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A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia

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Abstract. Epiphytism in Colombian Amazonia was described by counting vascular epiphytes in thirty 0.025-ha (5 × 50 m) plots, well-distributed over the main landscape units in the middle Caquetá area of Colombian Amazonia. Each plot was directly adjacent to a 0.1-ha plot at which the species composition of trees and lianas (diameter at breast height (DBH) ≥ 2.5 cm) had been recorded 3 years earlier. The purpose of the study was to explore abundance, diversity, and distribution of epiphytes between the principal landscape units. A total of 6129 individual vascular epiphytes were recorded belonging to 27 families, 73 genera, and 213 species (which included 59 morpho-species). Araceae, Orchidaceae, and Bromeliaceae were the most speciose and abundant families. A total of 2763 phorophytes were registered, 1701 (62%) of which with DBH ≥ 2.5 cm. About 40–60% of the woody plants with DBH ≥ 2.5 cm carried epiphytes, which points at low phorophyte limitation throughout all landscapes. Epiphytism was concentrated on stem bases. Just as trees, epiphyte species assemblages were well associated with the main landscapes. Contrary to trees, however, epiphyte abundance and diversity (species richness, Fisher's alpha index) hardly differed between the landscapes. This calls for caution when explanations for distribution and dynamics of tree species are extrapolated to growth forms with a totally different ecology.

Introduction

Northwestern Amazonia has been recognized as a region with high tree diversity (Valencia et al. 1994), but also where the epiphyte communities exhibit high abundance and diversity (Gentry and Dodson 1987b; Nieder et al. 2001). In the past decades, most studies carried out on vascular plants have focused on the tree component, despite the fact that the non-tree vegetation is responsible for a high percentage of the total diversity in the tropical forests (Gentry and Dodson 1987a; Galeano et al. 1998; Schnitzer and Carson 2000).

Epiphytes are plants that inhabit a discontinuous and three-dimensional landscape, directly in contact with the forest soil or not (Bennett 1986). Patterns of distribution and floristic composition of epiphytic plants have been related to factors of dispersal (Benzing 1986; Wolf 1993), humidity and soils

(Gentry and Dodson 1987b; Leimbeck and Balslev 2001), and variability of structure, superficial area and inclination and size of branches of host trees (phorophytes) (Nieder et al. 1999; Freiberg 1996, 2001). Recently, in nearby rain forests of the Yasuní area, Leimbeck and Balslev (2001) reported substantial differences in aroid epiphytism between floodplains of the Tiputini river and surrounding uplands, suggesting a strong role of phorophyte limitation in floodplain forests.

Here we make the first attempt to quantitatively describe vascular epiphytism in Colombian Amazonia. We counted vascular epiphytes in thirty 0.025-ha plots, well-distributed over the main landscape units in a part of the basin of the middle Caquetá river (Figure 1). Each plot was directly adjacent to a 0.1-ha plot at which the species composition of trees and lianas (diameter at breast

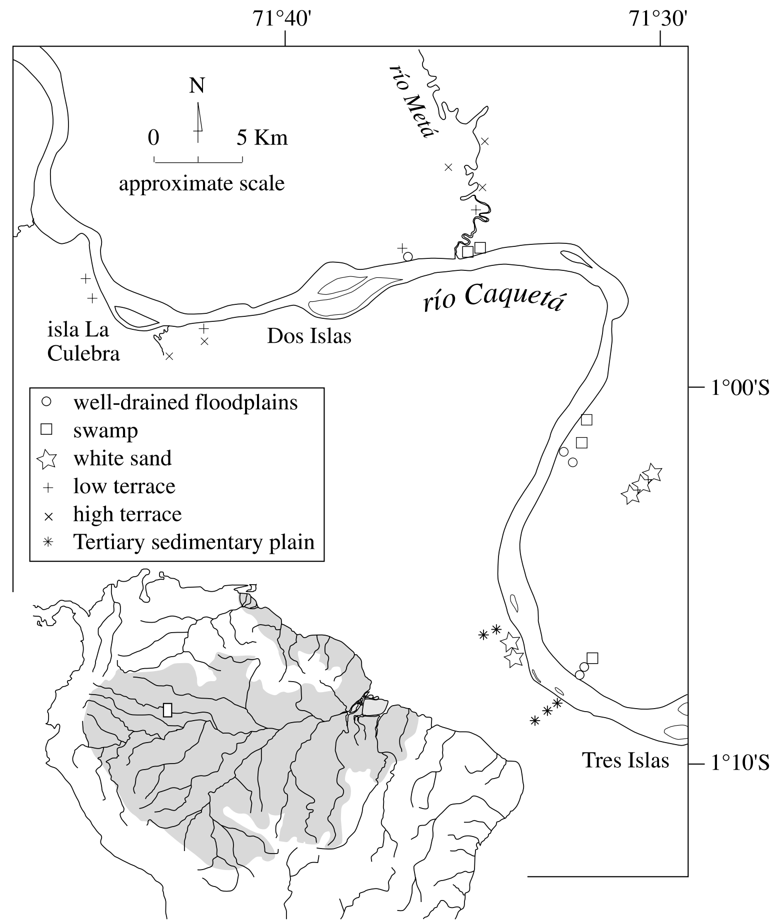

Figure 1. Location of the Metá area in Colombian Amazonia.

height (DBH) ≥ 2.5 cm) had been recorded 3 years earlier (Duque et al. 2001). The purpose of this paper is to present these species data, while focusing on the question whether or not there existed any difference in abundance, diversity, or distribution of epiphytes between the principal landscape units in the Metá area.

Study site

The study area comprised about 1000 km^2 and was situated along the middle stretch of the Caquetá River in Colombian Amazonia near the mouth of the Metá river, roughly between 1°–2° S and 70°–73° W (Figure 1). The principal landscape units found here were well-drained floodplains, swampy areas (including permanently inundated back swamps and basins in floodplains), 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 well-drained uplands or terra firme (never flooded by river water and including low and high fluvial terraces of the Caquetá river and a Tertiary sedimentary plain) (Duivenvoorden and Lips 1993; Lips and Duivenvoorden 2001). Soils were called well-drained when they showed a FAO drainage class of 2 or higher, and poorly drained when this class was below 2 (FAO 1977). The height of the studied forests varied between 10–15 m (white-sand areas), 15–25 m (well-drained floodplains and swamps), and 25–35 m (terra firme). Extensive forest structural information is given in Duque et al. (2001). The area received a mean annual precipitation of about 3060 mm (1979–1990) with a mean monthly rainfall always above 100 mm (Duivenvoorden and Lips 1993). Mean annual temperature was 25.7 °C (1980–1989) (Duivenvoorden and Lips 1993).

Methods

Rectangular plots of 5 × 50 m were established directly contiguous to the long side of previously established 20 × 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 (Figure 1). Plots were mapped with GPS. In 1997 and 1998, the density and species composition of lianas and trees with DBH ≥ 2.5 cm were recorded in these 0.1-ha plots (Duque et al. 2001, 2002). During a new fieldwork from March to June 2000, the adjacent 0.025-ha plots were censused for epiphytism.

The 5 × 50 m plots were subdivided into subplots of 5 × 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 m length. For trees, we calculated the conical superficial area of the phorophyte stems as 3.14 × 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). Only those epiphyte individuals that were in contact with the forest soil were recorded as hemi-epiphyte. All other epiphyte individuals were recorded as holo-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 Smilauer 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 10,000 permutations.

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 and Figure 2a). 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 2b). 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.

A total number of 2763 phorophytes were registered, 1701 (62%) of which with DBH $\geq$ 2.5 cm. On average, one phorophyte carried 2.2 (standard deviation = 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 $\geq$ 2.5 cm carried epiphytes, and about 50–85% in case of DBH $\geq$ 5 cm (Table 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 2). Stem bases also carried the highest number of epiphyte species, but differences with the upper parts of the phorophytes were less

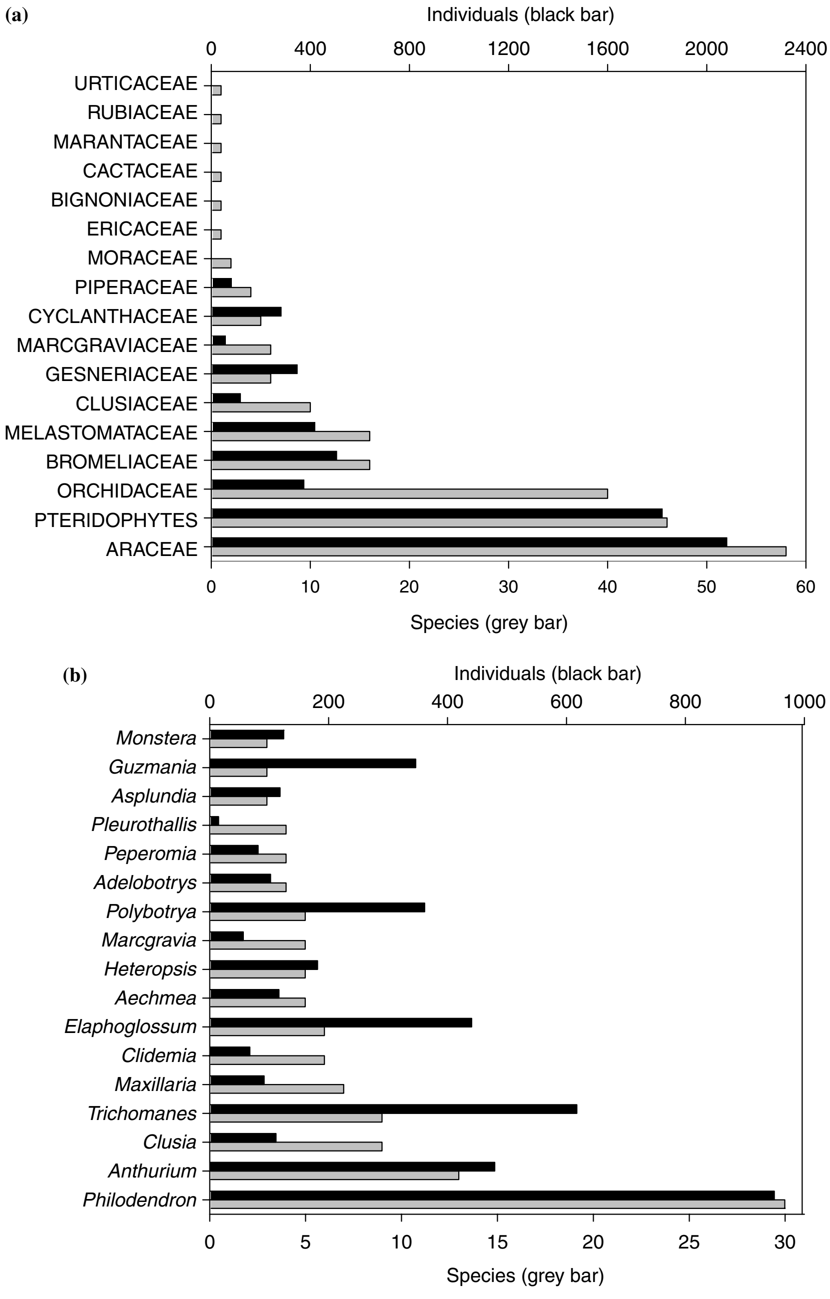

Figure 2. Number of epiphytic species and individuals belonging to the most speciose families and genera in 30 well-distributed 0.025-ha plots, in the principal landscape units of the Metá area in Colombian Amazonia. (a) Species richness and abundance of the most speciose epiphytic families. (b) Species richness and abundance of the most speciose epiphytic genera.

Table 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.

	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

Shown are averages ± one standard deviation. The numbers 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.

Table 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.

	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

Shown are averages ± one standard deviation.

pronounced (Table 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 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, Figure 3a, 3b). According to the Mantel test, the epiphytic floristic composition varied independently of the distance between the plots (Table 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 5).

Table 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.

	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

Also shown are the number and the superficial area of the phorophytes in these plots. Figures represent averages $\pm$ 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.

Table 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	

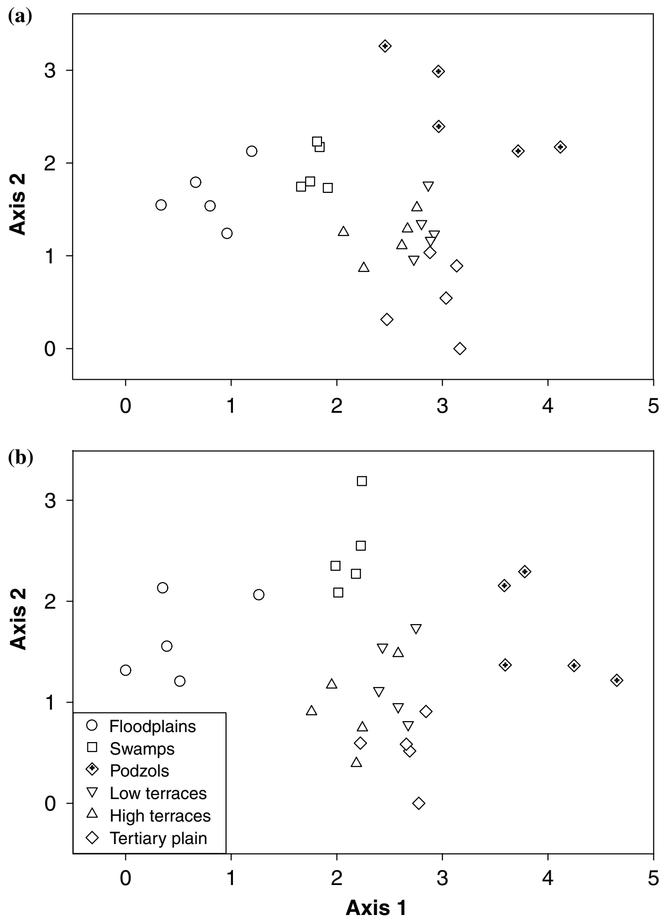

Figure 3. Detrended Correspondence Analysis of vascular epiphytes in the Metá area of Colombian Amazonia. (a) Based on the presence–absence of epiphyte species. (b) Based on the abundance (number of individuals) of epiphyte species.

Table 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.

		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

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.

Discussion

The 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 $\geq$ 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 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 1987a, b).

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 terra 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 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.

About 4–6 out of every 10 woody plants (DBH $\geq$ 2.5 cm) and 5–8 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 terra firme units this average number ranged between 14/0.025 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).

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. Second, 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 (Figure 3a, b and Table 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 autobiology 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.

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Appendix 1

Species found in 30 widely distributed 0.025-ha plots in the Metá area of Colombian Amazonia. Voucher codes are added between parentheses. Also, for each species, the number of plant individuals per habit is given, as well as the main landscape units where the species were recorded. Habit codes: Ep, Holo-epiphyte; He, Hemi-epiphyte. Landscape codes: TF, Terra firme; FP, Flood plains; Sw, Swamps; PZ, Podzol. *Species only found in one plot.

	Ep	He	Landscape
Angiosperms			
ARACEAE			
Anthurium acrobates Sodiro (AMB 821)	1		TF*
Anthurium atropurpureum Schult. and Maguire (AMB 429)	53	5	TF, SW, PZ
Anthurium clavigerum Poepp. (AMB 177)	1	1	FP*
Anthurium eminens Schott (AMB 142)	10	2	TF, SW, FP
Anthurium ernestii Engl. (AMB 621)	202	15	TF, SW, FP, PZ
Anthurium galactospadix Croat (AMB 245)	6		FP*
Anthurium gracile (Rudge) Schott (AMB 120)	51	4	TF, SW, FP
Anthurium obtusum (Engl.) Grayum (AMB 148)	17	1	TF, SW, FP, PZ
Anthurium pentaphyllum (Aubl.) G. Don (AMB 308)	13	29	TF, FP
Anthurium polydactylum Madison (AMB 141)	2	1	TF, SW
Anthurium sinuatum Benth. ex Schott (AMB 111)	5	24	TF, SW
Anthurium sp. 2 (AMB 175)	21	1	FP, PZ
Anthurium uleanum Engl. (AMB 642)	9	6	FP*
Heteropsis flexuosa (Kunth) Bunting (AMB 208)		58	TF, SW, FP
Heteropsis spruceana Schott (AMB 741)		62	TF, SW, FP
Heteropsis steyermarkii Bunting (AMB 306)	2	49	TF, SW, PZ
Heteropsis sp. 1 (AMB 1173)		2	TF*

Appendix 1. (Continued)

	Ep	He	Landscape
Heteropsis sp. 3 (AMB 803)		9	TF*
Monstera gracilis Engl. (AMB 808)		6	TF*
Monstera obliqua Miq. (AMB 770)		70	TF, SW, FP
Monstera spruceana (Schott) Engl. (AMB 342)	1	49	TF
Philodendron acutatum Schott (AMB 315)	7	7	TF, FP
Philodendron applanatum G.M. Barroso (AMB 597)	23	14	TF, SW, FP, PZ
Philodendron asplundii Croat and Soares (AMB 868)	4	4	TF, SW, PZ
Philodendron barrosoanum G.S. Bunting (AMB 339)	6	9	TF, FP
Philodendron buntingianum Croat (AMB 364)	8	13	TF
Philodendron chinchamayense Engl. (AMB 764)		36	TF, SW, FP
Philodendron elaphoglossoides Schott (AMB 583)	1		SW*
Philodendron fragantissimum Kunth (AMB 196)	35	119	TF, SW, FP, PZ
Philodendron guttiferum Kunth (AMB 215)	8	49	TF, FP
Philodendron hederaceum (Jacq.) Schott (AMB 545)	1	30	SW, FP
Philodendron herthae K. Krause (AMB 549)	7	16	TF, SW, FP, PZ
Philodendron holtonianum Schott (AMB 768)		1	FP*
Philodendron hylaeae Bunting (AMB 122)	17	1	TF, SW, PZ
Philodendron insigne Schott (AMB 358)	6	39	TF
Philodendron linnaei Kunth (AMB 121)	184	20	TF, SW, FP, PZ
Philodendron megalophyllum Schott (AMB 99)	56	10	TF, SW, FP, PZ
Philodendron melinonii Brongn. ex Regel (AMB909)	1	4	TF
Philodendron panduriforme (Kunth) Kunth (AMB 1145)		1	TF*
Philodendron pteropus Mart. ex Schott (AMB 173)	7	64	TF, SW, FP
Philodendron pulchrum Barroso (AMB 430)	14	4	TF, SW, PZ
Philodendron tripartitum (Jacq.) Schott (AMB 264)	15	18	TF, SW, FP
Philodendron venustum Bunting (AMB 489)	7	5	TF, SW, PZ
Philodendron sp. 1 (AVG 201)	1		SW*
Philodendron sp. 2 (AMB 785)	8	1	TF, PZ
Philodendron sp. 3 (AMB 851)	6	11	TF, SW, FP
Philodendron sp. 4 (AMB 816	3		TF*
Philodendron sp. 10 (AMB 1203)	1	4	TF
Philodendron sp. 11 (AMB 817)	2	23	TF
Philodendron sp. 12 (AMB 653)		11	TF
Philodendron sp. 13 (AMB 178	6	2	SW, FP
Rhodospatha venosa Gleason (AMB 805)	6	4	TF
Rhodospatha sp. 3 (AMB 739)	197	98	TF, SW, PZ
Stenospermation amomifolium Schott (AMB486)	14		TF, SW, PZ
Stenospermation sp. 1 (AMB 1247)	2		FP, PZ
Syngonium podophyllum Schott (AMB 270)	2	20	FP
BIGNONIACEAE			
Schlegelia sp. 1 (AMB 1201)		1	TF*
BROMELIACEAE			
Aechmea contracta (Mart. ex Schult.f.) Mez (AMB 252)	40		TF, SW, FP, PZ
Aechmea corymbosa (Mart. ex Schult. and Schult. f.) Mez (AMB 135)	15		TF, FP, PZ
Aechmea nivea L.B. Sm. (AMB 368)	41		TF, SW, FP, PZ
Aechmea tillandsioides (Mart. ex Schult. and Schult. f.) Baker (AMB 318)	19		TF, SW, PZ

Appendix 1. (Continued)

	Ep	He	Landscape
Aechmea sp. 1 (AMB 382)	2		TF, PZ
Brocchinia cf. *paniculata* Schult. f. (AMB 416)	3		TF*
Guzmania brasiliensis Ule (AMB 340)	50		TF, PZ
Guzmania lingulata (L.) Mez (AMB 428)	283		TF, SW, FP
Guzmania vittata (Mart. ex Schult. f.) Mez (AMB 877)	14		TF, SW
Neoregelia stolonifera L.B. Sm. (AMB 732)	1		SW*
Neoregelia sp. 1 (AMB 492)	2		PZ*
Pepinia sprucei (Baker) Varad. and Gilmartin (AMB 171)	11		TF, FP
Pepinia uaupensis (Baker) Varad. and Gilmartin (AMB 363)	5		TF, SW, PZ
Streptocalyx colombianus L.B. Sm. (AMB 303)	5		TF*
Streptocalyx poeppigii Beer (AMB 199)	15		TF, SW, FP
Tillandsia paraensis Mez (AMB 1076)	1		TF*
CACTACEAE			
Disocactus amazonicus (K. Schum.) D.R. Hunt (AMB 1199)	1		TF*
CLUSIACEAE			
Clusia cf . *amazonica* Planch. and Triana (AMB 490)	8		TF, SW, PZ
Clusia caudata (Planch. and Triana) Pipoly (AMB 1073)	1		TF*
Clusia flavida (Benth.) Pipoly (AMB 423)	27		TF, SW, PZ
Clusia grandiflora Splitg. (AMB 892)	6	1	TF*
Clusia hammeliana Pipoly (AMB 898)	4	1	TF
Clusia sp. 1 (AVG 374)	21	5	TF
Clusia sp. 2 (AVG 329)	17	1	TF
Clusia sp. 3 (AMB 624)	17		TF, FP, PZ
Clusia sp. 5 (AMB 152)	2	1	SW*
Clusiaceae sp. 1 (AMB 850)	7		SW*
CYCLANTHACEAE			
Asplundia vaupesiana Harling (AMB 292)	21	67	TF
Asplundia xiphophylla Harling (AMB 436)	7	24	TF, SW, FP, PZ
Evodianthus funifer (Poit.) Lindm. (AMB 123)	19	35	TF, SW, PZ
Ludovia lancifolia Brongn. (AMB 709)	28	6	TF, FP
Ludovia sp. 1 (AMB 885)	73	4	TF, PZ
ERICACEAE			
Psammisia sp. 1 (AMB 443)	11		TF, PZ
Satyria cf . *panurensis* (Benth. ex Meisn.) Benth. and Hook. f. ex Nied. (AMB 1097)	1		TF*
GESNERIACEAE			
Alloplectus sp.1 (AMB 457)	4	6	PZ*
Codonanthe calcarata (Miq.) Hanst (AMB 427)	90		TF, PZ
Codonanthe crassifolia (H. Focke) C.V. Morton (AMB 158)	175		TF, SW, FP, PZ
Codonanthopsis dissimulata (H.E. Moore) Wiehler (AMB 185)	20		TF, SW, FP
Paradrymonia ciliosa (Mart.) Wiehler (AMB 194)	36	16	TF, FP, PZ

Appendix 1. (Continued)

	Ep	He	Landscape
Gesneriaceae sp. 1 (AMB 160)	1		SW*
MARANTACEAE			
Monotagma laxum (Poepp. and Endl.) Schum. (AMB 304)	1		TF*
MARCGRAVIACEAE			
Marcgravia cf. *strenua* J.F. Macbr. (AMB 581)	8	13	TF, SW, PZ
Marcgravia sp. 1 (AVG 200)	1	6	TF, SW, FP
Marcgravia sp. 2 (AMB 1209)		1	TF*
Marcgravia sp. 3 (AVG 219)		5	TF
Marcgravia sp. 4 (AMB 184)	12	11	TF, FP, PZ
Marcgraviastrum sp. 1 (AMB 999)	1		TF*
MELASTOMATACEAE			
Adelobotrys linearifolia Uribe (AMB 738)	1	46	TF, SW
Adelobotrys marginata Brade (AMB 321)	1	39	TF
Adelobotrys praetexta Pilg. (AMB 902)		9	TF
Adelobotrys spruceana Cogn. (AMB 134)	4	2	SW, FP
Clidemia alternifolia Wurdack (AMB 1152)		2	TF
Clidemia epibaterium DC. (AMB 137)	2	17	TF, SW, PZ
Clidemia sp. 1 (AMB 1196)	1	2	TF
Clidemia sp. 2 (AMB 1061)		1	TF*
Clidemia sp. 3 (AMB 105)	2		SW*
Clidemia sp. 4 (AMB 917)	7	34	TF, PZ
Leandra candelabrum (J.F. Macbr.) Wurdack (AMB 341)		153	TF
Leandra sp. 1 (AMB 165)	1	2	SW*
Tococa lancifolia Spruce ex Triana (AMB 136)		1	SW*
Tococa cf . *ulei* Pilg. (AMB 1148)	1		TF*
Tococa sp. 1 (AMB 1127)	1		TF*
Melastomataceae sp. 2 (AMB 1115)		89	TF*
MORACEAE			
Ficus paraensis (Miq.) Miq. (AMB 1195)	1		TF*
Ficus sp. 1 (AMB 163)	1		TF*
ORCHIDACEAE			
*Adipe longicornis (*Lindl.) M. Wolfe (AMB 316)	4		TF, PZ
Braemia vittata (Lindl.) Jenny (AMB 110)	23	2	TF, SW, FP
Campylocentrum poeppigii (Rchb. f.) Rolfe (AMB 484)	4		FP*
Catacetum sp. 1 (AVG 288)	10		SW, FP
Dichaea hookeri Garay and Sweet (AMB 613)	9		SW
Dichaea rendlei Gleason (AMB 1092)	10		TF, PZ
Epidendrum cf. *nocturnum* Jacq. (AMB 1256)	1		PZ*
Epidendrum longicolle Lindl. (AMB 139)	83		SW, PZ
Epidendrum microphyllum Lindl. (AMB 523)	10		SW, PZ
Gongora quinquenervis Ruiz and Pav. (AMB 505)	6		PZ*
Masdevallia aff. *trigonopetala* Kraenzl. (AMB 223)	3		FP*
Maxillaria cf. *parkeri* Hook. (AMB 521)	53		TF, PZ
Maxillaria cf. *triloris* E. Morren (AMB 1056)	18		TF, PZ
Maxillaria sp. 1 (AMB 596)	1		PZ*
Maxillaria sp. 3 (AMB 1232)	1		SW*
Maxillaria sp. 4 (AMB 206)	1		FP*
Maxillaria superflua Rchb. f. (AMB 359)	17		TF, PZ

Appendix 1. (Continued)

	Ep	He	Landscape
Maxillaria uncata Lindl. (AMB 716)	1		TF*
Notylia sp. 1 (AMB 465	5		PZ*
Octomeria brevifolia Cogn. (AMB 371)	5		TF
Octomeria erosilabia C. Schweinf. (AMB 421)	7		TF
Octomeria sp. 1 (AMB 1219)	31		TF
Ornithocephalus cf. *cochleariformis* C. Schweinf. (AMB 262)	1		FP*
Paphinia cf. *seegeri* Gerlach (AMB 470)	9		TF, PZ
Pleurothallis aff. *aurea* Lindl. (AMB 500)	7		PZ
Pleurothallis cf. *flexuosa* (Poepp. and Endl.) Lindl. (AMB 517)	3		SW, FP, PZ
Pleurothallis grobyi Bateman ex Lindl. (AMB 717)	1		TF*
Pleurothallis miqueliana (H. Focke) Lindl. (AMB 609)	4		SW
*Polyotidium huebneri (*Mansf.) Garay (AMB 463)	10	4	TF, SW, PZ
Polystachya sp. 1 (AMB 774)	1		PZ*
Sobralia macrophylla Rchb. f. (AMB 182)	5		FP, PZ
Sobralia sp. 1 (AMB 1074)	1		PZ*
Vanilla cf. *columbiana* Rolfe (AMB 777)		1	FP*
Vanilla penicillata Garay and Dunst. (AMB 618)		2	SW, FP
Vanilla sp. 1 (AMB 140)		2	SW*
Orchidaceae sp. 1 (AMB 532)	6		PZ
Orchidaceae sp. 2 (AVG 360)	4		TF
Orchidaceae sp. 3 (AMB 758)	2		FP*
Orchidaceae sp. 4 (AMB 1294)	1		FP*
PIPERACEAE			
Peperomia cardenasii Trel. (AMB 240)	45		TF, SW, FP, PZ
Peperomia macrostachya (Vahl) A. Dietr. (AMB 181)	12		FP
Peperomia pseudopereskiaefolia C.DC (AMB 560)	8		TF, FP
Peperomia serpens Loud. (AMB 202)	17		FP
URTICACEAE			
Pilea sp. 1 (AMB 757)		1	
Pteridophytes			
ASPLENIACEAE			
Asplenium serratum L. (AMB 191)	41	9	TF, SW, FP, PZ
BLECHNACEAE			
Salpichlaena hookeriana (Kuntze) Alston (AMB 854)	3	26	SW*
DENNSTAEDTIACEAE			
Lindsaea klotzschiana Moritz (AMB 462)	18		PZ
Lindsaea lancea (L.) Bedd. (AMB 114)	8		TF, SW
DRYOPTERIDACEAE			
Polybotrya caudata Kunze (AMB 257)		107	TF, FP
Polybotrya polybotryoides (Baker) H. Christ (AMB 115)		16	TF, SW
Polybotrya pubens Mart. (AMB 350)	1	235	TF, SW
Polybotrya sessilisora R. C. Moran (AMB 986)	1		TF*
GRAMMITIDACEAE			
Cochlidium furcatum (Hook. and Grev.) C. Chr. (AMB 982)	11		TF, PZ
HYMENOPHYLLACEAE			
Hymenophyllum hirsutum (L.) Sw. (AMB 916)	2		TF*
Hymenophyllum sp. 1 (AMB 1254)	5		PZ*
Trichomanes ankersii C. Parker ex Hook. and Grev. (AMB 288)	9	325	TF, SW
Trichomanes arbuscula Desv. (AMB 616)	2	3	SW*

Appendix 1. (Continued)

	Ep	He	Landscape
Trichomanes bicorne Hook. (AMB 455)	89	7	PZ
Trichomanes botryoides Kaulf. (AMB 305)	1		TF*
Trichomanes crispum L. (AMB 840)		1	TF*
Trichomanes ekmanii Wess. (AMB 154)	15	2	SW, FP, PZ
Trichomanes elegans Rich. (AMB 1097)	3		TF*
Trichomanes martiusii C. Presl. (AMB 96)	116	30	TF, SW, FP, PZ
Trichomanes tanaicum J.W. Sturm (AMB 107)	5	7	SW, FP
Trichomanes tuerckheimii H. Christ (AMB 1008)		4	TF
Trichomanes sp. 1 (AMB 975)	1		TF*
LOMARIOPSIDACEAE			
Elaphoglossum discolor (Kuhn) C. Christ. (AMB 456)	248		PZ
Elaphoglossum flaccidum (Fée) T. Moore (AMB 225)	2	7	FP, TF
Elaphoglossum glabellum J. Sm. (AMB 467)	128		TF, PZ
Elaphoglossum luridum (Fée) H. Christ (AMB 183)	33	1	TF, SW, FP, PZ
Elaphoglossum obovatum Mickel (AMB 302)	15		TF, PZ
Elaphoglossum plumosum (Fée) T. Moore. (AMB 1126)	7		PZ
Lomagramma guianense (Aulb.) Ching (AMB 834)		11	SW*
Lomariopsis japurensis Mart. J. Sm. (AMB 100)	1	109	TF, SW, FP, PZ
POLYPODIACEAE			
Microgramma megalophylla (Desv.) de la Sota (AMB 113)	30		TF, SW, FP, PZ
Microgramma reptans (Cav.) A. R. Sm. (AMB 200)	8		FP, SW, PZ
Niphidium crassifolium (L.) Lellinger (AMB 762)	1		FP*
Pecluma pectinata (L.) M. G. Price (AMB 149)	9		SW, FP
Pleopeltis macrocarpa (Borq ex Willd.) Kaulf. (AMB 773)	1		FP*
Polypodium decumanum Willd. (AMB 792)	2		TF*
Polypodium triseriale Sw. (AMB 118)	3		SW, FP, PZ
PTERIDACEAE			
Adiantum terminatum Kunze ex Miq. (AMB 1159)	1		TF*
Adiantum tomentosum Klotzsch (AMB 860)	2	2	SW, PZ
SELAGINELLACEAE			
Selaginella amazonica Spring in Mart. (AMB 1245)	3		PZ*
Selaginella sp. 1 (AMB 104)	15		SW*
TECTARIACEAE			
Cyclodium meniscioides (Willd.) C. Presl. (AMB 640)	2		SW*
VITTARIACEAE			
Anetium sp. 1 (AMB 544)	22		SW, FP
Hecistopteris pumila (Spreng.) J. Sm. (AMB 151)	45		TF, SW, PZ
Not identified			
Pteridophyte sp. 1 (AMB 180)	5		FP
Indet. 1 (AMB1202)	3	12	TF, SW
Indet. 2 (AMB 950)	11	1	TF

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