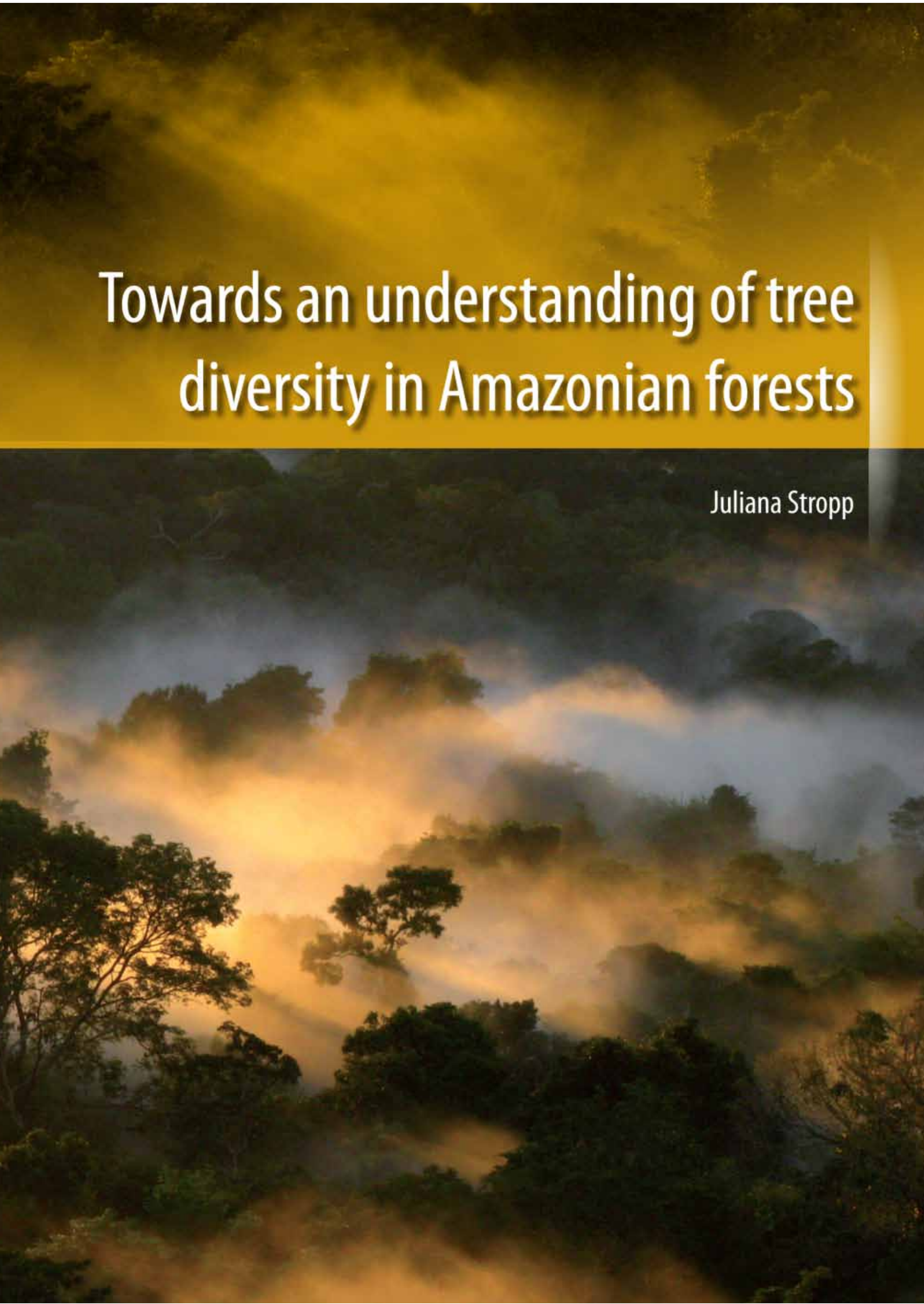

Towards an understanding of tree diversity in Amazonian forests

Juliana Stropp

TOWARDS AN UNDERSTANDING OF TREE DIVERSITY IN AMAZONIAN FORESTS

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Para minha mãe, Marilde Stropp

CONTENTS

1

INTRODUCTION

Amazonian forests arguably harbor the highest biodiversity of all terrestrial ecosystems on Earth. Both the origin of this extraordinary biodiversity and its current distribution are recently becoming better understood (ter Steege et al., 2003, Hoorn and Wesselingh, 2010). Processes such as long-term landscape evolution and climate change have been identified as important drivers of speciation and extinction, thus shaping the current patterns of biodiversity in Amazonian forests (Hoorn et al., 2010). Still, our knowledge about the relative contribution of processes operating at different spatial and temporal scales to the tree diversity in Amazonia remains surprisingly limited. Obtaining new scientific insight requires foremost collecting and analyzing additional empirical data. This thesis addresses parts of the existing knowledge gaps by presenting new data of tree inventory plots and by analyzing these in an integrated manner with previously established plots. The thesis thereby aims at deepening our understanding of the tree diversity in Amazonian forests and the ecological mechanisms shaping its current pattern at a local and regional scale.

HISTORY OF AMAZONIAN FORESTS

Forests have been a permanent feature in Amazonia for the past 55 million years (Ma) (Morley, 2000, Maslin et al., 2005). Throughout its history, Amazonia has experienced dynamic changes in its landscape and climate (Hoorn et al., 2010). Four important historical events have strongly contributed to the current pattern of diversity: a long period of isolation, the Andean uplift, the closing of the Panama isthmus, and changes in global climate (Fig. 1.1) (Burnham and Graham, 1999, Hoorn et al., 2010). This section shortly describes each of these historical events and discusses their impacts on the evolution of tree species diversity in Amazonia.

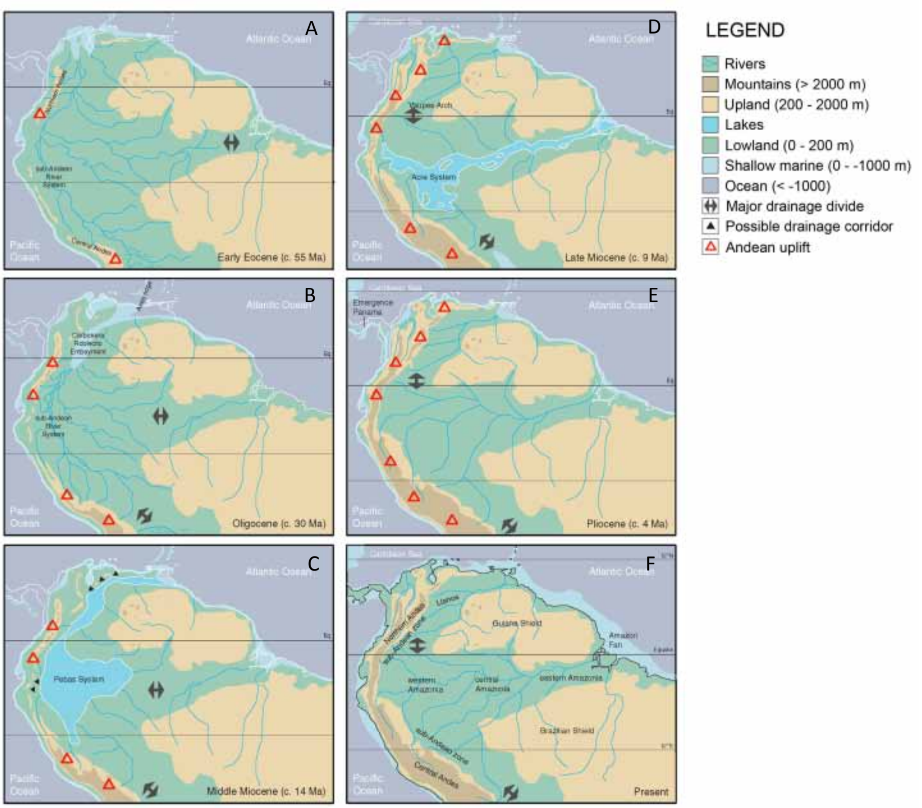

Figure 1.1: Palaeogeographic maps (A – E) and present configuration of Amazonia (F). **A:** ***rainforest diversification in the northern Andes***; uplift of the central and northern Andes; a major drainage divide is located in eastern Amazonia; **B:** ***intermediately/moderately diverse rainforest in the northern Andes***; the onset of the uplift of the northern Andes coincides with a period of a tropical wet climate with an intense dry season in western Amazonia; the major drainage divide is now located in central-eastern Amazonia; **C**: ***diverse rainforest in northwestern Amazonia;*** continued uplift of the central and northern Andes; origin of the Pebas megawetland in western Amazonia; the major drainage divide moves to central-eastern Amazonia; **D:** ***diverse rainforest in western Amazonia; diversification of sub-Andean forest***; the accelerated uplift of central Andes and northern Andes promotes the establishment of a transcontinental Amazon drainage system; **E:** ***diverse rainforest in western Amazonia*** **and** ***disappearance of Amazonian biota in northern Venezuela***; the strongly concerted uplift of the entire Andes and a dynamic low-relief river systems of western Amazonia favor the Andean derived nutrients spread over eastern Amazonia; the closure of the Panama isthmus promotes exchange of biota between North and South America ('Great American Biotic Interchange' - GABI); **F: diverse rainforest, especially in western Amazonia**; present configuration of Amazonia. Note that shield areas are geologically stable over the last 55 Ma. Modified after Hoorn and Wesselingh (2010) and Hoorn et al. (2010).

The long period of geologic isolation experienced by South America extended from about 100 to 3.5 Ma (Burnham and Graham, 1999). This isolation started when the South American and African plates began to separate and finished when South and North America became connected by the closing of the Panama isthmus. The period of isolation coincides with the period of great diversification of the angiosperms during the Cretaceous (Willis and McElwain, 2002). Isolation led to endemism. Several tree genera present in Amazonia, such as *Apeiba* (Malvaceae), *Ecclinusa* (Sapotaceae), *Siparuna* (Siparunaceae), and several genera of Annonaceae, have their distribution completely restricted to South America (Burnham and Graham, 1999, Couvreur et al., 2010), suggesting that several lineages currently present in Amazonia have originated *in situ*.

When in the Tertiary South America was still isolated, the Andean uplift, stretching from 65 to 4.5 Ma, considerably changed the landscape configuration as well as the climate of Amazonia (Hoorn et al., 2010). The Andean uplift dramatically modified relief configuration, drainage patterns, soil properties as well as regional patterns of rainfall in Amazonia. Because the Andean uplift caused such profound changes in the physical environment in Amazonia, this event is arguably one of the most important in shaping the current patterns of diversity (Hoorn et al., 2010). The Andean uplift created new habitats, such as montane and pre-montane habitats, and promoted the development of fertile soils. These new habitats may have induced the development of morphological and physiological adaptations, thereby offering opportunities for speciation (Fine et al., 2005). Additionally, the new mountain range may have caused geographic isolation of previously connected populations, favoring allopatric speciation. Moreover, the Andean uplift changed the rainfall regime in the east-west direction of Amazonia. When the Andes became a dominant landscape in the northwestern region of South America, it trapped the warm and wet air which blows from the Atlantic Ocean from east to west, favoring the occurrence of a stable rainfall regime in the east-west direction across an extensive area (Hooghiemstra and van der Hammen, 1998). In contrast, south and north regions of Amazonia were subject to more dynamic climate. The stable climate in the extensive area in the east-west direction prevented tree species from going extinct, whereas in area where climate was dynamic species were more vulnerable to extinction (ter Steege et al., 2010).

During the final phase of the Andean uplift, the closing of the Panama isthmus connected North and South America (~ 3.5 Ma). This coincided with the end of the mega wetland systems (Pebas and Acre) which were present from 16 to 7 Ma (Fig. 1.1). The connection between North and South America promoted exchange of fauna and flora between these two previously isolated areas. This exchange, named as ‘Great American Biotic Interchange’ (GABI), has caused extinctions among South American mammals, via competition or the presence of new pathogens (Stehli and Webb 1985 in Antonelli, 2008). Plants may have suffered similar impacts (Antonelli, 2008). Additionally, the end of the mega wetland systems promoted the expansion of terra-firme forest throughout a large area offering opportunists to tree species expand their distribution as well as to adapt to new environmental conditions. This expansion of terra-firme forest may have caused speciation as well as changes in tree species distribution. In fact, plant diversity increased by 10 to 15% after forest occupied the previously flooded areas (Hoorn et al., 2010).

Simultaneously with the tectonic dynamics of the South American plate, global climatic cycles have caused changes in the size and location of tropical forests (Hooghiemstra and van der Hammen, 1998, Dynesius and Jansson, 2000). These global climatic cycles, known as Milankovitch cycles, are driven by orbital variations. The ''precession cycle'', with a periodicity of about 20,000 years causes shift changes southwards and northwards of the location of the Intertropical Convergence Zone (ITCZ) (Martin et al., 1993, Martin et al., 1997, Haug et al., 2001). As a consequence, Amazonia has experienced a more stable climate in its centre than at its edges, which may have allowed a larger number of species to persist in this central area and may have caused species extinction in the more climatically dynamic borders. These variations in long-term climate may have made a large contribution to the current gradient of tree species diversity in Amazonia (ter Steege et al., 2010).

In short, at the broadest spatial and temporal scale, dynamics of plate tectonics and Earth orbital cycles have caused major changes in the landscape configuration as well as in climate throughout the history of Amazonian forests. Tree species have been responding to these changes, thereby creating the current pattern of tree species diversity.

CHARACTERIZATION OF CONTEMPORARY AMAZONIAN FORESTS

Amazonia encompasses an area of ca. 6.8 million km^2 located in the northern part of South America (Fig. 1.2) (Eva et al., 2005). Humid forests cover nearly 80% of Amazonia (5.5 million km^2); the remaining 20% is covered by dry forests (1%), flooded forests (3%), grass- and scrublands (5%), short or sparse vegetation (1%) as well as agriculture and urban areas (10%). Forests classified as 'lowland Amazonian rain forests' are defined as all natural forest types growing in areas with a mean annual temperature above 24°C, an elevation below 700 m asl (meters above sea level), and a mean annual rainfall above 1,400 mm (Eva et al., 2005). These lowland Amazonian rainforests grow both on flooded or non-flooded terrain and on a variety of tropical soil types, e.g., ferrasols, acrisols, arenosols, and podzols (Quesada et al., 2009). Rainfall seasonality varies across Amazonia. The south-eastern part has a marked dry season of 3 to 5 consecutive months with rainfall less than 100 mm per month, whereas in the north-western part climate is essentially a-seasonal (Sombroek, 2001). Additionally, soil fertility varies across Amazonia, being relatively fertile in the basins of the rivers: Putumayo-Içá, Purús, and Madeira and nutrient-poor in the basins of the Negro, Tapajós, Xingu as well as in the Guianas and in the Gurupí (Sombroek, 2000) (Fig. 1.2).

Figure 1.2: Geographical limits of Amazonia. This thesis uses the term "Amazonian forests" to refer to lowland rainforests present in the areas classified as "Gurupí", "Guianas", and "Amazonia *sensu stricto"*, according to Eva et al. (2005).

This thesis focuses on two floristically distinct Amazonian forest types: white-sand and terra-firme forests. White-sand forests refer to the lowland rainforests growing on non-flooded sandy soils (podzols) which are commonly referred to as 'campinarana' or 'caatinga alta' (Brazil), 'varillal' (Colombia and Peru), 'cunurí' or 'yaguácanan' (Venezuela), and 'wallaba forest' or 'white-sand forests' (Guyana, Suriname) (Anderson, 1981, Banki, 2010). White-sand forests cover ca. 5-10% of the total area of Amazonia (ter Steege et al., 2000). Canopy height of white-sand forests ranges from 20 to 30 m, the understory strata is relatively open and typical features of rainforests, such as tree buttresses, vines, and big woody climbers are relatively uncommon or absent (Anderson 1981). White-sand forests harbor a less diverse and distinct tree species community as compared to those encountered in the terra-firme forests (Fanshawe, 1952, Anderson, 1981, Dezzeo et al., 2000, ter Steege et al., 2000, Boubli, 2002, Banki, 2010). We refer here to 'terra-firme forests' as lowland rainforests growing on non-flooded clayey soils. The term 'terra-firme forests' is used across several countries in Amazonia. In the Guianas, however, this forest type is referred to as 'brown-sand forests' (Banki, 2010). Terra-firme forests are the dominant forest type, covering ca. 80% of the total area of Amazonia (ter Steege et al., 2000). Canopy height of terra-firme forests ranges from 25 to 35m and the understory is usually denser than that of white-sand forests, with palms and tree buttresses (Ribeiro et al., 1999). This forest type harbors one of world's most diverse tree communities; a single hectare of terra-firme forest can hold up to 300 tree species (DBH ≥ 10 cm) (Valencia et al., 1994, Oliveira and Mori, 1999).

UNDERSTANDING SPECIES DIVERSITY IN AMAZONIAN FORESTS

Efforts to understand the diversity of tropical forests have focused on ecological processes driving species co-existence (see review in Wright, 2002). Several hypotheses have been proposed to explain why a high number of species co-exists in tropical forests. These include local disturbance (Connell, 1978, Huston, 1979), predation (Janzen, 1970, Connell, 1972, Givnish, 1999), and competition for limiting resources (Tilman, 1982). The underlying ecological mechanisms of these hypotheses emphasize the importance of local species interaction as well as local environmental conditions. They thereby emphasize ecological processes operating at local spatial and short temporal scales. Recently, however, empirical data on species diversity and distribution covering a large geographic area (ter Steege et al., 2003, Malhi et al., 2006, ter Steege et al., 2006) as well as lineage-diversification (Richardson et al., 2001, Fine et al., 2005, Erkens and Maas, 2009) allowed ecologists to take a broad perspective and identify mechanisms shaping diversity at broad spatial and temporal scales. These analyses indicate that interactions between long-term evolutionary and short-term local ecological processes shape the current pattern of diversity of Amazonian forests (see Ricklefs and Schluter, 1993, Rosenzweig, 1995). To understand how these interactions operate it is important to clearly identify at which spatial and temporal scale evolutionary and ecological processes are most relevant (McGill, 2010).

Processes, such as speciation, extinction, and migration operate at large spatial and long temporal scales (Ricklefs and Schluter, 1993, Rosenzweig, 1995). At large spatial scales, the size of a habitat determines the number of species it can support: large habitats typically host more species, as a positive balance between speciation and extinction rates is often reached (Rosenzweig, 1995). At long temporal scales, environmental changes regulate speciation, extinction, and migration. If substantial environmental changes persist for long periods, species may 1) evolve adaptations to the new conditions, 2) go extinct, or 3) migrate to areas where suitable environmental conditions are still available (Rosenzweig, 1995). Thus, processes operating at large spatial and long temporal scales determine the number of species present in the regional community. Species are not randomly distributed across large regions. Dispersal limitation and environmental filtering determine *which* and *how many* species will be locally present (Hubbell, 2001, ter Steege and Zagt, 2002, Jabot et al., 2008, Banki, 2010). At local scale, diversity is mostly regulated by species interactions. Predation, competition, and local stochastic extinctions regulate how many species co-exist in the local community (Ricklefs and Schluter, 1993, Leigh et al., 2004). The categorical definition of regional and local communities is a simplification because evolutionary and ecological processes are linked in a continuum (Ricklefs, 2007). Nevertheless, this simplification allows us to improve our general understanding about the main drivers of species diversity.

SCOPE AND OUTLINE OF THIS THESIS

In this thesis, I apply a hierarchical approach in which regional and local communities are addressed explicitly (Fig. 1.3). I aim at identifying the contribution of regional and local processes for shaping variation in tree species diversity and in floristic composition across Amazonian forests.

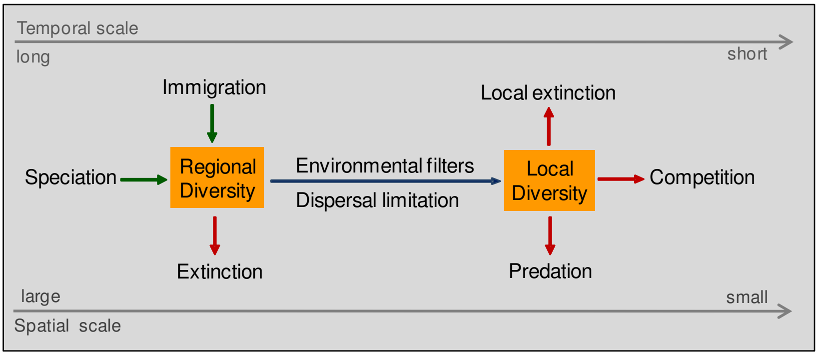

Figure 1.3: Processes shaping species diversity and the scale at which they are relevant. Green arrows indicate processes which increase diversity, red arrows those that decrease it. Regional diversity is controlled by processes such as speciation, immigration, and extinction, whereas local diversity is controlled by stochastic local extinction, interspecific competition, and predation. Regional and local diversity are linked via environmental filters and dispersal limitation (blue arrow). Modified after Ricklefs and Schluter (1993) and ter Steege and Zagt (2002).

In **Chapter 2**, I apply this hierarchical approach explicitly to a large dataset with the aim of identifying potential regional and local drivers for the variation in tree species diversity in the Amazonian forests. I hypothesize that regional tree diversity is influenced by large-scale and long-term processes, whereas local tree diversity is mainly regulated by small-scale and short-term processes. I analyze an extensive data set of 752 tree inventory plots spread over entire Amazonia. In this dataset, many localities have multiple plots, thereby offering a unique opportunity to analyze both regional and local variation of tree species diversity.

We will see in Chapter 2 that tree inventory plots are particularly scarce in the upper Rio Negro region. This shortcoming is relevant because unlike prevailing landscapes in Amazonia, where terra-firme forests are the dominant forest type, the upper Rio Negro consists of extensive areas of white-sand forests. Thus, in **Chapter 3**, I present data of eight new tree inventory plots established in white-sand and terra-firme forests of the upper Rio Negro. I analyze forest structure as well as tree species diversity and composition of these new plots. I discuss the role of habitat size and environmental filtering driving differences in diversity and composition in local tree communities of white-sand and terra-firme forests.

In **Chapter 4**, I address, in particular, the role of environmental filtering for the variation of tree species composition between white-sand and terra-firme forests of the upper Rio Negro. I test the hypothesis that a trade-off between seedling growth and herbivore defense drives habitat specialization in these two forest types in the upper Rio Negro. I do that by conducting a cross-transplanting field experiment. I analyze seedling performance, i.e., growth and insect herbivore defense, as well as seedling traits of seven white-sand and seven terra-firme habitat specialist tree species.

In **Chapter 5**, I characterize tree species diversity and composition of white-sand and terra-firme forests and their variability across a broad spatial scale. My aim is to understand how the regional tree community regulates variation in tree species diversity and composition of local communities of white-sand and terra-firme forests. I analyze a dataset containing 192 tree inventory plots established in white-sand and terra-firme forests placed in three regions of Amazonia: central Amazonia, the Guianas and the upper Rio Negro.

In **Chapter 6**, I integrate the key findings of this thesis and address the factors that drive tree species diversity at the scale at with they are most relevant. Furthermore, I discuss the strength and limitations of the data and analyses presented here. I conclude deriving implications for biodiversity conservation and by proposing a research agenda to expand our understanding of tree species diversity in Amazonian forests.

2

DISENTANGLING REGIONAL AND LOCAL TREE DIVERSITY IN AMAZONIA

with Hans ter Steege, Yadvinder Malhi, ATDN, and RAINFOR

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ABSTRACT

Amazonian forests are one of the most diverse and extensive forests in the world. So far, their regional and local tree diversity have been explained by current environmental factors such as rainfall seasonality and soil fertility. However, environmental factors have been far from stable over the history of Amazonia. Identifying the main drivers shaping the current pattern of tree diversity in Amazonia requires hence a proper historical perspective. Here, we partition tree diversity into its regional and local components. We hypothesize that regional diversity is influenced by large-scale, long-term processes, whereas local diversity is mainly regulated by small-scale, short-term processes. We analyze the most extensive dataset of tree inventory plots covering the Amazon Basin and the Guiana shield. We find that palaeo-climatic stability and long-term large-scale ecosystem dynamics explain 31% and 14%, respectively of the regional tree diversity. Actual rainfall seasonality is correlated with regional tree diversity (19%), but we argue that this is of little consequence for the evolutionary drivers of regional diversity. Local ecosystem dynamics explain 17% of the variation in local tree diversity. Our results suggest that reliable predictions of future changes of species diversity require an approach which considers evolutionary and ecological processes at the scale at which they are most relevant.

INTRODUCTION

Large-scale patterns of biodiversity are often explained by current climate. A well known example is the latitudinal gradient in species richness that is most often explained in terms of available energy, rainfall, or combinations thereof (Currie, 1991, Currie et al., 2004, O'Brien, 2006, Kreft and Jetz, 2007). The large-scale pattern of tree diversity in Amazonia (ter Steege et al., 2006) has also mostly been explained in terms of annual rainfall (Clinebell et al., 1995), seasonality (ter Steege et al., 2003), and soil fertility (Clinebell et al., 1995). Climate, however, has been far from stable over the history of the existence of Amazonian forests – viz the last c. 55 million years (Morley, 2000, Burnham and Johnson, 2004, Jaramillo et al., 2006). In fact, the current climate may be representative of only a small fraction of the history of Amazonia (ibid.). As species richness, the number of existing species, is ultimately the sum of three long-term processes – speciation, extinction, and immigration (Ricklefs and Schluter, 1993, Rosenzweig, 1995), the current pattern of diversity have to be interpreted in a proper historical perspective. Local diversity (here measured on 1-ha plots, see ter Steege et al., 2003) is also influenced by small-scale, short-term ecological processes such as competition, predation, and random local extinction. To understand which part of the variation of species diversity is regulated by long-term, large-scale versus short-term, small-scale processes a conceptual model linking them is needed (Ricklefs and Schluter, 1993, Rosenzweig, 1995, Willis and Whittaker, 2002). We propose a conceptual model with two species pools: a regional species pool, which is mainly influenced by the large-scale, long-term processes, and a local species pool, which is regulated by small-scale, short-term processes and receives species from the regional species pool. The link between regional and local species pool determines *which* and *how many* species from the regional species pool are present in the local species pool (Fig. 2.1). We, therefore, propose that an analysis of the tree diversity in Amazonian forests should take evolutionary and ecological processes into account at the scale at which they are relevant.

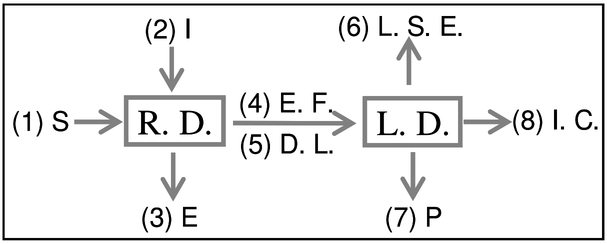

Figure 2.1: Diversity is influenced by regional and local processes (Hubbell, 2001, ter Steege and Zagt, 2002, Ricklefs and Schluter, 1993). Regional diversity is controlled by processes such as speciation (S, 1), immigration (I, 2), and extinction (E, 3), whereas the local diversity is controlled by local stochastic extinction (L. S. E., 6), interspecific competition (I. C., 8), and predation (P, 7). Regional and local diversity are linked via environmental filters (E. F., 4) and dispersal limitation (D. L., 5).

Regional tree diversity and regional processes

At low latitudes, the extent and location of the tropical rain forests are related to changes in global climate over time which, in turn, are influenced by the well-know 'Milankovitch cycles' (Gates, 1993). The global temperature and rainfall regime has a major cycle related to the 'eccentricity cycle' (ibid) with a periodicity of c. 100,000 years. During warm and wet interglacial periods, tropical rainforests covered a much larger latitudinal range than during cold and dry glacial periods (Morley, 2000, Mayle and Beerling, 2004, Maslin et al., 2005). The 'precession cycle', with a periodicity of 20,000 years causes shift changes southwards and northwards of the location of the Intertropical Convergence Zone (ITCZ) (Martin et al., 1993, Martin et al., 1997, Haug et al., 2001). As a consequence, Amazonia experienced a more stable climate in its centre than at its edges (Hooghiemstra and van der Hammen, 1998). As the ITCZ on the South American continent shifts slightly southward (see Martin et al., 1997), this stable area should have a centre just south of the equator. In the east-west direction, a more stable climate, in terms of rainfall, is found in western Amazonia due to the orographic rain caused by the Andes (Hooghiemstra and van der Hammen, 1998). Long-term climatic variability is considered to be one of the important explanations for low diversity in certain regions (Araujo et al., 2008). In general, species with small ranges size are thought to be more susceptible to extinction partially caused by long-term climate change than large-range size species (Dynesius and Jansson, 2000, Jetz et al., 2004, Araujo et al., 2008).

Additionally, there is a sharp contrast in landscape evolution in eastern and western Amazonia (Sombroek, 2000). In western Amazonia, soils developed on sediments originating from Andean orogeny during the Cenozoic (~66 Ma and more recent), while in the south-east and north-east, on the Brazilian and the Guiana shield, respectively, soils developed on crystalline bedrock from the Proterozoic (~2,500 Ma) and its sediments. The soils of these two major geological series differ markedly in fertility (Sombroek, 2000), productivity (Malhi et al., 2004), forest tree composition (ter Steege et al., 2006), wood density (Baker et al., 2004, ter Steege et al., 2006), and seed mass (ter Steege et al., 2006). Higher productivity leads to higher turn-over in the forest (ter Steege and Hammond, 2001, Phillips et al., 1994, Malhi et al., 2004). Species with fast growth rates have low wood density and high mortality and recruitment rates (Nascimento et al., 2005), and we assume, short generation times. These species would experience faster rates of evolution than species with long generation times (Marzluff and Dial, 1991, Verdú, 2002), consequently leading to higher diversification (Allen and Gillooly, 2006).

Local tree diversity and local processes

Local variation in tree species diversity has been documented for Amazonia (see e.g. Pitman et al., 2002, Oliveira and Nelson, 2001). Tree species diversity of 1-ha plots located close to each other and thus, under similar climatic conditions, can exhibit huge differences in tree species diversity (Valencia et al., 2004, ter Steege et al., 2003). Local differences are partially influenced by competitive exclusion, which is driven by local disturbance, such as gap formation by fallen trees or branches, as explained by the Intermediate Disturbance

Hypothesis (Connell, 1978, Huston, 1979, Huston, 1994), which predicts highest diversity at intermediate disturbance regimes or in the mid-term of a primary or secondary succession (but see Wright, 2002, Sheil and Burslem, 2003 for critical reviews). As shown in Fig. 2.1 predation is thought to decrease local tree diversity. Predation, however, can also increase tree local diversity through frequency dependent mortality (Janzen, 1970, Connell, 1972). Frequency-dependent mortality reduces the potential of species to become dominant in ecosystems (for Amazonia, see Givnish, 1999). Density-dependent mortality of plants may be caused more frequently by insects and infestation by microbes and fungi than by mammal herbivores (Hammond and Brown, 1998, Wright, 2002).

In this Chapter, we apply a hierarchical approach to identify regional and local patterns and potential drivers of variation in tree species diversity in Amazonia. We focus on the relative contribution of regional and local processes determining tree species diversity at the relevant scale. We analyze the Amazon Tree Diversity Network (ATDN) dataset, which contains 781 tree inventory plots and spans the entire area of the Amazon basin and the Guiana shield (here collectively called ‘Amazonia’). In this dataset, many localities have multiple plots, sometimes up to 80. This offers a unique opportunity to analyze both regional and local variation of tree species diversity in one of the largest and most ecologically diverse tropical forests in the world.

METHODS

Data

We updated the ATDN dataset (ter Steege et al., 2003) by adding 1) the number of tree species and 2) the number of individual trees with diameter at breast height ≥ 10 cm, compiled from both newly published and unpublished floristic inventory plots and plots included in the RAINFOR dataset (version FT29.06.06; Peacock et al., 2007). In total, we compiled data from 781 tree inventory plots spread across Amazonia and placed in different forest (and soil) types: terra-firme (latosol, oxisol, and ultisol), white-sand (podzol), swamp (histosols), and floodplain (alluvial). Out of this total, we selected 752 plots ranging from 0.23 ha to 1 ha to our analysis. Plots larger than 2 ha (29 plots out of 781) were excluded from the analyses to avoid inclusion of beta-diversity. The 752 plots were classified into two groups according to the age of the geological formation on which they occurred: Proterozoic/Palaeozoic versus Cenozoic. Plots located on and around the Brazilian and the Guiana shield were classified as Proterozoic, and plots located on the Andean sediments were classified as Cenozoic (Sombroek, 2000). For all 752 plots, we extracted rainfall seasonality (coefficient of variation; Bioclim 15 in the WORLDCLIM dataset) in the period of 1950-2000 with 30 arc-seconds resolution (~1 km) from WORLDCLIM (Hijmans et al., 2005).

We extracted the species list of 113 terra-firme plots (41 RAINFOR plots and 72 plots located in ‘Reserva Florestal Adolpho Ducke’, central Amazonia) for which the botanical identification is consistent among the plots. For the RAINFOR plots we calculated the percentage of individuals from softwood genera, i.e., with oven-dried wood density < 0.6 g cm^{-3}. For the plots at ‘Reserva Florestal Adolpho Ducke’ we first classified the genus on categories of pioneer and non-pioneer, afterwards we calculated the percentage of individuals belonging to pioneer genera. The wood density values and the classification of pioneer genera were extracted from Chave et al. (2006) and the RAINFOR dataset. The percentages are considered to be proxies for disturbance in the plots (ter Steege and Hammond, 2001).

Data analyses

Tree diversity was calculated with Fisher’s alpha, hereafter referred to as tree alpha-diversity, which is relatively insensitive to sample size (Fisher et al., 1943). To calculate tree alpha-diversity, we used the number of species and individuals given for each plot, which sometimes contain a considerable number of morpho-species. As a consequence of this approach, if the morpho-species are split artificially we over-estimate tree alpha-diversity. By contrast, if the morpho-species are grouped artificially we under-estimate tree alpha-diversity. We think, however, that it is of minor importance to the results as for those plots where the morpho-species were finally resolved, Fisher’s alpha changed little (Nigel Pitman, pers. obs.).

We applied a stepwise approach to analyze the total variation of tree alpha-diversity (TAD) as a function of regional tree diversity (RTD), which is a reflection of the regional species pool (RSP), and local tree diversity (LTD) plus error (ε):

$$\text{TAD} = \text{RTD} + \text{LTD} + \varepsilon \qquad (2.1)$$

We separated the signal of the RTD from that of the LTD + ε by means of spatial interpolation. First, we attempted to interpolate TAD using universal kriging (ter Steege et al., 2003); this, however, proved to be impossible because of high local variation of TAD in locations with several plots (see Fig. 2.2). The high local variation causes our data to show no significant spatial auto-correlation. We, therefore, applied local (loess) regression (Venables and Ripley, 1997, Kalunzy et al., 1998) to interpolate TAD for Amazonia. Loess regression is a non-parametric regression technique that allows for greater flexibility than traditional regression techniques because, unlike traditional regression techniques, it does not fit a single regression model to the entire dataset (Osborne et al., 2007). Instead, loess regression gives a predicted value at each point of the dataset by fitting a weighted linear regression to it. A smooth regression curve is used to connect the predicted values. The smoothness of the regression curve is affected by a span value, which controls the degree at which the weight of points decreases with distance from the point of interest. Therefore, small span values (close to zero) produce an over fitted model, in contrast high span values (close to one) cause an excessively smooth model. We fitted a 2nd degree polynomial equation to our data (i.e., degrees of latitude and longitude of each plot as independent variable and observed TAD as dependent one) using a span value of 0.5. With the fit of this loess model, we mapped TAD for the entire Amazonia at a spatial resolution of one degree grid cells. We assume that the fit of our loess regression model represents the signal of the RTD. We estimated the ordinary residuals of the loess model by subtracting the observed

TAD values from the estimated ones. These residuals represent the variation of TAD that is not explained by regional effects, i.e., LTD plus the error variance of our loess regression model.

We then assessed to what extent regional and local variables related to the variation in RTD (loess fit), LTD (loess residuals), the link between RTD and LTD (also in loess residuals), and original Fisher's alpha values of each plot in a stepwise fashion. The regional variables used were: 1) latitude and longitude as proxies for palaeo-climatic stability, 2) actual rainfall seasonality, and 3) bedrock age (Proterozoic vs. Cenozoic). We considered these variables as regional variables, because they, as we argued in the introduction, mainly affect the processes of speciation and extinction and hence the RTD. We used latitude and longitude as model variables for the loess regression and also as explanatory variables because we consider them to be important proxies for palaeo-climatic stability (see Introduction). The influence of current rainfall seasonality on RTD was also analyzed with loess regression. The influence of bedrock age on RTD was determined with single factor ANOVA.

The next set of analyses focused on local tree alpha-diversity and its interaction with regional tree alpha-diversity. We started by quantifying the contribution of soil type (as a proxy for environmental filters) to the local tree alpha-diversity. We performed a single factor ANOVA to determine whether LTD is explained by plot forest type. Finally, we determined the effect of actual forest dynamics on LTD, as hypothesized by the Intermediate Disturbance Hypothesis. One hundred and thirteen plots located in terra firme forest were included in this analysis. Out of this total, 41 plots are located at different regions of Amazonia and 72 plots are located at 'Reserva Florestal Adolpho Ducke' (central Amazonia). We used a quadratic regression model (consistent with the expectation of the Intermediate Disturbance Hypothesis), to model LTD as a function of the percentage of individuals with wood density < 0.6 g cm^{-3} for the 41 RAINFOR plots (our proxy for frequency of disturbance, see above). We analyzed the 72 terra-firme plots located at 'Reserva Florestal Adolpho Ducke', separately, as due to their geographical proximity there is no variation in RTD. For these plots, we analyzed the relationship between the percentage of individuals of pioneer species and TAD with a quadratic regression model. All statistical analyzes were performed in S-PLUS 2000 (Mathsoft Inc.).

RESULTS

Regional tree diversity and regional processes

The loess regression explained 46% of the total variation in TAD (see Table 2.11 and Fig. 2.22), i.e., 46% of the total variation of tree alpha-diversity occurred at the regional scale, whereas the remaining 54% residual variation occurred at the local scale or represented the residual error (Table 2.1). The spatial interpolation reveals two rather simple gradients, related to latitude and longitude. On the latitudinal gradient, species diversity peaks at 4°– 3° south and decreases towards a latitude of 15° south and 8° north. On the longitudinal gradient, diversity is low in the eastern areas of Amazonia and increases close to the western border of the study area (Fig. 2.3). Latitude accounted for 73% of the variation in this model and longitude 20% (Table 2.1) (Fig. 2.4). Current rainfall seasonality explained 37% of the variation in RTD and 19% in variation of total TAD. Fitted values for TAD explain observed values of TAD well, but at locations with many plots variation in TAD encompassed nearly all variation present in the model (Fig. 2.2). Average TAD differed among plots on the two different geological substrates (mean (Cenozoic) = 85.2; mean (Proterozoic) = 59.7) (Table 2.2). This two-class division explained 14% of the variation in RTD (ANOVA $F_{[1,750]} = 129.35$, $p < 0.001$) and 6% of the total variation of TAD. It is important to note that all regional variables, which we considered to be related to long-term evolutionary processes, had much higher explanatory power for RTD than for LTD (Table 2.1), consistent with our expectation.

Table 2.1: Contribution of regional and local drivers to the variation of total, regional, and local tree alpha-diversity in the Amazon basin and the Guiana shield. TAD: Tree Alpha-Diversity, observed value of Fisher's alpha for 752 tree inventory plots (ATDN 2008); RV: Regional Variation (fitted values of Fisher's alpha as a function of latitude and longitude estimated with Local regression model); LV: Local Variation (residuals of the Local regression model); Final effect: proportion of the total variation estimated by the Local regression model (0.46) that is explained by regional and local factors; LRM: loess regression model ; ANOVA: Analysis of Variance; QRM: Quadratic Regression Model. TF: terra firme forest, WS: white sand forest; SW: swamp forest; FL: floodplain forest. Regional variables (Latitude, Longitude, Age of Bedrock and actual rainfall seasonality) have mainly an effect (values in bold) on the RV, while local factors (forest type, frequency of disturbance) have mainly an effect on the LV. Bold values signify, the parameters we consider important at the scale at which they act

Factor	Variable	Scale	TAD	RV	LV	Final effect	Analysis
Regional diversity	latitude and longitude	R	**0.46**	0.99	0.08		LR
Palaeo-climatic stability	latitude	R	0.31	**0.73**	0.02	**0.34**	LR
Palaeo-climatic stability	longitude	R	0.14	0.2	0.03		LR
Actual rainfall seasonality	CV of rainfall	R	0.19	0.37	0.07		LR
Bedrock age	Categories: Cenozoic / Proterozoic	R	0.05	**0.14**	0	**0.06**	ANOVA
Forest/soil type	Categories: TF, WS, SW, FL	Link R-L	0.13	0.04	**0.28**	**0.15**	ANOVA
Actual ecosystem dynamics	% individuals with wood density < 0.6	L	n/a	n/a	**0.17**	**0.09**	QRM
Total						**0.64**	

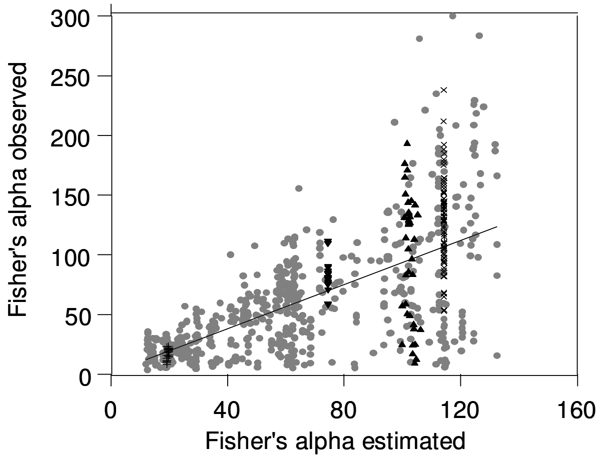

Figure 2.2: Relationship between observed tree alpha-diversity and estimated tree alpha-diversity for 752 1-ha plots in Amazonia, as modeled with a loess spatial regression (R^2 = 0.38). Plots located at the same geographical location show the full range of diversity for the value estimated in their 1 degree grid cell (● All plots; × Reserva Florestal Adolpho Ducke (central Amazonia); + Mabura Hill; ▼ Piste St. Elie (Guiana shield); ▲ Yasuní and surroundings (western Amazonia).

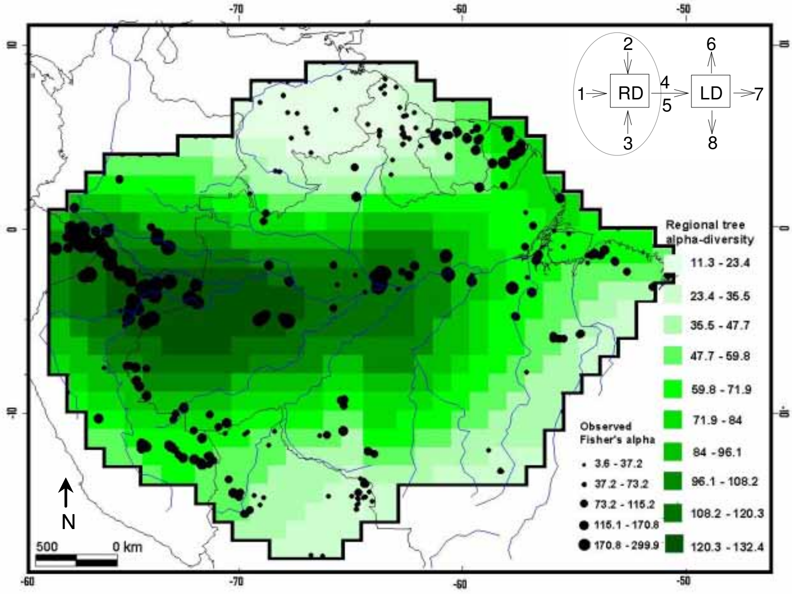

Figure 2.3: Regional variation of tree alpha-diversity (Fishers' alpha) based on a loess spatial regression. Tree alpha-diversity of 752 1-ha inventory plots modeled as a function of latitude and longitude and mapped on a one-degree grid cell scale for Amazonia. Inset on the upper right side represents Fig 2.1.

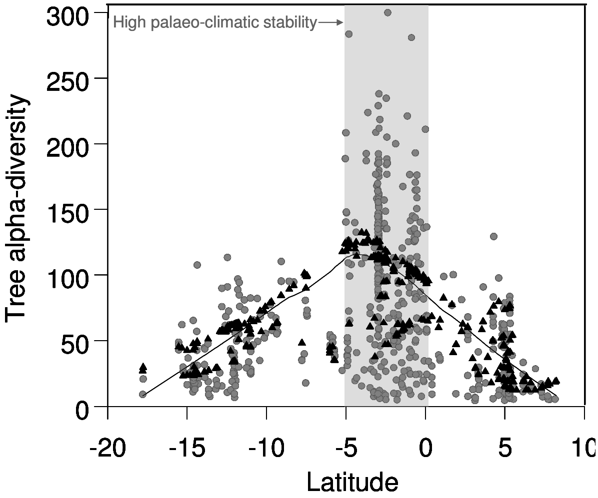

Figure 2.4: Relationship between tree alpha-diversity (● All data: observed value of Fisher's alpha for 752 tree inventory plots (ATDN 2008); ▲ RM: regional model (estimated values of Fisher's alpha as a function of latitude and longitude of each plot as obtained from the Loess regression model) and latitude used as a proxy for palaeo-climatic stability ($R^2 = 0.73$).

Local tree alpha-diversity and its interaction with regional tree alpha-diversity

The four forest types differed significantly in their LTD ($F_{[3,748]} = 89.91$; $p < 0.001$). We ascribe 28% of the variation in LTD, to environmental filtering (process 4 in Fig. 2.1). Local ecosystem dynamics, here analyzed as percentage of pioneer species in the RAINFOR plots (% of individuals with wood density < 0.6 g cm^{-3}), showed a significant quadratic relationship with LTD ($R^2 = 0.17$). In the plots at 'Reserva Florestal Adolpho Ducke' (Volkmer and Magnusson, unpublished data), TAD had a similar relationship ($R^2 = 0.20$) with the percentage of pioneer trees (Fig. 2.5).

Table 2.2: Average and standard deviation of Fisher's alpha for 1-ha plots (ATDN 2008) for 4 main forest types on soils originating the Cratonic (Proterozoic and Palaeozoic) origin and Andean Cenozoic origin; the number of plots is given in brackets

Soil origin/Forest type	White-sand	Swamp	Floodplain	Terra-firme	Total
Protero/Palaeozoic	16.5±16.2 (34)	34.9±33.9 (14)	20.6±16.0 (41)	68.2±48.6 (402)	59.7±48.4 (491)
Cenozoic	62.0±49.0 (3)	33.0±20.4 (13)	51.9±32.0 (82)	106.5±58.6 (163)	85.2±57.2 (261)
Total	20.2±23.1 (37)	34.0±27.7 (27)	41.5±31.4 (123)	79.2±54.5 (565)	68.5±53.0 (752)

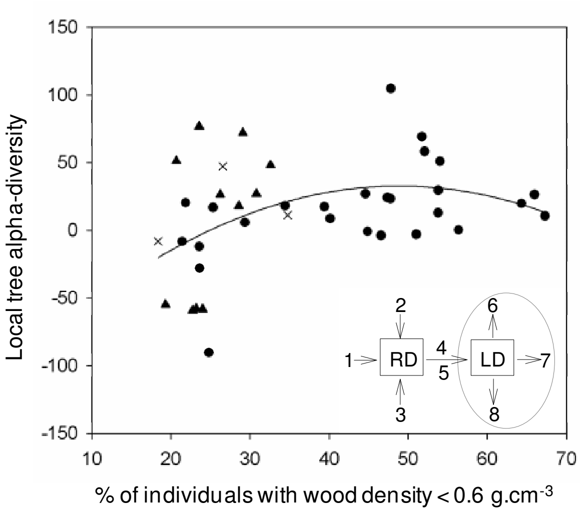

Figure 2.5: Relationship between variation in local tree alpha-diversity (residuals of Loess regression) and percentage of individuals with wood density lower than 0.6 g cm^{-3} (pioneer species) ($R^2 = 0.17$; $p < 0.01$), (● western Amazonia, × central Amazonia, and ▲ eastern Amazonia). Inset on the lower bottom side represents Fig 2.1.

DISCUSSION

Overview

Our analysis partitioned the variation of TAD in Amazonia into a regional and a local component. The proxies for palaeo-climatic stability (latitude and longitude) and bedrock age correlated significantly with the variation in RTD, but not in LTD. In contrast, LTD varied among forest types (i.e., ecological filters) and with local disturbance (Table 2.1). Our initial hypothesis that long-term and large-scale mechanisms mainly influence the RTD and short-term small-scale processes influence the LTD is therefore supported by these results. Regional drivers of TAD act mainly on the RTD, while local drivers act mainly on the LTD. It is important to point out that variables shaping RTD may also act at the local scale, whereas variables defined here as local, have typically only a minor influence on RTD (Ricklefs and Schluter, 1993). The classification of variables as either regional or local is hence a simplification, which however allows identification of the main drivers of tree alpha-diversity in Amazonia. In this section, we discuss how each of the palaeo-ecological and actual-ecological factors contributes to processes that shape tree alpha-diversity at each scale.

Regional tree alpha-diversity and regional processes

Forty-six percent of the total variation in TAD is explained by latitude and longitude. Latitude and longitude accounted for 73% and 20% for the variation of this model, respectively (Fig. 2.3). Actual rainfall seasonality explained just 19% of the total variation in

TAD. Because palaeo-climatic stability is probably closely related to latitude and longitude (see Introduction) and current climate is only a poor predictor for evolutionary drivers of regional diversity, we argue that variation in palaeo-climatic stability is the most likely cause for the variation in RTD. The correlation of TAD with latitude then reflects changes in forest area caused by orbitally forced climate change, while the correlation with longitude reflects persistent orographic rainfall in the western Amazonia due to the Andes. The use of latitude and longitude as a proxy for palaeo-climatic stability is obviously an oversimplification. Palaeo-vegetation simulation models, palynological records (Mayle et al., 2004), and the observation of southward shift of the ITCZ during glacial periods (Martin et al., 1997) suggest that central and western Amazonia experienced more stable climatic conditions than the northern and southern margins of the basin, providing a compelling argument to make use of such simple proxy.

The hypothesized stable palaeo-climate in central and western Amazonia favored persistence of tropical forest, whereas the more unstable palaeo-climate in south and north-eastern Amazonia forced shifts from open to dense forest (Mayle et al., 2004) and back. Such changes are still taking place as documented by recent forest increase on the southern edge of Amazonia in Bolivia (Mayle et al., 2000).

Climate change is thought to affect diversity because it may increase extinction rates (Araujo et al., 2008). In a period of climate change, species with poor dispersal ability and/or small ranges have lower chances to migrate to regions with suitable climate and are therefore more susceptible to extinction. As a result of this process, regions with historically instable climate have fewer species with small ranges (Dynesius and Jansson, 2000, Araujo et al., 2008). This phenomenon has been observed for reptiles, amphibians (Araujo et al., 2008), and trees in Europe (Svenning and Skov, 2007). Ter Steege et al. (2010) have shown a similar pattern for tree genera in Amazonia. The south-eastern Amazonia, with less stable palaeo-climate, has only half of the genera (257 genera in a sample of 52,182 trees) than western Amazonia (456 genera in 46,227 trees). The difference was mainly found in the rare genera. If their conclusion is correct, instable climate may have cost south-eastern Amazonia some 45% of its genera, either because they went extinct as they could not keep up with the forest decline, or failed to re-migrate either because low dispersal ability or species simply did not have enough time to spread their ranges (cf. Svenning and Skov, 2004, Svenning and Skov, 2008).

Fourteen percent of the variation in RTD is explained by bedrock age. Forests on young geological formations (Cenozoic, i.e., 66 Ma or younger) have higher tree diversity than forests on old geological formations (Proterozoic, i.e., 2,500 to 542 Ma). Soils originating from the Andes sedimentary bedrocks are considerably richer in nutrients than those originating from the Brazilian and Guiana crystalline shield bedrock (Sombroek, 2000). Ecosystems on rich soils are more dynamic than those on poor soils (Malhi et al., 2004, ter Steege et al., 2006). We suggest that the long-term large-scale ecosystem dynamics of these two contrasting landscapes (Andes foothill and Brazilian and the Guiana crystalline shields) may have played a role in the evolutionary processes that shaped current diversity. Speciation is driven by a combination of processes such as evolutionary speed, reproductive isolation, and biotic interactions (Mittelbach et al., 2007). We argue here that the landscape evolution Amazonia had a remarkable impact on the evolutionary speed of tree species. Dynamic ecosystems experience high wood productivity (Malhi et al., 2004), forest turn-over (Phillips et al., 2004), and abundance of pioneer species (ter Steege and Hammond, 2001, ter Steege et al., 2006). Tree species adapted to dynamic ecosystems have low wood density, small seed mass (ter Steege et al., 2006), short life span and, consequently, short generation time. Short generation time leads to faster evolution, thus higher speciation rates (Marzluff and Dial, 1991, Verdú, 2002, Allen et al., 2006). Based on this reasoning we suggest that the high diversity of forests on young western Amazonian geological formations could be the result of high speciation rates (Richardson et al., 2001, Erkens, 2007, Svenning et al., 2008). Species level phylogenies of families or genera occurring throughout Amazonia can be developed to test this hypothesis.

Local tree alpha-diversity and local processes

The reason why habitats differ in diversity and composition of tree species is partially explained by the fact that species are not drawn randomly from the regional species pool into the local species pool (Zobel, 1997). Environmental filters (Keddy, 1992, Zobel, 1997) and dispersal limitation (Hubbell, 2001, Zobel, 1997) determine *which* and *how many* species can occupy a local habitat. In our dataset we cannot test the effect of dispersal limitation which links the RTD and the LTD, as reliable broad-scale taxonomical information is not available for Amazonia (Hopkins, 2007) and there is a high number of morpho-species in our plots. The effect of environmental filtering, however, was quantified by analyzing local tree diversity in the four dominant forest types of Amazonia – terra-firme, white-sand, swamp and floodplain forests. The difference in local tree alpha-diversity is traditionally associated with differences in environmental conditions (Gentry, 1988, Tuomisto et al., 1998, Clark, 2004). There is little empirical evidence of a recurrent direct causal relationship between resource availability and local tree diversity, however (Pitman et al., 1999, Hubbell, 2001, Valencia et al., 2004). For white-sand forest, which occur on extremely poor soils, low frequency of disturbance events can explain part of the observed low tree alpha-diversity (see Molino and Sabatier, 2001, ter Steege and Hammond, 2001, Sheil and Burslem, 2003). Low frequency of disturbance, however, cannot explain the relatively low tree diversity in floodplains and swamps. We previously suggested (ter Steege et al., 2000) that alternative factor, shared by white-sand, swamp, and floodplain forests, namely their smaller area compared to terra-firme, could be responsible for their lower tree diversity. Hence, the cause for low diversity in these forest types could be the small and fragmented meta-populations of their constituent species, consistent with area (Terborgh, 1973, Rosenzweig, 1995, Fine and Ree, 2006) and neutral theory (Hubbell, 2001).

The variation of tree alpha-diversity at the local scale is enormous. It is surprising that different plots at one locality (‘Reserva Florestal Adolpho Ducke’ – central Amazonia) span almost the full range of alpha-diversity found in Amazonia (Fig. 2.2). A small percentage

(17% for the RAINFOR and 20% for 'Reserva Florestal Adolpho Ducke' plots) of the variation in local tree alpha-diversity could be explained by disturbance, here analyzed as percentage of individuals of pioneer species. This result is consistent with the Intermediate Disturbance Hypothesis (Connell, 1978). It is important to point out, however, that approximately 80% of the variation of LTD remains unexplained. Although perhaps disappointing, this is entirely consistent with the neutral theory of biodiversity and biogeography (Hubbell, 2001) and many previous findings (see e.g. Pitman et al., 1999, Valencia et al., 2004). As shown in Fig. 2.1, local tree alpha-diversity can be influenced by stochastic local extinction, predatory removal, and competitive exclusion. The effect of density-dependent mortality on local tree diversity could not be addressed by our dataset, but is clearly a candidate for promoting diversity (Connell, 1972). It may be both responsible for the higher local diversity in the wet western Amazonia (Givnish, 1999) and may also contribute to differences in tree composition between forest types (Fine et al., 2004).

Processes driving species diversity and their implication for conservation

Determining the relative contribution of long-term and large-scale as well as short-term and small-scale processes to the distribution of tree species diversity has important practical implications for biodiversity conservation. Modeling the impact of climate change on tree species diversity based on the relationship between tree species diversity and current climate can only be effective, if the distribution of tree species diversity is in equilibrium with current climate. However, as we suggest here, palaeo-climatic stability and palaeo-ecosystem dynamics are the main drivers regulating regional patterns of tree species diversity in Amazonia. Our results therefore suggest that only an approach which includes both evolutionary and current aspects of climate change will provide reliable predictions of the impacts of climate change on tree species diversity distribution in Amazonia (see Araujo et al., 2008).

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3

TREE COMMUNITIES OF WHITE-SAND AND TERRA-FIRME FORESTS OF THE UPPER RIO NEGRO

with Peter van der Sleen, Paulo Apóstolo Assunção,
Adeilson L. da Silva, and Hans ter Steege

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ABSTRACT

The high tree diversity and vast extensions of Amazonian forests challenge our understanding of how tree species abundance and composition varies across this region. Information about these parameters, usually obtained from tree inventories plots, is essential for revealing patterns of tree diversity. Numerous tree inventories plots have been established in Amazonia, yet, tree species composition and diversity of white-sand and terra-firme forests of the upper Rio Negro still remain poorly understood. Here, we present data from eight new one-hectare tree inventories plots established in the upper Rio Negro; four of which were located in white-sand forests and four in terra-firme forests. Overall, we registered 4703 trees ≥ 10 cm of diameter at breast height. These trees belong to 49 families, 215 genera, and 603 species. We found that tree communities of terra-firme and white-sand forests in the upper Rio Negro significantly differ from each other in their species composition. Tree communities of white-sand forests show a higher floristic similarity and lower diversity than those of terra-firme forests. We argue that mechanisms driving differences between tree communities of white-sand and terra-firme forests are related to habitat size, which ultimately influences large-scale and long-term evolutionary processes. The data presented here contribute to a better understanding of tree species composition and diversity of a region for which large gaps in our botanical knowledge persist.

INTRODUCTION

The Amazon basin contains 40% of the world's remaining tropical rainforests and harbors approximately 12,500 tree species (Hubbell et al., 2008). Attempts to systematically analyze tree species diversity and forest structure of Amazonian forests date back to 1930 (Davis and Richards, 1934, Pires et al., 1953). Over the past six decades, a total of about 800 one-hectare tree inventory plots has been established (Amazon Tree Diversity Network - ATDN, 2010). For the upper Rio Negro region, tree inventory plots are particularly scarce and thus under-represented in the ATDN dataset (ATDN, 2010). This shortcoming is relevant because unlike prevailing landscapes in Amazonia, where terra-firme forests are the dominant forest type, the upper Rio Negro harbors extensive areas of white-sand forests (IBGE, 1997).

White-sand forests are the dominant vegetation on non-flooded sandy soils in the upper Rio Negro regions. These forests are also classified as 'campinarana', 'campinarana arbustiva', or 'campinarana florestada' (IBGE, 1997) and are commonly referred as 'campinarana' (Brazil), 'varillal' (Colombia), 'wallaba' or 'white-sand forests' (Guyana) (Anderson, 1981, Banki, 2010). White-sand forests in the upper Rio Negro region are characterized by *Eperua leucantha* (Fabaceae), *Hevea* spp. and *Micrandra sprucei* (Euphorbiaceae) (Dezzeo et al., 2000, Boubli, 2002, Abraao et al., 2008). By contrast, terra-firme forests grow on non-flooded clayey soils (oxisols and latosols); they are also classified as 'floresta ombrófila' (IBGE, 1997). Previous tree inventories conducted in the upper Rio Negro region show that terra-firme forests are typically characterized by *Protium* spp. (Burseraceae), *Caryocar* spp. (Caryocaraceae), *Licania* spp. (Chrysobalanaceae), *Swartzia* spp. (Fabaceae), *Eschweilera* spp. (Lecythydaceae) and *Vochysia* spp. (Vochysiaceae) (Dezzeo et al., 2000, Boubli, 2002).

Tree communities of white-sand and terra-firme forests vary in their species diversity and composition (Dezzeo et al., 2000, ter Steege et al., 2000, Boubli, 2002, Banki, 2010). Tree communities of white-sand forests have a lower diversity and a distinctively different floristic composition in comparison to tree communities of terra-firme forests (ibid.). The lower diversity in white-sand forests has been explained mostly by 1) the indirect effects of soil nutrient availability on species diversity, e.g., low ecosystem dynamics, (ter Steege and Hammond, 2001), 2) 'density-dependence' effects (Janzen, 1974), as well as 3) the patchy configuration and the small size of the area in which white-sand forests occur (ter Steege et al., 2000). Each of these explanations emphasizes different mechanisms regulating tree species diversity of white-sand forests. In addition, variation in tree species composition has been attributed to the direct effect of physical environmental characteristics in these two forest types: white-sand and terra-firme forests differ in the availability of light in the understory (Coomes and Grubb, 1996), soil water (Luizao et al., 2007), as well as in edaphic features, especially H^+ (high in white-sand) and Al toxicity (high in terra-firme) (Luizao et al., 2007). As a consequence of different physical environmental conditions, tree species have become highly specialized in their habitat, and therefore may suffer a disadvantage when establishing in non-typical habitat. Moreover, an interaction between soil nutrient availability and herbivory may constrain species distribution in their typical habitat (Janzen, 1974, Fine et al., 2004).

Analyses of tree inventory plots have provided consistent information on the large scale pattern of tree species diversity across Amazonia since first publications (ter Steege et al., 2000, ter Steege et al., 2003, Stropp et al., 2009, but see Hopkins, 2007). Nevertheless, the question of what precisely is the tree species composition and how does tree diversity vary at local scales in the upper Rio Negro still remains poorly understood (Stropp et al., 2009). Here, we address this question by establishing eight new one-hectare tree inventory plots in the white-sand and terra-firme forests of the upper Rio Negro. We aim at analyzing forest structure, tree species composition, and tree species diversity of these plots.

METHODS

Study area

The study was carried out in Brazil in the upper Rio Negro region which is located at the south-western border of the Guiana shield formation (Fig. 3.1). The region have annual rainfall ranging from 2500 to 3000 mm and is one of the wettest and least seasonal regions in Amazonia (Sombroek, 2001). The average yearly temperature is 24°C (Bezerra *et al.*, 1976). The upper Rio Negro region belongs to the Rio Negro-Juruena geo-chronological province (Kroonenberg and de Roever, 2010). Its bedrocks are mainly classified as granites and gneisses, which originated during the Precambrian (Bezerra *et al.*, 1976). The relief in this region is influenced mainly by differences in the weathering resistance of the bedrocks (Kroonenberg and de Roever, 2010). In hilly areas, the dominant soils are well-drained clayey latosols and oxisols (Bezerra et al., 1976, Dubroeucq and Volkoff, 1998). By contrast, in the widespread flat areas, sandy podzols occur, the origin of which can be attributed to in-situ weathering, alluvial deposition, or podzolization (Anderson, 1981, Quesada, 2008).

Tree inventory plots and botanical identification

We established eight one-hectare tree inventory plots, four of which were placed in white-sand forests and four in terra-firme forests. Two plots were set up on indigenous land, in the 'Terra Indígena do alto Rio Negro', at the middle Içana River. The remaining six plots were set up in the vicinity of São Gabriel da Cachoeira: four at the air force area 'Comando Aéreo Regional – COMAR', one at Pico da Neblina National Park, and one at the indigenous community of 'Itacoatiara-Mirim' (Fig. 3.1, Table 3.1). To set up the plots, we collaborated with the 'Escola Indígena Baniwa Coripaco – Pamaáli' (EIBC – Pamaáli) and with the 'Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (Ifam), campi São Gabriel da Cachoeira e Tunuí)'.

In each plot, we measured the diameter of all trees with a diameter ≥ 10 cm at breast height, i.e., DBH at 1.3 m. We tagged trees of all morpho-species and collected at least one sample per morpho-species. The fertile botanical collections were deposited at the herbarium of the 'Instituto Nacional de Pesquisas da Amazônia' (INPA, Manaus) and at the herbarium of Ifam (campus São Gabriel da Cachoeira). The sterile material was deposited at the herbarium of the 'Instituto Federal de Educação, Ciência e Tecnologia do Amazonas' (EAF-Manaus). All tree species were identified at the INPA herbarium. Sterile material of the families Annonaceae, Moraceae, and Urticaceae was identified by P. J. M. Maas and C. C. Berg.). In the field, we collected at least one sample per morpho-species. The identification procedure revealed in a few cases that one morpho-species assigned to multiple trees during the field work, turned out to represent in fact two different species. To account for these cases, we created a 'complex of species' which reports the two species names assigned in the herbarium.

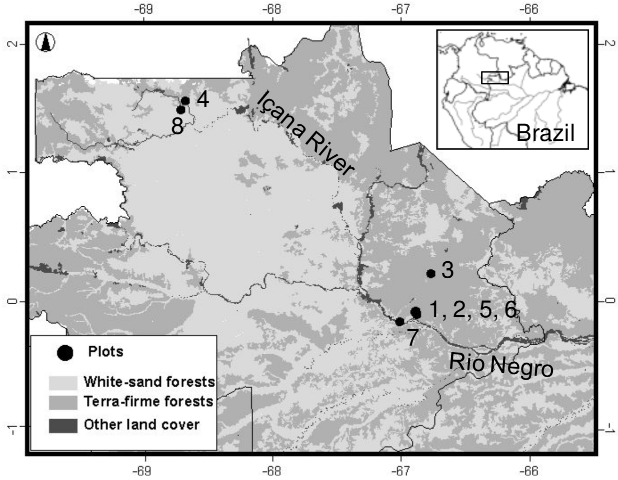

Figure 3.1: Locations of the eight one-hectare tree inventory plots established in the upper Rio Negro (black dots). Plots 1, 2, 3, and 4 were placed in terra-firme forests and plots 5, 6, 7 and 8 were placed in white-sand forests. The city of São Gabriel da Cachoeira is located nearby plot 7. Site names and plots' geographical coordinates are given in Table 3.1. The base map is a courtesy of Instituto Socioambiental (ISA).

Data Analysis

Forest structure

We calculated for each plot the total basal area and stem density. Additionally, we classified trees according to their DBH in 9 classes at increments of 5 cm (10 - < 15 cm, …, 45 - < 55 cm) and one including all trees with DBH ≥ than 55 cm. We then compared differences in the DBH class distributions between white-sand and terra-firme plots by plotting the proportion of trees belonging to each DBH class for each forest type. Finally, we tested whether the average basal areas as well as the stem densities varied between plots in white-sand and terra-firme forests.

Tree species composition and diversity

Hereafter we refer to the trees sampled in the four white-sand plots as tree community of white-sand forests and to the trees sampled in the four terra-firme plots as tree community of terra-firme forests. We established relative species abundance curves for the tree communities of white-sand and terra-firme forests. We tested differences in tree species composition among these two tree communities with a multi-response permutation procedure (MRPP). For this procedure, we calculated the Sørensen Index as a measure of floristic dissimilarity (FD) and we defined forest type (i.e., white-sand and terra-firme forests) as group variables. We assessed the variation in tree species composition by performing a non-metric multidimensional scaling (NMDS) (McCune *et al.*, 2002). We performed NMDS because we sampled tree communities in a discontinued manner (i.e., plots placed either in white-sand or terra-firme forests). For the NMDS, we first calculated the relative density of each species in each plot by dividing the absolute abundance of species *i* in plot *p* by the total absolute abundance of trees in plot *p.* We used relative density in the NMDS ordination (see Costa *et al.*, 2009). We used the Sørensen Index (Bray-Curtis) as a measure of floristic distance (FD) and 5000 runs for randomized data, as well as for real data. We calculated the percentage of variation explained by the two NMDS axes using the same Sørensen (Bray-Curtis) Index as used for the ordination. We determined whether family, genus, and species were indicators of either white-sand forests or of terra-firme forests by performing an *indicator species analysis* (ISA)*.* This analysis calculates an indicator index for each family, genus, and species. This indicator index is maximum when the respective taxa is present in all plots of one forest type and absent in all plots of the other forest type (Dufrene and Legendre, 1997). Finally, we estimated tree species diversity for each plot by calculating Fisher's alpha (Fisher et al., 1943). We performed a single factor analysis of variance (ANOVA) to test whether tree diversity varies among white-sand and terra-firme plots. For ANOVA, we used SPSS v.16. We used PC-ORD version 5.0 for performing MRPP, NMDS, and ISA analyses (McCune and Mefford, 1999).

RESULTS

Forest structure

The total basal area of the eight plots varied between 19.30 m^2 and 31.44 m^2. Interestingly, both maximum and minimum total basal area values were registered for white-sand plots: plot 8 (Jandú-Cachoeira) and plot 7 (Itacoatiara-Mirim), respectively. For terra-firme plots, total basal area ranged from 27.24 m^2 (plot 4, Igarapé Pamaáli) to 30.40 m^2 (plot 1, COMAR-01). For all plots, *Eperua leucantha* had the highest total basal area, followed by *Eperua purpurea* and *Monopteryx uaucu.* On white-sand plots, the three most abundant species also had the largest total basal area (*E. leucantha*, *E. purpurea*, *Aldina heterophylla*). By contrast, on terra-firme plots, *M. uaucu,* had the highest total basal area, although it was only the third abundant species. Additionally, *Micrandra spruceana* had the second highest total basal area (fifth in abundance) and *Clathrotropis macrocarpa* the third in total basal area. The differences in the average basal area between white-sand and terra-firme plots are non-significant (*F* = 5.98*; p* = 0.2*)*. Stem density varied between 547 and 724 trees*ha^{-1} in white-sand plots and between 505 and 614 trees*ha^{-1} in terra-firme plots. The stem density, was non-significantly different between white-sand and terra-firme plots ($F = 5.98$; $p = 0.09$).

Overall, 41% of trees had a DBH between 10 and 15 cm. On all white-sand plots, the density of these small trees ranged from 191 trees*ha^{-1} (34.91%) to 392 trees*ha^{-1} (54.14%). For terra-firme plots, this density varied between 195 trees*ha^{-1} (38.61%) and 292 trees*ha^{-1} (47.39%).

Tree species composition and diversity

We registered 4,703 trees ≥ 10 cm DBH, belonging to 49 families, 215 genera, and 603 species in eight one-ha plots. In white-sand plots, we found 2,524 trees, 39 families, 124 genera, and 290 species (Table 3.1). In terra-firme plots, we found 2,179 trees, 44 families and 183 genera, and 417 species. These inventories include potentially one new observation for Brazil (*Ephedranthus guianensis*) (Maas et al., 2010), a first observation for the upper Rio Negro region (*Pseudoxandra duckei* – P. J. M. Maas, pers. comm.), and an undescribed species (*Batocarpus* sp. nov. – C. C. Berg, pers. comm.). Twenty two individual trees (0.47% of all trees) were not identified at the family level. Additionally, 680 trees (14.45%), accounting for 142 morpho-species were only identified at the genus level, and 204 trees (4.33%), representing 64 morpho-species, remain to be confirmed (Appendix 1). For 112 trees belonging to 6 morpho-species we assigned the category 'complex of species' (see Methods).

Table 3.1: Total number of trees, total number of species, and Fisher's alpha index of eight one-hectare plots established in the upper Rio Negro. TF indicates terra-firme plots; WS indicates white-sand plots; SGC indicates plots established nearby the city of São Gabriel da Cachoeira; Içana indicates plots established at the middle Içana River

Plot No. (Forest type)	Site name	latitude	longitude	No. of trees	No. of species	Fisher's alpha
1 (TF)	COMAR-01 (SGC)	-0.084	-66.888	523	126	52.69
2 (TF)	COMAR-02 (SGC)	-0.086	-66.891	537	142	63.00
3 (TF)	Pico da Neblina National Park (SGC)	0.211	-66.771	505	155	76.35
4 (TF)	Igarapé Pamaáli (Içana)	1.553	-68.676	614	192	95.92
5 (WS)	COMAR-03 (SGC)	-0.101	-66.880	547	102	36.95
6 (WS)	COMAR-04 (SGC)	-0.111	-66.881	642	95	30.8
7 (WS)	Itacoatiara-Mirim (SGC)	-0.166	-67.011	611	87	27.73
8 (WS)	Jandú-Cachoeira (Içana)	1.481	-68.711	724	116	39.01

Overall, the most abundant family identified in white-sand and terra-firme forests was Fabaceae with 2,222 trees (47%), followed by Sapotaceae with 288 trees (6%) and Myristicaceae with 283 trees (6%). Fabaceae was the most abundant family in both white-sand and terra-firme plots, accounting for 1,451 trees (57%) and 771 trees (35%), respectively. In white-sand plots, the second and third most abundant families were Sapotaceae with 175 trees (7%) and Euphorbiaceae with 102 trees (4%), whereas in terra-firme plots, the second and third most abundant families were Myristicaceae with 220 trees (10%) and Euphorbiaceae with 165 trees (8%) (Fig. 3.2). The most abundant species in white-sand plots was *Eperua leucantha* with 681 trees (26%), followed by *Eperua purpurea* with 191 trees (8%), and *Aldina heterophylla* with 137 trees (5%). *Clathrotropis macrocarpa* was the most abundant species in terra-firme plots with 138 trees (6%), followed by *Pterocarpus* sp. with 126 trees (6%), and *Monopteryx uaucu* with 74 trees (3%). The range of relative abundance observed for the four most abundant species in white-sand plots is larger (0.26 – 0.05) than the same range observed for terra-firme-plots (0.06 – 0.03) (see Fig. 3.3 and Table 3.2).

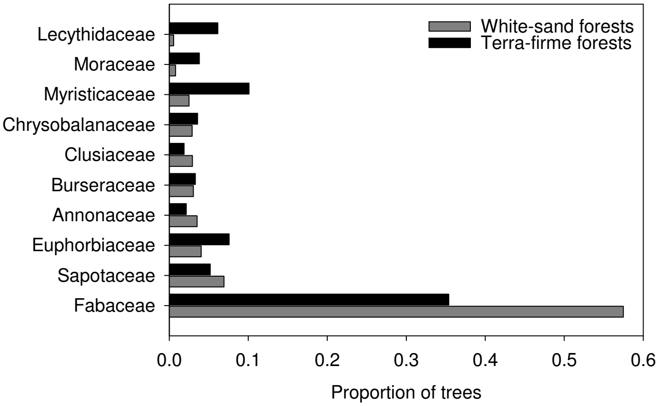

Figure 3.2: Proportion of trees of the ten most abundant families encountered in the eight one-hectare tree inventory plots. Proportion of trees is based on 2,524 trees encountered in four one-hectare white-sand plots and 2,179 trees registered in four one-hectare terra-firme plots.

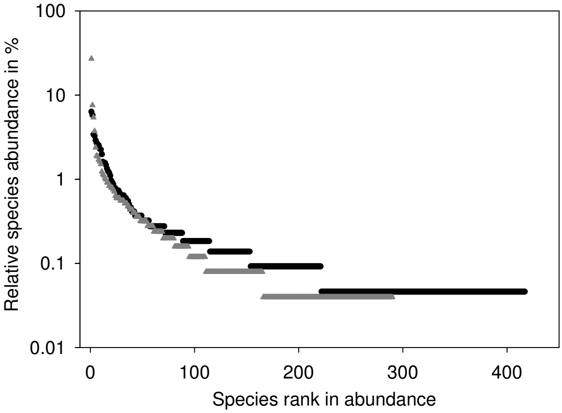

Figure 3.3: Relative species abundances in the four one-ha tree inventory plots established in white-sand forests (▲) and terra-firme forests (•). Total number of trees (DBH ≥ 10) encountered in white-sand and terra-firme plots is 2,524 and 2,179, respectively. The total number of species registered in white-sand and terra-firme plots are 290 and 417.

Table 3.2: Number of trees and relative abundance (in parenthesis) of the ten most abundant species encountered in four one-ha plots established in terra-firme forests (plots 1, 2, 3, and 4) and in white-sand forests (plots 5, 6, 7, and 8); plot codes and locations are given in Table 3.1

Family	Species	plot 1	plot 2	plot 3	plot 4
Euphorbiaceae	*Micrandra spruceana* (Baill.) R.E. Shult.	20 (0.04)	15 (0.03)	0 (0.00)	36 (0.07)
Fabaceae	*Andira unifloliolata* Ducke	9 (0.02)	20 (0.04)	0 (0.00)	34 (0.07)
Fabaceae	*Clathrotropis macrocarpa* Ducke	28 (0.05)	47 (0.09)	21 (0.03)	42 (0.08)
Fabaceae	*Monopteryx uaucu* Spruce ex Benth.	59 (0.11)	0 (0.00)	15 (0.02)	0 (0.00)
Fabaceae	*Pterocarpus* sp.2 INPA	63 (0.12)	42 (0.08)	0 (0.00)	21 (0.04)
Fabaceae	*Swartzia polyphylla* DC.	15 (0.03)	22 (0.04)	0 (0.00)	19 (0.04)
Fabaceae	*Swartzia tomentifera* (Ducke) Ducke	2 (0.00)	4 (0.01)	30 (0.05)	23 (0.05)
Lecythidaceae	*Eschweilera pedicellata* (Rich.) S. A. Mori	24 (0.05)	19 (0.04)	0 (0.00)	12 (0.02)
Myristicaceae	*Iryanthera ulei* Warb.	7 (0.01)	18 (0.03)	9 (0.01)	15 (0.03)
Myristicaceae	*Virola calophylla/pavonis*	7 (0.01)	7 (0.01)	35 (0.06)	1 (0.00)
		plot 5	**plot 6**	**plot 7**	**plot 8**
Fabaceae	*Eperua leucantha* Benth.	212 (0.39)	282 (0.44)	159 (0.26)	28 (0.04)
Fabaceae	*Eperua purpurea* Benth.	51 (0.09)	0 (0.00)	108 (0.18)	32 (0.04)
Fabaceae	*Aldina heterophylla* Spruce ex Benth.	33 (0.06)	25 (0.04)	44 (0.07)	35 (0.05)
Fabaceae	*Inga* sp.1	0 (0.00)	0 (0.00)	0 (0.00)	94 (0.13)
Fabaceae	*Monopteryx uaucu* Spruce ex Benth.	12 (0.02)	25 (0.04)	23 (0.04)	0 (0.00)
Fabaceae	*Taralea oppositifolia* Aubl.	11 (0.02)	12 (0.02)	16 (0.03)	9 (0.01)
Sapotaceae	*Pradosia* cf. *mutisii* Cronquist	2 (0.00)	10 (0.02)	12 (0.02)	23 (0.03)
Malvaceae	*Scleronema micranthum* (Ducke) Ducke	9 (0.02)	3 (0.00)	30 (0.05)	1 (0.00)
Euphorbiaceae	*Micrandra sprucei* (Müll. Arg.) R.E. Schult.	0 (0.00)	0 (0.00)	0 (0.00)	41 (0.06)
Clusiaceae	*Haploclathra paniculata* (Müll. Arg.) R.E. Schult.	0 (0.00)	10 (0.02)	0 (0.00)	28 (0.04)

Floristic composition differed between white-sand and terra-firme plots (MRPP: $A = 0.16$; $p = 0.007$). The floristic dissimilarity ranged from 0.38 to 1 among the pairs of eight plots, from 0.38 to 0.84 among pairs of white-sand plots, and from 0.48 to 0.87 among pairs of terra-firme plots. Considering pairs of white-sand and terra-firme plots, the floristic dissimilarity ranged from 0.81 to 1. The species indicator analysis revealed that there are fewer significant indicator families, genera, and species in white-sand (3 families, 8 genera, and 5 species) than in terra-firme forests (5 families, 12 genera, 9 species) (Table 3.4 and 3.5). Annonaceae, Apocynaceae, and Fabaceae were indicator families for white-sand forests. Lecythidaceae, Meliaceae, Moraceae, Myristicaceae, and Quiinaceae were indicator families for terra-firme forests (Table 3.4). Interestingly, Fabaceae, which represents the most abundant family in both forest types and which is an indicator family for white-sand forests, had a higher number of species in terra-firme forests than in white-sand forests. Four-hundred-one species occurred in only one of the eight plots; out of these 401 species, 154 were registered in only one of the white-sand plots and 247 in only one of the terra-firme plots. Two-hundred-sixty-two species occurred with only one individual. Out of this total, 92 species were encountered in white-sand forests and 170 species in terra-firme forests.

Table 3.4: Number of trees belonging to the families, which are significantly associated with one of the two forest types ($p < 0.05$); (*) indicates the forest type which the families are associated with

Family	Number of trees in white-sand	Number of trees in terra-firme
Annonaceae	89*	47
Apocynaceae	46*	12
Fabaceae	1451*	771
Lecythidaceae	14	134*
Meliaceae	1	10*
Moraceae	20	83*
Myristicaceae	63	220*
Quiinaceae	0	6*

Table 3.5: Number of trees belonging to the genera, which are significantly associated with one of the two forest types ($p < 0.05$); (*) indicates the forest type which the genera are associated with

Family	Genus	Number of trees in white-sand	Number of trees in terra-firme
Annonaceae	*Bocageopsis*	0	17*
	Fusaea	0	8*
	Xylopia	67*	4
Araceae	*Dendropanax*	7*	0
Clusiaceae	*Symphonia*	1	7*
Euphorbiaceae	*Sandwithia*	0	43*
Fabaceae	*Clathrotropis*	15	138*
	Eperua	872*	50
	Macrolobium	80*	5
	Swartzia	45	136*
	Taralea	48*	6
Lecythidaceae	*Couratari*	0	8*
	Eschweilera	14	112*
Moraceae	*Brosimum*	18	44*
Myristicaceae	*Virola*	6	90*
Rubiaceae	*Chimarrhis*	0	15*
	Pagamea	30*	1
Sapotaceae	*Manilkara*	42*	3
	Pradosia	52*	3
Vochysiaceae	*Erisma*	1	38*

The two axes of the NMDS captured 77% of the floristic variation. The first and the second axis explained 61% and 16% of the floristic variation among the eight one-ha plots, respectively. The variation on the first axis can be explained by forest type: plots placed in terra-firme forests are located on the left side of the Fig. 3.4, plots in white-sand forests on the right. The second axis is related to geographic distance: plots established close to São Gabriel da Cachoeira are clustered at the upper part of Fig. 3.4 and plots established at middle Içana River are found at the lower part (Fig.3.4).

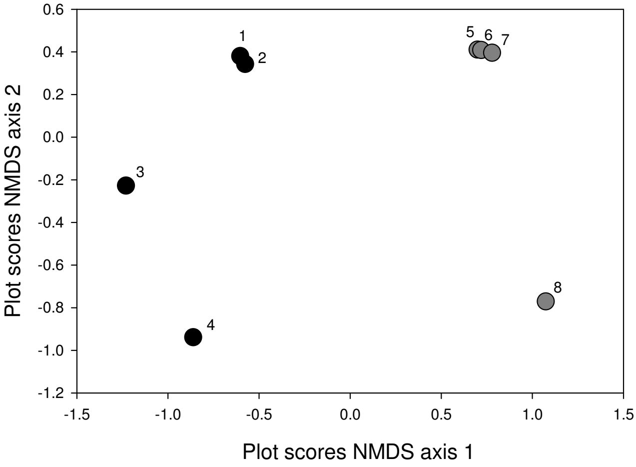

Figure 3.4: Ordination diagram of non-metric multidimensional scaling (NMDS) of the eight one-hectare tree inventory plots. The first and the second axis explained 61% and 16% of the floristic variation, respectively. Terra-firme plots are represented by black dots and white-sand plots by gray dots. The locations of the plots are given in Fig.3.1 and Table 3.1.

Tree diversity, measured here by Fisher's alpha, ranged from 27.3 (white-sand plots) to 95.9 (terra-firme plots, Table 3.1). For white-sand plots, tree diversity ranged from 27.7 (plot 7, Itacoatiara-Mirim) to 39.0 (plot 8, Jandú-Cachoeira), respectively. For terra-firme plots, tree diversity ranged from 52.7 (plot 1, COMAR-1) to 95.9 (plot 4, Igarapé Pamaáli), respectively. Tree diversity was on average significantly lower in white-sand plots than in terra-firme plots ($F = 15.66$; $p = 0.007$).

DISCUSSION

Overview

Tree communities of terra-firme and white-sand forests of the upper Rio Negro show a significant floristic dissimilarity. Tree communities of white-sand forests appear to be more similar to each other and less diverse than tree communities of terra-firme forests. This dissimilarity is to a large extent caused by 1) differences in relative abundance of highly abundant species, 2) the occurrence of families, genera, and species which are restricted to either of the two forest types, and 3) the low number of rare species registered for white-sand forests.

Forest structure

Total basal area, tree density, and DBH distribution observed here for white-sand and terra-firme forests are comparable to other tree inventory plots established in the upper Rio Negro (Dezzeo et al., 2000, Boubli, 2002) and in other regions of Amazonia (Amaral et al., 2000, Oliveira and Amaral, 2004, Oliveira et al., 2008).

Tree species composition

Patches of white-sand forests are usually surrounded by terra-firme forests in Amazonia. For most tree species, seed dispersal between these two forests types occurs regularly; therefore, dispersal may be of minor importance for limiting species occurrence in either forest type. Arguably, a main limitation to species establishment occurs at the seedling stage. In fact, tree seedling mortality seems to be higher when seedlings grow in their non-typical habitat (Chapter 4), indicating a habitat specificity that is likely to be related to the edaphic characteristics of these two forest types.

Several mechanisms have been proposed to explain habitat specificity of trees in white-sand and terra-firme forests. The hypothesis of a trade-off between plant investment in growth and herbivore defenses proposes that tree species which typically grow in nutrient-limited conditions, such as white-sand species, allocate more of their resources in herbivore defense and as a consequence have to allocate less in growth (Fine et al., 2004). Contrary, species occurring in less nutrient-limited conditions, such as terra-firme tree species, invest their resources in growth and relatively less in herbivore defenses. This divergence in the growth-defense strategy may be a result of long-term habitat specialization (Fine et al., 2004, Fine et al., 2006). The trade-off between growth and defense is thought to drive habitat specialization of trees in white-sand and terra-firme in western Amazonia (Fine et al., 2004). This trade-off seems to be of minor importance for habitat specialization in these two forest types in the upper Rio Negro. In Chapter 4, we will see that seedlings of white-sand and terra-firme habitat specialist species, including the highly abundant *E. purpurea* and *C. macrocarpa*, suffer similar herbivory rates and show similar growth performance regardless of the forest type in which they grow. An explanation for these diverging findings might be provided by additional soil characteristics: in the upper Rio Negro soil characteristics may have a more direct limiting effect on seedling establishment and growth. An experiment conducted in French Guiana (Guiana shield), has shown that tree seedlings growth of species typically occurring either in white-sand or terra-firme forests is not limited by phosphate, but seems to respond differently to soil drought (Baraloto et al., 2006). Although H^+ and Al toxicity seem to limit species distribution between white-sand and terra-firme forests in central Amazonia (Luizao et al., 2007), this toxicity apparently does not affect the occurrence of climax tree species in Guiana (ter Steege and Alexander unpubl. data – in Banki 2010). Additionally, differences in seed sizes influence how tree seedlings respond to soil nutrient conditions (Lawrence, 2003). We, therefore, suggest that a more general mechanism explaining habitat specificity should take into account both species characteristics, such as seed size, as well as edaphic properties of these two distinct habitats. So far, the general ecological mechanism driving habitat specificity of tree species to either forest types remains unknown in the upper Rio Negro.

Tree species diversity

The high floristic dissimilarity between white-sand and terra-firme forests suggests that these two forest types have a relatively independent evolutionary history. As the evolution of habitat specificity is a long-term process, it ultimately influences the current pattern of tree species diversity. The size of a habitat determines the number of species it can support: large habitats typically host a larger number of species than smaller ones do (Rosenzweig, 1995). This prediction holds for various habitats in different geographical regions and is explained by large-scale and long-term evolutionary processes that lead to higher speciation rates and low extinction rates in larger areas (ibid.). Amazonia covers ca. 6.8 million km^2 and rainforests extent throughout this area for as long as 55 Ma (Morley, 2000, Jaramillo et al., 2006, Wesselingh et al., 2010). Terra-firme forests cover ca. 80% of the total area of Amazonian forests, whereas white-sand forests cover only 5-10%. The number of species in the regional tree species pool in terra-firme forests is, therefore, expected to be much larger than the regional species pool of trees in white-sand forests (ter Steege et al., 2000, Banki, 2010).

The large habitat size of terra-firme forests may also explain the larger number of families, genera, and species associated with these forests. In the presence of two habitats, species may evolve to be habitat specialists or generalists. Assuming that two habitats differ considerably in their size, one would expect to find more habitat-specialist species in larger habitats than in smaller ones (Rosenzweig, 1995). If a habitat type occurs in small areas only, species specialized on that habitat may have a disadvantage as they might be more vulnerable to extinction. Hence, we suggest that collectively there might be more species associated with the large terra-firme forests than with the smaller white-sand forests. This hypothesis is supported by Banki (2010) who suggested that terra-firme species experience the most severe establishment limitation in white-sand forests.

How is regional tree diversity related to local diversity? By local diversity we mean the diversity observed at local communities, here analyzed based on one-hectare plots. The local-regional species diversity relationship and the species-area relationship, presented above, are tightly connected. Rosenzweig and Ziv (1999) named this connection the *echo pattern*. According to the *echo pattern*, the local-regional species relationship is a direct consequence of the species-area relationship (Fig. 3.5). The connection of these two relationships is strong because species composing the local community are “taken” from the regional community. Therefore, the richer the regional community the richer will be the local community.

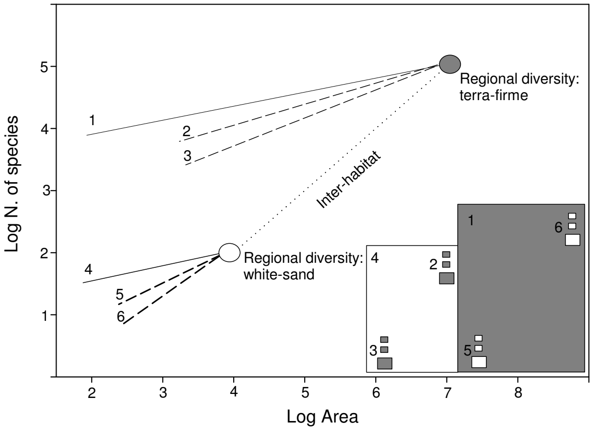

Figure 3.5: The species-area relationship and its connection with the local-regional species relationship (*echo pattern*). The dotted line represents the species area relationship of distinct habitats (big dots). White-sand and terra-firme forests are represented by white and gray squares, respectively. Differences in species diversity between habitats are mainly explained by evolutionary processes, which are largely influenced by the habitat size. The connection between regional and local diversity of the large areas is represented by the solid lines. The dashed lines represent the species-area relationships of 'islands', which are isolated patches of white-sand or terra-firme forests. Nearby islands (2, 5 have a less steep slope than islands further away from each other (3, 6) (Adapted from Rosenzweig and Ziv, 1999, Rosenzweig, 1995).

How does the *echo pattern* influence relative species abundance of tree communities in white-sand and terra-firme forests? As white-sand forests have few abundant species in the regional community, few species make up a large part of local community (see Fig. 3.3). Contrary, in the regionally and locally rich terra-firme forest, many species have low abundances; therefore, even the most abundant species in terra-firme forest will have lower abundance than the most abundant species in white-sand forest. In fact, we observed that the four most abundant species accounted for 44% (1,103 trees) of the total number of trees in white-sand forests, whereas this share was only 20% (409 trees) in terra-firme forests.

The low diversity of tree communities of white-sand forests also helps to explain the relatively low floristic dissimilarity of plots within this forest type. Because there are few regionally abundant species in white-sand forests, it is more likely that these few species disperse throughout most patches of this forest type. Indeed, we found that *E. leucantha* was the most abundant species in three of the four plots established in white-sand forests, thereby reducing the floristic dissimilarity of tree communities in white-sand forests. Contrary, the high diversity of tree communities, associated with low relative abundance of dominant tree species, in terra-firme forests causes relatively high floristic dissimilarity between individual plots.

Future directions

In our eight one-hectare plots we have collected potentially one new observation for Brazil (*Ephedranthus guianensis*) (Maas et al., 2010), a first observation for the upper Rio Negro (*Pseudoxandra duckei* – P. J. M. Maas, pers. comm.), and an undescribed species (*Batocarpus* sp. – C. C. Berg, pers. comm.). These findings highlight the lacuna we have in our botanical knowledge of the forests of the upper Rio Negro. Deepening our botanical knowledge can be achieved by long-term projects aiming at systematically collecting botanical material (Hopkins, 2007). We suggest that establishing long-term monitoring plots designed to capture variation in tree species diversity and composition at multiple spatial scales combined with flora projects planned to collect fertile material of rare species, would make an important contribution to our understanding of tree species diversity and composition in the upper Rio Negro. Long-term projects require long-term collaboration. Our experience shows that collaboration between research institutions and local schools proves to be effective for achieving that aim.

ACKNOWLEDGMENTS

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4

SEEDLING TRAITS AND HERBIVORY IN WHITE-SAND AND TERRA-FIRME FORESTS: AN ANALYSIS ACROSS A RESOURCE GRADIENT IN THE UPPER RIO NEGRO, BRAZIL

with Peter van der Sleen, Carlos Alberto Quesada, and Hans ter Steege

To be submitted

ABSTRACT

The hypothesis that a trade-off between plant growth and herbivore defense drives changes in species composition along a gradient of resource availability in Amazonian forests has recently been put forward. Nevertheless, gradients in resource availability in the tropics are still poorly understood and it remains controversial whether tree species communities vary in a predictable way depending on habitat resource availability. Here we tested in a transplanting experiment whether seedling traits as well as herbivory rates differ between habitat specialist species. We compared seedling traits, mortality, growth performance, and herbivore damage to assess the hypothesized trade-off between plant growth and herbivore defense. We focused on habitat specialist tree species of white-sand and terra-firme forests of the upper Rio Negro, the largest white-sand area in the world. We found that seedling traits vary in a similar way within and between these two groups of habitat specialists. Although habitat specialists showed lower mortality when growing on their original soil type, growth performance and herbivore damage were similar. We found no evidence that the growth defense trade-off drives habitat specificity in the white-sand and terra-firme forests of the upper-Rio Negro. We argue that the magnitude of the gradient of soil nutrient is crucial to trigger differences in seedling traits as well as the trade-off between growth and defense. If mechanisms driving changes in species composition are tightly connected to soil nutrient availability, such as the trade-off between growth and defense, we suggest that its importance might vary in a predictable manner across Amazonia.

INTRODUCTION

Tree beta-diversity in tropical forests is partially attributed to species' adaptations to resource availability (Markesteijn and Poorter, 2009, Andersen et al., 2010). These adaptations are shown in the high diversity of strategies of plant growth, dispersal, and herbivore defense (Hammond and Brown, 1995, Coley and Kursar, 1996, Wright and Westoby, 1999). Gradients in resource availability in the tropics are, nevertheless, still poorly understood (Townsend et al., 2007) and whether tree communities vary in a predictable way depending on habitat resource availability is still controversial (Hubbell, 2001).

Typically, species growing in habitats with limited resources are available tend to share functional traits, which reflect slow growth, such as long lived and tough leaves. If resource availability increases, species tend to switch gradually to traits which mirror fast growth, e.g., high leaf turnover and high specific leaf area (Wright et al., 2004). Moreover, herbivory is expected to remain low and relatively constant where resource availability is low, but gradually increases as resource availability increases (Herms and Mattson, 1992). The interaction between plant responses to resource availability and herbivory results in a trade-off between growth and defense (Shipley et al., 2006). In this trade-off, plants balance the allocation of their resources between growth and defense against herbivores (Coley and Kursar, 1996).

A trade-off between growth and defense is expected to contribute to tree beta-diversity (Marquis, 2004). In Amazonia, white-sand and terra-firme forests are known by their distinct flora as well as edaphic features (Anderson, 1981). Soils of white-sand forests (podzol) are poor in nutrients, whereas soils of terra-firme forests (latosols and oxisols) are clayey and relatively richer (ter Steege et al., 2000). In 1974, Janzen hypothesized that the main constraint for plants to grow on white-sand soils should be herbivory, rather than nutrient limitation itself. Only recently, however, rigid empirical testing was conducted to investigate this hypothesis in white-sand and terra-firme forests. By conducting a transplanting experiment in white-sand forests and terra-firme clay forests in western Amazonia (Peru), Fine et al. (2004) showed that terra-firme species grow significantly faster and invest less in defense than white-sand species. This difference in plant performance can be attributed to the trade-off between growth and defense (Fine et al., 2004, Fine et al., 2006).

Yet soils of terra-firme forests vary in their nutrient availability across Amazonia due to large scale difference in geology and geomorphology (Quesada et al., 2010). In western Amazonia, terra-firme forests grow on clay soils originated from Andean sediments (~66 Ma and much more recent). In the Guianas and in most of the Rio Negro basin, however, terra-firme forests occur in soils originated from the Guiana shield formation (~2,500 Ma) and for this reason are much less fertile than soils of terra-firme forest in western Amazonia. Interestingly, soils of white-sand forests from western Amazonia and from the Guiana shield might have similar origin. Therefore, difference in soil fertility between white-sand forests and the adjacent terra-firme forests may vary in a predictable way depending on the geological and geomorphological history. As in the Guiana shield soils are generally older, one can expect the gradient in soil nutrient availability to be relatively more subtle in the Guiana shield than in western Amazonia (Quesada et al., 2010). Nevertheless, the boundary between forest types on these soils is conspicuous and there is little overlap of tree species composition between white-sand and terra-firme forests in the Guiana shield (Dezzeo et al., 2000, ter Steege et al., 2000, Boubli, 2002, Banki, 2010). Therefore, whether the difference in resource availability between white-sand and terra-firme forests of the Guiana shield is enough to trigger differences in plant's functional traits related to growth and herbivore defense is still unclear.

Here, we investigate whether seedlings of habitat specialists of white-sand and terra-firme forests differ in their functional traits, growth performance, and herbivory rates. We randomly selected common habitat specialists from white-sand and terra-firme forests aiming at capturing traits which are often present in both habitats (see Westoby et al., 1995). We focus on the upper Rio Negro, a region which harbors the largest white-sand area in the world. We aim at answering the following questions: 1) How are seedling traits of white-sand and terra-firme habitat specialist associated? 2) Can we distinguish functional groups of white-sand or terra-firme habitat specialist species? 3) Is the variation in seedling traits caused by the environment in which they are growing or by intrinsic species characteristics? In other words: Do species show change in their traits when growing under different soil conditions? 4) Are there differences in seedling performance, i.e., mortality, growth, and herbivore damage among white-sand and terra-firme species under different soils conditions?

MATERIAL AND METHODS

Study site

The research was carried on the 'Terra Indígena do Alto Rio Negro', along the middle Içana River, Brazil (hereafter referred to as upper Rio Negro). This indigenous land encompasses an area of nearly 8 million hectares bordering Brazil, Colombia, and Venezuela (Cabalzar and Ricardo, 2006). We conducted our research in collaboration with and in close geographical proximity of an indigenous school ('Escola Indígena Baniwa Coripaco Pamaáli: EIBC – Pamaáli'), located at 1.52°N/68.66°W. White-sand forests occurring in non-flooded areas of sandy soils are the dominant vegetation type in our study site. The second dominant vegetation type is terra-firme forests that occurs on non-flooded areas of latosol or oxisols (Cabalzar and Ricardo, 2006). The few tree inventories plots that have been established at our study site (Chapter 3; Abraao et al., 2008) suggest that there is little overlap in tree species composition between white-sand and terra-firme forests. Tree inventory plots conducted in other regions in the upper Rio Negro support this finding and show that terra-firme forests are characterized by *Protium* spp. (Burseraceae), *Caryocar* spp. (Caryocaraceae), *Licania* spp. (Chrysobalanaceae), *Swartzia* spp. (Fabaceae), *Eschweilera* spp. (Lecythydaceae) and *Vochysia* spp. (Vochysiaceae). By contrast, white-sand forests are characterized by *Eperua leucantha* (Fabaceae), *Hevea* spp. and *Micrandra sprucei* (Euphorbiaceae) (Dezzeo et al., 2000, Boubli, 2002, Abraao et al., 2008). The climate of the study site is a-seasonal with a yearly precipitation of around 3000 mm and a mean monthly precipitation higher than 100 mm during all months (Sombroek, 2001).

Study species

We selected first-year tree seedlings of seven white-sand and seven terra-firme habitat specialists, hereafter referred to as white-sand species and terra-firme species, respectively. Our criteria for identifying first-year tree seedlings were: 1) absence of leaf scars on the seedling stem and 2) indications of recent masting on the harvest sites (e.g. seed and/or fruit remain still present on the ground). We selected seedlings which were at the same developmental stage at the forest floor. We collected a maximum of seven seedlings per mother tree.

We selected habitat specialist species based on species lists from tree inventory plots established in the upper Rio Negro (Dezzeo et al., 2000, Boubli, 2002). For white-sand habitat specialists, adult trees and seedlings of *Chamaecrista adiantifolia* (Fabaceae [nodulating]), *Macrolobium angustifolium* (Fabaceae), *Aspidosperma aracanga* (Apocynaceae), *Scleronema* cf. *micranthum* (Malvaceae), *Haploclathra* cf. *paniculata* (Clusiaceae) and *Micrandra sprucei* (Euphorbiaceae) were only found in white-sand forests; whereas adult trees and seedlings of *Eperua pururea* (Fabaceae) were found on both forest types, but with a much higher abundance in white-sand forest. For the terra-firme habitat specialist species, adult trees and seedlings of *Clathrotropis macrocarpa* (Fabaceae [nodulating]), *Monopteryx uaucu* (Fabaceae), *Swartzia* cf. *tomentifera* (Fabaceae [nodulating]), *Tetragastris panamensis* (Burseraceae), *Virola calophylla* (Myristicaceae) and *Micropholis guyanensis* (Sapotaceae) were only found in terra-firme forests, while *Mouriri ficoides* (Melastomataceae) was found on both forest types but with a higher abundance in terra-firme forests.

Experimental design and implementation

We selected 20 sites of which 10 were located in white-sand forests (sandy soil) and 10 in terra-firme forests (clayey soil) with similar light conditions. The minimum and maximum distance between the sites was 300 m and 9 km, respectively. In each of the 20 sites, we established a paired plot: one protected from herbivore insects (protected plots) and one unprotected plot. Protected plots consisted of cages of 3 m by 3 m by 2 m (length, width, height) completely covered with mosquito net (nylon net Ø = 1mm). The unprotected plots were composed of cages of the same dimensions as the protected plots but with the mosquito net covering only the roof in order to create similar light conditions as in the protected plots. Additionally, the unprotected plots were covered laterally with wire mesh (Ø = 5 cm) to avoid damage from mammal herbivores, e.g., agouties, deer, tapirs. At each site, the protected and non-protected plots were located approximately 5 m apart from each other. All litter fall and lichens growing on the nylon netting were continuously removed during the experiment. In total, 560 seedlings were transplanted (14 species: 7 white-sand species and 7 terra-firme species; x 2 soil types: sand and clay; x 2 herbivore treatments: protected and unprotected; x 10 sites per soil type). One seedling of each of the

14 species was planted in each plot. Before transplanting the seedlings, we carefully removed soil matter which was around the roots of the seedlings. Seedlings were placed in all the plots following a similar sequence at a distance of 0.5 m from each other. During the experiment, plots of one site located in white-sand forest had its mosquito net removed. We excluded this site from the analysis; we therefore considered 532 seedlings (560 minus 28). We set up the experiment in June 2007 and harvested in August 2008.

Light and soil measurements

We quantified the canopy openness of the 19 sites by taking four pictures for each plot (8 per site) using a fish-eye lens. The camera was placed perpendicularly to the forest floor with a fixed orientation to the north. Afterwards, we estimated the percentage of canopy openness using WinPhot version 5.0 (ter Steege, 1996). We averaged the percentage of canopy openness of each site and then we conduct a one-way ANOVA to compare means of canopy openness of white-sand sites and terra-firme sites.

We collected soil samples from 19 sites. Each sample was composed of eight collected soil cores (4 in protected and 4 in unprotected plots) collected at 30 cm depth. The litter layer was removed before sampling the soil. Soil samples were oven-dried at 80°C for 12 hours before being transported to the laboratory. Based on these soil samples, we determined the soil texture of the white-sand and terra-firme sites (Table 4.1). We tested differences in soil texture between white-sand and terra-firme with one-way ANOVA. Soil samples were also analyzed for their total soil phosphorus content by digestion with H_2SO_4 + H_2O_2 (Tiessen and Moir, 1993), nitrogen and carbon were determined in an automated analyzer (Vario Max, Elementar Instruments, Germany). All soil samples were analyzed at the 'Instituto Nacional de Pesquisas da Amazônia (INPA)', Brazil.

Table 4.1: Average and standard errors of sand (2.00 - 0.05 mm), silt (0.05 - 0.002 mm), clay (< 0.002 mm) (g kg^{-1}), total phosphorus (mg kg^{-1}), nitrogen (mg g^{-1}), and carbon (mg g^{-1}) of nine white-sand and ten terra-firme sites in the upper Rio Negro, Brazil

Soil parameter	White-sand	Terra-firme
Sand	946.6 ± 2.7	744.4 ± 3
Silt	34.5 ± 2.5	89.1 ± 1.4
Clay	18.9 ± 0.6	166.5 ± 3.1
Phosphorus	7.5 ± 1.4	54.4 ± 6.7
Nitrogen	0.4 ± 0.1	1.1 ± 0.1
Carbon	6.6 ± 1.0	16.2 ± 1.3

Tree seedling measurements

One month after the experiment had been set up (July 2007); we measured the number of surviving seedlings, the stem height, total leaf area and total leaf damage of the 560 seedlings. We considered these measurements as the initial conditions (t_0).

After 13 months (August 2008), we harvested the seedlings and measured the same parameters, which we considered the final conditions (t_1).

To calculate total leaf area and total leaf damage at t_0 and t_1, we took pictures of fresh leaves placed over a flat white board with a 0.5 x 0.5 cm grid. Afterwards, total leaf area and total leaf damage were calculated by digitizing the contour of each leaf and, if present, the damaged or missing areas. We performed these calculations with the program Image J (version 1.38) (Rasband, 2007). To calculate total leaf area, we summed up the area of individual leaves attached to the seedling. We furthermore calculated the proportional damage in each seedling (total leaf damage / total leaf area) at t_1. Based on the measurements, we calculated the relative height growth rate (*RHGR*) and relative leaf area growth rate (*RLGR*) as follows:

$$RHGR = \frac{\ln S_{t_0} - \ln S_{t_1}}{\Delta t} \; ; \qquad (4.1)$$

$$RLAGR = \frac{\ln LA_{t_0} - \ln LA_{t_1}}{\Delta t} \; ; \qquad (4.2)$$

where *S* is stem height (cm), *LA* is the total leaf area (cm^2) and Δt is the duration of the experiment in number of days (t_1-t_0).

After harvesting in August 2008, we dissected each seedling into roots, stem, petioles, leaves, and cotyledons, if present. With the fresh material, we measured the length of the main root (cm), stem volume, and leaf punch strength. We calculated stem volume as:

$$V = \frac{\pi L}{12}(D_{top}^2 + D_{top}D_{base} + D_{base}^2) \; ; \qquad (4.3)$$

where *V* represents stem volume (cm^3), *L* stands for stem length (cm), D_{top} for the diameter at the top of the stem (cm) just under the growth meristem and D_{base} for the diameter at the base of the stem (cm) just above the root. We measured leaf punch strength (LPS) of three fresh leaves of every seedling using a field penetrometer. The field penetrometer consisted of a needle with a flat tip of 4.98 mm^2 attached to a plastic Erlenmeyer. The needle was held straight by a plastic casing connected to a tripod. A leaf was placed between two thick acrylic plates, both containing a 6 mm diameter hole. The holes were positioned exactly above each other, creating an opening for the needle to touch the leaf (see Aranwela *et al.*, 1999). We calculated the punch strength with the volume of water in the Erlenmeyer necessary to penetrate a leaf. We considered the average of three leaves of each individual seedling as one statistical observation (Cornelissen et al., 2003).

After the measurements with the fresh material, all the seedlings were dried in a stove at 80°C for 48 hours the same day they had been harvested. At the laboratory, they were re-dried in a stove at 60°C for 48 hours. Dry weight of total roots, stem, petioles, leaves, and cotyledons, if present, were used to determine the biomass of each section and of the total seedling. Additionally, we determined the nitrogen, phosphorus, and potassium contents of the leaves with a continuous flow analyzer (Skalar, the Netherlands) after Kjeldal digestion.

We calculated leaf mass per area (LMA; dry leaf mass per unit of leaf area; g cm^{-2}), leaf area ratio (LAR; leaf area per unit dry plant mass; cm^2 g^{-1}), leaf, stem as well as root mass fractions (LMF, SMF, RMF; dry mass per unit dry plant; g g^{-1}), and stem density (SD; dry stem mass per unit stem volume; g cm^{-3}). In total, we analyzed 13 traits, which are considered to respond to the nutrient availability of the habitat and/or the seedling's tolerance for herbivore damage (Table 4.2).

Statistical analyses

We arcsine transformed proportional traits such as LMF, SMF, and RMF. The remaining traits were $\log_{10}$ transformed to assure normality. We estimated correlations between the 13 seedling traits by calculating Pearson's coefficient of the transformed trait values. We, furthermore, estimated Pearson's coefficient between soil nitrogen and leaf nitrogen content as well as soil phosphorus and leaf phosphorus content. We assessed association among seedling traits with principal components analysis (PCA). We calculated the average for each of the 13 traits for each species, which we arcsine or $\log_{10}$ transformed and subsequently standardized. We included in the PCA seedlings growing on the same soil type, i.e., both white-sand and terra-firme species growing on white-sand soil and white-sand and terra-firme species growing on clay soils. We calculated the Pearson correlation of the first two axes of the PCA with the average traits of the species. Furthermore, we calculated the difference between the scores of the first axis as well as the second axis of the PCA obtained for co-specific seedlings growing in distinct soil types, Δ_{axis1} Δ_{axis2}, respectively. Therefore, Δ_{axis1} is the score of the first axis obtained for species *'A'* when growing in white-sand soil minus the score of the first axis obtained for species *'A'* when growing in clay soil. Δ_{axis2} is calculated in the same way; however, it considers the scores of the second axis of the PCA. Afterwards, we calculated the Euclidian distance between Δ_{axis1} and Δ_{axis2}. We interpret these parameters (Δ_{axis1}, Δ_{axis2} and the Euclidian distance) as the shift in seedlings traits due to the soil on which they are growing.

To assess the effect of the transplanting experiment on seedlings performance, we conducted a nested-factorial analysis of variance (ANOVA). We analyzed the effect of soil type, herbivore protection and species origin on the following eight variables: proportional mortality, RHGR, RLAGR, proportional damage, leaf punch strength as well as leaf nitrogen, phosphorus, and potassium content with a nested-factorial analysis of variance (Sokal and Rohlf, 1995). We used a linear model including the terms: soil type (two levels; nested within site), herbivore protection (two levels), species origin (two levels) and species identity (14 levels; nested within species origin). We tested all interactions except soil type versus site and species origin versus species identity which cannot be estimated. Each of the variables was analyzed separately. Because there was only one individual per species growing in each plot, we evaluated the effect of the transplanting on seedling mortality without considering the site effect. We arcsine transformed data of proportional mortality and proportional damage. All analyses were conducted using SPSS 16.0 (SPSS Inc., Chicago).

For *C. adiantifolia* was not possible to measure leaf punch strength, leaf area, and leaf damage due its small leaflets; we therefore only included this species in the analysis of mortality and height growth.

RESULTS

Light and soil

Canopy openness was similar among white-sand and terra-firme sites (F = 0.157; p = 0.69). Soil texture differed between white-sand and terra-firme sites (sand: F = 180.3; p = 0.00 / silt: F = 6.64; p = 0.01 / clay: F = 75.90; p = 0.00).

Seedling traits

In general, seedlings traits were highly correlated with each other (Supplementary material S4.1). Leaf punch strength and leaf mass per area were negatively correlated with leaf nitrogen content (r^2 = -034; $p \leq 0.01$); and leaf phosphorus content (r^2 = -034; $p \leq 0.01$). Nodulating Fabaceae tended to have higher leaf nitrogen content and lower leaf punch strength than the other species analyzed here (Fig. 4.1A). White-sand species, on average, showed lower values of leaf nitrogen content and higher values of leaf punch strength than terra-firme species (Fig. 4.1B). Among all species, *M. ficoides* had the highest average of leaf punch strength (0.93 N mm^{-1}) and the lowest average of leaf nitrogen content (10.63 mg g^{-1}). Leaf mass fraction and root mass fraction were negatively correlated with each other. *M. ficoides* showed the highest average of LMF (0.47), whereas the highest average of RMF was found for *S.* cf. *micranthum* (0.42) (Supplementary material S4.2). Leaf nitrogen content was correlated with soil nitrogen for 11 species, whereas for phosphorus six species showed significant correlation between leaf phosphorus content and soil phosphorus.

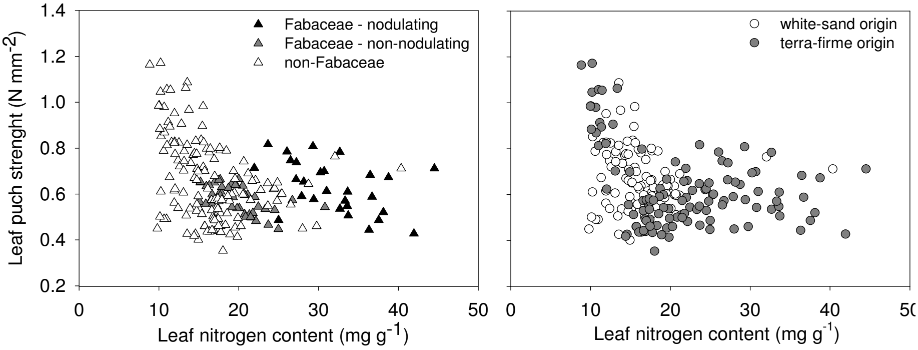

Figure 4.1: Correlation between leaf nitrogen content (mg g^{-1}) and leaf punch strength (N mm^{-2}) (r^2 = -0.34; $p \leq 0.01$). Each dot in the graphs represents one individual seedling. In A, symbols indicate species' family (Fabaceae – nodulating, Fabaceae – non-nodulating and non-Fabaceae) and in B symbols indicate species origin (white-sand origin and terra-firme origin).

The first two axis of the PCA of seedling traits explained 51% of the total variation. The first axis explained 30.6% of the total variation in seedling traits. Total leaf area, leaf nitrogen content, root length, and stem density were positively correlated with the first axis of the PCA. In contrast, leaf mass per area and leaf punch strength were negatively correlated with the first axis. The second axis accounted for 21.8% of the total variation. Leaf potassium content, root mass fraction, and root:shoot ratio were positively correlated with the second axis; whereas leaf mass fraction and leaf area ratio were negatively correlated with the second axis (Fig. 4.2; Table 4.2). The Δ_{axis2} resulted in negative values for 10 species (Fig.4.2; Table 4.3), implying that there is a directional shift of seedling traits, which might be caused by factors associated with the soil on which they are growing. The Euclidian distance between Δ_{axis1} and Δ_{axis2} ranged from 0.14 (*E. purpurea*) to 0.73 (*M. uaucu*).

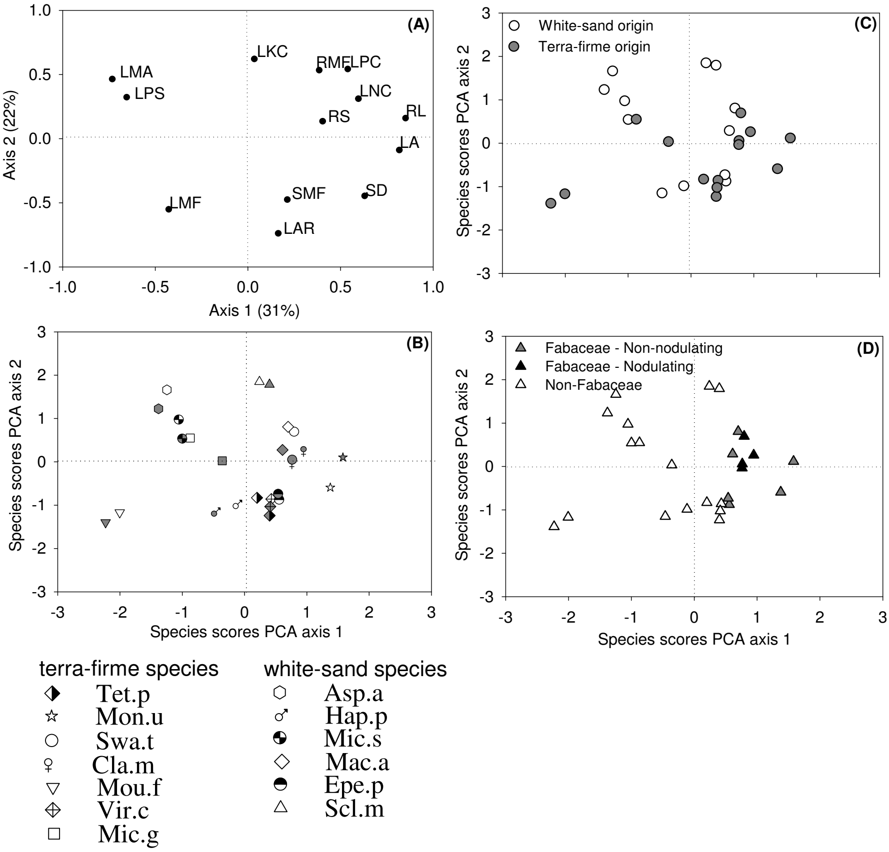

Figure 4.2: Ordination bi-plot and ordination diagrams of the Principal Component Analysis (PCA) of 13 seedling traits (see Table 4.2). (A) Each point in the graph represents the correlation between a trait and the first and second axis of the PCA. (B), (C), and (D) species score along the first two axes of the PCA. In graph (B) symbols represent different species (see Table 4.3); white symbols represent seedlings growing in white-sand forests and gray symbols those growing in terra-firme forests.

Table 4.2: Seedling traits and Pearson correlation (r^2) between seedling traits and the first two axes of the Principal Component Analysis (PCA); (* $p < 0.05$; ** $p < 0.01$); total seedling biomass was not included in the analysis

Trait	Abbreviation	Unit	r^2 PCA axis 1	r^2 PCA axis 2
Leaf area	LA	cm^2	0.689**	-0.066
Leaf area ratio	LAR	$cm^2\ g^{-1}$	0.208	-0.715**
Leaf mass per area	LMA	$cm^2\ g^{-1}$	-0.387**	0.480**
Leaf mass fraction	LMF	$g\ g^{-1}$	-0.440*	-0.541**
Leaf nitrogen content	LNC	$mg\ g^{-1}$	0.546**	0.256
Leaf phosphorus content	LPC	$mg\ g^{-1}$	0.442*	0.541**
Leaf potassium content	LKC	$mg\ g^{-1}$	0.004	0.617**
Leaf punch strength	LPS	$N\ mm^{-2}$	-0.676**	0.249
Root length	RL	cm	0.823**	0.188
Root mass fraction	RMF	$g\ g^{-1}$	0.381	0.545**
Root:shoot ratio	RS		0.397*	0.078
Stem density	SD	$g\ cm^{-3}$	0.680**	-0.391*
Stem mass fraction	SMF	$g\ g^{-1}$	0.219	-0.476*
Total seedling biomass	BIOM	g	-	-

Table 4.3: White-sand and terra-firme species analyzed in this study. r^2 N stands for the Pearson's correlation coefficient between leaf nitrogen content and soil nitrogen; r^2 P stands for the Pearson's correlation coefficient between leaf phosphorus content and soil phosphorus; (*$p < 0.05$; **$p < 0.01$); Δ_{axis1} and Δ_{axis2} stand for the difference between the scores of the first and second axis of the PCA for co-specific seedlings growing in distinct soil types (see methods)

Family	**Species**	**Abbreviation**	**Forest type**	**r^2 N**	**r^2 P**	**Δ_{axis1}**	**Δ_{axis2}**
Apocynaceae	*Aspidosperma aracanga*	Asp.a	white-sand	0.086	-0.069	-0.13	-0.43
Clusiaceae	*Haploclathra* cf. *paniculata*	Hap.p	white-sand	0.574**	0.344*	-0.35	-0.17
Euphorbiaceae	*Micrandra* sprucei	Mic.s	white-sand	-0.105	-0.183	0.06	-0.43
Fabaceae	*Chamaecrista adiantifolia*	Cha.a	white-sand	0.447**	0.361*	-	-
Fabaceae	*Macrolobium angustifolium*	Mac.a	white-sand	0.500**	0.323	-0.09	-0.52
Fabaceae	*Eperua purpurea*	Epe.p	white-sand	0.419*	0.480*	-0.02	0.1 5
Malvaceae	*Scleronema* cf. *micranthum*	Scl.m	white-sand	0.543**	0.231	0.16	-0.05
Burseraceae	*Tetragastris panamensis*	Tet.p	terra-firme	0.672**	0.276	0.20	-0.40
Fabaceae	*Monopteryx uaucu*	Mon.u	terra-firme	0.485*	0.568**	0.20	0.71
Fabaceae	*Swartzia tomentifera*	Swa.t	terra-firme	0.077	0.246	-0.03	-0.63
Fabaceae	*Clathrotropis macrocarpa*	Cla.m	terra-firme	0.383*	0.321	0.19	0.29
Melastomataceae	*Mouriri ficoides*	Mou.f	terra-firme	0.489**	0.357*	-0.23	-0.22
Myristicaceae	*Virola calophylla*	Vir.c	terra-firme	0.532**	0.269	-0.02	-0.16
Sapotaceae	*Micropholis guyanensis*	Mic.g	terra-firme	0.522**	0.501**	0.51	-0.51

Seedlings performance

One month after we set up the experiment, seedling mortality was 6% (32 out of 532 seedlings). At this stage, seedlings mortality might be attributed to a transplanting effect as we found no significant effect of soil type, protection, or interaction between soil type and species origin. When considering the deaths registered between t_0 and t_1, we found that seedlings had a significantly lower proportion of mortality when growing in their original soil type (soil × species origin: $p = 0.005$; $\eta^2 = 0.2$) (Fig. 4.3). For this period, seedling mortality was 19.8% (99 out of 500). *T. panamensis* (terra-firme species) showed the highest mortality (75%) when growing in white-sand forests. RHGR, RLAGR, and proportional damage were not normally distributed even when $\log_{10}$ or arcsine transformed. The lack of normality of these variables is attributed to the high number of replicates with zero RHGR, RLAGR, and proportional damage. Relative height growth rate and relative leaf area growth rate were zero for 11.4% and 10% of the white-sand and terra-firme seedlings, respectively. For individual seedlings, proportional damage by herbivores ranged from 0 to 0.20. Overall, 84.5% of the seedlings had less than 10% of their leaf area eaten by herbivores during the 13 months of the experiment. These results indicate a generally low and similar RHGR, RLAGR, and proportional damage for the seedlings growing under different treatments in our cross-transplanting experiment (Table 4.5).

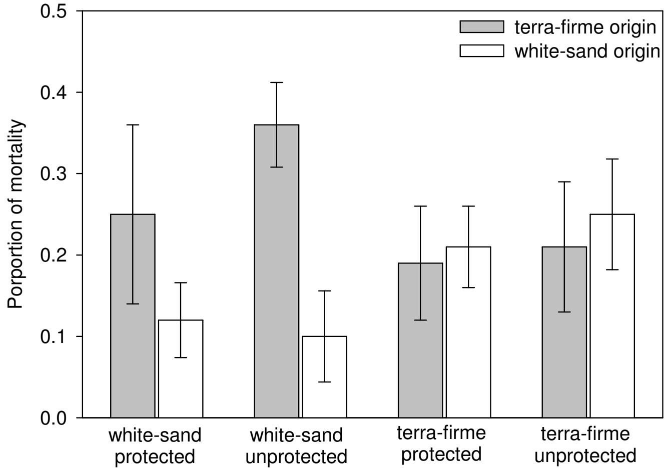

Figure 4.3: Proportion of mortality of white-sand and terra-firme habitat specialists in different treatments after 13 months (mean + SE). Seedlings growing on their non-original soil type show on average a significantly higher proportion of mortality than seedlings growing on their original soil type; $F = 8.825$; $p = 0.005$; $\eta^2 = 0.2$. Differences in the proportion of mortality between protected and unprotected plots are non-significant; $F = 0.72$; $p = 0.4$; $\eta^2 = 0.02$.

Table 4.5: Mean and standard deviation of relative height growth rate (RHGR), relative leaf area growth rate (RLAGR), proportional damage, leaf punch strength, and leaf nitrogen, phosphorus, and potassium content of seedlings analyzed in the cross transplanting experiment

Parameter	**Species Origin**	**White-Sand**		**Terra-firme**	
		Unprotected	**Protected**	**Unprotected**	**Protected**
RHGR	WS	0.011 ± 0.009	0.014 ± 0.015	0.012 ± 0.01	0.01 ± 0.007
RLAGH	WS	0.002 ± 0.002	0.002 ± 0.001	0.003 ± 0.005	0.002 ± 0.002
Proportional damage	WS	0.033 ± 0.036	0.022 ± 0.017	0.032 ± 0.028	0.018 ± 0.014
Leaf punch strength	WS	0.666 ± 0.108	0.674 ± 0.099	0.614 ± 0.093	0.631 ± 0.085
Leaf nitrogen content	WS	15.359 ± 1.851	17.16 ± 2.347	17.615 ± 2.46	18.407 ± 2.232
Leaf phosphorus content	WS	0.819 ± 0.201	0.982 ± 0.392	0.874 ± 0.203	0.974 ± 0.244
Leaf potassium content	WS	6.558 ± 2.541	6.877 ± 2.181	7.036 ± 2.217	7.043 ± 2.406
RHGR	TF	0.01 ± 0.01	0.01 ± 0.01	0.009 ± 0.004	0.014 ± 0.011
RLAGH	TF	0.002 ± 0.001	0.001 ± 0.001	0.002 ± 0.001	0.002 ± 0.003
Proportional damage	TF	0.027 ± 0.027	0.021 ± 0.029	0.019 ± 0.015	0.022 ± 0.02
Leaf punch strength	TF	0.635 ± 0.137	0.674 ± 0.167	0.641 ± 0.175	0.617 ± 0.155
Leaf nitrogen content	TF	18.571 ± 8.964	19.696 ± 9.162	22.474 ± 8.311	22.697 ± 8.021
Leaf phosphorus content	TF	0.749 ± 0.264	0.741 ± 0.306	0.868 ± 0.373	0.888 ± 0.37
Leaf potassium content	TF	5.204 ± 1.155	6.105 ± 1.822	5.764 ± 1.354	6.86 ± 2.331

Leaf punch strength ranged from 0.3 N mm^{-2} (*M. angustifolium*) to 1.2 N mm^{-2} (*M. ficoides*) (Table 4.5). Although we found that white-sand species showed slightly higher leaf punch strength than terra-firme species, the explanatory power of species origin for this variation is low (p = 0.01*;* η^2 = 0.01*).* Leaf nitrogen content ranged from 8.10 mg g^{-1} (*M. ficoides*) to 44.50 mg g^{-1} (*S. tomentifera* [nodulating species]) and differed between white-sand and terra-firme species as well as between soil type, being highest in terra-firme species and on clay soils. Additionally, seedlings growing in protected plots had higher leaf nitrogen content than seedlings growing in unprotected plots. For leaf phosphorus content, values ranged from 0.17 (*M. ficoides*) to 2.52 (*M. sprucei*). Similar to LNC, leaf phosphorus content was highest in seedlings growing on clay soils. However, white-sand species showed higher leaf phosphorus contents than terra-firme species. Finally, leaf potassium content varied from 1.34 (*H.* cf. *paniculata*) to 17.62 (*S. tomentifera*) and did not differ among forest type, but white-sand species showed greater leaf potassium contents than terra-firme species (see Supplementary material S4.2). Overall, species differed among each other on their leaf nitrogen, phosphorus and potassium contents (Table 4.6).

Table 4.6: Summary of *p*-values and partial Eta-squared (η^2) from a nested factorial ANOVA of leaf punch strength (LPS), leaf nitrogen content (LNC), leaf phosphorus content (LPC), and leaf potassium content (LKC); significant effects are indicated with asterisks (**p* < 0.05)

Effect	**LPS**		**LNC**		**LPC**		**LKC**	
	p	η^2	***p***	η^2	***P***	η^2	***p***	η^2
Soil	0.06*	0.18	0.00*	0.58	0.01*	0.33	0.23	0.08
Site (soil)	0.00*	0.17	0.00*	0.18	0.00*	0.12	0.00*	0.16
Protection	0.22	0	0.00*	0.04	0.01*	0.02	0.06	0.01
Species origin	0.01*	0.01	0.00*	0.15	0.00*	0.11	0.00*	0.05
Species identity (species origin)	0.00*	0.63	0.00*	0.77	0.00*	0.68	0.00*	0.51
Soil × protection	0.30	0	0.03*	0.01	0.51	0	0.93	0
Soil × species origin	0.35	0	0.01*	0.02	0.13	0.01	0.76	0
Protection × species origin	0.63	0	0.61	0	0.02*	0.01	0.16	0.01
Soil × protection × species origin	0.12	0	0.85	0	0.43	0	0.97	0

DISCUSSION

Overview

We analyzed morphological traits, leaf nutrient content, growth performance, and herbivore damage of seedlings of white-sand and terra-firme habitat specialist tree species. We found that seedling traits vary in a similar way within and between these two groups of habitat specialists. Although habitat specialists showed lower mortality when growing on their original soil type, growth performance and herbivore damage were similar regardless of protection and soil treatment. These findings suggest that the herbivores might be of little importance for the habitat specificity of trees in white-sand and terra-firme forests in the upper Rio Negro. Next, we discuss our findings with respect to seedling traits and growth performance in greater detail.

Seedling traits

Seedling traits, such as leaf nutrient content and biomass allocation, typically indicate plant growth strategies (Wright and Westoby, 1999, Markesteijn and Poorter, 2009). Interestingly, we found that white-sand and terra-firme species were equally spread along the first two axis of the PCA, implying that both groups span the whole range of variation in these seedling traits (Fig. 4.2). Variation in seedling traits along the first axis of the PCA corresponded to leaf traits, which typically reflect differences in growth and physical defense against herbivore strategies (Wright *et al.*, 2004). At one end of this axis were traits, which reflect slow growth and high physical herbivore defense (leaf punch strength and leaf mass per area). At the other end of this axis were traits, which reflect fast growth and low defense (leaf nitrogen content and total leaf area). Seedlings of Fabaceae were clustered together at one end of the first axis, sharing traits which are related to fast growth and low physical defense. This clustering can be due to the higher total leaf area of Fabaceae compared to non-Fabaceae. Moreover, for nodulating Fabaceae, this clustering can be explained by their common high leaf nitrogen content. The second axis in seedling traits represented features of seedling biomass allocation. At one extreme of the second axis were traits which indicate stronger below ground biomass allocation (RMF and RS), whereas on the other extreme were traits which indicate stronger above ground biomass allocation (LMF, SMF, and LAR).

Additionally, seedlings showed changes in their traits depending on whether they were growing in white-sand or terra-firme forests. The Δ_{axis2} resulted in negative values for 10 of the 13 species, suggesting that seedlings tend to shift their traits in the same direction when growing on similar soil types (Fig. 4.2; Table 4.3). For these 10 species (e.g., *S. tomentifera* and *M. angustifolium*), seedlings showed slightly higher shares of leaf mass in their total biomass when growing in terra-firme forests. The range of variation in Euclidian distance between co-specific species growing on different soil types plotted along the first two axes of the PCA (Δ_{axis1} and Δ_{axis2}) indicated that the extent to which seedlings adjust their traits vary among species.

Seedling performance

Mortality

The mortality observed during the first month of the experiment (6%) can be explained by the transplanting effect. Considering only seedlings, which survived after this first month, we find that seedlings had a significantly lower proportion of mortality when growing on their original soil type. According to the hypothesis of the trade-off between growth and defense, the higher mortality of terra-firme species on white-sand soils would be explained by the inherent fast-growth strategy of terra-firme species, which cannot be achieved under conditions of low nutrient availability (Fine et al., 2006). We did not observe this in our study, however. We found no differences in either growth or proportional damage between the white-sand and terra-firme species regardless of protection and soil treatment. Hence, it appears that mortality is not caused by leaf damage, if damage occurs at low levels such as found in the upper Rio Negro. Moreover, the trade-off hypothesis assumes that the higher mortality of white-sand species on terra-firme soils is attributed to their inherent slow growth strategies and thus inferior competitive ability when growing on clay soils in competition with terra-firme species. In our experiment, however, seedlings were planted about half a meter apart with no physical interference with each other, creating a low competitive environment. We, therefore, cannot conclude that white-sand species were out-competed by terra-firme species on clay soils. Though we were not able to identify the main factors affecting seedlings mortality in their non-original soil type, it seems clear that soil does have an effect on seedling establishment but this effect may not be attributed to a trade-off between growth and defense in our study.

Growth performance, herbivory and leaf strength

Despite changes in seedling traits, as well as differences in the proportion of mortality, we observed a similar and generally low RHGR, RLAGR, and herbivore damage. Although this fact hampered the testing for statistically significant differences, we considered it a highly relevant biological result (see Table 4.5). We attribute the similar and low growth performance and leaf damage of white-sand and terra-firme species to the overall low soil nutrient content of both white-sand and terra-firme soils of the upper Rio Negro. Our results show that the average leaf area growth rate for terra-firme species growing in protected plots on clay soil is only two times the leaf area growth rate of white-sand species growing under the same conditions. In contrast, Fine *et al.* (2006) found that, in western Amazonia, terra-firme species growing in protected plots on clay soil had on average a thrice higher leaf area growth rate than that of white-sand species. Regarding herbivory, we found that leaf damage was low in the unprotected plots. During the period of one year, 34% of the seedlings growing in unprotected plots had zero leaf damage and 92% of all seedlings had a proportional damage lower than 10%. Of all seedlings growing in the unprotected plots, only three individuals had more than 20% leaf damage (*S.* cf. *micranthum*, *E. purpurea* and *V. calophylla* growing in white-sand plots). These herbivory rates are low when compared to the study of Fine *et al.* (2006), who reported that terra-firme species lost nearly 23% of their new leaves per month, while white-sand plants lost almost 10%. Although there are differences regarding the design of the experiment presented here and the experiment presented by Fine et al. (2004, 2006) our findings suggest that seedlings grow slower and suffer lower herbivory rates in the upper Rio Negro than in western Amazonia.

The low herbivory rates observed here are consistent with our results of leaf punch strength, which ranged from 0.3 N mm^{-2} to 1.2 N mm^{-2}. These values are comparable to the data from San Carlos de Río Negro (Reich et al. 1991, Reich et al. 1995: range 0.4 N mm^{-2} to 1 N mm^{-2}). Compared to leaf punch strength registered by Fine et al. (2006) in the western Amazonia (0.1 N mm^{-2} to 0.2 N mm^{-2}), the species in the upper Rio Negro have up to 12 times tougher leaves. Similar to Fine et al. (2006), we found that both white-sand and terra-firme species increase their leaf strength when growing in white-sand soil. Fine *et al.* (2006) found that seedlings on average increase their leaf strength by 17% when growing on white-sand soils, whereas we found an increase of only 3%. This suggests that in the upper Rio Negro the need to defend leaves is rather similar in both forest types. Additionally, the low herbivory rates can be explained by the likely low insect abundance our study area. As white-sand forests represent the dominant habitat, the insect herbivores community might occur in low abundance also in the patches of terra-firme forests.

Why are herbivores of minor importance for tree habitat specificity in the upper Rio Negro?

Based on Herms and Mattson (1992), we suggest to express herbivory as a sigmoid function of resource availability (Fig. 4.4). Typically, herbivory remains low and relatively constant in habitats where resource availability is low, but gradually increases and eventually approaches its maximum, as resource availability increases. We argue that herbivory and consequently the trade-off between growth and defense only affects habitat specificity, if habitats are sufficiently distinct from each other along the sigmoid 'resource availability – herbivory' curve. Accordingly, we suggest that the range of resource availability and herbivory of both white-sand and terra-firme forests in the upper Rio Negro are located before the lower turning point of this sigmoid curve. Thus, herbivores are of minor importance for tree habitat specificity here.

A close proximity in terms of resource availability of white-sand and terra-firme forests of the upper Rio Negro in this 'resource availability – herbivory' curve is suggested by their relatively small difference in soils nutrient. Although soil nitrogen and carbon seem to be similar between soils of white-sand and terra-firme forests, absolute difference between soil phosphorus in these two forests types can be twice higher in western Amazonia than in the upper Rio Negro. As the input of phosphorus in the system comes mainly from the soil, differences in soil phosphorus can be explained by the differences in soil development and parent-material of the western Amazonia and the upper Rio Negro. White-sand and terra-firme forests in the upper Rio Negro grow on soils derived from Proterozoic rocks (~2,500 Ma), whereas the terra-firme forests in western Amazonia grow Cenozoic sediments (~66 Ma and much more recent) (Sombroek, 2000) and may have continuous volcanic input (Jan Sevink, pers. comm.), but the white-sands in western Amazonia might have a similar origin as those in the upper Rio Negro (Rässänen, 1993) (see Introduction). We therefore expected that differences between soil phosphorus of white-sand and terra-firme forests are more subtle in the upper Rio Negro than in western Amazonia. We suggest that plants traits might vary between habitats only if differences in soil nutrient are large enough to trigger differences in plants growth and herbivore defense strategy. Taken as a whole, our study suggest that gradient in soil nutrient vary among similar habitats across regions of Amazonia. This variation might influence ecosystem functioning as well as mechanisms shaping beta-diversity.

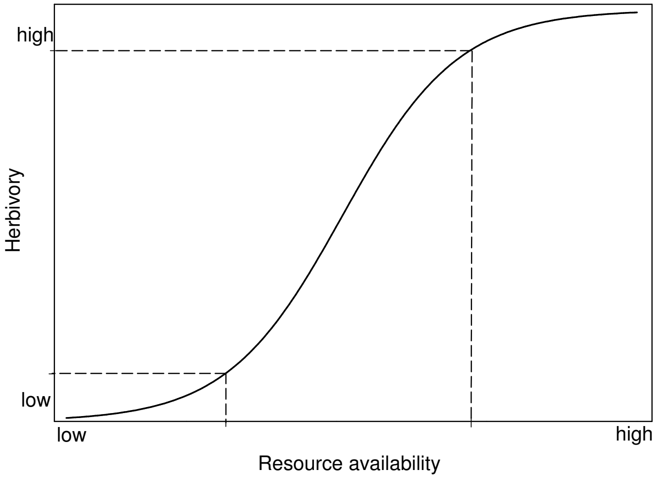

Figure 4.4: Theoretical function describing the relationship between resource availability and herbivory. The area between the turning points of the curve indicates the range in which resource availability substantially affects herbivory. The trade-off between growth and defense might influence habitat specificity only if the location of habitats assure sufficient gradient in herbivory and resource availability. Modified after Herms and Mattson (1992).

Table 4.7: Soil nutrient concentrations and leaf punch strength (LPS) compiled for white-sand and terra-firme forests in the Guiana shield (GS) and in western Amazonia. Differences in soil nutrient concentrations between clayey and sandy soils are given in bold. Soil nutrient concentrations values for the middle Içana River represent averaged values of sites presented in this study, LPS represents the range (min. – max.)

Site	Soil / difference between soils	Total P (mg kg^{-1})	N (mg g^{-1})	C (mg g^{-1})	LPS	Region, Country	Reference (soil, LPS)
San Carlos del Rio Negro	clayey	58.08	0.83	15.64	0.53 - 1.06	GS	Rainfor plot SCR-01, Reich et al. 1994
	sandy	22.54	0.70	13.38	*	GS	Rainfor plot SCR-05
	difference	**35.53**	**0.13**	**2.26**	*	GS	
Middle Içana River	clayey	53.80	1.07	16.22	0.95 - 0.46	GS	this study
	sandy	7.52	0.39	6.61	0.85 - 0.54	GS	this study
	difference	**46.28**	**0.68**	**9.61**		GS	
Allpahuayo	clayey	90.13	0.71	7.62	*	WA	Rainfor plot ALP-12
	sandy	7.59	0.15	1.80	*	WA	Rainfor plot ALP-03
	difference	**82.55**	**0.56**	**5.82**		WA	
Allpahuayo	clayey	80.17	1.02	10.75	*	WA	Rainfor plot ALP-22
	sandy	11.39	0.34	4.65	*	WA	Rainfor plot ALP-21
	difference	**68.78**	**0.68**	**6.10**		WA	
Allpahuayo, Mishana	clayey	*	*	*	0.12 - 0.06	WA	Fine et al. 2006
	sandy	*	*	*	0.23 - 0.06	WA	Fine et al. 2006

Conclusion

We found that the herbivory can be of minor importance for habitat specificity of trees when variation in resource availability is subtle, even for habitats, which have conspicuous boundaries. We argue that the low soil nutrient availability of both forest types analyzed here does not allow for variation in the continuum of the trade-off between growth herbivore defense (see Fig. 4.4). If mechanisms driving beta-diversity are tightly connected to soil nutrient availability, such as the trade-off between growth and defense, we suggest that its importance might vary in a predictable manner across Amazonia. Such mechanisms might be affected by geological and geomorphological history. In order to better predict in which range of resource availability the trade-off between growth and defense drives habitat specificity and plant traits, future research should aim at identifying the turning points of the ‘resource availability – herbivory’ curve. An approach combining empirical data and modeling might help to clear this problem.

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SUPPLEMENTARY MATERIAL: CORRELATION COEFFICIENTS AND AVERAGE SEEDLING TRAITS

Table S4.1: Pearson correlation coefficients of seedling traits (* $p < 0.05$; ** $p < 0.01$); abbreviations of traits are given in Table 4.3

	LA	**LAR**	**LMF**	**LNC**	**LPC**	**LKC**	**LPS**	**RL**	**RMF**	**RS**	**SD**	**SMF**	**BIOM**
LAR	0.335**												
LMF	0.208**	0.795**											
LNC	0.331**	0.043	-0.158*										
LPC	0.211**	-0.242**	-0.305**	0.575**									
LKC	-0.02	-0.141*	-0.188**	0.309**	0.378**								
LPS	-0.054	-0.174*	0.209**	-0.344**	-0.256**	0.056							
RL	0.477**	-0.194**	-0.238**	0.291**	0.381**	-0.037	-0.113						
RMF	-0.056	-0.340**	-0.416**	0.061	0.249**	0.084	-0.159*	0.354**					
RS	0.009	-0.112	-0.129	0.09	0.245**	-0.144*	-0.194**	0.703**	0.510**				
SD	0.401**	-0.115	-0.221**	0.08	-0.037	-0.201**	-0.105	0.272**	0.05	0.065			
SMF	-0.072	-0.191**	-0.347**	0.009	0.043	-0.033	-0.165*	-0.005	-0.377**	-0.205**	0.323**		
BIOM	0.896**	-0.119	-0.155*	0.328**	0.336**	0.046	0.025	0.594**	0.101	0.061	0.477**	0.014	
LMA	-0.138*	-0.339**	0.237**	-0.234**	-0.036	-0.082	0.559**	-0.03	-0.039	0.01	-0.13	-0.227**	0.015

Table S4.2: Average of seedling traits of 13 species included in the PCA analysis; abbreviations of traits are given in Table 4.3

Family	Species	Forest type	LA	LAR	LMA	LMF	LNC	LPC	LKC	LPS	RL	RMF	RS	SD	SMF	BIOM
Apocynaceae	*A. aracanga*	WS	10.01	0.05	6.68	0.34	16.86	1.25	9.72	0.68	7.15	0.36	0.69	69.54	0.27	213.30
Clusiaceae	*H.* cf. *paniculata*	WS	30.79	0.05	5.86	0.31	13.85	0.61	3.59	0.54	11.56	0.25	0.81	136.71	0.42	544.75
Euphorbiaceae	*M. sprucei*	WS	69.19	0.04	7.11	0.28	15.89	1.00	5.82	0.75	12.23	0.17	0.59	93.54	0.28	1427.68
Fabaceae	*E. purpurea*	WS	204.55	0.06	4.89	0.29	18.90	0.92	8.61	0.59	17.43	0.18	0.42	160.01	0.48	3060.07
Fabaceae	*M. angustifolium*	WS	93.96	0.06	5.38	0.30	19.35	0.77	6.14	0.57	21.65	0.44	1.03	126.71	0.23	1596.38
Malvaceae	*S.* cf. *micranthum*	WS	93.24	0.03	6.57	0.20	16.39	0.97	8.62	0.76	23.59	0.42	0.85	131.46	0.36	2887.57
Burseraceae	*T. panamensis*	TF	42.71	0.08	4.35	0.32	14.83	0.77	5.52	0.52	12.86	0.27	0.84	130.05	0.40	564.94
Fabaceae	*C. macrocarpa*	TF	323.30	0.05	5.19	0.27	27.12	1.18	6.89	0.68	22.92	0.23	0.55	146.17	0.44	5918.54
Fabaceae	*M. uaucu*	TF	326.31	0.06	5.10	0.31	21.80	1.29	4.18	0.54	30.50	0.35	0.99	168.48	0.30	5303.95
Fabaceae	*S. tomentifera*	TF	76.20	0.06	5.09	0.30	35.78	0.89	6.67	0.59	18.96	0.34	0.92	118.06	0.33	1231.38
Myristicaceae	*V. calophylla*	TF	97.18	0.09	4.56	0.36	16.31	0.70	6.41	0.50	14.91	0.28	0.93	113.91	0.34	1148.51
Myrtaceae	*M. ficoides*	TF	21.60	0.07	7.20	0.47	10.63	0.34	4.17	0.93	9.00	0.20	0.65	114.40	0.34	317.67
Sapotaceae	*M. guyanensis*	TF	38.31	0.04	6.03	0.23	21.40	0.58	7.02	0.63	9.57	0.20	0.55	117.24	0.30	860.59

Protected cage in white-sand forest,
nearby Tunuí-Cachoeira,
Içana River, Brazil

Romeu Brazão,
a student of EIBC,
monitoring
seedling mortality

A seedling of
Micrandra sprucei,
used for the
transplanting
experiment

5

COMPARING TREE COMMUNITIES OF WHITE-SAND AND TERRA-FIRME FORESTS ACROSS THREE AMAZONIAN REGIONS

with Ieda Leão do Amaral, Gerardo Aymard, Olaf Banki,
Carolina V. de Castilho, Cid Ferreira, Terry W. Henkel, Dairon C. Lopez, William Magnuson,
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To be submitted.

ABSTRACT

Amazonian forests harbor the world's most diverse tree communities. Tree species diversity and composition of local communities is partially regulated by local environmental conditions and local species interactions. Yet, local communities are embedded in regional communities which are regulated by long-term, large-scale evolutionary processes. The extent to which local tree communities in Amazonian forests are regulated by regional communities remains poorly understood. Here, we analyze a dataset containing 192 tree inventory plots placed in three Amazonian regions, central Amazonia, the Guianas, and the upper Rio Negro, covering white-sand and terra-firme forests. Our aim is to characterize how tree species diversity and composition of white-sand and terra-firme forests vary across these three regions. We evaluate whether tree diversity of regional communities influences tree diversity and floristic similarity of local communities. Furthermore, we assess if habitat association of trees families and genera with either the white-sand or the terra-firme forests is maintained across lower taxonomic levels. We found that tree communities of both white-sand and terra-firme forests are more diverse in central Amazonia than in the Guianas and in the upper Rio Negro. The floristic similarity of local communities of each forest type seems to be constrained by the diversity of the regional community. Furthermore, habitat association is, in general, maintained across taxonomic levels, i.e., families and genera that are significantly associated with either the white-sand or the terra-firme forests have the majority of their species associated with that particular forest type. This finding suggests that a large number of tree species may have retained requirements for their typical habitat during speciation events. The marked difference in tree species diversity between tree communities in central Amazonia and those encountered in the Guianas and in the upper Rio Negro suggests spatial variation in evolutionary processes. We argue that diversity and composition of local tree communities are largely influenced by regional communities. These results highlight the importance of considering a hierarchical approach for understanding how tree species diversity is regulated in Amazonian forests.

INTRODUCTION

Amazonian forests harbor the world's most diverse tree species communities. At the local scale, this high tree species diversity is partially explained by habitat heterogeneity (Gentry, 1988, Tuomisto et al., 2003). In places with high habitat heterogeneity, species are usually associated with one typical habitat, leading to little overlap in tree species composition between distinct habitats (Condit et al., 2002). The little overlap in tree species composition, i.e., high beta-diversity, has been mainly explained by species adaptations to distinct abiotic conditions as well as by herbivore-plant interactions operating at a local scale (Fine et al., 2004). Yet, species diversity and composition of local communities is largely influenced by the regional community, which is regulated by long term evolutionary processes operating at broad spatial and temporal scales (Ricklefs and Schluter, 1993, Stropp et al., 2009). The extent to which local tree communities are regulated by regional tree communities in Amazonian forests remains still poorly understood (see Banki, 2010).

One of the highest levels of tree beta-diversity observed in Amazonian forests is found between white-sand and terra-firme forests. White-sand forests growing on non-flooded sandy soils harbor a less diverse and a distinct tree species community as compared to those encountered on the clay soils of terra-firme forests (Fanshawe, 1952, Anderson, 1981, Dezzeo et al., 2000, ter Steege et al., 2000, Boubli, 2002, Banki, 2010). Several tree inventory plots have been established in white-sand and terra-firme forests revealing how floristic similarity varies between these two forest types at a local scale (ibid.). In white-sand and terra-firme forests of the upper Rio Negro *Eperua* (Fabaceae), contributes to the low floristic similarity between these two forest types (Dezzeo et al., 2000, Boubli, 2002). In central Amazonia, however, the low floristic similarity between these two forest types is apparently caused by differences in abundance of *Aldina* (Fabaceae) (Anderson, 1981). At a broader spatial scale, across Amazonian regions, however, variation in beta-diversity of white-sand and terra-firme forests remains unclear. White-sand forests are unevenly distributed across Amazonia. The upper Rio Negro and the Guianas harbor large and continuous patches of white-sand forests, whereas central and western Amazonia only hold small and isolated patches of white-sand forests surrounded by terra-firme forests. As at broad spatial scale, the size of a habitat determines the number of species it can support: large habitats typically host more species, and potentially more co-generic species than do smaller ones (Rosenzweig, 1995, Harnik et al., 2010). Variation in habitat size could, therefore, generate spatial gradients in alpha- and beta-diversity.

Additionally, beta-diversity originates in cases where species adapt over long time periods to a typical habitat. The contribution of phylogenetic niche conservatism, i.e., the tendency of lineages to maintain habitat requirements during speciation events (Wiens, 2004), to beta-diversity of white-sand and terra-firme forests is still poorly understood (Fine et al., 2005). If species-habitat associations are mostly explained by species inherited traits, lineages show phylogenetic niche conservatism; consequently, their current habitat requirements are inherited from their ancestors. In this case, habitat heterogeneity would be of minor importance for speciation. In contrast, if habitat associations have emerged frequently and separately among lineages, it indicates that current habitat characteristics play an important role driving speciation (see Fine et al., 2005). Trends in phylogenetic conservatism can be assessed by analyzing how often habitat association is maintained across different taxonomic levels in the regional community (Prinzing et al., 2001). Such information can contribute to the understanding of the role of habitat heterogeneity in the ecology of plants speciation (Fine et al., 2005), and therefore reveal how beta-diversity is generated in Amazonian forests.

Here we characterize how tree alpha- and beta-diversity of white-sand and terra-firme forests varies across broad spatial scales. We analyze 192 tree inventory plots established in white-sand and terra-firme forests of three regions: central Amazonia, the Guianas, and the upper Rio Negro. We aim at answering the following questions:

1. How does tree alpha- and beta-diversity of local communities of white-sand and terra-firme forests vary within and between regions?
2. Is the beta-diversity of similar forest types correlated with geographic distance?
3. Does regional diversity influence maximum floristic similarities between local communities?
4. Are tree families, genera, and species significantly associated with white-sand and terra-firme forests? Is this association maintained across lower taxonomic levels, i.e., is the typical habitat of a given family maintained/inherited by its subordinate taxa?

METHODS

Study sites and data collection

We analyze data from 192 tree inventory plots established in white-sand and terra-firme forests in the lowland tropical moist forests of the Guiana shield formation. The plots were located in three geographically separated regions: central Amazonia (CA), the Guianas (GS), here including Guyana and Suriname, and the upper Rio Negro (URN) (Fig. 5.1) (Appendix 2 and 3). The lowlands of the Guianas are characterized by a dry period of one to three months during which the monthly precipitation is less than 100 mm. Total annual rainfall ranges in this region from 1,800 mm to 3,200 mm (Sombroek, 2001). In central Amazonia and in the upper Rio Negro the climate is a-seasonal. Annual rainfall ranges from 2,400 mm to 2,800 mm in central Amazonia and from 2,500 to 3,000 mm in the upper Rio Negro (Sombroek, 2001). White-sand forests occur on sandy soils originated from *in-situ* weathering of crystalline rocks, alluvial deposition, or podzolization (Anderson, 1981, Quesada, 2008). In contrast, terra-firme forests grow on clayey soils (oxisols and ultisols) originated from *in situ* weathering of a distinct substrate. Although soils of white-sand forests are relatively poorer in nutrients than soils of terra-firme, soils of both forest types are considered poor in our study sites, as they typically originated from weathering of the ancient bedrocks of the Guiana shield formation (Quesada et al., 2010).

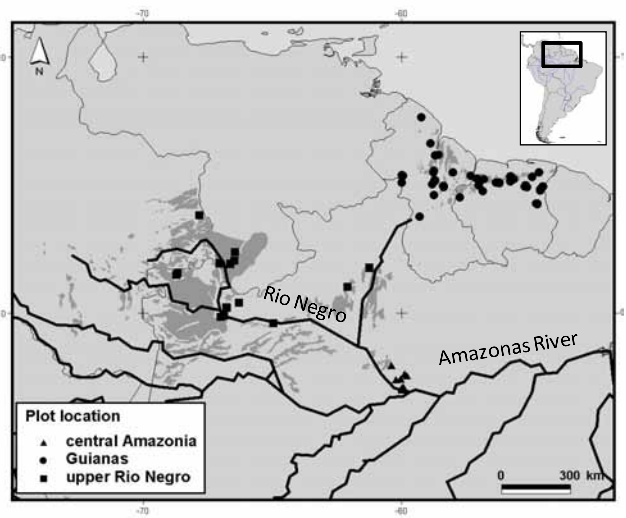

Figure 5.1: Location of the 192 tree inventory plots in the three Amazonian regions (central Amazonia, the Guianas, and the upper Rio Negro); individual locations may contain multiple plots. Areas of white-sand forests are represented in dark gray.

Plots are unequally distributed in white-sand and terra-firme forests; overall our dataset included 38 plots established in non-flooded white-sand forests and 154 plots established in non-flooded terra-firme forests. The plot size ranged from 0.25 to 1.08 ha (178 plots) and from 1.21 to 2.3 ha (14 plots). In each plot, all trees ≥ 10 cm DBH (diameter at breast height, i.e., 1.3 m) were measured for diameter. For 99 plots, all morpho-species were collected and identified in the herbarium, whereas for 74 plots only morpho-species, for which field identification was not possible, were collected and then identified (Appendix 2). Specimens for which taxonomic identification was not possible were sorted to morpho-species, i.e., recognized as morphologically similar at species level. We assumed that morpho-species collected in plots established by different researchers or during a different research project were restricted to the plot in which they were collected.

For each of the 192 plots, we compiled species lists and determined species abundances. We standardized species names and species synonyms using the Missouri Botanical Garden's TROPICOS dataset (MOBOT). This procedure reduced possible errors, e.g., a single species being considered as different entities. Nevertheless, it is well possible that trees identified by different research groups as one species are in fact different species because the research groups used different Herbaria and Floras for species identification. We, therefore, defined plot subsets which had its specimens identified at the same herbarium or by the same botanist. Overall, we defined three plot subsets: 1) central Amazonia (identified by specialists at the herbarium of the 'Insitituto Nacional de Pesquisas da Amazônia, INPA), 2) Guyana and Suriname (identified at the Nationaal Herbarium

Nederland by O. Banki and H. ter Steege), 3) upper Rio Negro (Venezuela) (indentified by G. Aymard at the Herbario Universitario, PORT, Venezuela), upper Rio Negro (Colombia) (identified by D. Cardenas at the Herbario Amazónico Colombiano, COAH, Colombia), upper Rio Negro (Brazil), and Roraima (identified by specialists at the Herbarium of the 'Insitituto Nacional de Pesquisas da Amazônia, INPA, or at the Herbarium of 'Museu Paraensi Emilio Goeldi'). Plots established in the upper Rio Negro were included in the same plot subset even if their species were identified by different research groups, due to their close spatial proximity. We consider the error due to species identification to be minor in this subset as there was a large overlap in species composition (average of *Jaccard* index = 0.94 ± 0.07 for terra-firme plots; average of *Jaccard* index = 0.93 ± 0.06 for white-sand plots).

Data Analysis

Tree species diversity

Hereafter we refer to the trees sampled in the white-sand plots as 'tree community of white-sand forests' and to the trees sampled in the terra-firme plots as 'tree community of terra-firme forests'. We established relative species abundance curves for the tree communities of white-sand and terra-firme forests. For this, we excluded 1,909 trees (9%) registered as 'indet.' in Volkmer and Magnusson's dataset (Appendix 2). We estimated tree alpha-diversity for each plot by calculating Fisher's alpha (Fisher et al., 1943). We tested whether tree-alpha diversity of white-sand and terra-firme forests varies within and between regions. To this end, we first applied a standard ANOVA and plotted fitted values against standardized residuals. We detected, however, heteroscedasticity due to the inherent heterogeneity of variance in tree alpha-diversity observed within and between forest types and regions (Stropp et al., 2009) – variance of each group, here forest types and region, increased with the average value of the group. For that reason, we applied an ANOVA with a generalized least square model (GLS) which allows the introduction of variance–covariate structures (Zuur et al., 2009). Because the explanatory variables used to explain the variance of the residuals were nominal, in this case, forest type, region as well as the interaction between forest type and region, we selected as function of variance structure the function 'varIdent' available in the 'nlme' package (Pinheiro et al., 2008) in the '*R'* statistical and programming environment (Ihaka and Gentleman, 1996).

Tree species composition

To evaluate variation in beta-diversity between the three regions (CA, GS, and URN) we performed two non-metric multidimensional scaling (NMDS) ordinations (McCune *et al.*, 2002). For the first NMDS ordination, we used the relative abundance of trees identified at family level. For the second, we used the relative abundance of trees identified at the genus level. We used the Sørensen Index (Bray-Curtis) as a measure of floristic distance (FD) in both NMDS ordinations. We calculated the percentage of variation explained by the axes of NMDS by computing the linear regression between the FD and the Euclidian distances between sites produced by the NMDS. To tested the correlation between floristic (Sørensen Bray-Curtis) and geographic distance (km) between the plots, we performed a Mantel test (Mantel, 1967).

We estimated the expected similarity for hypothetical random local communities, hereafter referred to as 'similarity simulated'. These hypothetical local communities were simply a random draw, with replacement, from the regional community. The number of individuals to be present in the random local communities was defined as the average number of individuals registered for plots established in the same forest type and in the same region. We obtained the regional communities by adding the total abundances of each species registered in plots established in the same forest type and in the same region. We obtained 1,000 hypothetical random local communities and then calculated the Sørensen floristic similarity between them. Afterwards, we tested difference between the mean floristic similarities obtained for the random local communities and mean floristic similarities observed by applying a Wilcoxon test. To assess whether floristic similarity is correlated with diversity, we calculated Pearson's correlation coefficient between average similarity simulated and average observed tree alpha-diversity.

We determined which families, genera, and species were associated with white-sand forests or terra-firme forests by performing an indicator species analysis (ISA) (Dufrene and Legendre, 1997). Because we expected that taxa with low numbers of individuals have low probability to be significantly associated with a given habitat type, we defined a cut-off value of 30 individuals. To define this cut-off value we first performed ISA including all trees. Afterwards, we plotted significance value against the total number of individuals and found that taxa with abundance below this cut-off value tended to show non-significant habitat associations (data not shown). For each family and genus we quantified how many subordinate taxa showed significant habitat associations and how many showed non-significant habitat associations.

We performed most of the analyses in the '*R*' statistical and programming environment (Ihaka and Gentleman, 1996). We used the package '*vegan*' (Oksanen et al., 2007) to calculate Sørensen Bray-Curtis indices as well as to perform the NMDS. To conduct the ANOVA with GLS we used the package '*nlme*' (Pinheiro et al., 2008). Geographic distances between plots were calculated using the package *'fossil'* (Vavrek, 2010) and the Mantel tests were performed using the package '*ade4´* (Dray and Dufour, 2007). For performing ISA, we used the software PC-Ord v.5 (McCune and Mefford, 1999). To obtain 1,000 random local communities we used a Matlab simulation algorithm developed by Mota de Oliveira (2010).

RESULTS

We registered 93,081 trees ≥ 10 cm DBH in the 192 plots. In 38 white-sand plots, we registered 21,483 trees, whereas in the 154 terra-firme plots we registered 71,598 trees (Fig. 5.2). The total number of trees identified at species level is 76,085 trees (82%). Overall, we registered 3,612 species, out of which 1,681 were identified at species level and but 1,931 (53%) are sorted to morpho-species (Table 5.1).

Table 5.1: Status of tree specimen identification (≥10 cm DBH); N. stands for the total number of trees; percentages are given in parentheses and refer to the total number of trees encountered in each forest type

Status of specimens identification	**N. of trees in white-sand plots**	**N. of trees in terra-firme plots**	**N. of trees in overall plots**
Family is not assigned	41 (0.19)	768 (1.07)	809 (0.87)
Family is not assigned, but specimens are sorted to morpho-species	10 (0.05)	75 (0.1)	85 (0.09)
Genus is not assigned	82 (0.38)	1613 (2.25)	1695 (1.82)
Genus is not assigned, but specimens are sorted to morpho-species	190 (0.88)	1920 (2.68)	2110 (2.27)
Genus is assigned[1]	79 (0.37)	3176 (4.44)	3255 (3.5)
Species is assigned	18,089 (84.2)	57,097 (79.75)	75,186 (80.77)
Species differ from herbarium material, but falls within the limit of variation of the species (aff.)	55 (0.26)	119 (0.17)	174 (0.19)
Species determination is uncertain (cf.)	186 (0.87)	415 (0.58)	601 (0.65)
Species is not assigned, but specimens are sorted to morpho-species	2,497 (11.62)	4,974 (6.95)	7,471 (8.03)
Species is not assigned and specimens are not sorted to morpho-species[2]	204 (0.95)	1,367 (1.91)	1,571 (1.69)
Species name not found in on-line herbaria datasets[3]	50 (0.23)	74 (0.1)	124 (0.13)
Total	**21,483**	**71,598**	**93,081**

[1] Family and genus are assigned. Species are stored as “indet.” in the original plot data.

[2] Family and genus are assigned. Species are stored as “sp.” in the original plot data.

[3] Missouri Botanical Garden’s TROPICOS dataset (MOBOT), International Plant Name Index dataset (IPNI, 2008), and New York Botanical Garden virtual herbarium (NYBG).

Table 5.2: Total number of tree inventory plots, trees, species, morpho-species presented per forest type and region; Fisher's alpha was calculated based on all species and morpho-species

Region	Parameter	White-sand	Terra-firme	Overall
All regions	Number of plots	38	154	192
	Number of trees	21,483	71,598	93,081
	Number of species	640	1572	1681
	Number of morpho-species	344	963	1200
	Fisher's alpha Mean (min-max)	19.8 (4.64 - 73.39)	82.19 (8.19 - 215.77)	-
Central Amazonia	Number of plots	4	75	79
	Number of trees	2,111	28,972	31,083
	Number of species	271	1018	1056
	Number of morpho-species	105	293	365
	Fisher's alpha Mean (min-max)	56.78 (32.48 - 73.39)	127.9 (45.58 - 215.77)	-
Guianas	Number of plots	26	65	91
	Number of trees	14,401	34,617	49,018
	Number of species	200	577	590
	Number of morpho-species	95	500	540
	Fisher's alpha Mean (min-max)	10.89 (4.64 - 24.53)	35.45 (8.19 - 78.86)	-
Upper Rio Negro	Number of plots	8	14	22
	Number of trees	4,971	8,009	12,980
	Number of species	327	769	903
	Number of morpho-species	144	171	296
	Fisher's alpha Mean (min-max)	30.27 (9.92 - 46.69)	54.39 (17.33 - 96.83)	-

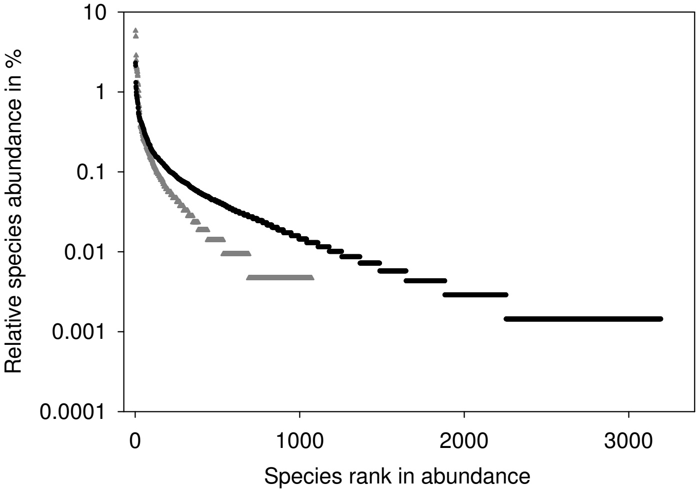

Figure 5.2: Relative abundance distribution of 38 one-ha tree inventory plots established in white-sand forests (gray dots) and 154 plots in terra-firme forests (black dots); the total number of species and morpho-species registered in white-sand and terra-firme plots are 1,072 and 3,194, respectively; number of singletons in white-sand is 383; number of singletons in terra-firme is 941.

Tree species diversity and composition

Overall, our dataset included 89 families, 412 genera, 1,681 identified species (including aff. and cf.). The three most abundant families were Fabaceae (21,652 trees), Lecythidaceae (9,938 trees), and Chrysobalanaceae (6,999 trees). The three most abundant genera were *Eperua* (6,936), *Eschweilera* (6,819), and *Licania* (5,262). In white-sand plots, the three most abundant species were *Eperua falcata* (2,823), *Catostemma fragrans* (1,245), and *Eperua grandiflora* (1,062). In terra-firme plots the three most abundant species were *Eschweilera coriaceae* (1,594), *Eschweilera sagotiana* (1,486), and *Lecythis corrugata* (908).

On average, tree diversity was significantly lower in white-sand plots than in terra-firme plots (average of Fisher's alpha of white-sand plots = 19.8; average of Fisher's alpha of terra-firme plots = 82.19; $F = 555.64$; $p < 0.001$). Among the three regions analyzed here, central Amazonia was the most diverse (F = 225.83; $p < 0.001$) (Fig. 5.3). Tree diversity of terra-firme forests showed higher residual variation than tree diversity of white-sand forests. Among the three regions, central Amazonia showed the highest residual variation in tree diversity (Table 5.3).

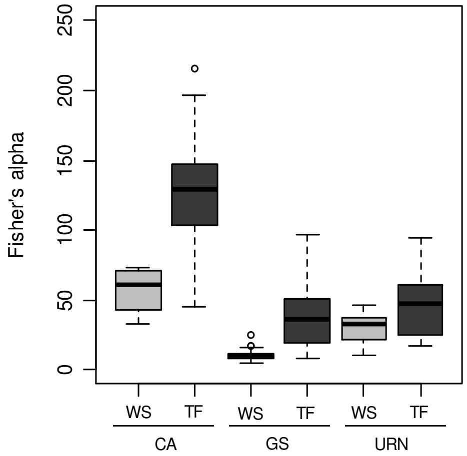

Figure 5.3: Tree alpha-diversity of white-sand (WS) and terra-firme (TF) forests in central Amazonia (CA), the Guianas (GS), and the upper Rio Negro (URN); tree diversity differed significantly between white-sand forests and terra-firme forests (ANOVA-GLS: F = 555.64, $p < 0.001$) as well as between regions (F = 225.83; $p < 0.001$).

Table 5.3: Summary of the ANOVA with generalized least square model for tree alpha-diversity; residual variation stands for the residual standard error (4.31) times the multiplication factors obtained for each group

Forest type	Region	Residual variation	Factors	F	p
White-sand	Central Amazonia	18.45	Forest type	555.64	< 0.0001
	Guianas	4.31			
	Upper Rio Negro	11.94	Regions	225.83	< 0.0001
Terra-firme	Central Amazonia	32.59			
	Guianas	19.19	Regions*Forest type	10.57	< 0.0001
	Upper Rio Negro	23.57			

The two axes of the NMDS captured 81% and 87% of the floristic variation at family and genus level, respectively. Ordination of both taxonomic levels revealed similar patterns. The variation on the first axis of the NMDS is related to the plots' geographic location. Plots located in central Amazonia and in the upper Rio Negro formed two groups along the first axis of the NMDS, whereas plots located in the Guianas were scattered along the first axis. Variation captured by the second axis of the NMDS is related to forest type.

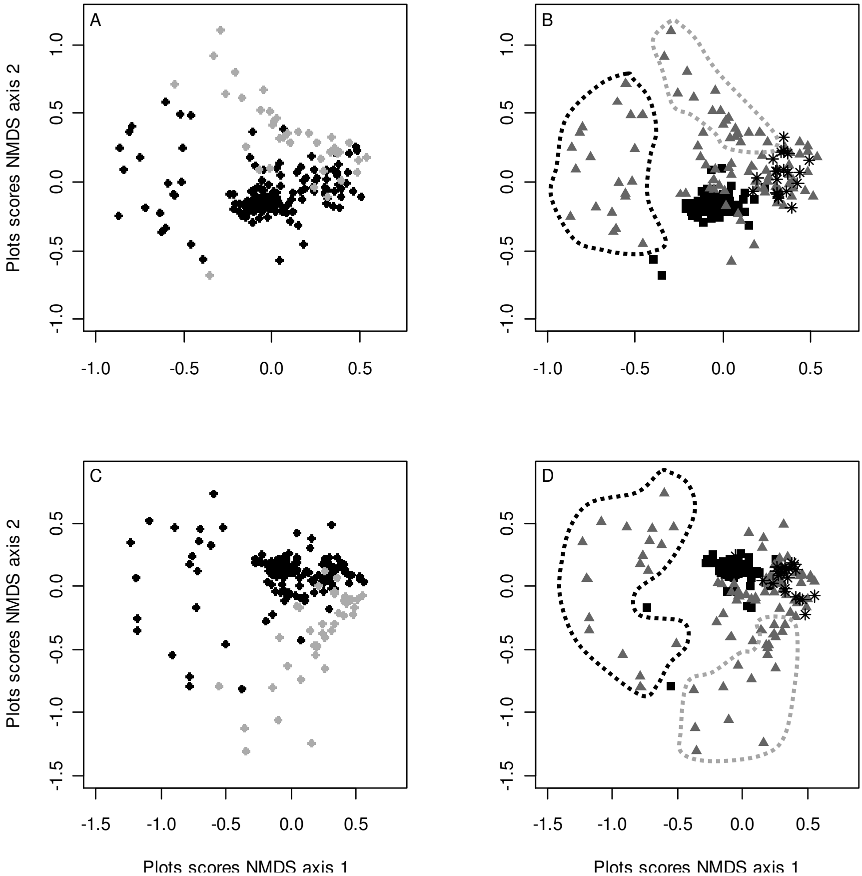

Figure 5.4: Ordination diagram of non-metric multidimensional scaling (NMDS) of the 192 one-hectare tree inventory plots; the first two axes of the NMDS explained 81% of floristic variation at family level (A and B) and 87% of the floristic variation at genus level (C and D); in A and C, symbols indicate forest type: • plots in white-sand forests and • plots in terra-firme forests; in C and D symbols indicate the regions in which the plots were established: ■ central Amazonia; ▲ the Guianas, ✳ the upper Rio Negro. In graphs B and D, the dotted lines are a visual aid to emphasize the separation of white-sand plots (gray line) and terra-firme plots (black line) in the Guianas.

Geographic and floristic distances between pairs of white-sand plots were significantly correlated in the Guianas and in the upper Rio Negro. For pairs of terra-firme plots, geographic and floristic distances were significantly correlated in central Amazonia and in the Guianas (Fig. 5.5). For all the three regions, the similarity simulated was significantly lower than the observed one ($p < 0.005$ – Wilcoxon test). Average similarity simulated and average observed tree alpha-diversity were negatively correlated (Pearson coefficient = -0.72).

Table 5.4: Floristic similarity observed between pairs of local communities of white-sand forests and terra-firme forests; floristic similarity simulated between pairs of 1000 random local communities obtained for each forest type and region; averaged Fisher's alpha observed in each forest type and region

Forest type	Region	Similarity observed Mean (SD)	Similarity simulated Mean (SD)	Average Fisher's alpha
White-sand	Central Amazonia	0.11 (0.06)	0.67 (0.02)	56.78
	Guianas	0.28 (0.2)	0.79 (0.02)	10.89
	Upper Rio Negro	0.19 (0.17)	0.57 (0.02)	30.27
Terra-firme	Central Amazonia	0.29 (0.09)	0.44 (0.02)	127.90
	Guianas	0.11 (0.11)	0.57 (0.02)	35.45
	Upper Rio Negro	0.11 (0.1)	0.72 (0.02)	54.39

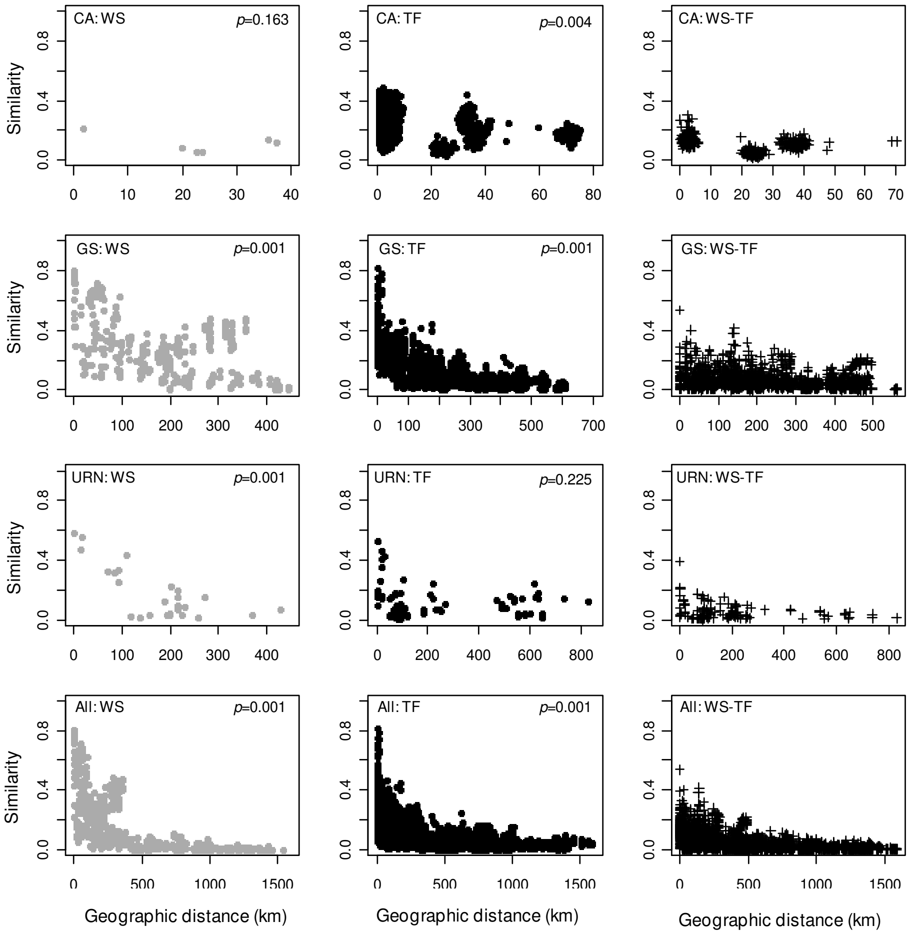

Figure 5.5: Sørensen Bray-Curtis similarity index as a function of geographic distance between pairs of tree inventory plots established in white-sand forests (•), terra-firme forests (•), and between pairs of plots established in either of these two forest types (WS-TF) (+). CA: central Amazonia, GS: Guianas, URN: Upper Rio Negro, All: CA, GS, and URN together. Statistical significance (*p* values) result from Mantel tests using the Sørensen Bray-Curtis dissimilarity index. The scale of x-axis varies among graphs to improve visibility. The similarity between pairs of plots for the three regions has to be interpreted with caution because species names have not been synchronized between plots established in different regions.

Among 63 families with total abundance ≥ 30 individuals, 11 were significantly associated with white-sand forests and 26 with terra-firme forests. Among the 238 genera (≥ 30 individuals), 28 were associated with white-sand forests whereas 84 were associated with terra-firme forests. Among the highly abundant families, Fabaceae was associated with white-sand forests. Although Fabaceae had the majority of its trees encountered in white-sand forests, this family showed a higher number of species associated with terra-firme than with white-sand forests. Out of the 93 species of Fabaceae included in the ISA, 12 were significantly associated with white-sand forests, whereas 21 were associated with terra-firme forests. By contrast, Lecythidaceae, highly abundant and significantly associated with terra-firme forests, had the majority of its species significantly associated with the same forest type, 21 out of 35 (Table 5.5). From this family, *Lecythis corrugata* was the only species associated with white-sand forests. Burseraceae, associated with terra-firme forests, had all genera and species associated with this forest type.

Among the three most abundant genera, *Eperua* (Fabaceae) and *Licania* (Chrysobalanaceae) were associated with white-sand forests while *Eschweilera* (Lecythidaceae) was associated with terra-firme forests. All species of the genus *Eperua* significantly associated with a forest type (*E. falcata, E. grandiflora, E. leucantha,* and *E. purpurea*), were associated with white-sand forests. *Licania*, however, had 5 species associated with white-sand (*L. bruxifolia, L. cuprea, L. divaricata, L. hypoleuca, L. leptostacya*) and 3 with terra-firme forests (*L. bracteata, L. heteromorpha, L. octandra*). *Eschweilera* had 12 species associated with terra-firme forests (Table 5.6).

Table 5.5: Overview of families that are significantly associated with white-sand or terra-firme forests; (WS) and (TF) indicates association with white-sand or terra-firme forests, respectively; N. indicates the number of genera or species; (WS/TF/NS) represents the total number of genera per family or species per family, which were significantly associated with white-sand or terra-firme forests, or which were not significantly associated with either forest type (NS); * indicates that no species in the family had an abundance ≥ 30 individuals

Family	N. of Genera (WS/TF/NS)	N. of Species (WS/TF/NS)
Annonaceae (TF)	1 / 6 / 5	2 / 6 / 10
Apocynaceae (WS)	1 / 1 / 6	1 / 1 / 9
Aquifoliaceae (WS)	1 / 0 / 0	*
Araliaceae (WS)	2 / 0 / 0	0 / 0 / 1
Arecaceae (TF)	0 / 2 / 5	0 / 2 / 6
Boraginaceae (TF)	0 / 1 / 0	0 / 1 / 3
Burseraceae (TF)	0 / 2 / 3	0 / 9 / 14
Calophyllaceae (WS)	1 / 0 / 2	2 / 0 / 2
Cardiopteridaceae (TF)	0 / 1 / 0	0 / 1 / 0
Caryocaraceae (TF)	0 / 1 / 0	0 / 0 / 1
Celastraceae (TF)	0 / 1 / 0	*
Chrysobalanaceae (WS)	1 / 1 / 3	5 / 5 / 25
Clusiaceae (WS)	3 / 1 / 0	4 / 1 / 3
Dichapetalaceae (TF)	0 / 1 / 0	0 / 1 / 1
Elaeocarpaceae (TF)	0 / 1 / 0	0 / 0 / 5
Fabaceae (WS)	5 / 12 / 25	12 / 21 / 60
Goupiaceae (TF)	0 / 1 / 0	0 / 1 / 0
Hypericaceae (TF)	0 / 1 / 0	*
Icacinaceae (TF)	0 / 1 / 0	0 / 1 / 0
Lacistemataceae (TF)	0 / 1 / 0	*
Lecythidaceae (TF)	0 / 5 / 1	1 / 21 / 13
Malvaceae (WS)	2 / 4 / 4	3 / 5 / 9
Melastomataceae (TF)	0 / 1 / 1	0 / 1 / 6
Meliaceae (TF)	0 / 2 / 1	0 / 1 / 11
Moraceae (TF)	0 / 8 / 2	0 / 10 / 8
Myristicaceae (TF)	0 / 3 / 0	0 / 7 / 10
Myrsinaceae (WS)	1 / 0 / 0	1 / 0 / 0
Olacaceae (TF)	0 / 2 / 3	0 / 1 / 3
Putranjivaceae (TF)	0 / 1 / 0	0 / 1 / 0
Quiinaceae (TF)	0 / 1 / 1	0 / 1 / 1
Rhabdodendraceae (WS)	1 / 0 / 0	1 / 0 / 0
Salicaceae (TF)	0 / 2 / 0	0 / 2 / 0
Sapindaceae (WS)	2 / 0 / 1	2 / 0 / 2
Siparunaceae (TF)	0 / 1 / 0	0 / 1 / 0
Urticaceae (TF)	0 / 1 / 1	0 / 2 / 3
Violaceae (TF)	0 / 2 / 0	0 / 3 / 2
Vochysiaceae (TF)	0 / 1 / 3	0 / 1 / 6

Table 5.6: Selected families and their genera, which are significantly associated with white-sand or terra-firme forests; (WS) and (TF) indicates association with white-sand or terra-firme forests, respectively; N. indicates the number of species; (WS/TF/NS) represents the total number of species per genus, which were significantly associated with white-sand or terra-firme forests, or which were not significantly associated with either forest type (NS)

Family	**Genus**	**N. of Species (WS/TF/NS)**
Burseraceae (TF)	*Protium* (TF)	0 / 8 / 11
“	*Tetragastris* (TF)	0 / 1 / 1
Chrysobalanaceae (WS)	*Licania* (WS)	5 / 3 / 20
Clusiaceae (WS)	*Clusia* (WS)	2 / 0 / 1
“	*Garcinia* (WS)	1 / 0 / 0
“	*Symphonia* (TF)	0 / 1 / 0
“	*Tovomita* (WS)	1 / 0 / 2
Fabaceae (WS)	*Albizia* (TF)	0 / 0 / 1
“	*Aldina* (WS)	1 / 0 / 1
“	*Bocoa* (TF)	0 / 1 / 1
“	*Chamaecrista* (WS)	1 / 0 / 1
“	*Copaifera* (TF)	0 / 1 / 0
“	*Dialium* (TF)	0 / 1 / 0
“	*Dipteryx* (TF)	0 / 2 / 0
“	*Enterolobium* (TF)	0 / 1 / 0
“	*Eperua* (WS)	4 / 0 / 3
“	*Inga* (TF)	0 / 4 / 2
“	*Ormosia* (WS)	2 / 0 / 0
“	*Pseudopiptadenia* (TF)	0 / 2 / 0
“	*Stryphnodendron* (TF)	0 / 1 / 0
“	*Swartzia* (WS)	3 / 3 / 13
“	*Tachigali* (TF)	0 / 2 / 4
“	*Zygia* (TF)	0 / 1 / 2
Lecythidaceae (TF)	*Cariniana* (TF)	0 / 1 / 0
“	*Corythophora* (TF)	0 / 2 / 1
“	*Couratari* (TF)	0 / 1 / 0
“	*Eschweilera* (TF)	0 / 12 / 7
“	*Gustavia* (TF)	0 / 1 / 4
Malvaceae (WS)	*Apeiba* (TF)	0 / 1 / 0
“	*Catostemma* (WS)	2 / 0 / 2
“	*Pachira* (WS)	1 / 0 / 2
“	*Quararibea* (TF)	0 / 0 / 2
“	*Sterculia* (TF)	0 / 1 / 0
“	*Theobroma* (TF)	0 / 2 / 0
Moraceae (TF)	*Brosimum* (TF)	0 / 2 / 3
“	*Helianthostylis* (TF)	0 / 1 / 0
“	*Helicostylis* (TF)	0 / 1 / 1
“	*Maquira* (TF)	0 / 1 / 2

Table 5.6: cont.

Family	Genus	N. of Species (WS/TF/NS)
Moraceae (TF)	*Naucleopsis* (TF)	0 / 1 / 0
"	*Pseudolmedia* (TF)	0 / 1 / 1
"	*Sorocea* (TF)	0 / 1 / 0
"	*Trymatococcus* (TF)	0 / 1 / 1
Myristicaceae (TF)	*Iryanthera* (TF)	0 / 3 / 5
"	*Osteophloeum* (TF)	0 / 1 / 0
"	*Virola* (TF)	0 / 3 / 5
Sapotaceae (NS)	*Pouteria* (TF)	1 / 7 / 12
"	*Pradosia* (WS)	1 / 0 / 1
"	*Sarcaulus* (TF)	0 / 1 / 0

DISCUSSION

Overview

Tree communities of white-sand and terra-firme forests are more diverse in central Amazonia than in the Guianas and in the upper Rio Negro. Within these three regions, floristic similarity of both white-sand and terra-firme forests is higher than between regions, indicating that at a large spatial scale, geographic distance structures floristic similarity between tree communities. At a small spatial scale, however, the range within which geographic distance structures floristic similarity appears to differ between white-sand and terra-firme forests. Furthermore, floristic similarity seems to be influenced by regional diversity: we found that highly diverse regional communities show a lower simulated similarity. Moreover, we found that habitat association is, in general, maintained across taxonomic levels, i.e., family and genera that are significantly associated with a forest type have the majority of their species associated with that particular forest.

For analyzing tree alpha- and beta-diversity across different forest types and regions in Amazonia we need to acknowledge two main constraints: the lack of complete and correct species identification for all tree inventory plots as well as the uneven spatial distribution of the plots. We found that out of 3,612 species or morpho-species, 1,681 were identified at species level, but 1,931 (53%) still remain to be properly identified. Additionally, even for specimens that have been identified at species level in each individual region, we are unable to assure whether they indeed belong to the same species, as Herbaria collections have not been synchronized yet. Furthermore, the number of tree inventory plots established is unevenly distributed between regions as well as forest types. Overall, the number of plots established in terra-firme forests is four times higher than the number of plots established in white-sand forests. Moreover, plots located in central Amazonia and in the Guianas, accounted for 90% of the total number of tree inventory plots present in our dataset, making tree communities of the upper Rio Negro under-represented. Despite these inherent constraints, the size of the dataset analyzed here and the regularity of the patterns observed across the three regions encourage us to discuss general mechanisms driving variation of tree alpha- and beta-diversity of white-sand and terra-firme forests at both regional and local scales.

Tree alpha-diversity

We found that the total number of species present in the regional community of white-sand forests is nearly 2.5 smaller than in the regional community of terra-firme forests. This difference is certainly influenced by the unequal number of plots established in these two forest types; therefore it should not be interpreted in absolute terms. The lower tree alpha-diversity of tree communities of white-sand forests in comparison to tree communities of terra-firme forests is consistently observed across the three regions analyzed here and has been widely reported across Amazonia (Anderson, 1981, Dezzeo et al., 2000, ter Steege et al., 2000, Boubli, 2002, Banki, 2010). We suggest that the main mechanisms causing differences in tree alpha-diversity between these two forest types, and subsequent in the regional community, is related to differences in their habitat sizes (Chapter 3; ter Steege et al., 2000). We have discussed in detail how differences in habitat size between white-sand and terra-firme forests determine the differences in tree alpha-diversity of these forests in Chapter 3. Here, we focus on the mechanisms driving differences in alpha-diversity between central Amazonia, the Guianas, and the upper Rio Negro.

Central Amazonia hosts one of the richest tree communities of Amazonia; a single hectare in this region can hold up to 285 tree species (DBH ≥ 10 cm) (Oliveira and Mori, 1999, Oliveira and Nelson, 2001). This extraordinary diversity has been explained by the occurrence of phytogeographic confluence (Oliveira and Daly, 1999) as well as by long-term climatic stability (Stropp et al., 2009). The contribution of phytogeographic confluence to the high tree alpha-diversity in central Amazonia is supported by a high floristic similarity observed between tree inventory plots established in western, central, and eastern Amazonia (Oliveira and Nelson, 2001). Our findings, however, show that tree communities in central Amazonia are different from those encountered in the Guianas and in the upper Rio Negro (see Fig. 5.4). Furthermore, ter Steege et al. (2006) have shown that floristic composition varies in a north east – south west gradient across Amazonia. We, therefore, do not attribute the higher tree alpha-diversity observed in central Amazonia to the overlap in species composition between this region and the Guianas and the upper Rio Negro. Regarding long-term climatic stability, central Amazonia has experienced a stable wet climate at least over the last 20,000 years, just as the upper Rio Negro (see Mayle et al., 2004). Therefore, past climatic differences do not help to explain differences in tree alpha-diversity between these three regions. Thus, both factors phytogeographic confluence and long-term climatic stability, are not sufficient to explain why tree communities of both white-sand and terra-firme forests are more diverse in central Amazonia than in the Guianas and in the Upper Rio Negro.

Tree communities in central Amazonia area functionally similar to those encountered in the Guianas and in the upper Rio Negro, being characterized by a high seed mass and high wood density (ter Steege et al. 2006). Nevertheless, the tree communities in central Amazonia are as diverse as those encountered in western Amazonia (Stropp et al., 2009). We found that the three most abundant families in our dataset have their highest numbers of species in central Amazonia. The number of species belonging to Fabaceae was 160 in central Amazonia, and decreased to 118 and 123 in the Guianas and in the upper Rio Negro, respectively. Chrysobalanaceae had 58 species in central Amazonia, but only 36 and 31 in the Guianas and in the upper Rio Negro, respectively. For Lecythidaceae the number of species in the three regions was 50 (CA), 27 (GS), and 36 (URN). This high number of species could be the result of high speciation rates in central Amazonia or high extinction rates in the northern part of the Guiana shield. Testing these two hypotheses could clarify which are the main drivers of the outstanding tree diversity found in central Amazonia. So far, this question remains open.

Tree communities of white-sand forests in the upper Rio Negro are more diverse than those in the Guianas. This can be explained by the large area that white-sand forests cover in the upper Rio Negro (see Fig. 5.1), which we expect to lead to a richer regional community. Interestingly, tree communities of white-sand forests in central Amazonia are more diverse than in the Guianas and in the upper Rio Negro. At a first sight, this appears odd, as the size of white-sand forests is considerably smaller in central Amazonia than in the Guianas and in the upper Rio Negro. Nevertheless, white-sand forests are not a closed system. In central Amazonia, local communities of white-sand and terra-firme forests share on average 21 tree species; this number is lower for the Guianas and the upper Rio Negro, averaging 8 and 10, respectively. In fact, we observe that in central Amazonia some highly abundant species in terra-firme forests, such as *Chrysophyllum sanguinolentum* (Sapotaceae), *Oenocarpus bacaba* (Arecaceae), and *Protium paniculatum* (Burseraceae), also occur, but with low abundance, in white-sand forests. We suggest that the higher diversity of tree communities of white-sand forests in central Amazonia as compared to the Guianas and the upper Rio Negro is influenced by the rich surrounding regional community of terra-firme forests. The same pattern has been observed for tree communities of white-sand forests surrounded by rich terra-firme forests in Peru (Fine et al., 2010).

Tree communities in central Amazonia not only show the highest diversity but also the highest variation in diversity (see Table 5.3). Interestingly, local communities of terra-firme forests can be remarkably poor, even when being surrounded by rich regional communities (Fig. 5.3). This variation of tree alpha-diversity at a local scale is caused by the high local abundance that a few species reach in some plots (Stropp et al., 2009). In 7 of the 14 plots in central Amazonia with Fisher's alpha values below 100, the *Oenocarpus* (Arecaceae) was the most abundant genus. In 5 of these plots, *Eschweilera coriacea* was most the abundant species. Finally, in the remaining 2 of these 14 plots, the most abundant species were *Micrandra spruceana* and *Pouteria* indet. The high local abundance found for the palm *Oenocarpus* can be explained by micro-habitat specialization which palms typically show (Svenning et al. 1999) or by past disturbance events (Pitman et al., 2005). For *Eschweilera coriacea*, the high local abundance maybe related to its high regional abundance, as this species is the most abundant in the regional community. The alternate high abundance of *M. spruceana* and *Pouteria* ident. maybe related to dispersal. Thus, micro-habitat specialization (Svenning, 1999), local disturbances (Pitman et al., 2005, Stropp et al., 2009) as well as dispersal (Vormisto et al., 2004) may all play an important role shaping variation in the local abundance of species. Variation of alpha-diversity in local communities is, therefore, related to local ecosystem dynamics (Ricklefs and Schluter, 1993). As local dynamics are largely driven by stochastic events, we may be unable to identify a single general mechanism explaining why some local communities enclosed in extremely diverse regional communities harbor low numbers of species.

Tree beta-diversity

The high tree beta-diversity between white-sand and terra-firme forests is related to species adaptations to the distinct edaphic features presented by these two forest types (Fine et al., 2004). We have further addressed the mechanisms driving such adaptations in Chapter 3 and Chapter 4. Our focus here is to discuss how tree species composition and beta-diversity of white-sand and terra-firme forests varies between central Amazonia, the Guianas, and the upper Rio Negro.

Tree species composition appears to be more variable in the Guianas than in central Amazonia and in the upper Rio Negro (see Fig. 5.4). This finding can be related to the spatial distribution of the plots. In the Guianas, the 91 tree inventory plots are located up to 600 km from one another, whereas in central Amazonia the distance between the 79 tree inventory plots is just 74 km. Despite differences in variability of floristic composition between the three regions, we do find that within each region floristic similarity, of both white-sand and terra-firme forests, is higher than between regions. Therefore, at a large spatial scale, geographic distance does structure floristic similarity between tree communities of white-sand and terra-firme forests at the family and genus levels.

At a smaller spatial scale, within each region, the range within which geographic distance structures floristic similarity between tree species communities appears to differ between white-sand and terra-firme forests. We found that tree communities of terra-firme forests seem to have a steeper decay of similarity than those of white-sand forests (Fig. 5.5). The rapid decay of floristic similarity at short distances followed by a gradual decay at larger distances can be explained by environmental conditions (Phillips et al., 2003) and by dispersal limitation (Condit et al., 2002). Plots located close to each other are more likely to have similar environmental conditions, thereby favoring establishment of species which are associated with these local environmental conditions. Furthermore, plots located nearby are likely to receive a large number of seeds from neighboring trees, thus increasing the chances of establishment of these shared species. Additionally to environmental conditions and dispersal limitation, regional diversity may influence the rate at which floristic similarity decreases as a function of geographic distance. We suggest that the high regional diversity of terra-firme forests may partially explain why its tree communities show a steeper decay of similarity than that of the white-sand forests. In diverse forests, a highly abundant species constitutes only a small share of the total number of individuals in the regional community. It is therefore unlike that this relatively abundant species reaches local communities, which are far apart from each other. As a consequence, floristic similarity between local communities enclosed in a highly diverse regional community may be lower than those enclosed in a less diverse regional community (see Chapter 3). We, hence, suggest that differences in regional diversity partially affect the structuring of floristic similarity between tree communities of white-sand and terra-firme forests.

Our results furthermore indicate that floristic similarity between local communities is constrained by regional diversity. In fact, we found a negative correlation between simulated similarity and regional diversity (Table 5.4). We propose that species with high regional abundance have better chances to reach and eventually to establish in the local communities than species with low regional abundance do. In low-diverse communities, few species make a large contribution to the total number of individuals of the regional community. As a consequence, when a vacant space becomes available in the local community, these few highly abundant species are most likely to establish in any local community. In this way, most local communities may end up being floristically similar to each other (see Chapter 3).

Habitat association

Our aim here was to provide an understanding of the ecology of plants speciation based on a qualitative analysis of our dataset. We found that all families which were associated with terra-firme and seven which were associated with white-sand forests showed a higher number of genera and species associated with their typical forest type. This suggests that for these families habitat association may be maintained across different taxonomic levels, indicating that they retain preference for their typical habitat over speciation events. Fabaceae and Malvaceae appear to present exceptions. These families proved associated with white-sand forests, but had higher numbers of genera and species associated with terra-firme forests. The association of Fabaceae with white-sand forests is caused by the high abundance and strong association of the genus *Eperua* with this forest. In fact, we ran the ISA excluding *Eperua* and found that Fabaceae was not significantly associated with either forests type. A non-significant habitat association of a family arises when 1) its subordinated taxa do not show habitat association, or 2) its subordinated taxa are restricted to white-sand or terra-firme forests, i.e., different genera and species are associated with different forest types. Then, as a group the family would not be associated with one specific forest type. The latter explanation best fits our observations (Table 5.5 and 5.6). We are unable to infer whether habitat associations have emerged independently across phylogeneticaly related taxa, as some of these non-associated families, such as Fabaceae without *Eperua*, contain monophyletic as well as paraphyletic groups. For the families which maintain their habitat association across subordinate taxonomic levels we speculate that adaptations to different soil conditions, such as presented today by white-sand and terra-firme forests, might have been of minor importance to the diversification of the ancestors of the current species pool (see Prinzing et al., 2001).

Conclusions

By integrating data of an extensive number of tree inventory plots established in white-sand and terra-firme forests across three Amazonian regions, we revealed how tree alpha- and beta-diversity of white-sand and terra-firme forests varies across broad spatial scales. We found a marked difference in tree alpha-diversity between communities in central Amazonia and those in the Guianas and in the upper Rio Negro. This finding suggests spatial variation in evolutionary processes. Moreover, our results indicate that the beta-diversity of local communities of each forest type is constrained by regional diversity. Furthermore, we have shown that most families and genera which are significantly associated with either forest type have the majority of their species associated with that particular forest type. This suggests that these genera and species may inherit habitat requirements from higher taxonomic levels, indicating that a large number of tree species have retained requirements for their typical habitat during speciation events.

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6

DISCUSSION AND PERSPECTIVES

This thesis addresses a long-standing problem in ecology: the contribution of processes operating at different spatial and temporal scales to the current pattern of species diversity. Understanding patterns of species diversity may seem like completing a hierarchical puzzle (Rosenzweig, 1995) that requires sorting out large and small pieces, which may belong together. In this thesis, I aimed at completing part of the puzzle for the tree species diversity in Amazonia. As large pieces, I considered large-scale, long-term processes, which influence regional tree communities. As small pieces, I considered small-scale, short-term processes, which influence local tree communities. This chapter first presents the key findings and discusses the strengths and limitations of the research presented in this thesis. Afterwards, the chapter concludes by deriving implications for biodiversity conservation and by proposing a research agenda to expand our understanding of tree species diversity in Amazonian forests.

KEY FINDINGS

- Tree alpha-diversity at regional scale can be explained by palaeo-climatic stability and long-term, large-scale ecosystem dynamics. Variation in tree alpha-diversity at local scale is enormous and is poorly explained by local ecosystem dynamics, here assessed as percentage of pioneer tree species present in the local community (Chapter 2).

- Tree communities of white-sand forests are less diverse than those in terra-firme forests (Chapter 3). Local tree diversity of white-sand forests appears to be influenced by regional diversity of both white-sand and terra-firme forests. We found that local tree communities, present in small patches of white-sand forests in central Amazonia, are more diverse than those occurring in the large white-sand areas of the upper Rio Negro. We explain the influence of the regional community of terra-firme forests on the local communities of white-sand forests by random invasion of tree species from the diverse regional community into the less-diverse local communities of white sand forests (Chapter 5).

- We found no indication that the trade-off between tree seedling growth and herbivore defense drives habitat association in white-sand and terra-firme forests of the upper Rio Negro. This probably is due to insufficient differences in nutrient availability between the soils of these two habitats. In the upper Rio Negro, soil may have a direct effect restricting seedling establishment in the forest type with which seedlings are generally associated with (Chapter 4).

- By assessing habitat association among 63 tree families and 238 genera occurring in white-sand and terra-firme forests, we found that most families and genera which are significantly associated with either forest type have the majority of their species associated with that particular forest type. This suggests that these genera and species may inherit habitat requirements from higher taxonomic levels, indicating that a large number of tree species have retained requirements for their typical habitat during speciation events (Chapter 5).

Regional tree species diversity

Regional tree alpha-diversity of Amazonian forests is spatially structured, showing two principal gradients related to latitude and longitude. Along the latitudinal gradient, regional tree alpha-diversity peaks at 4° – 3° degrees south and declines towards of 15° south and 8° north (Fig 2.3). Along the longitudinal gradient, regional tree alpha-diversity peaks close to the western limits of Amazonia and decreases towards the eastern limits of Amazonia. To interpret these gradients, we used palynological records, and palaeo- scenarios of climate as well as landscape evolution of Amazonia. We observed that areas with high regional diversity coincide with areas of high palaeo-climatic stability and long-term and high ecosystem dynamics. As these two factors strongly affect speciation and extinction and cause shifts in species distribution (Araujo and Pearson, 2005), we propose that they are important drivers of the current patterns of regional tree alpha-diversity in Amazonian forests (Chapter 2). The long-term rainfall stability in central and western Amazonia favored the persistence of tropical forests. In contrast, a more instable palaeo-climate in south and north-eastern Amazonia forced shifts to open up the dense forests. In a period of climate change, species with poor dispersal ability and/or small ranges have lower chances to migrate to regions with suitable climate and are, therefore, vulnerable to extinction. Thus, a dynamic palaeo-climate may have caused extinctions in south and north-eastern Amazonia.

We, furthermore, propose that long-term ecosystem dynamics in western Amazonia may have promoted fast speciation rates. In the fertile soils of western Amazonia, species have relatively short generations leading to faster evolution, thus higher speciation rates. It has been recently proposed that the origin of the high diversity in western Amazonia is caused by high sympatric speciation favored by marked differences in soil characteristics promoted by the Andean uplift (Hoorn et al., 2010).

Additionally, we investigated how tree alpha-diversity of white-sand and terra-firme forests varies at a large spatial scale. To this end, we compared tree alpha-diversity of three separate geographic regions: central Amazonia (CA), the Guianas (GS), and the upper Rio Negro (URN). We found that tree communities of both white-sand and terra-firme forests show higher diversities in central Amazonia than in the Guianas and in the upper Rio Negro. We, furthermore, confirm earlier findings reporting that tree communities of white-sand forests show a much lower tree alpha-diversity than those of terra-firme forests. Mechanisms driving differences in tree alpha-diversity of these two forest types are related to habitat size and are ultimately influenced by large-scale, long-term evolutionary processes. The marked difference in habitat size between white-sand and terra-firme forests may have promoted differences in speciation and extinction rates in these two forest types. As terra-firme forests represent 80% of Amazonian forests, and white-sand forests represent only 5-10%, the number of species present in the large terra-firme forests is expected to be much larger than the number of species in the small and fragmented white-sand forests (ter Steege et al., 2000, Banki, 2010).

Tree communities of white-sand and terra-firme forests are distinct in their species composition across Amazonia (Chapter 3 and 5) (Fanshawe, 1954, Anderson, 1981, Dezzeo et al., 2000, Banki, 2010, Fine et al., 2010). Habitat association rises from long-term adaptation of taxa to their typical habitat. The contribution of phylogenetic niche conservatism, i.e., the tendency of lineages to maintain habitat requirements during speciation events (Wiens, 2004), for floristic dissimilarity between white-sand and terra-firme forests is still poorly understood (Fine et al., 2005). In Chapter 5, we assessed trends in phylogenetic conservatism by evaluating how often habitat association is maintained across subordinated taxonomic levels in the regional community of white-sand and terra-firme forests. We found that that all 26 tree families that were associated with terra-firme and 7 out of 11 tree families that were associated with white-sand forests showed a higher number of genera and species associated with their typical forest type. This may suggest that for these genera and species habitat requirements may be inherited from higher taxonomic levels, indicating that tree species have retained requirements for their typical habitat during speciation events.

Local tree species diversity

The variation in tree alpha-diversity at the local scale is enormous: tree inventory plots established in one locality ('Reserva Florestal Adolpho Ducke' - central Amazonia) span nearly the full range of tree alpha-diversity found in Amazonia. A small percentage of this variation can be explained by local disturbances, here analyzed as percentage of individuals with low wood density (< 0.6 g cm^{-3}) (Chapter 2). Recently, similar results were reported for African tropical rainforests (Bongers et al., 2009). We suggest that the power of this explanation is low because local tree diversity is also subject to local ecosystem dynamics, such as disturbances, species association with micro-habitat conditions, ecological drift due to dispersal limitation, and occurrence of pathogens, such factors are largely variable from one location to another in Amazonian forests.

In Chapter 4, we evaluated the contribution of local interactions between soil type and herbivore pressure to the floristic dissimilarity observed between tree communities of white-sand and terra-firme forests in one particular region, the upper Rio Negro. To this end, we tested, in a transplanting experiment, whether a trade-off between plant growth and herbivore defense contributes to differences in tree species composition of white-sand and terra-firme forests (Fine et al., 2004). We found that species associated with either white-sand or terra-firme forests showed lower mortalities when growing on their typical forest type. Nevertheless, we found no difference in growth and herbivore damage. This finding may indicate that the growth-defense trade-off maybe of minor importance for tree habitat association in the white-sand and terra-firme forests in the upper Rio Negro (Chapter 4). We found that leaf toughness of seedlings associated with terra-firme forests in the upper Rio Negro is much higher than leaf toughness of white-sand species in western Amazonia. We suggest that soil characteristics, including, nutrients, acidity, Al toxicity, as well as soil biota, may directly prevent tree species to grow in their non-typical forest type. In the upper Rio Negro, Fabaceae is the most dominant tree family in white-sand as well as in terra-firme forests (Chapter 3, Dezzeo et al., 2000, Boubli, 2002). Their dominance in this region is not attributed to their nodulating ability, but to their high seed mass (ter Steege et al., 2006). Recently, it has been shown that seedlings of highly abundant adult trees are less vulnerable to soil pathogens than seedlings of lowly abundant tree species (Mangan et al., 2010, Comita et al., 2010). We suggest that in addition to their high seed mass, Fabaceae may show higher resistance to soil pathogens than less abundant tree families in the upper Rio Negro. Below ground species interactions are still poorly understood in Amazonian forests, and may be important for regulating relative species abundance in local and regional communities, including those of white-sand and terra-firme forests.

Integrating the puzzle: tree diversity and composition at regional and local scales

The conceptual framework presented in the Introduction links regional and local communities by environmental filtering and dispersal limitation (see Fig. 1.3). We observe that local tree communities of white-sand forests surrounded by terra-firme forest show a distinct floristic composition. For most tree species, seed dispersal between these two forests types occurs regularly; therefore, dispersal may be of minor importance as a limiting factor for species occurrence in either of the two forest types. Arguably, a main limitation to species establishment occurs at the seedling stage. As observed in Chapter 4, tree seedling mortality is higher when seedlings grow in their non-typical habitat, indicating a habitat specificity that is likely to be related to edaphic characteristics, including soil biota (see Mangan et al., 2010), of these two forest types. In the upper Rio Negro, soil might have a direct effect, limiting seedling establishment in their non-typical forest type. In western Amazonia, however, an interaction between soil nutrient availability and plant herbivore defense, i.e., a trade-off between plant growth and herbivore defense, limits the establishment of seedlings in their non-typical forest type (Fine et al., 2004). We suggest that the low soil nutrient availability of both forest types in the upper Rio Negro does not trigger the growth-defense trade-off because plant growth is generally severely limited there. White-sand and terra-firme forests in the upper Rio Negro both grow on soils derived from Proterozoic rocks (~2,500 Ma), whereas the terra-firme forests in western Amazonia grow on Cenozoic sediments (~66 Ma and much more recent) (Sombroek, 2000) and may have continuous volcanic input (Jan Sevink, pers. comm.). Interestingly, the white-sands in western Amazonia might have a similar origin as those in the upper Rio Negro (Rässänen, 1993). We therefore expect that differences between soil nutrient availability of white-sand and terra-firme forests are more subtle in the upper Rio Negro than in western Amazonia. This large-scale variation in soil nutrient availability, caused by geological and geomorphological history, may influence not only ecosystem functioning but also local species interactions (Chapter 4).

At broad spatial scale, the size of a habitat determines the number of species it can support: large habitats typically host more species (Rosenzweig and Ziv, 1999). We, thus, expected that local communities of white-sand forests in the Guianas and in the upper Rio Negro would harbor more diverse local communities than in central Amazonia. Our results, however, show the opposite pattern. We found that local communities occurring in white-sand forests in central Amazonia are more diverse than those occurring in the Guianas and in the upper Rio Negro. This pattern may be caused by random invasion of relatively highly abundant tree species from the diverse regional community of terra-firme forests into the less-diverse local communities of white sand forests. A similar pattern was recently reported for tree communities of white-sand forests surrounded by hyper diverse terra-firme forests in Peruvian Amazonia (Fine et al., 2010).

Dispersal limitation as well as environmental filtering determine *which* and *how many* species from the regional community will potentially occupy the local communities (ter Steege and Zagt, 2002). Dispersal limitation and environmental filtering therefore shape floristic similarity of tree communities. In cases where tree communities belong to similar forest types, geographic distance can be used as a proxy for dispersal limitation as well as environmental conditions (Condit et al., 2002, Phillips et al., 2003). This is because plots located close to each other are more likely to have similar environmental conditions, thereby favoring the establishment of species which are associated with these local environmental conditions. Furthermore, plots located near to each other are likely to receive a large number of seeds from neighboring trees, thus increasing the chances of establishment of these shared species. We suggest that, in addition to environmental conditions and dispersal limitation, regional diversity may influence the floristic similarity between local communities. In Chapter 5, we found a negative correlation between the average simulated floristic similarity for 1,000 neutral local communities and the actual, observed regional diversity (Table 5.4). We propose that in low-diverse regional communities, few species contribute importantly to the total number of individuals of the regional community. As a consequence, when a vacant space becomes available in the local community, these few highly abundant species are the most likely ones to establish in any local community. In this way, most local communities may end up being floristically similar to each other (see Chapter 3). Our results, thus, suggest that floristic similarity between local communities is influenced by regional diversity.

STRENGTHS AND LIMITATIONS OF THIS RESEARCH

Strengths

In this thesis we analyzed the most extensive dataset of tree inventory plots available to date, spread across entire Amazonia. Additionally, we compiled and analyzed the first dataset with tree species composition of tree inventory plots established in white-sand and terra-firme forests in central Amazonia, the Guianas, and in the upper Rio Negro. The environmental characteristics of these plots encompass nearly the full range of variation in current rainfall seasonality and soil fertility as well as palaeo-climatic stability and geological history. Analyzing this dataset revealed new insight in how tree diversity as well as composition varies at a regional and local scale. By combining current ecological data with palynological records, palaeo-climatic models, and scenarios of palaeo-landscape evolution of Amazonia, we have improved our understanding of drivers of tree diversity in Amazonian forests.

The simple model used to partition total tree alpha-diversity into its regional and local components provided a first quantitative estimation of the variation in tree alpha-diversity (Chapter 2). The parameters included in this model are simple and have empirical relevance. Such a model can be used as a starting point for identifying regional and local factors that are relevant for shaping current pattern of species diversity.

To compile our dataset of tree species composition of white-sand and terra-firme forests of central Amazonia, the Guianas, and the upper Rio Negro, we have standardized species names for synonymy in all tree inventory plots included in this dataset. We furthermore, have quantified the status of species identification of species collected in these plots. This contribution provides a quantitative estimation of the current status of species identification in these plots, and this has not been done before. We also extended our botanical knowledge of a biologically interesting and poorly studied area of Amazonia, the upper Rio Negro. The eight new tree inventory plots that we established in the upper Rio Negro represent 36% of the total number of plots established in this region. In these eight one-hectare plots we have collected potentially one new observation for Brazil (*Ephedranthus guianensis*) (Maas et al., 2010), a first observation for the upper Rio Negro (*Pseudoxandra duckei* – P. J. M. Maas, pers. comm.), and an undescribed species (*Batocarpus* sp. nov. – C. C. Berg, pers. comm.).

Limitations

Identifying evolutionary and ecological processes that regulate tree species diversity in tropical forests is challenging because data, empirical and modeled, are scarce for Amazonian forests. In Chapter 2, we propose that palaeo-climatic stability plays a major role shaping the current pattern of tree diversity. We used latitude as a proxy for palaeo-climatic stability. We support our choice with palynological records as well as palaeo-climatic scenarios (Hooghiemstra and van der Hammen, 1998, Mayle et al., 2004, Jaramillo et al., 2006). However, a more accurate approach would include a spatial model of palaeo-climate with a similar spatial resolution used to interpolate tree alpha-diversity. However, to our knowledge no such model is available for Amazonia.

Additionally, in Chapter 2, we hypothesized that the high diversity in western Amazonia may be explained by the relatively fast growing and short generation times experienced by tree species in this region. It has been suggested that life history traits of plants are correlated with the rate of molecular evolution (Smith and Donoghue, 2008). In fact, rates of molecular evolution are consistently lower in trees and shrubs, with relatively long generation times, than in herbaceous plants (Smith and Donoghue, 2008). Whether the variation in generation time within tropical trees is large enough to drive difference in the rate of molecular evolution is uncertain. In this sense, our hypothesis needs to be better supported by empirical data. Species level phylogenies of families or genera occurring throughout Amazonia need to be developed to test this hypothesis.

In Chapter 4, the analyses of our cross-transplanting seedling experiment led to non-significant differences in seedling growth performance and herbivore damage in habitat-specialist species in white-sand and terra-firme forests in the upper Rio Negro. This finding may be caused by the short duration of the experiment (one year). We make this assumption because we observed extremely low seedling growth. To properly evaluate the effect of herbivory in this particular area, field transplanting experiments should be carried out over longer time periods. An additional problem related to our experimental approach is that we are unable to identify exactly, which factor caused seedling mortality in the non-typical habitat. If we had also monitored seedlings growth and mortality growing under natural conditions, i.e., without transplanting, we would be able to better estimate to what extent the mortality is driven by soil properties and by the effects of transplantation. Studies about how interactions between tree species and soil biota differ in white-sand and terra-firme, are scarce (Perreijn, 2002), nevertheless such interactions may constitute an important driver for differences in tree species composition and abundances between these two forest types (Mangan et al., 2010). We think that our cross-transplanting experiment is a starting point to understand ecological dynamics in the upper Rio Negro. The area is biologically interesting and poorly known.

In Chapter 2 and 5, we analyzed an extensive dataset of tree inventory plots. Although this data set includes nearly all tree inventory plots that have been established in Amazonia, these plots represent only ca. 0.001% of the total area of Amazonian forests. To put it in perspective, ‘Reserva Florestal Adolpho Ducke’, located to the north of Manaus, covers an area of 100 km^2; therefore the total area covered by the tree inventory plots analyzed here would cover just 80% of the ‘Reserva Florestal Adolpho Ducke’. This highlights how small the sample of tree inventory plots still is. Additionally, by quantifying the status of species identification for a subset of 192 tree inventory plots we were able to estimate how limited our botanical knowledge is about tree communities in Amazonian forests. We found that out of 3,612 species or morpho-species, 1,681 were identified at species level, but 1,931 (53%) still remain to be properly identified. Thus, in analyses in which only trees identified at species level can be included, a large share of trees has to be disregarded. It is important to mention that species identification of plot studies are often made by comparing sterile plant collections with herbarium material. This procedure may lead to incorrect species identification (Hopkins, 2007, Tobler et al., 2007). As several plots included in our analyses do not belong to permanent research projects, we are unable to quantify this error. Information on species abundance and distribution, however, forms the basis for understanding patterns of biodiversity. To overcome this limitation we urgently need to expand data collection, integrate new and previously collected data as well as improve our taxonomic knowledge. Next, we propose actions aiming at overcoming some of the limitations presented here.

IMPLICATIONS FOR BIODIVERSITY CONSERVATION AND A FUTURE RESEARCH AGENDA

By studying processes operating at different spatial and temporal scales, we have contributed to a better understanding of the mechanisms that drive tree species diversity in Amazonian forests. Yet, exactly how these mechanisms interact to shape diversity remains partially unclear. Improving our understanding of tree diversity is urgently needed as Amazonian forests face ongoing global climate change (Phillips et al., 2009) as well as alarming deforestation rates (Soares-Filho et al., 2006). Here, we present some open research questions and propose a scientific approach which goes along with improvements of social welfare in Amazonia.

Obtaining new scientific understanding regarding Amazonian forests requires foremost the collection and analyses of more empirical data. The availability of baseline data on tree species abundance and composition is still a bottleneck for scientific progress. Our knowledge is still surprisingly limited. Collections from all Brazilian Amazonian herbaria total ca. 500,000 specimens, being equivalent to 1 specimen per km^2 (Hopkins, 2007). Additionally, species identification is uncertain at individual herbaria, and species names are not yet synchronized among different herbaria. As a consequence, up to 40% of the specimens of Amazonian plants in the world's herbaria may bear incorrect identifications (Hopkins and Hamada, unpublished data in Hopkins, 2007, Tobler et al., 2007). It is, therefore, of primary importance to expand plant collections as well as to improve the quality of species identification of Amazonian trees. By simply knowing how many and which species occur in different Amazonian regions we can better analyze relevant questions about the origin and maintenance of species diversity as well as propose effective biodiversity conservation plans.

Next to data collection, efforts should be made to quantify uncertainties related to species identification of previously collected data, especially those of tree inventories. Species identifications of tree inventory plots are often based on sterile material which often leads to erroneous identification. Quantifying this error is important for estimating the uncertainties associated with models of tree species diversity. We suggest that an estimation of errors in species identification could be done for permanent tree inventory plots which are monitored over long periods of time, such as plots monitored by the 'Biological Dynamics of Forest Fragments Project' (BDFFP) and the 'Amazon Forest Inventory Network' (RAINFOR). Botanical identifications for permanent tree inventory are constantly updated because new fertile material becomes available and botanists improve their knowledge about the local flora. During this process the total number of species and the species identity registered for a given plot change. Quantifications of these changes have not yet been done at, for instance, BDFFP (A. Andrade, pers. comm.).

Botanical collections are relatively abundant for central Amazonia (Ribeiro et al., 1999, Nelson et al., 1990), and indicate that this region harbors one of the world's richest tree communities (Oliveira and Daly, 1999). The origin of this diversity remains, however, largely unexplained. We suggest that molecular studies of speciation rates of highly abundant tree families, such as Chrysobalanaceae, Fabaceae, and Lecythidaceae, could clarify how and when these highly diverse tree communities evolved. To gain broad insights into factors driving speciation, molecular data should be interpreted in combination with palaeo-ecological scenarios. Elucidating how palaeo-climate and palaeo-landscape evolution influence speciation rates may help to predict how biodiversity adjusts to ongoing global climate change, which is expected to have a severe impact on the biodiversity of Amazonian forests.

The climate is expected to become drier and hotter in Amazonia in the twenty-first century (Cox et al., 2000, Cox et al., 2004). Predictions of how Amazonian forests will respond to these changes are a matter of debate (see Phillips et al., 2009, Jaramillo et al., 2010). It is agreed, however, that drier climate persisting over long periods of time, i.e., thousands of years (see Mayle et al., 2004), will reduce the size of the area that can support Amazonian forests. If a drier climate continues to be a permanent feature in Amazonia over even longer time periods, just the reduction in the size of the forest area can cause changes in long-term evolutionary processes. Tree species adaptations or shift in species distribution ranges happens at a time scale of 10^6 years. Reductions in the size of Amazonian forests, however, is happening in such rate that long-term species adaptations to new environmental conditions may be of minor importance for the future of Amazonian forests (ter Steege, 2010), especially for those forests occurring in seasonal climate. Over the last 30 years, deforestation in Brazilian Amazonia has cost 736,180 km^2 (18%) of its original forest cover (PRODES, 2010). This deforestation occurs mainly in forests in seasonal climate which have a distinctively different floristic composition from those occurring in the a-seasonal and wet parts of central and western Amazonia (Nelson et al., 2008, Emilio et al., 2010).

Effective biodiversity conservation and management programs are urgently needed. Progress in this direction should go together with increasing social welfare in Amazonia (see Putz and Zuidema, 2008). Education is thereby a key element. Forty percent of the inhabitants of Brazilian Amazonia (23 million) is younger than 17 years (UNICEF, 2009). Among these, only 36% of the 15-17 year old segment of the population attends to secondary education (ibid.).

Here, I recommend that efforts for improving education should be combined with our aspirations for scientific knowledge about tree diversity in Amazonian forests. Such a combination can be achieved by establishing student-scientist partnerships (see Harnik and Ross, 2003). My suggestion is to establish long-term research projects in collaboration with schools in the interior of Amazonia, where we lack botanical data and access to education is most difficult. Research could include long-term flora projects planned to collect fertile material of rare species (Hopkins, 2007) and long-term monitoring of tree inventory plots designed to provide quantitative information about tree community structures as well as ecosystem dynamics. These projects could start within a participatory framework in which scientists, teachers, and students get engaged in the early stages. During the projects, teachers and students have the opportunity to learn scientific techniques and gain insight into the functioning of the forest, matters that often relate to their everyday life. Additionally, researchers may get access to long-term ecological data which are scarce. Our own experience during field work in the upper Rio Negro has shown that establishing student-scientist partnerships is worthwhile and can benefit both tropical ecology and the inhabitants of Amazonia.

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Pressing plant material at EIBC, Içana River (top), and
at Pico da Neblina National Park (bottom), São Gabriel da Cachoeira, Brazil

APPENDIX 1: LIST OF ALL SPECIES AND MORPHO-SPECIES WITH TOTAL ABUNDANCE REGISTERED IN EIGHT ONE-HECTARE PLOTS IN THE UPPER RIO NEGRO

Table A.1: Tree species (≥ 10 cm DBH) registered in eight one-hectare plots established in the upper Rio Negro. Species that are significantly associated with one of the two forest types are given in bold ($p < 0.05$); (*) indicates in the respective column, the forest type the species are associated with (white-sand: WS, terra-firme: TF). The complete dataset of the eight one-hectare plots can be obtained on request to the author.

Family	Species	N. trees in WS plots	N. trees in TF plots
Anacardiaceae	*Tapirira guianensis* Aubl.	1	1
	Tapirira myriantha Triana & Planch.	8	0
	Thyrsodium guianense Sagot ex Marchand	0	1
Annonaceae	*Annona* sp.1	14	1
	Bocageopsis cf. *multiflora* (Mart.) R.E. Fr.	0	3
	***Bocageopsis pleiosperma* Maas**	0	**14***
	Diclinanona tessmannii Diels	0	1
	Duguetia sancticaroli Maas	0	4
	Duguetia cf. *surinamensis* R.E. Fr.	0	1
	Duguetia yeshidan Sandwith	0	1
	Ephedranthus guianensis R.E.Fr.	0	2
	***Fusaea longifolia* (Aubl.) Saff.**	0	**8***
	Guatteria cf. megalophylla Diels	1	0
	Guatteria guianensis (Aubl.) R.E. Fr.	0	1
	Guatteria insculpta R.E. Fr.	3	0
	Guatteria olivacea R.E. Fr.	0	3
	Guatteria sp.1	1	0
	Oxandra euneura Diels	1	1
	Pseudoxandra duckei Maas	0	1
	Pseudoxandra sp.	2	0
	Unonopsis duckei R.E. Fr.	0	2
	Xylopia calophylla R.E. Fr.	0	1
	Xylopia cf. *emarginata* Mart.	2	0
	Xylopia neglecta R.E. Fr.	1	0
	Xylopia spruceana Benth. ex Spruce	28	0
	Xylopia uniflora R.E. Fr.	31	3
	Xylopia sp.1	3	0
	Xylopia sp.2	2	0
Apocynaceae	*Aspidosperma* cf. *carapanauba* Pichon	1	0
	Aspidosperma nitidum Benth.	0	1
	Aspidosperma obscurinervium Azambuja	0	1
	Aspidosperma sp.1	2	0
	Aspidosperma sp.2	1	0
	Aspidosperma sp.3	1	0
	Couma guianensis Aubl.	6	5
	Couma cf. *macrocarpa* Barb. Rodr.	0	1
	Couma utilis Müll. Arg.	1	0
	Himatanthus articulatus (Vahl) Woodson	0	1
	Himatanthus obovatus (Müll. Arg.) Woodson	7	1
	Himatanthus sucuuba (Spruce ex Müll. Arg.) Woodson	2	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
	Himatanthus sp.1	2	0
	Rhigospira quadrangularis (Müll. Arg.) Miers	20	0
	Tabernaemontana macrocalyx Müll. Arg.	0	1
	Tabernaemontana macrophylla Lam.	1	0
	Tabernaemontana sp.1	0	1
	Indet.1	2	0
Araliaceae	*Dendropanax macropodus* (Harms) Harms	2	0
	Dendropanax sp.1	1	0
	*Dendropanax sp.*2	4	0
	Schefflera sp.1	0	1
	Schefflera sp.2	2	0
Arecaceae	*Euterpe precatoria* Mart.	0	4
	Mauritia aculeata Kunth	2	1
	Oenocarpus bacaba Mart.	0	5
	Oenocarpus bataua Mart.	2	1
Bignoniaceae	*Jacaranda* sp.1	0	3
	Tabebuia incana A.H. Gentry	0	1
Boraginaceae	*Cordia exaltata* Lam.	0	3
	Cordia cf. *fallax* I.M. Johnst.	0	1
	Cordia naidophila I.M. Johnst.	0	1
	Cordia sagotii I.M. Johnst.	0	1
Burseraceae	*Crepidospermum rhoifolium* (Benth.) Triana & Planch	4	2
	Dacryodes chimatensis Steyerm. & Maguire	0	1
	Dacryodes microcarpa Cuatrec.	0	6
	Indet.1	2	0
	Indet.2	1	0
	Protium altsonii Sandwith	0	1
	Protium aff. *amazonicum* (Cuatrec.) D.C. Daly	0	1
	Protium fimbriatum Swart	0	1
	Protium grandifolium Engl.	0	2
	*Protium guianensi*s (Aubl.) Marchand	1	0
	Protium hebetatum D.C. Daly	1	14
	Protium hebetatum tipo 1 D.C. Daly	1	19
	Protium nitidifolium (Cuatrec.) D.C. Daly	0	2
	Protium paniculatum Engl.	5	3
	Protium robustum (Swart) D.M. Porter	0	3
	Protium spruceanum (Benth.) Engl.	10	2
	Protium sp.1	7	0
	Protium sp.2	2	0
	Protium sp.3	1	1
	Protium sp.4	13	0
	Protium sp.5	0	1
	Protium sp.6	1	2
	Protium sp.7	0	1
	Protium sp.8	2	0
	Protium sp.9	1	0
	Protium sp.10	1	0
	Protium sp.11	18	4
	Protium sp.12	0	1

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	0	2
	Trattinnickia burseraefolia Mart.	0	1
	Trattinnickia glaziovii tipo 1 Swart	2	0
	Trattinnickia glaziovii tipo 2 Swart	1	1
	Trattinnickia sp.	3	1
Caryocaraceae	*Caryocar glabrum* Pers.	2	2
Chrysobalanaceae	*Couepia dolichopoda* Prance	0	1
	Couepia edulis (Prance) Prance	14	0
	Couepia elata Ducke	2	2
	Couepia longipendula Pilg.	1	3
	Couepia obovata Ducke	0	1
	Couepia spicata Ducke	1	0
	Couepia sp.1	0	1
	Hirtella racemosa Lam.	0	1
	Licania aff. *kunthiana* Hook. f.	2	0
	Licania apetala (E. Mey.) Fritsch	0	1
	Licania bracteata Prance	0	4
	Licania canescens Benoist	1	0
	Licania heteromorpha Benth.	6	3
	Licania kunthiana Hook. f.	2	0
	Licania latifolia Benth. ex Hook. f.	2	0
	Licania laxiflora Fritsch	9	0
	Licania cf. *licaniiflora* (Sagot) S.F. Blake	0	1
	Licania longistyla (Hook. f.) Fritsch	4	8
	Licania macrophylla Benth.	2	10
	Licania micrantha Miq.	1	5
	Licania octandra (Hoffmanns. ex Roem. & Schult.) Kuntze	0	6
	Licania parviflora Benth.	15	1
	Licania rodriguesii Prance	0	1
	Licania sandwithii Prance	1	0
	Licania sclerophylla (Mart. & Hook. f.) Fritsch	1	3
	Licania sprucei (Hook. f.) Fritsch	2	17
	Licania sp.1	5	0
	Licania sp.2	2	6
	Licania sp.3	0	1
	Parinari sp.1	0	2
Clusiaceae	*Calophyllum brasiliense* Cambess.	1	0
	Caraipa densifolia Mart.	1	2
	Caraipa heterocarpa Ducke	3	0
	Caraipa odorata Ducke	0	2
	Caraipa cf. *spuria* Barb. Rodr.	4	0
	Caraipa sp.1	2	0
	Caraipa sp.2	0	13
	Caraipa sp.3	1	0
	Caraipa sp.4	1	0
	Caraipa sp.5	1	0
	Clusia columnaris Engl.	1	0
	Clusia spathulaefolia Engl.	12	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Clusiaceae	*Dystovomita brasiliensis* D'Arcy	0	6
	Haploclathra paniculata (Mart.) Benth.	38	0
	Symphonia globulifera L. f.	1	7
	Tovomita caloneura A.C. Sm.	0	1
	Tovomita gracilipes Planch. & Triana	0	1
	Tovomita cf. *grata* Sandwith	0	2
	Tovomita cf. *obovata* Engl.	0	2
	Tovomita cf. *tenuiflora* Benth. ex Planch. & Triana	1	0
	Tovomita schomburgkii Planch. & Triana	2	0
	Tovomita sp.1	0	2
	Tovomita sp.2	3	0
	Tovomita sp.3	0	1
	Tovomita umbellata Benth.	1	0
	Vismia cayennensis (Jacq.) Pers.	0	1
	Vismia cf. *japurensis* Reichardt	0	1
	Indet.1	1	0
Combretaceae	*Buchenavia* cf. *congesta* Ducke	0	3
	Buchenavia oxycarpa (Mart.) Eichler	0	2
	Terminalia sp.1	0	2
	Indet.1	0	1
Cyrillaceae	*Cyrillopsis paraensis* Kuhlm.	1	7
Dichapetalaceae	*Tapura* cf. *amazonica* Poepp.	0	4
	Tapura guianensis Aubl.	1	0
Ebenaceae	*Diospyros* aff. *bullata* A.C. Sm.	0	4
	Diospyros capreifolia Mart. ex Hiern	0	1
	Diospyros cf. *cavalcantei* Sothers	0	1
	Diospyros guianensis (Aubl.) Gürke	1	0
	Diospyros sp.1	0	1
Elaeocarpaceae	*Sloanea duckei* Earle Sm.	3	0
	Sloanea eichleri K. Schum.	0	1
	Sloanea fendleriana Benth.	1	1
	Sloanea floribunda Spruce ex Benth.	10	0
	Sloanea latifolia (Rich.) K. Schum.	1	0
	Sloanea obtusifolia (Moric.) K. Schum.	7	35
	Sloanea cf. *oppositifolia* Spruce ex Benth.	1	0
	Sloanea pubescens Benth.	15	14
	Erythroxylum macrophyllum Cav.	0	1
Erithroxilaceae	*Amanoa* aff. *guianensis* Aubl.	0	1
Euphorbiaceae	*Anomalocalyx* sp.	1	0
	Anomalocalyx uleanus (Pax & K. Hoffm.) Ducke	0	1
	Aparisthmium cordatum Baill.	0	3
	Conceveiba guianensis Aubl.	0	5
	Conceveiba martiana Baill.	1	0
	cf. *Drypetes variabilis* Uittien	0	1
	Hevea benthamiana Müll. Arg.	6	0
	Hevea guianensis Aubl.	21	27
	Micrandra aff. *minor* Benth.	23	0
	Micrandra spruceana (Baill.) R.E. Schult.	4	71
	Micrandra sprucei (Müll. Arg.) R.E. Schult.	41	1

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Euphorbiaceae	*Nealchornea* sp.	0	1
	Pera bicolor (Klotzsch) Müll. Arg.	1	1
	Pera schomburgkiana (Klotzsch) Müll. Arg.	0	1
	Pera tomentosa (Benth.) Müll. Arg.	2	3
	Pera sp.1	0	1
	Podocalyx loranthoides Klotzsch	0	5
	***Sandwithia guyanensis* Lanj.**	0	**43***
	Indet.1	1	0
	Indet.2	1	0
Fabaceae	*Abarema* cf. *cochleata* (Willd.) Barneby & J.W. Grimes	0	2
	Abarema cf. *commutata* Barneby & J.W. Grimes	0	5
	Abarema jupunba (Willd.) Britton & Killip	0	3
	Abarema leucophylla (Spruce ex Benth.) Barneby & J.W. Grimes	8	0
	Abarema leucophylla / sp.1	4	0
	Acosmium cf. *nitens* (Vogel) Yakovlev	0	1
	Aldina discolor Spruce ex Benth.	0	3
	Aldina cf. *macrophylla* Spruce ex Benth.	1	0
	***Aldina heterophylla* Spruce ex Benth.**	**137***	4
	Aldina sp.1	6	0
	Andira inermis (W. Wright) Kunth ex DC.	1	0
	Andira cf. *micans* Taub.	0	1
	Andira micrantha Ducke	5	0
	Andira parviflora Ducke	0	1
	Andira unifoliolata Ducke	2	63
	Andira sp.1	0	3
	Andira sp.2	4	0
	Andira sp.3	9	0
	Calliandra tenuiflora Benth.	0	2
	Chamaecrista adiantifolia (Spruce ex Benth.) H.S. Irwin & Barneby	10	3
	Chamaecrista bahiae (H.S. Irwin) H.S. Irwin & Barneby	1	0
	***Clathrotropis macrocarpa* Ducke**	15	**138***
	Cynometra sp.1	0	3
	Cynometra sp.2	1	34
	Dialium guianense (Aubl.) Sandwith	0	4
	Dicymbe pharangiphila R.S. Cowan	1	0
	Dimorphandra coccinea Ducke	0	2
	Diplotropis sp.1	0	1
	Dipteryx cf. *magnifica* Ducke	1	3
	Dipteryx rosea Spruce ex Benth.	0	4
	Elizabetha speciosa Ducke	0	1
	Elizabetha sp.1	0	3
	***Eperua leucantha* Benth.**	**681***	21
	Eperua purpurea Benth.	191	29
	Hymenaea cf. *intermedia* Ducke	0	1
	Hymenolobium cf. *excelsum* Ducke	0	1
	Hymenolobium heterocarpum Ducke	1	0
	Hymenolobium modestum Ducke	1	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Fabaceae	*Inga alba* (Sw.) Willd.	0	2
	Inga cordatoalata Ducke	0	1
	Inga lateriflora Miq.	0	1
	Inga leiocalycina Benth.	0	3
	Inga longiflora Spruce ex Benth.	0	1
	Inga marginata Willd.	0	3
	Inga thibaudiana DC.	0	1
	Inga umbratica Poepp. & Endl.	0	1
	Inga sp.1	94	0
	Inga sp.2	5	0
	Inga sp.3	0	2
	Inga sp.4	1	0
	Macrolobium acaciifolium (Benth.) Benth.	1	0
	Macrolobium angustifolium (Benth.) R.S. Cowan	26	0
	Macrolobium bifolium (Aubl.) Pers.	23	0
	Macrolobium cf. *microcalyx* Ducke	4	0
	Macrolobium multijugum (DC.) Benth.	0	2
	Macrolobium unijugum Pellegr.	9	3
	Macrolobium sp.1	5	0
	Macrolobium sp.2	12	0
	Monopteryx uaucu Spruce ex Benth.	60	74
	Ormosia coarctata Jacks.	2	0
	Ormosia discolor Spruce ex Benth.	0	15
	Ormosia macrophylla Benth.	2	0
	Ormosia cf. *paraensis* Ducke	0	2
	Ormosia sp.1	0	1
	Ormosia/Swartzia coarctata/corrugata	0	16
	Parkia igneiflora Ducke	4	0
	Parkia cf. *multijuga* Benth.	0	2
	Parkia sp.1	1	0
	Peltogyne campestris Huber ex Ducke	3	0
	Peltogyne cf. *excelsa* Ducke	1	0
	Peltogyne cf. *paniculata* Benth.	0	1
	Pseudopiptadenia psilostachya (DC.) G. P. Lewis & M. P. Lima	1	1
	Pterocarpus amazonicus Huber	2	5
	Pterocarpus cf. *officinalis* Jacq.	1	6
	Pterocarpus rohrii Vahl	3	0
	Pterocarpus santilinoides L'Hér.	0	1
	Pterocarpus sp.1	11	126
	Sclerolobium chrysophyllum Poepp.	0	1
	Sclerolobium cf. *guianense* Benth.	2	8
	Sclerolobium sp.1	0	1
	Slerolobium micropetalum Ducke	0	5
	Stryphnodendron pulcherrimum (Willd.) Hochr.	0	2
	Stryphnodendron sp.1	0	2
	Swartzia arborescens (Aubl.) Pittier	0	4
	Swartzia cuspidata Spruce ex Benth.	3	16
	Swartzia laevicarpa Amshoff	1	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Fabaceae	*Swartzia polyphylla* DC.	7	56
	Swartzia tomentifera (Ducke) Ducke	3	59
	Swartzia sp.1	1	0
	Swartzia sp.2	1	0
	Swartzia sp.3	2	0
	Swartzia sp.4	14	0
	Swartzia sp.5	8	0
	Swartzia sp.6	2	1
	Swartzia sp.7	2	0
	Swartzia sp.8	1	0
	Tachigali cf. *venusta* Dwyer	0	1
	***Taralea oppositifolia* Aubl.**	**48***	6
	Vatairea guianensis Aubl.	3	0
	Vatairea paraensis Ducke	0	1
	Vatairea sericea (Ducke) Ducke	1	0
	Zygia cf. *claviflora* (Spruce ex Benth.) Barneby & J.W. Grimes	0	1
	Zygia cf. *ramiflora* (F. Muell.) Kosterm.	0	1
	Indet.1	1	0
Goupiaceae	*Goupia glabra* Aubl.	0	8
Humiriaceae	*Humiriastrum cuspidatum* (Benth.) Cuatrec.	1	1
	Humiriastrum sp.	2	0
	Hylocarpa heterocarpa (Ducke) Cuatrec.	16	0
	Sacoglottis guianensis Benth.	2	6
	Sacoglottis sp.1	1	0
	Schistostemon cf. *macrophyllum* (Benth.) Cuatrec.	2	0
	Schistostemon retusum (Ducke) Cuatrec.	4	0
	Vantanea cf. *guianensis* Aubl.	0	1
	Vantanea sp.1	4	0
Icacinaceae	*Dendrobangia* cf. *boliviana* Rusby	0	1
	Emmotum aff. *nitens* (Benth.) Miers	3	0
	Poraqueiba cf. *guianensis* Aubl.	1	0
	Poraqueiba sericea Tul.	2	1
Indet.	Indet.1	0	1
	Indet.2	1	0
	Indet.3	1	0
	Indet.4	0	1
	Indet.5	0	1
	Indet.6	1	0
	Indet.7	1	0
	Indet.8	1	0
	Indet.9	0	1
	Indet.10	0	1
	Indet.11	1	0
	Indet.12	1	0
	Indet.13	0	1
	Indet.14	1	0
	Indet.15	0	1
	Indet.16	1	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Indet.	Indet.17	0	1
	Indet.18	1	0
	Indet.19	0	2
	Indet.20	0	2
Lauraceae	*Aiouea* sp.	1	0
	Aniba affinis (Meisn.) Mez	0	1
	Aniba williamsii O.C. Schmidt	0	1
	cf. *Aiouea* or *Cinnamomum* sp.	0	2
	Licaria cannella (Meisn.) Kosterm.	0	3
	Licaria cf. *cannella cannella*	0	3
	Licaria guianensis Aubl.	0	3
	Mezilaurus cf. sp. INPA:169.296	0	1
	Mezilaurus duckei van der Werff	0	1
	Mezilaurus sp.1	6	0
	Mezilaurus sp.2	1	0
	Nectandra lanceolata Nees	0	3
	Nectandra cf. *lanceolata* Nees	0	1
	Nectandra cuspidata Ness	2	0
	Ocotea aciphylla (Nees) Mez	0	2
	Ocotea cernua (Nees) Mez	0	2
	Ocotea cinerea van der Werff	0	9
	Ocotea delicata Vicent.	0	2
	Ocotea cf. *douradensis* Vatt.	0	2
	Ocotea cf. *rhynchophylla* (Meisn.) Mez	3	2
	Ocotea cf. *tabacifolia* (Meisn.) Rohwer	0	2
	Ocotea nitida (Meisn.) Rohwer	0	1
	Ocotea rhodophylla Vicent.	0	1
	Ocotea splendens (Meisn.) Baill	0	1
	Ocotea suaveolens (Meisn.) Benth. & Hook. f. ex Hieron.	0	1
	Ocotea sp.1	0	17
	Ocotea sp.2	0	1
	Persea sp.	1	0
	Rhodostemonodaphne crenaticupula Madriñán	0	3
	Rhodostemonodaphne cf. *grandis* (Mez) Rohwer	0	1
	Rhodostemonodaphne negrensis Madriñán	1	0
	Rhodostemonodaphne sp.1	0	1
	Sextonia sp.1	7	0
	Indet.1	1	0
	Indet.2	1	0
	Indet.3	1	0
	Indet.4	0	1
	Indet.5	1	0
	Indet.6	0	1
Lecythidaceae	*Cariniana micrantha* Ducke	0	4
	Cariniana sp.	0	1
	Couratari gloriosa Sandwith	0	1
	Couratari stellata A.C. Sm.	0	7
	Eschweilera albiflora (DC.) Miers	0	5

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Lecythidaceae	*Eschweilera bracteosa* (Poepp. ex O. Berg) Miers	0	3
	Eschweilera carinata S.A. Mori	1	7
	Eschweilera decolorans Sandwith	1	1
	Eschweilera gigantea (R. Knuth) J.F. Macbr.	0	6
	Eschweilera cf. *macrocarpa* Pittier	0	1
	Eschweilera cf. *nana* (O. Berg) Miers	0	7
	Eschweilera coriacea (DC.) S.A. Mori	2	3
	Eschweilera ovata (Cambess.) Miers	0	2
	Eschweilera pedicellata (Rich.) S.A. Mori	8	55
	Eschweilera pseudodecolorans S.A. Mori	0	1
	Eschweilera revoluta S.A. Mori	2	0
	Eschweilera rionegrense S.A. Mori	0	4
	Eschweilera rodriguesiana S.A. Mori	0	1
	Eschweilera sp.1	0	1
	Eschweilera subglandulosa (Steud. ex O. Berg) Miers	0	2
	Eschweilera tessmannii R. Knuth	0	11
	Eschweilera wachenheimii (Benoist) Sandwith	0	2
	Gustavia elliptica S.A. Mori	0	2
	Lecythis gracieana S.A. Mori	0	1
	Lecythis parvifructa S.A. Mori	0	6
Linaceae	*Roucheria punctata* (Ducke) Ducke	7	0
Malvaceae	*Catostemma* sp.	1	0
	Erisma globosa (Aubl.) A.Robyns	8	2
	Pachira cf. *aquatica* Aubl.	2	0
	Pachira aff. *insignis* (Sw.) Sw. ex Savigny	1	0
	Pachira coriacea (Mart.) W.S. Alverson	1	0
	Pachira sp.1	2	0
	Quararibea ochrocalyx (K. Schum.) Vischer	0	1
	Scleronema micranthum (Ducke) Ducke	43	24
	Theobroma subincanum Mart.	0	8
	Theobroma sp.	0	1
Melastomataceae	*Miconia lepidota* Schrank & Mart. ex DC.	0	3
	Miconia punctata (Desr.) D. Don ex DC.	0	2
	Miconia pyrifolia Naudin	0	4
	Mouriri ficoides Morley	0	5
Meliaceae	*Carapa* cf. *guianensis* Aubl.	0	2
	Guarea convergens T.D. Penn.	0	4
	Guarea trunciflora C. DC.	0	2
	Trichilia sp.1	1	0
	Trichilia sp.2	0	2
Monimiaceae	*Siparuna decipiens* (Tul.) A. DC.	0	6
	Siparuna guianensis Aubl.	0	1
	Siparuna poeppigii (Tul.) A. DC.	1	1
Moraceae	*Batocarpus* sp.	0	1
	Brosimum acutifolium Huber	2	1
	Brosimum guianense Huber ex Ducke	4	8
	***Brosimum lactescens* (S.Moore) C.C. Berg**	1	**13***
	Brosimum melanopotamicum C.C. Berg	1	1
	Brosimum ovatifolium Ducke	2	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Moraceae	*Brosimum rubescens* Taub.	6	16
	Brosimum sp.1	1	0
	Brosimum sp.3	0	1
	Brosimum utile (Kunth) Oken ex J. Presl	1	4
	Clarisia sp.1	0	1
	Ficus americana Aubl.	1	0
	Ficus paraensis (Miq.) Miq.	0	1
	Helianthostylis sprucei Baill.	0	6
	Helianthostylis steyermarkii C.C. Berg	0	6
	Helicostylis scabra (J.F. Macbr.) C.C. Berg	1	4
	Helicostylis sp.1	0	1
	Helicostylis tomentosa (Poepp. & Endl.) Rusby	0	8
	Maquira sp.1	0	1
	Naucleopsis oblongifolia (Kuhlm.) Carauta	0	4
	Pseudolmedia macrophylla Trécul	0	1
	Trymatococcus amazonicus Poepp. & Endl.	0	5
Myristicaceae	*Iryanthera coriacea* Ducke	21	2
	Iryanthera crassifolia A.C. Sm.	0	2
	***Iryanthera elliptica* Ducke**	0	**20***
	Iryanthera laevis Markgr.	14	26
	Iryanthera lorentensis/lancifolia	5	6
	Iryanthera olacoides (A.C. Sm.) A.C. Sm.	0	2
	Iryanthera paraensis Huber	0	5
	Iryanthera sagotiana (Benth.) Warb.	0	1
	***Iryanthera ulei* Warb.**	5	**49***
	Iryanthera/Osteophloeum sagotiana/platyspermum	11	12
	Iryanthera sp.1	0	2
	Osteophloeum platyspermum (Spruce ex A. DC.) Warb.	0	1
	Otoba parvifolia (Markgr.) A.H. Gentry	0	2
	Otoba sp.1	1	0
	Virola calophylla/pavonis	0	50
	Virola macrocarpa A.C. Sm.	0	2
	Virola michelii Heckel	2	7
	Virola minutiflora Ducke	0	1
	Virola mollissima (Poepp. ex A. DC.) Warb.	0	2
	Virola cf. *theiodora* (Spruce ex Benth.) Warb.	0	3
	Virola surinamensis (Rol. ex Rottb.) Warb.	0	9
	Virola sp.1	0	6
	Virola sp.2	2	7
	Virola sp.3	2	3
Myrsinaceae	*Cybianthus fulvopulverulentus* (Mez) G. Agostini	2	0
Myrtaceae	*Calycolpus* sp.	0	1
	Calyptranthes cuspidata DC.	0	1
	Calyptranthes densiflora Poepp. ex O. Berg	0	1
	Campomanesia sp.1	0	2
	Eugenia diplocampta Diels	0	1
	Eugenia patrisii Vahl	0	1
	Myrcia magnoliifolia (O. Berg) Kiaersk.	0	1
	Myrcia sp.1	1	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Myrtaceae	*Myrcia* sp.2	1	0
Nyctaginaceae	*Guapira sancarlosiana* Steyerm.	1	0
	Neea cf. *obovata* 2 Spruce ex Heimerl	2	0
	Neea madeirana Standl.	2	0
	Neea oppositifolia Ruiz & Pav.	5	0
	Neea ovalifolia Spruce ex J.A. Schmidt	0	5
	Neea robusta Steyerm.	2	2
	Neea sp.1	0	1
	Neea sp.5	1	0
	Pisonia tomentosa Casar.	0	1
	Indet.1	0	1
Ochnaceae	*Ouratea discophora* Ducke	1	0
Olacaceae	*Cathedra* sp.1	0	1
	Dulacia guianensis (Engl.) Kuntze	0	1
	Heisteria densifrons Engl.	0	4
	Heisteria duckei Sleumer	0	1
	Heisteria krukovii A.C. Sm.	0	1
	Minquartia guianensis Aubl.	1	12
Quiinaceae	*Lacunaria crenata* (Tul.) A. C. Smith	0	2
	Lacunaria cf. *jenmanii* (Oliv.) Ducke	0	2
	Lacunaria sp.1	0	1
	Quiina sp.	0	1
Rhabdodendraceae	*Rhabdodendron amazonicum* (Spruce ex Benth.) Huber	11	0
Rubiaceae	*Botryarrhena pendula* Ducke	0	5
	Calycophyllum acreanum Ducke	1	0
	Capirona sp.1	0	1
	***Chimarrhis duckeana* Delprete**	0	**14***
	Chimarrhis sp.1	0	1
	Duroia cf. *macrophylla* Huber	0	4
	Duroia saccifera (Mart. ex Roem. & Schult.) Hook. f. ex Schumann	0	2
	Duroia velutina Hook. f. ex K. Schum.	0	1
	Ferdinandusa uaupensis Spruce ex K. Schum.	4	1
	Isertia hypoleuca Benth.	0	1
	Libertia sp.1	0	1
	Pagamea acrensis Steyerm.	1	0
	Pagamea coriacea Spruce ex Benth.	4	0
	Pagamea cf. *macrophylla* Spruce ex Benth.	5	1
	***Pagamea plicata* Spruce ex Benth.**	**20***	0
	Palicourea amapaensis Steyerm.	0	1
	Psychotria sp.1	0	1
	Remijia hispida Spruce ex K. Schum.	1	0
	Remijia aff. *ulei* K. Krause	0	2
	Remijia sp.1	0	1
	Warszewiczia schwackei K. Schum.	0	1
Rutaceae	*Hortia longifolia* Benth. ex Engl.	3	0
Sapindaceae	*Cupania emarginata* Cambess.	2	0
	Cupania hispida Radlk.	0	1

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Sapindaceae	*Cupania scrobiculata* Rich.	0	1
	Matayba elegans Radlk.	0	1
	Talisia pachycarpa Radlk.	0	1
	Talisia sp.	0	1
Sapotaceae	*Chromolucuma rubriflora* Ducke	0	2
	Chrysophyllum amazonicum T.D. Penn.	0	4
	Chrysophyllum cuneifolium (Rudge) A. DC.	0	1
	Chrysophyllum pomiferum (Eyma) T.D. Penn.	0	10
	Chrysophyllum prieurii A. DC.	1	4
	Chrysophyllum sanguinolentum (Pierre) Baehni	19	9
	Chrysophyllum sp.1	0	1
	Chrysophyllum sp.2	0	1
	Ecclinusa guianensis Eyma	0	1
	Ecclinusa sp.1	1	2
	Ecclinusa sp.2	0	1
	Ecclinusa sp.3	0	1
	Manilkara cf. *amazonica* (Huber) A. Chev.	15	3
	Manilkara bidentata (A. DC.) A. Chev.	13	0
	Manilkara bidentata/cuspidata	8	0
	Manilkara sp.1	5	0
	Manilkara sp.2	1	0
	Micropholis cf. *acutangula* (Ducke) Eyma	0	1
	Micropholis cylindrocarpa (Poepp. & Endl.) Pierre	0	1
	Micropholis cf. *grandiflora* Aubrév.	0	1
	Micropholis guyanensis (A. DC.) Pierre	3	32
	Micropholis splendens Gilly ex Aubréville	0	4
	Micropholis trunciflora Ducke	1	0
	Micropholis venulosa (Mart. & Eichler) Pierre	1	5
	Micropholis sp.1	0	2
	Pouteria cf. *ambelaniifolia* (Sandwith) T.D. Penn.	0	1
	Pouteria cf. *cladantha* Sandwith	5	2
	Pouteria cuspidata (A. DC.) Baehni	6	5
	Pouteria elegans (A. DC.) Baehni	8	1
	Pouteria eugenifolia (Pierre) Baehni	0	1
	Pouteria filipes Eyma	0	1
	Pouteria fimbriata Baehni	1	1
	Pouteria hispida Eyma	0	4
	Pouteria cf. *latianthera* T.D. Penn.	0	1
	Pouteria opposita (Ducke) T.D. Penn.	0	1
	Pouteria sp.1	0	2
	Pouteria sp.2	0	1
	Pouteria sp.3	1	0
	Pouteria sp.4	1	0
	Pouteria sp.5	6	0
	Pouteria sp.6	25	0
	Pouteria sp.7	0	1
	Pouteria sp.8	0	1
	Pouteria sp.9	1	0
	Pouteria sp.10	1	0

Table A1: cont.

Family	Species	N. trees in WS plots	N. trees in TF plots
Sapotaceae	*Pouteria* sp.11	0	1
	Pradosia beardii (Monach.) T.D. Penn.	1	0
	***Pradosia* cf. *mutisii* Cronquist**	**47***	0
	Pradosia schomburgkiana (A. DC.) Cronquist	2	3
	Pradosia sp.1	2	0
Sterculiaceae	*Sterculia* sp.1	0	4
Tiliaceae	*Apeiba echinata* Gaertn.	0	5
	Apeiba sp.1	0	1
Ulmaceae	*Ampelocera ruizii* Klotzsch	3	0
	Ampelocera sp.1	0	2
	Ampelocera sp.2	1	1
Urticaceae	*Cecropia* cf. *latiloba* Miq.	0	1
	Cecropia cf. *sciadophylla* Mart.	0	2
	Cecropia purpurascens C.C. Berg	0	6
	Pourouma bicolor Mart.	0	2
	Pourouma minor Benoist	0	3
	Pourouma sp.1	0	1
	Pourouma tomentosa Mart. ex Miq.	13	2
Verbenaceae	*Vitex calothyrsa* Sandwith	29	0
	Vitex orinocensis Kunth	0	3
Violaceae	*Rinorea falcata* (Mart. ex Eichler) Kuntze	0	1
Vochysiaceae	*Erisma bicolor* Ducke	1	0
	Erisma calcaratum (Link) Warm.	0	34
	Erisma japura Spruce ex Warm.	0	3
	Erisma sp.1	0	1
	Ruizterania cassiquiarensis (Spruce ex Warm.) Marc.-Berti	9	0
	Ruizterania sp.1	6	4
	Vochysia bicolor Ducke	1	0
	Vochysia spatiphylla Stafleu	0	1
	Vochysia vismiifolia Spruce ex Warm.	0	4
	Vochysia sp.1	0	3
	Vochysia sp.2	0	1
	Total	**2524**	**2179**

Paulo A. Assunção measuring DBH,
São Gabriel da Cachoeira, Brazil

APPENDIX 2: ATTRIBUTES OF TREE INVENTORY PLOTS

Table A2: Attributes of tree inventory plots analyzed in Chapter 5; TF: terra-firme forests; WS: white-sand forests

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
ANA-01	Est. Ecol. Anavilhanas	Brazil	-2.05	-60.37	TF	1	yes	Ieda L. Amaral, Francisca Matos	unpubl.
CAR-01	Caracarai	Brazil	1.03	-62.09	TF	1	yes	Juan Gabriel Soler Alarcón	(Arlacon and Peixoto, 2007)
CUI-01	Res. Biol. do Cuieiras	Brazil	-2.6	-60.21	WS	1	yes	Ieda L. Amaral	unpubl.
DUCKE-IPI	Team Ducke Ipiranga	Brazil	-3	-59.89	TF	1	yes	Team Ducke	unpubl.
DUCKE-SEDE	Team Ducke sede	Brazil	-2.93	-59.96	TF	1	yes	Team Ducke	unpubl.
DUCKE-WS	Ducke Campinarana	Brazil	-2.94	-59.94	WS	0.5	no	Hans ter Steege, Carolina Volkmer	unpubl.
ICANA-01	TF PAMAALI	Brazil	1.55	-68.68	TF	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
ICANA-02	CP Jandu Cachoeira	Brazil	1.48	-68.71	WS	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
LO1T0	Ducke LO1T0	Brazil	-2.93	-59.97	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T1000	Ducke LO1T1000	Brazil	-2.93	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T2000	Ducke LO1T2000	Brazil	-2.92	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T3000	Ducke LO1T3000	Brazil	-2.92	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T4000	Ducke LO1T4000	Brazil	-2.92	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T5500	Ducke LO1T5500	Brazil	-2.92	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T6500	Ducke LO1T6500	Brazil	-2.92	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO1T7500	Ducke LO1T7500	Brazil	-2.92	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T1000	Ducke LO2T1000	Brazil	-2.94	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T2000	Ducke LO2T2000	Brazil	-2.93	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T3000	Ducke LO2T3000	Brazil	-2.93	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T4500	Ducke LO2T4500	Brazil	-2.93	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T5500	Ducke LO2T5500	Brazil	-2.93	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T6500	Ducke LO2T6500	Brazil	-2.93	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO2T7500	Ducke LO2T7500	Brazil	-2.93	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
LO3T1500	Ducke LO3T1500	Brazil	-2.94	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO3T2500	Ducke LO3T2500	Brazil	-2.94	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO3T4500	Ducke LO3T4500	Brazil	-2.94	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO3T500	Ducke LO3T500	Brazil	-2.94	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO3T5500	Ducke LO3T5500	Brazil	-2.94	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO3T6500	Ducke LO3T6500	Brazil	-2.94	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO3T7500	Ducke LO3T7500	Brazil	-2.94	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T1500	Ducke LO4T1500	Brazil	-2.95	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T2500	Ducke LO4T2500	Brazil	-2.95	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T3500	Ducke LO4T3500	Brazil	-2.95	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T4500	Ducke LO4T4500	Brazil	-2.95	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T500	Ducke LO4T500	Brazil	-2.95	-59.93	WS	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T5500	Ducke LO4T5500	Brazil	-2.95	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T6500	Ducke LO4T6500	Brazil	-2.95	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO4T7500	Ducke LO4T7500	Brazil	-2.94	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T1500	Ducke LO5T1500	Brazil	-2.96	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T2500	Ducke LO5T2500	Brazil	-2.96	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T3500	Ducke LO5T3500	Brazil	-2.96	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T4500	Ducke LO5T4500	Brazil	-2.96	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T500	Ducke LO5T500	Brazil	-2.96	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T5500	Ducke LO5T5500	Brazil	-2.96	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T6500	Ducke LO5T6500	Brazil	-2.95	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO5T7500	Ducke LO5T7500	Brazil	-2.95	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO6T1500	Ducke LO6T1500	Brazil	-2.97	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO6T3500	Ducke LO6T3500	Brazil	-2.97	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO6T4500	Ducke LO6T4500	Brazil	-2.97	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO6T500	Ducke LO6T500	Brazil	-2.97	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
LO6T5500	Ducke LO6T5500	Brazil	-2.96	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO6T6500	Ducke LO6T6500	Brazil	-2.96	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO6T7500	Ducke LO6T7500	Brazil	-2.96	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T1500	Ducke LO7T1500	Brazil	-2.98	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T2500	Ducke LO7T2500	Brazil	-2.98	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T3500	Ducke LO7T3500	Brazil	-2.98	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T4500	Ducke LO7T4500	Brazil	-2.98	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T500	Ducke LO7T500	Brazil	-2.97	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T5500	Ducke LO7T5500	Brazil	-2.97	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T6500	Ducke LO7T6500	Brazil	-2.97	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO7T7500	Ducke LO7T7500	Brazil	-2.97	-59.89	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T1500	Ducke LO8T1500	Brazil	-2.99	-59.96	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T2500	Ducke LO8T2500	Brazil	-2.99	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T3500	Ducke LO8T3500	Brazil	-2.99	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T4500	Ducke LO8T4500	Brazil	-2.98	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T500	Ducke LO8T500	Brazil	-2.98	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T5500	Ducke LO8T5500	Brazil	-2.98	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T6500	Ducke LO8T6500	Brazil	-2.98	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO8T7500	Ducke LO8T7500	Brazil	-2.98	-59.89	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T1500	Ducke LO9T1500	Brazil	-3	-59.95	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T2500	Ducke LO9T2500	Brazil	-3	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T3500	Ducke LO9T3500	Brazil	-3	-59.94	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T4500	Ducke LO9T4500	Brazil	-2.99	-59.93	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T500	Ducke LO9T500	Brazil	-2.99	-59.92	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T5500	Ducke LO9T5500	Brazil	-2.99	-59.91	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T6500	Ducke LO9T6500	Brazil	-2.99	-59.9	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.
LO9T7500	Ducke LO9T7500	Brazil	-2.99	-59.89	TF	0.5	yes	Bill Magnuson, Carolina Volkmer	unpubl.

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
MAE-01	Mare	Brazil	1.75	-61.25	TF	1	yes	Willian Milliken	(Milliken, 1998)
PNNP-01	Neblina NP	Brazil	0.4	-66.3	TF	0.25	yes	Jean Paul Boubli	(Boubli, 2002)
PNNP-02	Neblina NP	Brazil	0.4	-66.3	WS	0.25	yes	Jean Paul Boubli	(Boubli, 2002)
RCAMP-01	Reserva Campinarana TF	Brazil	-2.58	-60.03	TF	1	yes	Cid Ferreira	unpubl.
RCAMP-02	Reserva Campinarana C	Brazil	-2.58	-60.03	WS	1	yes	Cid Ferriera	unpubl.
SGC-01	TF 1 COMARA	Brazil	-0.08	-66.89	TF	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
SGC-02	TF 2 COMARA	Brazil	-0.09	-66.89	TF	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
SGC-03	TF Torre do LBA	Brazil	0.21	-66.77	TF	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
SGC-04	CP 1 COMARA	Brazil	-0.1	-66.88	WS	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
SGC-05	CP 2 COMARA	Brazil	-0.11	-66.88	WS	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
SGC-06	CP Itacoatiara-Mirim	Brazil	-0.17	-67.01	WS	1	yes	Juliana Stropp, Hans ter Steege	Chapter 3, this thesis
SGC-07	SGC Torre LBA	Brazil	0.21	-66.76	TF	1	yes	Daniela Pauletto	unpubl.
SI-01	Santa Isabel	Brazil	-0.41	-64.95	WS	1	yes	Ieda L.Amaral, Francisca Matos	unpubl.
ZF2-PLATO	ZF2 Plato	Brazil	-2.6	-60.21	TF	1	yes	Ieda L. Amaral	unpubl.
ZF3-CF	Team ZF3 Cabo Frio	Brazil	-2.38	-59.86	TF	1	yes	Ieda L. Amaral, Atlila Oliveira	unpubl.
ZF3-KM37	Team ZF3 Km37	Brazil	-2.45	-59.78	TF	1	yes	Ieda L. Amaral, Atlila Oliveira	unpubl.
INIRIDA	Irinida	Colombia	3.79	-67.82	WS	1	yes	Dairon Cardenas Lopez	unpubl.
24MR-01	24 MR 1	Guyana	6.15	-58.66	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
24MR-02	24 MR 2	Guyana	6.15	-58.66	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
24MR-03	24 MR 3	Guyana	6.15	-58.68	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
24MR-04	24 MR 4	Guyana	6.15	-58.68	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BP107M	107 M BP road	Guyana	5.49	-58.76	TF	1.49	no	-	(Fanshawe, 1954)
BP90M	90 M BP road	Guyana	5.55	-58.74	WS	1.49	no	-	(Fanshawe, 1954)
CAMOUDI	Mabura Hill, Camoudi	Guyana	5.03	-58.8	TF	2.3	no	Raquel Thomas	(Thomas, 2001)
CHBR-01	Berbice	Guyana	4.95	-58.36	TF	1	no	Hans ter Steege, Olaf Banki	(Banki 2010)
CHBR-02	Berbice	Guyana	4.95	-58.35	WS	1	no	Hans ter Steege, Olaf Banki	(Banki 2010)
CHBR-03	Berbice	Guyana	4.95	-58.37	WS	1	no	Hans ter Steege, Olaf Banki	(Banki, 2010)

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
CHBR-04	Berbice	Guyana	4.92	-58.35	TF	1	no	Hans ter Steege, Olaf Banki	(Banki, 2010)
D1	D1	Guyana	5.08	-59.98	TF	1		Terry Henkel	(Henkel, 2003)
D2	D2	Guyana	5.08	-59.98	TF	1		Terry Henkel	(Henkel, 2003)
D3	D3	Guyana	5.37	-59.97	TF	1		Terry Henkel	(Henkel, 2003)
D4	D4	Guyana	5.37	-59.94	TF	1		Terry Henkel	(Henkel, 2003)
D5	D5	Guyana	5.38	-59.98	TF	1		Terry Henkel	(Henkel, 2003)
FTC-01	FTC 1	Guyana	6.63	-58.87	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
FTC-02	FTC 2	Guyana	6.63	-58.87	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
FTC-03	FTC 3	Guyana	6.63	-58.87	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
FTC-04	FTC 4	Guyana	6.63	-58.87	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
IWO-01	Iwo 1	Guyana	4.61	-58.73	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
IWO-02	Iwo 2	Guyana	4.52	-57.74	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
KWAK-01	Kwakwani	Guyana	5.5	-58	TF	1		James Comiskey	(Comiskey et al., 1994)
KWAK-02	Kwakwani	Guyana	5.5	-58	TF	1		James Comiskey	(Comiskey et al., 1994)
M1	M1	Guyana	5.37	-59.97	TF	1		Terry Henkel	(Henkel, 2003)
M2	M2	Guyana	5.35	-59.93	TF	1		Terry Henkel	(Henkel, 2003)
M3	M3	Guyana	5.35	-59.95	TF	1		Terry Henkel	(Henkel, 2003)
MAPSAV	Mapenna savanna LB	Guyana	5.35	-57.32	TF	0.74	no	-	(Fanshawe, 1954)
MB-GH	Moraballi green heart	Guyana	6.18	-58.55	TF	1.5	no	-	(Davis and Richards, 1934)
MB-MB	Moraballi, Morabukea	Guyana	6.18	-58.55	TF	1.5	no	-	(Davis and Richards, 1934)
MB-MX	Moraballi - mixed	Guyana	6.18	-58.55	TF	1.5	no	-	(Davis and Richards, 1934)
MB-WS	Moraballi, WALLABA	Guyana	6.18	-58.55	WS	1.5	no	-	(Davis and Richards, 1934)
MHF-0R3	MHFR 3	Guyana	5.18	-58.7	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
MHFR-01	MHFR 1	Guyana	5.18	-58.7	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
MHFR-02	MHFR 2	Guyana	5.16	-58.71	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
MHFR-04	Mabura Hill, FRMH 04	Guyana	5.18	-58.7	WS	2.3	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
MHFR-05	Mab. Hill, FRMH 05, Roza1	Guyana	5.17	-58.69	TF	1	no	Hans ter Steege, Roderick Zagt	unpubl.

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
MHFR-06	Mab. Hill, FRMH 06, Roza2	Guyana	5.17	-58.69	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
MHFRlAT1	Mabura Hill, FRMH, lat1	Guyana	5.16	-58.7	TF	1.5	no	Hans ter Steege.	unpubl.
MHFRlAT2	Mabura Hill, FRMH, lat2	Guyana	5.16	-58.7	TF	1.5	no	Hans ter Steege	unpubl.
MHFRlATRT	Mabura Hill, FRMH, lat3	Guyana	5.16	-58.69	TF	2.3	no	Raquel Thomas	(Thomas, 2001)
MORU-IR	Moruca Indian Reservation	Guyana	7.65	-59.23	TF	2.1	no	-	(Fanshawe, 1954)
SIM-CK	Simuni Ck. RB Rupununi	Guyana	3.77	-59.28	TF	1.08	no	-	(Fanshawe, 1954)
AL-01	Alberga 1	Suriname	5.34	-55.77	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
AL-02	Alberga 2	Suriname	5.34	-55.76	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
B-09S	BB9	Suriname	4.95	-55.19	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-01P	Brownsberg 1	Suriname	4.93	-55.22	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-02P	Brownsberg 2	Suriname	4.93	-55.19	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-03P	Brownsberg 3	Suriname	4.95	-55.19	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-04M	Brownsberg 4	Suriname	4.97	-55.18	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-05L	Brownsberg 5	Suriname	4.99	-55.2	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-06M	Brownsberg 6	Suriname	4.94	-55.18	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-07L	Brownsberg 7	Suriname	4.92	-55.13	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BB-08L	Brownsberg 8	Suriname	4.93	-55.14	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BIT-01	Bitagron 1	Suriname	5.07	-56.21	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BIT-02	Bitagron 2	Suriname	5.08	-56.2	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BIT-03	Bitagron 3	Suriname	5.08	-56.2	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BIT-04	Bitagron 4	Suriname	5.09	-56.19	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BLM-K	Blanche Marie Falls K	Suriname	4.75	-56.85	TF	1.21	-	Paul Maas	(Maas, 1971)
BSH-01	BSH 1	Suriname	5.14	-55.78	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BSH-02	BSH 2	Suriname	5.15	-55.78	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
BSH-03	BSH 3	Suriname	5.15	-55.78	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
GOL-01	Goliath 1	Suriname	5.22	-55.65	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
KABO-41	Kabo 41	Suriname	5.34	-55.77	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
KABO-43	Kabo 43	Suriname	5.34	-55.77	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
KAM-H	Kamisa Falls H	Suriname	5.1	-56.33	TF	0.91	-	Paul Maas	(Maas, 1971)
LM-01P	Lely 01	Suriname	4.27	-54.75	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010)
LM-02P	Lely 02	Suriname	4.26	-54.74	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010))
LM-03P	Lely 03	Suriname	4.27	-54.74	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010)
LM-04M	Lely 04	Suriname	4.25	-54.73	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010)
LM-06L	Lely 06	Suriname	4.26	-54.78	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010)
LM-07L	Lely 07	Suriname	4.27	-54.78	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010)
LM-08M	Lely 08	Suriname	4.27	-54.75	TF	1	no	Olaf Banki, Hans ter Steege	(Banki 2010)
NIR-01	Nickeri rivier 1	Suriname	4.98	-57	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NIR-02	Nickeri rivier 2	Suriname	4.98	-57	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NIR-03	Nickeri rivier 3	Suriname	4.99	-57	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NIR04	Nickeri rivier 4	Suriname	5	-57	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NM-01P	Nassau Mts 1	Suriname	4.78	-54.62	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NM-02P	Nassau Mts 2	Suriname	4.82	-54.61	TF	0.55	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NM-03P	Nassau Mts 3	Suriname	4.82	-54.6	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NM-04L	Nassau Mts 4	Suriname	4.93	-54.52	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NM-05L	Nassau Mts 5	Suriname	4.93	-54.52	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
NM-06P	Nassau Mts 6	Suriname	4.83	-54.61	TF	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
SIMCR-01	Simonskreek 1	Suriname	5.32	-54.94	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
SIMCR-02	Simonskreek 2	Suriname	5.32	-54.94	WS	1	no	Olaf Banki, Hans ter Steege	(Banki, 2010)
SNCR-B	Snake Creek B	Suriname	5.23	-56.8	WS	0.47	-	Paul Maas	(Maas, 1971)
SNCR-F3	Snake Creek FI	Suriname	5.23	-56.8	TF	1.25	-	Paul Maas	(Maas, 1971)
SUHO	Mapane Berg en Dal	Suriname	5.49	-54.67	TF	1	-	-	(Shulz & Lindeman 1960)
WIN-A	Winana Creek AI, AII	Suriname	5.25	-57.07	WS	0.54	-	Paul Maas	(Maas, 1971)

Table A2: cont.

Plot Code	Site name	Country	latitude	longitude	Forest	Area (ha)	morpho-sp. collected	Owner/contact	Reference
WIN-EI	Winana Creek EI	Suriname	5.25	-57.07	WS	0.68	-	Paul Maas	(Maas, 1971)
WIN-EII	Winana Creek EII	Suriname	5.25	-57.07	TF	0.9	-	Paul Maas	(Maas, 1971)
CASIQ-01	El Pijiguao - plot A	Venezuela	2.03	-66.47	TF	1	yes	Gerardo Aymard	unpubl.
CASIQ-03	La Ceiba - plot E	Venezuela	2.37	-66.45	TF	1	yes	Gerardo Aymard	unpubl.
CASIQ-04	El Peligro - plot F	Venezuela	1.92	-66.62	TF	1	yes	Gerardo Aymard	unpubl.
SCR-02	San Carlos, Yevaro	Venezuela	1.93	-67.05	TF	0.6	yes	Nelda Dezzeo	(Dezzeo et al., 2000)
SCR-03	San Carlos, Caatinga Alta	Venezuela	1.93	-67.05	TF	0.6	yes	Nelda Dezzeo	(Dezzeo et al., 2000)
SCR-04	San Carlos, Guaco	Venezuela	1.93	-67.05	WS	0.6	yes	Nelda Dezzeo	(Dezzeo et al., 2000)
SCR-05	San Carlos, Mixto	Venezuela	1.93	-67.05	TF	0.6	yes	Nelda Dezzeo	(Dezzeo et al., 2000)

APPENDIX 3: REFERENCES USED TO COMPILE THE DATASET ABOUT TREE INVENTORY PLOTS ESTABLISHED IN CENTRAL AMAZONIA, THE GUIANAS, AND THE UPPER RIO NEGRO

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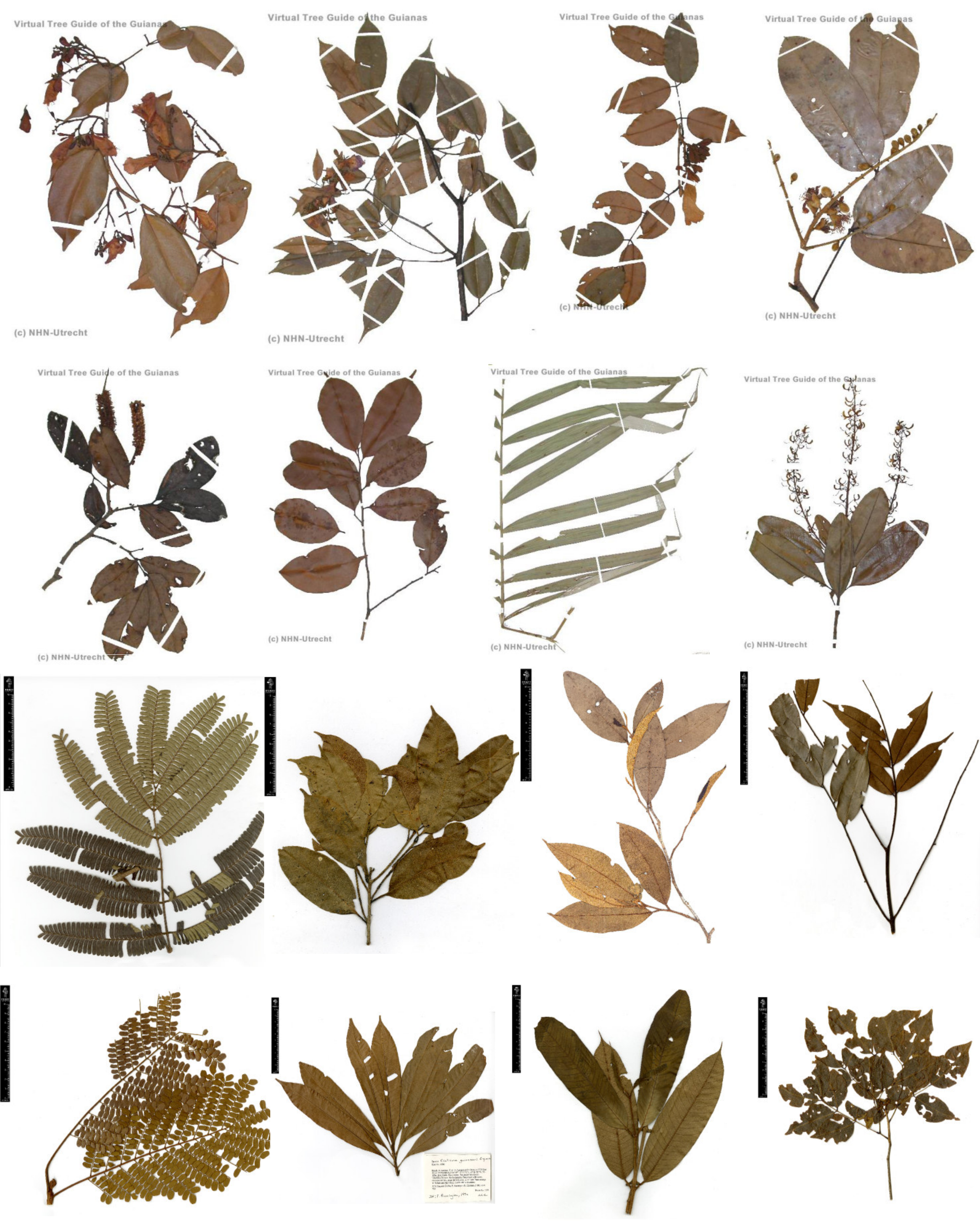

Pictures from the *Virtual Tree Guide of the Guianas* and from the *Virtual Flora of the Biological Dynamics of Forest Fragment Project* (BDFFP)

SUMMARY

Amazonian forests harbor the highest biodiversity of all terrestrial ecosystems on Earth. Both the origin of this extraordinary biodiversity and its current distribution are recently becoming better understood (ter Steege et al., 2003, Hoorn and Wesselingh, 2010). For example, long-term landscape evolution and climate change have been identified as important drivers of speciation and extinction, thus shaping the current patterns of biodiversity in Amazonian forests (Hoorn et al., 2010, see **Chapter 1**). Still, our knowledge of the contribution of processes operating at different temporal and spatial scales to the tree diversity in Amazonia remains surprisingly limited. Here we assess the contribution of long-term, large-scale as well as short-term, small-scale processes to the current pattern of tree diversity in Amazonian forests. To this end, we apply a hierarchical approach, which explicitly addresses regional and local tree communities.

We start out in **Chapter 2** by applying this hierarchical approach to a dataset of 752 tree inventory plots spread over entire Amazonia with the aim of identifying potential regional and local drivers for the variation in tree species diversity. We hypothesize that regional tree diversity is influenced by long-term, large-scale processes, whereas local tree diversity is mainly regulated by short-term, small-scale processes. We observed that areas with high regional diversity coincide with areas of palaeo-climatic stability and long-term high ecosystem dynamics. As these two factors strongly affect speciation and extinction rates and cause shifts in species distribution, we propose that they are important drivers of the current patterns of regional tree diversity in Amazonian forests. Variation in tree diversity at the local scale is enormous but only poorly explained by local disturbance, our proxy for local ecosystem dynamics. We suggest that the power of this explanation is low because local tree diversity is subject to local processes including disturbances, species association with micro-habitat conditions, ecological drift due to dispersal limitation, occurrence of pathogens, etc. such factors are largely variable from one location to another in Amazonian forests and difficult to be systematically measured in all tree inventory plots included in our analysis.

In Chapters 3, 4, and 5, we focus on tree communities of white-sand and terra-firme forests in Amazonia. Tree communities of these two forests types differ in diversity as well as in species composition, suggesting that these communities may have a relatively independent evolutionary history. In Chapter 3 and 4, we focus on tree communities of white-sand and terra-firme forests of the upper Rio Negro, a region for which empirical data are particularly scarce. This shortcoming is relevant because unlike prevailing landscapes in Amazonia, where terra-firme forests present the dominant forest type, the upper Rio Negro harbors extensive areas of white-sand forests. In **Chapter 3**, we present data of eight new tree inventory plots established in white-sand and terra-firme forests in the upper Rio Negro. For these plots, we analyzed forest structure as well as tree species diversity and composition. We found that tree communities of white-sand forests show a higher floristic similarity and lower diversity than those of terra-firme forests. We argue that differences in the tree communities of white-sand and terra-firme forests are related to habitat size, which influences speciation and extinction rates.

In **Chapter 4**, we address, in particular, the role of environmental filtering for differences in the tree species composition of white-sand and terra-firme forests in the upper Rio Negro. We tested the hypothesis that a trade-off between seedling growth and herbivore defense drives habitat association in these two forest types (Fine et al. 2004). To this end, we conducted a cross-transplanting field experiment. We analyzed seedling performance, i.e., mortality, growth, and insect herbivore defense, as well as seedling traits of seven white-sand and seven terra-firme habitat specialist tree species. Based on our cross-transplanting experiment we found no evidence that the trade-off between tree seedling growth and herbivore defense drives habitat association in white-sand and terra-firme forests of the upper Rio Negro. This finding may be explained by the extreme low nutrient availability of the soils of these two forest types in the upper Rio Negro. In this region, soil characteristics such as limited nutrient availability or soil biota may directly cause seedling mortality in their non-typical forest type as well as restrict seedling growth.

In **Chapter 5**, we characterize the tree species diversity and composition of white-sand and terra-firme forests across a broad spatial scale. We aim at understanding how regional tree communities regulate the variation in tree species diversity and composition of local communities of white-sand and terra-firme forests. Furthermore, we aim at assessing if habitat association is maintained across lower taxonomic levels. To address these objectives, we analyzed 192 tree inventory plots established in white-sand and terra-firme forests of three Amazonian regions: central Amazonia, the Guianas, and the upper Rio Negro. We found that local tree communities, present in small patches of white-sand forests in central Amazonia, are more diverse than those occurring in the larger white-sand areas of the upper Rio Negro. We explain this finding by the random invasion of tree species from the diverse regional community of terra-firme forests into the less diverse small local communities of white-sand forests. By assessing habitat association among 63 tree families and 238 genera occurring in white-sand and terra-firme forests, we found that most families and genera, which are significantly associated with either forest type, also have the majority of their species associated with that particular forest type. This finding suggests that associated genera and species inherit habitat requirements from higher taxonomic levels, indicating that a large number of tree species have retained requirements for their typical habitat during speciation events.

Taken as a whole, our findings indicate that patterns of tree diversity can only be understood if both current ecological and long-term evolutionary processes are taken into account. Elucidating how these processes influence diversity may help to predict how ongoing changes in climate and land use may re-shape biodiversity. At long-term, the size of forest areas in Amazonia is expected to decline in response to a predicted drier climate. At short-term, ongoing land use change reduces the size of forest areas by deforestation. As deforestation occurs at such rapid rates, long-term species adaptations to new environmental conditions may be of minor importance for the future of Amazonian forests (ter Steege, 2010).

Given the high rates at which Amazonia loses forests, our understanding of biodiversity is remarkably limited. This thesis includes nearly all tree inventory plots that have been established in Amazonia; yet these plots together cover only 0.001% of the total area of Amazonian forests. Of the total number of species and morpho-species encountered in a subset of 192 tree inventory plots, 53% remain unidentified. To address persisting knowledge gaps we urgently need to expand our data collection, integrate new and previously collected data of tree inventory plots, as well as improve our taxonomic knowledge. Here, I recommend that efforts to expand our understanding of tree diversity in Amazonian forests should be combined with efforts to improve the education of the inhabitants of Amazonia. Our own experience during field work in the upper Rio Negro has shown that establishing student-scientist partnerships is worthwhile and can benefit both tropical ecology and the inhabitants of Amazonia.

Seed of *Abarema* sp.

SAMENVATTING

De regenwouden van de Amazone herbergen de grootste biodiversiteit van alle terrestrische ecosystemen op aarde. Zowel het ontstaan van deze buitengewone biodiversiteit alsook de huidige ruimtelijke verdeling worden tegenwoordig beter begrepen (ter Steege et al., 2003, Hoorn and Wesselingh, 2010). Het ontstaan van het landschap over lange geologische tijdschalen en veranderingen in het klimaat gelden als belangrijke factoren voor het ontstaan en uitsterven van soorten en zijn dan ook bepalend voor huidige patronen van biodiversiteit in de Amazone (Hoorn et al., 2010, **Hoofdstuk 1**). Toch is onze kennis over de specifieke bijdrage van processen die op verschillende ruimtelijke en temporele schalen werken nog verassend klein. In dit proefschrift heb ik de rol van 'lange termijn – grote schaal' en 'korte termijn – kleine schaal' processen onderzocht. Ik heb hiervoor een hiërarchische methode gebruikt, die expliciet de regionale en lokale boomgemeenschappen onderzoekt.

In **Hoofdstuk 2** pas ik deze hiërarchische aanpak toe op een dataset van 752 1-ha boom-inventarisatieplots die verspreid over de Amazone liggen. Mijn aanname was, dat de regionale diversiteit voornamelijk door de processen die op de lange termijn en grote schaal opereren wordt bepaald, terwijl de lokale diversiteit door processen die op de korte termijn en kleine schaal werken wordt bepaald. Ik vond dat gebieden met een hoge regionale diversiteit nu juist ook de gebieden zijn met een hoge mate van stabiliteit in palaeoklimaat en hoge mate van ecosysteemdynamiek. Omdat deze processen sterk de soortvorming en extinctie beïnvloeden concludeer ik, dat deze processen voor een belangrijk deel de huidige regionale patronen in biodiversiteit kunnen verklaren. Lokale variatie in boomdiversiteit is erg groot en ik kan die maar in beperkte mate in termen van lokale ecosysteemdynamiek verklaren. Het verklarend vermogen van ecosysteemdynamiek is vermoedelijk zo laag, omdat er op lokale schaal veel variatie in dynamiek is, bijvoorbeeld als gevolg van random 'ecologische drift', pathogenen en relaties tussen soorten en de bodemeigenschappen.

In de hoofdstukken 3, 4 en 5 focus ik op boomgemeenschappen van bossen op witte zanden en op die van meer kleiige bodems (de zogeheten 'terra firmes'). De boomgemeenschappen van deze twee bodemtypes verschillen sterk in diversiteit en soortensamenstelling, hetgeen suggereert dat deze gemeenschappen een enigszins afzonderlijke evolutionaire geschiedenis hebben doorgemaakt.

In hoofdstuk 3 en 4 onderzoek ik de boomgemeenschappen van de witte zanden en 'terra firme' bossen van de boven Rio Negro, een gebied waarvan plot data schaars zijn. Het opnemen van plots in dit gebied was belangrijk, omdat juist hier grote gebieden met bos op wit zand voorkomen. In **Hoofdstuk 3** presenteer ik daarom de data van acht nieuwe 1-ha boomplots. Voor deze plots analyseerde ik zowel de structuur als de soortensamenstelling. Ik vond dat de boomgemeenschappen op wit zand onderling een grotere overeenkomst hadden dan de bossen op 'terra firme'. De verschillen tussen die boomgemeenschappen worden waarschijnlijk door de verschillen in habitatgrootte veroorzaakt, want die zijn van invloed op de snelheden van speciatie en extinctie.

In Hoofdstuk 4 kijk ik naar de rol van habitat als 'omgevingsfilter' op het voorkomen van planten. Ik testte de hypothese, die zegt dat er een zogeheten 'trade-off' zou zijn tussen de groeisnelheid en bescherming tegen herbivoren, en dat die verhouding in de twee habitattypen anders ligt (Fine et al. 2004). Om dit te toetsen voerde ik een kruisgewijs transplantatie-experiment uit. Ik analyseerde de groei van de zaailingen en de vraat door kleine herbivoren en ook mat ik de eigenschappen van zeven witzand-soorten en zeven terra-firme-soorten. In het transplantatie experiment vond ik geen bewijs dat de 'trade-off' tussen groei en bescherming tegen herbivoren voor de verschillen in samenstelling in de twee bostypes verantwoordelijk zou kunnen zijn. Wellicht dat de verschillen in voedselrijkdom tussen de twee bodemtypes niet voldoende zijn om een dergelijke 'trade-off', zo die al mocht bestaan, aan het licht te brengen. Maar het is ook mogelijk dat de bodemeigenschappen hier zo groot zijn, dat ze rechtstreeks bepalen of zaailingen zich al dan niet kunnen vestigen en uitgroeien en zo dus rechtstreeks de verschillen in samenstelling van het bos bepalen.

In **Hoofdstuk 5** onderzoek ik de soortensamenstelling en diversiteit van witzand- en terra-firme-bossen over een grotere ruimtelijke schaal. Ik probeer hierbij te onderzoeken hoe de regionale soortensamenstelling de lokale samenstelling van beide bostypes beïnvloedt. Ook onderzoek ik of habitat-associaties constant zijn over verschillende taxonomische niveaus. Ik onderzocht hiervoor 192 plots uit drie regio's: de centrale Amazone (Manaus), de Guianas, en de Boven Rio Negro. Ik vond dat de opnames van de witzandbossen in de centrale Amazone, die er als kleine eenheden tussen de uitgestrekte terra-firme-bossen voorkomen, veel diverser waren dan de opnames die in de veel grotere witzandgebieden van de Boven Rio Negro waren gemaakt. Dit kan men verklaren door een hoge willekeurige invasie in de witzandbossen van soorten uit de extreem soortenrijke terra-firme-bossen er omheen aan te nemen. In mijn onderzoek naar de habitat-associatie van 63 boomfamilies en 238 boomgenera vond ik dat de meeste families en genera, die kenmerkend zijn voor een van de twee bodems, ook wat betreft hun soorten voor die bodem kenmerkend zijn. Dit resultaat suggereert dat de habitat-associatie gedurende veel soortsvorminggebeurtenissen constant is gebleven.

Samenvattend kan ik stellen, dat patronen in biodiversiteit alleen goed kunnen worden begrepen als zowel de huidige ecologische als de lange-termijn evolutionaire processen in ogenschouw worden genomen (**Hoofdstuk 6**). Als we begrijpen hoe deze processen diversiteit beïnvloeden kunnen we ook beter voorspellen hoe klimaatsveranderingen and veranderingen in landgebruik op diversiteit van invloed zullen zijn. Op korte termijn wordt het bosareaal door ontbossing steeds kleiner. Op de lange termijn zal het oppervlak van het bosareaal door een droger klimaat afnemen. Aangezien ontbossing nog steeds op grote schaal plaats heeft zullen de aanpassingen van soorten aan een veranderend klimaat mogelijk van secundair belang zijn (ter Steege 2010).

Gezien de grote snelheid waarmee het bos in de Amazone verdwijnt, is onze kennis van de biodiversiteit nog steeds erg beperkt en neemt ze erg langzaam toe. In dit proefschrift zijn vrijwel alle boomplot-inventarisaties die in de Amazone gemaakt zijn opgenomen. Toch beslaan al deze plots tezamen slechts 0.001% van het landoppervlak van de Amazone. Van het totaal aantal soorten dat in een subset van 192 plots is gevonden blijft 52% vooralsnog zonder naam. Om deze gaten in onze kennis in te vullen zal op grote schaal meer informatie verzameld moeten worden, zullen we meer nieuwe en oude data moeten integreren en zal ook onze taxonomische kennis vergroot moeten worden. Ik stel dat we bij de vergroting van onze kennis ook aandacht besteden aan de scholing van de inwoners van de Amazone. Wat dit betreft heeft mijn ervaring gedurende het veldwerk voor dit proefschrift mij geleerd, dat de samenwerking tussen wetenschapper en lokale student zeer waardevol is en van nut is voor beide partijen.

Flower of a Chrysobalanaceae

RESUMO

As florestas na Amazônia abrigam uma das maiores biodiversidades do mundo. Recentemente, a origem e a distribuição desta imensa biodiversidade vêm sendo melhor entendidas (Hoorn and Wesselingh 2010, ter Steege et al. 2003). Mudanças no clima e na paisagem que ocorrem em grande escalas, espacial e temporal, afetam taxas de especiação e extinção de espécies; e portanto contribuem para a origem e também para distribuição da atual da biodiversidade na Amazônia (Hoorn et. al 2010, **capítulo 1**). Além disso, processos ecológicos que atuam em pequena escala, como interações inter-específicas, são também fundamentais para a manuntenção da biodiversidade. No entanto, a contribuição relativa destes processos evolutivos e ecológicos para a biodiversidade na Amazônia permanece ainda pouco entendida. Nesta tese, analisamos a diversidade de árvores das florestas da Amazônia considerando explicitamente processos ecológicos e evolutivos na escala em que são relevantes. Para isto, utilizamos uma abordagem hieráquica que considera explicitamente comunidades arbóreas regionais e locais.

No **capítulo 2**, aplicamos esta abordagem hierárquica a fim de identificar padrões regionais e locais de variação da diversidade de árvores. Propomos a hipótese de que a diversidade regional é influenciada por processos que operam em grande escala temporal e espacial, enquanto que a diversidade local é regulada principalmente por processos que operam em pequena escala. Para isto, utilizamos um banco de dados contendo 752 parcelas de inventários florísticos distribuídos em diferentes áreas da Amazônia. Nossos resultados indicam que áreas de alta diversidade regional ocorrem em áreas de longa estabilidade paleo-climática, como a Amazônia central, e em áreas de alta paleo-dinâmica de ecossistemas, como a Amazônia ocidental. Como estes dois fatores, estabilidade paleo-climática e paleo-dinâmica de ecossistemas, influenciam taxas de especiação e extinção e causam mudanças na distribuição espacial de espécies, propomos que estes fatores infuenciam o padrão atual da diversidade regional de árvores. Adicionalmente, encontramos uma grande variação da diversidade local árvores. Esta variação foi pouco explicada pela % de indivíduos de espécies pioneiras (*proxy* para dinâmica local e atual de ecossistemas) Sugerimos que este poder explanatório é baixo porque a diversidade local é influenciada por eventos como distúrbios, limites de dispersão, presença de patógenos, etc.,

Além destes fatores variarem de um local para o outro na Amazônia, uma amostragem sistemática destes fatores nas parcelas incluidas em nossas analises seria difícil.

Nos capítulos 3, 4 e 5 focamos nas comunidades arbóreas de florestas de campinarana e de terra-firme. Estas comunidades diferem em diversidade e composição florísticas, e portanto apresentam histórias evolutivas relativamente independentes. Nos capítulos 3 e 4, analisamos as comunidades de campinarana e terra-firme do alto Rio Negro, onde dados empíricos são particularmente escassos. Este fato é relevante porque diferentemente das demais regiões da Amazônia, onde florestas de terra-firme são a fisionomia dominante, o alto Rio Negro abriga extensas áreas de florestas de campinaranas. No **capítulo 3**, apresentamos dados de oito parcelas de inventários florísticos estabelecidas em florestas de campinarana e de terra-firme no alto Rio Negro. Para estas parcelas, analisamos estrutura florestal, diversidade e similaridade florística. Encontramos que comunidades arbóreas de florestas de campinarana apresentam maior similaridade florística entre si e menor diversidade do que as comunidades de terra-firme. Sugerimos que diferenças entre comunidades arbóreas de campinarana e de terra-firme estão relacionadas à diferença do tamanho do habitat, que indiretamente influencia taxas de especiação e extinção.

No **capítulo 4**, avaliamos a contribuição de filtros ambientais para dissimilaridade florística entre florestas de campinaranas e de terra-firme do alto Rio Negro. Testamos a hipótese de que um *trade-off* entre crescimento e defesa contra herbívoros causa associação ao habitat em espécies arbóreas que ocorrem em florestas de campinarana e de terra- firme (Fine et al. 2004). Para testar este *trade-off,* conduzimos um experimento de transplante de plântulas nestas duas fisionomias florestais no alto Rio Negro. Analisamos mortalidade, crescimento, defesa contra insetos herbívoros e características funcionais de plântulas de sete espécies associadas à campinarana e sete à terra-firme. Nossos resultados indicam que o *trade-off* entre crescimento e defesa não causa associação às florestas de campinarana ou às terra-firme do alto Rio Negro. Estes resultados podem ser explicados pela pouca diferença em disponibilidade de nutrientes nos solos dessas duas florestas no alto Rio Negro. Nesta região, características edáficas como disponibilidade de nutriente ou micro-biota de solo podem limitar diretamente o estabelecimento e crescimento de plântulas no ambiente em que estas não são características.

No **capítulo 5**, caracterizamos a diversidade e a composição florística de florestas de campinarana e de terra-firme em três regiões da Amazônia: Amazônia central, Guianas e alto Rio Negro. Nosso objetivo foi avaliar como a comunidade regional regula a diversidade e a composiçao florística das comunidades locais. Além disso, verificamos se famílias e gêneros que são tipicamente associados à uma destas duas fisionomias florestais mantém esta associação em níveis taxonômicos mais baixos. Para isto, compilamos dados de 192 parcelas de inventários forísticos. Encontramos que comunidades árboreas locais presentes nos pequenos fragmentos de campinarana na Amazônia central são mais diversas que aquelas presentes nas extensas florestas de campinaranas no alto Rio Negro. Este resultado pode ser explicado por invasões aleatórias de espécies presentes na rica comunidade das florestas de terra-firme que ocorrem na Amazônia central. Analisando associação de habitat em 63 famílias e 238 gêneros, encontramos que a maioria das famílias e gêneros que são associados à uma das fisionomias florestais, apresentam o maior número de espécies associados àquela mesma fisionomia. Este resultado sugere que gêneros e espécies parecem herdar requerimentos ao habitat de níveis taxonômicos mais altos, indicando que para um grande número de espécies os requerimentos pelo seu tipo de hábitat podem ter sido mantidos durante eventos de especiação.

Em síntese, os resultados apresentados aqui indicam que padrões de diversidade de espécies devem ser analisados considerando explicitamente tanto processos evolutivos tanto processos ecológicos atuais (**capítulo 6**). Entender como estes processos influenciam a diversidade de espécies podem ajudar a predizer como mudanças climáticas e do uso da terra podem alterar a diversidade e a composição de espécies na Amazônia. Em longa escala, esperamos que áreas cobertas por florestas na Amazônia sejam reduzidas em função do clima mais seco que é predito para o futuro desta região. A curto prazo, desmatamento reduz drasticamente áreas de florestas na Amazônia. Como desmatamento ocorre em taxas alarmantes, adaptação de espécies às novas condições ambientais pode ser de menor importância para o futuro das florestas da Amazônia (ter Steege, 2010).

Considerando as taxas alarmantes de desmatamento, nosso entendimento sobre a biodiversidade da Amazônia é surpreendentemente limitado. Para esta tese, analisamos quase todas as parcelas de inventários florísticos que já foram estabelecidas nesta região. No entanto, este conjunto de dados cobre somente 0,001% da área total de florestas da Amazônia. Além disso, do número total de espécies e morfo-espécies registrado em um sub-conjunto de 192 parcelas, 53% permanece para ser identificado. Para reduzir esta lacuna no conhecimento, é necessário expandir a coleta de dados, integrar novos dados aos dados previamente coletatos e ainda aprimorar o conhecimento taxonômico. Recomendamos aqui que esforços para expandir o conhecimento científico sobre a biodiversidade das florestas da Amazônia devem ser aliados aos esforços para aprimorar a educação de seus habitantes. Nossa experiência trabalhando no alto Rio Negro nos mostrou que a parceria entre pesquisadores e estudante é frutífera e pode beneficiar tanto pesquisas em ecologia tropical como a formação dos habitantes da Amazônia.

Kids playing at the Içana River, Brazil

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Our pet at EIBC

CURRICULUM VITAE

I was born on December 5, 1975 in Campinas, Brazil. From 1982 to 1993 I completed my primary and secondary education in Campinas. In 1994, I began to study Ecology. I received a B.Sc. degree in Ecology from the ‘Universidade Estadual Paulista’, campus Rio Claro, in 1999. Afterwards, I worked as a research fellow at the ‘Instituto Nacional de Pesquisas Espacias’ (INPE) analyzing tree diversity in the Atlantic forest, Brazil. In 2002, I moved to Manaus, Amazonas, to follow a Master program at the ‘Instituto Nacional de Pesquisas da Amazônia (INPA). I received my M.Sc. degree in Tropical Ecology in early 2004 with a dissertation on *Predictive models of tree species distribution in central Amazonia*. Between 2004 and 2005, I worked as a research fellow at INPA analyzing impacts of land use change on biodiversity in Amazonia. In 2005, I received an EU fellowship to work in collaboration with Utrecht University and Oxford University to analyze tree diversity in Amazonian forests. In 2006, I started my PhD research at the Ecology and Biodiversity Group, Utrecht University. Parallel to my PhD research, I have been working in collaboration with the Amazon Forest Inventory Network (RAINFOR).

Mr. Alberto, his grandson, and Juliana at Jandú-Cachoeira, Içana River, Brazil

LIST OF PUBLICATIONS

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