and Minchin 2002). This set of hierarchic models is composed of five models that vary in parameter numbers and complexity (Huisman *et al.* 1993). These are: type I (Flat), which shows no significant trend (*i.e.* null model); type II (Monotone), which shows an increasing or decreasing trend where the maximum is equal to the upper bound M; type III (Plateau), which shows an increasing or decreasing trend reaching an asymptotic value; type IV (symmetrical), which shows a Gaussian response curve; and type V (skewed), which represents an asymmetrical unimodal response curve. The last model is most complex and can be written as:

$$u = M \times \frac{1}{1+\exp(a+bx)} \times \frac{1}{1+\exp(c-dx)} \quad \text{(Oksanen and Minchin 2002)}$$

Where u is the expected response variable, x is the known explanatory variable, M is the maximum possible value (1 for the binomial case), and a, b, c and d the parameters of the function. The other four models can be obtained by fixing some parameters as constant values (Huisman *et al.* 1993, Oksanen and Minchin 2002). The final model is selected by means of backward elimination using a probability level of 0.05, which starts with the most complex model (Oksanen and Minchin 2002).

Table 7.1. Total soil elemental concentrations found in 80 plots located on floodplains, swamps, Tierra Firme and white sands in three different regions in NW Amazonia. SD: standard deviation. Rank represents the extreme values. Loadings of the first principal component are those obtained from a PCA analysis on soil elemental concentrations in all plots.

	Ca (mmol/kg)	Mg (mmol/kg)	K (mmol/kg)	Na (mmol/kg)	P (mmol/kg)	C (%)	N (%)
Mean ± SD	31.8 ± 50.8	162.1 ± 120.3	208.9 ± 151.5	87.8 ± 114.2	12.5 ± 9.02	3.4 ± 7.4	0.21 ± 0.39
Rank	0.58 – 237.7	0.6 – 423.5	0.3 – 575.5	0 – 478.5	0.3 – 36.5	0.1 - 35	0.02 – 1.8
First PCA axis loadings	0.37224	0.44325	0.42947	0.41421	0.4387	0.18332	0.28791

7.3 RESULTS

Gradient analyses

When all landscapes were considered, the species-based ordination diagram showed high eigenvalues and well distributed plots along the axes. Similar results were found with the genera-based and soil-based ordination analyses (Table 7.2, Figure 7.1). The first axis in the three ordination analyses represented a fertility gradient ranging from poorest soils, such as those in white sands, to richer soils, such as those in floodplains (Figure 7.1). In Tierra Firme alone, a similar fertility gradient ranging from poorer soils in Metá to richer soils in Ampiyacu and Yasuní (see also Lips and Duivenvoorden 2001) emerged in each of the ordination diagrams (Figure 7.1).

Response shapes

All landscapes
Of the 24 species analyzed along the DCA species gradient, 21% were skewed, 21% symmetrical, 29% plateau, 4% monotone, and 25% flat. Along the PCA soil gradient most of the species response models were symmetrical (42%) (Table 7.3). In total, 9 species (38%) had a similar non-flat model along the species gradient and the edaphic gradient (*i.e. Unonopsis stipitata* and *Virola elongata*) (Table 7.4, Figure 7.2).

The analysis of HOF models of 89 genera along the DCA genera gradient showed that 13% of the curve shapes were skewed, 19% symmetrical, 19% were plateau, 20% monotone, and 29% without a trend. Along the PCA soil gradient the percentage of symmetrical curves increased and the number of flat models decreased (Table 7.3). In total, 21 genera (24%) had the same response curve along the DCA genera gradient and the PCA soil gradient, but 8 of them had flat distribution. Thus, just 13 genera (15% [*i.e. Unonopsis* and *Brosimum*]) showed an edaphic-controlled distribution (Table 7.5, Figure 7.3).

Only Tierra Firme
Along the species gradient, 4 out of 8 species analyzed in Tierra Firme showed flat response curves. There were no skewed response curves for species in Tierra Firme (Table 7.3). Two species of *Virola* that displayed non-flat models along the PCA soil gradient showed flat responses along the species gradient. The 4 species with a non-flat response shape along the species gradient in Tierra Firme had flat responses along the PCA soil gradient (Table 7.4).

Among the 41 genera analyzed in Tierra Firme, 56% showed flat responses (no trend), 32% monotone, and 12% symmetrical (Table 7.3). There were 12 genera (29%) with a non-flat response model, which showed a similar response shape along the edaphic and genera gradients (*i.e. Matisisa* and *Guarea* [Table 7.5]).

7.4 DISCUSSION

This study does not support unimodal symmetrical Gaussian models (Gauch and Withaker 1972, ter Braak and Looman 1986) as the universal response shape for genera or species in tropical rain forests. Therefore, the first hypothesis was rejected since only a small percentage of the models showed symmetrical response shapes along the species and genera gradients, both in all landscapes and Tierra Firme forests. These results were similar to those found in Tasmania along an altitudinal gradient (Minchin 1989, Oksanen and Minchin 2002), where a higher proportion of non-symmetrical models prevailed. However, the results differed from those reported in Denmark, where symmetrical curves were the most common models (Lawesson and Oksanen 2002). The multiple ways by which species and genera responded to the complex gradients supports the continuum concept as the more appropriate model of vegetation organization in Amazonian rain forests

Table 7.2. Summary information of ordination analyses in all landscapes (80 0.1-ha plots) and Tierra Firme alone (31 0.1-ha plots). DCA were based on presence-absence data of genera and species composition, and PCA based on logarithmic transformations of soil elemental concentrations

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
All landscapes					
Species					
Eigenvalues	0.632	0.491	0.333	0.257	16.854
Length of gradient (sd units)	6.070	3.745	4.373	3.970	
Genera					
Eigenvalues	0.281	0.195	0.138	0.097	5.245
Length of gradient (sd units)	2.957	2.289	2.695	2.107	
Soils					
Eigenvalues	4.36	1.75	0.52	0.14	
Percent	62.31	25.12	7.36	2.05	
Tierra Firme					
Species					
Eigenvalues	0.670	0.335	0.289	0.259	8.456
Length of gradient (sd units)	4.337	3.184	3.114	2.314	
Genera					
Eigenvalues	0.327	0.153	0.112	0.093	3.097
Length of gradient (sd units)	2.340	1.733	1.539	1.381	
Soils					
Eigenvalues	4.26	0.97	0.60	0.45	
Percent	60.85	13.83	8.68	6.45	

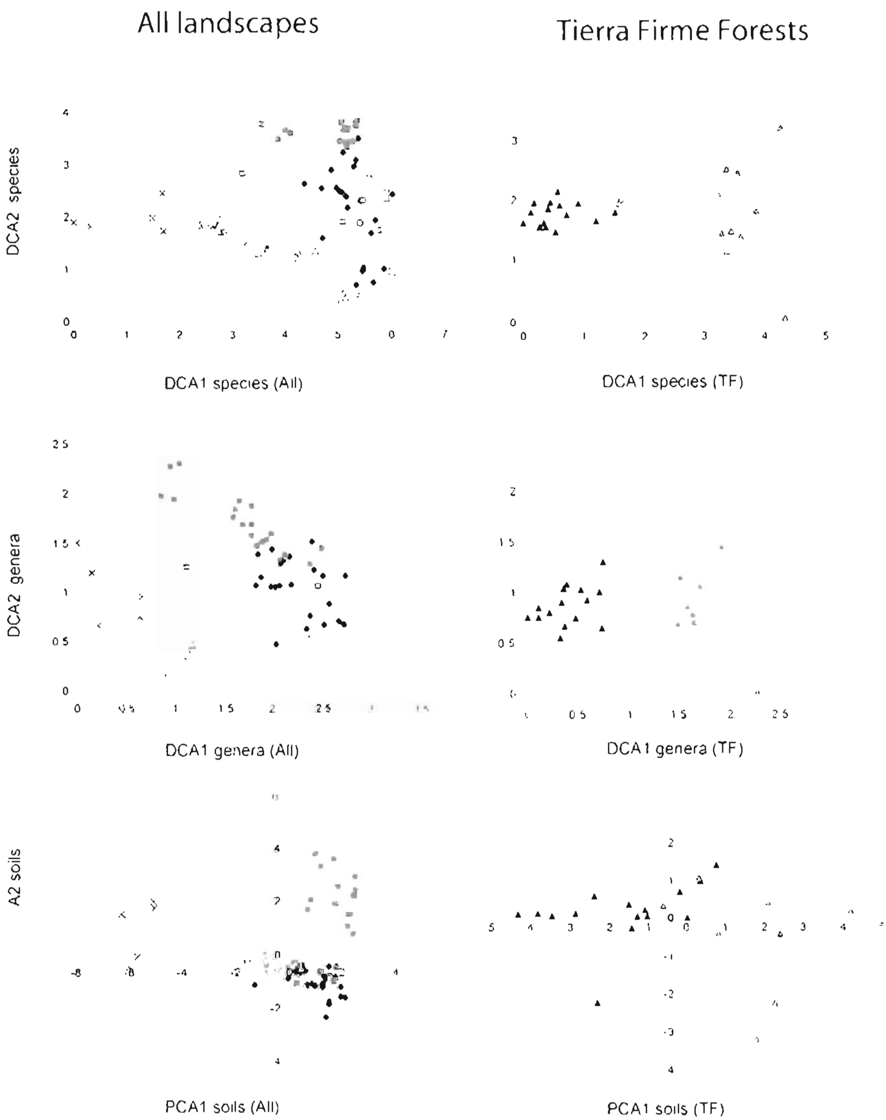

Figure 7.1. DCA based on genera and species and PCA based on soil elemental concentrations, in all landscapes (All), and Tierra Firme (TF) alone. Squares = flood plains, rhombus = swamps, triangles = Tierra Firme, and crosses = white sands. In Tierra Firme forests alone, black triangles represent Metá area, darker gray Yasuní, and lighter gray (with a darker line in the border) Ampiyacu.

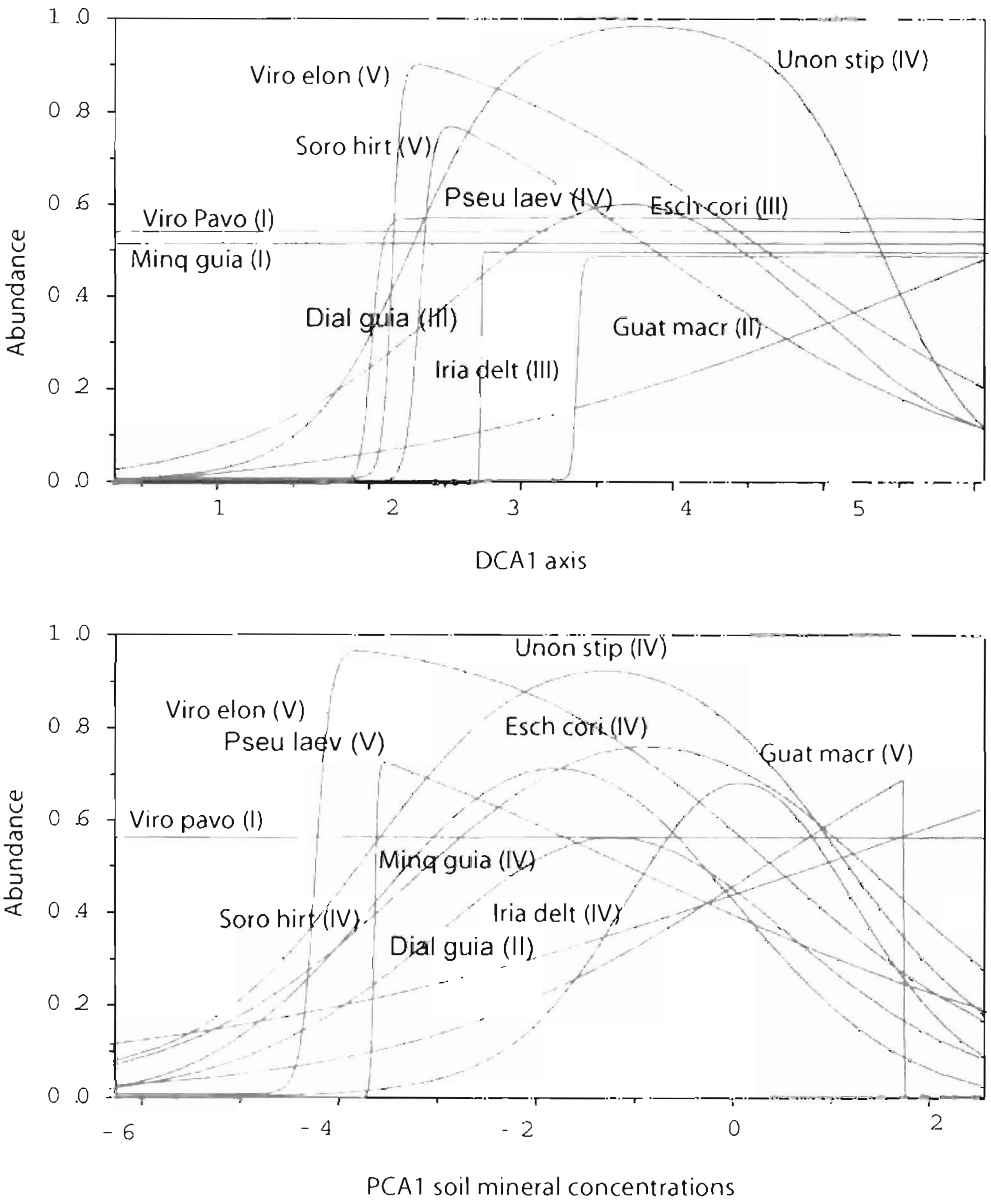

Figure 7.2. Examples of different response shapes of species along different gradients in 80 0.1-ha plots in NW Amazonia. Model types according to table 3 and species name as in table 4.

A circular reasoning is claimed when we use an analysis based on a Gaussian distribution assumption (Minchin 1989), as DCA does for extracting the coenocline. There was a high variety of response curves, of which the non-symmetrical curves were the most frequently occurring. Owing to the high number of species and genera considered in the ordination analysis, DCA sample scores still are a good niche measure of ecological gradients for individual species distribution (Lawesson and Oksanen 2002). However, the accuracy of methods based on an explicit model of vegetation response in tropical rain forests will remain controversial in the absence of a method which emphasizes different models (Austin 1985).

Table 7.3. Number of model types according with the response shape of genera and species along different gradients. DCA1 = first DCA axis based on the whole genera or species composition in both all landscapes (All) and Tierra Firme alone (TF). PCA1 soils = first axis from a PCA analysis based on logarithmic transformations of total soil elemental concentrations.

		Genera				Species			
Model		DCA1 genera		PCA1 soils		DCA1 species		PCA1 soils	
		All	TF	All	TF	All	TF	All	TF
V	Skewed	11	0	18	0	5	0	6	0
IV	Symetric	17	5	26	7	5	2	10	0
III	Plateau	17	0	16	0	7	0	4	1
II	Monotone	18	13	15	8	1	2	1	1
I	Flat	26	23	14	26	6	4	3	6

Monotone and plateau responses might be caused by a species range extending beyond the limits of the gradient sampled (Austin 2002), or by incomplete sampling of the gradient. Therefore, if the sample size is enlarged, more bell-shaped response curves might arise (Økland 1986). However, incomplete environmental gradient is not likely to occur in the present study as the sampled gradient included a wide edaphic gradient both across landscapes and within Tierra Firme alone (Lips and Duivenvoorden 2001). Also, the sampling frequency was at a similar level of that applied in other studies (Oksanen and Minchin 2002).

In Tierra Firme forests alone, compared to all landscapes, there is a stronger tendency for flat and monotonous response shapes for both genera and species along complex and soil gradients (Table 7.3). This result corresponds with the idea that in Tierra Firme forests the compositional turnover (beta diversity) of woody species is rather low (Duivenvoorden 1995, Pitman *et al.* 2001, Condit *et al.* 2002). Conversely, considering all landscapes, the number of taxa that show a preference for a part of the gradients as well as the number of symmetrical curves substantially increase, which supports a higher compositional turnover (Knut *et al.* 2003) in presence of pronounced environmental gradients

Table 7.4. Model type of species response shapes along different gradients in NW Amazonia. DCA1 = first DCA axis based on the whole species composition. PCA1 soils = first axis from a PCA based on logarithmic transformations of total soil elemental concentrations. Values between brackets are the model types found in Tierra Firme alone.

Species	DCA1	PCA1 soils
Cheiloclinium cognatum (Miers) A.C. Sm.	IV	III
Combretum laxum Jacq.	III	III
Cordia nodosa Lam.	III	III
Dialium guianense (Aubl.) Sandwith	III	III
Eschweilera coriacea (DC.) S.A. Mori	III (I)	IV (I)
Eugenia florida DC	V	IV
Euterpe precatoria Mart.	III	II
Garcinia macrophylla Mart.	I	I
Guarea macrophylla Vahl	II	V
Iriartea deltoidea Ruiz and Pav.	III	IV
Iryanthera juruensis Warb.	I	I
Licania heteromorpha Benth.	IV	IV
Minquartia guianensis Aubl.	I	IV
Ocotea aciphylla (Nees) Mez	V (II)	V (I)
Pouteria torta (Mart.) Radlk.	I	IV
Pseudolmedia laevigata Trécul	IV (IV)	V (I)
Socratea exorrhiza (Mart.) H. Wendl.	V	V
Sorocea hirtella Mildbr.	V (IV)	IV (I)
Tapirira guianensis Aubl.	IV	IV
Theobroma subincanum Martius in Buchner	III (I)	IV (I)
Unonopsis stipitata Diels	IV (II)	IV (I)
Virola calophylla (Spruce) Warb.	I	V
Virola elongata (Benth.) Warb	V (I)	V (II)
Virola pavonis (A. DC.) A.C. Sm.	I (I)	I (III)

The way that genera and species respond to an abstract complex gradient as the first DCA axis and to a soil fertility gradient was different for most taxa. Only few species in all landscapes (30%) and Tierra Firme alone (0%) showed a similar response model along the species gradient and soil gradient (Table 7.4). This tendency was also found for genera: only 15% (all landscapes) and 29% (Tierra Firme) of the genera shared a similar type of response models along the genera gradient and the soil gradient. Therefore, the second hypothesis was also rejected. This suggests that soil fertility (as quantified by the first PCA axis) is not the overridingly dominant factor affecting species distributions, as has been suggested by Gentry (1988). Other factors (e.g. pests influence, phylogenetical structure, resource competition, or dispersal; Condit 1996, Webb 2000, Enquist *et al.* 2002), are likely to have a stronger influence upon the distribution of species and genera.

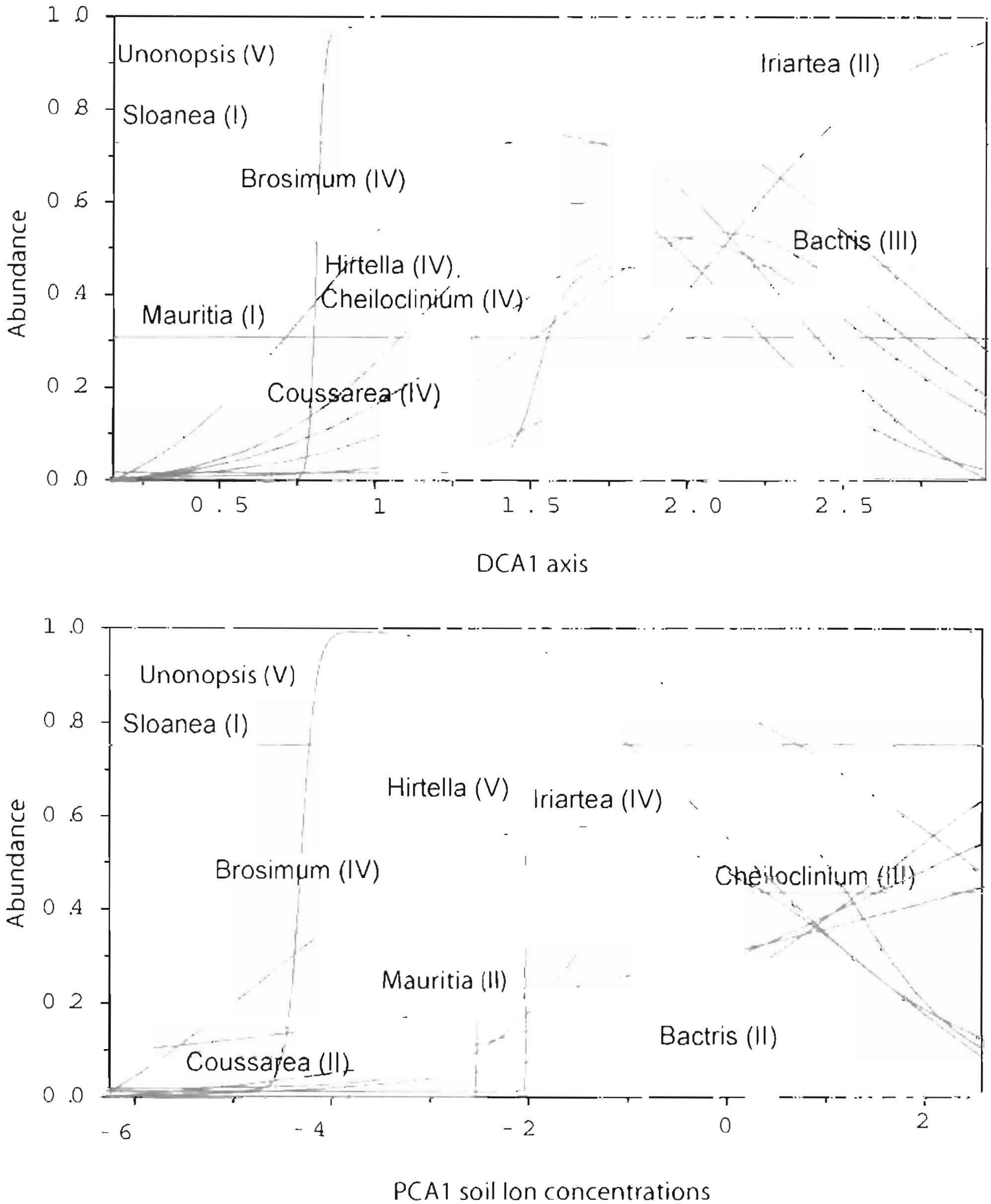

Figure 7.3. Examples of different response shapes of genera along different gradients in 80 0.1-ha plots in NW Amazonia. Model types according to table 3.

Table 7.5. Model type of genera response shapes along different gradients in NW Amazonia. DCA1 = first DCA axis based on the whole genera composition. PCA1 soils = first axis from a PCA based on logarithmic transformations of total soil elemental concentrations. Values between brackets are the model types found in Tierra Firme alone.

Genus	DCA1	PCA1soils	Genus	DCA1	PCA1soils
Abuta	I (I)	V (I)	*Mabea*	I (I)	IV (I)
Aniba	I	I	*Machaerium*	III (I)	III (I)
Annona	IV	III	*Macrolobium*	I	I
Aspidosperma	I	I	*Matisia*	II (II)	IV (II)
Astrocaryum	III	III	*Mauritia*	I	II
Bactris	III	II	*Memora*	II	IV
Bauhinia	II	IV	*Miconia*	III (I)	III (I)
Brosimum	IV (II)	IV (I)	*Micropholis*	I (I)	II (I)
Buchenavia	IV	I	*Minquartia*	I	IV
Calyptranthes	IV	II	*Mouriri*	IV (II)	V (II)
Casearia	III	II	*Myrcia*	III	III
Cheiloclinium	IV	III	*Naucleopsis*	II (I)	V (I)
Chrysophyllum	I (I)	II (I)	*Neea*	I (I)	I (I)
Clusia	V	II	*Ocotea*	I (II)	II (I)
Coccoloba	II	V	*Oenocarpus*	III	I
Combretum	II	III	*Ophiocaryon*	V (I)	IV (I)
Cordia	III (I)	V (I)	*Oxandra*	I	I
Couepia	V (II)	V (II)	*Paullinia*	II	IV
Coussarea	IV	II	*Perebea*	II (I)	IV (I)
Dacryodes	V (II)	IV (I)	*Pourouma*	III (I)	III (I)
Dialium	V	II	*Pouteria*	I (IV)	V (IV)
Dicranostyles	V	IV	*Protium*	I (IV)	V (IV)
Diospyros	IV	III	*Pseudolmedia*	IV (IV)	V (IV)
Doliocarpus	V	IV	*Pseudoxandra*	IV	III
Duguetia	I (I)	IV (I)	*Psychotria*	I	I
Endlicheria	IV (I)	III (IV)	*Rinorea*	III	IV
Eschweilera	III (I)	V (IV)	*Salacia*	II	III
Eugenia	II (I)	IV (I)	*Siparuna*	I (IV)	IV (IV)
Euterpe	I	II	*Sloanea*	I (II)	I (I)
Faramea	V	V	*Socratea*	III	V
Ficus	II	V	*Sorocea*	I (I)	IV (I)
Garcinia	IV	I	*Sterculia*	II	IV
Guarea	II (II)	IV (II)	*Strychnos*	IV	III
Guatteria	II (II)	II (II)	*Swartzia*	IV (I)	I (I)
Gustavia	III	IV	*Tachigali*	IV	I
Heisteria	I	III	*Talisia*	III (I)	IV (I)
Hevea	II	I	*Tapirira*	I	IV
Hirtella	IV	V	*Tapura*	III	III
Inga	I (I)	II (I)	*Theobroma*	III (II)	IV (II)
Iriartea	II	IV	*Trichilia*	III (I)	V (I)
Iryanthera	I (IV)	I (IV)	*Unonopsis*	V (II)	V (I)
Lacistema	IV	V	*Virola*	II (II)	II (I)
Leonia	II (I)	III (I)	*Xylopia*	V	IV
Licania	I (II)	IV (II)	*Zygia*	I (I)	II (I)
Licaria	V	V			

Gentry (1988) also suggested high predictability of families (and perhaps genera) according to the different substrates in NW Amazonia forests. Nevertheless, families and genera are artifacts of our propensity to classify nature (Brooks and McLennan 2002) and involve many different evolutionary and ecological traits that hamper the interpretation of response shapes along gradients. For example, in all landscapes the *Virola* genus showed a monotic response model along the genera-based gradient. However, the species *Virola calophylla*, *V. elongata* and *V. pavonis*, displayed flat and skewed response models (Tables 3 and 4). Speciose clades might produce species that are ecologically and phylogeneticaly similar, which might compete with each other restricting their distribution range more than unrelated species (Webb 2000). In the case of less speciose genera, the interpretation of the response along gradients is more straightforward, although caution remains needed. For example, *Mauritia* has been commonly associated with swamps (Urrego 1994, Duque *et al.* 2001, Romero *et al.* 2001, Grández *et al.* 2001). However, there is a clear separation between *Mauritia carana* and *M. flexuosa*, which occupy white sands and swamps respectively (Duivenvoorden and Lips 1995). Despite all this, genera-based analyses of response shapes could be an useful tool to infer about compositional turnover as shown above, as well as long-term processes such as speciation and extinction in larger geographical scales, which could help to understand macroecological patterns of species distribution (Enquist *et al.* 2002).

Chapter 8

SYNTHESIS

Alvaro J. Duque M.

8.1 ANSWERING THE RESEARCH QUESTIONS

Beta diversity at local and intermediate scales: a combined effect of environmental factors and spatial processes

At a local scale in Tierra Firme forests (Chapter 2), and according with the first research question, it was concluded that most big tree species are generalists. Thus, beta diversity was rather low, and to define a species as a 'true specialist' requires further and larger surveys. A species might be clasiffied at a local scale as a specialist, and at the same time it might be also known at a intermediate or regional scale as a generalist. At intermediate scale (Chapter 3), and in regards with the second research question, it was confirmed that canopy species tend to be more wide-spread and less soil-specialized than understory species (Webb *et al.* 1967, Zagt and Werger 1998, Ruokolainen and Vormisto 2001). The main land unit stratification in the study area was strongly correlated with the floristic patterns, and displayed a similar trend of different species assemblages for both canopy and understory species. However, at mesoscale in Tierra Firme forests in Colombian Amazonia, the enhanced effect of soil characteristics on understory species became evident. This is also a matter of growth form: trees react less than understory elements on changing conditions in a zonal forest covering slopes or land with drainage areas, such as streams, small swamps and small internal valleys. Spatial scaling laws (Brown 1995, Ritchie and Olff 1999, Haskell *et al.* 2002), which describe the interactions between mammals and the environment as a function of body size, could be an interesting approach to synthesize those contrasting patterns between canopy and understory plants in Amazonian Tierra Firme forests. This theory claims that larger species can detect larger patches, but requires lower resource concentrations, whereas smaller species require higher resource concentrations located in smaller patches (Ritchie and Olff 1999).

Vascular epiphytes in the Metá area: an unsaturated spatial system

Considering the third question, in Chapter 4 we concluded that there was a epiphyte-landscape association in Metá. It was hypothesized that some epiphyte species are more favoured by high humidity and better water supply (floodplains and swamps), or are better adapted to withstand drought (in low podzol forests) than others. The spatial configuration of the plots was independent of the recorded patterns, whereas the correlation between the woody floristic composition and the epiphytes was rather high and significant. However, it was not possible to conclude for a specific relationship between individual ephiphytic species and phorophytes. Furthermore, we found that vascular epiphytes fail to effectively colonize a substantial number of potential phorophytes in Metá. When comparing to Yasuní (Leimbeck and Balslev 2001), on a plot area basis, the forests of the Caquetá River contained less phorophytes covered with aroid epiphytes. The closeness of the Yasuní forests to the Andes, which have been recognized as a centre of diversity for epiphytes (Gentry 1982), may cause a greater saturation of epiphytes than in the Metá forests. This lack of large surrounding areas rich in epiphytes, along with the limited dispersal capability by wind of the bulk of individuals located in the forest understory, were hypothesized as the possible reasons for the ample availability of space for epiphyte individuals to settle.

Selected plant taxa as bioindicators for Amazonian forest diversity

Remote sensing tools, such as satellite images, and selected groups of plants that allow representative sample sizes (Clark and Grose 1999, Vormisto 2000), have been considered able to produce important information of forest biodiversity patterns in a cost-effective way (Vormisto *et al.* 2000, Tuomisto *et al.* 2003). However, in Chapter 5 of this study where the fourth question was considered, we did not find evidence that specific groups of plants, such as ferns and Melastomataceae, have more potential to predict the main patterns in species composition of forest types than soil characteristics, landscape unit stratification, or the spatial sampling set-up. The use of ecological indicators in tropical rain forests requires a prior test of their specific utility to avoid misinterpretations. When the main goal is to preserve biodiversity, an unsuitable use of bioindicators could translate into a loss of time and resources, which in the current situation is essential for timely and successful conservation planning.

Woody liana patterns in NW Amazonia

In Chapter 6 we tested the fifth question concluding that despite its uniform rainfall and geomorphology NW Amazonia was not homogeneous in its patterns of diversity and composition of woody lianas. Patterns of liana diversity and composition were not parallel. Liana diversity peaked in Ampiyacu, which might be due to the more central position of this area in the Amazon basin, compared to Yasuní and Metá. Soil fertility had no effect on liana diversity but was responsible for a strongly outlying liana composition of Tierra Firme forest in the Colombian area. The liana assemblages in Yasuní also differed from the other areas, possibly due to influx from Andean liana flora elements due to its close proximity to the Andes

Species response curves: building the bridge between statistical methods and ecological theory

In Chapter 7 the sixth question regarding the response shape of species and genera was tested. Most species (and genera) showed response curves different of the bell-shaped one, which has been widely postulated as the universal response shape of species to environmental gradients (Gauch and Withaker 1972, ter Braak and Looman 1986). Thus, this study supported the continuum theory (Austin 1985) as the most appropriate model for vegetation patterns in NW Amazonia. Whether species responses do or do not show Gaussian shapes has important implications for ecological modelling, because most of the techniques such as CA and its derivatives (DCA and CCA) assume unimodal symetrical curves as the standard response models. In the absence of a method that emphasizes different models, we take the risk of falling into a type I error, accepting a false hypothesis. Individual species analyses might help to illuminate understanding of the plant community structure, and so, help to get a clearer picture of how to find mechanistic explanations for the existing patterns (Minchin 1989).

8.2 METHODOLOGICAL CONSIDERATIONS

The present study focused on species distribution along environmental gradients by means of several approaches based on different methods, emphasizing the role of spatially structured factors. As pointed out by Dale *et al.* (2002), 'no single method can reveal all the important characteristics of spatial data, but the results of different analyses are not expected to be completely independent of each other'. In tropical rain forests the analytical methods in community ecology that assume a specific model, such as DCA, CCA, and PCA, are still controversial (Austin 2002). However, they all are still among of the more suitable tools to analyze spatial patterns of species assemblage distribution (Legendre and Legendre 1998).

The land unit approach in Amazonian rain forests proved to be very efficient in revealing the main floristic patterns at intermediate scales (see also Duivenvoorden and Lips 1995). In NW Amazonian forests, the local abundance and composition of species seems a random sample of the metacommunity with many singleton species. Dispersal rate functions come up as a key factor addressing this pattern. At a regional scale, the vegetation mosaic becomes more complex and historical and biogeographical factors become important (Ricklefs and Schluter 1993).

Sampling design

The stratified-random plot-based protocol used to sample both terrestrial and epiphytic plants showed advantages and disadvantages that may be considered in future studies. Large transects (≥1 ha) can detect well the floristic and geomorphological variation of big trees and lianas, but they produce a high edge effect that increases the amount of rare species and hampers the study of recruitment in dynamic-based studies (Sheil 1995). In long transects, there is also a considerable risk of falling into pseudo-replication (Hurlbert 1990). The series of spatially distributed compact 0.1-ha plots (DBH≥2.5 cm) employed to quantify the terrestrial woody vascular plants, require less effort in the field than larger plots (1-ha) including only big trees (DBH≥10 cm), and they reveal better the general diversity patterns. However, big trees could easily be undersampled and more individuals and species guilds mean a higher effort identifying species in the herbarium (Phillips *et al.* 2003b). A marked advantage using compact 0.1-ha plots instead of split 0.1-ha plots as those employed by Gentry (1988a), is that they allow us to choose for structural and geomorphological homogeneous forest-stands including soils, which avoid skewedness by tree falls or landscape ecotones.

A serie of rectangular 0.025-ha plots (5 x 50 m each) was used to sample herbs, vascular epiphytes, shrubs, and woody plants with DBH<2.5 cm. Species with smaller size require smaller sample units. This plot size used to study vascular understory species could be proposed as a good supplementary plot size to 0.1-ha plots in Amazonian forests. They also showed good performance sampling vascular epiphytes, and detecting the species assemblages in Metá. Series of sample transects are better than a compact plot or individual trees, since they show a higher capability to encounter epiphytic species with patchy distribution (Hietz and Wolf 1996, Van Dunné 2001). Since they also comprise more individuals, they can reveal much better the community structure. However, plot-based (or transect-based) inventories of epiphytes demand a higher effort in plant collecting. In this study, we used indigenous climbers along with poles and binoculars, and still there could be a possible bias in the tree crowns because of a lack of census of small elements, such as orchids and ferns. Another possible disadvantage of using plots in epiphyte inventories is the difficulty of comparing sample-volume or available superficies due to the three-dimensional structure of the forests, which is variable from one plot or forest type to another (Van Dunné 2001).

Local abundance and rarity
In Chapters 2 and 3, this study confirmed that NW Amazonia rain forests are characterized by a high amount of locally rare woody terrestrial species. However, the small sample size (and related undersampling) as well as the lack of a proper way to define the rarity of a species, hampered the identification of really endangered low-abundant species. For example, at mesoscale, considering species present in two or more plots (after Pitman *et al.* 1999), which might reduce the undersampling problem, rare species moved down from 43% to 21%. This reduction was particularly strong in Tierra Firme plots (from 50% to 32%), where species with one individual in only one plot were common due to the high alpha diversity in this forest type (Duivenvoorden 1996). The question remained whether or not rare species are always represented by a high portion of species, as suggested by Hubbell (2001), even if the sample size is enlarged.

Compared to woody trees and lianas, the amount of species with just one individual in vascular epiphytes was rather low (19%), as well as the total number of species with presence in only one plot (36%). Vascular epiphytes are known to be much less diverse than trees in Amazonian forests. A smaller regional diversity of vascular epiphytes results in a different local structure of relative species abundance than that observed for trees. Several mechanisms have been proposed for explaining this high amount of locally rare species in tropical forests: (1) recruitment reduction near conspecific adults due to pests (Janzen-Connell model), which creates space for other species; (2) ecological equivalence for all species that generates a random chance to reach any available regeneration site (Hubbell 2001); (3) Mass effect (Shmida and Wilson 1985), which promotes species to settle and regenerate in an unsuitable environment. However, there is no consensus yet how much each of these mechanisms contribute to the establishment and maintenance of local patterns of relative species abundance.

Growth forms and spatial scale: a complex vegetation model
When the unit size, shape spacing, or extent in a sample design are altered, statistical results are expected to change (Dungan *et al.* 2002). Indeed, diversity and floristic patterns at different spatial scales might be determined by different processes (Crawley and Harral 2001). A combination of growth form and spatial scale of analysis, might lead to an even more complex scenario that does not permit any generalization. For example, in Metá at intermediate scale, the species assemblages of both vascular epiphytes and woody species were highly correlated to each other, and arranged according to the main landscape units. Nevertheless, different processes appeared to be responsible for these similar patterns. In the case of woody species, as shown in Chapter 3, factors such as flooding, soil drainage and soil fertility, played a key role controlling the distribution patterns of the terrestrial plants (see also Duivenvoorden and Lips 1995). Regarding vascular epiphytes, as shown in Chapter 4, changes in environmental humidity (see also Leimbeck and Balslev 2001) and dispersal limitation came up as important factors determining distribution patterns. At a regional scale in the presence of a pronounced environmental gradient, woody lianas (Chapter 6) showed a density pattern that was not related to soil fertility. This might be due to the capability of lianas to reproduce by clones and to disperse by wind. However, at the same regional scale in NW Amazonia, Duivenvoorden *et al.* (in press) reported a negative relationship between

soil fertility and density of thin trees, possibly due to an increased treelet longevity and improved defense mechanisms against herbivory on poorer soils. Even though, as shown in the DCA analyses in Chapters 6 and 7, a similar pattern of floristic composition, in which regional processes and soil fertility had a remarkable influence, were found for trees and lianas. Our analyses of epiphytes, trees, and lianas suggested that patterns of diversity and composition do not have parallel explanations. Furthermore, they suggested 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.

8.3 IMPLICATIONS FOR CONSERVATION

The new insights into plant community biodiversity patterns and structure in NW Amazonian forests presented here, should help decision makers to focus their research and conservation strategies more accurately on some crucial points that deserve special attention. Some widely used criteria in conservation planning such as alpha diversity or taxonomic richness, spatial species turnover, population abundance, rarity, and environmental representativeness (Prendergast *et al.* 1999), are debated in this study, mainly for the Middle Caquetá area in Colombian Amazonia. However, there is not a single indicator or general procedure to identify areas to be protected as conservation planning is dependent on technical factors such as the scale of the survey as well as on political and socioeconomic imperatives.

Forest sampling in Amazonian rain forests faces some logistic obstacles, such as difficult access and high regional diversity, which increases effort and working time in the field. This is one of the reasons why most studies focussed on only a part of the total flora, leading to a lack of inventories considering different growth forms together. These difficulties also result in data sets with a high percentage of locally rare species, which usually produces undersampling of a considerable number of species (Duivenvoorden *et al.* 2002). A species should be rare in several ways (Rabinowitz 1981), and to be locally rare does not necessarily mean to be extinction-prone, now that locally rare species can also be wide spread in large geographical areas (Pitman *et al.* 1999). Therefore, there is still a need to improve the taxonomic knowledge on many groups and to know more precisely the geographic ranges for neotropical plant species, to be able to define better the terms endemic and rare in NW Amazonia (but see Pitman *et al.* 2002).

The results of this study suggest that at a regional scale, such as the area of NW Amazonian forests, where soil and climatic conditions hardly differed between the three studied areas, biological and historical processes have resulted into a clear floristic differentiation. The difficulty to integrate reserves in a continuous area of forest because of political boundaries among countries, creates the need to structure regional networks of reserves. Gap analysis, which identifies gaps in an existing reserve network (Prendergast *et al.* 1999), could be an interesting approach to combine factors that should enable to find where to site new reserves in the area. Within areas, a method based on geomorphological variation and landscape representativeness and connectivity, should fit the main goal of protecting and preserving the main species richness and species assemblage patterns currently existing there. A clear definition of 'forest type' depending on the contrasting 'niche-assembly' and 'dispersal-assembly' models is crucial to define areas for conservation.

The geopolitical fact of indigenous protected areas has shown to be a powerful mechanism for securing forest cover (van der Hammen 2003). The actual reserves in Amazonian rain forests can retain a substantial part of the whole biota, and serve as buffer zones for adjacent protected areas (Peres and Zimmerman 2001). However, the ongoing expansion of the agricultural frontier, oil exploitation, or illegal crops, which also causes severe social problems, constitute major threats for the (on paper) protected areas. The lack of experience of tribal communities in large scale agriculture and cattle production is likely to lead to a faster destruction of the forested areas inhabited since ancient times by indigenous people with a holistic environmental vision (van der Hammen 2003).

In Amazonian rain forests, exploitation of non-timber products might offer a way to preserve this ecosystem (Duivenvoorden *et al.* 2001, van Andel *et al.* 2003). The scarcity of big trees with large stem diameter along with the high variety in species composition, hamper the extraction of selected particular species, making selective and sustainable logging in Amazonian rain forest a difficult task (see also Bawa and Seidler 1998). A better understanding of the intrinsic value of biodiversity as well as the actual and potential preservation of the services provided for it, is still a challenge for local, national and international organizations (Thiollay 2002). For example, there is an ongoing debate on the capability of the tropical rain forests either to store or release carbon to the atmosphere (Phillips 1998, Clark *et al.* 2003). However, the additional services provided by the high diversity of natural Amazonian forest, such as scenic beauty and high cultural diversity of human ethnic groups, give these forests an extra value when compared to monoculture tree plantations, even if they are functionally similar in terms of carbon storage and evapotranspiration (Peres and Zimmerman 2001).

Finally, there is a need to strengthen the links between stake holders and land managers with those engaged in conservation research to improve the communication flow in both directions. Decision makers need to be more aware of how science can contribute to practical conservation, and vice versa (Prendergast *et al.* 1999). Basic ecological research presented here is the basis for addressing the conservation and restoration of natural ecosystems. Nevertheless, much information on population ecology, life history of species, species range distribution, taxonomy, and paleo-environmental history is still lacking. Furthermore, more detailed studies on both temporal and spatial components in tropical rain forests are urgent. I hope that this attempt to improve our understanding of Amazonian rain forest structure, based on ecological plant inventories and land unit surveys, will encourage new research and will serve as a new input for more useful discussions aiming at a science-based forest conservation.

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APPENDIX

Appendix I Results of contingency table (two degrees of freedom; Chi = 5.99) for each of the tree species respect to the physiographic factors LPT, HDT, and HPT respectively (*i.e.*, 0/+/0). (+) = species more frequent than expected, (-) = species less frequent than expected and (0) = indifferent species. (X) species present in 1–2 subplots and thus, with no sufficient information to be statistically tested.

Specialists LPT: *Iryanthera paraensis* (+/0/0), *Iryanthera ulei* (+/0/0), *Lacmellea arborescens* (-/0/0), Lauracea AD552 (+/0/0), *Micropholis guyanensis* (+/0/0), *Neea* AD319 (+/0/0), *Virola elongata* (+/0/0).

Specialists HDT: Chrysobalanaceae AD1030 (-/+/0), *Eschweilera alata* (-/+/0), *Hevea* AD911 (-/+/-), *Hevea benthamiana* (0/+/0), Lauraceae AD1321 (0/+/0), Lauraceae AD1384 (0/+/0), Melastomataceae AD1001 (0/+/0), *Micrandra spruceana* (-/+/-), Moraceae AD1214 (0/+/0), *Pithecellobium* AD966 (0/+/0), *Pourouma ovata* (-/+/0), *Pouteria* AD994 (-/+/0), *Protium fimbriatum* (0/+/0), *Rinorea racemosa* (0/+/0), *Senefeldera* AD891 (-/+/-), Vochysiaceae 1125 (0/+/0), *Warscewiczia* AD982 (-/+/-)

Specialists HPT: Chrysobalanaceae AD1633 (0/0/+), *Eschweilera tessmanii* (-/0/+), *Iryanthera polyneura* (0/-/+), *Mezilaurus itauba* (0/0/+), *Micropholis* cf. *cyrtobotrya* (0/0/+), *Pouteria* AD1518 (0/0/+), *Pouteria* AD1518 (0/0/+), *Protium grandifolium* (0/0/+), *Swartzia schomburgkii* (0/0/+), *Virola* AD1565 (0/0/+), Vochysiaceae AD1635 (0/0/+).

Intermediate LPT-HDT: *Eschweilera* AD685 (0/0/-).
Intermediate LPT-HPT: Burseraceae AD195 (0/-/0), *Pouteria* AD221 (0/-/0), *Qualea* AD348 (0/-/0).

Intermediate HDT-HPT: *Chrysophyllum sanguinolentum* (-/0/0), *Eschweilera* AD1299 (-/0/0), *Eschweilera parvifolia* (-/0/0), *Eschweilera punctata* (-/0/0), *Pouteria* AD947 (-/0/0).

Generalists (0/0/0): *Anisophyllea guianensis*, *Aspidosperma* AD264, *Aspidosperma* AD635, *Brosimum guianense*, *Brosimum lactescens*, *Brosimum rubescens*, *Brosimum utile*, *Buchenavia parviflora*, *Cariniana decandra*, *Carpotroche* AD277, *Caryocar glabrum* , Chrysobalanaceae AD1221, Chrysobalanaceae AD424, *Chrysophyllum superbum*, *Clathrotropis macrocarpa*, *Clathrotropis nitida*, Combretaceae AD1811, *Compsoneura capitellata*, *Dacryodes roraimensis*, *Dacryodes* AD291, *Dialium* AD204, *Dipteryx odorata*, *Drypetes variabilis*, *Elaeagia maguirei*, *Erisma bicolor*, *Erisma japura*, *Erisma laurifolium*, *Erisma splendens*, *Eschweilera undina*, *Eschweilera* cf. *laevicarpa*, *Eschweilera coriacea*, *Eschweilera itayensis*, *Eschweilera rufifolia*, Euphorbiaceae AD391, *Gavarretia* AD191, *Guarea cinnamomea*, *Guarea macrophylla*, *Heisteria* AD238, *Helicostylis tomentosa*, Humiriaceae AD1449, Humiriaceae AD426, *Inga* AD454, *Iryanthera crassifolia*, *Iryanthera elliptica*, *Iryanthera lancifolia*, *Iryanthera tricornis*, Lauracea AD1119, Lauraceae AD1165, Lecythidaceae AD932, Leguminosae AD1066, Leguminosae AD1304, *Leonia glycycarpa*, *Licania macrocarpa*, *Licania* AD17, *Licania* AD293, *Licania* AD471, *Licania* AD569, *Licaria* AD519, *Miconia punctata*, *Minquartia guianensis*, Moraceae AD1374, Myrtaceae AD440, *Naucleopsis amara*, *Naucleopsis* AD508, *Neea* AD437, *Ocotea aciphylla*, *Ocotea amazonica*, *Ocotea argyrophylla*, *Oenocarpus bataua*, Olacaceae AD416, *Osteophloeum platyspermum*, *Parkia panurensis*, *Pithecellobium* AD160, *Pithecellobium* AD324, *Pourouma minor*, *Pourouma tomentosa*, *Pouteria caimito*, *Pouteria* cf. *williamii*, *Pouteria guianensis*, *Protium decandrum*, *Protium hebetatum*, *Protium paniculatum* var. *paniculatum*, *Protium polybotryum*, *Pseudolmedia laevigata*, *Pseudolmedia laevis*, *Qualea paraensis*, Sapotaceae AD418, *Scleronema micranthum*, *Sterigmapetalum obovatum*, *Swartzia cardiosperma*, *Swartzia* AD1085, *Tachigali paniculata*, *Tachigali* AD413, *Tachigali* AD763, *Theobroma* *glaucum, Trymatococcus amazonicus, Virola calophylla, Virola multinervia, Virola pavonis, Virola* AD885, *Warscewiczia schwackei, Xylopia* AD307.

Rare species (X/X/X): *Abarema* AD1260, AD1765, *Albizia gongripii, Amaiona* AD1412, Anacardiaceae AD1971, *Anadenanthera peregrina, Aniba* cf. *williamsii, Aniba* AD1054, Annonaceae AD1325, Annonaceae AD1328, Annonaceae AD1961, *Anthodiscus* AD1929, *Aparithsmium cordatum, Aptandra* AD385, Arecaceae AD956, *Aspidosperma marcgravianum, Astrocaryum aculeatum, Astrocaryum gynacanthum, Botryarrhena pendula, Buchenavia* cf. *viridiflora, Buchenavia tetraphylla, Buchenavia* AD1146, *Buchenavia* AD203, *Calophyllum brasiliense, Cariniana* AD483, *Caryocar gracilis, Casearia suaveolens, Cecropia distachya, Cecropia ficifolia, Cecropia* AD634, Celastraceae AD234, cf. *Heteropteris* AD1089, cf. *Ixora* AD1347, cf. *Ryania* AD1129, cf. *Telitoxicum* AD1898, Chrysobalanaceae AD233, Chrysobalanaceae AD367, *Clusia* AD1044, Clusiaceae AD268, *Coccoloba* AD153, *Compsoneura ulei, Couepia* AD180, *Couratari stellata, Coussapoa* AD1003, *Coussarea* AD1591, *Cupania* AD1289, *Croton palanostigma, Cupania* AD1289, *Cynometra* AD36, Dichapetalaceae AD1113, *Dicranostyles* AD1729, *Doliocarpus* cf. *major, Doliocarpus confertus, Duroia saccifera, Ecclinusa lanceolata, Elaeagia* AD943, *Elaeoluma* AD1052, *Erisma* AD969, *Eschweilera bracteosa, Eschweilera juruensis, Euterpe precatoria, Ferdinandusa chlorantha, Ferdinandusa dissimiflora, Ferdinandusa* AD700, *Genipa williamsii, Goupia glabra, Guapira* AD662, *Guarea septentrionalis, Guarea trunciflora, Guarea* AD1592, *Guarea* AD1712, *Guatteria decurrens, Guatteria puncticulata, Guatteria schomburgkii, Guatteria* AD1124, *Guatteria* AD394, *Heisteria* AD1525, *Helicostylis heteroricha, Helicostylis scabra, Hippocratea* AD1623, *Humiria balsamifera, Hyeronima oblongifolia, Ilex guayusa,* unidentified *1*, unidentified *2, Inga acrocephala, Inga gracilifolia, Inga marginata, Inga plumifera, Inga* AD1334, *Inga* AD439, *Inga* AD831, *Iryanthera* AD1202, *Iryanthera* AD210, *Jacaranda macrocarpa, Kotchubaea* AD1233, *Ladenbergia* AD645, Lauraceae AD1235, Lauraceae AD194, Lauraceae AD497, Lauraceae AD579, Lauraceae AD688, Lauraceae AD968, Leguminosae AD1096, Leguminosae AD1276, Leguminosae AD1534, Leguminosae AD169, Leguminosae AD1723, Leguminosae AD1753, Leguminosae AD1950, Leguminosae AD228, Leguminosae AD333, Leguminosae AD677, Leguminosae AD976, *Licania apetala , Licania arachnoidea, Licania heteromorpha, Licania micrantha, LicaniaAD8, Licaria canella,* Loganiaceae AD562, *Machaerium* AD1957, *Macoubea guianensis, Macrolobium* AD683, *Manilkara bidentata, Maprounea guianensis, Maquira* AD1028, *Matayba purgans, Matisia ochrocalyx,* Meliaceae AD1529, Meliaceae AD341, Menispermaceae AD260, *Miconia* AD1151, *Miconia* AD2535, *Miconia* AD893, *Micropholis egensis, Micropholis madeirensis, Micropholis melinoniana, Micropholis venulosa,* Moraceae AD1703, Moraceae AD410, Moraceae AD560, Moraceae AD923, *Mouriri myrtifolia, Mouriri* AD1713, *Mouriri* AD24, *Moutabea guianensis, Moutabea* AD239, Myrtaceae AD1462, Myrtaceae AD396, Myrtaceae AD494, *Naucleopsis* AD240, *Nealchornea japurensis, Neocouma ternstroemiacea, Oenocarpus bacaba,* Olacaceae AD921, *Olmedia* AD980, *Pachira* AD518, *Parkia igneiflora, Parkia multijuga, Peltogyne* AD500, *Perebea* AD1208, *Perebea* AD1965, *Pinzona coriacea, Pithecellobium claviflorum, Pithecellobium leucophyllum, Pourouma bicolor, Pourouma herrensis, Pourouma myrmecophilla, Pourouma* AD1305, *Pouteria venosa, Pouteria vernicosa, Pouteria* AD1468, *Pouteria* AD756, *Pradosia cochlearia,* Proteaceae AD1611, *Protium* cf. *rubrum, Protium altsonii, Protium apiculatum, Protium aracouchini, Protium* cf. *divaricatum, Protium crassipetalum, Protium krukoffii, Protium* sp nov, *Protium trifoliolatum, Protium* AD1081, *Protium* AD1205, *Protium* AD1385, *Prunus sp, Qualea ingens, Qualea* AD740, *Roucheria punctata,* Rubiaceae AD1448, Rubiaceae AD1605, Rubiaceae AD300, *Sacoglotis amazonica, Sandwithia heterocalyx,* Sapindaceae AD526, Sapotaceae AD1110, Sapotaceae AD310, *Siparuna* AD532, *Siparuna* AD1838, *Sloanea macrophylla, Sloanea cf. obtusifolia, Sloanea* AD1253, *Sloanea* AD1543, *Sterigmapetalum* AD1885, *Sterigmapethalum guianense, Strychnos* AD1274, *Swartzia benthamiana, Swartzia racemosa, Swartzia* AD206, *Symphonia globulifera, Tapirira peckoltiana, Tapirira retusa, Tetragastris panamensis, Theobroma* *subincanum*, *Thyrsodium* AD1799, Tiliaceae AD1680, *Tovomita* AD1622, *Tovomita* AD607, *Tovomitopsis* AD1485, *Trattinickia* AD1114, *Trichilia micrantha*, *Unonopsis buchtieni*, *Vantanea peruviana*, *Virola sebifera*, *Vismia* AD1446, *Vochysia punctata*, *Vochysia venulosa*, Vochysiaceae AD754, *Xylopia micans*

Appendix 2. Vascular plant species recorded with more than 4 individuals (DBH ≥ 2.5 cm) in 30 plots of 0.1 ha, in the Metá area (Colombian Amazonia). N   total number of individuals; Min DBH = minimal DBH; max DBH = maximal DBH; F = number of individuals in well-drained floodplains; S = number of individuals in swamps; U - number of individuals in well-drained uplands; W = number of individuals in white sand areas

	N	Min DBH (cm)	Max DBH (cm)	F	S	U	W
Anacardiaceae							
Anacardium giganteum Hancock ex Engler	9	2.5	37.7			9	
Campnosperma gummiferum (Bentham) Marchand	10	6	21.6		10		
Tapirira guianensis Aublet	46	2.6	21.5		27	18	1
Thyrsodium herrerense Encarnacion	6	4.3	14.8			6	
Annonaceae							
Anaxagorea cf. *angustifolia* Timmerman	27	2.6	6.2	3	24		
Anaxagorea rufa Timmerman	8	2.5	4.7			8	
Annona dolichophylla R.E. Fries	15	2.6	24.5	9	1	5	
Annona hypoglauca Martius	7	4.5	29.7	7			
Annona MS3648	9	2.7	8			9	
Bocageopsis canescens (Spruce ex Bentham) R.E. Fr.	9	2.8	14.8			3	6
Bocageopsis multiflora (Martius) R.E. Fries	20	2.8	11.4		15	5	
Diclinanona calycina (Diels) R.E. Fries	6	2.5	29.8			6	
Diclinanona tessmannii Diels	16	2.5	17	5		7	4
Duguetia flagellaris Huber	7	2.5	3.8	2		5	
Duguetia macrophylla R.E. Fries	6	2.6	5.6	4		2	
Duguetia odorata (Diels) J.F. Macbride	10	2.6	14.8	6		4	
Duguetia stenantha R.E. Fries	5	2.5	5.3			5	
Duguetia cf. *ulei* (Diels) R.E. Fries	7	2.7	4.2			5	2
Ephedranthus amazonicus R.E. Fries	5	2.7	12			5	
Guatteria cf. *decurrens* R.E. Fries	40	2.7	16.6		6	10	24
Guatteria ferruginea St Hilaire	7	2.7	8.3			7	
Guatteria insculpta R.E. Fries	23	2.5	33.3		6	16	1
Guatteria macrocarpa R.E. Fries	6	2.8	9.3			6	
Guatteria macrophylla Blume	46	2.6	11.6	5		39	2
Guatteria MS3131	5	2.7	5	1			4
Guatteriasa tabapensis Aristeg. ex D.M. Johnson & A. Murray	18	2.5	26.5		7		11
Guatteriella tomentosa R.E. Fries	6	4.2	13.5			6	
Oxandra euneura Diels	49	2.7	7.3			49	
Oxandra leucodermis (Spruce ex Bentham) Warming	91	2.5	17.5				91
Oxandra mediocris Diels	8	2.6	17.6	8			
Oxandra polyantha R.E. Fries	1710	2.5	23.2		1710		
Oxandra xylopioides Diels	11	2.8	3.6				11
Pseudoxandra leucophylla (Diels) R.E. Fries	43	2.6	13	1	31	11	
Pseudoxandra aff. *polyphleba* (Diels) R.E. Fries	7	2.7	6.6	1		6	
Unonopsis elegantissima R.E. Fries	8	2.6	3.7			8	

Unonopsis floribunda Diels	15	2.5	12.8	15			
Unonopsis guatterioides (A.DC.) R.E. Fries	21	2.5	15.2	4	11	6	
Unonopsis stipitata Diels	48	2.5	7.8			48	
Unonopsis veneficiorum (C. Martius) R.E. Fries	9	2.6	12.1	9			
Xylopia cf. *calophylla* R.E. Fries	34	2.5	19.3		33	1	
Xylopia cuspidata Diels	7	2.6	4.2			7	
Xylopia nervosa (R.E. Fries) Maas	7	4	24.3	2	5		
Apocynaceae							
Aspidosperma excelsum Bentham	45	2.5	27.3		41		4
Aspidosperma MS3230	21	2.6	16	4	17		
Aspidosperma MS6443	10	4	37.4	10			
Aspidosperma cf. *multiflorum* A.DC.	6	2.5	48.7	6			
Couma catingae Ducke	5	3.5	29.6				5
Forsteronia affinis Muell. Arg.	7	3.2	7.3			7	
Lacmellea foxii (Stapf) Markgraf	11	2.7	10.8			10	1
Macoubea guianensis Aublet	18	3.8	28.7			7	11
Malouetia tamaquarina (Aublet) A.DC.	26	2.6	12.7	4	22		
Odontadenia funigera Woodson	11	3	5		11		
Tabernaemontana disticha A. DC.	10	3.3	6.4			10	
Aquifoliaceae							
Ilex guayusa Loesener	7	4	20		2	1	4
Ilex MS6237	6	2.7	6.6		6		
Araliaceae							
Dendropanax palustris (Ducke) Harms	225	2.5	21				225
Bignoniaceae							
Arrabidaea fanshawei Sandwith	12	2.7	8.5			12	
Arrabidaea prancei A.Gentry	8	2.5	7			8	
Digomphia densicoma (Martius ex DC.) Pilger	572	2.5	52.5				572
Distictis pulverulenta (Sandwith) A.Gentry	8	2.8	5.5			8	
Jacaranda macrocarpa Bureau & K. Schumann ex K. Schumann	28	2.5	17.5			28	
Memora bracteosa (DC.) Bureau ex K. Schumann	6	2.7	5.6	5		1	
Memora cladotricha Sandwith	13	2.5	4.3			13	
Paragonia pyramidata (L.C. Richard) Bureau	17	3	7.6	17			
Tabebuia insignis (Miquel) Sandwith var. *monophylla* Sandwith	84	2.7	9.3		1		83
Tabebuia ochracea (Chamisso) Standley	92	2.5	32				92
Bombacaceae							
Matisia lasiocalyx K. Schumann	14	3.7	17.8	14			
Matisia aff. *malacocalyx* (A. Robyns & Nilsson) W.S. Alverson	25	2.5	11			25	
Pachira brevipes (A. Robyns) W.S. Alverson	96	2.5	28.2				96
Pachira foscolepidota (Steyermark) W.S. Alverson	14	3.6	13				14
Scleronema micranthum (Ducke) Ducke	103	2.5	73.5			33	70
Boraginaceae							
Cordia nodosa Lamarck	14	2.7	7.5			14	
Burseraceae							
Crepidospermum prancei Daly	8	2.5	17			8	

Crepidospermum rhoifolium (Bentham) Swart	6	2.7	5.3			6	
Dacryodes MS2998	11	2.5	13.5			11	
Dacryodes MS3430	17	2.5	31.4			17	
Dacryodes nitens Cuatrecasas	8	2.8	19.5			8	
Dacryodes cf. *peruviana* (Loesener) J.F. Macbride	22	2.5	34.2	3		19	
Dacryodes cf. *roraimensis* Cuatrecasas	24	2.6	13.3			24	
Protium altsonii Sandwith	31	2.6	22.3			15	16
Protium apiculatum Swart	18	2.7	19			18	
Protium aracouchini (Aublet) Marchand	7	2.7	6.8			7	
Protium cf. *crassipetalum* Cuatrecasas	10	2.8	30			10	
Protium decandrum (Aublet) Marchand	11	3.3	24.8			11	
Protium cf. *divaricatum* Engler	7	3	11.6			7	
Protium hebetatum Daly	66	2.5	22.3			66	
Protium cf. *laxiflorum* Engler	7	2.7	8.3			7	
Protium MS2901	6	2.6	6.6	2	4		
Protium MS5830	5	2.7	3.7			5	
Protium nodulosum Swart	10	3.5	20.2	8		2	
Protium opacum Swart	12	3.3	27.8			12	
Protium paniculatum Engler var. *paniculatum*	51	2.5	17.3			51	
Protium unifoliolatum Engler	13	2.6	16.5	13			
Tetragastris cf. *altissima* (Aublet) Swart	6	2.7	16.6	1		5	
Trattinnickia cf. *lawrencei* Standley	5	2.7	8.2			5	
Capparidaceae							
Capparis schunkei Macbride	15	2.5	7.3			15	
Caryocaraceae							
Caryocar glabrum (Aublet) Persoon	6	4	25.8			6	
Caryocar cf. *nuciferum* Linnaeus	9	2.8	11.4		1	8	
Cecropiaceae							
Cecropia distachya Huber	8	4	22.7			8	
Coussapoa cf. *orthoneura* Standley	5	2.5	6.4		5		
Pourouma cucura Standley & Cuatrecasas	6	5.6	45.2	6			
Pourouma myrmecophila Ducke	14	2.7	15.2			14	
Pourouma tomentosa Martius ssp. *tomentosa*	15	2.7	15.8			15	
Celastraceae							
Goupia glabra Aublet	8	6.3	61.6			8	
Hippocratea MS3216	5	2.6	4.2	5			
Salacia bullata Mennega	6	2.7	4.3			6	
Salacia gigantea Loesener	23	2.5	16.5	22		1	
Salacia macrantha A.C. Smith	6	2.5	5.5		1	5	
Tontelea cf. *coriacea* A.C. Smith	6	2.7	8.3			6	
Tontelea aff. *corymbosa* (Huber) A.C. Smith	6	2.5	7.5			6	
Chrysobalanaceae							
Couepia canomensis (Martius) Bentham ex Hooker f.	5	2.8	28			5	
Couepia chrysocalyx (Poeppig & Endlicher)Benth ex Hooker	22	2.6	22.2	2		20	
Couepia guianensis Aublet	5	3	11.3			5	
Couepia MS4947	7	2.6	25.7			7	

Hirtella duckei Huber	8	2.7	5.2			8	
Hirtella guainiae Spruce ex Hooker f.	15	2.7	6.8	11	2	2	
Licania apetala (E.Meyer) Fritsch	18	2.7	24.3			18	
Licania granvillei Prance	18	2.7	23			18	
Licania guianensis (Aublet) Grisebach	8	2.8	7.7			8	
Licania harlingii Prance	5	3.8	16.4		1	4	
Licania heteromorpha (Martius ex Hooker f.) Bentham	41	2.5	22.6			41	
Licania heteromorpha (Martius ex Hooker f.) Bentham var. *glabra* (Martius ex Hooker f.) Prance	7	2.5	21.6	2	1	4	
Licania intrapetiolaris Spruce ex Hooker f.	8	2.8	41.4	2		4	2
Licania laevigata Prance	40	2.5	27.5			40	
Licania lata J.F.Macbride	6	2.5	62.3	6			
Licania longistyla (Hooker f.) Fritsch	21	2.8	12		21		
Licania micrantha Miquel	15	3.3	28.3	1	3	11	
Licania mollis Bentham	15	2.5	19.7			15	
Licania MS5402	6	3.4	21.7			6	
Licania octandra (Hoffsgg. ex Roemer & Schultes) Kuntze ssp. *grandifolia* Prance	11	2.6	13		10	1	
Licania triandra Martius ex Hooker f.	9	2.5	27.7	3		6	
Licania urceolaris Hooker f.	11	3	14.5			11	
MS3602	9	3.4	24.5			9	
Parinari klugii Prance	10	4	91.3		10		
Parinari cf. *rodolphii* Huber	36	2.5	19.7		35	1	
Combretaceae							
Buchenavia macrophylla Spruce ex Eichler	7	2.7	10.8	1	5	1	
Buchenavia MS6194	9	4.8	100		9		
Buchenavia cf. *viridiflora* Ducke	17	3.5	20.3		16	1	
Connaraceae							
Connarus ruber (Poeppig) Planchon	5	3.2	5.5	5			
Pseudoconnarus macrophyllus (Poeppig) Radlkofer	22	2.5	5			22	
Convolvulaceae							
Dicranostyles ampla Ducke	11	2.6	8.2			11	
Dicranostyles holostyla Ducke	10	2.5	5.8	1	3	6	
Maripa glabra Choisy	8	3.5	6.8			8	
Maripa janusiana D'Austin	18	2.5	9.5		16	2	
Turbina MS6375	8	2.5	5.8	8			
Costaceae							
Costus scaber Ruiz & Pavón	16	3	3	16			
Cucurbitaceae							
Cayaponia oppositifolia Harms	7	3.2	14	7			
Cyatheaceae							
Cyathea macrosora (Baker) Domin	6	2.7	5.5			6	
Dichapetalaceae							
Tapura peruviana K. Krause var. *petioliflora* Prance	7	2.7	5.3	1		6	
Dilleniaceae							
Doliocarpus cf. *macrocarpus* Martius ex Eichler	5	3.8	11.4			5	
Pinzona coriacea Martius & Zuccarini	11	3	10.6			11	

Dipterocarpaceae							
Pseudomonotes tropenbosii Londoño, Alvarez & Forero	20	2.5	77.5			20	
Ebenaceae							
Diospyros aff. *glomerata* Spruce	8	2.6	4.2			8	
Diospyros cf. *tetrandra* Hiern	6	2.8	3.7		1	5	
Elaeocarpaceae							
Sloanea AD4020	19	2.7	12				19
Sloanea durissima Spruce ex Bentham	12	2.6	21.6	1		11	
Sloanea gracilis Uittien	5	2.5	13.5	3		2	
Sloanea guianensis (Aublet) Bentham	6	3	10			6	
Sloanea laxiflora Spruce ex Bentham	5	3.8	35.8			5	
Sloanea longipes Ducke	5	3.2	9.9		4	1	
Sloanea parvifructa J.A. Steyermark	20	2.8	11.6				20
Ericaceae							
Satyria panurensis (Bentham ex Meisner) Bentham & Hooker f.	19	2.8	5			19	
Euphorbiaceae							
Alchornea aff. *schomburgkii* Klotzsch	10	2.5	22.4	1	6	3	
Amanoa guianensis Aublet	7	4.8	14.6			7	
Conceveiba guianensis Aublet	16	2.6	15.5		15	1	
Drypetes amazonica Steyermark	22	2.5	70	22			
Hevea nitida Martius ex Muell.Arg.	27	2.6	20.2				27
Hevea pauciflora (Spruce ex Bentham) Muell.Arg.	85	2.5	41	2	14	60	9
Hyeronima alchorneoides Allemão var. *alchorneoides*	5	7.6	65	3		2	
Hyeronima oblonga (Tulasne) Muell.Arg.	11	3.3	14.2			11	
Mabea aff. *angularis* G. Den Hollander	24	2.5	10.2			24	
Mabea maynensis Muell.Arg.	17	2.7	8.2			17	
Mabea cf. *occidentalis* Bentham	6	3	3.8				6
Mabea speciosa Muell.Arg	6	3	4.3			6	
Micrandra siphonioides Bentham	24	5.3	63.5		24		
Micrandra spruceana (Baillon) R.E. Schultes	67	2.6	53.3			67	
Nealchornea yapurensis Huber	8	2.6	15.5			8	
Omphalea diandra Linnaeus	6	3.8	7.2	6			
Podocalyx loranthoides Klotzsch	24	2.7	39	6	9	9	
Richeria grandis Vahl	5	2.7	3.7			5	
Sandwithia heterocalyx Secco	97	2.5	13.8			97	
Sapium marmieri Huber	8	6.5	25.4	8			
Senefeldera macrophylla Ducke	40	2.5	10.6			40	
Senefeldera cf. *verticillata* (Vell.) Croizat	53	2.5	14.4			53	
Flacourtiaceae							
Casearia cf. *arborea* (L.C. Richard) Urban	9	2.6	28.7	7		2	
Lindackeria paludosa (Bentham) Gilg	6	2.7	11.3			6	
MS6960	10	3.2	7.1		10		
Neoptychocarpus killipii (Monachino) Buchheim	54	2.5	6			54	
Ryania speciosa Vahl var. *tomentosa* (Miquel) Monachino	7	2.7	5.8			7	
Guttiferae							

Calophyllum AD3923	12	2.5	12.5				12
Calophyllum AD3969	6	5.2	51.7				6
Calophyllum longifolium Kunth	6	4	7.3		6		
Caraipa grandifolia Martius	30	2.6	17.3		29	1	
Caraipa myrcioides Ducke	5	2.8	41.8			5	
Chrysochlamys membranacea Planchon & Triana	6	2.5	12	2		4	
Clusia amazonica Planchon & Triana	6	2.8	5		3	3	
Clusia columnaris Engler	5	3	5			4	1
Clusia decussata Ruiz & Pavón	11	2.7	7.6			11	
Clusia gaudichaudii Choisy ex Planchon & Triana	6	2.7	4.8			6	
Clusia magnifolia Cuatrecasas	179	3	13.5				179
Clusia MS6280	11	2.5	6		1		10
Clusia spathulifolia Engler	67	3.5	21.8				67
Dystovomita AD3976	5	2.5	6.4				5
Dystovomita MS4875	52	2.5	13.2			22	30
Garcinia macrophylla Martius	14	2.6	26.6	5		9	
Garcinia spruceana (Engler) Hammel	5	2.5	17	2		3	
Haploclathra cf. *paniculata* (Martius) Bentham	10	2.8	35.5			10	
Lorostemon bombaciflorus Ducke	23	2.6	42.3		23		
Lorostemon colombianum Maguire	13	2.5	18			13	
Symphonia globulifera Linnaeus f.	5	3.1	5.5			5	
Tovomita cf. *brevistaminea* Engler	13	2.7	11.3	1		12	
Tovomita cf. *eggersii* Vesque	6	2.7	6.5			6	
Tovomita laurina Planchon & Triana	13	2.7	13.4			13	
Tovomita MS4222	44	2.5	6.8			44	
Tovomita MS4610	7	2.7	5.2			7	
Tovomita cf. *pyrifolia* A.C. Smith	6	4.3	13.1			6	
Humiriaceae							
Sacoglottis amazonica Martius	10	2.5	16.6			10	
Vantanea MS3381	16	2.7	23.3			16	
Vantanea spichigeri A. Gentry	5	2.7	38.5			5	
Vantanea? MS3304	16	3	19.5		16		
Icacinaceae							
Dendrobangia boliviana Rusby	5	3	9.8			5	
Discophora froesii Pires	16	2.5	10				16
Discophora guianensis Miers	10	2.7	9.5			10	
Lacistemaceae							
Lacistema aggregatum (Bergius) Rusby	20	2.7	17.5			20	
Lauraceae							
Anaueria brasiliensis Kostermans	11	2.7	14			11	
Aniba cf. *panurensis* (Meissner) Mez	5	2.5	6			2	3
Aniba cf. *williamsii* O.C. Schmidt	6	2.8	13.3			6	
Endlicheria bracteata Mez	11	2.8	4.3		9	2	
Endlicheria krukovii (A.C. Smith) Kostermans	7	2.5	9.6	6		1	
Licaria aurea (Huber) Kostermans	9	2.7	8.4	2	1	6	
Licaria cannella (Meissner) Kostermans	11	2.5	25.3		1	10	
Licaria macrophylla (A.C. Smith) Kostermans	8	2.5	8.2			8	

Licaria MS4941	5	2.6	5.5			5	
Mezilaurus itauba (Meissner) Taubert ex Mez	6	9 3	135.4			6	
Mezilaurus sprucei (Meissner) Taubert ex Mez	9	2.5	35.4	4		5	
MS2926	5	2.7	6		1	4	
MS3340	7	2.7	14.8			7	
MS3378	11	2.5	7.3			11	
MS3385	15	2.5	11.6			15	
MS3475	8	2.5	4.4			8	
Ocotea aciphylla (Nees) Mez	63	2 7	28.5	2		61	
Ocotea amazonica (Meissner) Mez	12	3.2	61.5			12	
Ocotea argyrophylla Ducke	20	2.8	21.3			20	
Ocotea bofo H.B.K.	17	2.5	14.7		2	15	
Ocotea cf. *javitensis* (H.B.K.) Pittier	44	2.6	15.3			5	39
Ocotea matogrossensis Vattimo	9	3	10.3			9	
Ocotea MS4959	8	2.9	13.4			8	
Ocotea neblinae C.K. Allen	20	2.7	23.7		1		19
Ocotea olivacea A.C. Smith	12	2.5	17.3			12	
Ocotea cf. *petalanthera* (Meissner) Mez	8	2.7	26.3	8			
Ocotea rubrinervis Mez	5	3	10.3			5	
Ocotea tomentella Sandwith cf	5	3	5.6			5	
Pleurothyrium panurense (Meisn.) Mez	9	2.7	6.8	9			
Lecythidaceae							
Cariniana decandra Ducke	6	2.7	6.3			6	
Cariniana multiflora Ducke	5	3.4	63			5	
Couratari oligantha A.C. Smith	28	2.5	32.8		28		
Couratari stellata A.C. Smith	14	2.5	18.2			14	
Eschweilera alata A.C. Smith	41	2.6	51.5			41	
Eschweilera albiflora (A.DC.) Miers	11	4.5	26.3	1	3	7	
Eschweilera andina (Rusby) J.F. Macbride	5	3	8.8	5			
Eschweilera bracteosa (Poeppig ex O. Berg) Miers	5	4.1	18.2			5	
Eschweilera coriaceae (A.DC.) S.A. Mori	95	2.5	39.5	5		90	
Eschweilera itayensis R. Knuth	10	2.6	23.2	3		7	
Eschweilera MS3354	24	2.6	7.8			24	
Eschweilera MS3719	21	2.5	25.8			21	
Eschweilera MS3776	67	2.8	34.7			67	
Eschweilera parvifolia Martius ex A.DC.	78	2.5	30			78	
Eschweilera punctata S.A. Mori	52	2.7	63.5			52	
Eschweilera rufifolia S.A. Mori	22	2.7	34.5			22	
Eschweilera tessmannii R. Knuth	29	2.5	25.2			29	
Gustavia poeppigiana O. Berg	9	3.3	26.8	9			
Lecythis chartacea O. Berg	10	2.7	37.5			10	
Leguminosae							
Abarema claviflora (Spruce ex Bentham) Kemhoonte	14	2.8	8.8		1	13	
Acacia MS6430	5	3.4	7.4	5			
Bauhinia guianensis Aublet	6	2 7	6.3	5		1	
Brownea cf. *macrophylla* Linden ex Masters	70	2.7	23.3	70			
Clathrotropis macrocarpa Ducke	177	2.5	19.6			177	

Clathrotropis nitida (Bentham) Harms	22	2.8	35			22	
Derris longifolia Bentham	13	2.5	58	13			
Diplotropis martiusii Bentham	21	2.8	27.7	2	17	2	
Dipteryx nudipes Tulasne	8	2.6	37.3		3	5	
Heterostemon conjugatus Spruce ex Bentham	48	2.6	12.6			48	
Heterostemon mimosoides Desfontaines	11	4.2	48			11	
Inga acrocephala Steudel	13	2.8	25.7	3	1	9	
Inga aggregata G. Don	5	2.8	18			5	
Inga archeri Britton & Killip	5	3.2	9.4			5	
Inga bourgoni (Aublet) DC.	6	2.7	5.3	5		1	
Inga cf. *brachyrhachis* Harms	43	2.5	25.6		33	10	
Inga capitata Desvaux	6	2.6	6.4			6	
Inga chartaceae Poeppig	8	3	6		7	1	
Inga edulis Martius	6	5	43.6	6			
Inga marginata Willdenow	9	3.5	17.2		3	5	1
Inga pruriens Poeppig	8	2.6	23.3			8	
Inga ruiziana G. Don	16	2.5	6.5	2	2	12	
Inga tenuistipula Ducke	14	2.7	13.8	14			
Inga umbellifera (Vahl) Steudel	5	3	17.8	5			
Lonchocarpus nicou (Aublet) DC.	7	2.7	5.1	2		5	
Machaerium acutifolium Vogel	13	2.8	18.5		12	1	
Machaerium cf. *cuspidatum* Kuhlmann & Hoehne	9	3.2	8	8		1	
Machaerium inundatum (Martius ex Bentham) Ducke	8	2.8	8.6	6		2	
Machaerium macrophyllum Martius ex Bentham	47	2.5	7.7			47	
Machaerium madeirense Pittier	9	2.6	5.3	8		1	
Machaerium quinata (Aublet) Sandwith	9	2.5	12		7	2	
Macrolobium cf. *angustifolium* (Bentham) R.S. Cowan	28	2.6	39			2	26
Macrolobium discolor Bentham	101	2.5	33.7				101
Macrolobium gracile Spruce ex Bentham	36	2.5	21				36
Macrolobium cf. *limbatum* Spruce ex Bentham	31	2.8	15.6		28		3
Macrolobium multijugum (DC.) Bentham	35	2.5	28.6		4	5	26
Macrolobium suaveolens Spruce ex Bentham	57	2.6	36.5			3	54
Macrosamanea amplissima (Ducke) Barneby & Grimes	18	2.6	6.3		18		
Monopteryx cf. *inpae* W. Rodrigues	6	2.8	12.6			6	
Monopteryx uaucu Spruce ex Bentham	13	4	67.5			13	
MS3170	10	3.8	52.2	3		7	
MS3208	5	3.1	8.5	5			
MS3300	12	2.5	9.2		6	6	
MS3451	7	2.7	14.3			7	
MS4865	7	2.8	15.4			7	
MS6749	5	2.8	3.7			5	
Parkia multijuga Benth.	10	2.8	18.5			10	
Parkia cf. *panurensis* Bentham & Hopkins	13	2.5	38		5	5	3
Pithecellobium cauliflorum (Willdenow) Martius	82	2.5	16.8	2	80		
Swartzia cardiosperma Spruce ex Bentham	9	2.5	17.7			7	2
Swartzia laurifolia Bentham	34	2.6	16.5		20	14	
Swartzia MS3534	41	2.5	12.6			41	

Swartzia parvifolia Schery	9	2.7	7.3			9	
Swartzia cf. *pendula* Spruce ex Bentham	6	2.6	6.6		5	1	
Swartzia racemosa Bentham	17	2.5	27.8	12		5	
Swartzia schomburgkii Bentham	45	2.6	73.5			45	
Tachigali cf. *colombiana* Dwyer	6	3.2	27.3		5	1	
Tachigali formicarum Harms	13	2.8	27.2	7	1	5	
Tachigali MS3476	24	2.6	40.8			24	
Tachigali MS3827	15	2.5	14			15	
Tachigali MS3846	7	2.7	49.5			7	
Tachigali paniculata Aublet	7	4.3	68			7	
Tachigali polyphylla Poeppig & Endlicher	6	2.5	13.4			6	
Tachigali ptychophysca Spruce ex Bentham	19	3	10.8				19
Tachigali tessmannii Harms	19	2.5	25.8			17	2
Tachigali ulei Harms	6	4.2	42.5			6	
Vatairea guianensis Aublet	35	3.3	27.5	1	33	1	
Zygia basijuga (Ducke) Barneby & Grimes	26	2.6	9			26	
Zygia latifolia (Linnaeus) Fawcett & Rendle	13	2.6	27.2	13			
Zygia macrophylla (Spruce ex Bentham) L. Rico	18	2.7	5.9	4	14		
Linaceae							
Hebepetalum humiriifolium (Planchon) Bentham	7	3.3	14			1	6
Roucheria calophylla Planchon	9	2.8	16.6		8	1	
Roucheria punctata (Ducke) Ducke	17	2.7	22.4			13	4
Loganiaceae							
*MS*3065	5	2.8	3.7	5			
Strychnos erichsonii Ri. Schomburgk ex Progel	5	2.5	6.5	5			
Strychnos cf. *peckii* B.L. Robinson	20	2.5	9.8		20		
Malpighiaceae							
Byrsonima coniophylla A. Juss.	12	3.5	6.6				12
*MS*3315	6	3.2	9		4	2	
Marcgraviaceae							
Marcgravia cf. *parviflora* L.C. Richard ex Wittmack	7	3	6		6	1	
*MS*2921	5	2.8	4.3		5		
Norantea guianensis Aublet	5	3.3	6.8			5	
Souroubea guianensis Aublet	9	2.7	5.4	8		1	
Melastomataceae							
Bellucia MS3064	5	4.7	20.8	5			
Bellucia MS6188	5	2.5	7.4		5		
Graffenrieda cf. *limbata* Triana	10	2.5	10.5				10
Macairea spruceana O. Berg ex Triana	11	3	5.2				11
Miconia cf. *elaeagnoides* Cogniaux	22	2.5	7.9	16	4	2	
Miconia spichigera Wurdack	8	2.7	4.5			8	
Miconia cf. *tomentosa* (L.C. Richard) D.Don	6	2.8	3.8			6	
Miconia cf. *trinervia* (Swartz) D. Don ex Loudon	24	2.7	8	2	22		
Mouriri cauliflora Martius ex DC.	17	2.5	7.4			17	
Mouriri huberi Cogniaux	5	2.7	22.5			5	
Mouriri nigra (DC.) Morley	19	2.5	14		1	18	
Mouriri vernicosa Naudin	6	3	15.6			6	

Meliaceae							
Guarea cinnamomea Harms	6	3.5	32.7			6	
Guarea MS4514	12	3	27.1	12			
Guarea grandifolia DC.	14	2.5	6.6			14	
Guarea kunthiana Adrien Jussieu	16	2.5	6.7	15		1	
Guarea macrophylla Vahl	5	2.6	5			5	
Guarea purusana C.DC.	41	2.6	49.5	41			
Trichilia martiana C.DC	7	3	9.4	2	1	4	
Trichilia micrantha Bentham	11	2.7	13.4			11	
Trichilia cf. *obovata* W. Palacios	12	4.5	18.7		12		
Trichilia pallida Swartz	7	2.6	7	1		6	
Trichilia septentrionalis C.DC.	6	2.7	9.6			6	
Trichilia stipitata T.D. Pennington	11	2.5	6		8	3	
Menispermaceae							
Abuta grandifolia (Martius) Sandwith	8	2.7	12.7			8	
Abuta imene (Martius) Eichler	25	2.5	7			25	
Abuta obovata Diels	8	3	12.1			8	
Sciadotenia cf. *toxifera* Krukoff & A.C. Smith	5	3	11.5			5	
Telitoxicum minutiflora (Diels) Moldenke	6	3	5.4		3	3	
Telitoxicum MS3816	15	2.6	7.8			15	
Monimiaceae							
Siparuna decipiens (Tulasne) A.DC	5	2.6	10.5			5	
Siparuna guianensis Aublet	18	2.6	8			18	
Siparuna MS3160	7	2.7	5.3	7			
Siparuna MS6928	5	3.6	43		5		
Siparuna pachyantha A.C. Smith	5	3.4	9.5			5	
Moraceae							
Brosimum lactescens (S. Moore) C. Berg	17	2.5	105	11	1	5	
Brosimum rubescens Taubert	11	2.7	29			11	
Brosimum utile (H.B.K.) Pittier ssp. *longifolium* (Ducke) C. Berg	13	2.5	23.1			13	
Brosimum utile (H.B.K.) Pittier ssp. *ovatifolium* (Ducke) C. Berg	14	2.7	48.5		3	9	2
Clarisia racemosa Ruiz & Pavón	6	4.2	37.4	2		4	
Ficus cf. *juruensis* Warburg ex Dugand	5	6.4	10	5			
Helicostylis elegans (J.F. Macbride) C. Berg	12	2.8	24.2			12	
Helicostylis scabra (J.F. Macbride)	11	2.8	29			11	
Helicostylis tomentosa (Poeppig & Endlicher) J.F. Macbride	6	2.6	9			6	
Maquira MS3114	5	3	69.3	5			
Naucleopsis glabra Spruce ex Pittier	6	3.2	26.8	3		3	
Perebea guianensis Aublet	12	2.7	6			12	
Perebea mennegae C. Berg	10	2.7	5.5			10	
Pseudolmedia laevigata Trécul	32	2.6	16.5		3	29	
Pseudolmedia laevis (Ruiz & Pavón) J.F. Macbride	15	2.8	25.7			15	
Sorocea hirtella Mildbraed ssp. *hirtella*	23	2.7	10.6			23	
Sorocea hirtella Mildbraed ssp. *oligotricha* Akkermans & C. Berg	24	2.5	22	10		14	

Sorocea muriculata Miquel	20	2.5	6.6	1	1	18	
Trymatococcus amazonicus Poeppig & Endlicher	16	2.7	9.4			16	
Myristicaceae							
Compsoneura cf. *capitellata* (A. DC.) Warburg	19	2.5	12.7			19	
Iryanthera elliptica Ducke	28	2.6	29			28	
Iryanthera juruensis Warburg	7	2.5	6.6			4	3
Iryanthera cf. *laevis* Markgraf	5	2.7	23			5	
Iryanthera lancifolia Ducke	13	2.6	17.8			13	
Iryanthera MS5064	9	3.3	13.5			9	
Iryanthera polyneura Ducke	113	2.5	22.8		1	78	34
Iryanthera tricornis Ducke	34	2.6	44			34	
Iryanthera ulei Warburg	56	2.5	16.5	12		44	
Osteophloeum platyspermum (A.DC.) Warburg	6	2.5	43.6			6	
Virola calophylla Warburg	37	2.7	31.8	13		24	
Virola duckei A.C. Smith	5	6.6	21			5	
Virola elongata (Bentham) Warburg	45	2.7	18		19	26	
Virola marlenei W.A. Rodrigues	15	2.5	6.7			15	
Virola MS3102	6	6.3	30	6			
Virola MS3311	5	2.7	5.2		5		
Virola MS3344	30	2.5	25.4			30	
Virola MS3580	18	2.5	21.7			18	
Virola MS4508	8	2.5	6.8	5		3	
Virola MS5088	5	2.5	21.5			5	
Virola MS6222	18	2.7	11.6		18		
Virola multinervia Ducke aff.	9	3.5	30.6			9	
Virola pavonis (A.DC.) A.C. Smith	44	2.5	36		5	38	1
Virola surinamensis (Rolander) Warburg	78	2.5	22.2	1	31		46
Myrsinaceae							
Stylogine cf. *longifolia* (Martius ex Miquel) Mez	12	2.6	6.4	12			
Myrtaceae							
Eugenia cf. *beaurepairiana* (Kiaersk.) Legrand	5	2.7	15.6	5			
Eugenia coffeifolia DC.	16	2.5	12.5			16	
Eugenia florida DC.	28	2.5	15	21	7		
Eugenia patens Poiret	8	3	8			8	
Marlierea caudata McVaugh	39	2.6	6.6		28	3	8
Marlierea cf. *schomburgkiana* Berg	17	3.3	10.2				17
Marlierea aff. *spruceana* O. Berg	30	2.5	7.7	1	29		
Marlierea cf. *umbraticola* (H.B.K.) O. Berg	18	2.6	7.7		15	3	
MS3412	6	3.3	21.7			6	
Myrcia fallax (L.C. Richard) DC.	9	2.6	15.3			9	
Myrcia splendens (Swartz) DC.	5	3	11.9			5	
Myrciaria cf. *floribunda* (West ex Willdenow) O. Berg	5	3.3	6	5			
Plinia cf. *duplipilosa* McVaugh	11	2.6	4.5			11	
Nyctaginaceae							
Neea cf. *macrophylla* Poeppig & Endlicher	8	2.5	5.5			8	
Neea parviflora Poeppig & Endlicher	7	2.8	17.6			7	
Neea spruceana Heimerl	12	2.7	10.5			11	1

Neea verticillata Ruiz & Pavón	9	2.7	5.4			4	5
Ochnaceae							
Ouratea chiribiquetensis Sastre	13	2.8	16.8		13		
Ouratea MS3608	6	2.6	9.8			6	
Olacaceae							
Aptandra caudata A. Gentry & Ortiz	9	2.7	4.8			9	
Aptandra cf. *tubicina* (Poeppig) Bentham ex Miers	31	2.6	38			1	30
Heisteria acuminata (Humboldt & Bonpland) Engler	5	3	4.8	4		1	
Heisteria barbata Cuatrecasas	11	2.7	10			11	
Heisteria duckei Sleumer	5	3	19			5	
Minquartia guianensis Aublet	11	3.6	29.8	2		9	
Tetrastylidium cf. *peruvianum* Sleumer	6	2.6	26			6	
Palmae							
Astrocaryum sciophillum (Miquel) Pulle	9	2.8	19	9			
Bactris maraja Martius var. *maraja*	19	2.5	5.5	19			
Euterpe precatoria Martius	70	2.5	18	24	44	2	
Iriartea deltoidea Ruiz & Pavon	18	4.4	25.5	16		2	
Iriartella setigera (Martius) H. Wendland	33	2.5	5.5			33	
Lepidocaryum tenue Martius	22	2.6	4			22	
Mauritia carana Wallace	12	10.6	48.5				12
Mauritia flexuosa L.f	72	3.2	44.7		72		
Mauritiella aculeata (Kunth) Burret	11	10	14.8				11
Oenocarpus bacaba Martius	5	3.4	11.6	1		4	
Oenocarpus bataua Martius	28	2.8	25.7		1	26	1
Socratea exhorriza (Martius) H. Wendland	28	2.7	14.5			28	
Wettinia augusta Poeppig & Endlicher	21	2.6	9.2			21	
Polygalaceae							
Moutabea cf. *guianensis* Aublet	24	2.6	14.7	9		15	
Quiinaceae							
Quiina peruviana Engler	13	2.9	11.6			13	
Rhamnaceae							
Ampelozizyphus amazonicus Ducke	21	2.5	7.4			21	
Rhizophoraceae							
Sterigmapetalum obovatum Kuhlman	5	2.5	16.4			5	
Rubiaceae							
Alibertia cf. *hispida* Ducke	24	2.5	9.6			23	1
Alseis MS3154	8	3.2	11	8			
Botryarrhena pendula Ducke	9	2.7	7.4		7	2	
Calycophyllum MS4415	5	3	20.8			5	
Calycophyllum obovatum (Ducke) Ducke	83	2.5	21.8				83
Chimarrhis gentryana Delprete	5	4.2	23.4			5	
Coussarea brevicaulis Krause	12	2.5	17.5	12			
Coussarea cf. *cephaeloides* C.M. Taylor	5	2.8	9	5			
Coussarea aff. *macrophylla* Muell.Arg.	7	2.7	6.8	7			
Duroia bolivarensis Steyermark	21	2.6	21.6		20	1	
Duroia succifera (Martius ex Roemer & Schultes) Hooker f. ex K. Schumann	17	2.7	8.8			17	

Faramea capillipes Muell.Arg.	6	2.5	3.8			6	
Faramea sessilifolia (H.B.K.) DC	5	2.6	9	4	1		
Ferdinandusa chlorantha (Wedd.) Standley	16	2.7	9.3		7	3	6
Ferdinandusa loretensis Standley cf	14	2.7	45.4	4		10	
Pagamea macrophylla Spruce ex Bentham	34	2.5	19.4			10	24
Palicourea nigricans Krause	7	2.5	14			7	
Platycarpum rugosum Steyermark	14	4.2	51.8		4	1	9
Posoqueria panamensis (Walp. & Duchass.) Walp.	8	2.8	7.2	3		5	
Psychotria cf. *sororiella* Muell.Arg.	6	2.5	4.2			6	
Remijia pedunculata (H. Karsten) Flueck	8	2.6	16.6			8	
Rudgea cf. *duidae* (Standley) Steyermark	7	2.5	4.1			7	
Rudgea loretensis Standley	7	2.7	6.8	5		2	
Warszewiczia coccinea (Vahl) Klotzsch	6	2.8	58.2	5		1	
Warszewiczia schwackei K. Schumann	17	2.7	17.6			17	
Sabiaceae							
Ophiocaryon heterophyllum (Bentham) Urban	23	2.6	12.3		1	22	
Ophiocaryon klugii Barneby cf	8	2.8	11.4			8	
Ophiocaryon manausense (W. Rodrigues) Barneby	25	2.6	8.8			25	
Sapindaceae							
Matayba inelegans Radlkofer	6	2.7	5.8			6	
Talisia eximia K.U. Kramer	13	2.7	7.4		2	11	
Talisia nervosa Radlkofer	17	2.7	7.3	1	7	8	1
Sapotaceae							
Chrysophyllum prieurii A.DC.	5	2.5	26.8			5	
Chrysophyllum sanguinolentum (Pierre) Baehni	52	2.5	45.8			25	27
Chrysophyllum sanguinolentum (Pierre) Baehni ssp. *balata* (Ducke) Pennington	8	7.6	34.8			4	4
Chrysophyllum superbum Pennington	6	2.8	5.2			6	
Ecclinusa lanceolata (Martius & Eichler) Pierre	16	2.5	6.6		2	14	
Micropholis casiquiarensis Aubréville	13	2.7	16.5			13	
Micropholis egensis (A. De Candolle) Pierre	5	2.6	7.6	2	3		
Micropholis guyanensis (A. De Candolle) Pierre	58	2.5	31	3		33	22
Micropholis maguirei Aubréville	35	2.6	39.8			4	31
Micropholis melinoniana Pierre	8	2.8	23			8	
Micropholis venulosa (Martius & Eichler) Pierre	6	3.7	31.8		1	4	1
MS3653	5	5.8	25.4			5	
Pouteria bangii (Rusby) Pennington	8	2.7	33.6	8			
Pouteria cuspidata (A. de Candolle) Baehni	49	2.5	20.4	5	7	36	1
Pouteria cf. *gongrijpii* Eyma	11	2.8	10.6			11	
Pouteria guianensis Aublet	34	2.5	23.8	5		29	
Pouteria MS3953	7	3.2	34.5			7	
Pouteria MS4770	5	3.8	5.2			5	
Pouteria MS5774	5	4	35.3			5	
Pouteria oblanceolata Pires	5	3.8	15.5			2	3
Pouteria reticulata (Engler) Eyma ssp. *reticulata*	9	2.8	19		2	3	4
Pouteria rostrata (Huber) Baehni	14	2.7	26.8			10	4
Pouteria torta (Martius) Radlkofer	31	2.6	30.5	23		8	

Pouteria cf. *williamii* (Aubréville & Pellegrin) Pennington	19	2.6	20.4			19	
Simaroubaceae							
Picramnia latifolia Tulasne	10	2.7	10	6		4	
Picramnia MS3384	7	2.7	8.8			6	1
Sterculiaceae							
Theobroma cacao Linnaeus	66	2.7	25.5	66			
Theobroma microcarpum Martius	9	3	35.8	9			
Theobroma subincanum Martius	13	2.8	12.3			13	
Violaceae							
Leonia cymosa Martius	27	2.5	6			27	
Leonia glycycarpa Ruiz & Pavón	8	2.5	30.5	6		2	
Leonia MS6512	18	2.6	31.3			18	
Rinorea MS3183	15	2.7	8.8	15			
Rinorea neglecta Sandwith	17	2.5	6.5	17			
Rinorea racemosa (Martius) Kuntze	64	2.5	13	24		40	
Vochysiaceae							
Erisma bicolor Ducke	11	2.6	16.2			11	
Erisma splendens Stafleu	5	3.3	10.8			5	
Qualea acuminata Spruce ex Warming	26	2.7	15		26		
Qualea ingens Warming	11	3.6	75.5	6	5		
Qualea paraensis Ducke	11	2.7	41.3			11	
Vochysia lomatophylla Standley	16	2.5	5.3	1		15	
Vochysia MS6230	19	2.6	39.5		19		

Appendix 3. Species found in thirty 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*
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

	Ep	He	Landscape
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
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 (AMB152)	2	1	SW*
Clusiaceae *sp.* 1 (AMB 850)	7		SW*
Cyclanthaceae			

	Ep	He	Landscape
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
Sanyria 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
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*

	Ep	He	Landscape
Catasetum 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
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
Polyradium 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			

	Ep	He	Landscape
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*
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			

	Ep	He	Landscape
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

Appendix 4. List of families and species of ferns and Melastomataceae employed as indicators. The figures represent the number of plants found in the main landscapes (FP = floodplains, SW swamps, TF = Tierra Firme, and WS = white sands). Note that 34 fern plants, which had remained without any identification, are not included

	FP	SW	TF	WS	Total
Blechnaceae					
Salpichlaena hookeriana (Kunze) Alston		10	2		12
Salpichlaena volubilis (Kaulf) J. Sm.		155	8		163
Cyatheaceae					
Cyathea lasiosora (Kuhn) Domin			35		35
Cyathea macrosora (Baker) Domin	1		108		109
Cyathea pungens (Willd.) Domin	1	2			3
Dennstaedtiaceae					
Lindsaea coarctata K. U. Kramer			156		156
Lindsaea guianensis (Aubl) Dryand.			1		1
Lindsaea klotzschiana Moritz ex Ettingsh				338	338
Lindsaea lancea (L.) Bedd.		35	186	29	250
Lindsaea quadrangularis Raddi	4	279	1		284
Lindsaea stricta (Sw.) Dryand.		100		52	152
Lindsaea ulei Hieron.			9		9
Saccoloma inaequale (Kunze) Mett.			19		19
Dryopteridaceae					
Cyclodium meniscioides (Willd.) C. Presl	8	142	114		264
Polybotrya caudata Kunze			329		329
Polybotrya polybotryoides (Baker) H. Christ	20	19			39
Polybotrya pubens Mart.			35		35
Polybotrya sessilisora R C. Moran	56		35		91
Polybotrya sp			65		65
Triplophyllum funestum (Kunze) Holttum			9		9
Triplophyllum dicksonioides (Fée) Holttum			5		5
Hymenophyllaceae					
Trichomanes arbuscula Desv.		912		478	1390
Trichomanes bicorne Hook.				483	483
Trichomanes cellulosum Klotzsch				16	16
Trichomanes elegans Rich.			17		17
Trichomanes hostmannianum (Klotzsch) Kunze		725			725
Trichomanes martiusii C. Presl				175	175
Trichomanes pinnatum Hedw	64	5	198		267
Trichomanes trollii Bergdolt			192		192
Trichomanes vandenboschii P G. Windisch	4797	2496		652	7945
Lomariopsidaceae					
Elaphoglossum discolor (Kunh) C. Chr				34	34
Elaphoglossum styriacum Mickel				2	2
Lomagramma guianense (Aubl.) Ching		2			2

	FP	SW	TF	WS	Total
Lomariopsis japurensis (Mart.) J. Sm.	17		11		28
Marattiaceae					
Danaea elliptica Sm.			573		573
Danaea grandifolia Underw.	5				5
Danaea trifoliata Rchb. Ex Kunze			1		1
Metaxyaceae					
Metaxya rostrata (Humb. & Bonpl. Ex Willd.) C. Presl	1	27	22		50
Nephrolepidaceae					
Nephrolepis biserrata (Sw.) Schott				26	26
Pteridaceae					
Adiantum petiolatum Sw.	7				7
Adiantum terminatum Kunze ex Miq.	10		25		35
Adiantum tomentosum Klotzsch	522	78	867		1467
Schizaeaceae					
Schizaea elegans (Vahl) Sw.		1	24	7	32
Schizaea fluminensis Miers ex J. W. Sturm		1	1		2
Selaginellaceae					
Selaginella amazonica Spring			154	319	473
Selaginella fragilis A. Br.		53			53
Selaginella humboldtiana A. Braun		40			40
Selaginella parkeri (Hook. & Grev) Spring		2	197		199
Selaginella sp.				3	3
Thelypteridaceae					
Thelypteris dentata (Forssk.) E.P. St. John	19				19
Melastomataceae					
Bellucia MS3064	5				5
Bellucia MS6188		5			5
Clidemia bernardii Wurdack			23		23
Graffenrieda limbata Triana				12	12
Henriettella AD6185		1			1
Leandra aristigera (Naud.) Cogn			3		3
Leandra glandulifera (Triana) Cogn.			10	5	15
Leandra rhodopogon (DC.) Cogn.			9		9
Loreya ovata Berg ex Triana			1		1
Macairea spruceana O. Berg ex Triana				41	41
Maieta guianensis Aubl			5		5
Melastomataceae AD6333		4			4
Melastomataceae AD7966			1		1
Melastomataceae AD8611			3		3
Melastomataceae MS5371			1		1
Miconia AD5237	2				2
Miconia AD5413			3		3
Miconia AD5972			1		1
Miconia AD6056			11		11

	FP	SW	TF	WS	Total
Miconia AD6297		60	10		70
Miconia AD6637			2		2
Miconia AD6706		6			6
Miconia AD7244			2		2
Miconia AD7582			4		4
Miconia AD8337			12		12
Miconia AD8614			5		5
Miconia AD8634			3		3
Miconia AD9068			5		5
Miconia AD9228	6	1			7
Miconia AD9394			1		1
Miconia AD9520			2		2
Miconia amnicola Wurdack	7				7
Miconia appendiculata Triana		8			8
Miconia argyrophylla DC			1		1
Miconia aulocalyx C. Martius ex Triana			1		1
Miconia aurea (D. Don) Naudin			3		3
Miconia barbinervis (Benth.) Triana			12		12
Miconia biglandulosa Gleason		1	4		5
Miconia carassana Cogn.			16		16
Miconia cautis Wurdack			5		5
Miconia chrysophylla (L.C. Richard) Urban			2		2
Miconia cionotricha Uribe			16		16
Miconia elaeagnoides Cogniaux	16	4			20
Miconia eugenioides Triana			2		2
Miconia klugii Gleason			3		3
Miconia mazanana J.F. Macbride	1				1
Miconia minutiflora (Bonpl.) DC.			1		1
Miconia MS4963			4		4
Miconia phanerostila Pilger			7		7
Miconia pilgeriana Ule			8		8
Miconia plukenetii Naudin			5		5
Miconia poeppigii Triana			1		1
Miconia prasina (Swartz) DC.			1		1
Miconia pterocaulon Triana			9		9
Miconia pubipetala Miquel		1			1
Miconia punctata (Desr.) D. Don ex DC			1		1
Miconia radulaefolia (Benth.) Naud.		24	2		26
Miconia rimachii Wurdack			2		2
Miconia spichigeri Wurdack			18		18
Miconia splendens (Swartz) Grisebach		1	27		28
Miconia tomentosa (L.C. Richard) D Don			6		6
Miconia traillii Cogniaux			2		2
Miconia trinervia (Swartz) D. Don ex Loudon	2	22			24

	IP	SW	TF	WS	Total
Miconia undata Triana			2		2
Mouriri 7034		2			2
Mouriri acutiflora Naudin	1		1		2
Mouriri cauliflora Martius ex DC			31		31
Mouriri chamissoana Cogniaux			1		1
Mouriri grandiflora A. DC			1		1
Mouriri huberi Cogniaux			8		8
Mouriri MS3104	4				4
Mouriri myrtifolia Spruce ex Triana	2	2	12		16
Mouriri nigra (DC.) Morley		2	28		30
Mouriri retentipetala Morley			1		1
Mouriri vernicosa Naudin			7		7
Myrmidone macrosperma (Mart.) Mart		8	17	68	93
Tococa AD5134	2		7		9
Tococa capitata Trail ex Cogn.	1				1
Tococa chuivensis Wurdack		2			2
Tococa guianensis Aubl.			2		2
Tococa macrophysca Spruce ex Triana				86	86
Tococa setifera Pilger		1			1

Appendix 5. List of fully identified liana species. For each species one selected voucher is added between brackets. Codes of collectors. MJM = M. Macía; MS = M. Sánchez; CG = C. Grández; APY = A. Yánez.

Amaranthaceae

Chamissoa altissima (Jacq.) Kunth (MJM3578)

Annonaceae

Annona hypoglauca Martius (MS5169)

Apocynaceae

Forsteronia acouci (Aublet) A. DC. (MS4756), *Forsteronia affinis* Muell. Arg. (MS5205), *Forsteronia brevifolia* Markgraf (MS5614), *Odontadenia funigera* Woodson (MS7022), *Odontadenia killipii* Woodson (MS6995), *Odontadenia macrantha* (Roemer & Schultes) Markgraf (MS4548), *Odontadenia verrucosa* (Roemer & Schultes) K. Schumann & Markgraf (MS6191)

Aristolochiaceae

Aristolochia goudotii Duch. (MJM1874)

Bignoniaceae

Adenocalymna impressum (Rusby) Sandwith (MJM3407), *Adenocalymna purpurescens* Rusby (MJM3367), *Amphilophium paniculatum* (L.) Kunth (MJM3726), *Arrabidaea chica* (Bonpl.) B. Verl. (MJM1984), *Arrabidaea cinnamomea* (A. DC.) Sandwith (MS4637), *Arrabidaea fanshawei* Sandwith (MS5117), *Arrabidaea florida* DC. (MJM3349), *Arrabidaea japurensis* Bureau & K. Schum. (MJM911), *Arrabidaea pearcei* (Rusby) K. Schum. ex Urb. (MJM3424), *Arrabidaea prancei* Gentry (MS4650), *Callichlamys latifolia* (L.C. Richard) K. Schumann (MS4703), *Clytostoma binatum* (Thunberg) Sandwith (MS2947), *Clytostoma sciuripabulum* Bureau & K. Schum. (MJM1321), *Cydista aequinoctialis* (L.) Miers (MS3742), *Distictella elongata* (Vahl) Urban (MS6089), *Distictella magnoliifolia* (H.B.K.) Sandwith (MS5733), *Distictella parkeri* (DC.) Sprague & Sandwith (CG15881), *Distictis granulosa* Bureau & K. Schum. (MS4869), *Distictis pulverulenta* (Sandwith) Gentry (MS5281), *Lundia densiflora* C. DC (MS5608), *Mansoa kerere* (Aublet) Gentry (MS3286), *Mansoa verrucifera* (Schltdl.) Gentry (MJM2776), *Memora bracteosa* (DC.) Bureau ex K. Schumann (MS6615), *Memora cladotricha* Sandwith (MS5052), *Memora juliae* Gentry (CG11890), *Mussatia hyacinthina* (Standl.) Sandwith (APY2434), *Paragonia pyramidata* (L.C. Richard) Bureau (MS6308), *Pleonotoma variabilis* (Jacquin) Miers (MS4612), *Schlegelia parviflora* (Oersted) Monachino (MS5372), *Schlegelia scandens* (Briquet & Spruce) Sandwith (CG12232), *Stizophyllum inaequilaterum* Bureau & K. Schum. (MJM2430), *Stizophyllum riparium* (Kunth) Sandwith (MJM2775)

Boraginaceae

Tournefortia bicolor Sw. (MJM3215), *Tournefortia coriacea* Vaupel (MJM2412)

Celastraceae

Cheiloclinium anomalum Miers (MS3216), *Cheiloclinium cognatum* (Miers) A.C. Sm. (MS6388), *Cheiloclinium hippocrateoides* (Peyr.) A.C. Sm. (MS6577), *Cheiloclinium klugii*

A.C. Sm. (CG11576), *Cuervea kappleriana* (Miq.) A.C. Sm. (MJM2504), *Hippocratea volubilis* L. (CG9212), *Hylenaea comosa* (Swartz) Miers (MS6348), *Salacia bullata* Mennega (MS5390), *Salacia cordata* (Miers) Mennega (MJM2609), *Salacia gigantea* Loesener (MS6313), *Salacia impressifolia* (Miers) A.C. Sm. (CG11120), *Salacia insignis* A.C. Sm. (MS3084), *Salacia macrantha* A.C. Sm. (MS5078), *Salacia multiflora* (Lam.) DC. (MJM2952), *Salacia opacifolia* (J.F. Macbr.) A.C. Sm. (MJM3126), *Tontelea attenuata* Miers (MS3390), *Tontelea coriacea* A.C. Sm. (MS5527), *Tontelea emarginata* A.C. Sm. (MS6438), *Tontelea ovalifolia* (Miers) A.C. Sm. (MS4925)

Combretaceae

Combretum laurifolium Mart. (MS6971), *Combretum laxum* Jacq. (MS3160), *Combretum llewelyni* Macbride (MJM1872), *Thiloa inundata* Ducke (CG13449), *Thiloa paraguariensis* Eichl. (MJM3600)

Compositae

Piptocarpha opaca (Benth.) Baker (MS4896), *Piptocarpha poeppigiana* (DC.) Baker (CG12668), *Piptocarpha triflora* (Aubl.) Benn. ex Baker (MJM1127)

Connaraceae

Connarus coriaceus Schellenb. (MS4981), *Connarus patrisii* (DC.) Planch. (APY2151), *Connarus punctatus* Planch. (MJM1746), *Connarus ruber* (Poeppig) Planchon (MS4526), *Pseudoconnarus macrophyllus* (Poeppig) Radlkofer (MS5130), *Rourea amazonica* (Huber) Radlkofer (MS6349), *Rourea sprucei* G. Schellenb. (MS5183)

Convolvulaceae

Dicranostyles ampla Ducke (MS4892), *Dicranostyles falconiana* (Barroso) Ducke (MS5330), *Dicranostyles globostigma* Austin (MS5147), *Dicranostyles guianensis* A. Mennega (MS3895), *Dicranostyles holostyla* Ducke (MS5152), *Dicranostyles integra* Ducke (MS4769), *Dicranostyles laxa* Ducke (MS6733), *Dicranostyles scandens* Benth. (MJM2331), *Dicranostyles sericea* Gleason (MS4984), *Ipomoea phyllomega* (Vell.) House (MJM2981), *Maripa axilliflora* D'Austin (MS6233), *Maripa elongata* Ducke (MS6739), *Maripa fasciculata* v. Ooststr. (MS6373), *Maripa peruviana* v. Ooststr. (MS6351)

Cucurbitaceae

Cayaponia glandulosa Cogn. (APY2326), *Cayaponia macrocalyx* Harms (MJM2172), *Cayaponia ophthalmica* R.E. Schult. (APY2236), *Cayaponia oppositifolia* Harms (MS4540), *Cayaponia selysioides* C. Jeffrey (CG14120), *Gurania spinulosa* (Poeppig & Endlicher) Cogniaux (MS6465)

Dichapetalaceae

Dichapetalum odoratum Baill. (CG10248)

Dilleniaceae

Davilla nitida (Vahl) Kubitzki (MS3207A), *Doliocarpus bolivianus* Aymard, ined. (MJM2763), *Doliocarpus brevipedicellatus* Garcke (MJM990), *Doliocarpus dasyanthus* Kubitzki (MS5161), *Doliocarpus dentatus* (Aublet) Standley (MS5978), *Doliocarpus hispidobaccatus* Aymard (MS4820), *Doliocarpus hispidus* Standl. & Williams (CG11545), *Doliocarpus macrocarpus* Martius ex Eichl. (MS6561), *Doliocarpus major* J.F. Gmel. (MJM3129), *Doliocarpus multiflorus* Standley (MS6299), *Doliocarpus novogranatensis* Kubitzki (MS3723), *Neodillenia coussapoana* Aymard (MJM2330), *Pinzona coriacea* Mart. & Zucc. (MS3674), *Tetracera hydrophila* Tr. & Pl. (MJM2530), *Tetracera volubilis* L. (MJM3113), *Tetracera willdenowiana* Steud. (MJM3368)

Ericaceae

Satyria panurensis (Benth. ex Meisner) Benth. & Hooker f. (MS5095)

Euphorbiaceae

Mabea pulcherrima Muell. Arg. (MS5037), *Omphalea diandra* L. (MS6428), *Plukenetia brachybotrya* Muell. Arg. (MJM950), *Plukenetia polyadenia* Muell. Arg. (MS4708)

Gnetaceae

Gnetum leyboldii Tulasne (MS4752), *Gnetum nodiflorum* Brongn. (CG10964)

Guttiferae

Haveliopsis flavida (Benth.) Pl. & Tr. (MS5455)

Icacinaceae

Leretia cordata Vell. (MJM3831)

Leguminosae

Acacia tenuifolia (L.) Willd. (MJM3125), *Bauhinia glabra* Jacq. (MJM3271), *Bauhinia guianensis* Aubl. (MS6374), *Bauhinia outimouta* Aubl. (MS5641), *Bauhinia rubiginosa* Bong. (MJM2789), *Bauhinia rutilans* Spr ex Benth. (MJM3106), *Bauhinia tarapotensis* Benth. ex J.F. Macbr. (MJM1571), *Calliandra carbonaria* Benth. (MJM3202), *Clitoria javitensis* (Kunth) Benth. (MJM1558), *Clitoria pozuzoensis* J.F. Macbr. (MJM3566), *Dalbergia monetaria* L. f. (MS5339), *Dalbergia riedelii* (Radlkofer) Sandwith (MS3670), *Deguelia scandens* Aubl. (CG8935), *Dioclea ucayalina* Harms (MJM3500), *Entada polyphylla* Benth. (CG9106), *Inga ciliata* C. Presl (MS3142), *Lonchocarpus nicou* (Aublet) DC. (MS3545), *Lonchocarpus utilis* A.C. Sm. (APY2100), *Machaerium cuspidatum* Kuhlmann & Hoehne (MS4707), *Machaerium ferox* (Benth.) Ducke (MS3262), *Machaerium floribundum* Benth. (MJM1037), *Machaerium inundatum* (Martius ex Benth.) Ducke (MS6345), *Machaerium kegelii* Meisn. (MJM3210), *Machaerium leiophyllum* (DC.) Benth. (MS3547), *Machaerium macrophyllum* Martius ex Benth. (MS3578), *Machaerium mutisii* Killip ex Rudd (MJM3464), *Machaerium paraense* Ducke (MS5170), *Machaerium quinata* (Aublet) Sandwith (MS4768), *Macrosamanea amplissima* (Ducke) Barneby & Grimes (MS6880), *Piptadenia anolidurus* Barneby (MS6430), *Piptadenia naupensis* Spruce ex Benth. (MJM2104)

Loganiaceae

Strychnos amazonica Krukoff (MS4013), *Strychnos asperula* Sprague & Sandwith (MS3657), *Strychnos barnhartiana* Krukoff (MS4662), *Strychnos darienensis* Seem. (MJM1736), *Strychnos erichsonii* Schomb. (MS3188), *Strychnos guianensis* (Aubl.) Mart. (MJM1682), *Strychnos mitscherlichii* Schomb. (MJM2846), *Strychnos panurensis* Sprague & Sandwith (MS4539), *Strychnos peckii* B.L. Robinson (MS6249), *Strychnos rondeletioides* Spruce ex

Benth. (MS4893), *Strychnos sandwithiana* Krukoff & Barneby (MS3470), *Strychnos toxifera* Schomb. ex Benth. (MJM887)

Malpighiaceae

Banisteriopsis lucida Small (MJM2924), *Banisteriopsis martiniana* (Juss.) Cuatrec. (MS4970), *Byrsonima hypoleuca* Turczaninov (MS5738), *Dicella julianii* (J.F. Macbr.) W.R. Anderson (MS3758), *Diplopterys cabrerana* (Cuatrec.) B. Gates (MJM3201), *Heteropterys aurosericea* Cuatrec. (MJM3144), *Heteropterys cristata* Benth. (MS2927), *Heteropterys multiflora* (DC.) Hochreutiner (MS7042), *Hiraea fagifolia* (DC.) A. Juss. (MS5648), *Hiraea reclinata* Jacq. (CG13229), *Jubelina uleana* (Nied.) Cuatrec. (MJM1953), *Mascagnia benthamiana* (Griseb.) W.R. Anders. (MS5856), *Mascagnia dissimilis* Morton & Moldenke (MJM1559), *Mascagnia macrodisca* (Tr. & Pl.) Nied. (MS3240), *Tetrapterys crispa* Nied. (MS6391), *Tetrapterys mucronata* Cavanilles (MS6371), *Tetrapterys nitida* Mart. ex A. Juss. (MJM732)

Melastomataceae

Blakea rosea (R & P.) Don (MJM449), *Henriettea spruceana* Cogn. (MS6185)

Meliaceae

Trichilia elsae Harms (MS6307)

Menispermaceae

Abuta grandifolia (Martius) Sandwith (MS5528), *Abuta grisebachii* Triana & Planchon (MS5007), *Abuta imene* (Martius) Eichler (MS3603), *Abuta obovata* Diels (MS4873), *Abuta pahni* (Martius) Krukoff & Barneby (MS3940), *Abuta rufescens* Aubl. (MS5751), *Abuta solimoesensis* Krukoff & Barneby (APY2166), *Abuta velutina* Gleason (MJM2969), *Anomospermum grandifolium* Eichl. (CG12079), *Curarea tecunarum* Barneby & Krukoff (MJM3335), *Curarea toxicofera* (Wedd.) Barneby & Krukoff (MJM3603), *Orthomene schomburgkii* (Miers) Barneby & Krukoff (CG11624), *Sciadotenia toxifera* Krukoff & A.C. Sm. (MS6444), *Telitoxicum krukovii* Moldenke (MS4787), *Telitoxicum minutiflorum* (Diels) Moldenke (MS4885)

Myrtaceae

Calyptranthes simulata McVaugh (MS6279), *Eugenia anastamosans* DC. (MS4590)

Olacaceae

Heisteria scandens Ducke (MJM3403)

Palmae

Desmoncus giganteus Hend. (MJM948), *Desmoncus orthacanthos* Mart. (MJM2469)

Passifloraceae

Dilkea acuminata Masters (MS3698), *Passiflora nitida* H.B.K. (MS5747), *Passiflora spinosa* (Poepp. & Endl.) Mast. (CG9159)

Phytolaccaceae

Trichostigma octandrum (L.) H. Walter (MJM1433)

Piperaceae

Piper heterophyllum R. & P. (CG14175), *Piper hispidum* Swartz (MS6457), *Piper laevigatum* H.B.K. (MS5750), *Piper tenuistylum* C. DC. (CG10494)

Polygalaceae

Bredemeyera floribunda Willdenow (MS4237), *Moutabea aculeata* (R. & P.) Poepp. & Endl. (MJM409), *Moutabea guianensis* Aubl. (MS5131), *Securidaca paniculata* L.C. Richard (MS6357)

Polygonaceae

Coccoloba densifrons Martius ex Meissner (MS6310)

Rhamnaceae

Ampelozizyphus amazonicus Ducke (MS3583), *Gouania lupuloides* Urb. (CG11513)

Rubiaceae

Chomelia malaneoides Muell. Arg. (MJM1019), *Guettarda acreana* K. Krause (MJM2277), *Randia altiscandens* (Ducke) C.M. Taylor (MS5172), *Sabicea paraensis* (Schumann) Wernham (CG15499), *Uncaria guianensis* (Aubl.) J.F. Gmel. (MJM2449), *Uncaria tomentosa* (Willdenow ex Roemer & Schultes) DC. (MS6359)

Sapindaceae

Paullinia alata (R. & P.) Don (CG13416), *Paullinia bracteosa* R.E. Fries (MS6346), *Paullinia capreolata* (Aublet) Radlkofer (MS3769), *Paullinia clathrata* Radlkofer (MJM1909), *Paullinia elegans* Griseb. (MJM3291), *Paullinia eriocarpa* Tr. & Pl. (MJM3695), *Paullinia faginea* Radlkofer (CG9232), *Paullinia fimbriata* Radlkofer (MJM1158), *Paullinia fuscescens* Kunth (CG14040), *Paullinia grandifolia* Benth. ex Radlkofer (MJM1770), *Paullinia mariae* J.F. Macbr. (MJM1918), *Paullinia mazanensis* J.F. Macbr. (MS6370), *Paullinia microneura* Cuatrec. (MJM2829), *Paullinia nobilis* Radlkofer (MS4537), *Paullinia pachycarpa* Benth. (MJM1657), *Paullinia rugosa* Benth. ex Radlkofer (MJM730), *Paullinia serjaniifolia* Tr. & Pl. (MJM3353), *Serjania leptocarpa* Radlkofer (MJM3348)

Smilacaceae

Smilax panamensis Morong (CG9763)

Solanaceae

Lycianthes sprucei (Van Huerck & Müll. Arg.) Bitter (CG13776), *Markea coccinea* Rich. (MJM2397), *Markea ulei* (Dammer) Cuatrec. (MS3542)

Sterculiaceae

Byttneria ancistrodonta Mildbr. (MS4579), *Byttneria asterotricha* Mildbr. (MJM2805), *Byttneria coriacea* Britton (CG13163), *Byttneria fulva* Poepp. (CG12645)

Ulmaceae

Celtis iguanaeus (Jacquin) Sargent (MS6462)

Verbenaceae

Aegiphila glandulifera Moldenke, *Aegiphila smithii* Moldenke (CG14962), *Petrea maynensis* Huber (MJM3494), *Petrea volubilis* L. (MS3115)

Violaceae

Corynostylis arborea (L.) S. F. Blake (CG14360)

Vitaceae

Cissus microcarpa Vahl (MJM3756), *Cissus ulmifolia* (Baker) Pl. (MJM3004), *Cissus verticillata* (L.) Nichols. & Jarvis (MJM3393)

SUMMARY

The major goal of this Thesis was the study of the spatial distribution and abundance of different growth forms of tropical rain forest plants, at different spatial scales, in relation to their ecological response to major environmental gradients in methodological NW Amazonia. Basic knowledge of the distribution of individual species and species assemblages is necessary for the conservation of the Amazonian rain forests. Amazon forests are well known for harboring a high plant biodiversity. However, it is still not clear which mechanisms address the species assemblages and the distribution patterns of different growth forms at different spatial scales.

In this study, new insights into comparative environmental control on herbs and woody understory plants, tree, epiphytes and lianas species composition at different spatial scales are presented. These main issues were addressed with a new series of well distributed high resolution relevés of terrestrial vascular plant species composition. These were sampled along the principal environmental gradients in a wide rain forest area in Colombian Amazonia, and adjacent (Amazon) areas of Ecuador and Peru. This study is one of the few at plot level in Amazon forests, which compares different growth forms, including (near)-total epiphyte species, in relation to environmental control in one survey design. As the study is limited to NW Amazonia, humidity (in terms of total annual rainfall) and geomorphology is quite similar between sample sites, thus allowing a more robust analysis of the effect of finer environmental variables as soil elemental contents.

In Chapter 2 the goal was to define differences in species richness and tree and liana species-assemblages in three adjacent terra firme forests in the middle Caquetá, Colombia. A vegetation survey of trees and lianas equal to or more than 10 cm diameter breast height (DBH) was carried out along a single longitudinal transect (10 m x 2160 m) passing through a low plain terrace, a high dissected terrace, and a high plain terrace. Species were classified as either locally abundant or locally rare. Abundant species were defined as "generalists" (in all environments), "intermediate" (in two environments), and "specialists" (in only one environment) using 2x3 contingency table. There were 146 (39%) species classified as locally abundant and 231 (61%) as locally rare. Among the abundant species, 70 percent were generalists, 25 percent were specialists and 5 percent were intermediate. Although there was a significant number of rare species, for those species with sufficient number to statistical test spatial distribution, the results suggest that many species are generalists and that beta diversity at the local scale (2.16 ha) is rather low. Larger data sets over larger geographical areas should be analyzed to determine the degree of species turnover in Amazonian forests.

In Chapter 3 distribution patterns of vascular plants with DBH $\geq$ 2.5 cm were studied on the basis of compositional data from 30 small plots located in the Meta area in Colombian Amazonia. The research questions were: How are distribution patterns of species in relation to local abundance in plots? Do understorey species (defined as species with individuals that never attained DBH $\geq$ 10 cm anywhere) show better correlations with soils and environment than canopy species (defined as species with individuals that attained DBH $\geq$ 10 cm)? Are patterns found in the entire range of landscape units comparable to those found in well-drained uplands alone? Species that occurred in more than one plot showed higher local abundances.

This pattern was consistent among environmental generalists and specialists. Locally rare species (with maximum one individual per plot) occurred mostly in well-drained uplands. Considering all landscape units, Mantel tests showed substantial correlations between environmental data (soil chemical data, drainage and flooding) and species composition. Canopy species were only slightly less correlated with environmental data than understorey species. Elimination of the spatial component in the data did not reduce these correlations. In well-drained uplands, understorey species were better correlated with soils than canopy species. Here, however, the spatial configuration of the plots became more important in explaining species patterns.

In Chapter 4 epiphytism in Colombian Amazonia was described by counting vascular epiphytes in thirty 0.025-ha (5 x 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 (DBH $\geq$ 2.5 cm) had been recorded three 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 $\geq$ 2.5 cm. About 40-60% of the woody plants with DBH $\geq$ 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.

In Chapter 5 in a case-study from Colombian Amazonia, species information from ferns and Melastomataceae was used to explain the compositional patterns of other vascular plant species in 40 widely distributed 0.1-ha plots. Canonical correspondence analysis was applied to regress vascular plant species composition in the forests against information from these two indicator groups (summarized as axes of principal coordinate analyses), together with that from soils, landscape, and the spatial sampling design. In total, 53941 individuals of 2480 vascular plant species were recorded. Of these, 17473 individuals and 132 species were from ferns and Melastomataceae. In 19 well drained upland (tierra firme) plots 19622 vascular plant individuals and 1716 species were found, with 3793 plants and 91 species from ferns and Melastomataceae. In both the set of all landscapes and the subset of tierra firme forests the principal PCoA axes of the two indicator groups were highly related to the main patterns of forest species composition. In principle, therefore, ferns and Melastomataceae can be used to detect and forecast changes in the forest composition of the study area. However, evidence was not obtained that ferns and Melastomataceae show more potential to predict the main patterns in species composition of forests than soil, landscape, and spatial variables. The partioning of the total variation in forest composition showed that the effect of ferns and

Melastomataceae was quite independent from that of soil, landscape, and space. It was suggested that correlative studies of plant indicators with other subsets of tropical forest plants may not allow to separate direct effects from those derived from indirect correlations, given the complexity of the factors governing tropical forest compositional patterns.

In Chapter 6 the aim was to assess patterns of diversity and composition of woody lianas in NW Amazonia. The study was carried out in three different areas in northwestern Amazonia: Metá, forming part of the middle Caquetá basin in Colombia; Yasuní in Ecuador; and Ampiyacu pertaining to the Maynas Province in Peruvian Amazonia Woody lianas with DBH $\geq$ 2.5 cm were surveyed in 0.1-ha plots, that were laid out in floodplains, swamps, and well drained uplands (Tierra Firme) in each of the three study areas. Plot density, diversity (family, genus and species richness as well as Fisher's alpha based on species), and species composition of lianas were regressed against region (or plot coordinates), landscape, extension of landscape units surrounding the plots, soil chemical information, and forest structure using ANOVA, multiple regression and canonical ordination analysis. A total number of 2670 woody lianas were found in 77 0.1-ha plots, including 46 vascular plant families, 126 genera, 263 fully identified species, and 122 morpho-species. Liana density did not respond significantly to landscape, regions, or the interaction of these two factors. However, landscapes and regions differed significantly in liana diversity. Swamps contained the lowest diversity. Ampiyacu plots stood out in their high species richness and Fisher's alpha, while Metá and Yasuní differed far less. In multiple regression the latitudinal position of the plots had the strongest effect on liana Fisher's alpha, but soil and forest structure information did not. In contrast, liana species composition was best related to soil fertility, leading to a distinct position of the tierra firme plots in Colombia. Also important was a longitudinal effect separating the Yasuní plots from the other areas. Despite its uniform rainfall and geomorphology NW Amazonia was not homogeneous in diversity and composition of woody lianas. Patterns of liana diversity and composition were not parallel. The peak in liana diversity in Ampiyacu had no relationship with soil fertility, and might be due to the more central position of this area in the Amazon basin, compared to Yasuní and Metá. Soil fertility was responsible for a strongly outlying liana composition of tierra firme forest in the Colombian area. Independent from soils, the liana assemblages in Yasuní differed from the other areas, possibly due to influx from Andean liana flora elements.

In Chapter 7 the response shape of 24 species and 89 genera of woody vascular plants (DBH$\geq$2.5 cm) to environmental gradients was studied on the basis of 80 0.1-ha plots located across the main landscape units in three different rain forest areas in Colombia, Ecuador, and Peru, NW Amazonia. The following hypotheses are considered: (1) Most genera and species respond to complex environmental gradients with a symmetrical Gaussian function; (2) The response shape of species and genera along a soil gradient is the same as that along a complex species or genera derived gradient. Complex gradients were obtained from ordination analyses (DCA and PCA). For the description of genera and species response shapes, five logistic regression hierarchic models known as HOF models, which range from flat to skewed, were used. In all landscapes, along all gradients, most species showed a response shape different to a symmetrical model. In Tierra Firme forests alone, compared to all landscapes, there were much more flat response shapes for both genera and species along all gradients. Regardless of flat models (no trend) in both all landscapes and Tierra Firme alone, a small proportion of species and genera displayed a similar response shape along the complex and the edaphic gradients. Both hypotheses were rejected. This study supports the continuum concept as the more appropriate model of vegetation organization in Amazonian rainforests. In Tierra Firme, most taxa did not show any preference for a part of the gradient, which corresponds with the idea that compositional species turnover (beta diversity) in this landscape unit is low. In all landscapes, the number symetrical models increased, which supports a higher compositional turnover. Soil fertility (as quantified by the first PCA axis) is not the overridingly dominant factor affecting species distributions. Other factors (e.g. the influence of pests, phylogenetic structure, resource competition, or dispersal) are likely to have a stronger influence upon the distribution of species and genera.

Chapter 8 details the main conclusions of the previous chapters, accompanied by methodological considerations and the general implications for conservation. The main methodological issues discussed were the advantages and disadvantages of the sampled protocol employed, which emphasizes on the undersampling problem and the respective high abundance of rare species in plant inventories in tropical rain forests. It is also concluded that when different growth forms and different spatial scales are merged, a much more complex vegetation model arises. General strategies to preserve the Amazon forests as non-timber forests resource exploitation, and the creation of protected areas are proposed. Finally, it is suggested as necessary to strengthen the links between stake holders and land managers with those engaged in conservation research to improve the communication flow in both directions. Decision makers need to be made more aware of how science can contribute to practical conservation, and vice versa.

SAMENVATTING

Het voornaamste doel van dit proefschrift was het bestuderen van de abundantie en de ruimtelijke verbreiding – op verschillende schalen – van verschillende groeivormen van tropische regenwoudplanten. De relatie tussen deze patronen en de belangrijkste omgevingsgradiënten in het noordwestelijk Amazonegebied werd onderzocht. Basale kennis over de verbreiding van soorten en soortengemeenschappen is noodzakelijk voor de bescherming van het Amazone-regenwoud, dat bekend staat om zijn hoge planten-diversiteit. Het is echter nog niet duidelijk welke mechanismen de samenstelling van soortengemeenschappen en de verbreidingspatronen van groeivormen beinvloeden.

In dit werk laat ik nieuwe inzichten zien betreffende omgevingsinvloeden op de soortensamenstelling van kruiden, houtige ondergroei, bomen, epifyten en lianen. Gegevens hiervoor werden verkregen uit een nieuwe serie gedetailleerde vegetatieopnamen. Deze werden gelegd langs de belangrijkste omgevingsgradiënten in een groot gebied, dat gedeelten van het Colombiaanse, Ecuadoriaanse en Peruaanse Amazonegebied omvat. Dit onderzoek behoort tot de weinige in Amazone-regenwoud dat groeivormen – inclusief bijna alle epifytensoorten – in relatie tot de abiotische omgeving combineert. Het noordwestelijk Amazonegebied, waar het onderzoek plaatsvond, is behoorlijk homogeen wat betreft vochtigheid (gemeten als jaarlijkse neerslag) en geomorfologie, en daarmee zijn de onderzochte gebieden goed vergelijkbaar. Hierdoor konden de abiotische variabelen die op gedetailleerdere schaal variëren, bijvoorbeeld mineraalgehalten in de bodems, beter onderzocht worden.

Hoofdstuk 2 behandelt de verschillen wat betreft soortenrijkdom en floristische samenstelling van bomen en lianen, tussen drie landschapstypen van *tierra firme* (hoogland) in het midden-Caquetá gebied van Colombia,. In een transect door de drie typen (10 m x 2160 m), zijnde laag terras, geaccidenteerd (heuvelig) hoog terras en vlak hoog terras, werden de bomen en lianen met een DBH (diameter op borsthoogte) van minstens 10 cm geïnventariseerd. De soorten werden geclassificeerd als lokaal abundant en lokaal zeldzaam. De abundante soorten werden beschouwd als "generalisten" (voorkomend in alle landschapseenheden), "intermediairen" (in twee landschapseenheden), of "specialisten" (in één landschapseenheid), gebaseerd op contingentie-tabellen van 2 bij 3. Van alle soorten werden 146 (39%) gekwalificeerd als lokaal abundant, en 231 (61%) als lokaal zeldzaam. Van de abundante soorten was 70% generalist, 25% specialist en 5% intermediair. Hoewel er veel zeldzame soorten zijn gevonden, suggereren de resultaten dat veel soorten generalist zijn, en dat de bètadiversiteit op lokale schaal (2,16 ha) laag is. Om de daadwerkelijke graad van ruimtelijke floristische diversiteit (*turnover*) in Amazonewouden te bepalen is een veel grotere hoeveelheid gegevens nodig.

In Hoofdstuk 3 worden patronen van verbreiding van vaatplanten in het Metá-gebied gepresenteerd. Planten met DBH van minstens 2,5 cm werden geregistreerd in 0,1 ha plots, met als doel het beantwoorden van de volgende drie vragen: Hoe zijn de verbreidingspatronen van soorten gerelateerd aan lokale abundantie in de plots? Zijn ondergroeisoorten (soorten met individuen die in de hele opname nooit een DBH boven 10 cm hebben) sterker gecorreleerd aan het abiotische milieu dan kronendaksoorten (soorten met individuen met een DBH van 10 cm of meer)? Zijn de in alle landschapseenheden gevonden patronen vergelijkbaar met die van alleen de hooglandplots? De soorten die in meer dan één plot werden gevonden waren ook lokaal meer abundant. Dit patroon gold voor zowel generalisten als specialisten. De lokaal zeldzame soorten (met maximaal één individu per plot) kwamen meestal in het hoogland voor. Een Mantel-test waarin alle landschapseenheden werden verwerkt gaf hoge correlaties tussen omgevingsvariabelen (chemische eigenschappen van de bodems, drainage en overstroming) en floristische samenstelling. De kronendaksoorten gaven een zwakkere correlatie met de omgeving dan ondergroeisoorten. Het elimineren van de ruimtelijke component maakte de correlaties niet zwakker. Anderzijds waren in het hoogland de ondergroeisoorten sterker gecorreleerd met de bodemgesteldheid dan de kronendaksoorten, en bleek de ruimtelijke configuratie de belangrijkste factor voor de floristische patronen.

In Hoofdstuk 4 wordt de samenstelling van vasculaire epifyten in het Metá-gebied beschreven. Deze werden bemonsterd in 30 plots van 5 x 50 m, gelegd in de belangrijkste landschapseenheden van dit gebied. Elke plot werd naast een 0,1 ha plot gelegd, waarvan de bomen- en lianensamenstelling drie jaar daarvoor al bestudeerd was. Het doel van deze epifytenstudie was het verkennen van abundantie, diversiteit en verbreiding van epifyten in de betreffende landschapseenheden. In totaal werden 6129 individuen bemonsterd, behorende tot 27 families, 73 genera, en 213 soorten (waarvan 59 morfo-soorten). De belangrijkste families wat betreft soortenvertegenwoordiging en abundantie waren Araceae, Orchidaceae en Bromeliaceae. In totaal werden 2763 epifytendragende bomen (forofyten) geregistreerd, waarvan 1701 (62%) met een DBH van minstens 2,5 cm. Tussen 40 en 60% van de houtige planten met een DBH van 2,5 cm of meer droeg epifyten, dus er was geen sterke forofyten-limitatie in de landschapseenheden. Het epifytisme was meestal beperkt tot de stammen en de boomvoeten. Evenals bij de bomen was epifytensamenstelling sterk gerelateerd aan het landschapstype. Anderzijds waren de verschillen in abundantie en diversiteit (uitgedrukt in soortenrijkdom en Alfa-Fisher waarden) tussen de landschapseenheden verwaarloosbaar, dit in tegenstelling tot het gevonden patroon bij bomen. Deze resultaten manen tot grote voorzichtigheid bij het extrapoleren van conclusies gebaseerd op verbreiding en dynamiek van boomsoorten naar andere groeivormen met een sterk afwijkende ecologie.

Hoofdstuk 5 handelt over de vraag of de floristische samenstelling van vaatplanten in Amazone-regenwoud voorspeld kan worden door een inventarisatie van indicatieve plantengroepen: varens en Melastomataceae. Gegevens van 40 ruimtelijk goed verspreide vegetatieopnamen werden hiertoe geanalyseerd met behulp van Canonische Correspondentie-Analyse (CCA), oftewel een regressie van de samenstelling van vaatplanten over verklarende variabelen. Voor deze variabelen werd informatie gebruikt afkomstig van de twee genoemde indicator-plantengroepen (samengevat als assen van een Principale Coördinaten-Analyse), en daarnaast de bodemgesteldheid, landschapseenheden en de ruimtelijke configuratie van de opnamen. In totaal werden 53.941 individuen bemonsterd, behorend tot 2480 soorten. Hiervan waren 17.473 individuen en 132 soorten varens of Melastomataceae. Het deel van de opnamen dat in hoogland (*tierra firme*) werd gemaakt gaf 19.622 individuen en 1716 soorten, waarvan 3793 planten en 91 soorten tot de indicatorgroepen behoorden. Zowel in de gehele dataset, dus met alle landschapseenheden, als in de sub-set met alleen de hoogland-opnamen, waren de belangrijkste assen van de Principale Coördinaten-Analyse (PCoA) sterk gerelateerd aan de patronen van soortensamenstelling in de bossen. Hieruit volgt dat varens en Melastomataceae gebruikt kunnen worden voor het typeren en voorspellen van veranderingen in de floristische samenstelling in het bestudeerde gebied. Tegelijk concludeerden we dat er geen statistische aanwijzing is dat varens en Melastomataceae een sterkere voorspellende waarde hebben dan bodems, landschapstypen en ruimtelijke variabelen. Het onderverdelen van de verklaarde variatie in de samenstelling van de bossen liet zien dat het verklarende effect van de indicator-plantengroep grotendeels onafhankelijk was van bodemfactoren, landschap en de ruimtelijke verbreiding van de plots. Dit geeft aan dat bij het correleren van indicatorsoorten(groepen) aan andere plantengroepen de directe causale verbanden moeilijk onderscheiden kunnen worden van de indirecte correlaties, als gevolg van de vele factoren die mogelijk de verbreiding van tropische regenwoudplanten beinvloeden.

Hoofdstuk 6 behandelt de diversiteit en samenstelling van houtige lianen in het noordwestelijke Amazonegebied. Deze werden onderzocht in drie gebieden: het Metá-gebied in de vallei van de midden-Caquetá in Colombia, het Yasuní-gebied in Ecuador, en Ampiyacu in de Peruaanse Amazone-provincie Maynas. In plots van 0,1 ha werden alle houtige lianen met een DBH van minstens 2,5 cm bemonsterd. In elk van de drie regio's werden plots gelegd in bossen op vloedvlaktes van de rivieren, in moerasbossen en in hoogland-bossen. De dichtheid, diversiteit (soorten-, genera- en familierijkdom en Alfa-Fisher waarden) en samenstelling van lianen in de plots werd geanalyseerd met behulp van multiple regressies, ANOVA en CCA. De verklarende variabelen die we gebruikt hebben zijn: regio (geografische coördinaten van de plots), landschapstype, oppervlakte van het betreffende landschapstype rondom de plot, bodemchemische eigenschappen, en structuur van het bos. In totaal werden in de 77 plots 2670 lianen gevonden, behorend tot 46 families, 126 genera, 263 soorten en 122 morfosoorten (niet geïdentificeerd tot op soortsniveau). De lianendichtheid verschilde niet significant tussen landschapstypen of regio's, noch tussen interactietermen van deze twee. Anderzijds verschilde de diversiteit wel tussen landschapstypen en regio's: de moerasbossen vertoonden de laagste diversiteit. De plots gelegd in Ampiyacu hadden de hoogste soortenrijkdom en Alfa-Fisher waarden; deze waarden waren voor Metá en Yasuní ongeveer gelijk.

Hoofdstuk 7 rapporteert over de respons van 24 soorten en 89 genera van houtige vaatplanten (DBH van minstens 2,5 cm) op enkele abiotische omgevingsgradiënten. De gegevens hiervoor werden genomen van 80 vegetatieopnamen van 0,1 ha, gelokaliseerd in de belangrijkste landschapstypen van drie regenwoudgebieden in Colombia, Ecuador en Peru. De onderzochte hypothesen waren: (1) de meeste genera en soorten vertonen een symmetrische Gaussiaanse respons op complexe omgevingsgradiënten, (2) de vorm van de responscurve van genera en soorten op een bodemgradiënt is dezelfde als die op een complexe gradiënt op basis van soorten- en genera-samenstelling van de gehele vegetatie. De omgevingsgradiënten werden verkregen door middel van ordinaties. Vijf hiërarchische logistische modellen werden gebruikt voor de beschrijving van de vorm van de responscurves, bekend onder de naam HOF-modellen. Deze variëren van vlak (geen respons) tot scheef (*skewed*). De meerderheid van de soorten vertoonde een niet-symmetrische respons op alle gradiënten en in alle landschapstypen. In vergelijking tot de andere landschapstypen, waren alleen in de hoogland-bossen meer soorten en genera die een vlakke (dus geen) respons vertoonden op alle omgevingsgradiënten. Als men de vlakke respons buiten beschouwing laat, waren er weinig soorten en genera die op de bodemgradiënt eenzelfde type curve vertoonden als op de andere complexe gradiënt. Dit gold zowel voor de analyse van alle landschapstypen bij elkaar, als voor de analyse van alleen de hoogland-bossen. Beide hypothesen werden dus verworpen. Deze resultaten suggereren dat het zogenaamde continuümconcept het sterkst van toepassing is op het model van vegetatie-organisatie in Amazone-regenwouden. In hoogland-bossen had het grootste deel van de taxa geen voorkeur voor een bepaald deel van de gradiënt. Dit duidt erop dat de soorten-vervanging (*turnover*) of bètadiversiteit in dit landschapstype laag is. Bij de analyse van alle landschapstypen samen werden meer symmetrische responscurven gevonden, wat suggereert dat er een vrij sterke graad van soorten-vervanging is over de gradiënt. De bodemvruchtbaarheid (uitgedrukt als de eerste as van de Principale Componenten-Analyse) bleek geen dominerende factor die soortenverbreiding bepaalt. Andere factoren, zoals ziekten, fylogenetische structuur, competitie, of zaadverspreiding, hebben waarschijnlijk een grotere invloed op het verbreidingspatroon van soorten en genera.

Hoofdstuk 8 belicht de belangrijkste conclusies van de voorafgaande hoofdstukken, bediscussieert de methodologie en bespreekt de implicaties voor natuurbehoud. De belangrijkste methodologische punten die besproken worden zijn de voor- en nadelen van het bemonsteringsprotocol, in termen van problemen met onderbemonstering en het daaruit voortvloeiende hoge aantal gevonden zeldzame soorten in tropische regenwouden. Daarnaast concludeer ik dat het door elkaar gebruiken van verschillende groeivormen en ruimtelijke schalen leidt tot een complex vegetatiemodel. Verder worden strategieën gesuggereerd voor het behoud van Amazone-wouden, de exploitatie van non-timber producten, en het creëren en onderhouden van reservaten. Als laatste wordt benadrukt dat communicatie tussen beleidsmakers en onderzoekers noodzakelijk is voor natuurbehoud. Beide groepen moeten zich er sterk van bewust zijn wat de bijdrage voor natuurbehoud is die de andere groep kan leveren

RESUMEN

El principal objetivo de este trabajo fue estudiar la abundancia y distribución espacial de diferentes formas de crecimiento vegetal en bosques húmedos tropicales, a diferentes escalas espaciales, como respuesta ecológica a los mayores gradientes ambientales en la Amazonía noroccidental. Ampliar el conocimiento básico acerca de la distribución de especies individuales y grupos de especies, es necesario para la conservación de los bosques húmedos Amazónicos. Estos ecosistemas boscosos son conocidos por albergar una alta biodiversidad vegetal. Sin embargo, aún no es claro cuales mecanismos determinan los agrupamientos de especies y los patrones de distribución de las distintas formas de crecimiento a diferentes escalas espaciales.

En este estudio, se presentan nuevos aportes respecto al control ambiental sobre la distribución y composicion florística de hierbas, arbustos, árboles, epífitas y lianas. Los respectivos análisis de los diferentes tópicos expuestos anteriormente, fueron basados en información proveniente de una nueva serie de parcelas que incluyen una alta resolución muestral de plantas vasculares. Dichas parcelas fueron localizadas a lo largo de la principales unidades de paisaje en una amplia area de bosques tropicales en la Amazonía Colombiana, y áreas adyacentes de la Amazonía Ecuatoriana y Peruana. Esta investigación, es una de las pocas al nivel de parcelas en bosques Amazónicos que compara formas de crecimiento, incluyendo (casi) el total de especies epífitas, y su relación con el medio ambiente en un mismo diseño de muestreo. Debido a que está limitado a la Amazonía noroccidental, la humedad (en términos de precipitación annual) y la geomorfología son bastante similares entre los sitios de muestreo. Esto permite por tanto un análisis más robusto del efecto de variables abioticas más finas como, por ejemplo, el contenido de minerales en los suelos.

En el capitulo 2 se deseaba saber si era posible definir diferencias en cuanto a la riqueza de especies y los agrupamientos florísticos de árboles y lianas sobre tres unidades del paisaje en tierra firme en el medio río Caquetá, Colombia. Se llevó a cabo un inventario de los árboles y lianas con diámetro a la altura del pecho (DAP) igual o mayor de 10 cm, a través de un transecto longitudinal (10 m x 2160 m) pasando sobre una terraza plana baja, una terraza alta disectada y una terraza alta plana. Las especies fueron clasificadas como localmente abundantes y localmente raras. Las especies abundantes fueron definidas como "generalistas" (en todas las unidades de paisaje), "intermedias" (en dos unidades) y "especialistas" (en unicamente una unidad), usando tablas de contingencia de 2x3. 146 (39%) especies fueron clasificadas como localmente abundantes y 231 (61%) como localmente raras. Entre las especies abundantes, el 70 por ciento fueron generalistas, el 25 por ciento especialistas y el 5 por ciento intermedias. Aunque hubo un gran número de especies raras, para aquellas especies con abundancia y frecuencia suficiente para que su distribución fuera analizada estadísticamente, los resultados sugieren que muchas especies son generalistas y que la diversidad beta a escala local (2.16 ha) es baja. Son necesarias bases de datos mucho más grandes para determinar el grado de recambio de las especies en los bosques amazónicos.

En el capítulo 3, patrones de distribución de especies de plantas vasculares con DAP $\geq$ 2.5 cm fueron estudiados basados en datos de composición florística provenientes de 30 parcelas de 0.1-ha localizados en el area del Metá, Amzonía Colombiana. Las preguntas de investigación fueron: ¿Cómo son los patrones de distribución de

especies en relación con la abundancia local en las parcelas? ¿Muestran las especies de sotobosque (definidas como las especies con individuos que en todo el inventario nunca alcanzan DAP $\geq$ 10 cm) mejor correlación con el medio ambiente que las especies del dosel (definidas como las especies con individuos que presentan DAP $\geq$ 10 cm)? ¿Son los patrones encontrados en todas las unidades del paisaje comparables con los que se encuentran en solamente Tierra Firme? Las especies encontradas en más de una parcela presentaron mayor abundancia local. Este patrón fue consistente entre generalistas y especialistas. Las especies localmente raras (con máximo un individuo por parcela) ocurrieron principalmente en Tierra Firme. Cuando se consideraron todas las unidades de paisaje, el test de Mantel presentó altas correlaciones entre los datos medio ambientales (propiedades químicas de los suelos, drenaje e inundación) y la composición florística. La especies del dosel fueron ligeramente menos correlacionadas con el ambiente que las especies de sotobosque. La eliminación de el componente espacial en los datos no redujo las correlaciones. Sin embargo, en Tierra Firme, las especies de sotobosque estuvieron mejor correlacionadas con los suelos que las especies del dosel. En este caso la configuración espacial de las parcelas aparece como el factor explicatorio más importante de los patrones florísticos.

En el capítulo 4 el epifitismo de plantas vasculares en la Amazonía Colombiana fue descrito por medio de 30 parcelas de 0.025-ha (5 x 50 m) localizadas en las principales unidades de paisaje en el área Metá, Amazonía Colombiana. Cada parcela fue localizada adyacentemente a una parcela de 0.1-ha en la cual la compsición de árboles y lianas (DAP $\geq$ 2.5 cm) había sido estudiada tres años antes. El objetivo de este estudio fue explorar la abundancia, diversidad y distribución de epífitas en las principales unidades del paisaje. En total fueron muestreados 6129 individuos de epífitas vasculares que pertenecen a 27 familias, 73 géneros, y 213 especies (dentro de las cuales se incluyen 59 morfo-especies). Araceae, Orchidaceae, and Bromeliaceae fueron las familias más abundantes y especiosas. Un total de 2763 forofitos fueron registrados, de los cuales 1701 (62%) tuvo un DAP $\geq$ 2.5 cm. Entre el 40-60% de las plantas leñosas con DAP $\geq$ 2.5 cm tenía epífitas, lo cual significa una baja limitación de forofitos en todas las unidades de paisaje. El epiftismo estuvo principalmente concentrado sobre los troncos y las bases. Similar que los árboles, los agrupamientos de especies epífitas estuvieron bien asociados con las unidades de paisaje. Sin embargo, al contrario que los árboles, la abundancia y diversidad (riqueza de especies y valores del Alfa de Fisher) escasamente difieren entre paisajes. Estos resultados proponen máxima precaución cuando se desean extrapolar explicaciones de la distribución y dinámica de especies arbóreas a otras formas de crecimiento con una ecología totalmente diferente.

En el capitulo 5, en un estudio de caso en la Amazonia Colombiana, información de especies de helechos y Melastomataceae fue usada para explicar los patrones de composición florística de otras plantas vasculares en 40 parcelas ampliamente distribuidas. Análisis de Correspondencia Canónicos (ACC) fueron empleados para regresar la composición de especies de plantas vasculares en los bosques. Como variables explicatorias se usó información proveniente de estos dos grupos indicadores (resumidos como ejes de Análisis de Coordenadas Principales), suelos, paisajes y el diseño espacial del muestreo. En total, 53941 individuos que pertenecen a 2480 especies de plantas vasculares fueron registrados. De estos, 17473 individuos y 132 especies fueron helechos y Melastomataceae. En 19 parcelas localizadas en Tierra Firme fueron registrados 19622 individuos y 1716 especies, de las cuales 3793 plantas y 91 especies fueron helechos y Melastomataceae. Tanto en el set de datos considerando todos los paisajes como sólo Tierra Firme, los ejes principales derivados del Análisis de Coordenadas Principales (PCoA) fueron fuertemente relacionados con los principales patrones de composición de especies en los bosques. Por lo tanto, en principio, helechos y Melastomataceae pueden ser usados para detectar y predecir cambios en la composición florística de los bosques en el área de estudio. Sin embargo, no se obtuvo evidencia estadística de que helechos y Melastomataceae tienen un mayor potencial predictivo de los principales patrones florísticos que suelos, paisajes y variables espaciales. La partición de la variación en la composición de los bosques mostró que el efecto proveniente de helechos y Melastomataceae fue bastante independiente de los suelos, el paisaje y el espacio geográfico. Esto sugiere por tanto que estudios correlativos de especies vegetales indicadoras con respecto a otros subsets de plantas tropicales podria no permitir la separación de efectos directos, de aquellos derivados de correlaciones indirectas, dada la complejidad de los factores que goviernan los patrones de composición de los bosques tropicales.

En el capítulo 6 el objetivo fue evaluar patrones de diversidad y composición de lianas leñosas en la Amazonía noroccidental. Este estudio fue llevado a cabo en tres diferentes áreas de la Amazonía noroccidental: Metá, que forma parte de la cuenca del medio Caquetá en Colombia; Yasuní, en Ecuador; y Ampiyacu que pertenece a la provincia de Maynas en la Amazonía Peruana. Lianas leñosas con DAP $\geq$ 2.5 cm fueron muestreadas en parcelas de 0.1-ha, localizadas sobre planos inundables, pantanos y Tierra Firme, en cada una de las tres áreas de estudio. La densidad, diversidad (riqueza de familias, generos y especies, así como valores del Alfa de Fisher basado en especies), y composición de lianas por parcela, fue analizada por medio de regresiones múltiples, ANOVA, y ACC. Las variables explicatorias empleadas fueron: región (coordenadas geográficas de las parcelas), paisaje, extensión de las unidades de paisaje alrededor de cada parcela, propiedades químicas de los suelos, y estructura del bosque. En total fueron encontradas 2670 lianas en 77 parcelas de 0.1-ha, las cuales incluyen 46 familias, 126 géneros, 263 especies botánicas y 122 morfo-especies. La densidad de lianas no mostro diferencias significativas con respecto a el paisaje y la región, o la interacción de estos dos factores. Sin embargo, paisaje y region diferieron significativamente en cuanto a la diversidad. Los pantanos presentaron la menor diversidad. Las parcelas de Ampiyacú presentaron la mayor riqueza de especies y valores de Alfa Fisher, mientras que Metá y Yasuní difieren muy poco.

En el capítulo 7 la forma de respuesta a gradientes ambientales de 24 especies y 89 géneros de plantas leñosas vasculares (DAP $\geq$ 2.5 cm), fue estudiada sobre la base de 80 parcelas de 0.1-ha localizadas en las principales unidades de paisaje en tres areas boscosas en Colombia, Ecuador y Perú, Amazonía noroccidental. Las hipótesis de trabajo son las siguientes: (1) La mayoría de los géneros y especies responden a gradientes ambientales complejos con forma de una función Gaussiana simétrica. (2) La forma de respuesta de géneros y especies a lo largo de un gradiente edáfico es la misma que a lo largo de un gradiente complejo derivado de los datos de especies o géneros. Los gradientes ambientales fueron obtenidos por medio de análisis de ordenación. Para la descripción de la forma de respuesta de los géneros y especies, fueron usados cinco modelos jerárquicos de regresiones logísticas conocidos como los modelos HOF, los cuales varían desde planos a sesgados. En todos los paisajes y a lo largo de todos los gradientes, la mayoría de las especies presentaron formas de respuesta distintas del modelo simétrico. En unicamente los bosques de Tierra Firme, comparado con todos los paisajes, hubo mucho más modelos planos (ninguna tendencia) tanto para géneros como para especies a lo largo de todos los gradientes ambientales. Sin considerar los modelos planos, tanto en todos los paisajes como en Tierra Firme unicamente, una pequeña proporción de géneros y especies presentó un modelo de respuesta similar a lo largo del gradiente edáfico y los otros gradientes complejos. Ambas hipótesis fueron rechazadas. Este estudio soporta el concepto del continuo como el modelo de organización de la vegetación más apropiado en los bosques húmedos Amazónicos. En Tierra Firme, la mayor parte de los taxones estudiados no mostraron ninguna preferencia por una parte específica del gradiente. Este resultado corresponde con la ideade que el recambio de especies (diversidad Beta) en esta unidad de paisaje es bajo. En todos los paisajes, el número de modelos simétricos aumentó, lo cual soporta un mayor recambio de especies a lo largo del gradiente. La fertilidad del suelo (cuantificada por el primer eje del Análisis de Componentes Principales-ACP-), no es el factor dominante que determina la distribución de las especies. Otros factores (por ejemplo la influencia de pestes, la estructura filogenética, la competición por recursos, o la dispersión) tienen probablemente una influencia más fuerte sobre la distribución de especies y géneros.

El capítulo 8 resalta las principales conclusiones de los capítulos previos, acompañado de consideraciones metodológicas, e implicaciones generales para la conservación. Los principales temas metodológicos discutidos fueron las ventajas y desventajas del protocolo muestral empleado, el cual hace énfasis en el problema del sub-muestreo y la respectiva alta abundancia de especies raras en los inventarios en bosques húmedos tropicales. Se concluye, además, que cuando diferentes formas de crecimiento y escalas espaciales son mezcaladas, emerge un modelo de vegetación mucho más complejo. Se proponen estrategias generales para preservar los bosques Amazónicos como la explotación de recursos no maderables, y el mantenimiento y creación de áreas protegidas. Finalmente, se sugiere la necesidad de reforzar los vínculos y la comunicación entre los tomadores de decisiones y los planificadores del uso de la tierra con aquellos comprometidos en la investigación para la conservación. Quienes toman decisiones necesitan estar más conscientes de cómo la ciencia contribuye a la conservación y viceversa.

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CURRICULUM VITAE

Alvaro J. Duque M. was born on 30th November 1965 in Medellín, Colombia. He received his BSc degree in Forestry Engineering at Universidad Nacional de Colombia, Medellín, in 1995. His research project to obtain his BSc entitled *'Correlación suelos-bosques en la Amazonía Colombiana'* was considered meritorious. Afterwards he participated in the research project *Comparación de los paisajes de Orinoquia y Amazonia (ORAM)* in the Instituto Geográfico Agustín Codazzi for two and a half years. Then, he got involved in an international project entitled *"Non-timber forest plant resources in NW amazonia"*, which was founded by the European Commision and carried out at the Universidad de Los Andes, Colombia, where he continued with the ecological studies of Amazon forests. He has also participated as a consultant in several projects, as for example, the environmental impact of the Central Oil Pipeline of Colombia (CIA, Universidad de Antioquia), and Plan management of several watersheds in the Amazon area (Corporación para la Investigación y el Desarrollo agropecuario –CINDAP-). During his Ph.D thesis he has participated in symposiums and workshops on invitation. He has presented his work in several international institutions as the Missouri Botanical Garden in USA, The Smithsonian Institute in Panamá, The University of Amsterdam in the Netherlands and the Universidad de Valladolid in Spain. He also followed graduate courses in the University of Amsterdam, the Netherlands, and Aarhus University, Denmark. He has been awarded with grants from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), the Francisco José de Caldas Institute for the Development of Science and Technology (COLCIENCIAS) in Colombia, and the Netherlands organization for international cooperation in higher education (Nuffic). During his PhD. he studied the patterns of distribution of different plant growth forms along spatial and environmental gradients in three different areas of NW Amazonia. His main interest is focus on the structure, dynamic, and functioning of rain forest ecosystems; ecology and diversity of plants in tropical rain forests; and the conservation, restoration and use of forest and tropical ecosystems.

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