Chapter 1

INTRODUCTION

Alvaro J. Duque M.

1.1 INTRODUCTION

Northwestern Amazonian forest conservation: a challenge for ecologists

The actual deforestation rates in Amazonian rain forests are extremely high. The worst case scenario could lead to an almost total disappearance of the largest tropical forest mass that nowadays exists on the earth, in a relatively short time (Laurance *et al.* 2001). Patterns of rain forest plant diversity in northwestern (NW) Amazonia have particular importance as plant diversity in this area reaches exceptional high values per unit area (Gentry 1988a, Valencia *et al.* 1994, ter Steege *et al.* 2003). To guarantee an effective conservation planning, basic knowledge on the distribution of individual species and species assemblages is necessary. In spite of the fact that information concerning to plant communities has much increased in the last decade, most studies have focused on trees because they are the most conspicuous elements in the forests (Gentry 1988b, Duivenvoorden 1995, 1996, Pitman *et al.* 1999, 2001, ter Steege *et al.* 2000, Condit *et al.* 2002). However, it is well known that vascular plant diversity in tropical rain forests is also well represented by other growth forms, such as climbers, shrubs, epiphytes and herbs (Gentry and Dobson 1987, Duivenvoorden 1994, Balslev *et al.* 1998, Galeano *et al.* 1998). In addition to this lack of knowledge on non-tree growth forms, most studies have been based on different methodological approaches at individual species or community level, different sample designs, and different spatial scales, which hampers the comparisons and extrapolations among independent case studies.

The Pleistocene and Miocene-Pliocene climate history has been considered as the cornerstone to understand the origin of the plant and animal biodiversity and biogeography in Amazonian rain forests (Haffer 1969, Colinvaux 1987, Van der Hammen and Absy 1994, Hooghiemstra and van der Hammen 1998). The refugia hypothesis claims a repeated expansion and retreat of forests and savannas due to cyclic drier periods, which created forest refuge centers of endemism and promoted allopatric speciation (Haffer 1969, Prance 1982). The additional cooling hypothesis, based on the idea that temperatures were lower during the Pleistocene glaciations, results in a past-time with a constant migration of montane forests that promoted parapatric and sympatric speciation (Colinvaux 1987). However, adequate pollen records to test these two hypotheses are still lacking (H. Hooghiemstra, pers. comm. 2004). Furthermore, biogeographical predictions of the two climate-based hypothesis are quite similar, which make it difficult to draw conclusions based on the present-day patterns of species distributions (Tuomisto and Ruokolainen 1997).

The measure of diversity at local and regional scale has often been related to the definition of alpha and beta diversity, respectively. Alpha diversity measures, which include species richness and species abundance models, are employed to define the diversity within a habitat. Beta diversity, in contrast, is essentially a measure of the rate of change in the floristic composition between habitats in a landscape or along environmental gradients (Magurran 1988). The extent at which biotic and abiotic processes influence species diversity varies according to the scale of organization of the ecological systems. Local-scale processes such as canopy gap formation, dispersal limitation, competition, pests or insect attacks, and niche specialization, determine the structure and interactions of individuals within a population. Regional-scale processes such as migration, speciation, extinction, river dynamics, recruitment limitation, climatic and landscape variation, determine the structure and organization of the ecological communities (Hubbell 1997, 2001; van Gemerden 2004). Despite of regional processes patterns play an important role structuring the compositional local-scale patterns (Hubbell 2001, Huston 1999), local processes still remain quite important (Gaston 2000). Diversity patterns vary according to the spatial scale (Crawley and Harral 2001), but no single mechanism can explain a given pattern (Gaston 2000).

In tropical rain forests it is still unknown how, and at which extent local and regional scale processes address species distribution, diversity maintenance, and species co-existence (Tilman 1982, Brown 1995, Gaston 2000, Hubbell 2001, Wright 2002). In NW Amazonia, light gap disturbance and microclimatic conditions were found as important factors addressing floristic differences at local scale (Denslow 1987, Terborgh and Mathews 1999, Svenning 2000). In contrast, recruitment limitation was found to be a powerful force that limits the predictability of species richness or species composition, even in those lighter places such as forest gaps (Hubbell *et al.* 1999). The demographic disequilibrium diversity maintenance hypothesis (Connell 1978), which claims short-term and small-scale spatial denographic variation, was supported by a population analysis of the canopy palm *Iriartea deltoidea* (Svenning and Balslev 1997). The escape hypothesis or Janzen-Connell model (Janzen 1970, Connell 1971), which claims recruitment reduction near conspecific adults due to pests, was partially supported when tested with two single species in Amazonian rain forest (*Astrocaryum murumuru* and *Dipteryx micrantha*) (Cintra 1997), but rejected for most tree species analyzed in Panamá (Condit *et al.* 1992). Based on multi-species approaches, contrasting results arose as well. Harms *et al.* (2000), on the basis of data from seed traps and seedling recruitment in Barro Colorado Island, argued that even partial effects of Janzen-Connell mechanisms play an important role promoting species co-existence. Nevertheless, Hyatt *et al.* (2003), based on a meta-analysis from published papers dealing with this hypothesis, simply denied any probability that diversity maintenance and species survival should increase with distance from the parent plant.

In the same way, regional and local species diversity is strongly influenced by the interaction between environmental heterogeneity and dispersal (McLaughin and Roughgarden 1993). Upper Amazonian forests have been conceived as a dense mosaic of different forest types, each characterized by local assemblages of tree species, among which many are edaphic specialists (e.g. Gentry 1988a; see also Tuomisto *et al.* 1995, and Clark *et al.* 1998). On the other hand, beta diversity of relatively big trees among forest types has been considered rather low, at least in well drained uplands (Tierra Firme) where tree alpha diversity is highest (Duivenvoorden 1995, Pitman *et al.* 2001). However, a high sampling error is a common feature in tropical forest tree inventories (Duivenvoorden *et al.* 2002), due to the fact that most species are locally rare (Hubbell and Foster 1986, Pitman *et al.* 1999). The way that a species can be classified as abundant or rare, which largely depends on the plot size, minimum plant size, growth form, and geographical scale considered, is a relevant question in conservation biology (Rabinowitz 1981, Pitman *et al.* 1999). Forests with high degrees of local endemic plant species occurring in dense mosaics of different floristic assemblages require completely different strategies of conservation than forests built up by populations of locally rare but widely distributed generalist species.

Another fundamental issue in understanding ecological theory concerns the species response shape along complex environmental gradients. The unimodal bell-shaped curve, which in ecology finds its origin in niche-assembly rules, has been commonly recognized as a fundamental response shape to environmental gradients (Gauch and Whittaker 1972, ter Braak and Looman 1986). However, there is not sufficient evidence to support this view as a general law in plant ecology. Species response shapes might differ among gradient types (Austin and Smith 1989), growth forms (Minchin 1989), biological interactions (Austin 1999), and gradient locations (Austin and Gaywood 1994). Whether or not species display response shapes other than Gaussian and if they are continuously distributed along environmental gradients, have strong implications on an accurate prediction of spatial species distribution. An appropriate link between ecological theory and statistical modelling, largely depends on these conditions (Austin 2002). The shape of the species response curve itself is, above all, a parametric concept (Oksanen and Minchin 2002). Information on the shape of response curves from tropical rain forest species, highly needed for theory building of rain forest structure and composition (Austin 1987, 1990; Økland 1992; Austin *et al.* 1994), is hardly available (Gartlan *et al.* 1986; Svenning 1999).

Non tree growth forms: a black box in Amazonian rain forests

Climber plants, as well as other plant groups like epiphytes, have mostly been ruled out from inventories and vegetation models in spite of their ecological and functional importance (Schnitzer and Carson 2000). Lianas are a polyphyletic group of plants that have anatomical differences with trees, and need support to grow up and settle (Carlquist 1991, Schnitzer and Bongers 2002). They have been reported as an increasingly important element in tropical rain forest, which could induce the future forest into drastic changes in dynamics, diversity, and carbon fixation capability (Phillips *et al.* 1994, Dewalt *et al.* 2000, Schnitzer *et al.* 2000, Phillips *et al.* 2002). Vascular epiphytes, which depend of trees and lianas to establish, are well known for their active role in the hydrological regulation cycle of the forests (Veneklaas 1990, Wolf 1993). Epiphytes are plants that inhabit a discontinuous and three-dimensional organic landscape, mostly not in contact with the forest soil (Bennett 1986). Patterns of distribution and floristic composition of epiphytic plants have been related to factors such as dispersal ability (Benzing 1986; Wolf 1993), relative humidity (Leimbeck and Balslev 2001), soil fertility (Gentry and Dodson 1987b), and variability in forest structure and host tree features (Nieder *et al.* 1999, Freiberg 1996, 2001, van Dunné 2001). However, the way by which different growth forms are related to each other and depend on abiotic and biotic factors, is still poorly known. For example, holo-epiphytes do not seem to have any direct relationship with soils. However, as soils affect floristic patterns and forest structure (Duivenvoorden 1996), they indirectly determine factors as humidity and light, which control establishment and growth of epiphytes. Therefore, the analysis of different growth forms combined will help to obtain a better understanding of floristic patterns related to soils and not related to soils in Amazonian rain forests.

Regarding only terrestrial plants in tropical rain forests, few studies have, as yet, taken into account the relationships among different growth forms, such as herbs, shrubs and trees, and abiotic factors, such as soils (Webb *et al.* 1967, Ruokolainen *et al.* 1997, Vormisto *et al.* 2000). A pioneer study carried out in Australia (Webb et al 1967) arrived at two main conclusions: (1) larger trees and woody lianas primarily reflect the macro-ecological patterns, which largely depend on climatic factors and are quite independent of site conditions; (2) understory species, such as shrubs and herbs, display low influence from macro-climatic conditions, but are more dependent on micro-environmental factors, which include also biological processes. Indeed, independent studies in NW Amazonia based on canopy trees (Duivenvoorden 1995, Pitman *et al.* 2001, Condit *et al.* 2002) and understory species (Tuomisto *et al.* 1995, 2003a) suggested that plants with different sizes, growth forms, or pertaining to different guilds have a different ecology leading to different patterns of floristic composition in relation to environmental factors (Zagt and Werger 1998, Ruokolainen and Voormisto 2001). In contrast, recent studies in NW Amazonia also claimed that terrestrial growth forms ranging from herbs to big trees, might show important common trends in patterns of floristic composition that are largely determined by edaphic variability (Ruokolainen *et al.* 1997, Vormisto *et al.* 2000). In these latter studies, the authors apply and advocate the use of selected plants groups –mostly understory species, such as ferns, palms and Melastomataceae– as bioindicators.

Justification

The effect of scale on species distribution and diversity patterns has a particular importance for conservation and decision-making in natural ecosystems. In NW Amazonia from local to intemediate scales, and in accordance with landscape variation, insights into relevant patterns of tree species have become available in the last decades (*i.e.* Duivenvoorden 1995, Pitman *et al.* 1999). However, in the Amazon basin, only a few attempts to link floristic patterns at local and intermediate scale to larger scales have been done so far (Pitman *et al.* 1999). Since trees are the most conspicuous component of the forests, which creates support and conditions for the establishment of other growth forms, understanding the relationship between trees and other growth forms might help to simplify the conservation planning of the whole forest ecosytem. Nevertheless, it is virtually uknown how to extrapolate the knowledge acquired from trees to other growth forms, such as lianas, herbs, shrubs and epiphytes. This is why, in this study, we used and enhanced already existent information of forest inventories with new supplementary data, which comprised a wide environmental gradient in a range of spatial scales (from local to regional), and a variety of different growth forms in NW Amazonia.

1.2 OUTLINE OF THIS THESIS

In this thesis, the main issues mentioned above are addressed in more detail with a new series of well distributed high resolution relevés of terrestrial vascular plant species composition. They all have been sampled along the principal environmental gradients in a wide rain forest area in Colombian Amazonia, and adjacent (Amazon) areas of Ecuador and Peru (Fig. 1.1). 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 better analysis of the effect of other environmental variables. This in contrast to other spatial studies in Amazonia where annual rainfall varies between study sites (Clinebell *et al.* 1995, ter Steege *et al.* 2000, Pitman *et al.* 1999, 2001). New insight on comparative environmental control on understory, tree, epiphytes and lianas species composition at different spatial scales is obtained. Furthermore, strategies of habitat occupation (generalists, specialists) in relation to patterns of local abundance, relationships between different growth forms, use of selected plant taxa as bioindicators of patterns of plant distribution, and species response curves to complex environmental gradients, will be presented.

Aims

The principal aim was to study the spatial distribution and abundance of different growth forms of rain forest plants at different spatial scales (on the basis of a substantial set of new relevés, which includes (near)-total vascular plant species composition such as big trees, lianas, epiphytes, shrubs and herbs) in relation to their ecological response to major environmental gradients in a wide area of NW Amazonia. Spatial scales have been arbitrarily subdivided into local, meso or intermediate, and regional. Local scale is referred to plot scale, which in this study ranges from 0.1 ha to 2.16 ha. Mesoscale is considered for those surveys carried out within a country, which range from 3 ha to 2000 km^2. Regional scale is defined for those analyses that involved more than 2000 km^2 and included areas in the three countries.

The principal research questions addressed are:

At local scale (Tierra Firme in Colombian Amazonia):

- How are big tree species (DBH$\geq$10.0 cm) distributed along a narrow environmental gradient crossing three geomorphological units (low plain terrace, high dissected terrace, and high undissected terrace) in Tierra Firme forests?

At mesoscale (Metá and Chiribiquete areas, Middle Caquetá basin, Colombian Amazonia):

- Is beta diversity higher among woody understory species than among big trees?
- Are the distribution and diversity patterns of vascular epiphytes related to the main landscape units and woody species composition in the Metá area?
- Can we use some selected plant species as bioindicators to predict the floristic pattern of all other plant species present in a plot-based survey in different landscape units?

At regional scale (NW Amazonia):

- What are the local and regional patterns of diversity and composition of woody lianas (DBH>2.5 cm) in NW Amazonia?
- What is the predominant response shape of woody (DBH>2.5 cm) species and genera to complex environmental gradients in NW Amazonia?

Study area

The study was carried out in four different areas in northwestern Amazonia: middle Caquetá basin, which includes the Chiribiquete and Metá areas in Colombian Amazonia (roughly between 0°-2°S and 70°-73°W); Yasuní area in Ecuadorian Amazonia (roughly between 0°-1.1°S and 76°-76.5°W); and Ampiyacu area pertaining to the Maynas Province in Peruvian Amazonia (roughly between 3-3.5°S and 71.5°-72.5°W) (Fig. 1.1). All areas are in the Humid Tropical Forest life zone (bh-T) according to Holdridge *et al.* (1967). The average annual temperature is near 25°C, and annual precipitation varies around 3000 mm. All months show an average precipitation above 100 mm. In the Metá and Yasuní areas the lowest rainfall is in January and February, whereas in Puerto Isanga it is in August and September (Lips and Duivenvoorden 2001).

Northwestern Amazonia has been geologically divided into two Cenozoic sedimentary basins: "pericratonic" or Andean basin and "intracratonic" or Amazonian basin (Räsanen 1993). The Middle Caquetá area in Colombia and the Ampiyacu area in Peru are located within the Amazonian basin, while the Yasuní area is within the Andean basin (Lips and Duivenvoorden 2001). The principal landscape units found here are well-drained floodplains, swampy areas (including permanently inundated backswamps and basins in floodplains or fluvial terraces), areas covered with white-sand soils (found on high terraces of the Caquetá River and in less dissected parts of the Tertiary sedimentary plain), and well-drained uplands or Tierra Firme forests (which are never flooded by river water and include low and high fluvial terraces and a Tertiary sedimentary plain) (Duivenvoorden and Lips 1995). Soils and landscape units are called well-drained when soil drainage (according to FAO 1977) is imperfectly to well-drained (FAO drainage class ≥ 2), and poorly drained when soils are poorly to very poorly drained (FAO drainage class < 2).

All the areas studied are predominantly covered by 'primary' forests that lack recent evidence of disturbance. These forests are mainly inhabited by indigenous communities. In the Colombian study area the surveys were carried out in forest lands owned by the people of the Muinane and Miraña groups, which live along the Caquetá River in small groups that do not exceed 200 in number each (Sánchez 2001). The Chiribiquete area, which was inhabited in the past by the Carijona indigenous tribe, is located within the Chiribiquete National Park. There are almost no people living in this area nowadays (Peñuela and von Hildebrand 1999). The Yasuní area has been historically inhabited by the Huaorani community. Until just a couple of decades ago, the Huaorani people were nomads. However, after the incursion of the oil companies they became sedentary (Macía 2001). The Yasuní National Park is a protected zone in the Ecuadorian Amazonia with a very low population density. This area is very well known for harbouring a high plant diversity (Valencia *et al.* 1994). In the Ampiyacu area, in Peruvian Amazonia, the indigenous communities in the study area are part of three main indigenous tribes: Boras, Huitotos and Okaina. In the period of the rubber exploitation, most members of these communities migrated southward from Colombia into this area, expelled by the violence or forced by the rubber tree employers (García 2001).

Main properties of the field data

The current study addresses the research questions by means of three datasets: (1): data from a survey carried out on only trees (DBH>10 cm) along a transect of 10 x 2160 m (2.16 ha) in Tierra Firme forests in Colombian Amazonia; (2): quantitative data on (near)-total vascular plant composition in Colombian Amazonia from 40 0.025-ha well distributed plots covering a total area of 1 ha; and (3): data concerning woody plant species composition (DBH>2.5 cm) in a total of 90 0.1-ha plots, located in pilot areas in the Amazon basin of Colombia (Caquetá basin, 40 plots), Ecuador (Yasuní area, 25 plots), and Peru (Ampiyacu area, 25 plots). 80 of these 90 plots came from an EU funded project to assess non-timber forest resources in NW Amazonia (Duivenvoorden *et al.* 2001). Plot position was recorded using a GPS.

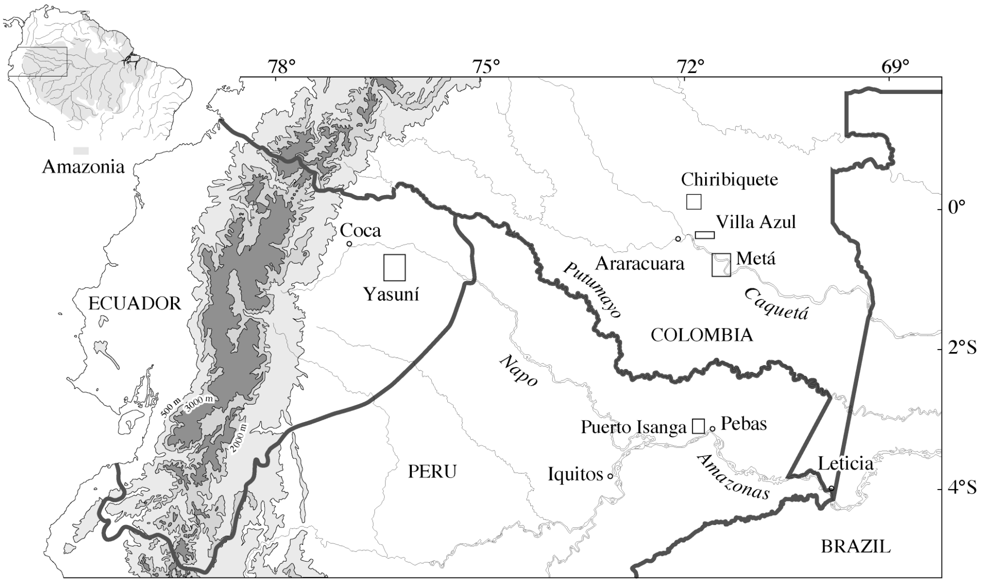


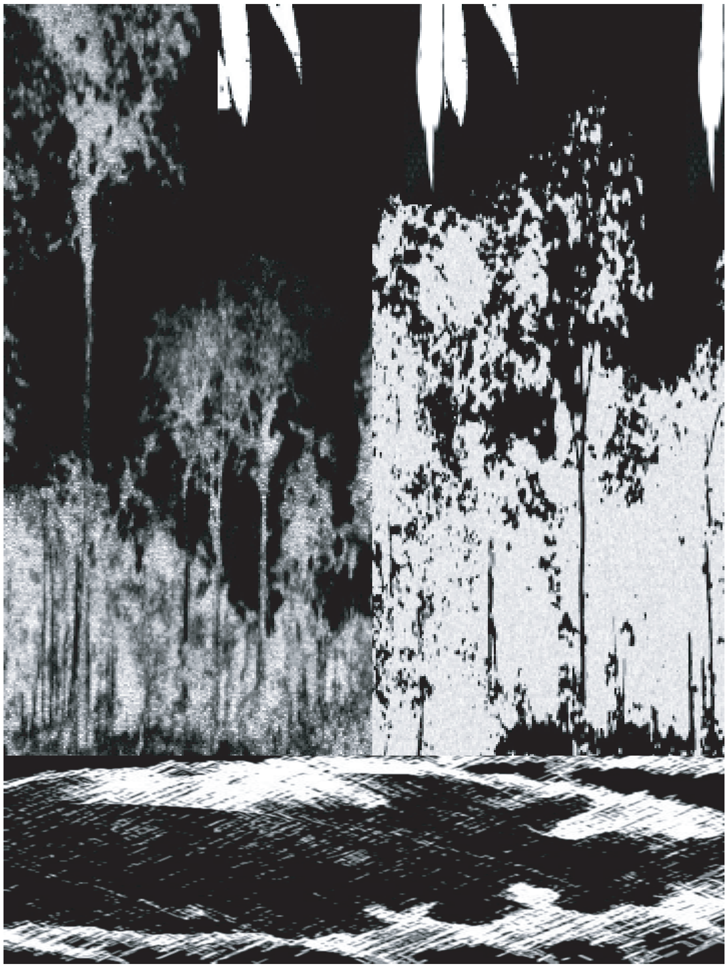
Figure 1.1. Location of the different sampled areas in NW Amazonian.

Botanical collections were made of all vascular plant species found in each plot, according to the minimum plant size included in the sampled design. Identification took place at the herbaria COAH, HUA, COL, QCA, QCNE, AMAZ, USM, MO, NY and AAU (Holmgren *et al.* 1990). The nomenclature of families and genera follows Mabberley (1989). Visual interpretation of satellite imagery and aerial photographs were carried out to define the study area as well as the geomorphological maps of the different study areas (Duivenvoorden and Lips 1993, Tuomisto and Ruokolainen 2001, Duivenvoorden 2001, von Hildebrand *et al.* in prep.). In the central part of each one of the 90 0.1-ha plots, a soil description until 120 cm depth was done, and a soil sample was taken at a depth of 65-75 cm. Chemical soil analyses were carried out at the soil laboratory of the Institute for Biodiversity and Ecosystem Dynamics (IBED) of the Universiteit van Amsterdam.

1.3 A BRIEF SUMMARY OF THE CHAPTERS

This PhD. thesis presents a compilation of several articles, which have already been published in, accepted by or submitted to, in international peer-reviewed journals. The different chapters are specially arranged in accordance with the spatial scale, which starts from a local scale (Chapter 2), going by several topics at intermediate (Chapters 3, 4 and 5) and regional scales (Chapters 6 and 7), and finishing with a synthesis that includes implications for forest conservation planning in NW Amazonia (Chapter 8).

In Chapter 2, contingency tables were used to test whether or not locally abundant species were randomly distributed along three different kinds of alluvial terraces from the Caquetá River. Most of the abundant species that allowed statistical analysis were classified as generalists. In Chapter 3, Mantel and partial Mantel tests were carried out to analyze the effect of geographical space and environment on the observed patterns of woody understory and canopy species distribution. It was concluded that canopy species had a wider distribution and were less depending on soil specialization than understory species. Hence, for understory plants the spatial configuration of the plots became more important in explaining species patterns. In Chapter 4, just as trees, the ordination diagram of Detrended Correspondence Analysis (DCA) showed that epiphyte species assemblages were well associated with the main landscapes units. Mantel correlation analysis showed a non significant correlation between the epiphytes composition and the spatial sampling set-up of the plots. According to one-way ANOVA analyses, and contrary to trees, vascular epiphyte abundance and diversity (species richness, Fisher's alpha index) hardly differed between the landscapes. In Chapter 5, by means of a Canonical Correspondence Analysis (CCA), species information from ferns and Melastomataceae, together with that from soils, landscape, and spatial sampling design, was used to explain the compositional patterns of other vascular plant species in 40 widely distributed 0.1-ha plots. No evidence was obtained that ferns and Melastomataceae showed more potential to predict the main patterns in species composition of forests than soil, landscape, and spatial variables. In Chapter 6 the main aim was to assess patterns of diversity and composition of woody lianas in three different areas in NW Amazonia. Woody lianas with DBH $\geq$ 2.5 cm (DBH = diameter at breast height) 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 analyzed in response to 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. 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. In contrast, liana species composition was best related to soil fertility, leading to a distinct position of the Tierra Firme plots in Colombia. 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. We used a hierarchic set of logistic regression models to test if response curves were skewed, symmetrical or monotonic. The continuum concept appeared as the most appropriate model of vegetation organization in the forests. Predictions of response curves of woody species based on soil fertility gradients tended to be inaccurate. Factors other than soils probably had a strong influence on the way how species were distributed along complex abstract gradients. Finally, Chapter 8 presents the general conclusions, including some general methodological considerations and implications for conservation.



Chapter 2

STRATEGIES OF TREE OCCUPATION AT A LOCAL SCALE IN TERRA FIRME FORESTS IN THE COLOMBIAN AMAZON

Alvaro J. Duque M., Jaime Cavelier and Alberto Posada

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2.1 INTRODUCTION

Amazonian forests and tropical coral reefs are known to have the highest species richness in the world (Connell 1978). Within Amazonian forests, those closer to the Andes are known to have higher species richness than those in the central Amazonian watershed (Valencia *et al.* 1994, Clinebell *et al.* 1995). Gentry (Gentry 1988a,b, Clinebell *et al.* 1995) hypothesized that the forests along the Andean foothills are richer than those in the central basin because of a general positive relationship between species richness, precipitation, and mineral nutrient contents in soils. Nevertheless, when the number of individuals per unit area is considered, this hypothesis no longer holds (Ter Steege *et al.* 2000). Plots located in the central Amazonian have higher tree density, resulting in equal or even higher tree species diversity, that is, the ratio of species to individuals (Ter Steege *et al.* 2000).

Whether species richness is considered as the number of species per unit area or in relation to the number of individuals, there is still much debate on the causes of high species number and the way these species are related to one or more environments. Two opposing hypothesis have been proposed to explain tree species in tropical wet forests, the hypothesis of deterministic niche-assembly, and the hypothesis of probabilistic dispersal-assembly. According to the deterministic niche-assembly theory, plant communities are composed of groups of species that coexist in interactive equilibrium with each other, and one species is the best competitor for a given niche (Tilman 1982). This hypothesis implies a fine partitioning of the environment as shown for understory shrubs and ferns in the understory of Peruvian Amazonia (Tuomisto *et al.* 1995). In contrast, the theory of dispersal-assembly suggests that plant communities are the collection of species that overlap in environmental requirements for geographical or historical reasons. According to this theory, the species in a community are in non-equilibrium, that is, they co-exist in changing relative abundances (Hubbell 1998). Since data have been recently published in favor of both, the deterministic niche-assembly theory (Clark *et al.* 1998, Tuomisto *et al.* 1995) and the probabilistic dispersal-assembly (Harms *et al.* 2001), the explanation of species distribution may fall between these two hypothesis (Hubbell 1998).

According to Gentry (1988a,b), high levels of species richness in the Tambopata region of the Peruvian Amazon can be attributed to high beta-diversity due to habitat specialization. This conclusion came from comparison of tree species (≥10 cm DBH) in nearby 1 ha plots located in Tierra Firme and flooded forests. More recent studies of tree species composition in Tierra Firme forests at a larger geographical scale have shown that, Beta diversity is rather low, most tree species appear as habitat generalists, and there is a low proportion of local specialists (Duivenvoorden and Lips 1998, Pitman *et al.* 2001). Beta diversity in Tierra Firme forests may increase when the woody understory species are considered. These species seem to show higher specialization to soil conditions and higher dispersal limitation (Zagt and Werger 1998, Ruokolainen and Vormisto 2001).

In the present study, we describe the species richness and the floristic composition of three adjacent geomorphological units in Tierra Firme forests in the middle Caquetá area, Colombian Amazonia. We address the following questions: (1) is there an effect of the physiographic changes on the species richness across three landscape units? (2) are there tree species unique to each landscape unit or are tree species mainly distributed across all three units? Two extremes are possible: a large list of "specialists" for each forest type, and thus high beta diversity, or a large list of generalist species and low beta diversity.

2.2 METHODS

Study site

The study was carried out in the middle Caquetá of the Colombian Amazon. In particular, vegetation surveys were carried out in three adjacent geomorphological units in Tierra Firme forests: low plain terrace, high dissected terrace, and high plain terrace in the Villa Azul area of the Muinane indigenous community (0° 32' S; 72 ° 6' W). These three units are all of Quaternary age and are not subject to flooding from the Caquetá River. The low plain terrace (LPT), 15-20 m above the average water level in the river, is a flat well-drained unit with deep soils ($pH_{0\text{-}40\ cm}$ =3.7-4.0; total bases = 4.4 meq/100 g) classified as Paleudults (Botero *et al.* 1993). The high dissected terrace (HDT), 30-40 m above the river, is composed of hills 20-30 m tall, moderately to well drained, with stable tops and unstable hillsides (slopes 50-60%) with signs of active geomorphological processes like mass movements, resulting in "steps" varying in height from a few centimeters to 1-3 m. Soils are shallow in the hill tops and deeper on the slopes and valley bottoms. Soils have low mineral nutrient content ($pH_{0\text{-}40\ cm}$ = 3.7; total bases = 2.9 meq/100 g) and are classified as Kandiudults (Botero *et al.* 1993). The high plain terrace (HPT), 40-50 m above the river, is a flat, well-drained unit with no signs of erosion (*i.e.* creeks). Soils are also deep with low mineral nutrient contents ($pH_{0\text{-}40\ cm}$ =3.7; total bases = 2.3 meq/100 g) and classified as Kanhapludults (Botero *et al.* 1993). Average mean annual rainfall (1979-1990) is 3059 mm with no month with less than 100 mm. The elevation is approximately 90 m.a.s.l. and the mean annual temperature (1980-1989) was 25.7°C (Duivenvoorden and Lips 1993).

Sampling methods

The vegetation survey was carried out along a single longitudinal transect 10 m x 2160 m located in a west-east direction, and passing through a low plain terrace (720 m), a high dissected terrace (720 m), and a high plain terrace (720 m). For every tree and liana more than 10 cm DBH, distance from the origin of the transect and the diameter were recorded. Specimens of each individual were collected and determined by means of comparisons at the Herbario Amazónico (COAH) and Herbario Nacional Colombiano (COL). Voucher specimens (AD 001-2044) are deposited in COAH and the Herbarium of the Botanical Garden of Medellin (JAUM).

Data analysis

For data analysis, the continuous transect was divided in subplots 10 m x 30 m resulting in 24 plots in each of the three landscape units. The species were classified as "locally abundant" if they had more than one individual per hectare (after Pitman *et al.* 1999), and if they were present in three or more subplots. Otherwise, species with two or fewer individuals in the entire 2.16 ha and present in two subplots or fewer, were defined as "locally rare". To determine if the abundant species distributed along this transect were restricted to one, two, or three landscape units, a 2 x 3 contingency table was analyzed using the "Ecological Profile" method (Ezcurra and Montaña 1984). In this method, the contingent table contains three factors (*i.e.* landscape units) and the frequency of presence and absence of the species within the subplots in each landscape unit. The null hypothesis is that every species belongs to a single population and is distributed at random, thus occurring in all three units. Observed values of G (with distribution Chi-square) were compared with the expected value of Chi-square for two degrees of freedom (5.9). If the observed value was higher than the expected value, the null hypothesis was rejected, and thus the distribution of the species was restricted to one or two units. To determine which unit(s) the species was restricted to, the following procedure was used. For each factor, observed values of G were compared with Chi-square for one degree of freedom. If the observed value was higher than tabulated (3.84), the species was either more (+) or less (-) abundant than expected. On the contrary, if the observed value was lower than tabulated, the species was considered to be indifferent to this factor (0). Thus, a species could be restricted to one geomorphological unit when only one value was positive (*i.e.* 0/+/0; -/+/-), to two geomorphological units when two values were positive (*i.e.* +/-/+) or evenly distributed when all values were zeros (0/0/0). These species are referred here as "specialists", "intermediates" and "generalists", respectively. The Jaccard coefficient (J), which is designed for presence-absence data (Legendre and Legendre 1998), was used as a measure of similarity (beta diversity) in the floristic composition among landscape units.

2.3 RESULTS

Along the 2160 m x 10 m transect, there were a total of 51 families, 140 genera, and 377 morphotypes of trees more than 10 cm DBH. Determination of morphotypes was possible at different levels: 189 (50%) to the species level, 120 (33%) to the genus level, and 66 (17.5%) to the family level. Only two morphotypes (0.5%) were not identified. All the different morphotypes will be refered to as species. The most abundant families were Lecythidaceae with 204 individuals (13%), Leguminosae with 160 individuals (10.2%) and Myristicaceae with 151 individuals (9.6%) (Fig. 2.1)

Species richness was higher in the high dissected terrace (229 species/0.72 ha) followed by the high plain terrace (178 species/0.72 ha) and the low plain terrace (174 species/0.72 ha). When species richness was considered as the ratio between the number of species and the number of individuals collected in each forest type, the LPT showed the highest value (0.382), followed by HDT (0.376) and HPT (0.361).

Comparison between forest types using the Jaccard Index showed that the LPT and HDT, as well as the LPT and HPT, had 26 % of the species in common, while the HDT and HPT had 30 % of the species in common. There were 146 (39%) species classified as "locally abundant" and 231 (61%) classified as "locally rare". The

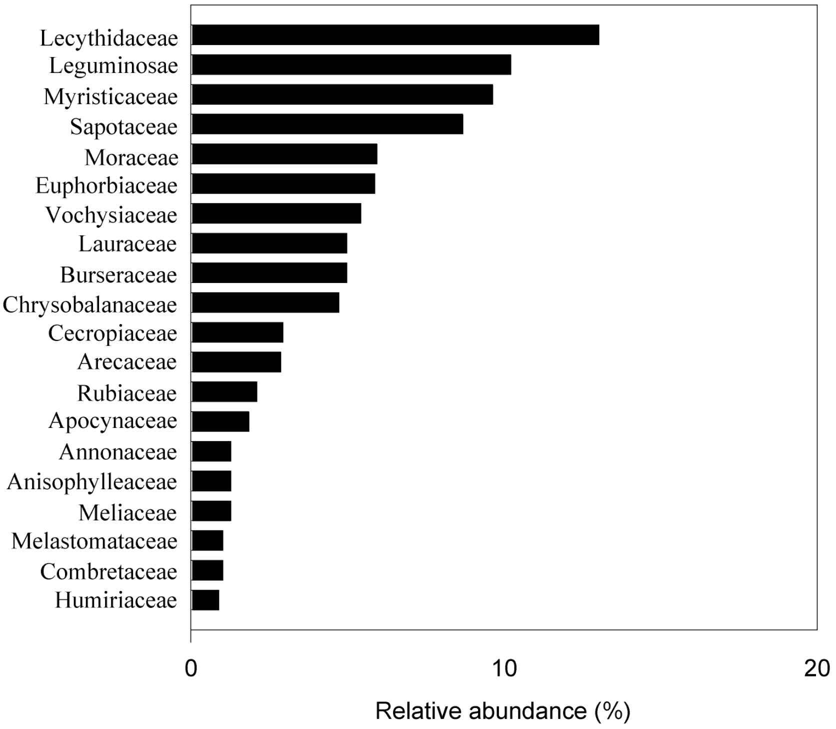

Figure 2.1. Relative abundance of plant families in the 2.16 ha longitudinal plot covering a low plain terrace, a high dissected terrace, and a high plain terrace.

results of the "Ecological Profile" method, showed that the abundant species occurred in one, two or three forest types. The largest group was composed of those species that were present in all three forest types (102 species of 146; 70%) (Table 2.1). *Oenocarpus bataua* is a very good example of this strategy (Fig. 2.2). A second group was composed of species that were located in only one of the three forest types: those restricted to the low plain terrace (seven species; 4.8%), the high dissected terrace (17 species; 11.6 %) and the high plain terrace (11 species; 7.5%) (Table 2.1). Species as *Lacmellea arborescens* in LPT, *Senefeldera* AD891 in HDT and *Swartzia schomburgkii* in HPT belong to this group (Fig. 2.2). A third group was composed of the species that were present in two of the three forest types; those that occur in LPT and HDT (one species; 0.7%), HDT and HPT (five species; 3.4%), and LPT and HPT (three species; 2%) (Table 2.1). Species such as *Eschweilera* AD685 in LPT and HDT, *Qualea* AD348 in LPT and HPT, and *Eschweilera parvifolia* in HDT and HPT are examples (Fig. 2.2). For the rest of the species (231 species; 61%) (Table 2.1), and due to low occurrence in the entire transect (present in one or two subplots), it was not possible statistically to discriminate to which group they belonged. These species are referred here as "rare" species. A list of all species is given in the Appendix 1.

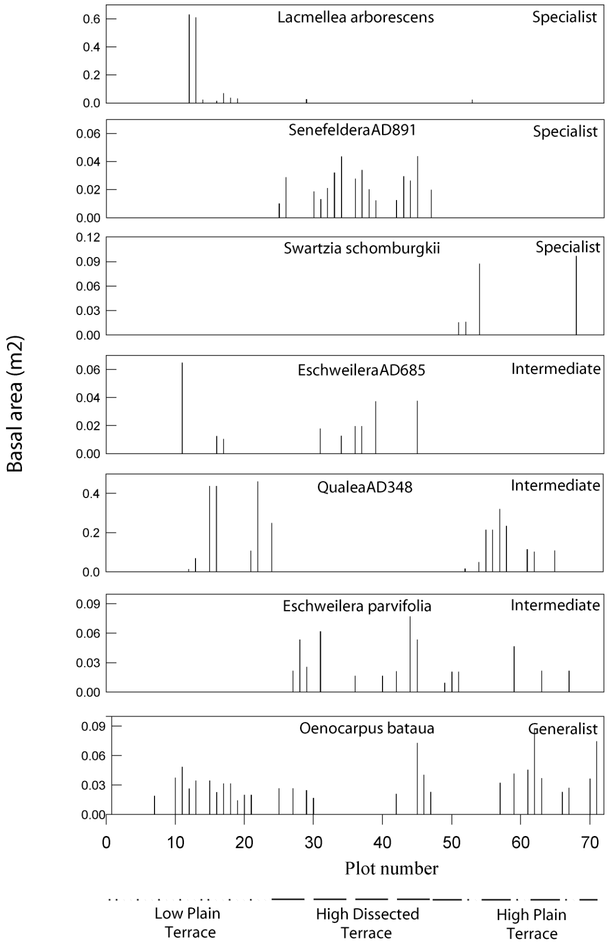

Figure 2.2. Examples of the different strategies of tree occupation for abundant species: specialists (occur in only one forest type), intermediate (occur in two forest types) and generalists (occur in all three forest types). The total length of the transect is 2160 m and each contiguous plot is 10 m x 30 m.

2.4 DISCUSSION

Species richness, species distribution, and environmental factors

All three forest types are rich in species of trees and lianas (≥ 10 cm DBH) with the highest species richness in the high dissected terrace, HDT (229 species/0.72 ha). This high value, when compared to that in the relatively flat land types [low plain terrace (174 species/0/72 ha) and high plain terrace (178 species/0.72 ha)] may be the result of several environmental and biological factors. The forest of the high dissected terrace has the highest number of "specialists" (17 species only occurring in that unit) and "rare" species (95 species). Although these species are associated with an environment that is both unstable (*i.e.* mass movements, resulting in "steps" from a few centimeters to 1-3 m), and heterogeneous (*i.e.* hilltops, slopes and valley bottoms with variable soils and water content), no data is available on specific correlations between species occurrence and micro-environments. Further research is needed to clarify the role of landscape instability and environmental heterogeneity (*i.e.* Tuomisto *et al.* 1995, Clark *et al.* 1998) as proximal causes of species distribution and abundance at the mesoscale in Amazonian forests.

Strategy of occupation and beta diversity

In the present study, the "specialists" and "rare" species are defined here at a very local scale (2.16 ha) and not in absolute terms or in reference to other classification schemes (Rabinowitz *et al.* 1986). The presence of specialist species in each of the three non-flooded forests in this study suggests that there is some degree of determinism (association of species to environmental units) in the distribution of these tree species at least at a local scale. If the occurrence of these species is not only considered locally, as we have done in this study, but in a wider biogeographical sense (*i.e.* Colombian or NW Amazonian), it is likely that some of these "unique" species actually occur in other forest types but at different densities (Pitman *et al.* 1999). For instance, *Micropholis guyanensis*, a specialist of the LPT in the study site, occurs in a variety of flooded and non flooded forests (Lescure and Boulet 1985, Duivenvoorden and Lips 1993, Urrego 1997). Other specialists of the HDT (*Micrandra spruceana*, *Hevea benthamiana*, and *Rinorea racemosa*) and HPT (*Swartzia schomburgkii*, *Protium grandifolium* and *Mezilaurus itauba*) have been reported in other forest types as well (Duivenvoorden and Lips 1993, Sánchez *et al.* 2001).

Table 2.1. Number of species according to occupation strategy. S = specialist, I = intermediate, G = generalist.

	Abundant			Rare	Sub-total
Landscape Units \ Strategy	S	I	G		
Low Plain Terrace (LPT)	7			64	71
High Dissected Terrace (HDT)	17			92	109
High Plain Terrace (HPT)	11			51	62
LPT and HDT		1		8	9
LPT and HPT		3		9	12
HDT and HPT		5		7	12
Generalists			102		102
TOTAL	35	9	102	231	377

Considering those species with sufficient individuals to run statistical analysis, beta diversity is low at local scale: most species are generalists with a random distribution on the three landscape units. These results contrast with those reported in a similar study at fine scale in Peruvian Amazonian, in which the authors demonstrated that most tree species were differentially distributed with respect to environmental conditions (Vormisto *et al.* 2000). Low tree beta diversity in Tierra Firme forests has been demonstrated at both mesoscale and large scale as well (Duivenvoorden and Lips 1998, Pitman *et al.* 2001, Condit *et al.* 2002).

If all species are considered in the analysis of spatial occupation (with or without sufficient individuals to run statistical analysis), beta diversity or the turnover of species from one environment to another, seems to be rather high. The high abundance of rare species and the autocorrelated patterns of species with limited dispersal (Condit *et al.* 1996, Plotkin *et al.* 2000), makes difficult analyzing species from the point of view of their association with one or more environments. This in turn, makes difficult our understanding of the proximal causes of species richness and turnover. The existence of true specialists can only be determined with a complete survey of the potential distribution range of these species, or the analysis of all information of tree plots already collected by various research group.

Chapter 3

DIFFERENT FLORISTIC PATTERNS OF WOODY UNDERSTORY AND CANOPY PLANTS IN COLOMBIAN AMAZONIA

Alvaro J. Duque M., Mauricio Sánchez, Jaime Cavelier and Joost F. Duivenvoorden.

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3.1 INTRODUCTION

The identification and explanation of plant distributions at local and regional scales in Amazonia, and the humid tropics in general, are gaining increasing attention (Caley and Schluter 1997, Hubbell 1997, Pitman *et al.* 1999, Terborgh and Andresen 1998). In humid tropical forests, spatial patterns of species are aggregated (Condit *et al.* 2000, Denslow 1987, Hubbell 1979), and tend to show high numbers of scattered and rare species (Hubbell 1995, 1997). Recent comparisons at regional scales in Peruvian Amazonia show that many locally rare tree species have wide regional distributions (Pitman *et al.* 1999, see also Murray *et al.* 1999).

In upper Amazonia, Gentry (1988, see also Tuomisto *et al.* 1995) suggested that forests are a fine-grained mosaic of many different forest types, each characterised by local assemblages of edaphic specialists. Spatial studies of canopy trees (in this study defined as plants with DBH $\geq$ 10 cm; DBH = diameter at breast height) in Colombian (Duivenvoorden 1995, Duivenvoorden and Lips 1998) and Peruvian Amazonia (Pitman *et al.* 1999), however, showed that beta diversity at mesoscales (*i.e.* over geographical distances of 1-103 km) is low, especially in the well-drained upland forests which are the most widespread forest type in this region.

Better understanding of plant distribution patterns is highly relevant as forests with high levels of local endemic species occurring in fine-grained patches require completely different strategies of conservation than forests built up by populations of locally scarce but widely distributed generalist species. Insights into the degree of environmental preference of forest taxa are also highly necessary for calibration of the growing body of palynological data from the lowland tropics (van der Hammen and Hooghiemstra 2000).

Most studies on plant-edaphic relationships in tropical forests (e.g. Baillie *et al.* 1987, Clark *et al.* 1998, 1999; Duivenvoorden 1995) focused on canopy trees. However, tropical forests contain many more plant species among the individuals in the understory (Duivenvoorden 1994, Gentry and Dodson 1987). It may well be that understory species show greater edaphic specificity than large, well-established trees (Zagt and Werger 1998). Chance elements related to unpredictable events of gap formation influence the successful establishment of large trees. Also, it might be argued that for understory plants which live predominantly in shaded conditions, edaphic heterogeneity might be an important source of variation for genetic selection. On the other hand, several authors have reported on evidence for spatial heterogeneous light conditions at forest floors and effects on plant performance (Nicotra *et al.* 1999, Terborgh and Mathews 1999, Svenning 2000).

The current study was set up to compare patterns of these species groups in a series of 0.1-ha plots, well distributed in the principal landscape units of a part of Colombian Amazonia. The research questions were: How are the principal distribution patterns of species in relation to local abundance in plots? Do understory species show better correlations with soils and environment than canopy species? Are patterns found in the entire range of landscape units comparable to those found in well-drained uplands alone?

3.2 METHODS

Study area

The study area comprises about 1000 km^2 and is situated along the middle stretch of the Caquetá River in Colombian Amazonia, roughly between 1°-2°S and 70°-73°W. The principal landscape units found here are well-drained floodplains, swampy areas (including permanently inundated backswamps and basins in floodplains or fluvial terraces), areas covered with white-sand soils (found on high terraces of the Caquetá River and in less dissected parts of the Tertiary sedimentary plain), and well-drained uplands (which are never flooded by river water and include low and high fluvial terraces of the Caquetá River and a Tertiary sedimentary plain) (Duivenvoorden and Lips 1993, Lips and Duivenvoorden 1996). Soils and landscape units are called well-drained when soil drainage (according to FAO 1977) is imperfectly to well-drained (FAO drainage class ≥ 2), and poorly drained when soils are poorly to very poorly drained (FAO drainage class < 2). A previous ordination analysis of forest compositional patterns of the current data set (Duque *et al.* 2001), allowed the recognition of four forest types which correspond closely to the main landscape units: well-drained floodplain forest, well-drained upland forests (Tierra Firme), swamp forests (excluding any white sand forests), and white sand forests. The area receives a mean annual precipitation of about 3060 mm (1979-1990) and monthly rainfall is never below 100 mm (Duivenvoorden and Lips 1993). Mean annual temperature is 25.7°C (1980-1989) (Duivenvoorden and Lips 1993).

Vegetation sampling and identification of botanical vouchers

In each of the above-mentioned landscape units, 30 plots were located (Fig. 3.1). In order to establish the plots, starting locations along the Caquetá River and the direction of the tracks along which the forests were entered, were planned on the basis of the interpretation of aerial photographs (Duivenvoorden 2001). During the walk through the forests, soils and terrain forms were rapidly described, and the forest was visually examined. In this way sites with homogeneous soils and physiognomically homogeneous forest stands were identified. In these stands, rectangular plots were delimited by compass, tape and stakes, working from a random starting point, with the restriction that the long side of the plot was parallel to the contour line. Plots were located without bias with respect to floristic composition or forest structure (including aspects of density and size of trees, and presence of lianas). All plots were established in mature forests that did not show signs of recent human intervention, at a minimum distance of 500 m between plots (Fig. 3.1). Plots were mapped with GPS. Plot size was 0.1 ha and most plots had rectangular shape (20 x 50 m). Plots were subdivided into subplots of 10 x 10 m, in which all vascular plant individuals with DBH $\geq$ 2.5 cm were numbered. The DBH of all individuals was measured with tape. Their height was estimated using long poles as a reference measure. Fieldwork took place in 1997 and 1998

Botanical collections (numbers MS2900-7049 and AD3900-4092) were made of all species found in each plot. Identification took place at the Herbario Amazónico (COAH), the herbarium of the Missouri Botanical Garden (MO), the herbarium of the Universidad de los Andes in Santafé de Bogotá, and the Herbarium of the University of Aarhus (AAU). The nomenclature of families and genera follows Mabberley (1989). Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics, were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens.

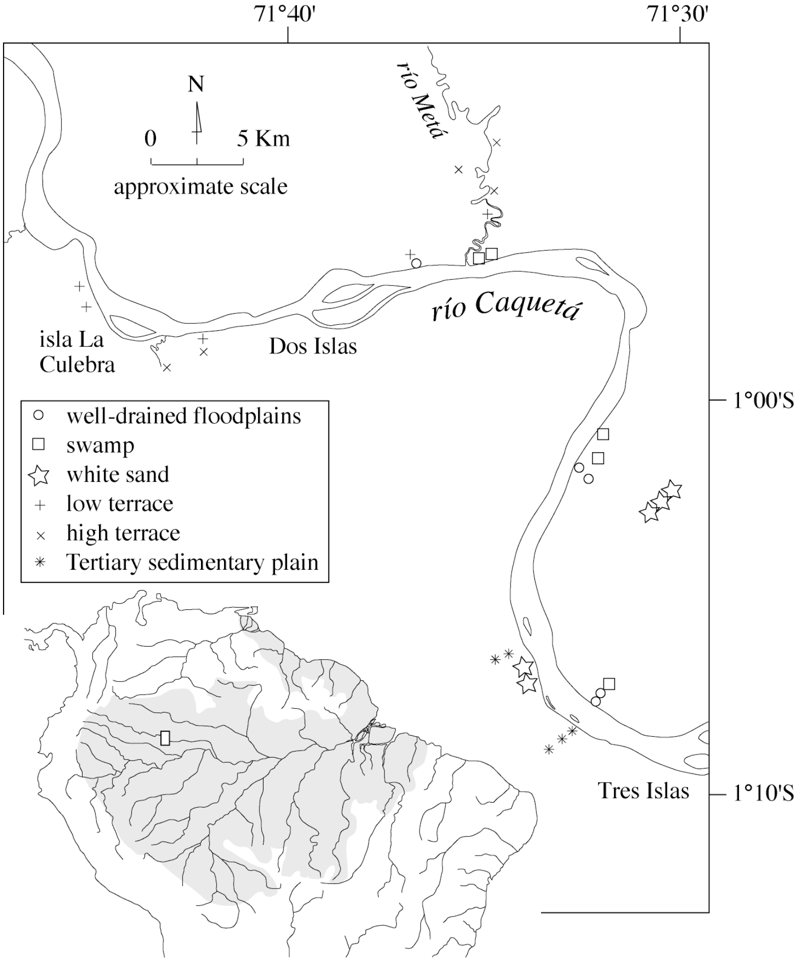

Figure 3.1. Location of 0.1-ha sample plots in the Metá area (Colombian Amazonia).

Soil data

Roughly in the central part of each plot, a soil core was taken to 120 cm depth in order to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions, and texture) and to define soil drainage (in classes of FAO 1977). At each augering position a soil sample was taken at a depth of 65-75 cm. Due to an unplanned delay in soil sampling in one floodplain plot and two plots in white sand forests, samples from only 27 plots were analysed. For analyses, soil samples were dried at temperatures below 40°C, crumbled and passed through a 2-mm sieve. At the soil laboratory of the Institute of Biodiversity and Ecosystem Dynamics at the University of Amsterdam, total content of Ca, Mg, K, Na and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H_2SO_4 (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser.

Categories of floristic composition

Three categories of floristic data are considered in the analysis: all species (DBH $\geq$ 2.5 cm); canopy species (species with individuals that were found with DBH $\geq$ 10 cm; and understory species (species with individuals recorded with a maximal DBH of less than 10 cm, anywhere in the plots). Understory species are thus represented by plants that will never attain DBH $\geq$ 10 cm, or by juvenile individuals of plants that may develop into big canopy trees. For the species-environment analysis in well-drained uplands (see Table 3.6), only understory species among individuals with heights below 10 m are considered (Welden *et al.* 1991).

Distribution patterns and forest preference

Species found with a maximum density of 1 stem per plot, are defined as locally rare (after Pitman *et al.* 1999). Otherwise species are referred to as locally abundant. Species are called environmental specialists when found in only one of the main landscape units defined in this study. When recorded in more than one of these landscape units, species are considered environmental generalists.

Correlation of species with soils, landscape units, and geographical space

The correlations between species, environmental variables, and geographical space, were calculated by Mantel and partial Mantel tests (Leduc *et al.* 1992, Legendre and Legendre 1998), as made available in R-Package (Casgrain and Legendre 2000). In these tests, geographical space is used in much the same way as environmental variables, to define and test correlation between matrices (Legendre 1993).

In all Mantel tests, matrices of similarity coefficients were used. Species matrices were calculated with the Steinhaus index. This asymmetrical quantitative coefficient permits usage of species abundance data (Legendre and Legendre 1998). Environmental matrices were calculated with Gower's symmetrical similarity coefficient. This coefficient permits simultaneous incorporation of both nominal and quantitative variables (Legendre and Legendre 1998). Spatial information was quantified by means of Euclidean distances between plots. Probabilities of r-values were defined on the basis of 999 permutations.

3.3 Results

Floristic data

A total of 13,989 individual vascular plants (DBH ≥ 2.5 cm) was recorded in the 30 plots of 0.1 ha each. A total number of 4343 botanical collections were made, representing 89 families, 378 genera, and 1502 species, including 478 morphospecies (31% of all species). The most common species found in the area are listed in Appendix 2 (a complete species listing is annexed to Sánchez *et al.* 2001). 303 morphospecies (20% of all species) were identified only to genus, and 159 only to family (10% of all species). In the 15 plots of 0.1 ha established in the well-drained uplands, 81 families, 310 genera, and 1124 species were found. 650 canopy species were recorded (43% of all species found), 16 of which were liana species. 852 understory species (57% of all species) were found. Of these, 161 species were lianas.

Distribution patterns

Average plot densities of individuals (DBH ≥ 2.5 cm) in the main landscape units ranged between 273-669 per 0.1 ha (Table 3.1). A proportion of 15-32% of these individuals had DBH ≥ 10 cm. Average species densities (DBH ≥ 2.5 cm) fluctuated between 36-183 per 0.1 ha. Average canopy species densities were between 16-54 per 0.1 ha.

Many species were restricted to only a few plots (Fig. 3.2). For example, almost half of all the species (DBH ≥ 2.5 cm) were found in only one plot, and 80% of the species were found in three plots or less. Most species were also represented by only a few individuals (Fig. 3.3). About 43% of all species were only found as 1 individual, and 80% of the species as three individuals or less (Fig. 3.3). In both cases, patterns in well-drained uplands were quite similar to patterns in all landscape units together.

Table 3.1. Densities of species and plant individuals in two DBH classes, recorded in 0.1-ha plots in the main landscape units of the Metá area (Colombian Amazonia). Shown are averages ± standard deviation of n plots.

	species	individuals	species	individuals	n
	DBH ≥ 2.5 cm		DBH ≥ 10 cm		
well-drained floodplains	93 ± 16	273 ± 53	35 ± 9	57 ± 9	5
swamps	72 ± 18	669 ± 302	27 ± 8	160 ± 115	5
white sands	36 ± 18	521 ± 212	16 ± 7	111 ± 40	5
well-drained uplands	183 ± 21	436 ± 68	54 ± 7	79 ± 14	15

There were slightly more locally abundant species (57% of all species DBH ≥ 2.5 cm) than locally rare species (43% of all species DBH ≥ 2.5 cm) (Table 3.2). Most species occurred in only one landscape unit. Those species that were found in more than one plot tended to achieve higher local abundance than species restricted to a single plot. Among the entire set of species recorded, including the species that were found in only one plot, the number of locally rare species in relation to that of the locally abundant species was higher. In the well-drained uplands the locally rare species contributed almost 50% of the total species richness (Table 3.3). In all other landscape units, locally abundant species prevailed. When the species that were found in only one plot were excluded, local abundance became proportionally more important, especially in the well-drained uplands.

Species-environment correlations

The abiotic variables used to correlate species data with environmental information included flooding, drainage, and physico-chemical soil variables (Table 3.4). When the entire data set derived from plots in all landscape units was analysed, the species composition of both canopy and understory was strongly correlated with soils and flooding (Mantel r = 0.55 and Mantel r = 0.64, respectively; see Table 3.5). The spatial configuration of the plots correlated rather poorly with species patterns, even though this correlation was just significant (P = 0.05) for understory species. When the effect of soils and flooding was removed, the correlation between species patterns and spatial positioning of the plots improved. The environmental information and location of the plots were just significantly correlated (Mantel r = 0.11, P = 0.04).

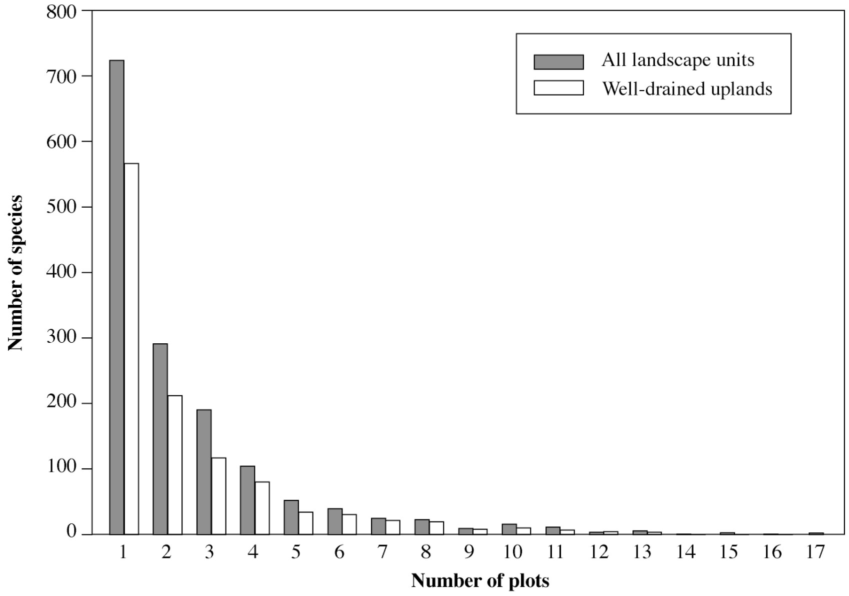

Figure 3.2. Number of species (DBH $\geq$ 2.5 cm) recorded in an increasing number of plots of 0.1 ha, in the Metá area (Colombian Amazonia)

Table 3.2. Number of locally rare and locally abundant vascular plant species (DBH ≥ 2.5 cm) in view of species presence in one or more landscape units in the Metá area (Colombian Amazonia). Landscape units considered are well-drained floodplains, swamps, well-drained uplands, and 'white sand' areas.

	Species in two or more plots				All species
	number of landscape units where species are found				
	4	3	2	1	
Locally abundant species	3	42	170	404	861
Locally rare species	0	2	29	127	641

Table 3.3. Number of locally rare and locally abundant vascular plant species (DBH ≥ 2.5 cm) in different landscape units, in the Metá area (Colombian Amazonia).

	Landscape units				
	Well-drained flood plains	Swamps	Well-drained uplands	White sands	All
All species					
Locally abundant	200 (61%)	141 (62%)	563 (50%)	85 (69%)	861 (57%)
Locally rare	127 (39%)	88 (38%)	555 (50%)	38 (31%)	641 (43%)
Species found in two or more plots					
Locally abundant	137 (71%)	108 (68%)	436 (68%)	62 (75%)	614 (79%)
Locally rare	57 (29%)	52 (32%)	201 (32%)	21 (25%)	163 (21%)

Restricting the analyses to the well-drained uplands, the species-environment relationships were less pronounced (Table 3.6). It became particularly poor among canopy species (Mantel r = 0.15, P = 0.12). Understory species composition continued to show a significant correlation with soils (Mantel r = 0.30; P = 0.004), even when the spatial effect of the positioning of the plots was taken away (partial Mantel r = 0.33; P = 0.0002). The location of the plots became an important factor in explaining species patterns, particularly among understory species (Mantel r = 0.52), also after correction for the environmental effect on species patterns (partial Mantel r = 0.53 for understory species). The environmental information and location of the plots were not significantly correlated (Mantel r = 0.04, P = 0.27).

3.4 DISCUSSION

Amazonia, and 74% claimed by Romero-Saltos *et al.* (2001) in Ecuadorian Amazonia). The unidentified specimens in this study (31% of all species) were mostly sterile and largely taken from juvenile individuals, which tend to show high morphological variability (Romoleroux *et al.* 1997). Some of the morphospecies might turn out to represent species new to science (R. Liesner and H. van der Werff, *pers. comm.*). However, other morphospecies may well correspond to one of the identified species, despite the efforts to simultaneously compare all specimens from the same genus or family

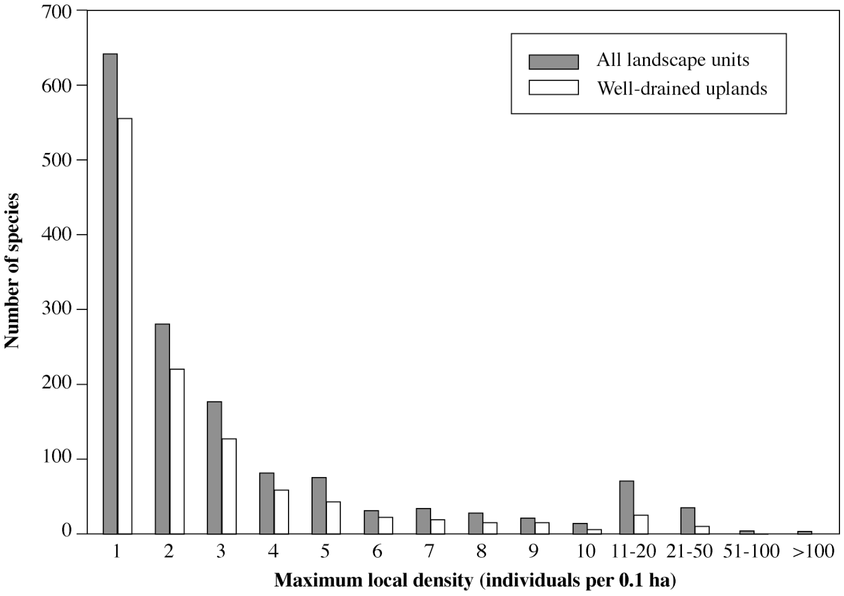

Figure 3.3. Number of species (DBH ≥ 2.5 cm) recorded with an increasing number of individuals in plots of 0.1 ha, in the Metá area (Colombian Amazonia).

Species distribution

Species that occurred in more than one plot showed higher local abundances. Positive abundance-distribution relationships are often found in many organisms and at a variety of spatial scales (see an overview in Gaston and Kunin 1997, see also Brown 1984, Hanski *et al.* 1993). The most important explanations mentioned are sampling artifacts (locally rare species are less likely to be included in small sample plots and hence may appear with a more limited regional distribution), metapopulation dynamics (details in Hanski 1982, and Hanski *et al.* 1993) and different degrees of ecological specialization (generalists would be able to exploit a wider range of resources and show less habitat specialization). In the current study generalist species (found in more than one main landscape unit) and specialist species (found in only one main landscape unit), showed a more-or-less similar abundance-distribution pattern. However, the estimates of local population size or environmental preference of many species were crude as the plot samples contained only a few individuals of these species. Also, the applied definition of local rareness and local abundance is arbitrary. It should be stressed that the great majority of the so-called locally abundant species are found with a low number of individuals per plot (see Fig. 3.3). This makes that the term 'locally abundant' in this context may be considered as somewhat misleading (Pitman *et al.* 1999).

Table 3.4. Environmental variables used in the Mantel analyses, and their variation (average ± standard deviation in case of quantitative variables and frequencies in case of nominal variables) recorded in 27 plots distributed over all landscape units, in the Metá area (Colombian Amazonia) (see also Fig. 3.1).

	Well-drained flood plains	Swamps	Well-drained uplands	White sands	All
number of plots	4	5	15	3	27
Quantitative variables					
Drainage	3 ± 0.6	0 ± 0.0	4 ± 0.0	0 ± 0.0	2 ± 1.9
Soil elemental concentration					
Ca (mmol kg^{-1})	130 ± 92	5 ± 1.8	2 ± 0.6	2 ± 1.2	20 ± 56
Mg (mmol kg^{-1})	320 ± 119	83 ± 34.8	30 ± 20.1	2 ± 0.3	80 ± 114
K (mmol kg^{-1})	370 ± 41	173 ± 77.9	53 ± 37.5	1 ± 0.7	120 ± 129
Na (mmol kg^{-1})	290 ± 174	29 ± 12.7	9 ± 6.8	0 ± 0.0	50 ± 117
P (mmol kg^{-1})	10 ± 4	17 ± 8.2	5 ± 1.4	1 ± 0.3	10 ± 6
C (%)	0 ± 0.1	15 ± 15.3	0 ± 0.1	3 ± 1.0	3 ± 8.2
N (%)	0 ± 0.0	1 ± 0.7	0 ± 0.0	0 ± 0.0	0 ± 0.5
Nominal variables (frequencies in %)					
Flooding by river water	100	100	0	0	40
Texture					
Sand	0	0	0	100	11
Clay-loam	0	0	20	0	11
Sandy clay	0	0	7	0	4
Silty clay	0	0	7	0	4
Organic clay	0	60	0	0	11
Clay	100	40	67	0	59

When poorly distributed species (found in only one plot) are removed, the contribution of locally rare species to the entire species pool decreases most in well-drained upland forests. Species that occur with one individual in only one plot are therefore relatively common in well-drained uplands, and contribute to the high alpha diversity in these uplands.

Species-environment patterns in all landscape units (whole area)

Most species occur in only one landscape unit (Table 3.2). Because the plots are well distributed in the area this result suggests that species have rather strong preferences for one of the principal landscape units in the area. However, processes of dispersal among species may have led to relatively high species overlap between neighbouring plots in one landscape unit. The Mantel tests serve to quantify these spatial effects.

Table 3.5. Mantel and partial Mantel correlation of species composition with space and environment in all landscape units (27 plots). Matrix A is composed of Steinhaus similarity coefficients between species data. Environment is the matrix composed of Gower's similarity coefficients between environmental data. Space is the matrix composed of Euclidean distances between plots. Mantel r is the Mantel correlation coefficient between matrix A and matrix B. Partial Mantel r is the Mantel correlation between matrix A and matrix B when the effect of matrix C is removed.

All landscape units		Mantel r	partial Mantel r	Probability
Matrix A = All species (DBH ≥ 2.5 cm)				
Matrix B				
Environment		0.63		0.001
Space		0.08		0.105
Matrix B	Matrix C			
Environment	Space		0.65	0.001
Space	Environment		0.19	0.004
Matrix A = Canopy species				
Matrix B				
Environment		0.55		0.001
Space		0.09		0.09
Matrix B	Matrix C			
Environment	Space		0.57	0.001
Space	Environment		0.17	0.005
Matrix A = Understory species				
Matrix B				
Environment		0.64		0.001
Space		0.11		0.05
Matrix B	Matrix C			
Environment	Space		0.66	0.001
Space	Environment		0.24	0.002

The Mantel analysis of species found among all individuals (DBH ≥ 2.5 cm) recorded in all landscape units (Table 3.5) shows a substantial amount of correlation between the matrices of species and environmental data (Table 3.5). Despite their rather low plot densities, canopy species are only slightly less correlated with environmental variables than understory species. Elimination of the spatial component in the data, does not reduce these correlations. It seems therefore that forest plots which share certain properties of flooding, drainage and soil fertility (including white sand soils) contain more-or-less similar assemblages of vascular plant species. Conclusions about environmental preferences of species should always be corroborated by experiments to discover causative mechanisms and underlying eco-physiological processes

Table 3.6. Mantel and partial Mantel correlation of species composition with space and environment in the well-drained uplands (15 plots). Matrix A is composed of Steinhaus similarity coefficients between species data. Environment is the matrix composed of Gower's similarity coefficients between environmental data. Space is the matrix composed of Euclidean distances between plots. Mantel r is the Mantel correlation coefficient between matrix A and matrix B. Partial Mantel r is the Mantel correlation between matrix A and matrix B when the effect of matrix C is removed.

Uplands well-drained		Mantel r	partial Mantel r	Probability
Matrix A = All species (DBH ≥ 2.5 cm)				
Matrix B				
Environment		0.24		0.034
Space		0.56		0.001
Matrix B	Matrix C			
Environment	Space		0.26	0.034
Space	Environment		0.57	0.001
Matrix A = Canopy species				
Matrix B				
Environment		0.15		0.12
Space		0.29		0.002
Matrix B	Matrix C			
Environment	Space		0.15	0.14
Space	Environment		0.29	0.002
Matrix A = Understory species (height < 10 m)				
Matrix B				
Environment		0.3		0.004
Space		0.52		0.001
Matrix B	Matrix C			
Environment	Space		0.33	0.002
Space	Environment		0.53	0.001

Indications for recurrent patterns of vascular plant species composition in similar landscape units in NW Amazonia are not new (e.g. Duivenvoorden 1995, Tuomisto *et al.* 1995). Pitman *et al.* (1999) concluded that beta diversity among tree species in SW Amazonia (Manu area, Peru) is weak, and found that 26% of tree species (DBH ≥ 10 cm) were restricted to one forest type (with species from two or more plots). In the present study, this percentage is slightly higher (35%). Perhaps the variation in soils and flooding among the plots studied by Pitman *et al.* was lower than in the current study. This may be due to their larger plot size (0.825-2.5 ha) which increases within plot environmental heterogeneity or to smaller gradients among soils in the footslope zone of the Andes (less white sand soils, ubiquitous enrichments by volcanic ash) compared to wider soil gradients found further downstream. Pitman *et al.* found plot densities of individuals with DBH ≥ 10 cm ranging between 282-858 ha^{-1}. These densities are in the same range as those found with DBH ≥ 2.5 cm in the 0.1-ha plots (Table 3.1).

Species-environment patterns in well-drained uplands

In the well-drained uplands, where the factor of flooding and drainage is held more or less constant, the Mantel correlation between the overall set of species (found among all individuals of DBH ≥ 2.5 cm) and soils is low but significant (Table 3.6). This correlation is due to understory elements, because patterns in canopy species are no longer associated with soils. The understory species-to-soil correlation remains significant when effects of space are removed. In a comparable sampling design of well-distributed 0.1-ha plots, Duivenvoorden (1995) claimed low but significant species-to-soil relationships in well-drained uplands of the middle Caquetá area (Colombia) for trees (DBH ≥ 10 cm). When correcting for effects of space and forest structure a partial canonical correspondence analysis showed that about 6% of the tree species patterns were significantly correlated with soils (Duivenvoorden 1995). The lack of correlation with canopy species in the current study might be due to the comparatively low number of plots analysed (15 versus 39 by Duivenvoorden 1995). Comparison of Mantel tests and correspondence analysis is outside of the scope of this study (see Legendre and Legendre 1998).

In the well-drained uplands, the spatial configuration of the plots is more important than soils in explaining species patterns. Many soil independent processes (Condit 1996), like herbivory, seed dispersal by animals, plagues and attacks by fungi, species migration, colonisation and competition for space and light in dynamic forest ecosystems affect species composition at scales wide enough to influence species composition in neighbouring plots in the area of the current study. The spatial effect is more pronounced in well-drained uplands than in the whole of the study area, both in absolute terms and in comparison to the environmental effect. Apparently, the wider the gradient in soils and flooding, the less important the role of the above-mentioned spatial processes.

Canopy species versus understory species in relation to environment

In the well-drained uplands, just as in the whole data set, understory species are better correlated with soils than canopy species. Also the spatial configuration of plots has a greater effect on understory species patterns than on canopy species patterns. It seems likely that the current presence of many canopy individuals in the plots is an unpredictable result of light-induced growth due to events of gap formation in the recent past. The presence of understory individuals, on the other hand, might be more limited by seed dispersal, germination, and survival in heterogeneous light environments (Hubbell 1997, Nicotra *et al.* 1999, Terborgh and Mathews 1999). Better adaptation to specific local soil properties might improve the competitive strength of these species. As indicated above, such processes might take place at scales sufficiently wide to facilitate some spatial dependence among the plots included in the current survey.

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Chapter 4

A FIRST QUANTITATIVE CENSUS OF VASCULAR EPIPHYTES IN RAIN FORESTS OF COLOMBIAN AMAZONIA

Ana María Benavides D., Alvaro J. Duque M., Joost F. Duivenvoorden, Alejandra Vasco G. and Ricardo Callejas

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4.1. INTRODUCTION

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

Epiphytes are plants that inhabit a discontinuous and three-dimensional landscape, directly in contact with the forest soil or not (Bennett 1986). Patterns of distribution and floristic composition of epiphytic plants have been related to factors of dispersal (Benzing 1986; Wolf 1993), humidity and soils (Gentry and Dodson 1987b; Leimbeck and Balslev 2001), and variability of structure, superficial area and inclination and size of branches of host trees (phorophytes) (Nieder *et al.* 1999; Freiberg 1996, 2001). Recently, in nearby rain forests of the Yasuní area, Leimbeck and Balslev (2001) reported substantial differences in aroid epiphytism between floodplains of the Tiputini river and surrounding uplands, suggesting a strong role of phorophyte limitation in floodplain forests.

Here we make the first attempt to quantitatively describe vascular epiphytism in Colombian Amazonia. We counted vascular epiphytes in thirty 0.025-ha plots, well distributed over the main landscape units in a part of the basin of the middle Caquetá River (Fig. 3.1). Each plot was directly adjacent to a 0.1-ha plot at which the species composition of trees and lianas (DBH ≥ 2.5 cm) had been recorded three years earlier (Duque *et al.* 2001). The purpose of this paper is to present these species data, while focusing on the question whether or not there existed any difference in abundance, diversity, or distribution of epiphytes between the principal landscape units in the Metá area.

4.2 METHODS

Study site

The study area comprised about 1000 km^2 and was situated along the middle stretch of the Caquetá River in Colombian Amazonia near the mouth of the Metá river, roughly between 1°-2° S and 70°-73° W (Fig. 3.1). The principal landscape units found here were well-drained floodplains, swampy areas (including permanently inundated back swamps and basins in floodplains), areas covered with white-sand soils (found on high terraces of the Caquetá River and in less dissected parts of the Tertiary sedimentary plain), and well-drained uplands or Tierra Firme (never flooded by river water and including low and high fluvial terraces of the Caquetá River and a Tertiary sedimentary plain) (Duivenvoorden and Lips 1993; Lips and Duivenvoorden 2001). Soils were called well-drained when they showed a FAO drainage class of 2 or higher, and poorly drained when this class was below 2 (FAO 1977). The height of the studied forests varied between 10-15 m (white sand areas), 15-25 m (well drained floodplains and swamps), and 25-35 m (Tierra Firme). Extensive forest structural information is given in Duque *et al.* (2001). The area received a mean annual precipitation of about 3060 mm (1979-1990) with a mean monthly rainfall always above 100 mm (Duivenvoorden and Lips 1993). Mean annual temperature was 25.7°C (1980-1989) (Duivenvoorden and Lips 1993).

Field work data

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

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

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

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

Numerical analysis

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

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

4.3 RESULTS

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

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

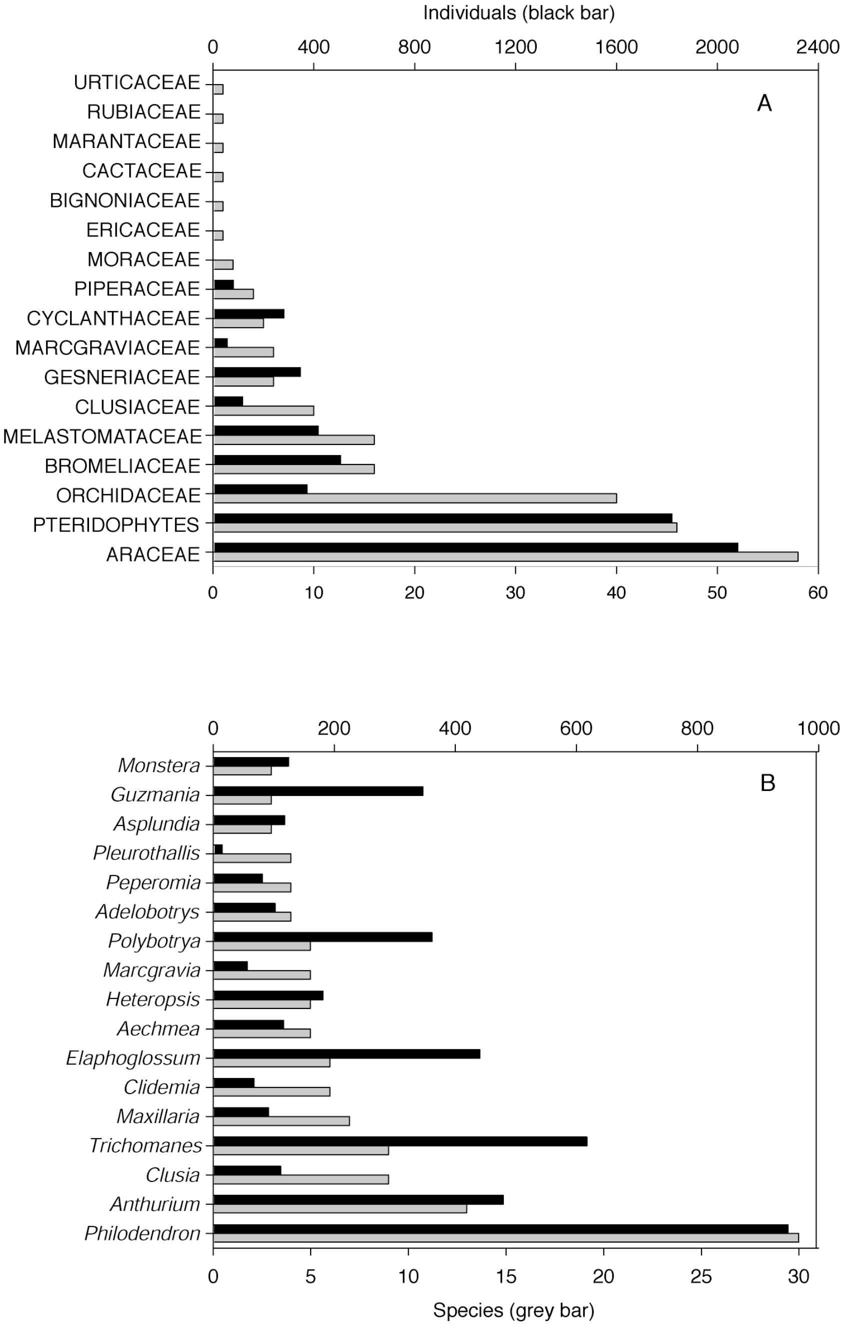

Figure 4.1. Number of epiphytic species and individuals belonging to the most speciose families and genera in thirty well distributed 0.025-ha plots, in the principal landscape units of the Metá area in Colombian Amazonia. A. Species richness and abundance of the most speciose epiphytic families. B.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

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

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

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

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

4.4 DISCUSSION

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

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

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

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

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

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

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

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

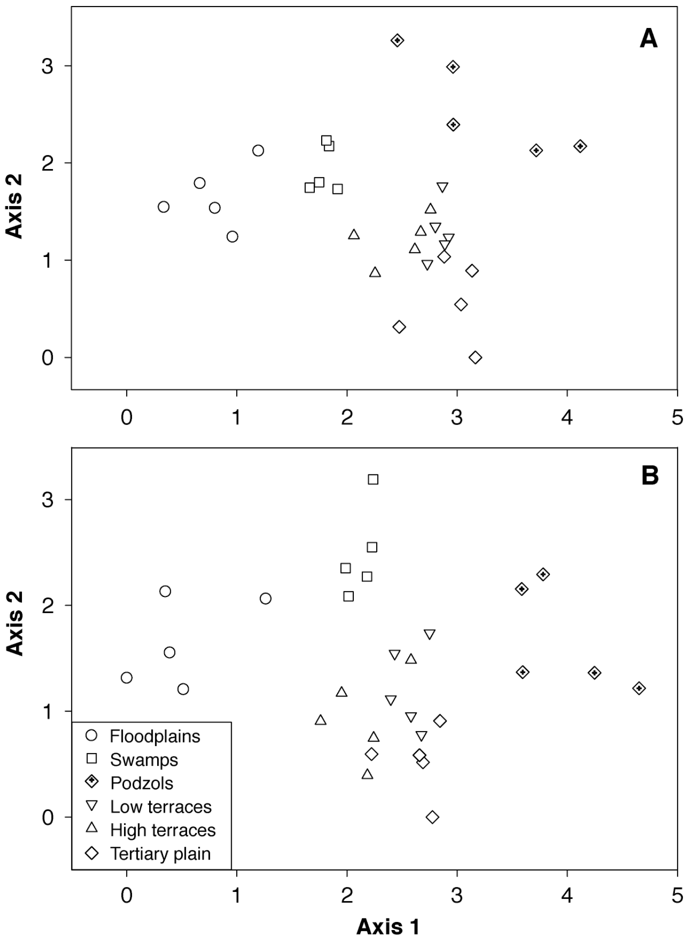

Figure 4.2. Detrended Correspondence Analysis of vascular epiphytes in the Metá area of Colombian Amazonia. A: based on the presence-absence of epiphyte species. B: based on the abundance (number of individuals) of epiphyte species.

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

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

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

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

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

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

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

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

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

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

Chapter 5

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

Alvaro J. Duque M., Joost F. Duivenvoorden, Jaime Cavelier,
Mauricio Sánchez, Carolina Polanía and Andrea León
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5.1 INTRODUCTION

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

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

5.2 METHODS

Study site

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

Field and laboratory work

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

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

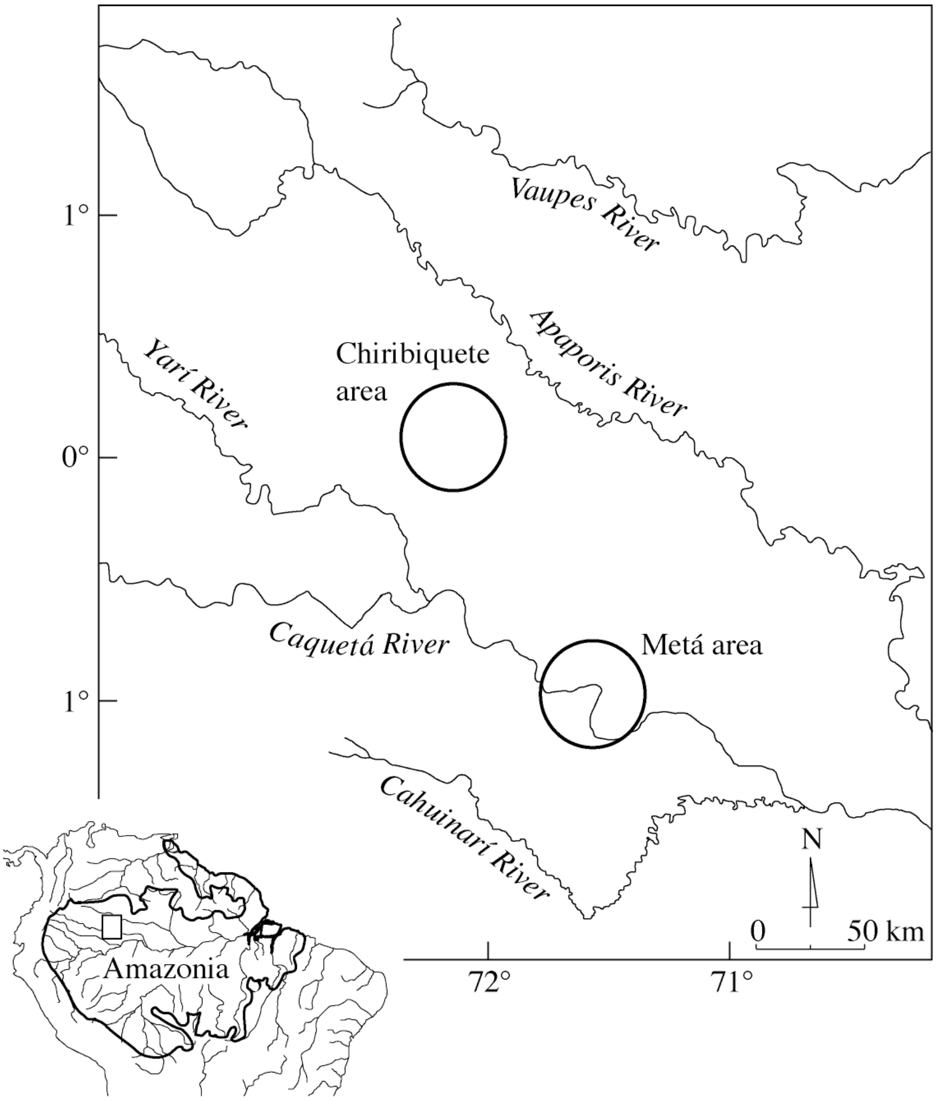

Figure 5.1. Location of the Metá and Chiribiquete sites in the middle Caquetá area.

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

Data analysis

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

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

5.3 RESULTS

All landscape units

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

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

Tierra firme forests

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

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

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

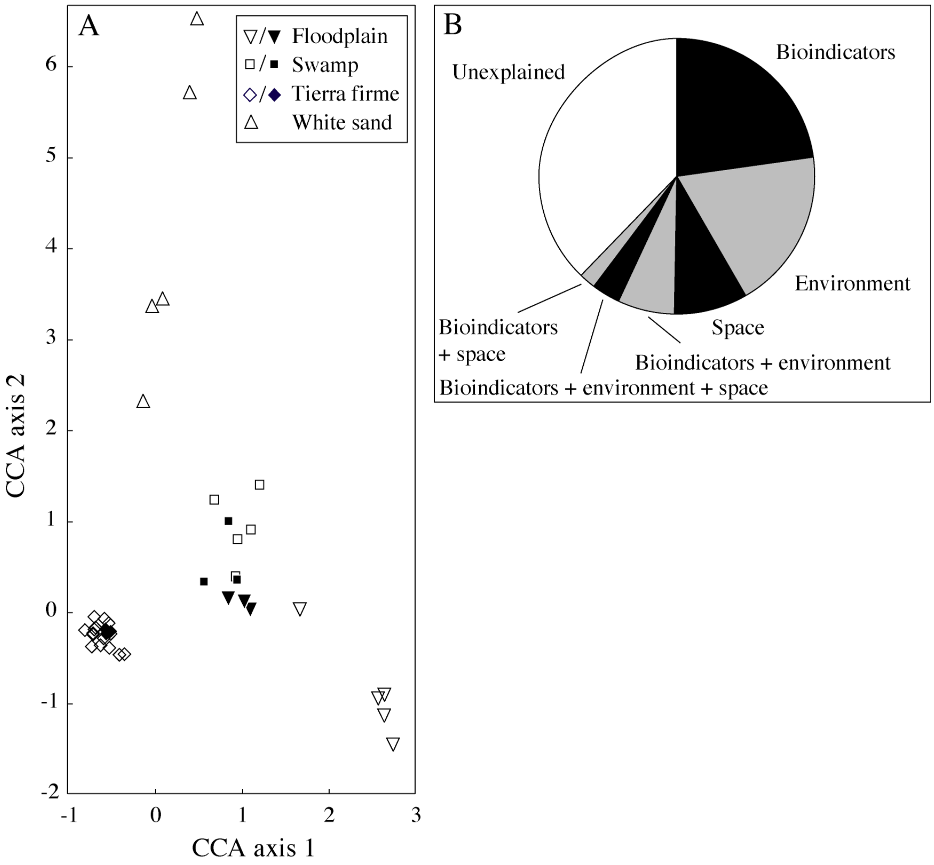

Figure 5.2. CCA of vascular plant composition (excluding ferns and Melastomataceae) in 40 0.1-ha plots, located in Metá and Chiribiquete areas in Colombian Amazonia. A: Ordination diagram showing sample scores derived from the species from the Metá area (open symbols) and the Chiribiquete area (closed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

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

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

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

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

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

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

5.4 DISCUSSION

Indicators of rain forest plant composition?

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

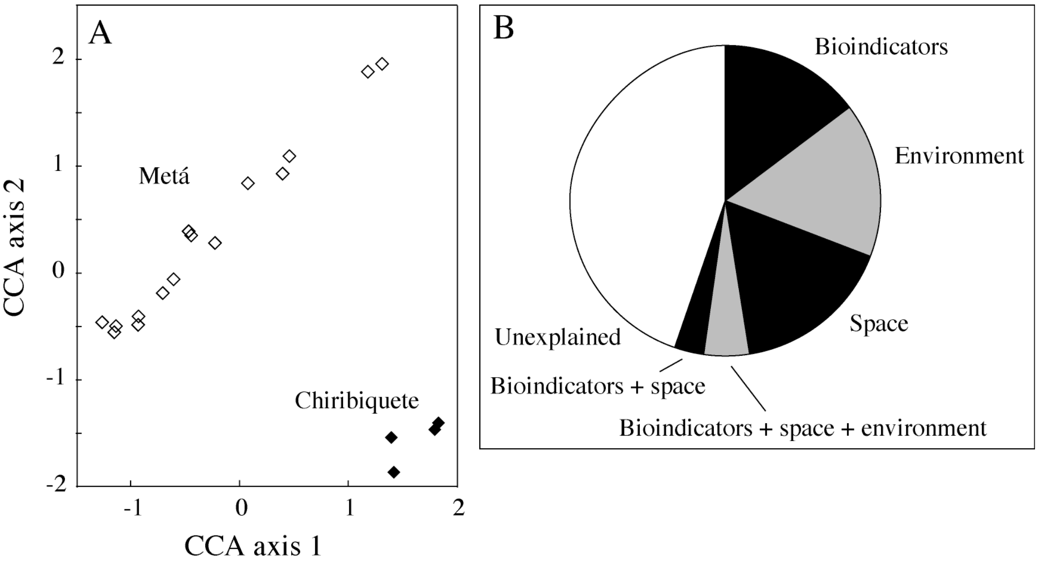

Figure 5.3. CCA of vascular plant composition (excluding ferns and Melastomataceae) in 19 Tierra Firme of 0.1-ha each, located in Metá and Chiribiquete areas in Colombian Amazonia. A: Ordination diagram showing sample scores derived from the species from the Metá area (open symbols) and the Chiribiquete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

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

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

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

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

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

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

Overall variation in species composition

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

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

Chapter 6

DIVERSITY AND COMPOSITION OF WOODY LIANAS IN NW AMAZONIA

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

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6.1 INTRODUCTION

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

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

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

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

6.2 METHODS

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

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

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

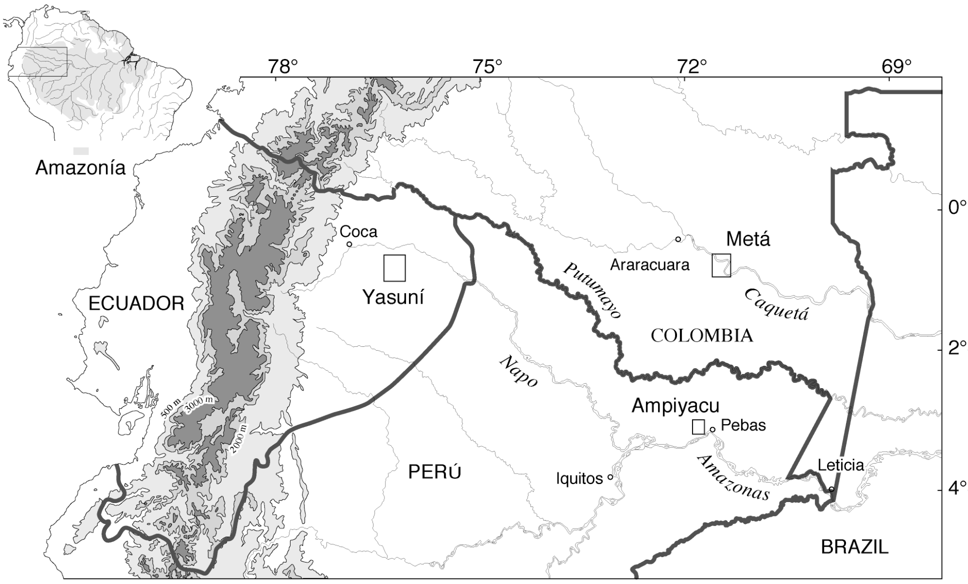


Figure 6.1. Location of the three study sites in NW Amazonia.

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

Data analysis

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

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

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

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

6.3 RESULTS

Diversity patterns

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

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

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

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

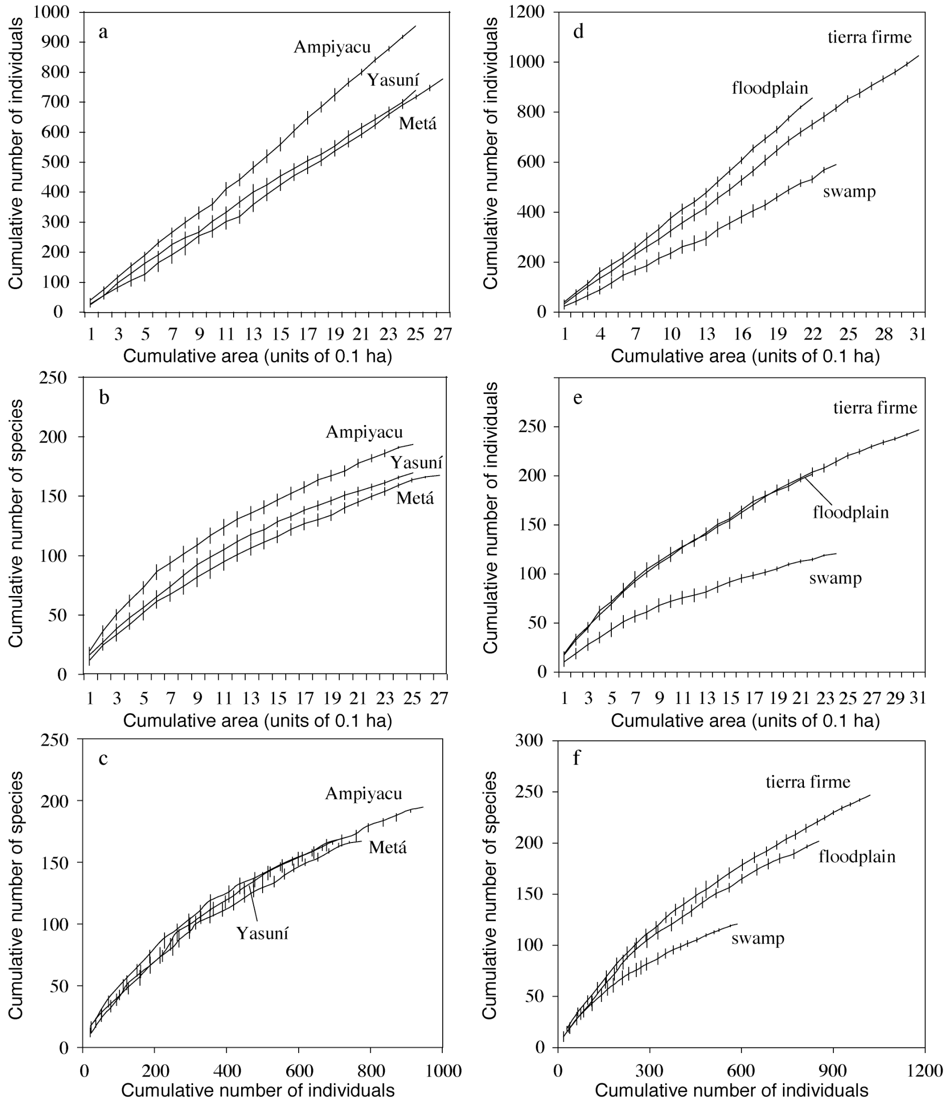


Figure. 6.2 Accumulation curves of liana individuals and species, based on 77 0.1-ha plots where lianas with DBH ≥ 2.5 cm were found. The lines are smoothly drawn through means based on 10 series of randomly ordered plots; vertical bars represent one standard deviation of each mean.

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

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

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

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

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

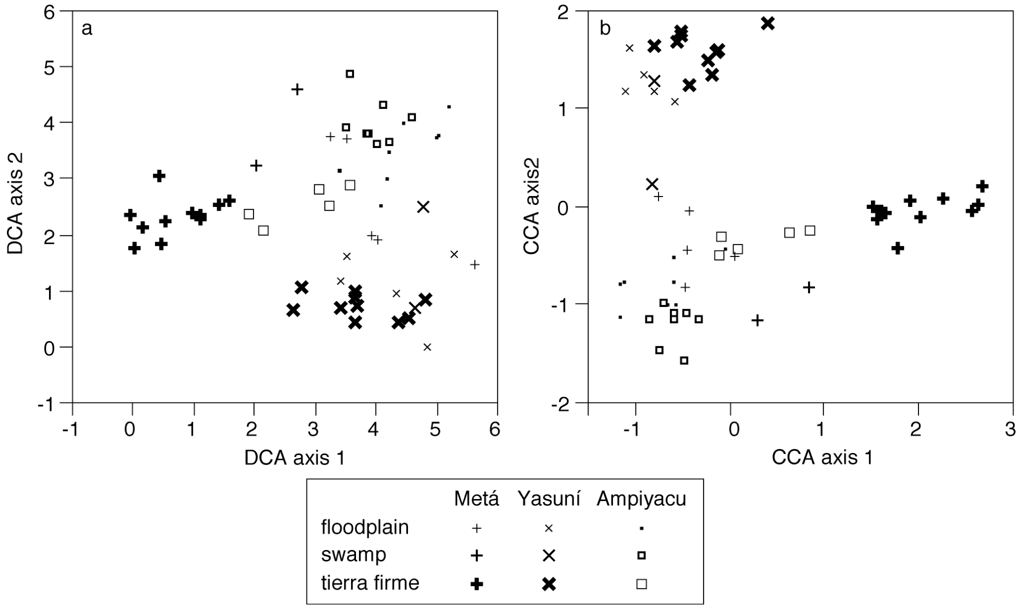


Figure 6.3. Ordination diagrams of DCA (left) and CCA (right) of composition of woody liana species (DBH ≥ 2.5 cm) in 56 0.1-ha plots. In the CCA diagram, plot scores are weighted mean species scores.

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

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

Compositional patterns

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

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

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

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

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

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

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

	swamp surroundings	Tierra Firme surroundings	PCAsoil1	PCAsoil2	PCAforest1	PCAforest2	latitude	longitude
floodplain surroundings	0.68	-0.60	0.33	-0.02	-0.03	-0.29	-0.08	-0.33
swamp surroundings		-0.84	0.44	0.22	-0.15	-0.21	-0.21	-0.47
Tierra Firme surroundings			-0.57	-0.07	0.17	0.20	0.36	0.44
PCAsoil1				0.00	-0.56	0.03	-0.33	0.14
PCAsoil2					0.13	0.03	-0.03	-0.10
PCAforest1						0.00	0.12	-0.28
PCAforest2							0.06	0.26
latitude								0.51

6.4 DISCUSSION

Liana diversity

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

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

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

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

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

	canonical coefficients		interset correlations	
	axis1	axis2	axis1	axis2
floodplains	-0.28	-0.08	-0.45	-0.14
swamps	-0.06	-0.23	-0.24	-0.47
Tierra Firme	-	-	0.62	0.52
latitude	0.37	0.24	0.36	0.75
longitude	-0.54	0.70	-0.34	0.89
floodplain surroundings	0.02	-0.18	-0.16	-0.49
swamp surroundings	0.09	0.14	-0.15	-0.60
Tierra Firme surroundings	0.16	0.07	0.37	0.63
pca1soil	-0.54	-0.05	-0.85	-0.23
pca2soil	0.10	-0.08	0.21	-0.25
pca1structure	-0.01	-0.01	0.52	-0.05
pca2structure	-0.03	-0.07	-0.09	0.23

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

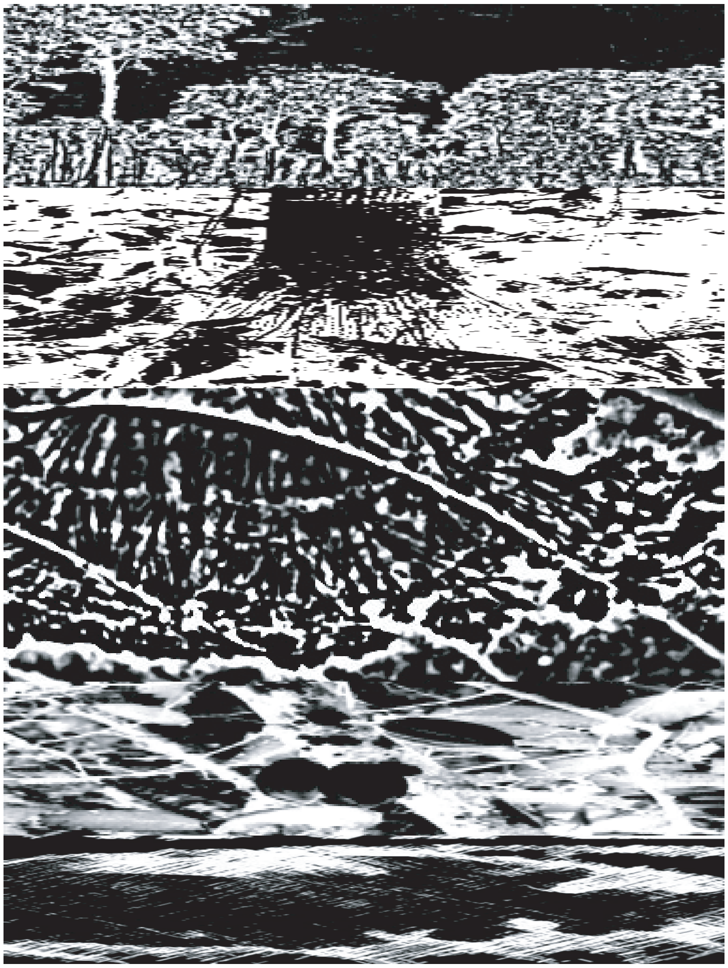
The ANOVA and multiple regression analysis also pointed out that liana diversity was consistently lower in floodplains and swamps that in Tierra Firme forests. The lack of interaction in the ANOVA indicated that these effects were similar in all three areas. A negative association between Amazonian plant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

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

Liana species patterns

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

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



Chapter 7

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

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

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

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

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

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

7.2 METHODS

Study site and sample design

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

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

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

In the central part of each plot, a soil augering was carried out to 120 cm depth in order to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions, and texture) and to define soil drainage (in classes of FAO 1977). At each augering a soil sample was taken at a depth of 65-75 cm. For analyses, soil samples were dried at temperatures below 40°C, crumbled and passed through a 2-mm sieve. The total content of Ca, Mg, K, Na, and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H2SO4 (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser. Soil analyses were done at the soil laboratory of Institute for Biodiversity and Ecosystem Dynamics of the Universiteit van Amsterdam.

Data analysis

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

Response models

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

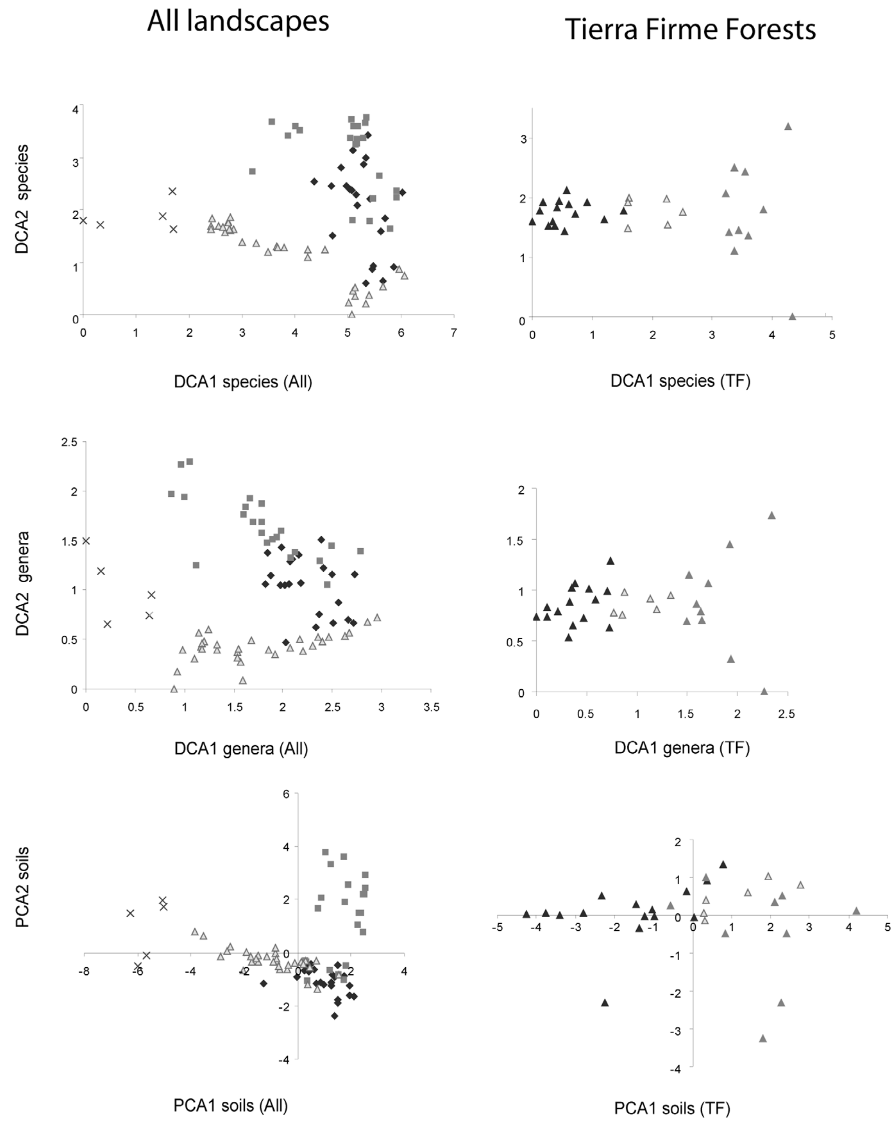


Figure 7.1. DCA based on genera and species and PCA based on soil elemental concentrations, in all landscapes (All), and Tierra Firme (TF) alone. Squares = flood plains, rhombus = swamps, triangles = Tierra Firme, and crosses = white sands. In Tierra Firme forests alone, black triangles represent Metá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

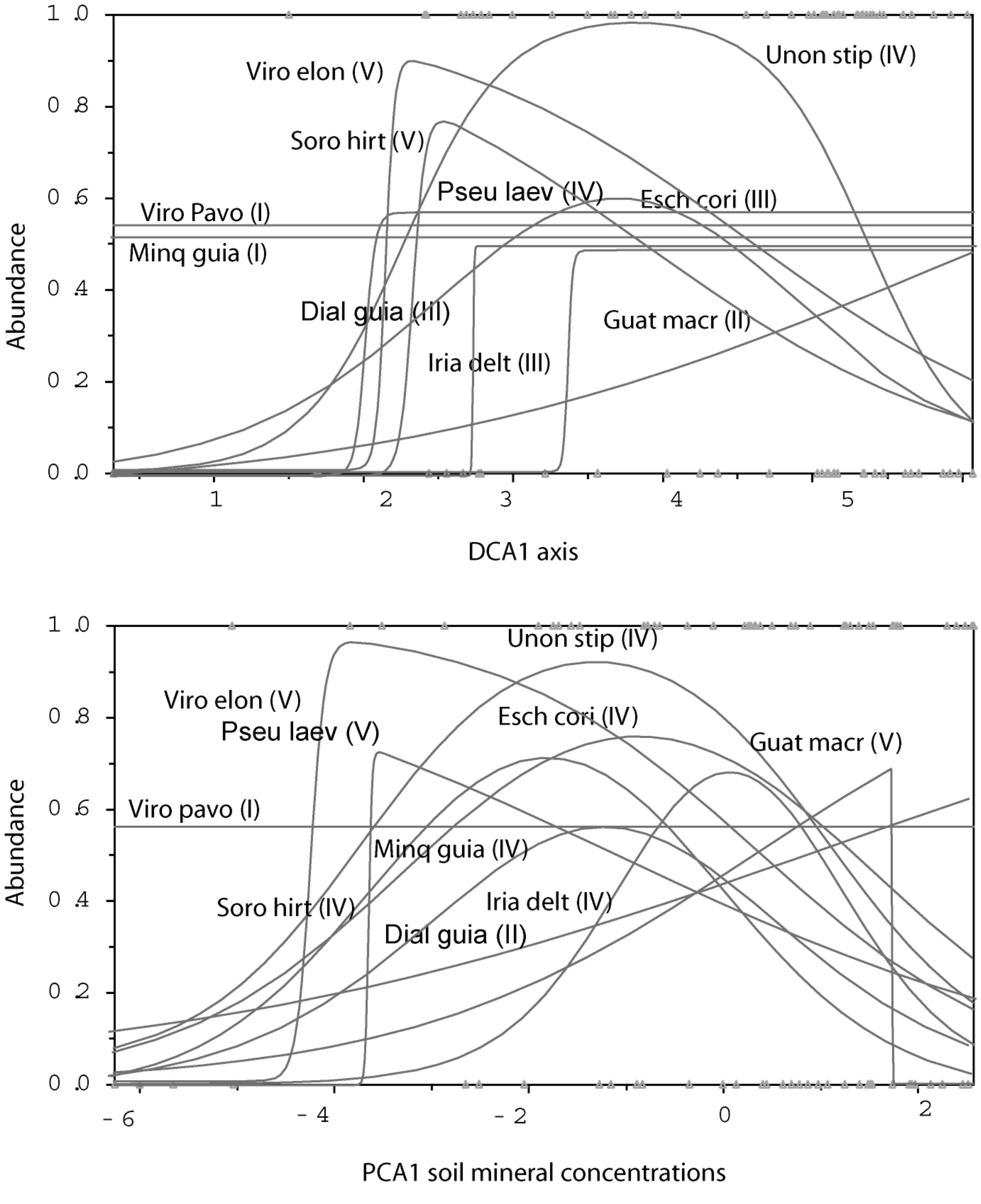


Figure 7.2. Examples of different response shapes of species along different gradients in 80 0.1-ha plots in NW Amazonia. Model types according to table 3 and species name as in table 4.

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

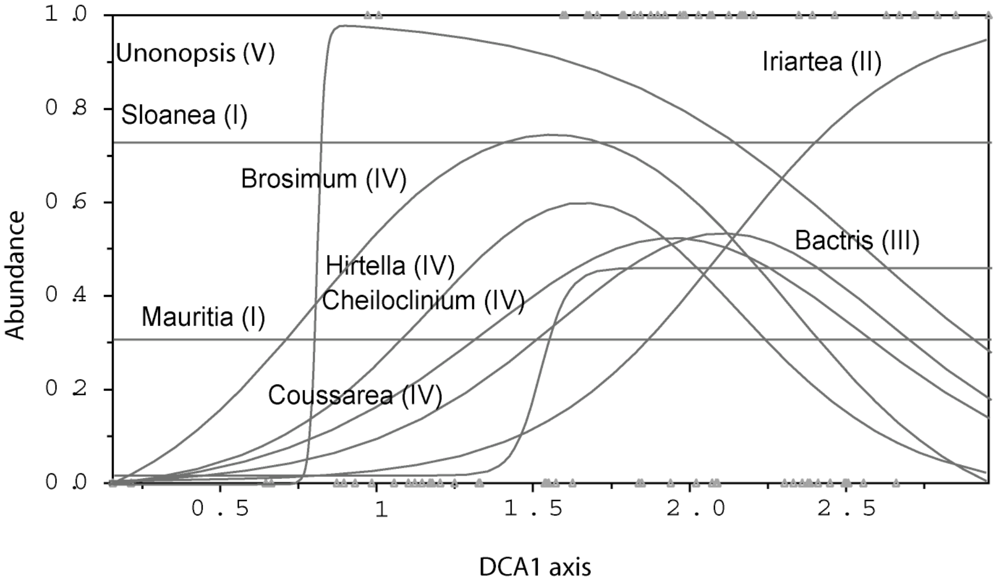
Monotone and plateau responses might be caused by a species range extending beyond the limits of the gradient sampled (Austin 2002), or by incomplete sampling of the gradient. Therefore, if the sample size is enlarged, more bell-shaped response curves might arise (Økland 1986). However, incomplete environmental 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.



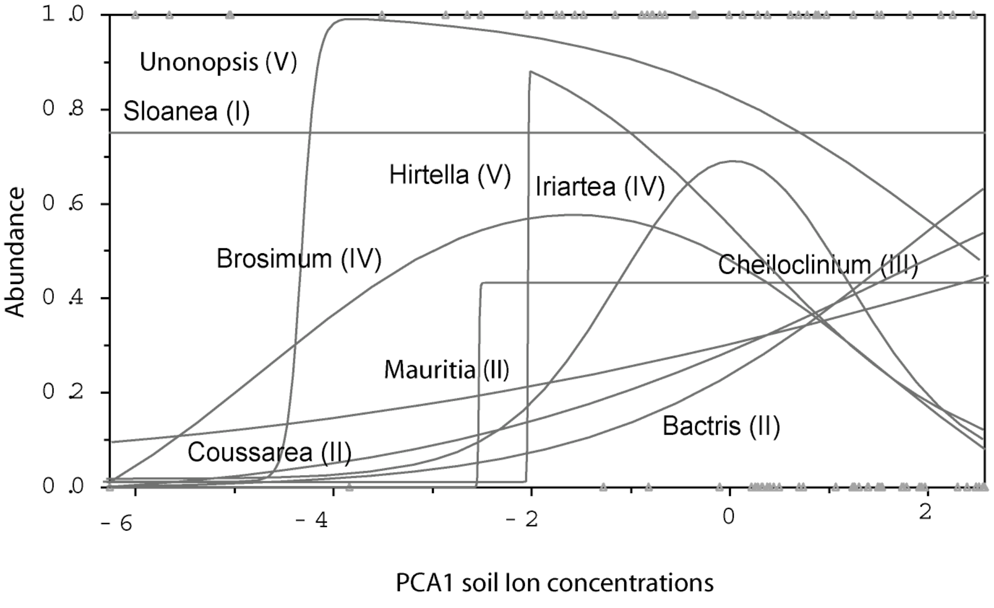


Figure 7.3. Examples of different response shapes of genera along different gradients in 80 0.1-ha plots in NW Amazonia. Model types according to table 3.

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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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 capítulo 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 epifitas 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 capítulo 5, en un estudio de caso en la Amazonía 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.

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

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 ≥ 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 ≥ 2.5 cm. About 40-60% of the woody plants with DBH ≥ 2.5 cm carried epiphytes, which points at low phorophyte limitation throughout all landscapes. Epiphytism was concentrated on stem bases. Just as trees, epiphyte species assemblages were well associated with the main landscapes. Contrary to trees, however, epiphyte abundance and diversity (species richness, Fisher's alpha index) hardly differed between the landscapes. This calls for caution when explanations for distribution and dynamics of tree species are extrapolated to growth forms with a totally different ecology.

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.

Appendix 1. 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 andina, 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, Amaioua* 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 marmierii 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 Ruíz & 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) Keinhoonte	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	
*MS*3451	7	2.7	14.3			7	
*MS*4865	7	2.8	15.4			7	
*MS*6749	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 Ruíz & 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 (Ruíz & 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 Ruíz & 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 saccifera (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 Ruíz & 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*
Clusiacea*e 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
Satyria cf. *Panurensis* (Benth. Ex Meisn.) Benth. and Hook. F. Ex Nied. (AMB 1097)	1		TF*
Gesneriaceae			
Alloplectus sp.1 (AMB 457)	4	6	PZ*
Codonanthe calcarata (Miq.) Hanst (AMB 427)	90		TF, PZ
Codonanthe crassifolia (H. Focke) C.V. Morton (AMB 158)	175		TF, SW, FP, PZ
Codonanthopsis dissimulata (H.E. Moore) Wiehler (AMB 185)	20		TF, SW, FP
Paradrymonia ciliosa (Mart.) Wiehler (AMB 194)	36	16	TF, FP, PZ
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
Catacetum sp. 1 (AVG 288)	10		SW, FP
Dichaea hookeri Garay and Sweet (AMB 613)	9		SW
Dichaea rendlei Gleason (AMB 1092)	10		TF, PZ
Epidendrum cf. *nocturnum* Jacq. (AMB 1256)	1		PZ*
Epidendrum longicolle Lindl. (AMB 139)	83		SW, PZ
Epidendrum microphyllum Lindl. (AMB 523)	10		SW, PZ
Gongora quinquenervis Ruiz and Pav. (AMB 505)	6		PZ*
Masdevallia aff. *trigonopetala* Kraenzl. (AMB 223)	3		FP*
Maxillaria cf. *parkeri* Hook. (AMB 521)	53		TF, PZ
Maxillaria cf. *triloris* E. Morren (AMB 1056)	18		TF, PZ
Maxillaria sp. 1 (AMB 596)	1		PZ*
Maxillaria sp. 3 (AMB 1232)	1		SW*
Maxillaria sp. 4 (AMB 206)	1		FP*
Maxillaria superflua Rchb. F. (AMB 359)	17		TF, PZ
Maxillaria uncata Lindl. (AMB 716)	1		TF*
Notylia sp. 1 (AMB 465)	5		PZ*
Octomeria brevifolia Cogn. (AMB 371)	5		TF
Octomeria erosilabia C. Schweinf. (AMB 421)	7		TF
Octomeria sp. 1 (AMB 1219)	31		TF
Ornithocephalus cf. *cochleariformis* C. Schweinf. (AMB 262)	1		FP*
Paphinia cf. *seegeri* Gerlach (AMB 470)	9		TF, PZ
Pleurothallis aff. *aurea* Lindl. (AMB 500)	7		PZ
Pleurothallis cf. *flexuosa* (Poepp. and Endl.) Lindl. (AMB 517)	3		SW, FP, PZ
Pleurothallis grobyi Bateman ex Lindl. (AMB 717)	1		TF*
Pleurothallis miqueliana (H. Focke) Lindl. (AMB 609)	4		SW
Polyotidium huebneri (Mansf.) Garay (AMB 463)	10	4	TF, SW, PZ
Polystachya sp. 1 (AMB 774)	1		PZ*
Sobralia macrophylla Rchb. F. (AMB 182)	5		FP, PZ
Sobralia sp. 1 (AMB 1074)	1		PZ*
Vanilla cf. *Columbiana* Rolfe (AMB 777)		1	FP*
Vanilla penicillata Garay and Dunst. (AMB 618)		2	SW, FP
Vanilla sp. 1 (AMB 140)		2	SW*
Orchidaceae sp. 1 (AMB 532)	6		PZ
Orchidaceae sp. 2 (AVG 360)	4		TF
Orchidaceae sp. 3 (AMB 758)	2		FP*
Orchidaceae sp. 4 (AMB 1294)	1		FP*
Piperaceae			
Peperomia cardenasii Trel. (AMB 240)	45		TF, SW, FP, PZ
Peperomia macrostachya (Vahl) A. Dietr. (AMB 181)	12		FP
Peperomia pseudopereskiaefolia C.DC (AMB 560)	8		TF, FP
Peperomia serpens Loud. (AMB 202)	17		FP
Urticaceae			
Pilea sp. 1 (AMB 757)		1	
Pteridophytes			
Aspleniaceae			
Asplenium serratum L. (AMB 191)	41	9	TF, SW, FP, PZ
Blechnaceae			

	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 hostmanianum (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 parkerii (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

	FP	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

Havetiopsis 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 uaupensis* 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)