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## A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest

J. Vormisto, O. L. Phillips, K. Ruokolainen, H. Tuomisto and R. Vásquez

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We carried out a comparison among the floristic patterns of four different plant groups (palms, trees, melastomes and pteridophytes) in a lowland rainforest site in Peruvian Amazonia. The study site consisted of a mosaic of edaphic patches reflecting the different geological formations that can be found on the surface. We collected the data along a linear transect (500 m long, divided into 20 × 20 m or 5 × 20 m subplots), and recorded of the four plant groups all individuals that exceeded a minimum size limit predefined for each plant group. We also recorded the drainage conditions and soil type classes in each subplot of the transect. The results indicated that different plant groups can produce similar floristic patterns in local spatial scales, and that these patterns reflect similarities in edaphic conditions. All matrix correlations calculated between pairs of the four plant groups were positive and statistically significant. Floristic composition in all plant groups correlated with soil class, and to a somewhat lesser degree with drainage. These results imply that any one of the four plant groups could serve as a rough indicator of more general floristic patterns, and that even the inventory of a limited part of the flora can shed light on the floristic variation found in Amazonian forests.

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Any study that aims at understanding the structure and function of tropical forest plant communities can only sample a part of the flora. The use of a limited set of species is a practical necessity because the extreme species richness, inadequate taxonomic knowledge and logistic difficulties make it prohibitively laborious to sample all plant species. Thus, floristic studies traditionally deal only with trees (e.g. Ashton 1969, Lieberman et al. 1985, Gentry 1988a, b, ter Steege et al. 1993, Duivenvoorden 1995, Clinebell et al. 1995). More recently, studies have also been done on ground herbs (Poulsen and Balslev 1991, Poulsen 1996), palms (Kahn and de Castro 1985, Kahn and de Granville 1992), pteridophytes (Young and León 1989, van der Werff 1990, Tuomisto and Ruokolainen 1994, Tuomisto et al. 1995, Tuomisto and Poulsen 1996, Ruokolainen et al.

1997), Lauraceae (van der Werff 1992), and Melastomataceae (Tuomisto and Ruokolainen 1994, Tuomisto et al. 1995, Ruokolainen et al. 1997). However, if the results of studies on restricted components of the flora are to be used as models for making generalisations concerning the flora in general, and potentially for developing conservation strategies, then it is important to assess how well the studied part of the flora represents the unstudied part. In other words: are the studied groups good “indicators” of floristic patterns in the rest of the flora?

Although all plants need light, water and nutrients, different plant groups may have different responses to these resources (Cox and Larson 1993). An obvious way to study the variation in ecological behaviour among plant groups is to measure if the plant groups

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reproduce the same pattern of floristic similarities and differences among different study sites. To our knowledge, in tropical rain forests this has been done only on two occasions, and the results have been partly contradictory. Webb et al. (1967) found in Australian rain forests that out of several different plant groups (e.g. large trees, lianas, epiphytes, herbs), only the distribution patterns of trees over 10 cm dbh (diameter at breast height) corresponded well to floristic distribution patterns found in the whole flora. On the other hand, in Amazonian rain forests the floristic similarity patterns measured separately by trees over 2.5 cm dbh, pteridophytes and Melastomataceae were found to be well correlated with each other and with soil texture and nutrient content (Tuomisto et al. 1995, Ruokolainen et al. 1997, Ruokolainen and Tuomisto 1998).

In those studies that have compared the floristic patterns among different plant groups, study plots have typically been separated from each other by large distances (up to hundreds of kilometres). However, there are good theoretical reasons for expecting that plant groups might behave differently from one another at much finer scales. Herbs, for example, may distinguish fine-scale environmental variation that passes undetected by the emergent trees due to the sheer difference in size (Wiens 1989).

Several studies have addressed the fine-scale correlations between single plant groups and environmental factors in tropical forests. For example, Johnston (1992) observed that tree species distributions correlated with several soil characteristics in montane forest in Puerto Rico; especially strong correlations were found with extractable bases (Ca, Mg and Na) and pH. Sabatier et al. (1997) concluded that many tree species in the Guianan rain forests have a clear preference for particular soil characteristics, since they tend to prevail under some edaphic conditions and be scattered in or absent from others. Clark et al. (1995) demonstrated that distributions of five common palm species in old-growth lowland forest in Costa Rica are related to soil type, topographic position and slope angle. Later they also showed that the distributions of 14 tree species are linked with the same environmental factors as the palm distributions (Clark et al. 1998). Kahn (1987) observed that palm populations on well-drained soil in Peruvian Amazonia differ according to topography. Other studies have found similar relationships between species distributions and local environmental conditions for palms (e.g., Kahn and de Castro 1985, Kahn 1987, Baillie et al. 1987, Basnet 1992), trees (Lieberman et al. 1985, Hubbell and Foster 1986, Chen et al. 1997), pteridophytes and Melastomataceae (Tuomisto and Ruokolainen 1994), and ground herbs (Poulsen and Balslev 1991, Poulsen 1996). However, it is unknown if these plant groups respond to the same environmental factors and with equal or close to equal intensity when observed in the same area.

Here we report the first fine-scale comparison in a lowland tropical forest site among floristic patterns produced by plant groups representing several different growth forms: palms (with variable sizes), trees (> 10 cm dbh), Melastomataceae (mostly shrubs, some vines and small trees) and pteridophytes (terrestrial to low-epiphytic herbs). The study area comprises a mosaic of edaphic patches with contrasting conditions that range from nutrient poor quartz sand soils to richer clayey soils. The extremes of this gradient are known to support structurally and floristically different forests (Encarnación 1985, Ruokolainen and Tuomisto 1993, Ruokolainen et al. 1997) but floristic changes across this ecotone have previously only been documented with pteridophytes and Melastomataceae (Tuomisto and Ruokolainen 1994).

## Materials and methods

### The study site

The study site is situated ca 25 km south of the city of Iquitos in the Peruvian Amazonia (3°57'S, 73°26'W; Fig. 1), within the Allpahuayo reserve that is administered by the Peruvian Inst. for Amazonian Research (IIAP). The climate in the area is humid and hot (average annual precipitation ca 3000 mm and average temperature 26°C; Marengo 1998). The altitude above sea level in the reserve varies between 110 and 180 m. Soils in the area present a mosaic of patches varying in texture from clayey to almost pure sand, and in drainage from water-logged swamps to excessively drained hill tops (Vásquez 1997). This edaphic variation reflects the geological formations that can be found on

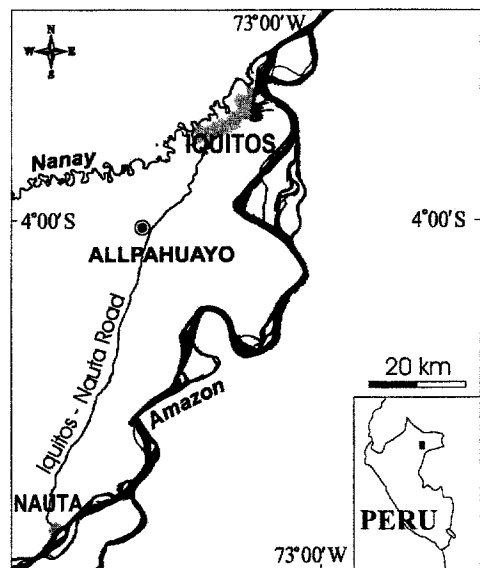


Fig. 1. Location of Allpahuayo in Peruvian Amazonia.

the surface (Räsänen et al. 1998). Generally, the highest hills are covered with sandy fluvial sediments that were repeatedly eroded and redeposited during the Pleistocene. This recycling efficiently leached the soils of nutrients and often resulted in characteristically white quartz sand. Below these sand deposits there are often loamy Middle to Late Miocene estuarine sediments. In the topographically lowest sites one can find clay-rich sediments of the semimarine Pebas formation of Middle Miocene age (Hoorn 1993, Räsänen et al. 1998). Typically, nutrient concentrations are higher in soils derived from the Pebas formation than in soils derived from other formations (Linna et al. 1998, Räsänen et al. 1998).

The vegetation at the study site appeared to be primary forest, although some palm trees *Oenocarpus bataua* Mart. had been cut for harvesting their fruits. The forests in the area are extraordinarily diverse in species: the 3750-ha Allpahuayo-Mishana Reserve has at least 1729 vascular plant species (Vásquez 1997), and a 0.1-ha sample of woody plants within the reserve has the highest species richness and Fisher's Alpha values out of > 200 such samples world-wide (Clinebell et al. 1995, Phillips and Raven 1997, Phillips and Miller unpubl.).

### Floristic survey

In 1990 R. Vásquez established a 20 × 500 m tree transect divided into 20 × 20 m subplots. All trees (self-supporting plants > 10 cm dbh) were recorded, and voucher specimens of all individuals were collected for later identification. We reinventoried the transect for trees in 1996, and the reinventory data are used here. A 5-m wide strip within the transect, divided in 5 × 20 m subplots, was sampled in 1996 for palms, melastomes and pteridophytes. We recorded all individuals of these plant groups, except those pteridophytes that had no leaves longer than 10 cm, or that were epiphytic or climbing and had the lowest green leaves at > 2 m above ground. In addition, melastomes species composition was recorded in subplots of 20 × 20 m because of the relatively low density of melastomes. For each species we collected representative voucher specimens, and deposited them in several herbaria. Tree vouchers (Grández et al. 7952-8035, Vásquez et al. 15247-15829) are in the herbaria of Univ. Nacional de la Amazonia Peruana (AMAZ), Inst. para Investigaciones de la Amazonia Peruana (IIAP), Univ. Nacional Mayor de San Marcos (USM), Univ. Agraria La Molina (MOL) and Missouri Botanical Garden (MO). Palm vouchers are in IIAP, Univ. of Aarhus (AAU), and Univ. of Turku (TUR); melastomes and pteridophytes are in IIAP and TUR.

### Description of edaphic conditions

The topography of the transect was measured along one of the 500 m long sides of the transect, taking measurements every 20 m with a Suunto clinometer. Drainage conditions of each subplot were recorded using ten subjectively defined drainage classes, where 1 is permanently waterlogged and 10 is the most excessively drained. The visual assessment is based on relative topographic position, vegetation physiognomy that indicates seasonal or permanent water-logging, soil texture, and evidence for an impermeable or waterlogged layer in the soil in accordance with a manual for Peruvian students and forestry professionals (Phillips et al. unpubl.). Not all drainage classes were represented within the transect. For the numerical analyses, we also defined four soil classes on a visual basis: white sand soil (coded 1 in the analyses), brown sand soil (coded 2), loamy soil (3) and clayey soil (4). Definitions of these soil classes are based on earlier soil surveys made in the Iquitos area (Kauffman et al. 1998). Soil samples for more detailed analyses of soil texture and nutrients in different parts of the topography were taken from one or more representative 20 × 20 m subplots. These soil samples were used for descriptive purposes only, and all numerical analyses were performed on the visually assessed soil and drainage classes. The samples represent the surface mineral soil (top 10 cm of the Ah horizon) of three soil classes (white sand, brown sand and loam) excluding the layer of pure organic matter (O horizon). Analyses included pH (in 1 M KCl), percentage loss on ignition at 420°C (LOI; a proxy for soil organic matter), extractable Ca, Mg, K and Na (in 1 M NH<sub>4</sub>-Ac at pH 7), extractable Al (in 1 M KCl), extractable P (in 0.03 M NH<sub>4</sub>F + 0.025 M HCl) and percentage of sand (grain size > 0.063 mm) of total sample weight. Soil analyses were done in the Agricultural Research Centre of Finland.

### Numerical analyses

The numerical analyses are based on similarity matrices consisting of all possible pair-wise comparisons of the subplots. We used seven different criteria for measuring similarity: four based on floristic composition (of trees, palms, melastomes and pteridophytes separately), two based on edaphic characteristics (soil class and drainage) and one based on horizontal geographical distance.

For the floristic similarity matrices, we used the Sørensen coefficient (which is designed for presence-absence data) and the Steinhaus coefficient (which is designed for abundance data); these are mathematically similar (Legendre and Legendre 1998). In this study, the two similarity measures gave practically the same results, so here we only report the results based on the

Sørensen coefficient. Before calculating the similarity coefficients, we made minor adjustments in the tree and palm datasets because of problems in species identification. Thirty-one individual trees could not be identified to species, and we therefore excluded them from the analysis. Two palm species (*Socratea exorrhiza* (Mart.) H. Wendl. and *Iriartella stenocarpa* Burret) were treated as one because we could not reliably distinguish all young individuals in the field. For the melastomes, we used the 20 × 20 m subplots when calculating the Sørensen coefficient, and the 5 × 20 m subplots when calculating the Steinhaus coefficient.

A small fraction of the tree individuals are palms or melastomes, so we computed three different similarity matrices for trees: one that includes all trees, one that includes those trees that are not palms, and one that includes those trees that are not melastomes. In the correlation analyses we used the second matrix when comparing trees and palms, and the third matrix when comparing trees and melastomes, in order to ensure independence of the matrices to be compared. We used Euclidean distance in computing a distance matrix on the basis of each of the categorical soil variables (soil class, drainage). For the correlation analyses, the Euclidean distance coefficient ( $D$ ) was converted to a similarity coefficient ( $S$ ) using the formula  $S = 1 - D$ .

To illustrate floristic relationships among the subplots, we used two methods of clustering (one with and the other without spatial constraint) and one method of ordination. The clusterings present concisely a limited number of groups of similar subplots and the ordination illustrates in a more detailed way the pattern of similarities and differences among the subplots.

Both clustering methods use a proportional-link linkage algorithm. In the non-constrained method (later referred to as proportional-link linkage clustering), a hierarchical classification is produced in which subplots are allowed to fuse irrespective of their position along the transect. In the constrained method (later referred to as chronological clustering), a unidimensional constraint (in the sense of Legendre et al. 1985; see also Legendre 1987, Galzin and Legendre 1987) is applied that only allows the fusion of subplots or subplot groups if they are contiguous along the transect. The chronological clustering therefore helps in identifying the places where the most significant changes occur in the species composition. In the present study, the connectedness level for the proportional-link linkage algorithm was set to 0.5, and in the chronological clustering we used an alpha significance level of 0.05.

Principal co-ordinate analysis (PCoA, Legendre and Legendre 1998) is an ordination method that uses a distance (or similarity) matrix to map study objects in a space of reduced dimensionality in such a way that the distances in the original matrix are conserved as well as possible.

We analysed correlations among all floristic and edaphic similarity matrices using the Mantel test (Mantel 1967). A standardised form of this test was used, in which the values of the correlation coefficient  $r$  vary between  $-1$  (perfect negative correlation) and  $+1$  (perfect positive correlation, Smouse et al. 1986). We estimated the probability of error ( $p$ ) for  $r$  by comparing the observed value of  $r$  to the distribution of random values of  $r$ , having obtained random values by permuting one of the matrices and recalculating  $r$  999 times.

Since most ecological data are spatially autocorrelated (Legendre and Troussellier 1988, Legendre and Fortin 1989, see also Borcard et al. 1992), we also used the Mantel test to study the correlations between the matrix of horizontal geographical distances and all the other matrices. The Mantel test calculates a linear correlation coefficient, so the presence of statistically significant correlation when a geographical distance matrix is involved indicates that there is a linear spatial gradient in the values of the other matrix. When a Mantel test was performed between two matrices that both showed such a spatial correlation at  $p < 0.05$ , a partial Mantel test was performed in addition to the simple Mantel test. The partial Mantel test calculates the correlation between two matrices after removing the effect of the correlation with a third matrix, in this case horizontal distance (Smouse et al. 1986).

We used programs of the R-package (Legendre and Vaudor 1991) for all numerical analyses.

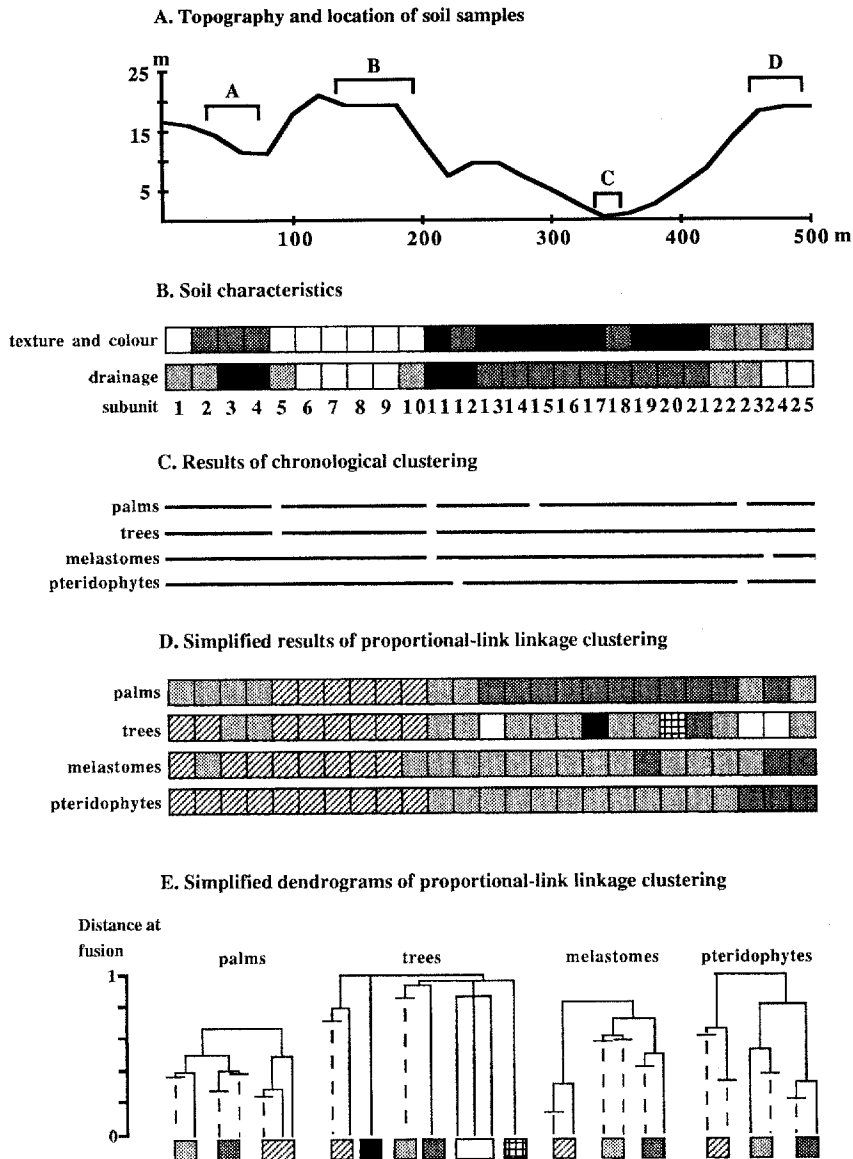
## Results

The floristic inventory of the 20 × 500 m transect yielded 289 tree species (560 individuals) and 27 melastomes species. The mean number of tree species in one 20 × 20 m subplot was 19, which equals 7% of the tree species recorded in the entire transect. The mean number of melastomes in a subplot was 5, equalling 19% of all melastomes recorded.

The 5 × 500 m transect within the 20-m wide transect yielded 26 palm species (1754 individuals), 20 melastome species (187 individuals), and 41 pteridophyte species (880 individuals). The mean number of palm species in one subplot of 5 × 20 m was 7, which equals 27% of the palm species recorded in the entire transect. The mean number of pteridophyte species in a subplot was 6, equalling 15% of all pteridophyte species recorded.

The topography of the transect, the visual classification of soil texture and colour, and the drainage classes are shown in Fig. 2 (A, B). The most elevated parts of the transect had sandy soils; at the beginning of the transect the sand consisted of almost pure white quartz, while in the end of the transect the sand consisted of

Fig. 2. Topography, some soil characteristics and the results of floristic clusterings in the transect in Allpahuayo, Peruvian Amazonia. A) Topography of the transect and locations where soil samples A–D were collected. B) Characteristics of surface soil in the different subunits of the transect. Texture and colour: from lightest to darkest the shadings indicate whitesand, brownsand, loam and clayey soil. Drainage: from lightest to darkest the shadings indicate excessively drained, well-drained, adequately-drained and wet. C) Cluster limits according to chronological clustering based on the floristic composition of four plant groups. ( $\alpha$ -significance level in all cases 0.05). D) Simplified results of proportional-link linkage clustering based on four different plant groups. Main clusters are shown with different shadings for each floristic group. The hierarchical clustering is shown in Fig. 2E. E) Simplified dendrograms of proportional-link linkage clustering. The distance at fusion varied between 0 and 1.



brown quartz. The texture in both sandy parts was relatively coarse; only a small proportion of the soil was silt and/or clay (Table 1). The sandy areas were mostly well-drained, and had the most nutrient-poor soils in the transect. The two loam soil samples (A and C in Table 1) differed from each other in pH, Ca, P and Al content. Our visual classification of the soil in subplot 18 was loam (Fig. 2B), but the soil sample C that represented this subunit was taken near a creek in the bottom of the valley and was surrounded by clay soils, so it presents characteristics intermediate between these two soil classes.

The distribution patterns of the most abundant species in each plant group (Fig. 3) seemed to respond especially to the patches of white sand soil at 0–20 m and 80–200 m. The clearest white sand specialists

were *Macrolobium microcalyx* Ducke, *Micrandra elata* (Diedr.) Muell. Arg., *Tachigali tessmannii* Harms, *Lindsaea divaricata* Kl. and *Clidemia epibaterium* DC. *Bactris simplicifrons* Mart. was found along most of the transect but was significantly more abundant on white sand than elsewhere ( $\chi^2$ -test,  $p < 0.001$ ). On the other hand, *Lepidocaryum tenue* Mart., *Astrocaryum murumuru* Mart., *Polybotryx osmundacea* Willd., *P. pubens* Mart., *Lomariopsis japurensis* (Martius) J. Smith, *Maieta guianensis* Aubl., *Miconia elata* (Swartz) DC., *M. nervosa* (Sm.) Tr. and *Clidemia epiphytica* (Tr.) Cogn were evidently avoiding white sand. Of the 21 species presented in Fig. 3, only one, *Virola pavonis* (DC.) Smith, seemed to be indifferent to the variation in edaphic conditions within the transect.

Table 1. Results of some chemical and textural analyses on soil samples from Allpahuayo, Peruvian Amazonia. For location of soil samples within the 500-m long transect, see Fig. 2A.

soil sample	soil class	pH	Ca mg kg <sup>-1</sup>	K mg kg <sup>-1</sup>	Mg mg kg <sup>-1</sup>	Na mg kg <sup>-1</sup>	P mg kg <sup>-1</sup>	Al mg kg <sup>-1</sup>	loss on ignition %	clay and silt content (<0.063 mm) %
A	loam	2.84	34	40.5	22.9	2	6.51	76	7.63	16
B	white sand	3.15	27.3	21.4	11.8	0.2	5.73	1	1.92	7
C	loam	4.07	436	40.8	21.4	1.97	2.45	329	4.99	48
D	brown sand	3.74	8.1	15.1	4.5	0.16	4.9	77	2.28	14

## Clustering

The chronological clustering identified several significant discontinuities in the variation of species composition in the transect. With trees, melastomes, and pteridophytes, two points of discontinuity were recognised, and with palms, four points (Fig. 2C). In most cases, the points of discontinuity were repeated in at least two plant groups, and they also corresponded to edaphic changes (Fig. 2B). There was a clear discontinuity for all four plant groups in the slope at 200 m (between subplots 10 and 11 or 11 and 12), where white sand soil graded into clayey soil. All plant groups except trees showed a floristic change on the last hill at 440 m (between subplots 22 and 23 or 23 and 24), where the well-drained brown sand soil started to occur. Both palm and tree species compositions changed in the first depression at 80 m (between subplots 4 and 5). The only group-specific discontinuity was the change in palm species composition at 280 m; at this point there was no observable edaphic change.

Chronological clustering with trees did not show any floristic discontinuity at the start of the brown sand soil, but when proportional-link linkage clustering (i.e., no spatial constraint) was used, two of the subunits on this substrate were classified apart from the preceding subunits with clayey soils (Fig. 2D). With palms, the third floristic discontinuity detected by chronological clustering had no exact counterpart in the non-constrained clustering, but a limit between recognised clusters in the latter was found only 40 m earlier.

Overall, the non-constrained clusterings with the four plant groups show rather similar structures. The subplots between 80 m and 180 m are always classified together, with one or a few subplots from either side entering the same cluster. Similarly, the subplots between 240 m and 440 m form a well-defined cluster, although there is some lability with a few of the subplots there. The clearest differences in the non-constrained clusterings produced by the four plant groups are found in the classification of the first four subunits. The patterns produced by trees and the melastomes are rather similar, but those produced by palms and pteridophytes differ from this (Fig. 2D).

The simplified dendrograms of the proportional-link linkage clusterings (Fig. 2E) show that the clusters identified on the basis of palm, melastomes and pteri-

dophyte species composition are rather clearly defined, while the clusters defined on the basis of trees are much less so.

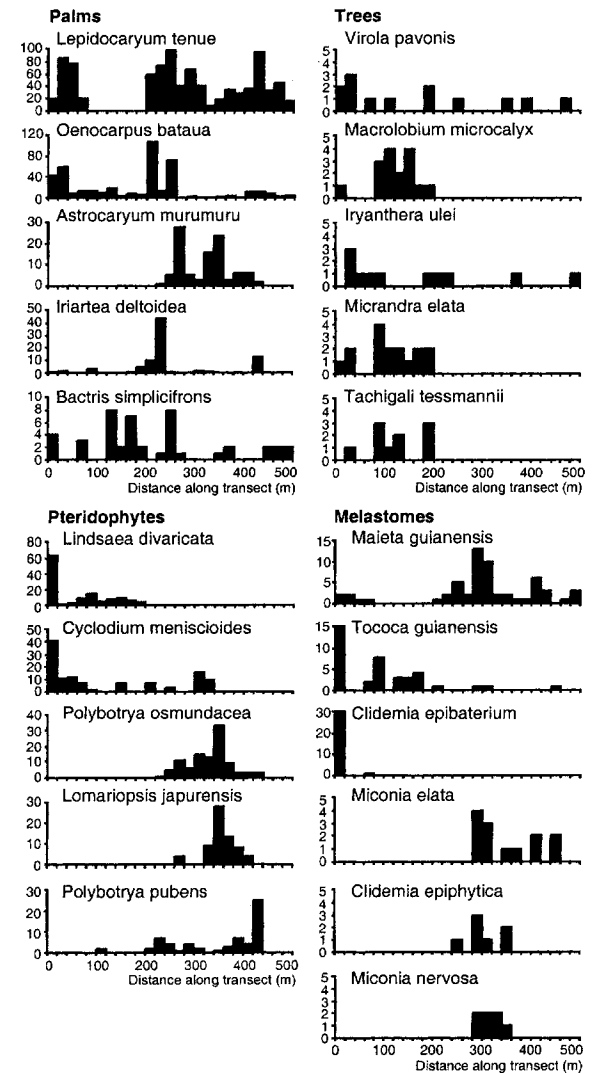
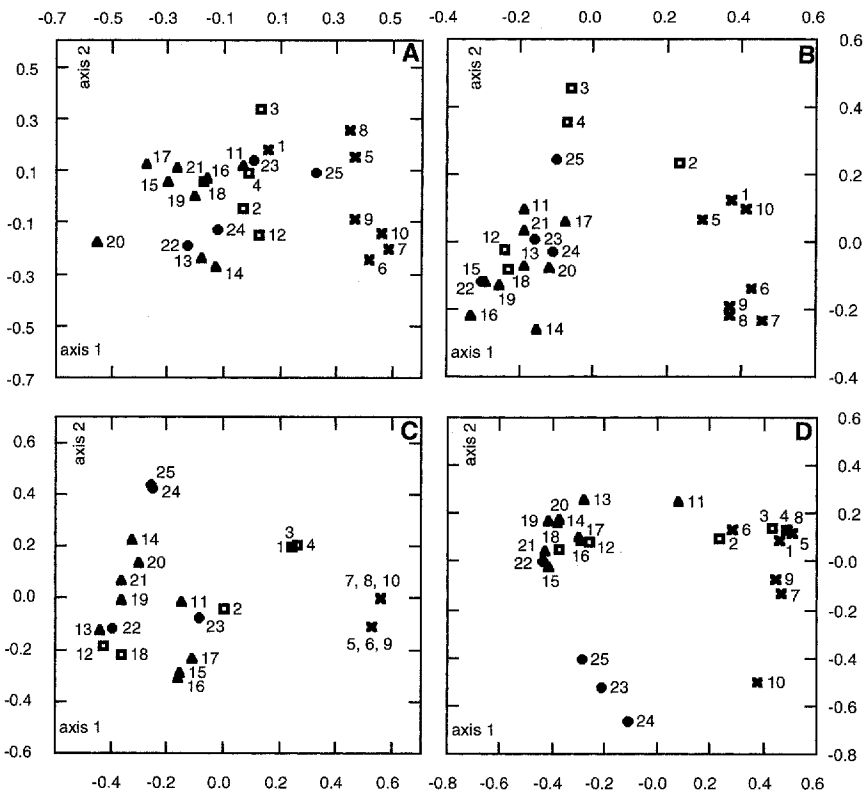


Fig. 3. Distribution patterns of the five most abundant species (in order of decreasing number of individuals) of four plant groups. For melastomes, the abundances of six species are shown because *Clidemia epiphytica* and *Miconia nervosa* had the same number of individuals.

Fig. 4. Ordination of subunits within a 500-m long transect in Allpahuayo, Peruvian Amazonia. Ordination based on the floristic composition of palms (A), trees (B), melastomes (C) and pteridophytes (D). Soil texture and color classes are indicated with different symbols; white sand (cross), brown sand (circle), loam (square) and sandy clay (triangle).



## Ordinations

The four ordinations produced with the principal co-ordinates analysis (Fig. 4A–D) show a roughly comparable pattern: white sand soil subplots are found on the right side and clayey soil subplots on the left side of the ordinations. The loamy soil subplots 2, 3 and 4 are more or less in the middle of the ordination, except in the case of pteridophytes where they are placed among the white sand subplots. The remaining loamy soil subplots 12 and 18 are usually found on the left hand side of the ordinations. Of the subplots on brown sand soil, subplot 25 is the only one that consistently comes out as floristically distinct, whereas subplots 22–24 show in most cases strong affinity to the clay soil subplots. Only with pteridophytes is there clear tendency for the brown sand subplots to form a floristically distinct group. These results parallel those obtained with cluster analyses.

## Mantel tests

All correlations between the four plant groups were positive and statistically significant (Fig. 5). Since the floristic similarities were correlated also with spatial distances, we calculated partial Mantel tests between the plant groups controlling for the effect of horizontal distance. Calculated in this way, the correlations were

lower, but still clearly positive and statistically significant. To verify whether the high correlations were just due to the distinctness of the white sand soils, we repeated the Mantel tests between the plant groups after having removed white sand subplots from the matrices. Even these conservative analyses showed significant positive correlations between the plant groups. The highest correlations were found between pteridophytes and melastomes, and between melastomes and trees. The lowest correlations were those between palms and trees.

Both of the environmental factors (soil class and drainage) were positively correlated with the plant groups (Fig. 6). Because soil class was well correlated also with horizontal distance, we performed partial Mantel tests for all the comparisons involving soil class; the correlations remained positive. All plant groups showed high correlations with soil class, and somewhat lower correlations with drainage.

## Discussion

Earlier studies (Tuomisto et al. 1995, Ruokolainen et al. 1997) have documented that at the regional scale in western Amazonia, different plant groups can reproduce similar patterns of floristic distribution, and that these reflect similarities in edaphic conditions. The re-



sults of the present study indicate that such correlations can also exist at much more local spatial scales, within a transect only 500 m long.

In both cluster and ordination analyses, the four plant groups (palms, trees, melastomes and pteridophytes) differed between those parts of the transect with clayey soil, and those parts with white sand soil. In some of the cluster analyses, and to a lesser degree in the ordinations, the brown sand soil parts of the transect stood out as floristically intermediate. The similarity of the species distribution patterns of the different plant groups was further confirmed by the positive correlations obtained in Mantel tests between the corresponding floristic similarity matrices. In a comparable regional study (Ruokolainen et al. 1997), correlation coefficients ranging from 0.5 to >0.8 were found. Although the values of the correlation coefficients were not as high in our study (ranging between 0.2 and 0.5, with a mean 0.4), they were consistent and statistically significant. Together with the significant correlations between floristic and edaphic similarity matrices, these results suggest that deterministic processes (such as taxon-specific preferences for particular soil nutrient conditions, perhaps modified by interspecific competition) affect plant species distributions in Allpahuayo.

In our study, the rather small sample sizes may have limited the potential of obtaining higher correlation coefficients between the plant groups, by introducing substantial sampling error. Sample sizes were especially small for trees (the mean number of individual trees sampled per species was only 1.9), which makes it difficult to unravel the true distribution patterns and possible edaphic preferences of the species. It is likely that sampling error was a factor behind the small differences that were observed between the subplot

clusters identified on the basis of tree species composition; clusters identified on the basis of the three other plant groups were more clearly defined. However, in spite of the greatly differing sampling intensities for the four plant groups, the degree of similarity in their floristic patterns was remarkably high.

The life forms in the four plant groups ranged from understorey herbs (pteridophytes) through shrubs (melastomes) to canopy trees. Palms are the most heterogeneous group in terms of size: some are understorey species, others canopy species; some have a single stem while others are multi-stemmed. Such differences among organisms affect the relevant scales of investigation, because environmental or other variation at spatial scales that are relevant for understorey species may not be essential to canopy trees (Wiens 1989). Also the impacts of the mass effect on floristic distribution patterns are likely to be scale-dependent. It has been suggested that mass effects are most important at the meso-scale (10–10<sup>6</sup> m<sup>2</sup>), especially in transition zones between distinct floras (Auerbach and Shmida 1987). Since the mass effect is expected to obscure the relationships between species and environment (Shmida and Wilson 1985), it is conceivable that large-sized trees with a species pool of several hundreds within a small area would not show clear environmental relationships in a fine-scale study. However, our results suggest that the subplots used (5 × 20 m and 20 × 20 m) are appropriate for revealing general distributional patterns in the four floristic groups, including trees.

Somewhat surprisingly there is little indication that the smaller-statured plant groups (pteridophytes and melastomes) were responding to a finer scale of environmental variation than the larger plants. A counterexample was found in the classification of subplots 1

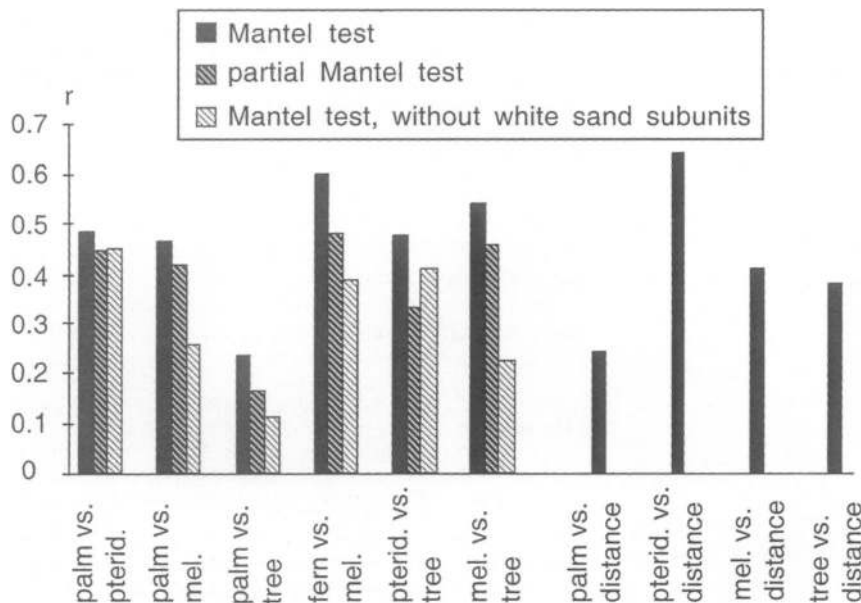
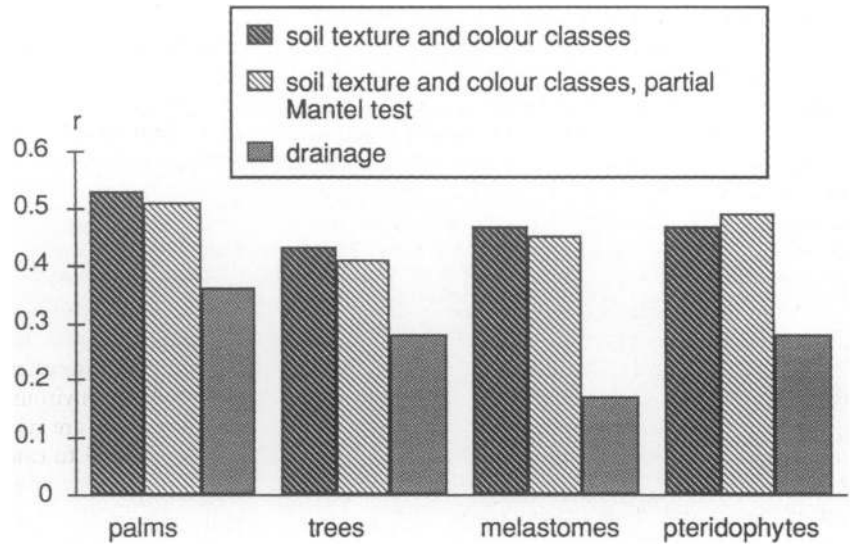


Fig. 5. Coefficients of correlation (Mantel test, partial Mantel test) between floristic similarity matrices based on different plant groups in Allpahuayo, Peruvian Amazon. Partial Mantel test was performed after the effect of geographic distance was excluded. Mantel test without white sand subunits was calculated after having removed white sand subunits from the matrices. All correlations were significant at the  $p < 0.01$  level, except two of the correlations between palms and trees (Mantel test,  $p < 0.05$ ; Mantel test without white sand subunits, not significant).

Fig. 6. Coefficients of correlation (Mantel test) between each of the floristic groups, and some soil characteristics. Because of the high positive correlation between geographical distance and soil texture and color ( $r = 0.62$ ), also the partial Mantel test was computed (i.e. the effect of geographic distance were excluded) when comparing them with similarity matrices of floristic groups. For all correlations,  $p < 0.01$ .



through 4: in this case, trees reflected the drainage patterns more exactly than any of the other plant groups (Fig. 2D). On the other hand, pteridophytes responded most clearly of all plant groups to the brown sand soils (Fig. 2D).

The palm results are somewhat different from the results obtained with the other plant groups. In the spatially constrained clustering, floristic discontinuities between palms correspond to all those in the other plant groups, plus one that is not repeated by any other plant group. The correlation between the floristic similarity matrices of palms and trees was lower than the corresponding correlations between the other plant groups. These differences may indicate that the heterogeneity in life forms among palms plays a role, or that palms have somewhat distinctive ecological preferences, but it is also possible that these patterns are the result of human interference, as palms include more harvested species than any of the other plant groups. Sampling error (Newbery 1991) is an unlikely explanation for the peculiar behaviour of palms since they have the highest individuals:species ratio among the four sampled groups.

The present study is based on one transect, which of course represents only a small part of the floristic variation in Amazonia. However, this fine-scale study shows that even a single hectare of non-flooded forest can be edaphically and floristically very heterogeneous. In Allpahuayo, there are patches of at least three different geological formations on the surface, which has created the conditions for a mosaic of different soils (Räsänen et al. 1998, Linna et al. 1998). Although this edaphic mosaic is more extreme than those found in some other localities in Amazonia, it is by no means unique (Lescure and Boulet 1985, Sabatier et al. 1997). This local-scale patchiness is an important aspect to keep in mind when discussing the representativeness of

1-ha plots, and when considering the extent to which such samples reflect within-habitat diversity (alpha diversity) or between-habitat diversity (beta-diversity). In the Allpahuayo plot  $\beta$ -diversity is strongly represented.

Our results are consistent with the hypothesis that different plant groups show broadly similar floristic patterns at the local scale, and that much of the floristic variation is correlated with edaphic variation. Therefore, any one of the four plant groups could serve as a rough indicator of more general floristic patterns within the transect. However, further studies are needed to obtain detailed information on the responses of different floristic groups, and especially for trees it will be necessary to sample many more individuals in order to understand distributional patterns at the specific level.

Our results have two important implications for the practical concern of making rapid and efficient biological assessments in species-rich tropical forests. First, it is possible to capture important floristic variation with relatively small samples. Second, a single group of plants, which may include only a small part of the total flora, may predict floristic patterns in other groups of plants even at the local scale. Consequently, it may be possible to study and understand much of the floristic variation found in Amazonian forests on the basis of a rather limited part of the whole flora.

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