PLANT DIVERSITY SCALED BY GROWTH FORMS ALONG SPATIAL AND ENVIRONMENTAL GRADIENTS

A study in the rain forests of NW Amazonia

Alvaro Javier Duque Montoya

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CONTENTS

To all those plants, animals, and human beings inhabiting the forests.
And to all those striving to preserve this.

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≥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.

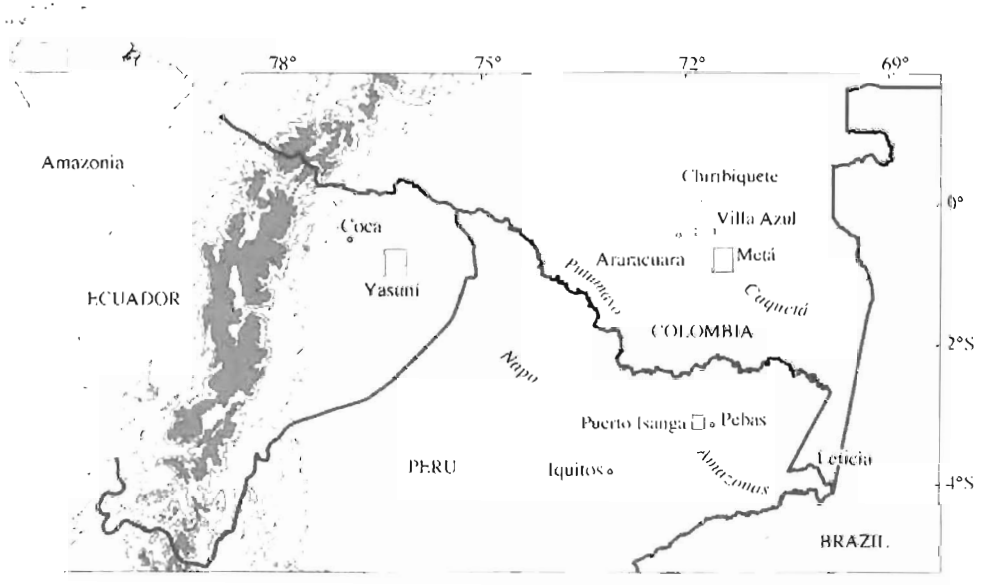

Figure 1.1. Location of the different sampled areas in NW Amazonian.

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
Biotropica 35(1): 20-27 (2003)

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 Medellín (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

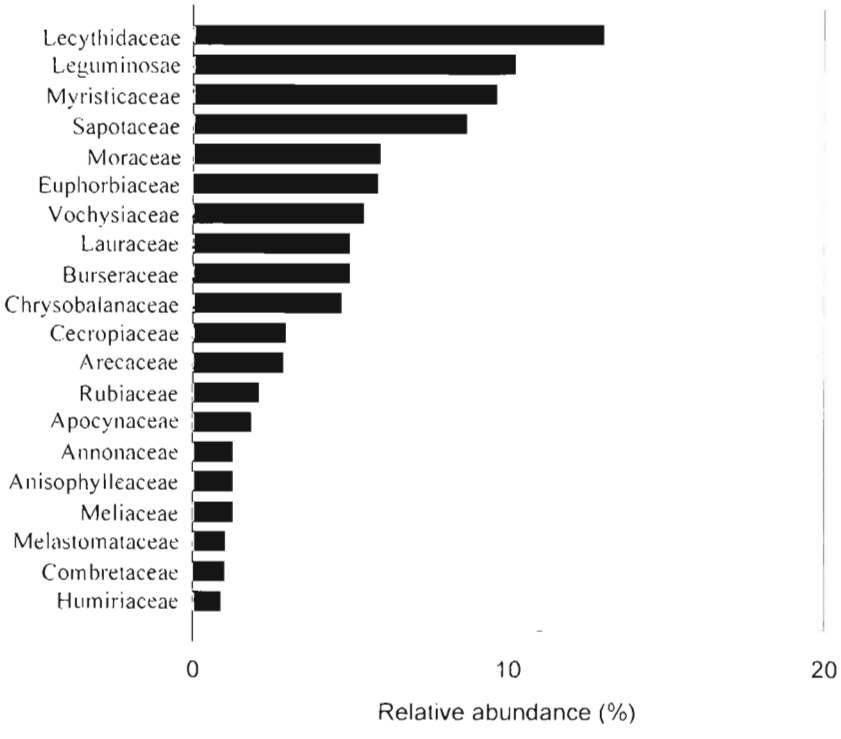

Figure 2.1. Relative abundance of plant families in the 2.16 ha longitudinal plot covering a low plain terrace, a high dissected terrace, and a high plain terrace.

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.

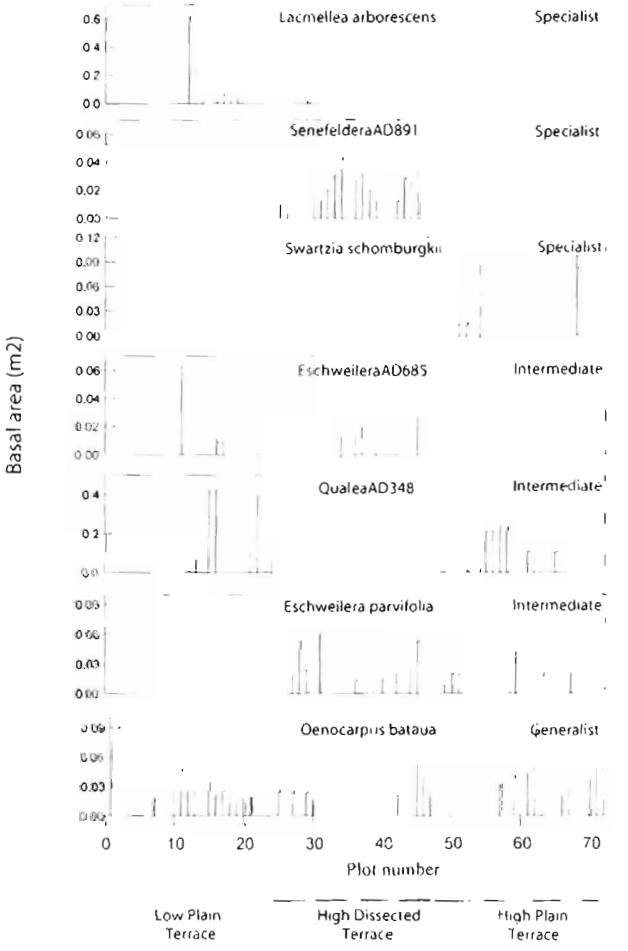

Figure 2.2. Examples of the different strategies of tree occupation for abundant species: specialists (occur in only one forest type), intermediate (occur in two forest types) and generalists (occur in all three forest types). The total length of the transect is 2160 m and each contiguous plot is 10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

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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.

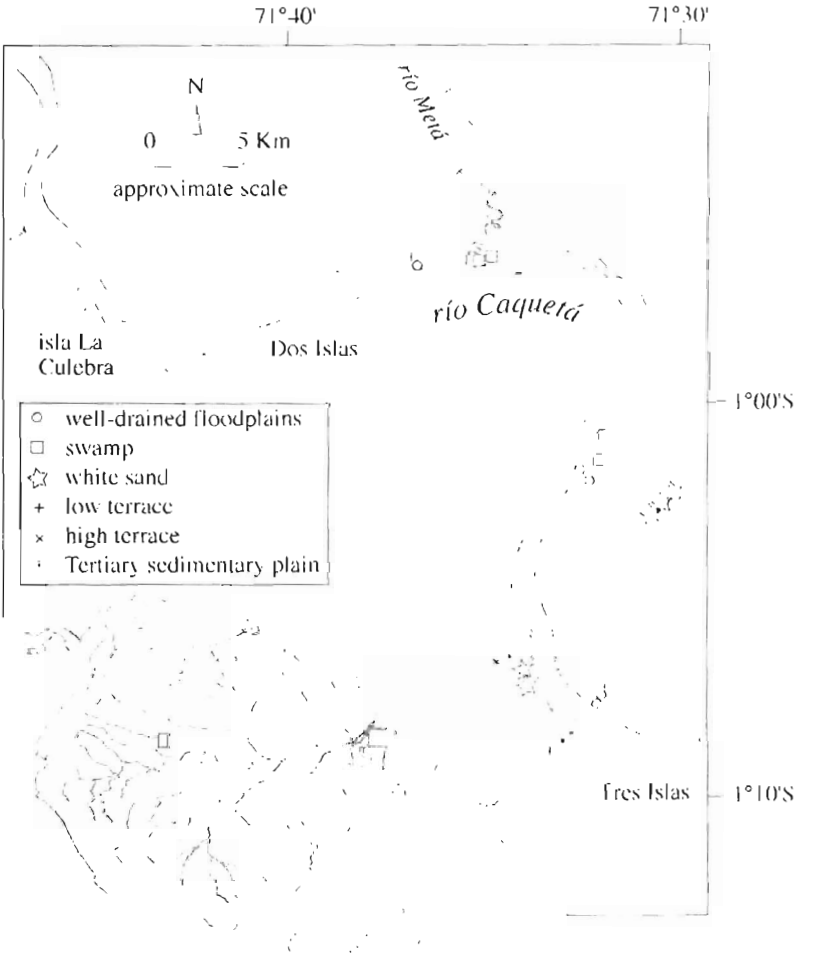

Figure 3.1. Location of 0.1-ha sample plots in the Metá area (Colombian Amazonia).

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 ≥ 2.5 cm); canopy species (species with individuals that were found with DBH ≥ 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 ≥ 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 Meta area (Colombian Amazonia). Shown are averages ± standard deviation of n plots.

	species DBH ≥ 2.5 cm	individuals	species DBH ≥ 10 cm	individuals	n
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).

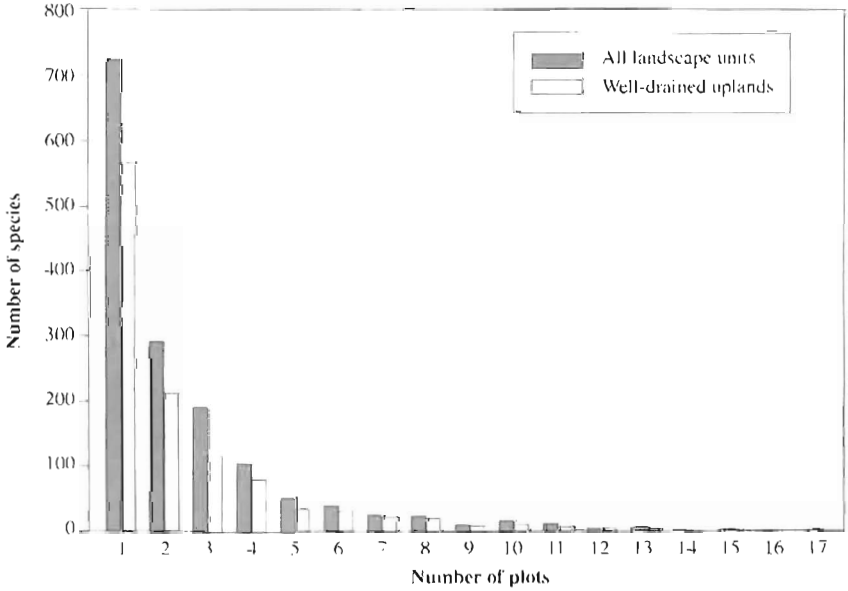

Figure 3.2. Number of species (DBH ≥ 2.5 cm) recorded in an increasing number of plots of 0.1 ha. in the Metá area (Colombian Amazonia)

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

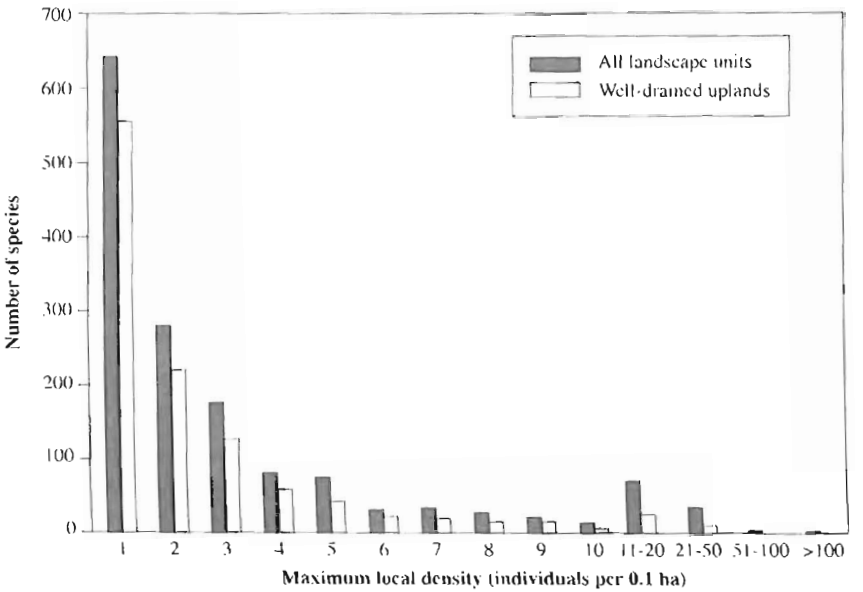

Figure 3.3. Number of species (DBH ≥ 2.5 cm) recorded with an increasing number of individuals in plots of 0.1 ha, in the Metá area (Colombian Amazonia).

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.

Chapter 4

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

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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 Yasuni 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