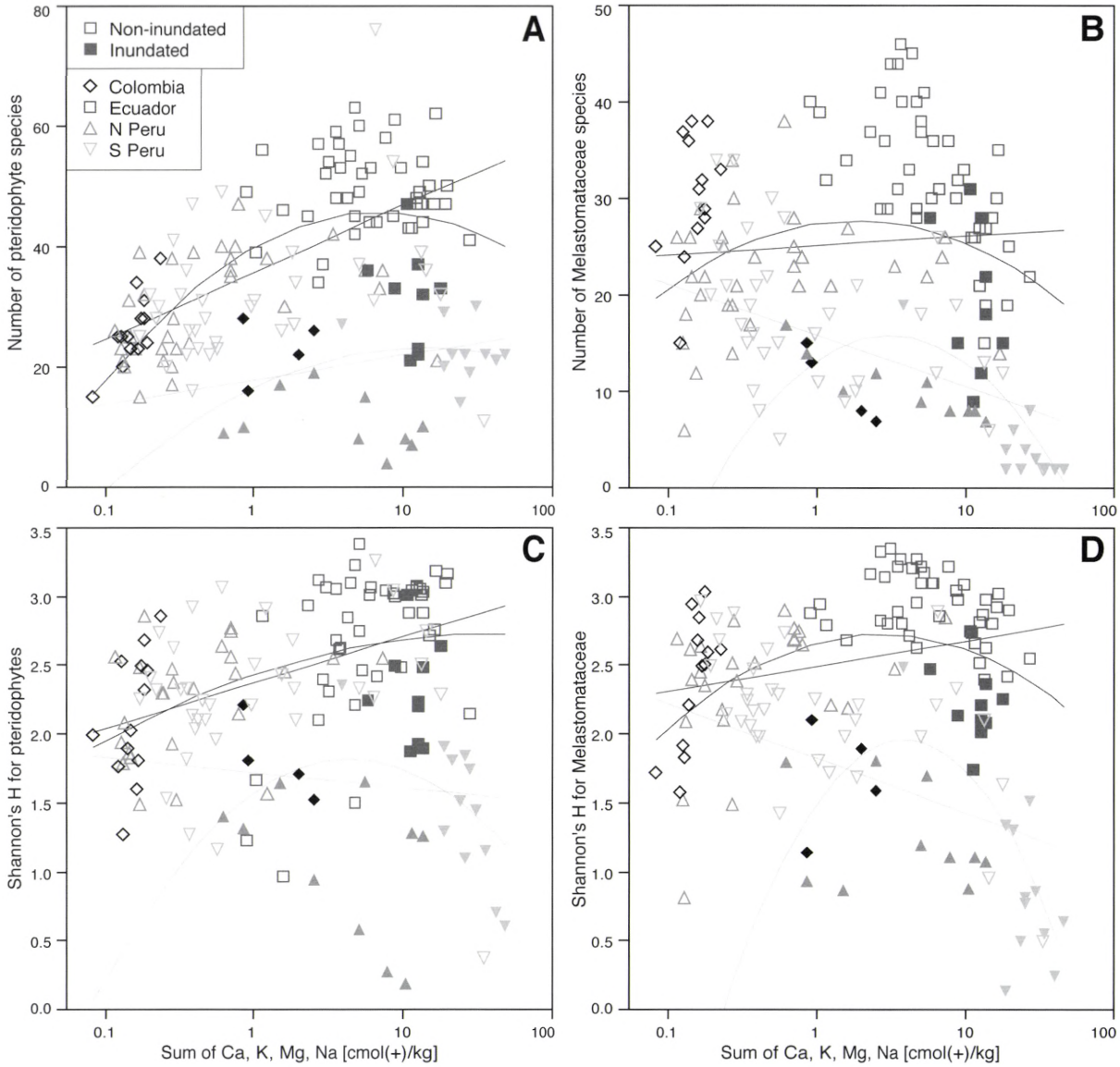

Fig. 3. Species richness (A, B) and Shannon's H diversity index (C, D) of pteridophytes (A, C) and Melastomatacese (B, D) as a function of logarithmically transformed soil cation content in 160 transects (5 m by 500 m) in western Amazonia. Linear and quadratic regressions are shown separately for transects in non-inundated areas (black lines) and inundated areas (grey lines). For R-squares and P values, see Tables 2 and 3.

characteristics are illustrated in Figures 3-6, and the statistical details are given in Tables 2-3.

In *terra firme* forests, both pteridophyte species richness and diversity increased linearly with the logarithm of soil cation content (Fig. 3, Table 2). The quadratic term was significant only in the regression of species richness, and even there it contributed relatively little to the

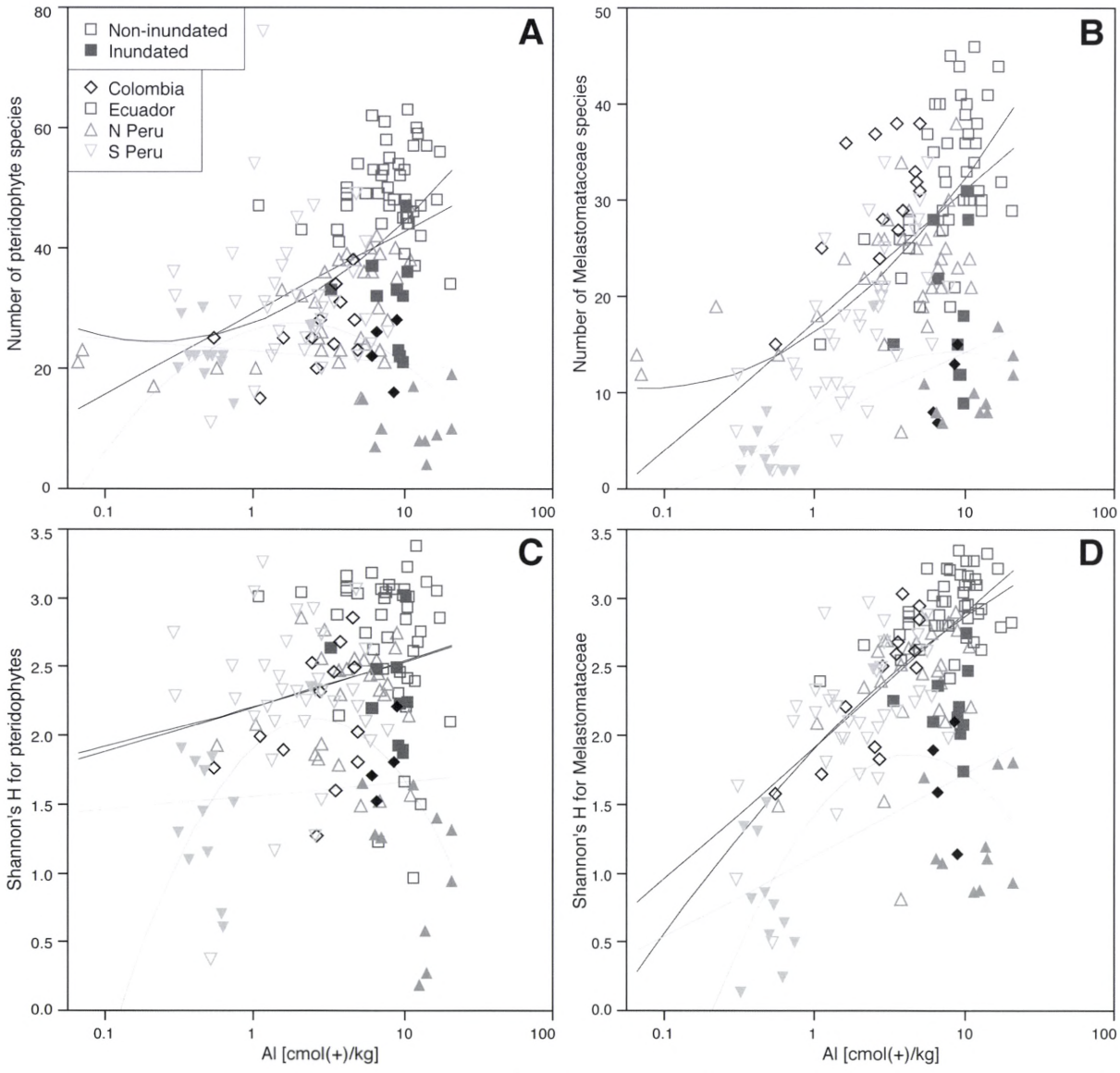

Fig. 4. Species richness (A, B) and Shannon's H diversity index (C, D) of pteridophytes (A, C) and Melastomatacese (B, D) as a function of logarithmically transformed soil aluminium content in 160 transects (5 m by 500 m) in western Amazonia. Linear and quadratic regressions are shown separately for transects in non-inundated areas (black lines) and inundated areas (grey lines). For R-squares and P values, see Tables 2 and 3.

coefficient of determination. In inundated forests (Fig. 3, Table 3), neither pteridophyte species richness nor diversity showed significant responses along the soil cation gradient. Melastomataceae species richness and diversity were best fit by the quadratic regression on soil cation content both in inundated and in *terra firme* forests.

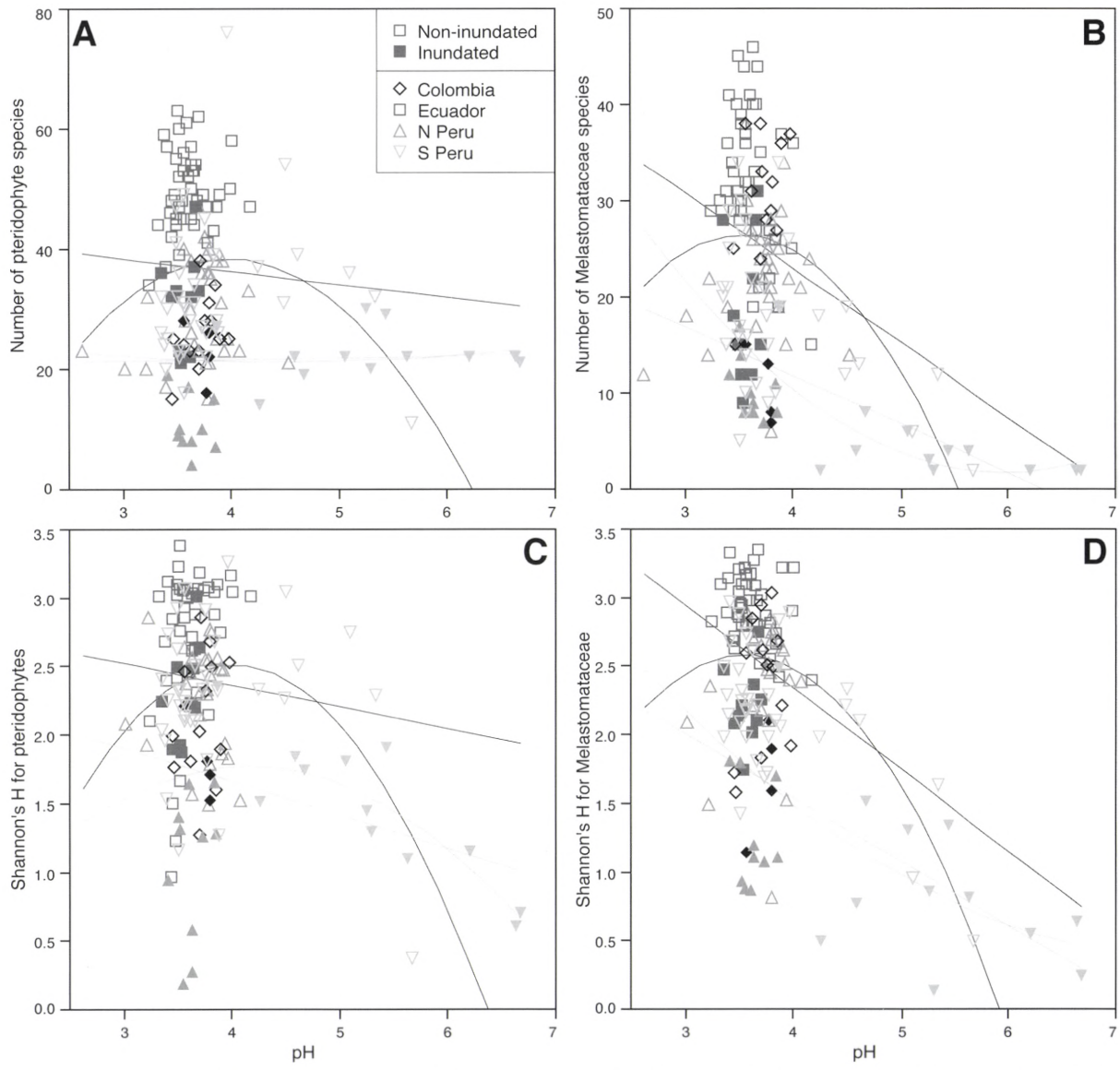

Fig. 5. Species richness (A, B) and Shannon's H diversity index (C, D) of pteridophytes (A, C) and Melastomatacese (B, D) as a function of soil pH in 160 transects (5 m by 500 m) in western Amazonia. Linear and quadratic regressions are shown separately for transects in non-inundated areas (black lines) and inundated areas (grey lines). For R-squares and P values, see Tables 2 and 3.

Along the soil aluminium content gradient in tierra firme, species richness and diversity of both pteridophytes and Melastomataceae showed a linear response; although the quadratic term was statistically significant for species richness, its contribution to the coefficient of determination was small. For pteridophyte species diversity, even the linear fit was

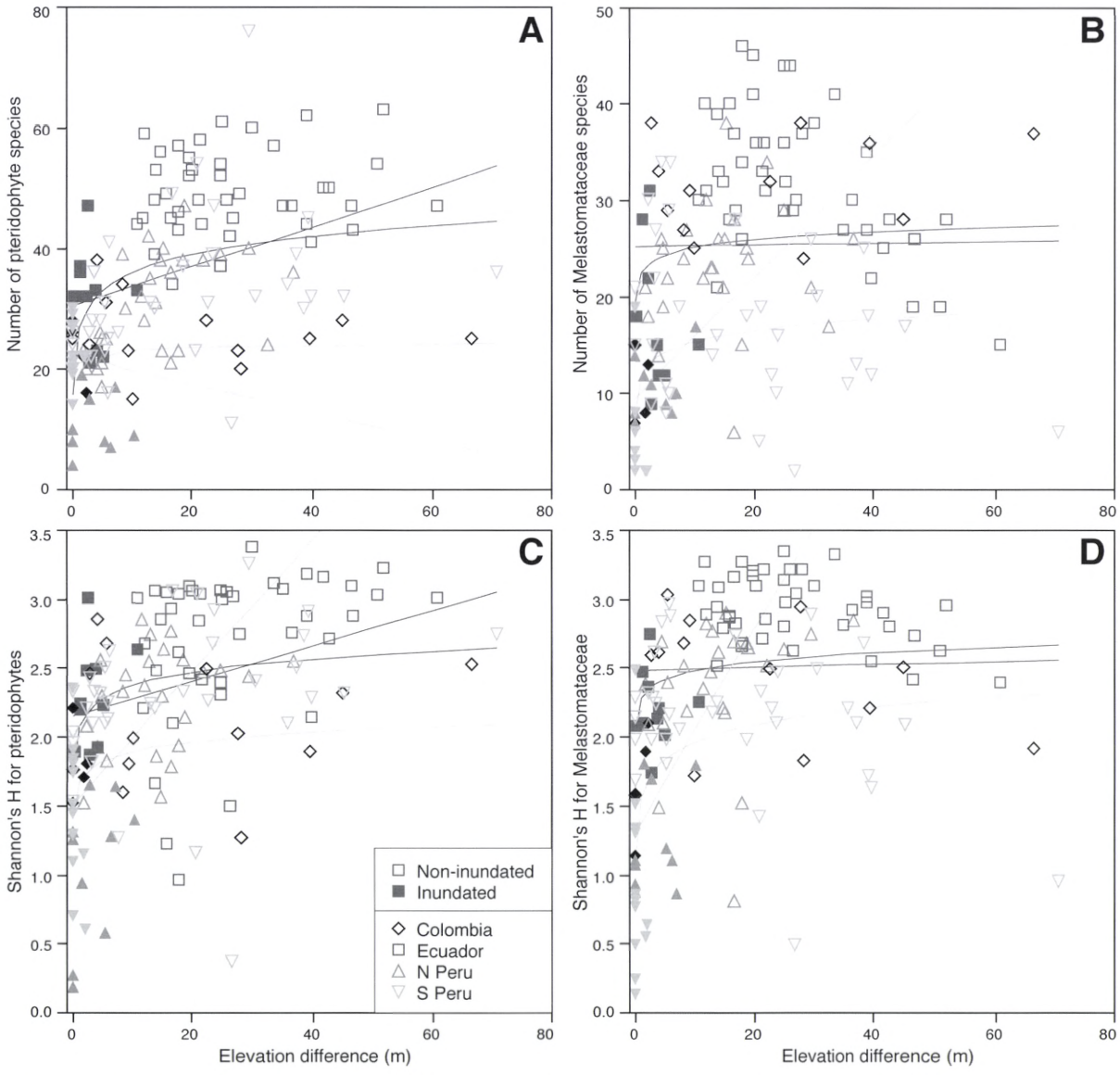

Fig. 6. Species richness (A, B) and Shannon's H diversity index (C, D) of pteridophytes (A, C) and Melastomatacese (B, D) as a function of elevation difference within 160 transects (5 m by 500 m) in western Amazonia. Linear and quadratic regressions are shown separately for transects in non-inundated areas (black lines) and inundated areas (grey lines). For R-squares and P values, see Tables 2 and 3.

poor (Fig. 4, Table 2). In inundated areas, Melastomataceae species richness showed a clear linear response and diversity a unimodal response along the Al content gradient. For pteridophytes, no statistically significant response was detected for species richness, but species diversity showed a unimodal response (Fig. 4, Table 3).

Along the soil pH gradient, pteridophyte species richness and diversity showed weak unimodal responses in tierra firme, but only species diversity yielded a statistically significant relationship in inundated forests, and then only with the linear model (Fig. 5, Tables 2-3). For Melastomataceae, both the linear and quadratic terms were significant in *terra firme*, but only the linear term was significant in inundated areas. Species richness and diversity decreased with increasing pH in all cases.

Environmental heterogeneity within the transects did not provide very strong explanations for species richness and diversity (Tables 2 and 3, Fig. 6). The best fits for pteridophytes were in *terra firme*: species richness showed a linear regression on standard deviation of log-transformed cation content, and a logarithmic regression on elevation difference. None of the regressions in inundated areas were significant for pteridophytes. For Melastomataceae, the situation was different: the strongest regressions were for elevation difference and SD of Al content in inundated areas, and even though more regressions were statistically significant in *terra firme*, their coefficients of determination were lower.

When the alpha-diversity patterns of pterido-

Table 4. Linear correlation (Pearson's coefficient) in alpha-diversity between pteridophytes and Melastomataceae, and the degree of beta-diversity in four areas in western Amazonia. Alpha-diversity was measured as both species richness (number of species per transect) and diversity (Shannon's H within a transect). Statistically significant correlation coefficients are emphasized in bold. Beta-diversity was measured as the 1-complement of the Jaccard index computed between pairs of transects and expressed in percentages; means (and ranges in parentheses) are given for each region.

		Correlation in alpha-diversity between pteridophytes and Melastomataceae		Degree of beta-diversity within a region (%)	
		species richness	Shannon's H	pteridoph.	Melastom.
All transects (n=160)	Colombia	0.25 (p>0.10)	0.38 (p>0.10)	74 (41-100)	77 (39-100)
	Ecuador	**0.63** (p<0.001)	**0.35** (p=0.0076)	61 (29-93)	71 (26-100)
	Northern Peru	**0.76** (p<0.001)	**0.76** (p<0.001)	78 (36-100)	87 (14-100)
	Southern Peru	**0.45** (p=0.0016)	**0.73** (p<0.001)	82 (30-100)	85 (0-100)
	All areas	**0.64** (p<0.001)	**0.70** (p<0.001)	82 (29-100)	89 (0-100)
Tierra firme transects (n=124)	Colombia	0.12 (p>0.10)	0.37 (p>0.10)	64 (41-86)	65 (39-86)
	Ecuador	0.25 (p=0.0953)	0.10 (p>0.10)	56 (29-82)	66 (29-98)
	Northern Peru	**0.50** (p=0.0045)	**0.43** (p=0.0365)	75 (37-100)	82 (34-100)
	Southern Peru	0.30 (p=0.0817)	**0.50** (p=0.0021)	74 (36-100)	81 (37-100)
	All areas	**0.51** (p<0.001)	**0.50** (p<0.001)	78 (29-100)	86 (29-100)

phytes and Melastomataceae were compared in the entire data set, high correlations were found both for species richness (r = 0.64) and species diversity (r = 0.70; Table 4). If only *terra firme* transects were included in the analyses, the correlations were somewhat weaker (0.51 and 0.50, respectively), but still statistically significant. Within three of the four regions, correlations between pteridophyte and Melastomataceae species richness and diversity were found in the entire data set, and for one region, both correlations remained significant when only *terra firme* transects were considered.

Mean values of beta-diversity (species turnover between transects) were highest in the two Peruvian regions, both when all transects were compared to each other, and when only *terra firme* transects were considered (Table 4).

In the partial correlation analyses for the *terra firme* transects, soil Al content proved to be the only environmental variable that clearly reduced the correlation coefficient between pteridophyte and Melastomataceae species richness, from r = 0.51 ($P < 0.001$) to r = 0.29 ($P = 0.0011$) with linear regression model, and to r = 0.25 ($P = 0.0048$) with quadratic regression model. The correlation between pteridophyte and Melastomataceae species diversity decreased from 0.50 to 0.44 when the effect of soil cation content was taken into account, but in all other cases the effect of environmental variables was negligible. Because few environmental variables provided significant regressions for both pteridophytes and Melastomataceae in inundated areas, partial regressions were only computed for the *terra firme* data set.

Discussion

General alpha-diversity patterns

The great ecological difference between inundated and *terra firme* forests has been acknowledged for a long time, and tree diversity has been found to be lower in inundated forests than in *terra firme* (Campbell *et al.* 1986; Balslev *et al.* 1987; Clinebell *et al.* 1995; ter Steege *et al.* 2000). Our results show that a similar pattern exists also for pteridophytes and Melastomataceae. Both plant groups presented much lower alpha-diversity in inundated forests than in non-inundated forests, no matter whether species richness or Shannon's diversity index was considered.

So far, our results confirmed what could be expected on the basis of earlier studies. However, when exploring diversity trends along soil gradients within the two major landscape types, it was more difficult to foresee the outcome. The only Amazonian study that has concentrated on such comparisons before is that of Clinebell *et al.* (1995), and their results indicated that climatic humidity is the most important factor for tree species richness; the role of soil properties was found negligible in comparison. Also ter Steege *et al.* (2003) argue for the importance of climate in explaining the variation in Amazonian tree alpha-diversity. In our data, Melastomataceae did indeed show lower alpha-diversity in southern Peru (with lower annual precipitation and more pronounced rainfall seasonality) than in the three northern regions. However, pteridophyte alpha-diversity was no lower in southern Peru than in northern Peru or Colombia.

Alpha-diversity along edaphic gradients

All three soil factors that we explored are related to soil fertility, although their relationship with actual site productivity is rather complex. The content of base cations (Ca, K, Mg, Na) is a resource gradient sensu Pausas and Austin (2001), while pH is a direct environmental gradient whose high (or rather, neutral) values are often used as indicators of high soil fertility (*e.g.*, Sollins 1998), and Al content is a direct environmental gradient whose high values may reduce productivity due to toxicity.

The ranges of these soil variables in our data are close to the ranges reported in earlier studies for Amazonian forests (Sanchez & Buol 1974; Botschek *et al.* 1996), and all these gradients yielded statistically significant relationships with species richness and diversity. However, the forms of the response functions were not always easy to describe, and they had relatively little consistency between the two plant groups.

For pteridophytes, the trends in alpha-diversity along the edaphic gradients were clearer within *terra firme* forests than within inundated forests. For example, variation in species richness could not be explained by any of the edaphic gradients within inundated areas, whereas both soil cation content and soil Al content provided statistically significant regression models within *terra firme*. This contrasts with the situation for Melastomataceae, for which the trends in the two landscape types were more similar. Overall, more statistically significant regression models were found in *terra firme* than in inundated areas, and the coefficients of determination were generally higher in *terra firme*. These differences between the landscape types may occur because alpha-diversity in inundated areas is more strongly affected by such ecological gradients that were not measured in the present study (*e.g.*, the duration or depth of inundation), but it may also reflect our smaller sample size for inundated than *terra firme* areas.

In the *terra firme* areas, the most obvious difference between the two plant groups was found in their response to the soil cation content gradient. Pteridophyte species richness and diversity were best explained by an increasing monotonic response to soil cation content, whereas Melastomataceae species richness and diversity showed unimodal patterns (albeit rather weakly so).

Along the soil pH gradient, species richness and diversity of both plant groups showed unimodal patterns, but the explanative power of soil pH was very poor, especially for pteridophytes. Because the vast majority of the transects has soil pH values between 3.5 and 4, the general trend was set by a few transects whose pH was well outside these limits. Consequently, the observed relationships of species richness and diversity with soil pH are not robust. Soil Al content proved to be the best explanatory factor for Melastomataceae species richness and diversity, with clearly monotonic response functions. The responses of pteridophyte species richness and diversity along the soil Al content gradient were also monotonic, but the explanatory powers of these models were poorer.

Is alpha-diversity predictable?

To sum up, the two plant groups differed in which soil factors best explained the trends in their species richness and diversity, and in some cases also in the type of response function (monotonic or unimodal). Similar inconsistencies exist between earlier studies relating alpha-diversity and soil characteristics in tropical forests (Huston 1980; Gentry 1988; Ashton 1992; Rosenzweig & Abramsky 1993; Duivenvoorden 1994, 1996; Clinebell *et al.* 1995; Austin *et al.* 1996; Tuomisto & Poulsen 1996; Pausas & Austin 2001; Tuomisto *et al.* 2002).

What should be concluded from all this? One obvious possibility is that all plant groups behave in an individualistic way along ecological gradients, and consequently, alpha-diversity patterns are idiosyncratic and cannot be generalized from one plant group to others. Another possibility is that there is a general pattern of alpha-diversity, but we have failed to identify those ecological factors that are most important for defining that pattern. We did not measure the contents of such important plant nutrients as nitrogen or phosphorus in the soil samples, and the most important diversity-regulating factors may actually not be related

to soils at all. For example, specialized herbivores have been repeatedly advocated as a main factor in promoting alpha-diversity in tropical rain forests (Janzen 1970; Connell 1978; Givnish 1999; Wright 2002). It may also be that reliable results can only be obtained when all factors are analyzed together rather than in isolation (cf. Pausas & Austin 2001), or when such analysis methods that are able to detect ceiling effects are used (cf. Thomson *et al.* 1996).

In any case, if any factors affect the alpha-diversity of plants in general in a systematic way, then a correlation between the alpha-diversities of different plant groups should exist. We did indeed observe such a correlation. Both species richness and diversity showed statistically significant correlation between pteridophytes and Melastomataceae within *terra firme* forests. However, this correlation can be due to neither soil cation content nor soil pH, because the shapes of the response functions of both plant groups along these gradients were different, or the coefficients of determination were too low, or both. Soil Al content did seem to have some effect on the correlation between pteridophyte and Melastomataceae species richness (but not diversity), as taking it into account in a partial correlation analysis clearly decreased the correlation between plant groups.

Another possible explanation for a correlation between alpha-diversity of two plant groups is that the degree of within-transect habitat heterogeneity varies between transects: transects that include more habitat heterogeneity should have higher numbers of species. We investigated this possibility by correlating species richness and diversity with four measurable sources of environmental variation within a transect: elevational range, and the standard deviations of soil cation content, soil Al content, and soil pH. However, none of these features explained alpha-diversity particularly well, and statistically significant results were rarely obtained with the same variable for both pteridophytes and Melastomataceae.

Unfortunately, our measures of habitat heterogeneity were rather crude (*e.g.*, usually only three soil samples were taken in each transect), so these results cannot rule out the possibility that habitat heterogeneity does play a role. Indeed, it has been documented that elevation differences of less than 25 m are sufficient to affect the local distribution of plant species, and to create floristically different patches within sites (*e.g.*, Poulsen & Balslev 1991; Tuomisto *et al.* 1995; Clark *et al.* 1995, 1998; Svenning 1999; Tuomisto & Poulsen 2000). Furthermore, we did not measure succession in any way, even though it is known that tree fall gaps may harbor successional species that are not represented in the closed-canopy parts of the forest.

Importance of gamma-diversity

It has repeatedly been observed that local species richness is not independent of regional species richness, but that the two correlate positively (*e.g.*, Ricklefs 1987; Ricklefs & Schluter 1993; Pärtel *et al.* 1996). However, in our data such a pattern is only partly present. For Melastomataceae, Ecuador stands out as the region with the highest and southern Peru as the region with the lowest within-transect species richness, even though the regional species richness in both is about the same (and lower than in the other two regions). For pteridophytes, the within-transect species richness is also highest in Ecuador, although its regional species richness is about the same as in the two Peruvian regions. Unfortunately, all estimates of the sizes of regional species pools are affected by collection intensity, and our sample sizes vary among regions. Therefore, our estimates of regional species richness are not strictly comparable, and even their rank order may be incorrect. Consequently, we cannot

even begin to estimate the sizes of the regional species pools sensu Pärtel *et al.* (1996), i.e. the number of species that are both present in the region and able to grow in the plant community of interest (*e.g.*, inundated forests); this would require information on which species are able to grow in which kinds of forests, which is not available either.

Using the gamma-diversity estimates obtained from the literature would not clarify the picture much, because they are based on data that are even less standardized than our inventory data: they cover areas of very different surface areas and botanical exploration histories. For example, southern Peruvian gamma-diversity is obviously underestimated in the literature sources; even though we sampled southern Peru less intensively than any of the other regions, our inventories included more species of both pteridophytes and Melastomataceae than the published checklists.

Importance of beta-diversity

The regional species pool may explain differences in local diversity between regions, but it cannot explain the variation in alpha-diversity within one region. The correlations between the alpha-diversities of pteridophytes and Melastomataceae within both Peruvian regions, therefore, call for some explanation at a more local scale. The degree of beta-diversity within the two Peruvian regions was higher than in the Ecuadorian and Colombian regions, i.e., mean floristic similarity between sites was lower. This suggests that alpha-diversities of two plant groups are more likely correlated in areas where species composition differences between sites are high than in areas where they are low. This is, of course, a very tentative result, because four geographical areas can hardly be considered a sufficient sample to establish such general patterns.

The main problem with analyzing trends in alpha-diversity is that the observed level of diversity in any given site is the product of a multitude of factors, many of which are difficult or impossible to measure. Factors that have been considered important in this respect include, for example, size of the regional species pool, dispersal abilities of the species, competitive abilities of the species, disturbance history, herbivory, climatic humidity, temperature, productivity, and edaphic factors. Present theoretical knowledge about each of these factors is still inadequate, and therefore it is not possible to predict their effects on local diversity. On the contrary, both observations and theoretical considerations have produced contradicting models concerning their effects (Huston 1994; Abrams 1995; Waide *et al.* 1999).

It is easy to imagine that all these factors could contribute to alpha-diversity, but that their relative importance would vary so much from site to site that a generally valid predictive model would be either impossible to construct or so complex that, in practice, its parameters would be impossible to estimate. Furthermore, the importance of many of the factors may vary among plant groups. For example, the size of the regional species pool of a particular taxon is to a large degree defined by its evolutionary and biogeographical history, and there are many reasons why these might not be congruent between unrelated plant groups at the continental scale (Givnish 1999). Furthermore, it can be suggested that the alpha-diversities of groups such as cacti and ferns are unlikely to peak at the same sites, because they are adapted to different levels of air humidity. Even within Amazonian rain forests, it has been reported that some plant genera or families are more speciose on poor soils while others are more speciose on rich soils (Gentry 1988; Tuomisto 1998). Consequently, there is little reason to suggest that the correlation between the alpha-diversities of independent plant groups should always be positive.

This ambiguity is in striking contrast with the

situation when predicting beta-diversity, or species turnover between sites. It is by now universally recognized that all plants grow better in some ecological conditions than in others, and from this it logically follows that there must be species turnover along such ecological gradients that affect plant growth. In Amazonian forests, such universally recognized gradients include the transitions between inundated forests and *terra firme*, and between extremely nutrient-poor white sand soils and more nutrient-rich fine-textured soils.

It is inconsequential to the resulting floristic patterns whether the actual mechanism of species replacement is by the physiological inability of the species to grow in unfavorable conditions, or by changes in the relative competitive abilities of different species along the ecological gradients. In either case, the net result is that environmentally similar sites tend to have similar floristic compositions, whereas environmentally different sites tend to have different floristic compositions. This leads unambiguously to the prediction that floristic similarities of independent plant groups should be positively correlated. Obviously, when the observed ecological differences are so small as to be inconsequential for plant growth, the correlation between plant groups may be zero, but there is no ecologically sound reason to expect a negative correlation.

Indeed, all studies that have analysed the question have found that floristic similarities are positively correlated between plant groups (Tuomisto *et al.* 1995, 2002, 2003a, b, c; Ruokolainen *et al.* 1997, Ruokolainen & Tuomisto 1998; Vormisto *et al.* 2000; Higgins & Ruokolainen 2004). In an earlier study, we compared the correlations of (similarity in) local diversities with correlations of similarity in species composition in Ecuador, and found that the latter were much higher (Tuomisto *et al.* 2003a). Furthermore, the correlations between pteridophyte and Melastomataceae floristic similarities reported in Tuomisto *et al.* (2003c) were much higher than the correlations reported in the present paper between the species richnesses and diversities of the same plant groups in the same data set. This difference is especially remarkable because Mantel correlation coefficients (which were reported in Tuomisto *et al.* 2003c) are generally lower than Pearson correlation coefficients (reported in the present study) when computed from the same data (Tuomisto & Poulsen 2000; Tuomisto *et al.* 2003a). This means that when one plant group is used to predict patterns in another plant group, similarity in species composition can be predicted much more reliably than similarity in species richness.

Conclusions

The practical conclusion of all this is that when conservation planners look for shortcuts in gaining useful information about the distribution of species diversity, indicators of beta diversity provide more reliable predictions than indicators of alpha diversity. This is actually not bad news. Indicators of changes in species composition can be used to evaluate whether all different habitats are included in conservation programs, and to assess the complementarity value of new conservation area proposals (Flather *et al.* 1997). After all, the ultimate aim of conservation is to ensure the viability of all species in a region, not just those that occur in the habitats that happen to have the highest local species richness.

Acknowledgements

We especially wish to thank the following persons for their contributions to field data collection: in Peru: Melchor Aguilar, Illich Arista, César Bardales, Glenda Cárdenas, Guillermo Criollo, Simón Cortegano, Lizardo Fachín, Manuel Flores, Alberto García, Mildred García

de Panduro, César Grandez, Nestor Jaramillo, Juha Järvinen, Hannele Koivunen, Antonio Layche, Elina Lusa, Isabel Oré, Richer Ríos, Juan Ruiz, Abel Sarmiento, Alberto Torres, Gustavo Torres, José Torres, Rodolfo Vásquez, Victor Vargas and Adriana Zegarra; in Ecuador: Jorge Celi, Gustavo Cañas, Manuel Macía, Rommel Montúfar, Sami Markkanen, Robbin C. Moran, Axel Poulsen, Catalina Quintana, Hugo Romero and Renato Valencia; and in Colombia: Jaime Cavelier, Alvaro Duque, Joost Duivenvoorden and Mauricio Sanchez. The inhabitants of many villages close to the field work sites provided invaluable practical help and hospitability. Funding was primarily provided by the Academy of Finland, the European Union, and the Finnish Foreign Ministry.

Literature cited

Abrams, P.A. 1995. Monotonic or unimodal diversity-productivity gradients: What does competition theory predict? *Ecology* **76**: 2019-2027.

Ashton, P.S. 1992. Species richness in plant communities. *In*: Fiedler, P.L. & Jain, S.K. (eds.), *Conservation Biology*. Chapman and Hall, New York. Pp. 3-22.

Austin, M.P., Pausas, J.G. & Nicholls, A.O. 1996. Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. *Austral. J. Ecol.* **21**: 154-164.

Austin, M.P. & Smith, T.M. 1989. A new model for the continuum concept. *Vegetatio* **83**: 35-47.

Balslev, H., Luteyn, J., Øllgaard, B. & Holm-Nielsen, L.B. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* **92**: 37-57.

Botschek, J., Ferraz, J., Jahnel, M. & Skowronek, A. 1996. Soil chemical properties of a toposequence under primary rain forest in the Itacoatiara vicinity (Amazonas, Brazil). *Geoderma* **72**: 119-132.

Brako, L. & Zarucchi, J.L. 1993. Catalogue of the flowering plants and gymnosperms of Peru. *Monogr. Syst. Bot. Missouri Bot. Gard.* **45**.

Campbell, D.G., Daly, D.D., Prance, G.T. & Maciel, U.N. 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* **38**: 369-393.

Clark, D.B., Clark, D.A. & Read, J.M. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *J. Ecol.* **86**: 101-112.

Clark, D.A., Clark, D.B., Sandoval, R. & Castro C., M.V. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* **76**: 2581-2594.

Clinebell II, R.R., Phillips, O., Gentry, A.H., Stark, N. & Zuuring, H. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* **4**: 56-90.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1309.

Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *Amer. Naturalist* **137**: 27-49.

Duivenvoorden, J.F. 1994. Vascular plant species counts in the rain forests of the middle Caquetá area, Colombian Amazonia. *Biodiversity and Conservation* **3**: 685-715.

Duivenvoorden, J.F. 1996. Patterns of tree species richness in rain forests of the middle Caquetá area, Colombia, NW Amazonia. *Biotropica* **28**: 142-158.

Flather, C.H., Wilson, K.R., Dean, D.J. & McComb, W.C. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecological Applications* **7**: 531-542.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* **75**: 1-34.

Gentry, A.H. (ed.), 1990. *Four neotropical rainforests*. Yale University Press, New Haven and London.

Givnish, T.J. 1999. On the causes of gradients in tropical tree diversity. *J. Ecol.* **87**: 193-210.

Higgins, M. & Ruokolainen, K. 2004. Rapid tropical forest inventory: a comparison of techniques using inventory data from western Amazonia. *Conservation Biol.* **18**: 799-811.

Hoffmann, A.J.J. 1975. *Climatic Atlas of South America*. WMO and Unesco, Cartographia, Budapest.

Huston, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. *J. Biogeogr.* **7**: 147-157.

Huston, M. 1994. *Biological diversity: The coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *Amer. Naturalist* **104**: 501-528.

Jørgensen, P.M. & León-Yánez, S. (eds.), 1999. Catalogue of the Vascular Plants of Ecuador. *Monogr. Syst. Bot. Missouri Bot. Gard.* **75**.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watt, A.D. 1998. Biodiversity inventories, indicator

taxa and effects of habitat modification in tropical forest. *Nature* **391**: 72-76.

Legendre, P. & Legendre, L. 1998. *Numerical Ecology*. Elsevier, Amsterdam.

Lips, J. & Duivenvoorden, J.F. 2001. Caracterización ambiental. *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. Pp. 19-45.

Magurran, A.E. 1988. *Ecological diversity and its measurement*. Croom Helm Limited, Sydney.

Marengo, J.A. 1998. Climatología de la zona de Iquitos, Perú. *In*: Kalliola, R. & Flores Paitán, S. (eds.), *Geoecología y desarrollo Amazónico: estudio integrado en la zona de Iquitos, Perú*. Ann. Univ. Turku., A, II 114. Pp. 35-57.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: An appraisal. *J. Veg. Sci.* **12**: 153-166.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* **75**: 111-117.

Poulsen, A.D. & Balslev, H. 1991. Abundance and cover of ground herbs in an Amazonian rain forest. *J. Veg. Sci.* **2**: 315-322.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**: 335-337.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**: 168-171.

Ricklefs, R.E. & Schluter, D. 1993. Species diversity: regional and historical influences. *In*: Ricklefs, R.E. & Schluter, D. (eds.), *Species diversity in ecological communities*. University of Chicago Press. Pp. 350-363.

Rosenzweig, M.L. & Abramsky, Z. 1993. How are diversity and productivity related? *In*: Ricklefs, R.E. & Schluter, D. (eds.), *Species diversity in ecological communities*. University of Chicago Press. Pp. 52-65.

Ruokolainen, K., Linna, A. & Tuomisto, H. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographic patterns in Amazonian rain forests. *J. Trop. Ecol.* **13**: 243-256.

Ruokolainen, K. & Tuomisto, H. 1998. Vegetación natural de la zona de Iquitos. *In*: Kalliola, R. & Flores Paitán, S. (eds.), *Geoecología y desarrollo Amazónico: estudio integrado en la zona de Iquitos, Perú*. Ann. Univ. Turku., A, II 114. Pp. 253-365.

Ruokolainen, K., Tuomisto, H., Vormisto, J. & Pitman, N. 2002. Two biases in estimating range sizes of Amazonian plant species. *J. Trop. Ecol.* **18**: 935-942.

Sanchez, P.A. & Buol, S.W. 1974. Properties of some soils of the upper Amazon basin of Peru. *Soil Sci. Soc. Amer. Proc.* **38**: 117-121.

Shmida, A. & Wilson, M.W. 1985. Biological determinants of species diversity. *J. Biogeogr.* **12**: 1-20.

Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forests: does soil matter? *Ecology* **79**: 23-30.

Svenning, J.-C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol.* **87**: 55-65.

ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., van der Hout, P., Daly, D.C., Silveira, M., Phillips, O., Vásquez, R., van Andel, T., Duivenvoorden, J., de Oliveira, A.A., Ek, R., Lilwah, R., Thomas, R., van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Nuñez Vargas, P., Mogollón, H. & Morawetz, W. 2003. A spatial model of tree α-diversity and -density for the Amazon. *Biodiversity and Conservation* **12**: 2255-2277.

ter Steege, H., Sabatier, D., Castellanos, H., van Andel, T., Duivenvoorden, J., de Oliveira, A.A., Ek, R., Lilwah, R., Maas, P. & Mori, S. 2000. An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *J. Trop. Ecol.* **16**: 801-828.

Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S. & Legendre, P. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. *Ecology* **77**: 1698-1715.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.

Tryon, R.M. & Stolze, R.G. 1989-1994. Pteridophyta of Peru. *Fieldiana, Bot.* **20**, **22**, **27**, **29**, **32**, **34**.

Tuomisto, H. 1998. What satellite imagery and large-scale field studies can tell about biodiversity patterns in Amazonian forests. *Ann. Missouri Bot. Gard.* **85**: 48-62.

Tuomisto, H. & Poulsen, A.D. 1996. Influence of edaphic specialization on pteridophyte distribution in neotropical rain forests. *J. Biogeogr.* **23**: 283-293.

Tuomisto, H. & Poulsen, A.D. 2000. Pteridophyte diversity and species composition in four Amazonian rain forests. *J. Veg. Sci.* **11**: 383-396.

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. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *J. Veg. Sci.* **5**: 25-34.

Tuomisto, H., Ruokolainen, K., Aguilar, M. & Sarmiento,

A. 2003b. Floristic patterns along a 43-km long transect in an Amazonian rain forest. *J. Ecol.* **91**: 743-756.

Tuomisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W. & Rodriguez, Z. 1995. Dissecting Amazonian biodiversity. *Science* **269**: 63-66.

Tuomisto, H., Ruokolainen, K., Poulsen, A.D., Moran, R.C., Quintana, C., Cañas, G. & Celi, J. 2002. Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. *Biotropica* **34**: 516-533.

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. 4th ed.* Technical Paper 9, International Soil Reference and Information Centre, Wageningen.

Vandermeulen, M.A., Hudson, A.J. & Scheiner, S.M. 2001. Three evolutionary hypotheses for the hump-shaped productivity-diversity curve. *Evolutionary Ecology Research* **3**: 379-392.

Vormisto, J., Phillips, O.L., Ruokolainen, K., Tuomisto, H. & Vásquez, R. 2000. A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. *Ecography* **23**: 349-359.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. 1999. The relationship between productivity and species richness. *Annual Rev. Ecol. Syst.* **30**: 257-300.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**: 1-14.