monthly rainfall always above 100 mm (Duivenvoorden and Lips 1993). Mean annual temperature was 25.7°C (1980-1989) (Duivenvoorden and Lips 1993).

Field work data

Rectangular plots of 5 x 50 m were established directly contiguous to the long side of previously established 20 x 50 m plots. These latter plots were installed in each one of the above-mentioned landscape units, which had been recognized on aerial photographs (Duivenvoorden 2001). During walks through the forests, soils and terrain forms were rapidly described, and the forest was visually examined. In this way, forest stands with more or less homogeneous soils were identified. In these stands, plots were located without bias with respect to floristic composition. Recent gaps due to fallen canopy trees were avoided. All plots were established in mature forests that did not show signs of recent human intervention, at a minimum distance of 500 m between plots (Fig. 3.1). Plots were mapped with GPS. In 1997 and 1998, the density and species composition of lianas and trees with DBH $\geq$ 2.5 cm were recorded in these 0.1-ha plots (Duque *et al.* 2001). During a new fieldwork from March to June 2000, the adjacent 0.025-ha plots were censused for epiphytism. The 5 x 50 m plots were subdivided into subplots of 5 x 10 m, in which all vascular epiphytes occurring on trees and lianas with a stem basis inside the plot area were recorded.

Field collection of epiphytes was done with the help of indigenous climbers. Binoculars were used to examine epiphyte individuals occurring in distant crowns. With the help of poles, crowns were surveyed and all observed individual epiphyte plants were collected. For each epiphyte plant, the position above ground (in the case of hemi-epiphytes the maximum height was considered), and position on the phorophyte (main stem or branches) were recorded. Three plant positions were considered: (1) base: individuals found at or below 3 m above ground level; (2) stem: individuals found above 3 m and below the first branch; (3) branches or crowns: individuals found on stems or branches in crowns.

For each phorophyte, the following variables were recorded: (1) DBH (from phorophytes with height lower than 1.3 m the stem diameter was recorded at half of the total height). (2) Total height and height of first branch, measured or estimated by means of poles of 8 meters length. For trees, we calculated the conical superficial area of the phorophyte stems as 3.14 times the product of the stem radius and the height of the first branch (if there were no branches, the total height was employed).
All species in each plot were collected applying vouchers numbered AMB 100-1300. Species identification took place at the Herbario Universidad de Antioquia (HUA), Herbario Amazónico Colombiano (COAH), and Herbario Nacional Colombiano (COL), by means of taxonomic keys, comparison with herbarium collections, and consultations of specialists. The nomenclature of families follows Cronquist (1988) for angiosperms and Tryon and Tryon (1982) for pteridophytes. Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics, were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens.

In this study, the term epiphyte is used, in a broad sense, for plants that spend most of their life cycle attached to other plants (Benzing 1987), including true epiphytes (holo-epiphytes) and hemi-epiphytes. Only those epiphyte individuals that were in contact with the forest soil were recorded as hemi-epiphyte. Clones from rhizomatous plants were considered as one individual.

Numerical analysis
To calculate the diversity, Fisher's alpha index was employed (Fisher *et al.* 1943, Condit *et al.* 1996). Differences of diversity, species richness, epiphyte abundance, and superficial area of the phorophytes between the landscapes were analyzed by ANOVA and subsequent Tukey-Kramer tests. The condition of normal distribution of residuals was checked by means of Shapiro-Wilk tests. The analyses were developed using JMP 3.2.2 (SAS 1994).

Patterns of epiphyte species composition were explored by Detrended Correspondence Analysis (DCA, Hill 1979) in CANOCO version 4 (ter Braak and Šmilauer 1998), applying plot data of abundance and presence-absence. Correlations between epiphyte species, trees and liana species in the adjacent plots, and the spatial position of the plots, were analyzed by Mantel and partial Mantel tests (Legendre and Legendre 1998), applying R-package for Macintosh (Casgrain and Legendre 2002). The floristic similarity matrices were constructed on the basis of the abundance data using the Steinhaus index. A Euclidean distance matrix was calculated using the geographical coordinates of the plots (Legendre and Legendre 1998). The significance of the Mantel r coefficient was tested by means of 10000 permutations.

4.3 RESULTS

A total of 6129 individual vascular epiphytes were recorded in the 30 plots of 0.025 ha each. Precisely 1200 botanical collections were made pertaining to 27 families, 74 genera, and 213 species (which included 59 morpho-species). A total of 141 species (66%) were found in more than one plot and just 17 species (8%) represented 50% of the total number of individuals registered. Many species (78) were found both as hemi-epiphyte and holo-epiphyte. Most species (107), however, were strictly holo-epiphytic, while 28 species were always hemi-epiphytic.

Araceae, Orchidaceae, and Bromeliaceae were the most speciose and abundant families (see Appendix 3 and Figure 4.1A). Of these, Araceae was the most diverse family in all landscape units. Two genera of Araceae, *Philodendron* and *Anthurium*, had the highest species richness (Figure 4.1B). There were 117 monocotyledonous species (5 families, 36 genera), 45 species of pteridophytes (12 families, 20 genera), and 49 dicotyledonous species (10 families, 18 genera). Five species were found in all landscape units: *Aechmea nivea* (Bromeliaceae), *Asplenium serratum* (Aspleniaceae), *Codonanthe crassifolia* (Gesneriaceae), *Anthurium ernestii* (Araceae), and *Philodendron linnaei* (Araceae). *Trichomanes ankersii* (Hymenophyllaceae) was the most abundant species, being present mainly in upland forests.

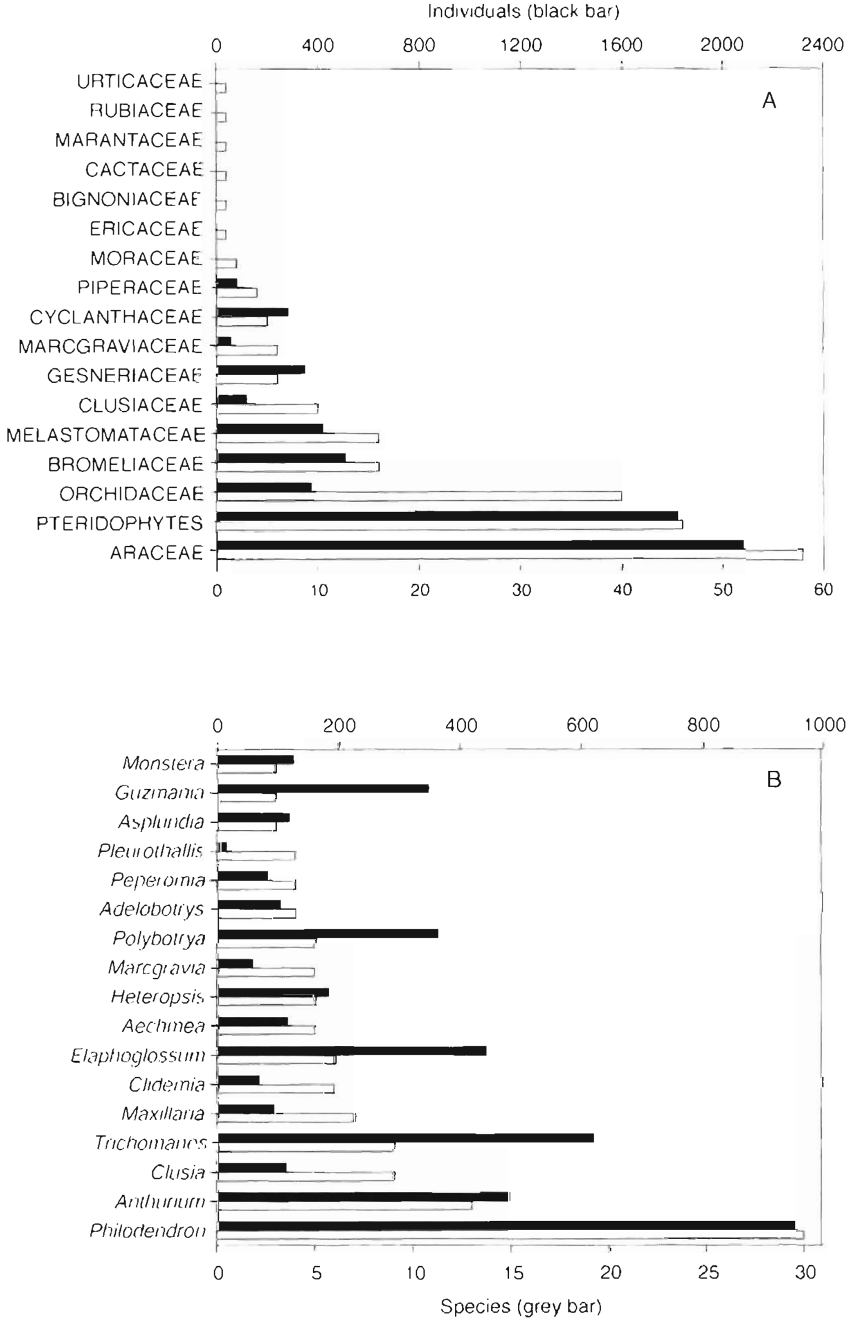


Figure 4.1 Number of epiphytic species and individuals belonging to the most speciose families and genera in thirty well distributed 0.025-ha plots, in the principal landscape units of the Metá area in Colombian Amazonia. A. Species richness and abundance of the most speciose epiphytic families. B. Species richness and abundance of the most speciose epiphytic genera.

A total number of 2763 phorophytes were registered, 1701 (62%) of which with DBH ≥ 2.5 cm. On average, one phorophyte carried 2.2 (standard deviation (sd) = 1.9) epiphyte individuals and 1.8 (sd = 1.2) epiphyte species. Based on the density of trees and lianas in the adjacent 0.1-ha plots (Duque *et al.* 2001) about 40-60% of the woody plants with DBH ≥ 2.5 cm carried epiphytes, and about 50-85% in case of DBH ≥ 5 cm (Table 4.1).

Many (44-60%) epiphyte individuals were found 0-3 m above the ground, and far less (4-12%) were in the crowns or on the branches, throughout all landscape units (Table 4.2). Stem bases also carried the highest number of epiphyte species, but differences with the upper parts of the phorophytes were less pronounced (Table 4.2). Thus, on a species-to-individual basis, epiphyte diversity was highest in the crown/branches, and lowest on the stem bases.

Epiphyte species richness, abundance of epiphytes, phorophyte density, and superficial area did not differ between landscapes (Table 4.3). Epiphyte diversity (Fisher's alpha index) showed a slight difference between landscapes, mostly due to high values in some plots on the low terrace compared to those in the white-sand areas and the Tertiary sedimentary plain.

The DCA diagrams showed how the recorded epiphyte species assemblages tended to be associated with the landscape units (Table 4.4, Figs 4.2A,B). According to the Mantel test, the epiphytic floristic composition varied independently of the distance between the plots (Table 4.5). On the other hand, the floristic composition of epiphyte species and that of trees and lianas with DBH ≥ 2.5 cm in the adjacent 0.1-ha plots (Duque *et al.* 2001) was strongly correlated (r = 0.7). This high correlation remained after controlling for the geographic distance between the plots by means of a partial Mantel test (Table 4.5).

4.4 DISCUSSION

The percentage of species belonging to the most speciose families in this study were more similar to those reported for wet and moist forests in lowlands (Gentry and Dodson 1987b, Foster 1990, Balslev *et al.* 1998), than those located in drier forests where the aroid component decreased, and Orchidaceae and Pteridophytes increased (Wolf and Flamenco-S. 2003). Three of the most speciose families (Araceae, Orchidaceae, and Bromeliaceae) have been reported within the most abundant and diverse families in other studies that included epiphytes as well (Gentry and Dodson 1987b, Balslev *et al.* 1998, Galeano *et al.* 1998).

The recorded number of epiphyte species is within the range of other reports from Neotropical forests (Gentry and Dodson 1987b) and among the highest for the Amazonian region (Gentry and Dodson 1987b, Prance 1990, Balslev *et al.* 1998, Carlsen 2000, Nieder *et al.* 2000). Our total of 213 vascular epiphyte species comprised 14% of the species of trees and lianas (DBH ≥ 2.5 cm) found in the adjacent plots. In the same area, Duivenvoorden (1994) found that (hemi-)epiphytes represented about 5% of the vascular plant species, but he reported undersampling of the upper stems and crowns of high trees. All these figures remain well below the

Table 4.1 Density of phorophytes and the total number of trees and lianas in n 0.025-ha plots in different landscape units in the Metá area of Colombian Amazonia. Shown are averages ± one standard deviation. The number of trees and lianas were based on 0.1-ha plot data (Duque et al. 2001), adjacent to the plots where the phorophytes were counted.

	n	Phorophyte density			Total number trees and lianas	
		total	DBH ≥ 2.5 cm	DBH ≥ 5 cm	DBH ≥ 2.5 cm	DBH ≥ 5 cm
floodplains	5	65 ± 12	42 ± 7	25±5	73 ± 13	36 ± 6
swamps	5	84 ± 25	69 ± 21	47±18	166 ± 75	95 ± 59
podzols	5	132 ± 93	68 ± 38	36±18	129 ± 52	75 ± 46
low terrace	5	84 ± 28	55 ± 21	36±11	91 ± 12	42 ± 7
high terrace	5	93 ± 26	61 ± 15	35±7	117 ± 12	52 ± 4
Tertiary sedimentary plain	5	94 ± 30	64 ± 21	38±11	119 ± 11	55 ± 7
All landscape units	30	91 ± 46	60 ± 24	36±13	116 ± 46	59± 35

Table 4.2. Abundance (number of individuals) and species richness of epiphytes in three positions in the forest, as recorded on phorophytes present in five 0.025-ha plots in different landscape units of the Metá area in Colombian Amazonia. Shown are averages ± one standard deviation.

	Floodplains	Swamps	Podzols	Low terrace	High terrace	Tertiary	Total
Abundance							
Base	81.8 ± 21.1	127 ± 107.5	281 ± 251.4	108 ± 50.0	103 ± 37.9	103 ± 61.1	123 ± 104.2
Stem	42.4 ± 13.8	78 ± 25.9	347 ± 34.0	63.8 ± 42.6	79 ± 43.6	47.6 ± 33.5	59.2 ± 34.8
Crowns/branches	19.6 ± 6.5	25.4 ± 19.8	12 ± 1.4	25.6 ± 6.0	24.2 ± 11.4	20.2 ± 14.2	22.1 ± 11.7
Species richness							
Base	15.6 ± 3.6	20.8 ± 8.8	22.7 ± 7.0	25.4 ± 6.6	20.4 ± 8.7	13.2 ± 5.5	19.4 ± 7.5
Stem	15.2 ± 4.3	19.4 ± 6.4	11 ± 4.4	21.4 ± 6.3	20.4 ± 6.8	14.4 ± 6.3	17.3 ± 6.4
Crowns/branches	11 ± 2.5	10.4 ± 7.2	7 ± 1.4	14.4 ± 2.3	11.2 ± 1.9	11 ± 4.5	11.2 ± 4.1

Table 4.3. Species richness, abundance (number of individuals), and diversity (Fisher's Alpha index) of epiphytes found on phorophytes in n 0.025-ha plots in different landscape units of the Metá area in Colombian Amazonia. Also shown are the number and the superficial area of the phorophytes in these plots. Figures represent averages ± one standard deviation. The right column gives the F values of the ANOVA between landscape units (ns = non significant, * = 0.05 < P < 0.01). The letter codes (a), (ab), and (b) indicate the result of the Tukey-Kramer post-hoc test of difference between landscape units.

	Floodplains (n=5)	Swamps (n=5)	Podzols (n=5)	Low terrace (n=5)	High terrace (n=5)	Tertiary sedimentary plain (n=5)	All landscapes (n=30)	ANOVA F
Species richness	25 ± 7	32 ± 10	29 ± 7	36 ± 7	32 ± 10	23 ± 7	29 ± 9	2.1 ns
Number of individuals	143 ± 33	230 ± 107	278 ± 214	197 ± 96	206 ± 81	170 ± 92	204 ± 115	0.8 ns
Fisher's Alpha index	9.3 ± 3.1 (ab)	16.1 ± 13.8 (ab)	9.6 ± 2.7 (a)	13.2 ± 1.1 (b)	10.6 ± 4.3 (ab)	7.6 ± 2.3 (a)	11 ± 6.4	3.4 *
Number of phorophytes	65 ± 13	84 ± 28	132 ± 93	84 ± 32	93 ± 29	94 ± 33	92 ± 46	1.2 ns
Superficial area (m^2)	59.7 ± 19	71.2 ± 29.3	57 ± 26	68.6 ± 26	76.2 ± 22	89.3 ± 23	70.3 ± 24.1	1.2 ns

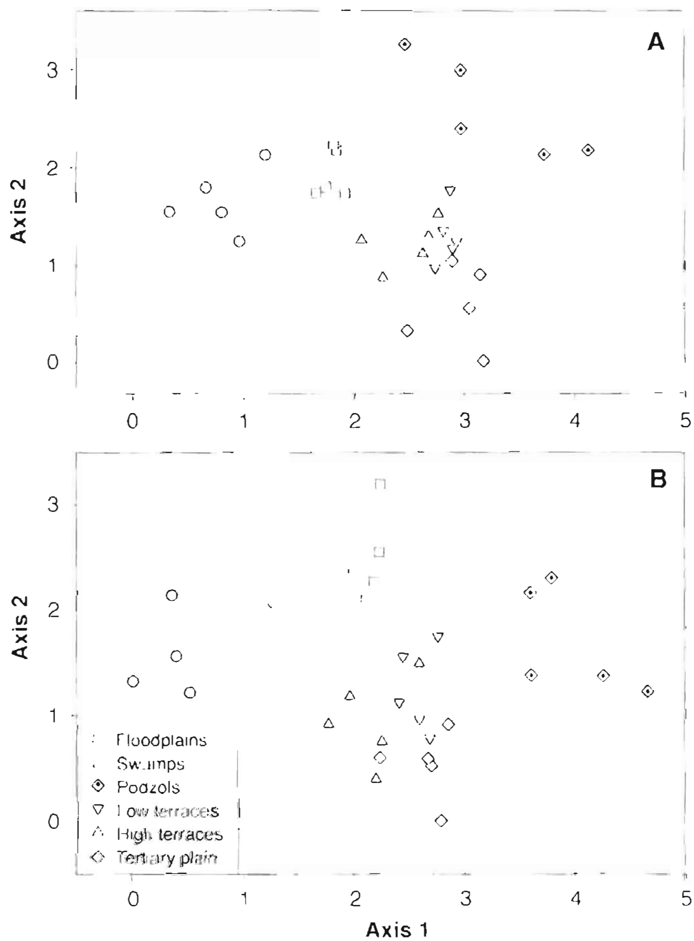


Figure 4.2. Detrended Correspondence Analysis of vascular epiphytes in the Metá area of Colombian Amazonia. A: based on the presence-absence of epiphyte species. B: based on the abundance (number of individuals) of epiphyte species.

estimates of studies in western Ecuador and Costa Rica where between 25 and 35%)of vascular species in small plots pertained to epiphytes (Whitmore *et al.* 1985, Gentry and Dodson 1987ab

Recording epiphytes in forest canopies with binoculars is common practice (e.g., Leimbeck and Balslev 2001). However, even though much care has been taken to observe and sample the epiphytes by climbing into tree crowns, it remains possible that small epiphyte plants have been missed in our study, especially in high trees of floodplains, swamps and Tierra Firme, accounting partially for the high density and species richness of epiphytes at the stem basis. Only by more intensive sampling, for example including careful destructive felling of all branches, an exhaustive census of epiphyte diversity in tree crowns can be made. To test if the branches and crowns might have been undersampled, we cut down 30 trees with a DBH between 20 cm and 30 cm well outside the plot areas but close to each plot. Each of these trees had a visually defined large epiphyte load along the stem and in the crown. Contrary to our expectations, the analyses of these data, which are still in a preliminary stage of species identification and therefore not shown here, did not reveal significant differences in the number of epiphyte individuals and epiphyte species in branches and crowns compared to the phorophytes in similar diameter-class sampled in the plots

Table 4.4. Summary information of Detrended Correspondence Analyses (DCA), based on vascular epiphyte species composition on phorophytes in thirty 0.025-ha plots.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
A. Presence-absence data					
Eigenvalues	0.45	0.28	0.17	0.12	4.23
Length of gradient (sd units)	4.1	3.3	2.8	2.2	
B: Abundance data					
Eigenvalues	0.54	0.27	0.16	0.12	4.78
Length of gradient (sd units)	4.7	3.2	2.3	1.9	

About 4 to 6 out of every 10 woody plants (DBH $\geq$ 2.5 cm) and 5 to 8 out of every 10 woody plant with DBH $\geq$ 5 cm carried epiphytes, suggesting that epiphytes fail to effectively colonize a substantial number of potential phorophytes in the Metá area. Leimbeck and Balslev (2001), in floodplains of nearby Yasuní, found that 98% of the trees with DBH $\geq$ 5 cm carried aroid epiphytes. These authors hypothesized that aroid epiphytes experienced limitation for phorophytes in floodplains. Their floodplain saturation percentage of 98% corresponded to about 25 phorophytes with aroid epiphytes per 0.025 ha when based on the tree density (DBH $\geq$ 5 cm) of 1012/ha reported by these authors. In the five floodplain plots of the Metá area, the average number of phorophytes with aroid epiphytes was 21/0.025 ha, corresponding to 58% of the trees and lianas with DBH $\geq$ 5 cm. So, on a plot area basis, the forests of the floodplain of the Caquetá River contained 16% less phorophytes covered with aroid epiphytes, and their phorophyte saturation level for aroids was about 40% lower than in Yasuní. It seems unlikely, in this light, that the aroid epiphytes in the Metá experience phorophyte limitation to the same degree as might take place in Yasuní floodplains. For the transition and upland areas in Yasuní, about 31 and 32 phorophytes with aroids were found in sample areas of 0.025 ha, which corresponded to 82-86% of the total tree density (DBH $\geq$ 5 cm). In the three Tierra Firme units this average number ranged between 14/0.025 ha and 29/0.025 ha, corresponding to 26-70% of the tree and liana density (DBH $\geq$ 5 cm). This comparison suggests that a lower number of trees and lianas are covered by aroid epiphytes in upland forests of the Metá area compared to Yasuní, and that the saturation level and phorophyte limitation is comparatively low too, just as in the floodplains. Overall climate and humidity levels of the Yasuní area and Metá areas hardly differ (Lips and Duivenvoorden 2001). Yasuní forests might be subjected to a greater immigration of aroid epiphytes from the surrounding forests, especially from the nearby Andes, compared to the Caquetá area. The Andes have been mentioned as a rich centre of diversity for aroid epiphytes (Gentry 1982).

Table 4.5. Mantel and partial Mantel test results of vascular epiphyte species against species of trees and lianas, and geographic distance (space) in the Metá area of Colombian Amazonia. Matrix A is composed of Steinhaus similarity coefficients between epiphytic species data from thirty 0.025-ha plots. Trees is the matrix composed of Steinhaus similarity coefficients between species data of trees and lianas (DBH $\geq$ 2.5 cm) from thirty 0.1-ha plots, each directly adjacent to the 0.025-ha plots where epiphytes were recorded. Space is the matrix composed of Euclidean distances between plots. Mantel r is the Mantel correlation coefficient between matrix A and matrix B. Partial Mantel r is the Mantel correlation between matrix A and matrix B when the effect of matrix C is removed.

		Mantel r	Partial Mantel r	Probability
Matrix A = All vascular epiphytic species				
Matrix B				
Trees		0.7		0.0001
Space		- 0.05		0.18
Matrix B	Matrix C			
Trees	Space		0.7	0.0001
Space	Trees		-0.02	0.33

In the Metá area, epiphytes showed a more or less similar abundance and species diversity in all landscapes. This is remarkably different from trees, which show a well-documented gradient in species diversity from swamps and podzols to well drained floodplains and well-drained uplands (Duivenvoorden 1996; Duque et al 2001). Why might landscape factors not affect epiphyte diversity in the same way as they do for trees? Epiphytes in upper canopies in all lowland forests are generally subjected to high temperatures and low levels of air humidity (ter Steege and Cornelissen 1989), leading to energetic losses by tissue respiration and water balance stress (Andrade and Nobel 1997; Zotz and Andrade 1997). In forest understories stress factors differ between forest types. In the understory of tall forests, air humidity tends to be higher and more constant but light availability and associated rates of carbon fixation lower (Kessler 2002). In the understory of low forests, light penetration in understory is higher, but temperature and drought are also higher leading to less favorable growth conditions for epiphytes. Therefore, the epiphytes in both high and low forests in the various landscape units might experience a more or less similar net degree of stress. Secondly, epiphytes are claimed to have a high dispersal ability (Benzing 1987; Nieder *et al.* 1999), which would allow a more rapid colonization reducing possible effects of forest development on epiphyte species diversity. This explanation, however, seems only valid for epiphytes occuring in upper canopy crowns, but not for understory environments where dispersal by wind is less effective. A high epiphyte dispersal ability should lead to a wide distribution of many epiphyte species in all landscapes, which is not in correspondence to the high epiphyte-landscape association recorded in the Metá area.

Epiphyte species compositional patterns were well related to the principal landscape units (Figs 4.3AB and Table 4.4). In view of the dominance of epiphytes in the understory this is hardly a surprise. The floodplain and swamp plots are subjected to an annual inundation by the Caquetá River, during which water levels may rise several meters above the forest soil. This, plus the closer proximity of river and swamp water during periods of low river water levels likely produce a higher humidity (including mist in early mornings), at annual and daily time-scale, compared to upland conditions. Yearly sedimentation of silty deposits, which are partially of Andean origin, makes the rooting environment at the trunk bases more fertile than in upland forests. Leimbeck and Balslev (2001) further mentioned enhanced vegetation reproduction due to mechanical damage or separation of plant parts into ramets when submerged. The lower stand height and simpler structure of white-sand forests might induce less habitat diversity, as well as better light penetration and wider daily amplitude in temperature and humidity in the understory environment, compared to the generally taller forests in the other landscape units.

Contrary to trees, landscape patterns of species diversity and species composition for epiphytes are uncoupled. In conclusion, we hypothesize that some epiphyte species are more favoured by high humidity (floodplains and swamps), or are better adapted to withstand drought (in low podzol forests) than others without leading to competitive exclusion as this latter process is effectively counterbalanced by immigration from regional pools in situations of low phorophyte limitation. We need more explorative studies, and additional studies on the dispersal ability and auto-biology of epiphytic taxa and the dynamics of epiphyte populations (Benzing 1995; Nieder and Zotz 1998). Our results suggest that caution is needed when knowledge of tree species distribution and dynamics are extrapolated to growth forms with a totally different ecology and vice versa.

Chapter 5

FERNS AND MELASTOMATACEAE AS INDICATORS OF VASCULAR PLANT COMPOSITION IN RAIN FORESTS OF COLOMBIAN AMAZONIA

Alvaro J. Duque M., Joost F. Duivenvoorden, Jaime Cavelier,
Mauricio Sánchez, Carolina Polanía and Andrea León
Submitted to *Plant Ecology*

5.1 INTRODUCTION

Ecological indicators can be defined as a discrete expression or portion of the environment that provides quantitative information on ecological resources reflecting the status of large systems (Hunsaker and Carpenter 1990). Organisms may be employed to test conditions of resources or exposure of biological components to stress. For instance, invertebrates or lichens have been used as indicators for forest degradation (Rodriguez *et al.* 1998, Clarke and Grosse 1999) and water quality (EPA 2003). Ferns and Melastomataceae have been used as indicators of patterns of tree species distribution at different spatial scales (Ruokolainen *et al.* 1997, Vormisto *et al.* 2000). How subsets of understory plants might provide information about patterns of other vascular plant taxa in tropical forests has, however, never been examined in detail. Plot records of vascular floristic composition, including large canopy trees, herbs, shrubs, and small trees are still scarce (Gentry and Dodson 1987, Duivenvoorden 1994, Balslev *et al.* 1998, Galeano *et al.* 1998).

Recently, a new set of near-total vascular plant species composition in a series of widely distributed small plots in Colombian Amazonia has become available (Fig. 5.1). The aim of this case-study is to use these data to examine to which degree species information from ferns and Melastomataceae might explain the composition of the other vascular plant species in these plots. In general, ferns and Melastomataceae may influence the settlement and growth of other forest plants in a direct way (for example, analogous to the well-known allelopathy of *Pteridium aquilinum* (L.) Kuhn in temperate forests), or they may correlate to other forest plants by chance, or because of a common response to external factors (e.g. flooding, topography, etc.). Previous work suggests that ferns and Melastomataceae in NW Amazonian forests are associated with soils, topography, and physiographic units or landscapes (e.g. Tuomisto *et al.* 2003). As these same factors, including space, have also been significantly related to patterns of tropical tree composition (Phillips *et al.* 2003), we expected to find a correlation of ferns and Melastomataceae with the other plant taxa found in the forests. Canonical analysis was applied to regress vascular plant species composition in the forests against information from these two indicator groups, together with that from soils, landscape, and the spatial sampling design. We focused on two questions: 1) Are the main patterns in forest plant composition, as extracted by the principal ordination axes, better related to ferns and Melastomataceae than the soil chemical properties, spatial location of the sample plots or the overall effect of the main landscape? 2) Do ferns and Melastomataceae explain any part of the total variation in forest plant composition after having accounted for effects of space, soils, or landscape? The first question addresses the practical indicator potential of ferns and Melastomataceae, relative to the other types of information that are frequently obtained in reconnaissance inventories. The second question may falsify the hypothesis that ferns and Melastomataceae are simply related to the composition of other forest plants because of a common response to soils or the main landscape.

5.2 METHODS

Study site

The study area covers about 2000 km^2 and is situated along the stretches of the middle Caquetá and Mesay Rivers in Colombian Amazonia, roughly between 72° 37' and 71 ° 18' W longitude, and 0 ° 55' S and 0 ° 9' N latitude (Fig. 5.1). The principal landscape units found here are well-drained floodplains, swampy areas (including permanently inundated backswamps and basins in floodplains or fluvial terraces), areas covered with white-sand soils (found on high terraces of the Caquetá River and in less dissected parts of the Tertiary sedimentary plain), and Tierra Firme (which are never flooded by river water and include low and high fluvial terraces and a Tertiary sedimentary plain) (Duivenvoorden and Lips 1995, Lips and Duivenvoorden 1996). Soils and landscape units are called well-drained when soil drainage (according to FAO 1977) is imperfectly to well-drained (FAO drainage class ≥ 2), and poorly drained when soils are poorly to very poorly drained (FAO drainage class < 2). The area receives a mean annual precipitation of about 3060 mm (1979-1990) and monthly rainfall is never below 100 mm (Duivenvoorden and Lips 1995). Mean annual temperature is 25.7°C (1980-1989) (Duivenvoorden and Lips 1995).

Field and laboratory work

We conducted a survey of 40 0.1-ha plots that were located in the four landscape units mentioned above. In order to establish the plots, starting locations along the Caquetá, Mesay, and Cuñare rivers and the direction of the tracks along which the forests were entered, were planned on the basis of the interpretation of aerial photographs and satellite images (Duivenvoorden *et al.* 2001). The topography was rapidly described and the forest was visually examined in order to identify more or less homogeneous terrain units. In these units, rectangular plots were located without bias with respect to floristic composition or forest structure, and were delimited by compass, tape and stakes, starting at a random point. All plots were mapped by GPS and were established in mature forests that did not show signs of recent human intervention, at a minimum distance from each other of 500 m. In each plot all vascular plants with DBH ≥ 2.5 cm (DBH diameter at breast height) were described, counted and collected. Thirty of these plots were located in the Metá area (Duque *et al.* 2001, 2002). Here, a subplot of 0.025 ha (5 x 50 m) was established directly bordering each plot, in order to count and collect all herbs as well as all other vascular plants of height > 1 m (and DBH<2.5 cm). Ten other 0.1-ha plots were established in the Chiribiquete area. There, the 0.025 ha subplots were located inside instead of just outside the 0.1-ha plots. Fieldwork took place from April to December in 1997, and from March to November in 2001

The identification of the botanical collections took place at the herbaria COAH, COL, HUA, MO, and AAU (Holmgren *et al.* 1990). Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens. Hereafter the term species refers to both morpho-species and botanical species.

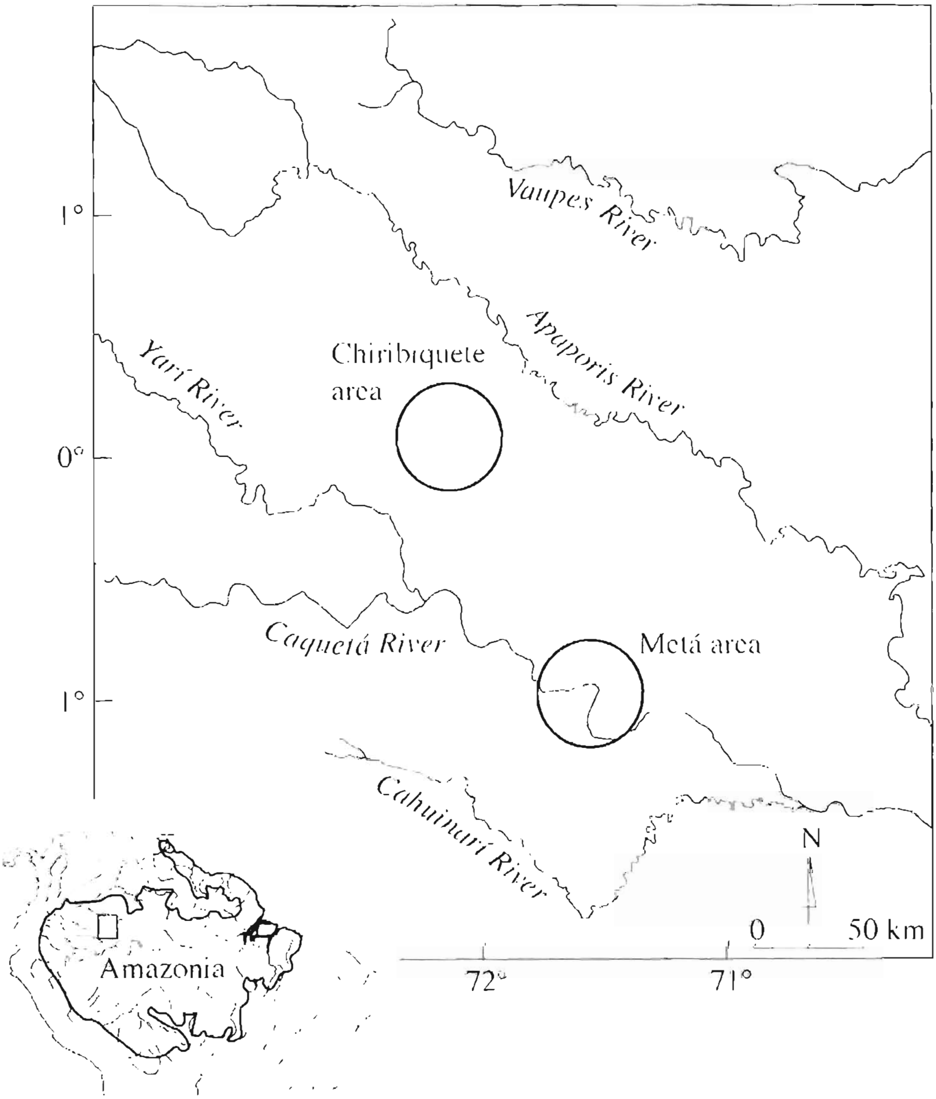


Figure 5.1. Location of the Metá and Chiribiquete sites in the middle Caquetá area.

Roughly in the central part of each 0.1-ha plot, a soil core was taken to 120 cm depth in order to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions, and texture) and to define soil drainage (in classes of FAO 1977). At each augering position a soil sample was taken at a depth of 65-75 cm. For analyses, soil samples were dried at temperatures below 40°C, disaggregated and passed through a 2-mm sieve. In the soil laboratory of the Institute for Biodiversity and Ecosystem Dynamics at the Universiteit van Amsterdam, total content of Ca, Mg, K, Na and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H_2SO_4 (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser

Data analysis

The similarity of plots on the basis of species from ferns and Melastomataceae was calculated using Jaccard's index (J). Bioindicators were then defined as the axes of a Principal Coordinate Analysis (PCoA) on a matrix of distances between plots, in which the distance was expressed as 1-J (Legendre and Legendre 1998). The association between bioindicators and presence-absence information from ferns and Melastomataceae was given by the Spearman correlation coefficient. Geographical space was quantified by means of the axes of a PCoA of neighbor matrices using a threshold between-plot distance of 35 km (Borcard and Legendre 2002). Environment was represented by log-transformed soil elemental reserves (Table 5.1) and physiography, the latter included as four dummy variables representing the main landscape units. The analyses described above were done with R-Package (Casgrain and Legendre 2000).

We used detrended correspondence analysis (DCA) and canonical ordination analysis (CCA) by means of CANOCO 4.0 (ter Braak and Šmilauer 1998) in order to examine patterns in floristic composition (excluding ferns and Melastomataceae). The CCA was conducted in relation to bioindicators, geographical space, and environment. In CCA, a manual forward selection with 999 permutations was conducted for each of these explanatory sets separately. Variables with $P \leq 0.15$ were picked out for the final CCA, in which all selected variables together acted as explanatory descriptors. The significance of first axis and all axes combined from this final CCA was determined by Monte Carlo tests using 999 permutations. The relative contribution of the sets of selected variables to explaining the patterns of floristic composition was determined by variation partitioning (Borcard *et al.* 1992; Anderson and Gribble 1998). In all CCA, we focused scaling on inter-species distances and applied the biplot scaling type. The analyses were conducted on data from the full set of 40 plots in all landscapes, and on a subset of 19 plots made only in Tierra Firme. In the latter CCA, physiography did not enter as an explanatory variable.

5.3 RESULTS

All landscape units

In total 53941 individuals of vascular plants belonging to 2480 species were recorded in the 40 0.1-ha plots in the Metá and Chiribiquete areas. Of these, 17473 individuals and 132 species were from ferns and Melastomataceae (see Appendix 4; the names of the other species will be published elsewhere). The gradient length of the principal axes of the DCA of the species data (excluding ferns and Melastomataceae) was 7.5 (first axis) and 3.5 (second axis), warranting subsequent ordinations by means of reciprocal averaging (ter Braak 1987). The forward selection yielded ten bioindicators which together explained 61% of the variance in ferns and Melastomataceae. The three principal bioindicators were mostly related to *Trichomanes pinnatum* (r_s = 0.77), *Cyathea macrosora* (r_s = 0.71), *Danaea elliptica* (r_s = 0.69), *Mouriri cauliflora* (r_s = 0.65), *Polybotrya caudata* (r_s = 0.60), *Lindsaea* *coarctata* (rs = 0.58) (all bioindicator 1); *Adiantum tomentosum* (rs = 0.81), *Miconia* AD6297 (rs = 0.60), *Mouriri myrtifolia* (rs = 0.54) (all bioindicator 2); and *Lomariopsis japurensis* (rs = 0.63) (bioindicator 3). These three axes were more strongly associated with the selected spatial and environmental variables than the less important axes (Table 5.2). Bioindicator 1 contained information quite similar to that of the Tierra firme class (rs = 0.88). Bioindicator 2 was well associated to the first spatial PCoA axis (rs = -0.68), while bioindicator 3 showed a strong positive correlation with the soil content of Ca, Mg, K, and P.

The main axes of the CCA ordination displayed a strong separation of the main forest types (Fig. 5.2A; Table 5.3), mostly due to the influence of the Tierra firme unit along axis 1, and bioindicator 3 and Mg along axis 2 (Table 5.4). The interset correlation coefficients showed that bioindicator 1 was also important, together with Ca and the White sand class. On the other hand, the spatial configuration of the sample plots had hardly any impact. Incorporating all canonical axes, the entire set of bioindicators explained 23-35% of the forest composition (Fig. 5.2B). Soil and physiography accounted for 19-30%, while space explained 9-15%.

Tierra firme forests

Tierra firme forests were analysed separately in order to minimise possible effects of flooding and drainage on the correlation between bioindicators and forest composition. In the 19 0.1-ha plots in Tierra Firme forests 19622 vascular plant individuals were recorded from 1716 species. Of these, 3793 plants and 91 species were from ferns and Melastomataceae. A DCA analysis of the forest species (excluding ferns and Melastomataceae) revealed a gradient length of 3.0 along the first DCA axis and 3.5 along the second axis, both just large enough to proceed with CCA (ter Braak 1987). By forward selection three bioindicator PCoA axes were chosen which together explained 41% of the variance. Bioindicator 1 was mostly correlated with *Polybotrya caudata* (rs = 0.73), *Miconia cionotricha* (rs = 0.68), *Mouriri nigra* (rs = 0.58), *Cyathea macrosora* (rs = 0.54), *Tococa guianensis* (rs = 0.53), and *Myrmidone macrosperma* (rs = 0.52). Bioindicator 2 was mostly associated with *Miconia carassana* (rs = 0.74), *Cyathea lasiosora* (rs = 0.70), *Miconia* MS4963 (rs = 0.53), and *Maieta guianensis* (rs = 0.53), and bioindicator 3 with *Mouriri vernicosa* (rs = 0.64) and *Selaginella parkerii* (rs = 0.50). Also selected were the three principal spatial PCoA axes and the soil reserve levels of Mg, K, and N. The first two bioindicators were strongly related to the spatial configuration of the plots (Table 5.5). In the final CCA, space and Mg (with regard to the canonical coefficients), in addition to bioindicator 1 and N (with regard to the interset correlations) largely determined the main patterns of species composition in the forests (Fig. 5.3A; Table 5.6). Taken together, the bioindicators explained 15-23% of the forest composition, a level similar to that of soils (17-23%) and space (17-25%).

Table 5.1 Soil elemental reserves measured at 70 cm soil depth in the different landscape units in the Metá and Chiribiquete areas in Colombian Amazonia. Shown are averages ± one standard deviation of n plots

	n	Ca	Mg	K	Na	P	C	N
		mmol kg					%	
Flood plains	8	105.6 ± 98.7	215.7 ± 171.7	275.4 ± 161.7	207.8 ± 203.4	9.6 ± 4.4	0.5 ± 0.1	0.1 ± 0.02
Swamps	8	3.7 ± 2.0	71.7 ± 32.3	160.2 ± 69.6	27.7 ± 11.2	12.9± 8.4	9.5 ± 13.7	0.6 ± 0.7
Tierra firme	19	1.8 ± 0.7	30.9 ± 21.7	60.0 ± 54.7	14.5 ± 14.6	5.2 ± 1.5	0.5 ± 0.3	0.05 ± 0.03
White-sands	5	1.4 ± 1.0	1.4 ± 0.7	1.1 ± 0.5	1.0 ± 1.4	0.6 ± 0.3	1.6 ± 1.5	0.02 ± 0.01

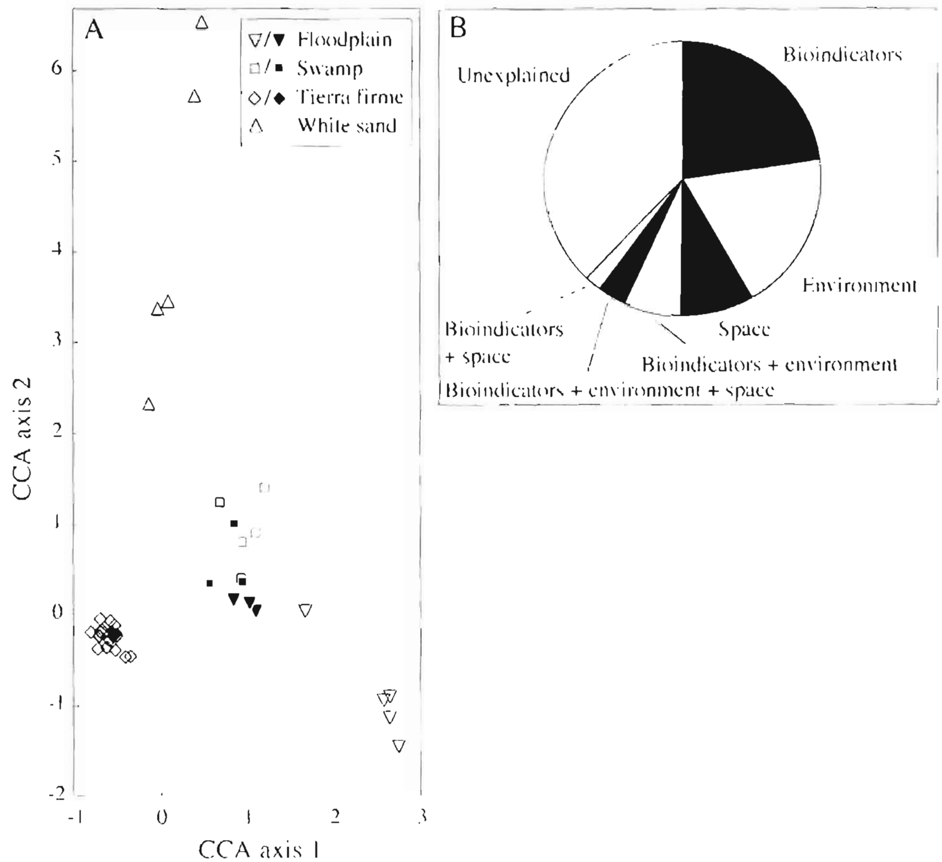


Figure 5.2. CCA of vascular plant composition (excluding ferns and Melastomataceae) in 40 0.1-ha plots, located in Metá and Chiribiquete areas in Colombian Amazonia. A. Ordination diagram showing sample scores derived from the species from the Metá area (open symbols) and the Chiribiquete area (closed symbols); B: partitioning of the variation explained by the different sets or combinations of sets of explanatory variables. Only portions of the variation >1% are shown. The first CCA axis (F-ratio = 0.885) and all axes together (F-ratio = 1.246) were significant at $P = 0.001$.

Table 5.2. Pearson correlation coefficients of bioindicators with spatial and environmental variables, selected for CCA analyses of vascular plant composition (excluding ferns and Melastomataceae) in 40 0.1-ha plots, located in Metá and Chiribiquete areas in Colombian Amazonia.

	spatial axis											
	1	2	3	17	Ca	Mg	K	P	C	N	Tierra firme	White sand
bioindicator 1	0.31	-0.29	0.25	-0.23	-0.19	0.20	0.19	0.30	-0.22	-0.10	0.88	-0.52
bioindicator 2	-0.68	-0.29	-0.17	-0.04	-0.21	0.28	0.43	0.36	0.12	0.37	0.09	-0.50
bioindicator 3	0.04	-0.18	0.00	0.1	0.80	0.83	0.75	0.68	-0.02	0.24	-0.26	-0.55
bioindicator 4	0.19	-0.05	-0.34	-0.28	0.05	0.06	-0.03	0.02	0.43	0.30	-0.12	0.19
bioindicator 5	0.37	0.21	-0.41	0.1	0.01	0.04	0.06	0.23	0.37	0.21	-0.13	-0 03
bioindicator 6	0.22	-0.34	0.34	0.12	-0.27	-0.06	-0 05	0.12	0.37	0.32	-0.01	-0.07
bioindicator 7	-0.08	-0.34	-0.19	0.27	-0.01	-0.04	-0.08	-0.01	0.15	-0.07	0.06	0.08
bioindicator 8	-0.29	0.22	0.20	0.06	0.11	0.14	0.10	0.20	0.11	0.09	-0.02	-0.22
bioindicator 11	-0.01	0.17	-0.28	0.06	-0.07	0.10	0.08	0.18	0.20	0.07	-0.14	-0.07
bioindicator 12	0.17	-0.12	0.16	-0.08	-0.05	-0.07	-0.05	-0.12	-0.29	-0.25	-0.06	0.14

Table 5.3. Summary table of CCA analyses of vascular plant composition (excluding ferns and Melastomataceae) in 40 0.1-ha plots in all landscape units (A), and in19 0.1-ha plots located in Tierra Firme (B).

	Eigenvalues				Inertia
A: All landscapes	axis1	axis2	axis3	axis4	
	0.66	0.62	0.59	0.50	
Sum of all unconstrained eigenvalues					13.3
Sum of all canonical eigenvalues					8.2
B: Tierra firme					
	0.49	0.45	0.40	0.33	
Sum of all unconstrained eigenvalues					5.8
Sum of all canonical eigenvalues					3.1

Table 5.4. Canonical coefficients and interset correlation of CCA analyses of vascular plant composition (excluding ferns and Melastomataceae) in 40 0.1-ha plots, located in Metá and Chiribiquete areas in Colombian Amazonia.

	canonical coefficient		interset correlation	
	axis 1	axis 2	axis 1	axis 2
Bioindicator 1	-0.01	-0.47	-0.65	-0.54
Bioindicator 2	-0.08	-0.69	-0.20	-0.10
Bioindicator 3	0.37	1.03	0.76	-0.47
Bioindicator 4	0.00	0.33	0.22	0.21
Bioindicator 5	-0.07	0.33	-0.01	0.06
Bioindicator 6	-0.11	0.29	-0.12	0.11
Bioindicator 7	0.02	0.16	-0.05	-0.02
Bioindicator 8	0.16	-0.36	0.10	-0.08
Bioindicator 11	-0.01	0.12	0.14	0.09
Bioindicator 12	0.05	0.07	0.11	-0.03
spatial axis 1	0.06	-0.46	-0.01	0.00
spatial axis 2	0.01	-0.01	0.20	0.21
spatial axis 3	-0.10	-0.02	-0.21	-0.19
spatial axis 17	0.01	-0.09	0.17	0.01
Ca	0.04	0.18	0.85	-0.26
Mg	0.16	0.93	0.64	-0.53
K	-0.07	-0.53	0.54	-0.53
P	-0.02	-0.08	0.42	-0.56
C	0.05	0.06	0.20	0.41
N	-0.05	-0.07	0.28	0.10
Tierra firme	-0.63	-0.25	-0.87	-0.41
White sand	-0.06	0.04	0.03	0.84

5.4 DISCUSSION

Indicators of rain forest plant composition?

Ignoring the animal kingdom, reliable ecological indicators of tropical forest composition should belong to plant groups that are widespread, and occur in many habitats with sufficient abundance to allow representative and sizeable samples for analysis (Clark and Grosse 1999). They should also have the capacity to reveal important patterns of variation in forest composition in a cost-effective way. Because lowland tropical forests contain so many plant species, and because the tropical flora is still poorly described, any field information that can be obtained quickly without a large error and that helps to distinguish the main patterns of forest composition in a reliable way is an important survey tool. In both the entire set of all landscapes and the subset of Tierra Firme forests, information from ferns and Melastomataceae, as summarized in PCoA axes, was highly related to the main patterns in forest species composition. In principle, therefore, ferns and Melastomataceae can be used to detect and forecast changes of forest composition in the study area. However, there are a number of constraints to this conclusion.

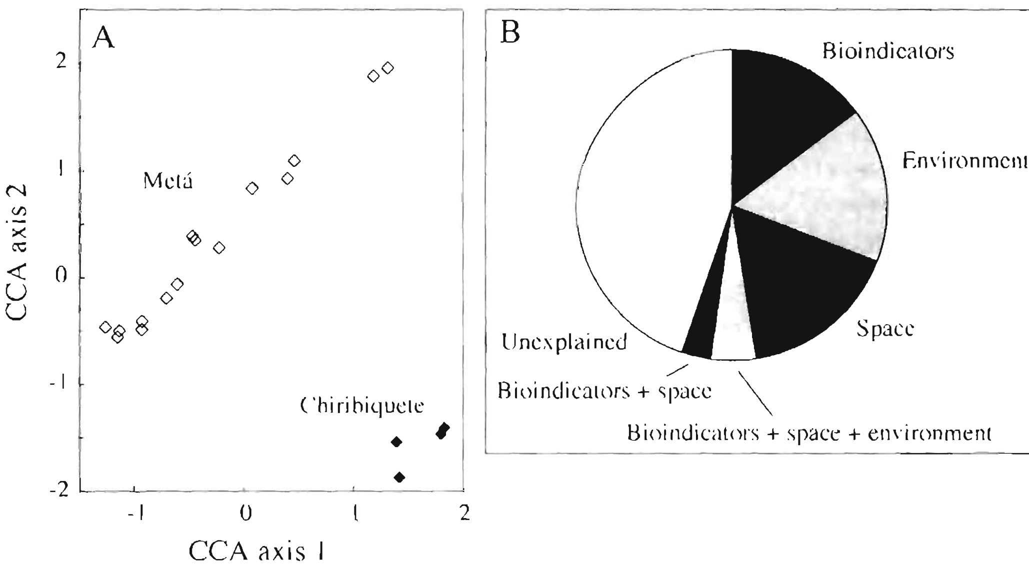


Figure 5.3. CCA of vascular plant composition (excluding ferns and Melastomataceae) in 19 Tierra Firme of 0.1-ha each, located in Metá and Chiribiquete areas in Colombian Amazonia. A. Ordination diagram showing sample scores derived from the species from the Metá area (open symbols) and the Chiribiquete area (closed symbols); B: partitioning of the variation explained by the different sets or combinations of sets of explanatory variables. Only portions of the variation >1% are shown. The first CCA axis (F-ratio = 0.830) and all axes together (F-ratio = 1.167) were significant at $P = 0.001$.

Table 5.5. Pearson correlation coefficients of bioindicators with spatial and environmental variables, selected for CCA analyses of vascular plant composition (excluding ferns and Melastomataceae) in 19 Tierra Firme plots of 0.1 ha each, located in Metá and Chiribiquete areas in Colombian Amazonia.

	spatial axis					
	1	2	3	Mg	K	N
bioindicator 1	0.85	0.33	-0.21	-0.33	-0.34	-0.60
bioindicator 2	0.02	-0.56	-0.64	0.13	-0.06	0.09
bioindicator 3	0.33	-0.29	0.44	0.42	0.38	0.05

Table 5.6. Canonical coefficients and interset correlation of CCA analyses of vascular plant composition (excluding ferns and Melastomataceae) in 19 Tierra Firme plots of 0.1 ha each, located in Metá and Chiribiquete areas in Colombian Amazonia.

	canonical coefficient		interset correlation	
	axis 1	axis 2	axis 1	axis 2
bioindicator 1	0.31	0.08	-0.75	0.37
bioindicator 2	0.20	0.21	0.48	0.46
bioindicator 3	0.08	0.04	0.07	0.51
spatial axis 1	-1.09	0.46	-0.71	0.70
spatial axis 2	-0.24	-0.19	-0.53	-0.52
spatial axis 3	-0.02	-0.03	-0.12	-0.03
Mg	1.03	1.11	0.57	0.52
K	-0.42	-0.43	0.46	0.38
N	-0.25	-0.40	0.64	-0.03

We used PCoA in order to reduce redundancy and to concentrate the information from ferns and Melastomataceae into a few variables (Gauch 1982, Legendre and Legendre 1998). Any a priori selection out of the large pool of individual indicator taxa would have been biased by subjective judgment. Ordination axes, however, do not contain practical field information, which implies that further research is required to quantify the indicator potential of individual species. In the Middle Caquetá area those species that were most correlated with the first bioindicator axes might well be used for such studies.

The principal bioindicator axes were substantially correlated with the supplied soil, landscape and spatial variables. These results confirm that ferns and Melastomataceae have a potential to indicate general patterns of soil and landscape variation in Amazonia, as has been reported from studies elsewhere (e.g. Ruokolainen *et al.* 1997, Tuomisto *et al.* 2003). However, these same high correlations implied that the canonical coefficients for the principal CCA axes were not stable, hampering their use in comparing the relative effect of ferns and Melastomataceae with those of the other supplied variables (ter Braak 1987). Because of the high interset correlations of the bioindicators for the principal CCA axes, no evidence was obtained that ferns and Melastomataceae show more potential to predict the main patterns of forest composition than the other variables. This implies that when botanical experts are available, information from ferns and Melastomataceae might offer an effective way to map the main patterns in forest composition. In other circumstances, field data of soils and main landscapes might offer quite similar information. The cost-effectiveness of these two indicator methods was outside the scope of this case-study.

Overall variation in species composition
The variation partitioning yields a biased outcome, as small sample sizes in diverse tropical lowland forests, either by small or by few large plots (or transects), inevitably leads to undersampling of locally rare species. As a result, between-plot similarity tends to be underestimated (Pitman 2001) which, in turn, might reduce the overall amount of variation explained. There is no easy solution for this old survey problem (e.g., Schulz 1960), as increased sampling intensities will yield more locally rare species and, therefore, more noise. On the other hand, most of the variation is concentrated in the principal ordination axes that are built up by the main similarity patterns, and are less influenced by the sampling effect than subordinate axes.

The relationships of ferns and Melastomataceae to the patterns of other plants in the forests was to a substantial degree independent from that of the other sets of explanatory variables, both in the entire analysis as in that from the tierra firm forests (Figs. 2B and 3B). This is probably due to the effect of the subordinate bioindicators, because the principal ones were well correlated to the soil, landscape and spatial variables (see also Legendre and Legendre 1998). It is hard to distinguish between direct or indirect effects here. The vascular plant composition of tropical forests depends on a variety of factors, many of which lack any relationship to soils or abiotic environment (Condit 1996, see also Enquist *et al.* 2002). Any large subset of plants taken from the forests will show this dependency. Therefore, it is highly likely that, by default, subsets of forest plants will be correlated to each other. Indeed, apart from ferns and Melastomataceae, palms and other taxa have been reported as indicators of Amazonian forest composition as well (Vormisto *et al.* 2000). Correlative studies of plant indicators to other subsets might simply not yield sufficient information to separate direct effects from those derived from indirect correlations, given the complexity of the factors governing tropical forest compositional patterns. Evidence of direct effects may come from detailed experimental studies of between-plant interactions. Most ferns and Melastomataceae belong to different functional plant groups than trees and lianas. With regard to the understory habitat and predominant herbaceous and shrublike appearance of ferns and Melastomataceae, future studies to detect such interactions should to concentrate on the seedling or juvenile stages of trees and lianas, both above-ground as well as in the rooting environment.

Chapter 6

DIVERSITY AND COMPOSITION OF WOODY LIANAS IN NW AMAZONIA

Alvaro J. Duque M., Joost F. Duivenvoorden, Mauricio Sánchez, Jaime Cavelier, Hugo Romero-Saltos, Renato Valencia, Manuel Macía, César Grández and Alberto García

Submitted to *Global Ecology and Biogeography*

6.1 INTRODUCTION

Woody lianas are a significant plant group contributing to the total plant diversity and the dynamics of the tropical forests (Putz 1984, Phillips and Gentry 1994, Schnitzer *et al.* 2000, Phillips *et al.* 2002). These climber plants, as well as other groups like epiphytes, shrubs, and herbs, have been ignored in many inventories and vegetation models (Schnitzer and Carson 2000). As a result, information of the ecology and function of lianas is still scanty and sometimes even contradicting. Lianas were considered light demanding species (Putz 1984) but recent studies showed that they are also tolerant to low light intensities on the forest floor (Nabe-Nielsen 2000). Wind has often been mentioned as important for the dispersal of lianas (Gentry 1991b, Killeen *et al.* 1998). Many lianas, however, may reproduce by clones (Nabe-Nielsen 2000). The density and species richness of lianas at local scale have been related to forest architecture and structure (Putz 1984, Nabe-Nielsen 2000), but also to the successional stage of the forests (Dewalt *et al.* 2000). A positive relationship between soil fertility and density of lianas has been suggested for Amazonian and Malaysian forests (Putz and Chai 1987, Gentry 1991a) but was not found in Mexico (Ibarra-Manríquez and Martínez-Ramos, 2002). Clumps of vines were also interpreted as biological markers of forest disturbance (Balée and Campbell 1989, Hegarthy and Caballé, 1991). Increased seasonality in precipitation was positively associated with the abundance of lianas (Gentry 1991a, Pérez-Salicrup *et al.* 2001) but negatively with their species richness (Clinebell *et al.* 1995). Rising atmospheric concentrations of CO_2 might enhance density and dominance of lianas in western Amazonian rain forests, but failed to have a clear effect on their floristic composition, distribution, and compositional turnover rates (Phillips *et al.* 2002).

With so many biotic and abiotic environmental factors playing a role in the establishment and maintenance of liana diversity, and the likeliness that these act together, a search for a single explanatory variable is not useful (Balfour and Bond 1993). Spatial mechanisms may also determine the floristic composition of a local community, embedded in a larger and heterogeneous landscape (Holt 1993, Legendre and Legendre 1998). Species diversity at regional and local spatial scales is strongly influenced by the interaction between environmental heterogeneity and dispersal (McLaughin and Roughgarden 1993). When the local species richness in a similar habitat type but in different regions varies significantly, the historical and biogeographical influence may become more relevant (Ricklefs and Schluter 1993).

This paper aims to assess the hitherto unexplored patterns of liana diversity and composition at local and regional scales in NW Amazonia (Fig. 6.1). NW Amazonia has become known for its high plant diversity, mainly recorded in the surroundings of three centres of field research that were located in each of the three countries involved (Iquitos area in Peru: Gentry 1988; Yasuní area in Ecuador: Valencia *et al.* 1994; Araracuara area in Colombia: e.g. Duivenvoorden and Lips 1995). NW Amazonia is still largely covered by non-fragmented 'virgin' rain forests (no fragmentation), which are situated in a lowland setting (neglectable altitudinal gradient). The whole area has a largely similar geomorphology comprised by sedimentary plains that are more or less dissected in dense subdentritic drainage systems (Dumont *et al.* 1990). It has a humid rain fall regime with a low seasonality,

and has probably undergone a similar rainfall in the Pleistocene and Holocene (e.g. Colinvaux *et al.* 2000, Hooghiemstra and van der Hammen 1998). As these important environmental factors show relatively little regional variation, NW Amazonia is especially suitable for wide-scale comparisons of rain forest diversity.
Diversity and composition of woody lianas that occurred with a minimum density of 25 rooted stems in series of scattered 0.1-ha plots made in each of the 'hotspot areas' mentioned above, were related to physiography, soil, and forest structure in multiple regression and canonical ordination analysis. With respect to the regional location and the fine resolution (applying diameter cut-off of 2.5 cm), our study is complementary to comparative studies at wide tropical scales (Clinebell *et al.* 1995) or Amazonian scales (Terborgh and Andresen 1998, Pitman *et al.* 1999, 2001, Ter Steege *et al.* 2003).

6.2 METHODS

Study site
The study was carried out in three different areas in NW Amazonia: Metá, forming part of the middle Caquetá basin in Colombia; Yasuní in Ecuador; and Ampiyacu pertaining to the Maynas Province in Peruvian Amazonia (Fig. 6.1). All areas are in the Humid Tropical Forest life zone (bh-T) according to Holdridge *et al.* (1971). The average temperature is near 25°C, and annual precipitation varies around 3000 mm. All months show an average precipitation above 100 mm (Lips and Duivenvoorden 2001).

Vegetation sampling and identification of botanical vouchers
A total of 80 0.1-ha plots were established: 30 in Metá and 25 in both Yasuní and Ampiyacu. In order to establish the plots, starting locations and the direction of the tracks along which the forests were entered, were planned on the basis of the interpretation of aerial photographs (Duivenvoorden 2001) and satellite images of Landsat TM (Tuomisto and Ruokolainen 2001). During the walk through the forests, soils and terrain units were rapidly described, and forests were visually examined. In this way sites with homogeneous soils and physiognomically uniform forest stands were identified. In these stands, rectangular plots (mostly 20 x 50 m) were delimited by compass, tape and stakes, working from a random starting point, with the restriction that the long side of the plot was parallel to the contour line. Plots were located without bias with respect to floristic composition or forest structure (including aspects of tree density, thickness and height, and presence of lianas). They were made in forest that lacked signs of human intervention. The only exception to this were some swamp plots in the floodplain of the Ampiyacu River in Peru, where few palms had been cut recently to harvest fruits from *Mauritia flexuosa* L.f. Plots were established at a minimum between-plot distance of 500 m and were mapped with GPS. They were subdivided into subplots of 10 x 10 m, in which all lianas with DBH ≥ 2.5 cm were numbered and measured with tape. Lianas were defined as those woody plants that established as seedlings on the forest soil, gained access to upper canopy by using other plants as support, and remained rooted in the soil throughout their lives. According to these criteria, epiphytes and hemi-epiphytes were excluded (Schnitzer and Bongers, 2002). Fieldwork took place in 1997 and 1998.

Botanical collections were made of all liana species (DBH ≥ 2.5 cm) found in each plot. Identification took place at the herbaria COAH, QCA, QCNE, AMAZ, USM, MO, NY and AAU (Holmgren *et al.* 1990). The nomenclature of families and genera followed Mabberley (1989). Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics, were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens.

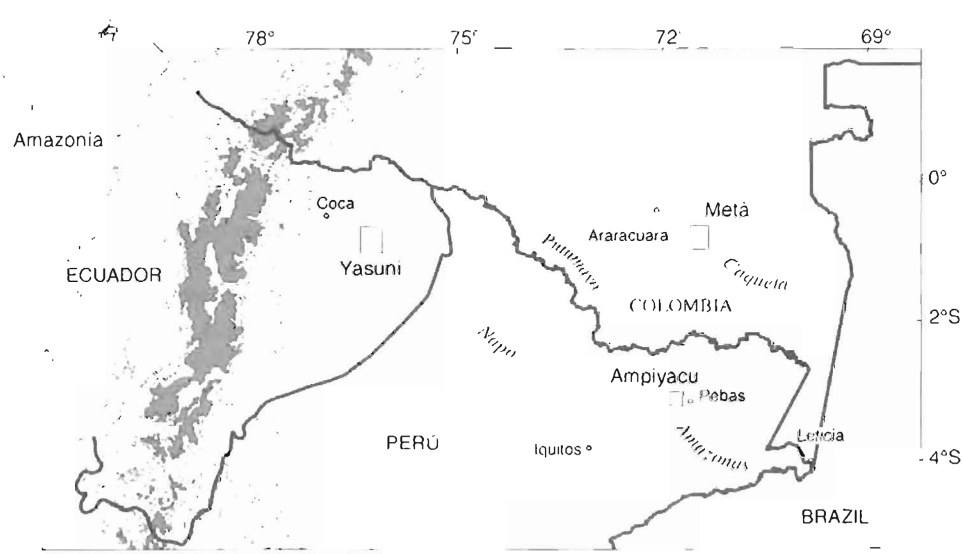


Figure 6.1. Location of the three study sites in NW Amazonia.

In the central part of each plot, a soil augering was done to 120 cm depth in order to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions, and texture) and to define soil drainage (in classes of FAO 1977). At each augering a soil sample was taken at a depth of 65-75 cm. For analyses, soil samples were dried at temperatures below 40°C, crumbled and passed through a 2-mm sieve. Total content of Ca, Mg, K, Na, and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H_2SO_4 (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser. Soil analyses were done at the soil laboratory of Institute for Biodiversity and Ecosystem Dynamics of the Universiteit van Amsterdam.

Data analysis

Plot-based accumulation curves (Gotelli and Colwell 2001) were made by successively pooling of liana species and individuals recorded in randomly ordered plots. A total of 56 plots, each with 25 lianas or more, were used for ANOVA and regression analyses of diversity, and ordination analyses of species patterns. Differences in number of individuals, families, genera, species, and Fisher's alpha based on species were analyzed by means of a two-way ANOVA with landscape and region as factors. For this ANOVA, landscape was classified in the three physiographic units where the plots were made: well-drained floodplains, swamps, and well-drained uplands (Tierra Firme). The first two landscape units were periodically flooded by river water (all swamps pertained to the floodplains of the main rivers), the last unit not. The region was simply taken as the area where plot were located (Metá, Yasuní, Ampiyacu). Fisher's alpha was calculated using Newton's method (Fisher *et al.* 1943; Condit *et al.* 1998). All response variables in the ANOVA's were ln-transformed.

Multiple regression was done of Fisher's alpha against environmental and spatial variables that were also used in the canonical correspondence analysis (CCA) of liana species patterns. In addition to the landscape factor (see above) the following explanatory variables were used in this analysis:

- Cover of each of the three landscape units, determined with Landsat TM imagery and aerial photographs in a circle with radius of 1 km, centred on each plot. When the area around the plot was part of a river, it was taken as flood plain. Before analyses, the three cover variables were ln-transformed.
- Forest structure summarized in the first two axes of a principal components analysis (PCA) of plot densities of non-liana individuals (hereafter simply called trees) in six DBH classes ($2.5 \leq$ DBH < 5 cm, $5 \leq$ DBH < 10 cm, $10 \leq$ DBH < 20 cm, $20 \leq$ DBH < 40 cm, $40 \leq$ DBH < 60 cm, and DBH ≥ 60 cm). Before PCA, densities were ln-transformed and standardized.
- Soil chemical information summarized in the first two axes of a PCA of total concentrations of Ca, Mg, K, Na, P, C and N, sampled at 65-75 cm soil depth in each of the plots. Before PCA, soil variables were ln-transformed and standardized.
- Latitudinal and longitudinal coordinates of the plots in decimal degrees.

In ANOVA and multiple regression, samples were visually inspected for homoscedasticity. Residuals from all analyses were not different from normal (Shapiro-Wilk W test, $p > 0.05$), They also did not show any spatial dependence, as tested by means of the significance of Moran's I, after progressive Bonferroni corrections using nine equal-width classes of ln-transformed distances in the Autocor module of R-Package R 4.0 (Casgrain *et al.* 2000). The distance matrix for this analysis was calculated in km with the Geographic Distance module in R package R 4.0 (Casgrain *et al.* 2000), applying the latitudinal and longitudinal coordinates of the plots in decimal degrees. ANOVA, PCA and multiple regression were done with JMP 3.1 (SAS Institute 1994). Detrended Correspondence Analysis (DCA) and CCA of log-transformed basal area of species were done with CANOCO 4 (ter Braak and Smilauer 1998). The significance of the first CCA axis and all CCA axes combined was determined by Monte Carlo tests using 199 permutations under reduced model (ter Braak and Smilauer 1998). All regressor variables selected in the final models showed variance inflation factors less than five.

6.3 RESULTS

Diversity patterns

A total number of 2670 woody lianas (DBH ≥ 2.5 cm) were found in 77 0.1-ha plots, 2464 of which were identified to species or morpho-species. In total 46 vascular plant families, 126 genera, 263 fully identified species, and 122 morpho-species were encountered. The most speciose families (including identified species and morpho-species) were Leguminosae (48 spp.), Bignoniaceae (44 spp.), Malpighiaceae (31 spp.), Celastraceae (25 spp.), Sapindaceae (23 spp.), Convolvulaceae (22 spp.), Menispermaceae (21 spp.), Dilleniaceae (19 spp.), Connaraceae (17 spp.) and Loganiaceae (15 spp.). The five most frequently recorded species were *Combretum laxum* Jacq. (173 individuals), *Machaerium cuspidatum* Kuhlmann and Hoehne (115 ind.), *Machaerium macrophyllum* Martius ex Benth. (52 ind.), *Paragonia pyramidata* (L.C Richard) Bureau (50 ind.), and *Machaerium floribundum* Benth. (40 ind.). Most species were only found with one (34% of all species), two (17%), or three individuals (8%). A list of fully identified species is in the Appendix 5.

On a cumulative basis, the Ampiyacu plots contained more individuals and liana species than the Yasuní and Metá plots (Figs 6.2a and 6.2b). However, on a species-to-individuals basis the liana diversity in the three areas was fairly similar (Fig. 6.2c). Also the thickness of the lianas differed hardly. In Ampiyacu the average liana DBH was 5.0 cm (standard deviation = 2.5 cm), in Metá 4.5 cm (sd = 2.5 cm), and Yasuní 4.5 cm (sd = 3.0 cm). The thickest liana was found in Metá (a giant *Combretum laurifolium* Mart. of 43 cm DBH). However, thick lianas were scarce. In all areas the great majority (97.5%) of lianas had a DBH ≤ 12 cm. Pooling all plot data by landscape revealed that swamps contained the lowest density and diversity of lianas (Figs 6.2d and 6.2e). The floodplain plots contained more individuals than the Tierra Firme plots (Fig. 6.2d), but a similar number of species (Fig. 6.2e) resulting in lower cumulative estimates of Fisher's alpha (Fig. 6.2f).

In 21 plots (nine in Metá, eight in Yasuní, and four in Ampiyacu, and four in floodplains, 12 in swamps and five in Tierra Firme), liana density remained below the arbitrary threshold of 25 that was used in the subsequent analyses. In the 56 remaining plots, liana density did not respond significantly to landscape, regions, or the interaction of these two factors (Table 6.1). However, landscapes and regions differed significantly in liana diversity. Between regions, the Ampiyacu plots stood out in their high species richness and Fisher's alpha, while plot differences between Metá and Yasuní were small. The interaction effect (landscape x region) on richness and Fisher's alpha was small and not significant.

Multiple regression was applied to examine the effect of a larger set of potential factors on the Fisher's alpha in liana-rich plots. Information of soil analyses and forest structure (Table 6.2) was summarized by PCA. The first soil component (PCAsoil1) was positively associated with concentrations of Ca, Mg, K, Na, and P. For this reason it is referred to hereafter as 'soil fertility factor' (Table 6.3). This factor showed high positive correlations with the cover swamps and floodplains around the plots, as soils tend to be enriched by sediments during flooding (Table 6.4).

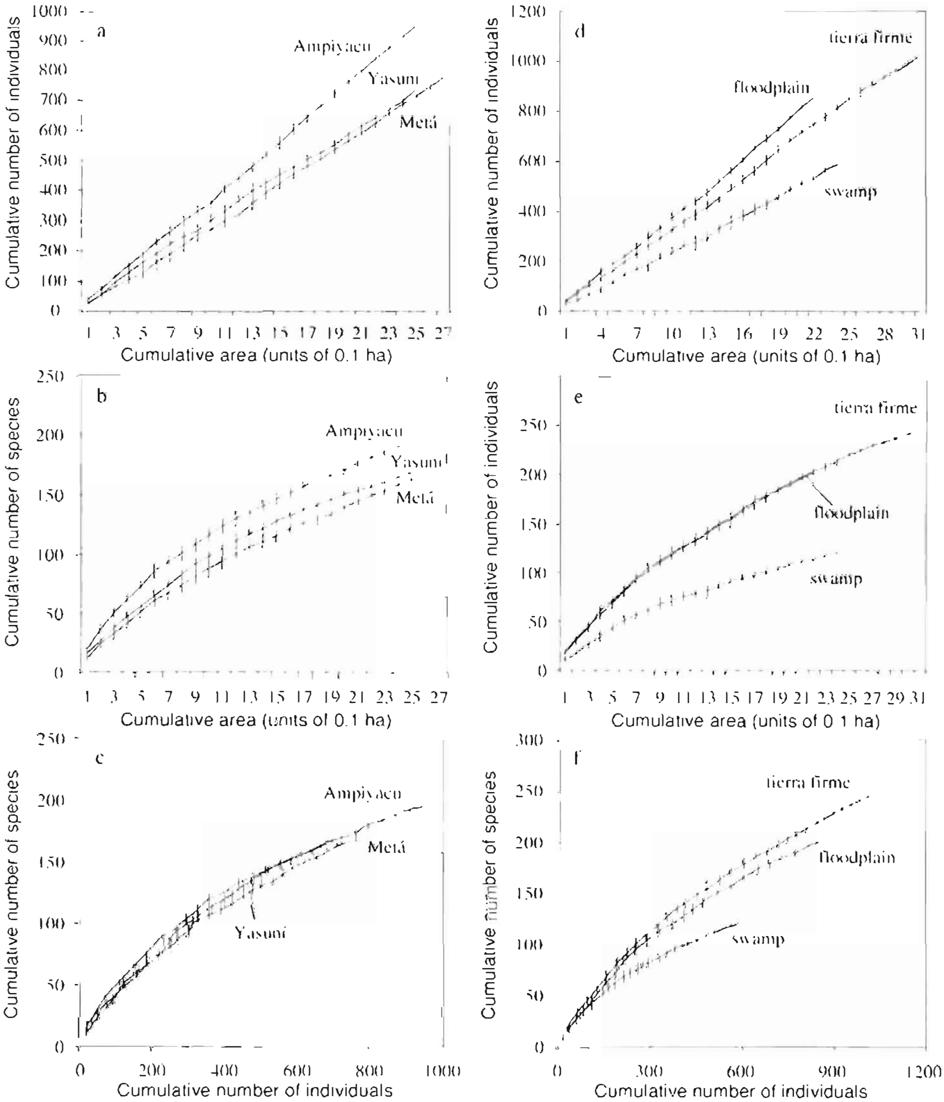


Figure. 6.2 Accumulation curves of liana individuals and species, based on 77 0.1-ha plots where lianas with DBH ≥ 2.5 cm were found. The lines are smoothly drawn through means based on 10 series of randomly ordered plots; vertical bars represent one standard deviation of each mean.

The second soil component (PCAsoil2) explained 28% and was mostly loaded by C and N percentages, separating swamp soils from well drained floodplain and upland soils. Forest physiognomy was included by means of tree density, subdivided into six DBH classes. The first forest component (PCAforest1) mostly ordered plots with high density of slender trees (Table 6.3), and was negatively associated with soil

Table 6.1 Individuals, families, genera, species, and species' Fisher's alpha of woody lianas (DBH ≥ 2.5 cm) in 56 0.1-ha plots containing 25 lianas or more. Legend of two-way ANOVA results: $^{n.s}$ = non significant: * = 0.05 ≤ p < 0.01; ** = 0.01 ≤ p < 0.001, *** = p ≤ 0.001

	plots	Individuals		Families		Genera		Species		Fisher's alpha (species)	
		total	average±sd	total	average±sd	total	average±sd	total	average±sd	total	average±sd
Floodplains	18	848	47.1±19.0	34	12.1±2.7	84	14.9±4.3	186	19.4±7.2	73.6	14.1±10.4
Metá	5	210	42.0±21.4	24	10.8±1.6	41	12.6±3.3	56	15.0±4.9	25.0	9.3±3.8
Yasuní	5	211	42.2±13.2	22	10.6±3.0	40	13.8±3.8	62	16.6±4.8	29.6	10.3±3.5
Ampiyacu	8	427	53.4±20.8	29	13.8±2.4	60	17.1±4.5	112	23.9±7.5	49.4	19.6±13.6
Swamps	12	532	44.3±13.6	26	10.5±2.6	51	12.5±3.3	106	17.6±5.2	39.8	11.5±5.0
Metá	2	63	31.5±0.7	12	8.0±1.4	17	9.5±2.1	22	11.5±2.1	12.0	6.7±2.4
Yasuní	2	57	28.5±0.7	12	8.0±0.0	19	10.5±0.7	21	11.0±0.0	12.0	6.6±0.1
Ampiyacu	8	412	51.5±10.7	22	11.8±2.3	38	13.8±3.2	78	20.8±2.9	28.5	14.0±4.3
Uplands	26	1021	39.3±12.8	41	12.0±2.7	94	15.8±4.3	237	19.9±4.9	96.9	18.8±10.6
Metá	11	426	38.7±13.3	26	10.9±2.7	51	13.7±3.9	103	17.4±4.2	43.2	12.4±2.6
Yasuní	10	428	42.8±12.9	34	13.2±3.0	65	18.6±4.1	118	21.8±5.1	53.8	18.6±4.7
Ampiyacu	5	167	33.4±11.2	22	11.8±1.1	40	14.8±2.0	76	21.8±4.1	53.9	33.2±16.3
All landscapes Metá	18	699	38.8±14.9	34	10.6±2.4	76	12.9±3.7	155	16.1±4.5	61.7	10.9±3.5
All landscapes Yasuní	17	696	40.9±12.6	34	11.8±3.3	77	16.2±4.8	154	19.0±5.9	61.2	14.8±6.3
All landscapes Ampiyacu	21	1006	47.9±16.9	36	12.5±2.2	77	15.3±3.7	183	22.2±5.3	65.5	20.7±13.5
Two-way ANOVA											
Landscape	56		F=1.5$^{n.s}$		F=4.9*		F=5.0*		F=6.7**		F=21.5***
Region	56		F=1.9$^{n.s}$		F=5.6**		F=3.6*		F=13.2***		F=21.9***
Landscape*Region	56		F=2.2$^{n.s}$		F=2.0$^{n.s}$		F=1.5$^{n.s}$		F=1.9$^{n.s}$		F=0.5$^{n.s}$

Table 6.2. Average ± standard deviation of soil chemical variables and landscape cover, in n 0.1-ha plots arranged according to landscape unit and region.

	n	Ca	Mg	K	Na	P	C	N	Floodplains	Swamp	Uplands
		mmol kg^{-1}					%				
Floodplains	18	54.3±65.8	254±101.3	327±104.8	173±128.7	12.6±3.9	0.50±0.20	0.06±0.02	57±28	13±10	30±35
Metá	5	131.9±80.1	320±102.6	374±35.4	290±150.4	12.1±3.6	0.40±0.09	0.05±0.01	68±10	27±2	5±11
Yasuní	5	39.2±18.1	215±31.4	227±26.6	145±29.3	13.9±4.7	0.43±0.15	0.07±0.02	32±26	4±5	64±31
Ampiyacu	8	15.3±21.5	237±117.7	359±124.9	119±114.4	12.0±3.9	0.52±0.26	0.06±0.02	65±28	10±6	25±33
Swamps	12	46.5±31.1	243±114.6	340±164.4	84±73.9	18.7±9.8	8.0±10.3	0.52±0.56	41±26	48±35	11±22
Metá	2	2.9±1.3	95±33.9	213±3.5	34±7.8	13.1±6.9	5.6±5.20	0.88±0.60	41±4	59±4	0±0
Yasuní	2	61.5±24.8	144±129.4	126±93.3	49±41.7	22.5±2.1	18±24.40	0.94±1.20	42±25	6±5	52±30
Ampiyacu	8	53.7±27.7	306±67.3	425±121.3	106±81.9	19.1±11.4	6.2±6.80	0.35±0.31	41±31	55±36	4±8
Uplands	26	8.8±29.7	101±81.8	126±93.4	40±53.4	8.3±5.6	0.47±0.14	0.06±0.02	11±13	4±6	85±16
Metá	11	1.6±0.6	30±22.4	51±42.6	8±7.5	5.1±1.5	0.43±0.12	0.05±0.02	22±12	8±7	70±14
Yasuní	10	19.6±47.4	162±79.9	156±82.0	81±68.2	9.8±2.3	0.47±0.15	0.07±0.02	5±6	1±1	94±6
Ampiyacu	5	2.7±0.8	133±41.4	231±59.5	27±4.0	12.4±11.2	0.57±0.09	0.06±0.01	1±1	0±0	99±2

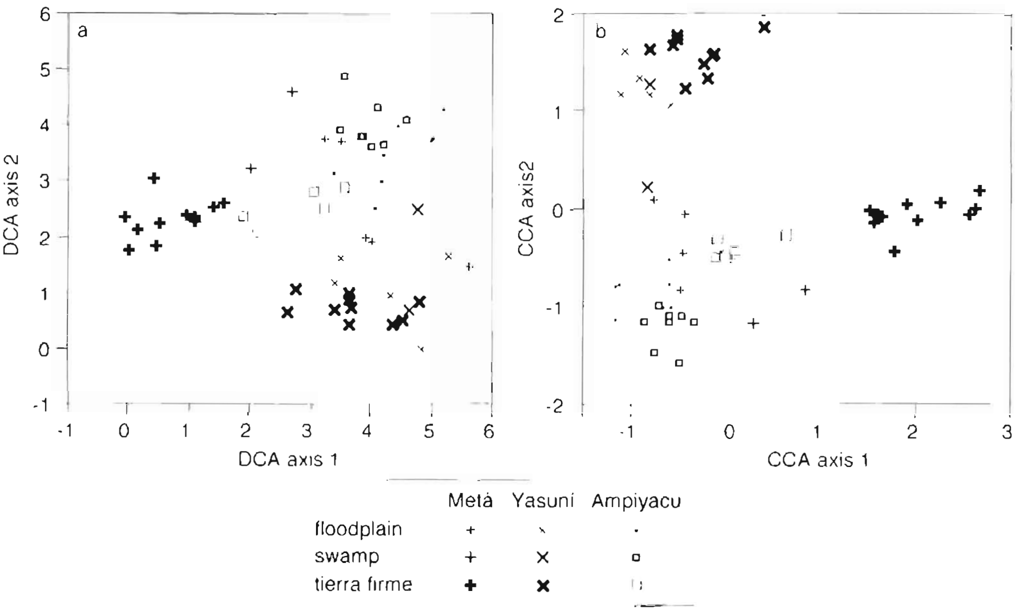


Figure 6.3. Ordination diagrams of DCA (left) and CCA (right) of composition of woody liana species (DBH > 2.5 cm) in 56 0.1-ha plots. In the CCA diagram, plot scores are weighted mean species scores.

nutrient levels (Table 6.4). The second forest component (PCAforest2) was mostly loaded by the number of thick trees in the plots. The PCA thus showed that the plot densities of slender and thick trees were poorly related to each other. In both PCA's, the third and higher axes contributed little to the variation and were not considered for further analyses.

A fair amount (70%) of the variation in Fisher's alpha was explained by the regression model (Table 6.5). Latitude yielded the strongest effect on Fisher's alpha (while keeping constant the other effects), showing that diversity peaked in the Peruvian area in comparison with the Ecuadorean and Colombian sites. Local plot surroundings of floodplains as well as swampy soils (the second PCA axis of the soil data) negatively influenced liana diversity.

Compositional patterns

The first DCA axis (Fig. 6.3a) separated the Metá Tierra Firme plots from the rest, while the second axis mostly separated Yasuní from Ampiyacu. The Metá floodplain plots appeared scattered among the Ampiyacu and Yasuní plots. The eigenvalues of the principal CCA axes (Table 6.6) as well as the main patterns shown in the CCA ordination diagram (Fig. 6.3b) were quite similar to those of the DCA ordination. Liana species patterns were best related to soil fertility, which showed a high canonical coefficient and a high interset correlation coefficient for the first CCA axis (Table 6.7). The Tierra Firme landscape factor also influenced species patterns, as illustrated by the position of the Tierra Firme plots to the right and upper part of the

CCA diagram. The second CCA axis mostly showed influence of longitude, separating upward the Yasuní plots (Table 6.7). The Yasuní plots were also separated due to the high degree of Tierra Firme forests surrounding these plots (Table 6.7 and Table 6.2). The two soil PCA axes retained a significant effect on liana species patterns after cancelling out the effects of all other variables (the eigenvalue of the first CCA axis was 0.40, with a permutation test result P = 0.015 and F-ratio = 1.3, and with canonical coefficients of -1.9 and 0.5 for pca1soil and pca2soil, respectively). Latitude and longitude kept a significant effect on the first CCA axis after accounting for the effect of all other variables (the eigenvalue of this axis was 0.50, with a permutation test result P = 0.005 and F-ratio = 1.6, and with canonical coefficients of -0.2 and -1.2 for latitude and longitude, respectively).

Table 6.3. Loadings of soil and forest structure variables on the principal components in PCA analyses

	soil			forest structure	
	PCA1	PCA2		PCA1	PCA2
percentage explained	57%	28%		45%	20%
soil variables			tree density in DBH class		
Ca	0.41	-0.07	2.5 ≤ DBH < 5 cm	0.49	0.13
Mg	0.45	-0.24	5 ≤ DBH < 10 cm	0.56	-0.11
K	0.42	-0.21	10 ≤ DBH < 20 cm	0.53	0.08
Na	0.42	-0.32	20 ≤ DBH < 40 cm	0.31	0.53
P	0.42	0.20	40 ≤ DBH < 60 cm	-0.16	0.72
C	0.23	0.61	DBH ≥ 60 cm	-0.22	0.41
N	0.22	0.61			

Table 6.5. Effect tests of a multiple regression model of ln-transformed Fisher's alpha values derived from species among liana individuals (DBH ≥ 2.5 cm) in 56 0.1-ha plots against spatial, soil, and forest structure regressors (model F-ratio = 9.5; $p<0.0001$, $r^2 = 0.70$)

	F Ratio	Prob > F
landscape	1.0	0.39
latitude	21.0	<0.0001
longitude	0.7	0.40
floodplain surroundings	10.6	0.002
swamp surroundings	0.0	0.99
Tierra Firme surroundings	0.0	0.97
pca1soil	0.2	0.69
pca2soil	4.2	0.05
pca1structure	0.0	0.87
pca2structure	0.9	0.35

Table 6.4. Pearson correlation coefficient between the quantitative explanatory variables used in multiple regression of liana diversity and CCA analyses of liana species patterns.

	swamp surroundings	Tierra Firme surroundings	PCAsoil1	PCAsoil2	PCAforest1	PCAforest2	latitude	longitude
floodplain surroundings	0.68	-0.60	0.33	-0.02	-0.03	-0.29	-0.08	-0.33
swamp surroundings		-0.81	0.44	0.22	-0.15	-0.21	-0.21	-0.47
Tierra Firme surroundings			-0.57	-0.07	0.17	0.20	0.36	0.44
PCAsoil1				0.00	-0.56	0.03	-0.33	0.14
PCAsoil2					0.13	0.03	-0.03	-0.10
PCAforest1						0.00	0.12	-0.28
PCAforest2							0.06	0.26
latitude								0.51

6.4 DISCUSSION

Liana diversity

In several ways the conclusions from the accumulation curves that were based on all plots differed from the ANOVA comparisons that were based on liana-rich plots. The accumulation curves suggested substantial differences in liana density between regions (highest density in Ampiyacu) and landscapes (lowest densities in swamps). On the basis of the liana-rich plots in the ANOVA, region nor landscape showed a significant effect on density Also the small between-landscape differences in liana species per individual in the accumulation curves contrasted with the strong landscape effect on Fisher's alpha in the liana-rich plots. These discrepancies are due to the unbalanced distribution of the liana-poor plots, which were mostly made in swamps in Metá and Yasuní. The relatively low frequency of liana-poor swamp and floodplain plots in Peru might well be due to the recent cuttings of adult palms of *Mauritia flexuosa* in the floodplain of the Ampiyacu River Opening of the forest canopy often stimulates vigorous liana growth (Putz 1984, Balée and Campbell 1989, Hegarthy and Caballé 1991).

Table 6.6. Summary table of DCA and CCA of 56 0.1-ha plots with species composition of woody lianas (DBH ≥ 2.5 cm) (see also Fig. 6.3).

	axis1	axis2	axis3	axis4	Inertia
DCA					
Eigenvalues	0.70	0.62	0.49	0.39	
Lengths of gradient (sd units)	5.7	5.0	5.0	3.9	
CCA					
Eigenvalues	0.65	0.63	0.45	0.44	
Sum of all canonical eigenvalues					4.3
Sum of all unconstrained eigenvalues					17.6

Inferential statistics to test regional differences in forest diversity may seem useless in view of the fact that any null hypothesis of statistical populations being identical is trivially wrong in living nature (Hurlbert 1984 as summarized by Oksanen 2001). The zero hypothesis of no regional differences does not exist and cannot be tested. However, in this exploratory study the ANOVA's (Table 6.1) do help showing that Ampiyacu, in each of the three landscapes considered in the present study, stood out in liana diversity compared to Yasuní and Metá. This conclusion refers to forest stands with liana densities > 25 /0.1 ha, which comprised 66% of the plots sampled. We speculate that the high liana diversity in Ampiyacu is due to more continued disturbances by fluvial action throughout the Pleistocene and Holocene history favouring maintenance of liana diversity, in combination with a larger and more supply of propagules by river water, compared to areas located more in the upper catchments of the Amazon basin. In view of the comparatively central position of Ampiyacu in the Amazon basin its liana diversity peak might be also seen as a kind of mid-domain effect of Amazonian lianas (Colwell and Lees 2000).

Table 6.7. Canonical coefficients and interset correlation coefficients regarding the first two axes of a CCA of composition of woody lianas (DBH > 2.5 cm) in 56 0.1-ha plots (see also Fig 6.3).

	canonical coefficients		interset correlations	
	axis1	axis2	axis1	axis2
floodplains	-0.28	-0.08	-0.45	-0.14
swamps	-0.06	-0.23	-0.24	-0.47
Tierra Firme	-	-	0.62	0.52
latitude	0.37	0.24	0.36	0.75
longitude	-0.54	0.70	-0 34	0.89
floodplain surroundings	0.02	-0.18	-0.16	-0.49
swamp surroundings	0.09	0.14	-0.15	-0.60
Tierra Firme surroundings	0.16	0.07	0.37	0 63
pca1soil	-0.54	-0.05	-0.85	-0.23
pca2soil	0.10	-0.08	0.21	-0.25
pca1structure	-0.01	0.01	0.52	-0.05
pca2structure	-0.03	-0.07	-0.09	0.23

Soil heterogeneity in northern Peruvian Amazonia (Gentry 1988) cannot explain this peak, as the middle Caquetá area to which the Metá area pertains is characterized by a soil setting that is equally or even more variable (Duivenvoorden and Lips 1995; Lips and Duivenvoorden 1996). Hubbell (1997) warned for over-interpretation of diversity figures from static survey data ('snapshots'), and suggested that between-area differences in diversity might level out to similar (average) figures over a longer period of sampling time. The liana species richness in Tierra Firme forests in Yasuní (21.8 ± 5.1 species/0.1 ha; see Table 6.1), was quite similar that of 20.5 ± 6.2 species/0.1 ha in reported by Nabe-Nielsen (2001) for that area. The species richness in Metá floodplains (15.0 ± 4.9 species/0.1 ha) and Tierra Firme forests (17.4 ± 4.2 species/0.1 ha; Table 6.1) was well above the values of 8.5 ± 2.1 species/0.1 ha and 11.5 ± 6.0 species/0.1 ha for these two forest types respectively, as reported by Duivenvoorden (1994) for the area near Araracuara. Gentry (1991a) reported values of 42 and 50 liana species/0.1 ha, which are above the maximum species richness of 38 species/0.1 ha found in Ampiyacu in the present study.

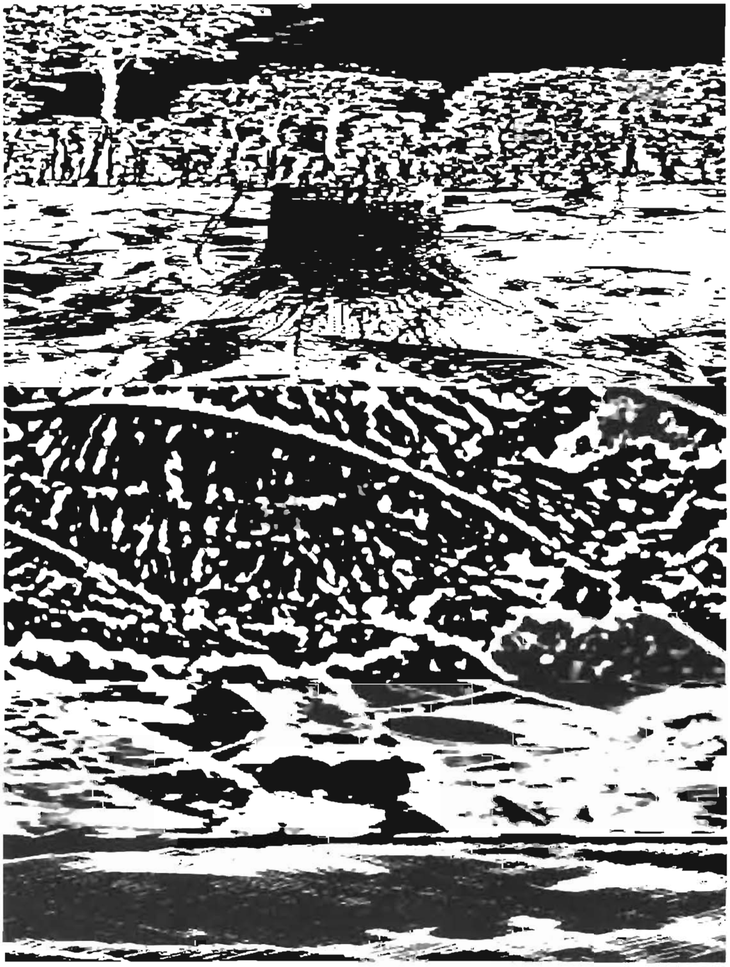
The ANOVA and multiple regression analysis also pointed out that liana diversity was consistently lower in floodplains and swamps that in Tierra Firme forests. The lack of interaction in the ANOVA indicated that these effects were similar in all three areas. A negative association between Amazonian plant diversity and flooding and water logging has been found in several other studies (Duivenvoorden and Lips 1995). Forest in floodplains and swamps may be rather young, and time may have been insufficient for liana species to immigrate, also in view of the limited size of these forests compared to well drained upland areas in NW Amazonia. In addition, less species may have adapted to the physiologically hostile root environment in water logged soils, and to the high and unpredictable rate of disturbance by flooding.

Despite the strong differences in soil fertility between Yasuní and Metá (Table 6.2), the average plot density and diversity of lianas did not differ substantially between these areas. The lack of difference in liana diversity between these two areas lead to the insignificant role of the soil fertility factor in the multiple regression of Fisher's alpha. Our results, therefore, do not support the notion that soil fertility is relevant for liana abundance (Ibarra-Manríquez and Martínez-Ramos 2002), as has been suggested in earlier studies (Putz and Chai 1987, Gentry 1991a). In this way, lianas respond differently to soil fertility than trees (DBH ≥ 2.5 cm) in the three study sites. Duivenvoorden *et al.* (in press) reported significant higher thin tree densities in Metá compared to both Ampiyacu and Yasuní, and suggested that this might be due to increased longevity and better defense mechanisms against herbivory on less fertile soils in Metá. The falling down of host trees or lianas because of the liana weight, clonal reproduction and effective dispersal by wind might provide means by which lianas successfully establish and maintain levels of stem densities in a way that is independent from soil fertility.

Liana species patterns

Soil fertility was the most important factor in the canonical analysis of liana species patterns and explained the distinct composition of the Tierra Firme plots of Metá compared to the forest in other landscapes and areas. Soils in the Metá Tierra Firme plots showed distinctively lower reserves of cations and P, than soils from the other two areas. Lips and Duivenvoorden (1996) suggested that the low levels of the soil nutrient reserves in uplands from the middle Caquetá area were due to the highly weathered status of the soil parent material that originated from the Guayana shield area (Hoorn 1994). In the middle Caquetá basin, just as part of the Rio Negro basin of Venezuela and in well-drained upland forests of lowland Borneo (Ashton 1989, see also Potts *et al.* 2002), soils with such low nutrient reserve levels are covered by thick and acid humus profiles. These are probably a result of lower litter decomposition (Lips and Duivenvoorden 1996), and more closed nutrient cycling (Baillie 1989, Burnham 1989) and associated mechanisms of nutrient conservation (Jordan 1985) compared to forests on more nutrient rich soils. In the wide spatial context and the geologically long time during which these soil differences have occurred in the Amazon basin, it is conceivable that liana species have adapted differentially to such soil differences.

The second important factor explaining liana species patterns was longitude or proximity to the Andes, mostly separating Yasuní from the other two areas. This longitudinal factor is poorly correlated to soil fertility (Table 6.4) due to the comparatively high soil mineral concentrations in Ampiyacu (Table 6.2). This result shows that generalizations of increased soil fertility in the vicinity of the footslope zone of the Andes compared to more eastern areas in the Amazon basin are not permitted. Gentry (1986, 1990) reported migration of Andean floral elements into wet lowland forests of Chocó and Central America. Perhaps the distinct assemblage of lianas in Yasuní compared to Ampiyacu and Metá is due to a relatively high and recent influx from Andean liana taxa from the nearby Andes.



Chapter 7

RESPONSE SHAPE OF PLANT GENERA AND SPECIES ALONG GRADIENTS IN NW AMAZONIA

Alvaro J. Duque M., Joost F Duivenvoorden, Jaime Cavelier, Alberto García, César Grández, Manuel Macía, Hugo Romero-Saltos, Mauricio Sánchez and Renato Valencia
Submitted to *Journal of Vegetation Science*

7.1 INTRODUCTION

A commonly accepted idea in plant ecology is that species responses to environmental gradients have a Gaussian shape with the optimum located at a particular point along an environmental gradient (Gauch and Withaker 1972). A symmetrical unimodal response shape has been the only ecological model for which parameters can be well estimated (ter Braak and Looman 1986). A basic assumption in Niche theory is that both fundamental and realized niches have symmetrical Gaussian curves (Austin 1999). However, the use of such a symmetrical response model as a paradigm in ecological modelling has been strongly criticized (Austin and Meyers 1996, Austin 2002). The continuum concept, which maintains that species response curves have different shape, amplitudes, widths and optima along environmental gradients (Austin 1985), has gained support in recent years. Biological interactions and factors such as dispersal, competition, succession, disturbance and pest pressure could modify the species response into non-Gaussian shapes along these gradients (Austin *et al.* 1990, Guisan and Zimmermann 2000). Indeed, biotic processes are rarely considered in statistical models of species distributions and need further attention (Condit 1996, Austin 2002).

Although several ways of testing skewedness and analyzing the response shapes of species along gradients have been employed, few methods provide sufficiently accurate results (Oksanen and Minchin 2002). Some of the most common problems (Oksanen and Minchin 2002) are unrealistic shapes of polynomial functions (Austin *et al.* 1990), bias and subjective judgment in methods that are based on visual analysis (Okland 1986) and in smooth generalized additive models (GAM, Hastie and Tibshirani 1990), as well as confusion in the location of the maximum in beta functions (Austin *et al.* 1994, Oksanen 1997). However, a set of five hierarchical models, which range from flat to skewed and include symmetrical responses as proposed by Huisman *et al.* (1993), appear to give more success in solving parametric questions of response shapes (Oksanen and Minchin 2002). This set of equations could be applied to different environmental gradients as long as the models are only used for descriptive purposes (Huisman *et al.* 1993).

Species are the most common hierarchical taxonomic unit employed to analyze response shapes (Minchin 1989, Austin and Meyers 1996, Lawesson and Oksanen 2002). Individual species analyses might help to understand plant community structure, and so, how to find mechanistic explanations for existing patterns (Minchin 1989). In NW Amazonia still only a few studies have focused on the behaviour of individual species along environmental gradients (*i.e.* Duivenvoorden and Lips 1995, Svenning and Balslev 1997, Svenning 1999, Tuomisto *et al.* 1998, Phillips *et al.* 2003). In ecological inventories, a high proportion of species occurs with very few individuals (Pitman et al 1999), which appears as a constraint to get data sets of sufficient size to analyze species response curves. Therefore, a higher taxa as genus provides a good alternative to overcome the sample error in tropical inventories. Genera-based analyses, might help to understand better the role of environment-vegetation interactions at wider temporal and spatial scales, such as those included in paleoecological studies (Hooghiemstra and van der Hammen 2000, Colinvaux 1987).

The goal of this study is to analyze the distribution and response curves of selected genera and species along abstract complex ecological gradients in NW Amazonia forests. The following hypotheses are considered: (1) Genera and species respond to complex environmental gradients, such as those derived from ordination analysis, with a symmetrical Gaussian function; (2) The response shape of individual species and genera along a soil gradient is similar to that found along a complex gradient that is constructed by ordination of complete inventory data of species or genera. If the first hypothesis is accepted, niche-preemptioning prevails and may be accepted as the dominant model for woody species in NW Amazonia; if not, continuum model is accepted as the most suitable one. If the second hypothesis is accepted, soil fertility should be employed to predict species distribution along more complex environmental gradients in NW Amazonia; if not, that would indicate the importance of other factors like biotic ones.

7.2 METHODS

Study site and sample design

The study was carried out in three different areas in north-western Amazonia: (1) the Metá area, which forms part of the middle Caquetá basin in Colombian Amazonia; (2) the Yasuní area in Amazonian Ecuador; and (3) the Ampiyacu area pertaining to the Maynas Province in Peruvian Amazonia (Figure 6.1). All areas are in the Humid Tropical Forest life zone (bh-T) according to Holdridge *et al.* (1971). The average temperature is near 25°C, and annual precipitation oscillates around 3000 mm. All months show an average precipitation above 100 mm. In Metá and Yasuní the lowest rainfall is in January and February, whereas in Ampiyacu this occurs in August and September (Lips and Duivenvoorden 2001).

A total of 80 0.1-ha plots were established; 30 in Metá and 25 in both Yasuní and Ampiyacu. Plots were located and distributed across the main landscape units as follows: 31 in Tierra Firme or well drained upland areas (15 in Metá, 10 in Yasuní, and 6 in Ampiyacu); 22 in well drained floodplains (5 in Metá, 8 in Yasuní, and 9 in Ampiyacu); 22 in swamps (5 in Metá, 7 in Yasuní, and 10 in Ampiyacu) and 5 in white sands (only sampled in Metá). A detailed description of each of these landscape units can be found in Lips and Duivenvoorden (2001). In order to establish the plots, starting locations and the direction of the tracks by which the forests were entered were determined on the basis of the interpretation of aerial photographs (Duivenvoorden 2001) and satellite images of Landsat TM (Tuomisto and Ruokolainen 2001). During the walk through the forests, soils and terrain units were rapidly assessed, and forests were visually examined. In this way, sites with homogeneous soils and physiognomically uniform forest stands were identified. In these sites, rectangular plots (mostly 20 x 50 m) were delimited by compass, tape and stakes, working from a random starting point, with the restriction that the long side of the plot was parallel to the contour line. Plots were located without bias with respect to floristic composition or forest structure (including aspects of tree density, thickness and height, and presence of lianas). They were made in forest that lacked signs of human intervention. The only exceptions to this were some of the swamp plots in the floodplain of the Ampiyacu River in Peru, where palms had recently been cut to harvest fruits from Mauritia flexuosa. Plots were established at a minimum between-plot distance of 500 m and were mapped with GPS. Plots were subdivided into subplots of 10x10 m, in which all vascular plant individuals with DBH≥2.5 cm were numbered and measured with tape. Fieldwork took place in 1997 and 1998.

Botanical collections were made of all species (DBH≥2.5 cm) found in each plot. Identification took place at the herbaria COAH, QCA, QCNE, AMAZ, USM, MO, NY and AAU (Holmgren *et al.* 1990). The nomenclature of families and genera followed Mabberley (1989). Within families, or groups of closely allied families, specimens that could not be identified as a species because of a lack of sufficient diagnostic characteristics were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens. Hereafter the term 'species' refers to both morpho-species and botanical species.

In the central part of each plot, a soil augering was carried out to 120 cm depth in order to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions, and texture) and to define soil drainage (in classes of FAO 1977). At each augering a soil sample was taken at a depth of 65-75 cm. For analyses, soil samples were dried at temperatures below 40°C, crumbled and passed through a 2-mm sieve. The total content of Ca, Mg, K, Na, and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H_2SO_4 (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser. Soil analyses were done at the soil laboratory of Institute for Biodiversity and Ecosystem Dynamics of the Universiteit van Amsterdam.

Data analysis

Three standardized gradients or coenoclines (Lawesson and Oksanen 2002) were employed in analysis of the response shapes of genera and species. (1) The first axis from a detrended correspondence analysis (DCA) based on presence-absence of all species (2157). (2) The first axis from a detrended correspondence analysis (DCA) based on presence-absence of all genera (527). Both these gradients represent a complex environmental and spatial gradient determining the distribution of either genera or species. (3) The first axis from a principal component analysis (PCA) of soil elemental concentrations (Table 7.1). DCA was performed with CANOCO 4.0 (ter Braak and Šmilauer 1998) using default options (Lawesson and Oksanen 2002). PCA was carried out by means of JMP 3.0, based on the correlation matrix of logarithmically transformed variables. All analyses were done on the basis of the data from 80 plots made in all landscapes and 31 plots made in Tierra Firme forests.

Response models

Following the criteria of minimum frequency proposed by Oksanen and Minchin (2002), in all landscape units, 89 genera and 24 species that were present in 25 or more plots were selected for the analyses. In only Tierra Firme, 41 genera and 8 species that were present in 20 or more plots, were employed in the analyses. For description of genera and species response shapes the hierarchic models proposed by Huisman *et al.* (1993) were employed by using the HOF program which maximizes a log-likelihood function instead of minimizing the squared residuals, and by considering presence-absence data or binomial with denominator m = 1 (Oksanen