

**Does Neutral Theory explain
Community Composition in the
Guiana Shield Forests?**

The research presented in this thesis was carried out within the framework of the Plant Ecology and Biodiversity group, Institute of Environmental Biology, Utrecht University.

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Does Neutral Theory explain Community Composition in the Guiana Shield Forests?

Verklaart de neutrale theorie gemeenschapssamenstelling van
de bossen op het Guyana Schild?

(met een samenvatting in het Nederlands)

Proefschrift

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Voor Endre & Hanne

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Chapter 1

General Introduction

Why a species occurs at a certain site and not at another has puzzled ecologists for much more than a century. The interest in this question has led to a staggering number of hypotheses, making the classification of these hypotheses a research in itself (Palmer, 1994). Recently the question 'what determines species diversity' was chosen as one of the top 25 Science questions of our times (Pennisi, 2005). With the numerous factors that could influence diversity in species rich ecosystems like tropical rainforests, one can imagine that a satisfying answer to such a question is not readily available. Therefore, ecologists are constantly seeking for general principles in ecology, and with the current threats the global biodiversity faces today (e.g. habitat fragmentation and destruction, climate change), it is clear that a general theory on biodiversity is much needed.

In his revolutionary publication of 1898, Schimper was one of the first to put plant geography in a physiological context, and to relate plant form and structure to functional responses due to (abiotic) environmental factors (Schimper, 1898). Tansley later described the problems of getting this new upcoming research field of 'ecology' accepted, and proposed two types of ecological research: a descriptive and an experimental approach. Both these ecological research approaches should interact and involve: "*an attempt to determine why plants which live together on a definite area with definite environmental conditions come to be thus associated – how they come to exhibit, and what are their detailed functional relations to one another and to their inorganic surroundings*" (Tansley, 1904). Not long after, it became clear that species could outcompete one another, and this was later termed competitive exclusion (Gause, 1934; Hardin, 1960; Tansley, 1917). Species were also found to be related to other non environmental factors, such as area (Gleason, 1922).

In ecology today, the interaction between the abundance of individual species and the diversity patterns that emerge from these abundances are still not fully understood (Lennon *et al.*, 2004). An intrinsic aspect of ecological communities is that there are few common species and lots of rare species (Ricklefs, 2000). A major milestone in the study on relative species abundances was the introduction of the logseries and the associated diversity measure Fisher's alpha (Fisher *et al.*, 1943; Taylor *et al.*, 1976). The logseries is part of a

statistical and sampling theory. It describes the relation between individuals and species in random samples taken from ecological communities. Fisher's alpha is widely used as a measure for alpha-diversity, the diversity of a single point location such as a forest plot, as it is relatively independent on sample size (Taylor *et al.*, 1976; ter Steege *et al.*, 2006). Preston (1948) quickly opposed Fisher's logseries, arguing that the logseries was an artifact of small sample size, and postulated that ecological communities were better described by a lognormal distribution. The lognormal is however based on observation rather than being statistical and predicts too few rare species and too many abundant species (see Chave, 2004). Because both theories describe distributions that are found in the field, they are still widely discussed today (Hubbell *et al.*, 2008; McGill, 2003). Neither Fisher's nor Preston's theory was derived from fundamental birth, death, and migration processes, however. The theory on Island Biogeography of MacArthur and Wilson (1967) was one of the first neutral theories and included the processes of immigration and extinction. The problem with this theory was that all species were treated as identical as to immigration and extinction probabilities; an assumption not very likely to be correct. In the next 40 years the study on community dynamics focussed more on explaining the coexistence within ecological systems with only few species and limited resources, and not with the complexity of species rich systems (McGill *et al.*, 2006a; Tilman, 1982). This changed drastically with the rebirth of neutral models in community ecology (Bell, 2000; Hubbell, 2001).

Neutral Theory

In its version without dispersal limitation Hubbell's model (2001) evolves on the basis of three assumptions: 1) the landscape is saturated with individuals, 2) individuals have the same chance of death, and 3) the probability of recruiting a vacant spot is determined by the abundance of the species present. The first assumption is also referred to as the 'zero-sum game': no species can increase in abundance without a death of an individual in the community, and a vacant spot is instantly taken by a new individual such that the total amount of individuals in the local community remains constant. The other two assumptions are referred to as 'neutral', as every demographic event for each individual of each species is the same, and all individuals are assumed to be ecologically equivalent (Hubbell, 2006). If the model is run without the possibility of immigration, there will be only one species left whose individuals completely dominate the local

community. Processes such as speciation, density dependent mortality, and environmental stochasticity are excluded from the model (Hubbell, 2001).

In the case the local community is connected to a metacommunity in Hubbell's model (2001), a vacant spot can either be taken by a local descendent or an individual that migrated into the local community from the metacommunity. In the metacommunity neutral dynamics reign as well, and each individual of every species has the same chance of migrating into the local community. Dispersal is thus also neutral. Local communities are only connected with each other through the metacommunity, and local communities are not connected with one another through direct dispersal. Dynamics in the metacommunity are regulated by neutral extinction and neutral speciation. The zero-sum rules also apply for the metacommunity, thus its total size in the number of individuals is fixed, although Etienne et al. (2007) showed that models without the zero-sum assumption generated similar results (for further explanation of the model see also Alonso *et al.*, 2006; Chave, 2004).

Two important parameters in Hubbell's neutral model (2001) are the immigration probability m , and the fundamental biodiversity number θ (theta), which is a measure of regional diversity (the diversity of the metacommunity). Theta can be described by the Ewens formula, a sampling formula for neutral alleles (Ewens, 1972). Hubbell's theory makes in fact a lot of use from advancements in population genetics (Chave, 2004; Hu & He, 2006; and see for a complete history Leigh, 2007). Analytically, Hubbell could only make the case for $m = 1$, meaning that the probability of occupying a vacant spot in a local community is the same for individuals of the local and the metacommunity (there is no dispersal limitation). For all the cases where dispersal limitation between a metacommunity and a local community occurred ($m < 1$), simulations were used.

Not long after the publication of Hubbell's neutral theory (2001) the model was analytically solved (McKane *et al.*, 2004; Vallade & Houchmandzadeh, 2003). This led to new research lines in the neutral theory commonly referred to as the 'forward in time' approach. This approach makes use of a mean field master equation with a Markovian description of states and transitions (Alonso & McKane, 2004; McKane *et al.*, 2000; 2004; Vallade & Houchmandzadeh, 2003; 2006; Volkov *et al.*, 2003; 2007). The implications of the approach are that each species is considered against the background of a combination of all other species in such a way that the problem is reduced to a two-species problem. This results in exact analytical expressions for the probability that a single species has a particular abundance in a dispersal-limited local community, but to obtain the

expected number of multiple species with a certain abundance various approximations are needed (Etienne & Alonso, 2005; Etienne & Olff, 2004).

Another approach to the neutral theory is referred to as the 'backward in time' approach (Etienne, 2005; Etienne & Olff, 2004). This genealogical approach is based on coalescent theory, where each individual in the local community can be traced back to a single ancestor that migrated from the metacommunity. The ancestors are a random sample of the metacommunity. This approach leads to the full and exact analytical expression for the multivariate probability of observing a specific species abundance distribution in a sample of a certain number of individuals from the local community (Etienne, 2005; 2007; 2009; Etienne & Alonso, 2005; Etienne & Olff, 2004; Jabot *et al.*, 2008; Munoz *et al.*, 2007).

The neutral theory has received a lot of critique, especially on its neutrality assumption (Clark, 2009), its predictions on speciation (Hubbell, 2003; Ricklefs, 2003; 2006), and in its failing to predict other processes relevant for a general biodiversity theory, such as in ecosystem functioning (Leigh, 2007). The literature on tests of the neutral theory is overwhelming, and stretches over a range of organisms and ecosystems, including tropical trees (Chave, 2004; Condit *et al.*, 2002), coral reefs (Dornelas *et al.*, 2006; Pandolfi, 2006), tropical arthropod communities (Ellwood *et al.*, 2009), birds (McGill, 2003), temperate grasslands (Adler, 2004; Harpole & Tilman, 2006), fynbos vegetation (Etienne *et al.*, 2006; Latimer *et al.*, 2005), freshwater fishes (Muneepeerakul *et al.*, 2008), and intertidal communities (Wootton, 2005), etc. Testing has been difficult mostly because the neutral theory is difficult to falsify, the alternative niche model is not clearly defined, and because the neutral theory is treated as a real null model while it is not (Gotelli & McGill, 2006; McGill *et al.*, 2006b). Chave identified the neutral theory as a special case of niche theory involving equal fitness, and often such niche models generate the same patterns as neutral models (Chave, 2004). However, there is general consensus that the neutral theory has generated several merits by placing an emphasis on dispersal limitation as the prime deterministic process, placing diversity in a historic context, and by providing null hypotheses (Alonso *et al.*, 2006; Beeravolu *et al.*, 2009; Chave, 2004; Leigh, 2007; Ricklefs, 2006). The different lines of research on the neutral theory can also generate new tools, such as the comparison of species abundance models through likelihood theory (Chave *et al.*, 2006a).

Diversity patterns in Amazonian forests

The introduction of neutral models has spurred discussions on the role of ecology in driving diversity patterns (Bell, 2000; 2001; 2003; Hubbell, 1997; 2001). These models assume that species composition changes randomly over geographical distances with dispersal limitation (spatially clumped species) as the main driving process of beta-diversity, the change in species composition over landscapes (Bell, 2000; 2001; Hubbell, 2001, see for explanation below). This has raised a hot debate in rainforest ecology as to the importance of geographical distance (dispersal limitation) and environmental conditions in determining species composition and diversity (Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Ruokolainen *et al.*, 2002; Tuomisto *et al.*, 2003). Before, tree species in the Amazonian forests were seen as habitat specialists, and the richness in habitats was assumed to be the driver of the species richness of these forests (Gentry, 1992; Tuomisto *et al.*, 1995). Seen from this perspective, the Amazonian forests were a predictable assemblage of numerous species. Nevertheless, some studies indeed found that patterns could be well described by predictions of the neutral models. In the forests of Western Amazonia species composition was found to be uniform over large distances, and some species were thought to be habitat generalists (Pitman *et al.*, 1999; 2001; 2002). Another example was the decay in similarity over geographical distance between forest plots and the potential role of dispersal limitation (Condit *et al.*, 2002). A decay in similarity between ecological communities over geographical distances could very well be an intrinsic pattern in various biological groups (Morlon *et al.*, 2008; Nekola & White, 1999; Soininen *et al.*, 2007). Nevertheless, species abundance distributions, species–area and species–time relations, and the distance decay of compositional similarity, appear to be general statistical patterns not unique to ecology. These statistical patterns may be characteristic of many complex dynamical systems, and therefore not necessarily the result of ecological mechanistic processes (Nekola & Brown, 2007). The patterns itself cannot always inform us about mechanism involved, because the scale of resolution at which the mechanism generates the data cannot be discerned (Nee, 2002). Diversity is influenced by regional and local processes, and regional and local diversity interact through processes of dispersal limitation and environmental filtering (Ricklefs, 1987; 2004; Ricklefs & Schluter, 1993; ter Steege & Zagt, 2002). We are still deficient in our understanding on how local diversity is shaped by regional diversity. One of the questions of this study is how local diversity is derived from regional diversity, and to what extent this is

caused by random processes and dispersal limitation (neutral theory) or by environmental filters (niche differentiation theory).

The Guianas

Within the Amazonian forests, the Guiana Shield forms a separate biogeographical region and a distinct floristic province (Huber & Foster, 2003; Lindeman & Mori, 1989). The Guiana Shield, of Pre-Cambrian age, is one of the oldest surfaces of the world (Gibbs & Barron, 1993, see for the geology of the Guiana Shield below). The political deliniation of the Guiana Shield includes French Guiana, Guyana, and Suriname and extends underneath parts of Central Venezuela, Southeastern Colombia, and northern Brazil (Huber, 1995; Huber & Foster, 2003). The Venezuelan Guayana stretches over three states South of the Orinoco River: Amazonas, Bolivar, and Delta Amacuro. These states cover an area of approximately 458 345 km², and hold a population of 1 383 297 inhabitants¹ (see also Huber, 1995). Guyana is approximately 214 970 km² in area, and has a population size of 751 223 inhabitants². Suriname covers an area of 163 820 km², and holds a population of 492 829 inhabitants³, while the territory of French Guiana stretches over an area of 91 000 km², and its population size is estimated at 216 000⁴. In all the countries most populations reside in the coastal areas.

Relevant areas for the current research are the Central and Northern parts of French Guiana, Guyana, and Suriname, and the state of Bolivar in Venezuelan Guayana (see Figure 1.1). Precipitation varies in the Guianas from 1700 – 5000 mm y⁻¹, and is dependent upon topography and the distance and position from the coast line (Huber, 1995; Jetten, 1994; Lindeman & Mori, 1989; Schulz, 1960). In most parts of the Guianas the climate is under influence of the coastal trade winds and the Intertropical Convergence Zone (ITCZ). The movements of the ITCZ causes seasonal changes in the annual distribution of rainfall, and in most parts of the Guianas there are two dry seasons, approximately from September to November and February to April, and two rainy seasons, approximately from May to August and December to January. The timing of the dry and wet seasons differ slightly over the Guianas, and yearly variations in timing and the length of the seasons do occur (Huber, 1995; Jetten, 1994; Lindeman & Mori, 1989; Schulz, 1960; van Kekem *et al.*, 1996). Tree species

¹ <http://www.statoids.com/uve.html>, based on census data from 2001

² <http://www.statisticsguyana.gov.gy>, based on census data from 2002

³ <http://www.statistics-suriname.org>, based on data from 16 January 2007

⁴ <http://www.cr-guyane.fr>, based on data from 2008

respond to these shifts in dry and rainy seasons and show distinct peaks in their flowering and fruiting (Norden *et al.*, 2007; ter Steege & Persaud, 1991).

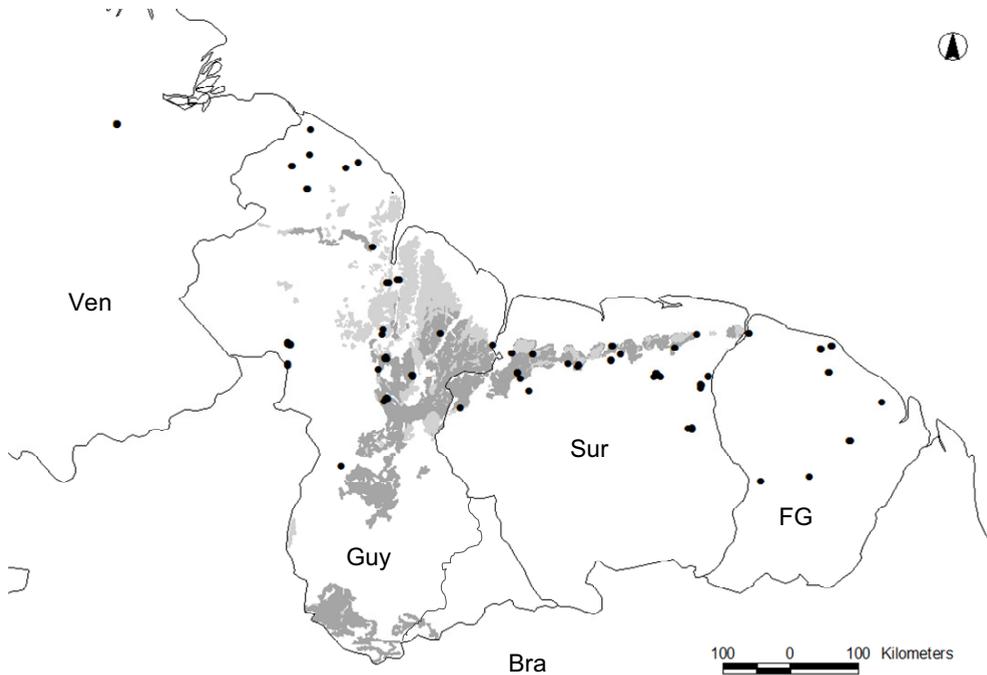


Figure 1.1

Map of the Guianas with the sites of the 156 forest plots used in this study indicated as dots. The grey and lighter grey areas indicate the brown and white sands of the Berbice/Zanderij formation. From left to right the map shows a part of Venezuela (Ven), Guyana (Guy), Suriname (Sur), French Guiana (FG), and at the bottom Brasil (Bra).

There are frequent droughts in the Guianas due to a consistent El Niño–Southern Oscillation (ENSO), that causes each 14 or more years extreme dry years in which the rainfall can drop significantly (Hammond & ter Steege, 1998; Lindeman & Mori, 1989). Such dry spells can have significant effects on tree mortality in the region and in the Amazon forests in general (Davis & Richards, 1933; 1934; Phillips *et al.*, 2009). Moreover, these extreme dry years can cause massive fires that mostly affect forests on well drained white and brown sands, and on man-made savannah areas, swamp and even mangrove forests (Hammond & ter Steege, 1998; Schulz, 1960; Teunissen, 1993; van Anandel, 2003). In fact all over Central Guyana charcoal has been found, that dates back to recent and more ancient times and suggests a peak in fire events between 1000 and 2000 years before present, all over Eastern Amazonia (Hammond *et*

al., 2006). Frequent fires unrelated to the ENSO years can also be observed in the white sand forests and savannahs. These induce the proliferation of certain types of fire climax forests, with tree species such as *Dimorphandra conjugata* and *Humiria balsemifera* (see e.g. Heyligers, 1963). Still, in general the Guiana Shield is an area that is thought to be geologically stable for quite some time, causing very little large scale disturbances for the Guianan forests (Hammond, 2005).

Geology of the Guiana Shield in a nutshell

The Guiana Shield is composed of crystalline rocks mostly of Proterozoic origin, consisting mainly of granites and gneisses that were roughly formed in different phases between 3.6 to 0.8 billion years ago. It is one of the world's oldest earth crusts and it formed the Western part of the continent of Gondwana, with the Western African Shield forming the Eastern Gondwana lands, and the Brazilian Shield the Southern. Approximately 150 million years ago Gondwana broke up and the Atlantic ocean was formed between South America and Africa. Near the end of the Tertiary (25 million years ago) the crystalline basement complex of the Guiana Shield approached its present configuration. In Venezuelan Guayana this basement complex was filled with sediments during various phases between 1.6 and 1 billion years ago, a process that resulted in the quartzite and sandstone rocks of the Roraima group. During the Paleozoic and Mesozoic times the last major rock formation of the Guiana Shield occurred; these are referred to as intrusive rocks because these penetrated the crystalline shield and the sedimentary cover (like the Roraima group) (the above is interpreted from Huber, 1995). In the Tertiary, ironstone caps were formed in the landscape at lower and higher altitudes due to lateritization processes (Gibbs & Barron, 1993; van Kekem *et al.*, 1996). In the late Pliocene, early Pleistocene (around 1.6 million years ago) sediments mainly from the Roraima Formation were deposited in the slowly subsiding basin, covering the Northeastern half of Guyana. Subsequently, the original sedimentary plain has been uplifted and tilted towards the coast. This uplift and tilting also exposed some of the crystalline basement complex (e.g. the granite Inselbergs). The sediments that were deposited in these times are part of the Berbice formation, the White Sand Plateau, that consists of unconsolidated white and brown sands and brown sandy loams, and stretches over Central Guyana, and parts of Suriname (Zanderij/Coesewijne formation) and French Guiana (the above interpreted after Gibbs & Barron, 1993; Jetten, 1994; Schulz, 1960; van Kekem *et al.*, 1996).

Deposits of the Zanderij formation can also have other such as marine origins (Schulz, 1960). In Guyana the white sands can make up layers of more than 2000 m in depth. Where the sandy layers of the Berbice formation are thin, streams have cut through these sandy layers to the crystalline basement complex and have formed more clayey soils. Dolerite dykes are examples of intrusion rocks that are thought to have produced more fertile clays through erosion. A long time period of weathering and the interplay with vegetation changes due to climate, has resulted in a multitude of mostly infertile soils that cover the Guianas in mosaics (Schulz, 1960; van Kekem *et al.*, 1996). The coastal areas in the Guianas, also referred to as the Coropina and Demerara formations, were formed in the Quaternary, mostly in the Holocene (Schulz, 1960; van Donselaar, 1965).

Forest composition in the Guianas

The Guianas beg to disagree with a neutral community structure. Forests in the Guianas are generally thought to be more species poor with a lower tree alpha-diversity compared to Western Amazonian forests (ter Steege *et al.*, 2003; ter Steege *et al.*, 2006; ter Steege *et al.*, 2000b). Forest composition and diversity clearly respond to the mosaic of different soil types in the Guianas (Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Lindeman & Moolenaar, 1959; Maas, 1971; Schulz, 1960; ter Steege *et al.*, 1993). There are several endemic tree species, and these show clear habitat specificity (Davis, 1941; ter Steege *et al.*, 2000a). Very marked floristic differences are found between forests on white sands and forests on brown sands and laterite soils. Forest composition changes immediately at the beginning of white sand patches, and forests are dominated by a few species such as *Eperua falcata*, locally referred to as walaba (Davis & Richards, 1933; 1934). The distribution of *Eperua falcata* and its abundances across soil types in the Guianas is of interest. In Guyana the species is without doubt a dominant of white sand forests. But on the scale of the Northern Guianas it is also the most dominant species, occurring on various soil types, ranging from white sands to laterite soils (Schulz, 1960). Moreover, although flood plain forests at geographical distances in Guyana are dominated by the same tree species (*Mora excelsa*), each forest plot still floristically better resembles a terra firme forests in its direct vicinity, than a flood plain forests at a distance (ter Steege unpublished data). So, despite an important role for environmental conditions in shaping forest composition, at the same time forest composition also tends to change along geographical distance in the Guianas.

Aim of this study

The central question in this thesis is if neutral theory can explain community composition in the Guiana Shield forests. Our objectives are to assess what drives forest composition between forest types, and to what extent do plant attributes respond to environmental conditions? We use a dataset of 156 mostly 1-ha plots in six forest types, ranging over a gradient of 1400 km in the Guianas (see Figure 1.1). Of interest to this thesis is also how the local species pool is derived from the regional species pool in tropical rainforests. Is this mainly through random processes (neutral theory) and influenced principally by dispersal limitation or are environmental filters (niche differentiation theory) important as well? We test both questions based on species abundances of two different forest plot datasets. One dataset involves 38 1-ha plots that are paired in forests on brown and white sands ranging over a gradient of 450 km. These forests on brown and white sands in the Guianas show marked floristic differences and are ideal to study environmental filtering. And another dataset is based on approximately 23 1-ha plots in the lowlands, on the slopes, and on the plateaus of three bauxite mountains in Northeastern Suriname. These bauxite mountains are destined for bauxite mining and may constitute a rare and endangered landscape type.

The specific research questions in this thesis are:

1. What causes the difference in composition between terra firme rain forests on brown and white sands in the Guianas?
2. How does composition differ between forest types in the Guianas, and how much of the floristic variation can be explained by environmental conditions?
3. Can novel neutral-like community models help explain differences in composition and diversity of white and brown sands forests?
4. Can the predictions of the neutral theory aid in an assessment of the conservation value of forests on bauxite mountains in Suriname?

Outline of thesis

Chapter two deals with the question on what causes the difference in species composition between brown and white sands? The original set-up was to develop a natural phytometer to investigate whether dominant tree species performed best, had most leaf nutrients, when growing on their preferred soil type. This set-up did not deliver publishable results, as the dominants of laterite and brown sands soils never occurred on white sands. Instead a review was written on the current state of knowledge on the drivers of species composition between brown and white sand forests.

In **Chapter three** the first biogeographical assessment on a species level, concerning 156 forest plots across the Guianas, is made to determine what the patterns in tree composition and diversity are in the Guianan forests, which plant attributes correlate with composition and diversity, and what that can tell us about the functioning of these forests.

In **Chapter four** the different hypotheses on the low diversity found in white sand forests are tested with neutral-like dynamical community models. We make use of the largest paired plot data set of rainforests on brown and white sands within Amazonia.

Chapter five deals with the predictions of the neutral theory and what these could contribute to the debate on the management of tropical rainforests in respect to conservation approaches. The nature value in terms of tree diversity is assessed of several bauxite mountains in Northeastern Suriname that are prone for bauxite mining of aluminum ore.

Chapter six gives a synthesis on the usefulness and predictive power of neutral models concerning the species abundance distributions in the rainforests of the Guianas. The findings of this thesis are also summarized and discussed.

Next page: *Pachira flaviflora*, white sand forest at Akintosula, Suriname



Chapter 2

What drives the difference in species composition between Amazonian forests on white and brown sands?

Olaf S. Bánki, Hans ter Steege, and Suzanne Rotthier

Abstract

It has long been known that tropical rain forests on white sand differ markedly in species composition from forests on brown sands. What abiotic and/or biotic factors constitute the environmental filter between brown and white sands is less understood and still debated. Here we hypothesize that this environmental filter must act continuously and already at the seedling stage, and we discuss several factors that could be involved in this environmental filter.

Introduction

Amazonian high forests on white sand have considerable floristic affinity to one another mostly at the family and genus level, while the species that dominate these forests may differ (Anderson, 1981; Coomes & Grubb, 1996; Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Fine *et al.*, 2004; Heyligers, 1963; Jiménez *et al.*, 2009; Klinge & Herrera, 1983; Maas, 1971; ter Steege *et al.*, 2000b; Villacorta *et al.*, 2003; this study). Legumes, especially species belonging to the Caesalpinioideae, often dominate these forests (Coomes & Grubb, 1996; ter Steege *et al.*, 2006, this study). Amazonian forests on brown sands have more species overlap with other soil types compared to forests on white sands, and may show substantial decrease in floristic similarity along geographical distances (Davis & Richards, 1933; 1934; ter Steege *et al.*, 2000b; this study). We restrict our discussions here to the non-inundated naturally occurring, fully developed so-called tall forests on white and brown sand soil.

The tall white sand forests can occur on higher topographic grounds with well drained soils and without a distinct root mat, such as is often found in the Guianas (Brouwer, 1996, this study). Or these forests are found at lower topographic positions with a fluctuating ground water table at shallow depths and sometimes with a thick root mat in the upper layer of the soil, such as is often

found in Venezuela (Coomes, 1997; Jordan & Herrera, 1981). Forests on brown sands rather have a tendency to occur on the slopes of the terrain and have well drained soils (van Kekem *et al.*, 1996; this study). In the upper Rio Negro forests on brown sands also have a thick root mat on top of the soil (Jordan & Herrera, 1981).

Tall white sand forests differ structurally from brown sand forests in having a more uniform and lower canopy between 20 to 30 meters in height, a higher number of individual trees above 10 cm dbh but with few trees in the highest dbh classes, and lower species richness per 1 ha plot (based on 38 1-ha plots the first author inventoried in the Guianas). The tall forests on brown and white sands do not differ in standing biomass (Coomes & Grubb, 1996; ter Steege, 2001; but see Klinge & Herrera, 1983). The canopy of white sand forests is relatively open, so more light penetrates into the forest compared to brown sands forests (Coomes & Grubb, 1996; Davis & Richards, 1934). The forests on brown sands have a taller canopy of 35-40 meters in height, with emergent trees, broad tree crowns, and a denser and more developed subcanopy, hence less light is able to penetrate these forests (Davis & Richards, 1933; 1934).

The floristic boundary between white sands and adjacent soil types is so sharp that the species composition changes immediately when one steps from the brown sand onto the white sand (Davis & Richards, 1934, this study). When in Guyana a *Chlorocardium rodiei* (greenheart) tree occurs on the white sand, closer inspection reveals this is merely a shallow layer of white sand on top of a brown sand soil. Our large plot study on brown and white sands in the Guianas confirms a strong environmental filter between these forests. We also provide compelling evidence that environmental filtering of tree species between brown and white sands is asymmetric: dominant tree species on brown sands do not occur or hardly occur on white sands (e.g. *Astrocaryum sciophilum*, *Chlorocardium rodiei*, *Dicorynia guianensis*, *Eschweilera sagotiana*, *Licania alba*, *Mora gongrijpii*, *Vouacapoua americana*), and only few dominant tree species from white sands enter the brown sands with a limited amount of individuals (e.g. *Aspidosperma excelsum*, *Catostemma fragrans*, *Eperua falcata*, *Lecythis corrugata*, *Swartzia bannia*). Additionally, during our field work we observed neither seedlings nor young treelets of brown sand dominants on white sand, while we did observe seedlings of several white sand dominants on brown sands (e.g. *Aspidosperma excelsum*, *Catostemma fragrans*, *Eperua falcata*, *Lecythis corrugata*). Therefore, we hypothesize that the environmental filter between brown and white sands must act continuously and already at the seedling stage.

Factors that are proposed to play a role in the difference between brown and white sands are light availability, water availability, H⁺ and aluminium toxicity, and soil nutrient status. In this paper we discuss to what extent each of these factors on its own account may explain the floristic differences between brown and white sands. We furthermore discuss plant responses to the different growth conditions on brown (haplic ferralsols and ferralic arenosols) and white sands (albic arenosols).

Light availability

As stated above, the canopy of white sand forests is more open, enabling more light to penetrate these forests compared to brown sand forests (Coomes & Grubb, 1996; Davis & Richards, 1934). This can result in a dense understorey of small trees, often belonging to a single species, such as *Anaxagorea dolichocarpa* and *Clusia fockeana* in Suriname (Lindeman & Moolenaar, 1959, this study). Interestingly, the dominant species on white sand, such as *Eperua falcata* (walaba; Davis & Richards, 1934; this study), apparently do not benefit from the presumably better light conditions, as we never find large seedling banks of these species in the white sand forests. Davis and Richards (1934) suggest that *Eperua falcata* is a light demander, and ter Steege (1990, page 54) also classified its seedlings as light-demanding. However, we never observed *Eperua falcata* seedlings on the open savannah areas on white sands. Based on the 38 1-ha plots and our additional field observations several (semi-) dominant species in white sand forests in the Guianas (e.g. *Clusia fockeana*, *Licania incana*, *Matayba opaca*, and *Swartzia bannia*) also occur in thickets and bushes on the open white sand savannas (Heyligers, 1963; van Donselaar, 1965). Moreover, these species also occur in forests on brown sands, albeit in small numbers. In contrast, species from the brown sands that require higher light intensities for germination, such as *Goupia glabra* and *Jacaranda copaia*, hardly occur on white sands even under more open better illuminated conditions. Consequently, light perhaps explains at best only a small part of the differences in species composition between brown and white sands.

Water availability

Several authors have attributed the differences in species composition between brown and white sands to water availability (see Luizão *et al.*, 2007; ter Steege *et al.*, 1993). The white sands have indeed a significantly lower soil moisture retention capacity compared to brown sands (van Kekem *et al.*, 1996). Drought could potentially occur on the deep and well drained white sands in Guyana, but detrimental effects for trees are only expected during prolonged dry periods (Jetten, 1994). It is obvious that such prolonged dry periods do not occur each year, but these infrequent spells could have a significant effect (Davis & Richards, 1933; ter Steege, 1994). The drying of the topsoil could affect the establishment of tree seedlings, especially those with shallow root systems (Engelbrecht & Kursar, 2003; Engelbrecht *et al.*, 2007; Paine *et al.*, 2009). In fact the cohorts of small trees of a single species observed on white sand could be explained by increased survival during more favourable years. Unfortunately we do not know of any reports on seedling mortality of white sand forest species. Even on the brown sands some especially dry years might lead to unusual dry top soils and consequently to massive seedling death. Davis and Richards (1933) reported heavy mortality among *Mora gonggrijpii* seedlings and some other canopy trees in 1925-1926. Those years were exceptionally dry and Davis and Richards suggested: "It is therefore likely that these droughts prevent the vegetation from being as hygrophilous a type as is allowed by the average climate". Severe droughts such as in 1925-1926 also occurred in 1911-1912 and 1931-1932 as well as in more recent years such as in 1997-1998 and are not uncommon in Guyana (Hammond & ter Steege, 1998; ter Steege, 1993). Overall, when drought occurs it causes tree mortality throughout the Amazon on various soil types (Phillips *et al.*, 2009). On the seasonally waterlogged white sands at San Carlos de Rio Negro there is no supporting evidence that soils dry out on a regular basis (Franco & Dezzeo, 1994). The same counts for the white sands at La Esmeralda, where during drier months the water table drops to more than 1 meter depth in the soil, but tensiometers at 30 cm depth did not indicate significant water shortage (Coomes & Grubb, 1996). Nevertheless, the differences in floristic composition of the forests on white or brown sands are large in both La Esmeralda and San Carlos de Rio Negro. The differences in water retention capacities in the top soil layers on white and brown sand substrates may at times be a significant explanative factor for the strong differences in floristic composition of the two forest types.

H⁺ and aluminium toxicity

Both brown and white sands are acid soils. The white sands consist for almost 100% of pure quartz sand with low clay content, and this causes a low buffering capacity of acidity (van Kekem *et al.*, 1996). The difference in effective cation exchange capacity (ECEC) between brown and white sands is significant in Central Guyana, white brown sands having higher ECEC values (ANOVA, $F_{[1,98]} = 11.867$, $p = 0.001$). On white sands the ECEC is mostly determined by H⁺ ions that occupy the negatively charged sites of the soil particles (van Kekem *et al.*, 1996; Table 2.1). This has led some authors to hypothesize that H⁺ toxicity could be operative on the white sands, while conversely aluminium toxicity could be operative on brown sands (Luizão *et al.*, 2007; Proctor, 1999). Both H⁺ and aluminium toxicity can occur on acid soils and can have detrimental effects on plants, although plants may also tolerate or evade such toxicities. Evasion of H⁺ toxicity can be achieved by changes in the rhizosphere like pH increase, and in the case of aluminium for example by the release of chelators (Marschner, 1991). Klinge *et al.* (1977) and Luizão *et al.* (2007) both reported high H⁺/Al³⁺ ratio's for white sands (Table 2.1). While van Kekem *et al.* (1996) reported significantly lower levels of aluminium on white sands (Mann-Whitney U $p = 0.000$, Table 2.1). The ECEC on brown sands is mostly determined by both H⁺ and Al³⁺, and the concentration of H⁺ ions is at times similar to that found on white sands (van Kekem *et al.*, 1996; Table 2.1). The pH (both H₂O and KCl) between the brown and white sands is not significantly different (van Kekem *et al.*, 1996; Table 2.1).

Inorganically bound aluminium is released from the soil if the pH drops below 3.5 (see Figure 16 in ter Steege *et al.*, 1996). Such low pH values do occur in gaps, but are uncommon under normal forested conditions (Brouwer, 1996; ter Steege *et al.*, 1996). Ter Steege and Alexander (unpubl. data) found that both brown and white sand climax species were equally affected by aluminium (Al³⁺). Concluding from this evidence there is little direct support for H⁺ and aluminium toxicity as the driving forces for the difference in species composition between forests on brown and white sands.

Table 2.1 Exchangeable soil nutrients between white and brown sands under forested conditions at several sites in Amazonia.

Location	Soil (white=bold) (brown=italic)	Depth cm	pH H2O	pH KCl	CEC	ECEC	BS (%)	BT	Exchangeable Acidity (H+Al)	AI	H+/Al3+ ratio	C (%)	N (%)	P-Bray mg Kg-1	C:N
Brazil, Manaus ¹	Podzol	0-30	3.97	-	3.06	-	-	0.56	-	-	14.53	-	0.04	-	34.7
	<i>Oxisol</i>	0-30	4.1	-	15.51	-	-	0.35	-	-	0.24	-	0.07	-	25.53
	Entisol	0-10	4.7	-	1.98	-	7	0.1	-	0.6	-	0.76	0.03	2	-
Manaus ²	<i>Oxisol</i>	0-10	4.4	-	8.49	-	7.7	0.58	-	1.6	-	2.26	0.25	4	-
	Podzolised soils	0-20	-	3.1	4	-	23	0.6	0.5	-	-	1.40	-	3	-
Aracacura ³ Aracacura	<i>Acric-Ferralsols</i>	50-100	-	3.7	2	-	27	0.5	0.2	-	-	0.15	-	1	-
		0-20	4.2	-	16*	-	9	0.6	1.6	-	-	1.39	-	2	-
		50-100	4.9	-	14*	-	13	0.6	1.2	-	-	0.34	-	1	-
Guyana, Mabura Hill ⁴	Albic Arenosol	0-30	-	-	1.1	-	-	0.05	-	-	-	-	-	4	-
	<i>Ferralsol / Ferralic Arenosol</i>	0-30	-	-	3	-	-	0.048	-	-	-	-	-	2.8	-
Guyana, Mabura Hill ⁵	Albic Arenosol	0-40	4.37	3.2	4.96	0.87	4	0.19	0.56	0	-	1.54	0.08	1.29	17.00
	<i>Ferralsol / Ferralic Arenosol</i>	70-200	5.93	4.85	0.3	0	0	0.13	0	0	-	-	-	0.13	-
Venezuela, San Carlos do Rio Negro ⁶		0-45	4.40	3.82	4.09	1.62	8.31	0.36	1.26	0.70	-	1.32	0.08	1.52	13.79
	Podzol	100-300	4.83	4.42	2.42	0.71	8.53	0.12	0.59	0.33	-	0.14	0.02	0.22	5.00
		0-40	4.33	-	-	-	-	1.51	-	-	19.30	9.19	-	-	-
		100-140	4.54	-	-	-	-	0.07	-	-	14.70	13.21	-	-	-

CEC, ECEC, BT, Al in cmol/kg; BT = sum of exchangeable cations Ca, K, Mg, Na; BS = base saturation

* CEC7 clay corrected for C

¹ (Luizão *et al.*, 2007)

² (Anderson, 1981)

³ (Duijvenvoorden & Lips, 1995, table 2.5 B & C)

⁴ (Brouwer, 1996, table 3.3)

⁵ (van Kekem *et al.*, 1996, profiles 2,4,6-8,10-12,15,23,26-28,30-32,35)

⁶ (Klinge *et al.*, 1977)

Table 2.2 Total soil nutrients in white and brown sands under forested conditions at several sites in Amazonia.

Location	Soil (white=bold) (brown=italic)	Depth (cm)	Al	B	C	Ca	Cu	Fe	K	Mg	Mn	Mo	N	Na	P	S	Zn
Brazil ¹	Podzol	0-3	-	-	-	40	3.8	1193	100	136	17	-	1577	28	tr*	-	-
		60-62	-	-	-	37	2.5	1515	68	40	31.6	-	354	35	tr*	-	-
Colombia ²	Podzol	0-20	-	-	-	27	-	92	92	30	-	-	440	38	26	-	-
Aracuara	<i>Acric-Ferralsols</i>	20-50	-	-	-	45	-	61	61	19	-	-	85	40	16	-	-
		0-20	-	-	-	64	-	270	270	210	-	-	1040	104	124	-	-
		50-100	-	-	-	65	-	490	490	340	-	-	380	160	143	-	-
Guyana ³	Albic Arenosol	0-30	30	4.5	5800	70	-	70	19.1	16.6	2.8	0.3	330	17.5	15	36.3	1.9
	<i>Ferralsol / Ferralic Arenosol</i>	0-30	11600	4.1	8640	40	-	5130	84.8	82.9	22	0.67	690	29.5	52.7	80	6.3
Mabura Hill	<i>Arenosol</i>	60-62	-	-	-	500	7.3	14	38	200	0.5	-	1050	20	25	-	-
Suriname ¹	Albic Arenosol	0-3	-	-	-	750	5	83	37	100	0.5	-	800	10	0	-	-
Jodensavanne	Albic Arenosol [#]	0-3	-	-	-	900	9	13500	500	1400	2.8	-	2620	40	113	-	-
	<i>Laterite</i>	60-62	-	-	-	700	9	63	38	900	0.5	-	1500	20	tr	-	-
Venezuela ⁴	Albic Arenosol	0-10	-	-	-	-	-	-	-	-	-	-	3000**	-	85**	-	-
La Esmeralda		0-20	-	-	-	-	-	-	-	-	-	-	3570***	-	72***	-	-
		0-20	-	-	-	-	-	-	-	-	-	-	450****	-	35****	-	-
		40-45	-	-	-	-	-	-	-	-	-	-	0	-	7	-	-
	<i>Ferralsol / Ferralic Arenosol</i>	0-10	-	-	-	-	-	-	-	-	-	-	2950	-	44	-	-
		0-20	-	-	-	-	-	-	-	-	-	-	1210	-	27	-	-

¹ (Stark, 1970); * tr = trace < 1 mg kg⁻¹; # bare white sand, not forested;

² (Duivenvoorden & Lips, 1995, table 2.6)

³ (Brouwer, 1996, table 3.4)

⁴ (Coomes, 1997), this soil is seasonally waterlogged creating a landscape of bumps (hummocks) and trenches (hollows); ** soil measurement on hummocks + hollows; *** soil measurement on hummocks, **** soil measurement on hollows.

Available and total soil nutrients

In general the white sands are thought to be poorer in nutrients and this could cause the difference in species composition between brown and white sands. Both brown and white sands in the Guianas and the Upper Rio Negro are exceedingly weathered and leached. Cation exchange capacity (CEC, Mann-Whitney U $p= 0.001$) and sum of bases (BS, Mann-Whitney U $p= 0.022$) were significantly higher on brown compared to white sands in Central Guyana, while N, P, Ca, Mg, Na, K, organic C, C/N, were not significantly different (van Kekem *et al.*, 1996; Table 2.1). In fact, several studies imply that the differences in exchangeable cations, N and P are not large between the brown and white sands (Table 2.1). This could lead to the suggestion that available soil nutrients are similar between brown and white sands (Klinge *et al.*, 1977; Raaimakers, 1994). However, when total nutrients are compared, the brown sands have far more nutrients, including for N and P, than the white sands (Brouwer, 1996, Table 2.2). On the other hand, the methods used to quantify available nutrients may not fully reflect the nutrient availability for plants in tropical soils (see Quesada *et al.*, 2009b). Binding of cations such as with sesquioxides might immobilize the nutrients for plant up take in the brown sands (Raaimakers, 1994). It is unclear whether trees are able to draw on the inorganically bound nutrient resources (Brouwer, 1996; Silver, 1994).

Mycorrhizae (Jordan & Herrera, 1981; Torti *et al.*, 2001) or other adaptations of plants, such as ericoid-, proteoid- (or cluster-) roots (Lambers *et al.*, 2008) might also aid in releasing inorganically bound nutrients. There was no support however that the occurrence of ectomycorrhizas or arbuscular mycorrhizas was very different between forests on brown and white sands in Venezuela (Moyersoen *et al.*, 2001).

Jordan (1982) suggests that forest at San Carlos de Rio Negro maintain itself through nutrient input from the atmosphere, and prevention of leaching nutrients from the top soil layers through tight nutrient cycling (Jordan & Herrera, 1981). Although forests on brown and white sands are thought to depend on phosphorous derived from organic matter (Jordan, 1982; Tiessen *et al.*, 1994), recent studies indicate that phosphorus cycling is more complicated (Chacón *et al.*, 2008; Chacon *et al.*, 2006; McGroddy *et al.*, 2008; Peretyazhko & Sposito, 2005; Quesada *et al.*, 2009b). Under soil conditions where temporary anaerobic conditions occur, due to inundation or high rainfall, phosphorous bound to Fe and Al oxides could be transferred to organic layers and become available for plant uptake (Chacón *et al.*, 2008; Peretyazhko & Sposito, 2005).

Additionally, Quesada *et al.* (2009b) suggested that soil phosphorus levels exert an important influence on nitrogen cycling, and low P availability may very well lead to N-limitation. White sands as well as some brown sands (ferralic arenosols) have very low phosphorus levels compared to other soil types in Amazonia (Quesada *et al.*, 2009b). Although it is not reflected in available nutrients, the differences in total nutrients between the brown and white sands are large and this may affect the floristic differences found on the two soil types.

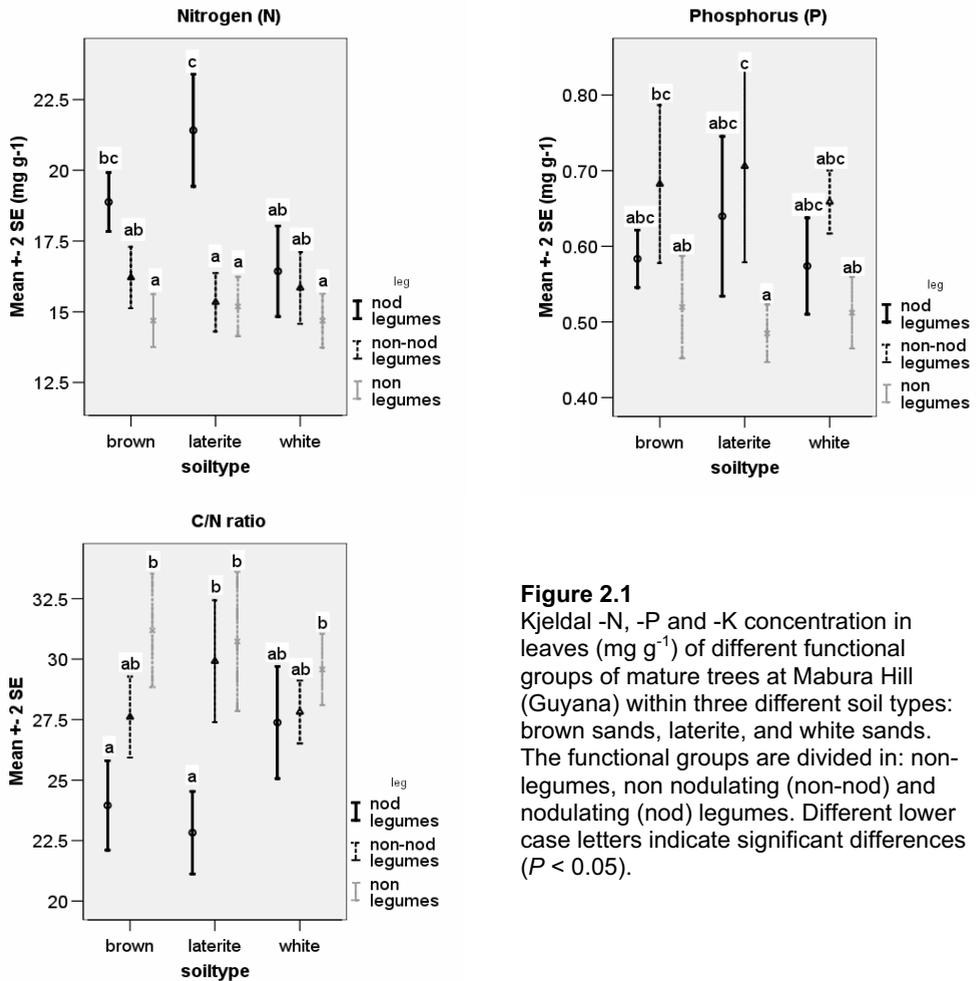


Figure 2.1 Kjeldal -N, -P and -K concentration in leaves (mg g^{-1}) of different functional groups of mature trees at Mabura Hill (Guyana) within three different soil types: brown sands, laterite, and white sands. The functional groups are divided into: non-legumes, non nodulating (non-nod) and nodulating (nod) legumes. Different lower case letters indicate significant differences ($P < 0.05$).

Foliar nutrients

Foliar nutrients seem to correlate well with the overall nutrient status of trees, and with soil fertility (Fyllas *et al.*, 2009; Vitousek & Sanford, 1986). In Amazonia, tree species that tend to occupy more fertile soils have higher intrinsic N, P, K, Mg, and $\delta^{13}\text{C}$ (Fyllas *et al.*, 2009). There is also a genetic effect on leaf nutrient status (Fyllas *et al.*, 2009; Watanabe *et al.*, 2007). Some foliar characteristics like P, K, Ca, $\delta^{13}\text{C}$ seem to be more determined by local growth conditions in Amazonia, while others like C, N, and Mg seem to be highly taxonomically constrained (Fyllas *et al.*, 2009). All legumes have significantly higher foliar N compared to non-legumes, although some genera such as *Eperua*, a genus that dominates on white sands both in the Guianas and in the Rio Negro, have on average lower foliar N compared to other legume genera (Fyllas *et al.*, 2009).

Two studies in Mabura Hill found significant differences in foliar N between tree species in forests on brown and white sands (ANOVA, $F_{[1,4]} = 10.683$, $p = 0.031$, Brouwer 1996; ANOVA, $F_{[1,32]} = 9.300$, $p = 0.005$, Perreijn 2002; see Table 2.3). We found significantly higher foliar N at Mabura Hill on laterite and white sand, but not in brown as compared to white sands (ANOVA, $F_{[2,136]} = 3.755$, $p = 0.026$; Bonferroni, $p = 0.008$) (see Table 2.4 for data, and Rotthier, 2007 for methods). Perreijn (2002) found significantly higher foliar N in nodulating legumes compared to non-nodulating legumes and non-legumes across four soil types, including brown and white sands (ANOVA, $F_{[2, 550]} = 89.22$, $p = 0.000$). In our study foliar N of nodulating legumes was significantly higher on laterite, although not on white sands (ANOVA, $F = 34.873$, $p = 0.000$; Figure 2.1). Foliar P did not differ between soil types, and differed hardly between functional groups, (Figure 2.1, see also Perreijn, 2002). Foliar K showed no significant difference at all. C:N ratio showed significant differences between functional groups (ANOVA, $F = 21.624$, $p = 0.000$), although not on white sands (Figure 2.1). At San Carlos de Rio Negro one study found significantly lower foliar N, while another study found significantly higher foliar Mg (data not shown) and K on white sands (Cuevas & Medina, 1988; Reich *et al.*, 1994, Table 2.3). Other studies in Amazonia showed no significant differences in foliar N between brown and white sands (Table 2.3).

Keeping in mind the large differences in species composition between brown and white sands, the differences in foliar nutrients are less sharp than expected. The above lends little support to the suggestion that the concentration of foliar nutrient levels on white sands is lower than those on brown sands.

Leaf litter and productivity

While foliar nutrients did not show clear differences, several studies in forests on brown and white sands showed significantly lower leaf litter fall (ANOVA, $F_{[1,32]} = 20.922$, $p = 0.000$), and a significantly lower total small litter fall (ANOVA, $F_{[1,36]} = 6.630$, $p = 0.014$) in forest on white sand (see Figure 2.2). Productivity in terms of leaf and total small litter fall is a factor 1.35 lower in forests on white sands. Of the leaf litter nutrients only leaf N is significantly lower in forests on white sands (ANOVA, $F_{[1,30]} = 22.013$, $p = 0.000$). The total N in leaf litter per year (see Figure 2.2) is two times higher in forests on brown sands compared to forest on white sands (ANOVA, $F_{[1,26]} = 36.082$, $p = 0.000$). This suggests N-limitation in white sand forests. The rate of decomposition of (leaf) litter is slower as well in white sand forests compared to forests on brown sands (Cuevas & Medina, 1988). Studies in Mabura Hill and in La Esmeralda found high P-resorption before leaf fall in tree species on both brown and white sands, suggesting P-limitation on both soils (Coomes, 1997; Raaimakers, 1994). The N-limitation on white sands may slow overall growth on white sands. Wood productivity at San Carlos de Rio Negro is $1.53 \text{ mg C ha}^{-1}\text{a}^{-1}$ on white sand, while on brown sands this was 1.76 and $2.47 \text{ mg C ha}^{-1}\text{a}^{-1}$ with an average of $3.1 \text{ Mg C ha}^{-1}\text{a}^{-1}$ for all Neotropical plots (see data in Malhi *et al.*, 2004). At Zafira in Colombia wood productivity on a white sand plot was $1.3 \text{ mg C ha}^{-1}\text{a}^{-1}$ (Aragao *et al.*, 2009). Thus white sand forests indeed seem to show slower growth, and seem to be N-limited as well as P-limited.

N₂-fixation

If N is limiting on white sands, why do N₂-fixers not have an overriding competitive advantage in these forests? Forest inventories across Amazonia (ter Steege *et al.*, 2006) showed that N₂-fixation cannot explain the dominance of legumes on poor soils. Our 38 1-ha plots did not show significant differences in the percentage of individual trees belonging to N₂-fixers on brown and white sands in the Guianas. Reliable estimates of N₂-fixation for white sand forests are troublesome as available soil nitrogen ($\delta^{15}\text{N}$) is isotopically similar to fixed-N₂ (Perreijn, 2002; Roggy *et al.*, 1999a). There is substantial evidence that symbiotic N₂-fixation is contributing to high amounts of soil available N in forests on brown sands in Guyana and French Guiana (Perreijn, 2002; Pons *et al.*, 2007; Roggy *et al.*, 1999a; Roggy *et al.*, 1999b). Nardoto *et al.* (2008) found to the

contrary that leguminous trees did not fix atmospheric N in the Brazilian Amazon. Houlton *et al.* (2008) suggested that N₂-fixation is an advantage in P-limited ecosystems as more N could be assigned to P acquisition from organic pools (see also Davidson, 2008). It is also possible that P is limiting the ability to fix nitrogen (Perreijn, 2002; Pons *et al.*, 2007). On white sands a co-limitation of P and N could seriously diminish the ability to fix nitrogen, especially on the brown sands (arenosols) and white sands where both low P- and low N-availability occur in the soils (Quesada *et al.*, 2009b).

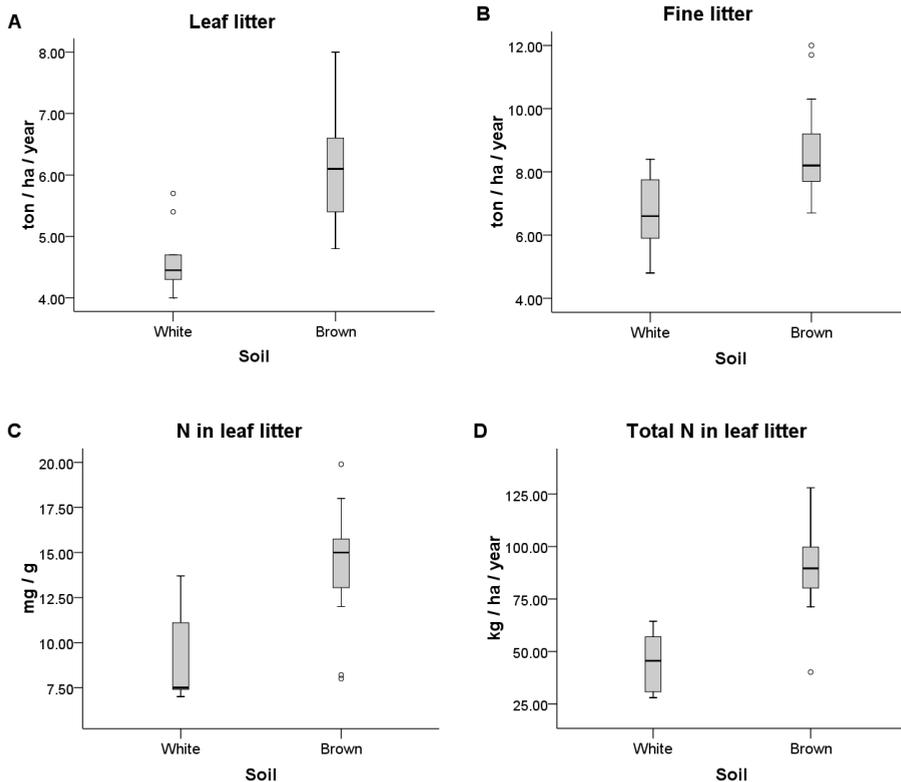


Figure 2.2

Above the average leaf litter (A) and fine litter fall (B) of various studies in forests on white and brown sands in South America is shown. The N concentration in leaf litter (C) is also given, as well as the total N (D) that is thought to pass through the leaf litter into the system in the white and brown sands. White sands have significantly lower leaf litter fall, fine litter fall, N concentration in leaf litter, and total N on a yearly basis compared to brown sands ($P < 0.05$). The following data is used: (Coomes, 1997; Cooper, 1982; Dantas & Phillipson, 1989; Luizao, 1989). Also data is used from references cited in: (Brouwer, 1996; Duivenvoorden & Lips, 1995; Lips & Duivenvoorden, 1996; Proctor, 1984; Scott *et al.*, 1992; Thomas, 2001).

Table 2.3 Nutrient concentration, specific leaf area (SLA) and C:N ratio of mature leaves from adult trees of species on white sand and brown sand on various locations across the Amazon. Values are given as average element concentration per soil per publication. Bold indicates a significant difference ($P < 0.05$) between brown and white sands.

Location	N mg.g ⁻¹		P mg.g ⁻¹		K mg.g ⁻¹		C mg.g ⁻¹		SLA m ² .kg		C/N g.g ⁻¹	
	White	Brown	White	Brown	White	Brown	White	Brown	White	Brown	White	Brown
	Brazil ¹	28.3		2.5		6.5						
Brazil, Manaus ²	10.8		0.56		5.8							
Brazil, Manaus ³	12.8											40.2
French Guiana Piste st Elie ⁴	20.7	21.7										
French Guiana Paracou ⁵	15.8			0.59					7.1			
Guyana Mabura Hill ⁶	10.8	14.0	0.19	0.17	1.6	1.1						
Guyana Mabura Hill ⁷	16.4	16.8	0.6	0.6								
Guyana Mabura Hill ⁸	14.8	20.5	0.49	0.57	3.9	3.9	515	519			35	27
Guyana Mabura Hill ⁹	15.2	17.1	0.56	0.59	3.6	3.0	519	525	6.7	7.1	28.7	26.8
Suriname, Zanderij ¹	20.4*	16.2**	1.4	1.25	1.5*	14.25**						
Venezuela La Esmeralda ¹⁰	7.5		0.18		2.0							
Venezuela San Carlos ¹¹	9.2	13.4	0.91	0.63	7.5	4.4	510	520	7.7	6.7	56.9	40.5
Venezuela San Carlos ¹²	12	12	0.7	0.6								
Venezuela San Carlos ¹³	10	16.2										
Averages	14.5	16.4	0.81	0.63	4.1	5.3	513	520	7.1	7.1	39.7	31

* data of one species *Dimorphandra conjugata* a dominant species of a fire climax forest with a very thick leaf litter layer and the presence of numerous mycorrhizal fungi.

** data from a laterite soil

¹ (Stark, 1970), ² (Klinge, 1985), ³ (Mardegan et al., 2008), ⁴ (Roggy et al., 1999a), ⁵ (Guehl et al., 1998), ⁶ (Brouwer, 1996), ⁷ (Raaimakers, 1994), ⁸ (Perreijn, 2002), ⁹ this study, ¹⁰ (Coomes, 1997), ¹¹ (Cuevas & Medina, 1988), ¹² (Medina et al., 1990), ¹³ (Reich et al., 1994).

Table 2.4. Below the nitrogen and phosphorus concentrations of mature sunlit leaves of canopy trees of dominant species on the white sand, brown sand, and the laterite soils at Mabura Hill are given (Guyana). Average concentration of species per soil type is given with standard deviation between brackets. Bold numbers are used for species dominant on the specific soil type. Functional legume status of species (nodulation) is given with numbers: non-legumes (0); non-nodulating legumes (1) and nodulating legumes (2) (see for methods Rothier, 2007).

Genus	Species	nod	white sand			brown sand			laterite		
			n	N (SD)	P(SD)	n	N (SD)	P (SD)	n	N (SD)	P (SD)
<i>Chamaecrista</i>	<i>adiantifolia</i>	2	4	16.2 (3.7)	0.60 (0.12)						
<i>Licania</i>	<i>buxifolia</i>	0	5	16.5 (2.1)	0.41 (0.07)						
<i>Ormosia</i>	<i>coutinhoi</i>	2	5	14.4 (1.4)	0.47 (0.07)						
<i>Talisia</i>	<i>squarrosa</i>	0	5	11.8 (1.6)	0.57 (0.09)						
<i>Aspidosperma</i>	<i>excelsum</i>	0	5	15.2 (0.7)	0.46 (0.12)	5	15.7 (0.9)	0.50 (0.12)	3	15.4 (1.5)	0.50 (0.08)
<i>Catostemma</i>	<i>fragrans</i>	0	5	14.8 (1.5)	0.62 (0.05)	4	14.0 (1.9)	0.57 (0.06)	4	13.7 (2.2)	0.58 (0.07)
<i>Eperua</i>	<i>falcata</i>	1	5	14.5 (1.3)	0.62 (0.05)	5	15.9 (1.8)	0.65 (0.05)	5	14.9 (1.5)	0.74 (0.36)
<i>Licania</i>	<i>alba</i>	0				3	11.9 (3.0)	0.38 (0.09)			
<i>Talisia</i>	<i>furfuracea</i>	0				3	12.0 (1.1)	0.53 (0.14)			
<i>Chlorocardium</i>	<i>rodiei</i>	0				5	17.5 (0.9)	0.46 (0.06)	5	17.3 (1.2)	0.46 (0.05)
<i>Eschweilera</i>	<i>sagofiana</i>	0				5	14.7 (1.5)	0.62 (0.34)	5	14.1 (2.2)	0.43 (0.05)
<i>Mora</i>	<i>gonggrijpii</i>	1				5	14.4 (1.2)	0.69 (0.14)	5	13.7 (1.2)	0.65 (0.22)
<i>Chamaecrista</i>	<i>apoucouita</i>	2	4	19.1 (1.1)	0.66 (0.04)	5	18.0 (2.0)	0.54 (0.03)	5	22.1 (5.9)	0.79 (0.31)
<i>Dicymbe</i>	<i>altsonii</i>	1	5	17.2 (1.6)	0.69 (0.07)	5	18.2 (1.2)	0.67 (0.05)			
<i>Clairotropis</i>	<i>brachypetala</i>	2				4	18.0 (1.5)	0.62 (0.07)	5	19.0 (1.2)	0.58 (0.06)
<i>Swartzia</i>	<i>leioalycina</i>	2				5	20.5 (1.3)	0.60 (0.09)	5	23.1 (1.8)	0.55 (0.07)
<i>Voacapoua</i>	<i>macropetala</i>	1				4	16.3 (3.7)	0.73 (0.52)	5	17.4 (1.3)	0.73 (0.16)

Plant responses to low nutrients: possibly trade-offs

Overall it would appear that, even though it has not been firmly proven, nutrients must play a pivotal role in the differentiation of forest composition of brown and white sands. One of the questions that need to be answered to further support this is what the underlying mechanism(s) would be.

Over the full area of the Amazonian rainforest there exists a gradient of soil fertility. This gradient in fertility is followed closely by a gradient in productivity (see Malhi *et al.*, 2004), composition and diversity, and average community and seed mass (ter Steege *et al.*, 2006). The largest average seed size was found and was related to the dominance of legumes, on the nutrient poor soils of the Guianas (ter Steege *et al.*, 2006). Based on our 38 1-ha plots in the Guianas community weighted seed mass was higher in forests on white sand compared to forests on brown sands, suggesting that more trees with larger seeds occur on the white sand (ANOVA, $F_{[1,36]} = 16.15$, $p = 0.0003$). Bigger seeds suggest shade tolerance of seedlings (Poorter & Rose, 2005) and may provide extra nutrients for the growth of seedlings on poor soils (but see Coomes & Grubb, 2003). Highest leaf P and N concentrations were indeed found in leguminous saplings on white sands compared to brown sands in Mabura hill (Raaimakers, 1994). Nutrient additions at Manaus increased the survival of seedlings growing in the high white sand forests, but had no effect on seedling survival in forests on brown sands (Luizão *et al.*, 2007). The above supports the role of low nutrients, especially N and P, in determining the difference in composition between brown and white sands.

Moreover, adaptive trade offs for growth on white sands could explain the difference in species composition observed with brown sands. One such trade off is proposed by Fine *et al.* (2004), based on fast growth and juicy leaves versus slow growth and tough leaves (Marquis, 2004; Shipley *et al.*, 2006; Whitfield, 2006; Wright *et al.*, 2004). White sand dominants grew slower on white sands, but were better protected against herbivore attacks, while laterite dominants grew faster on both laterite and white sands but suffered more herbivore attacks with detrimental effect on the white sands (Fine *et al.*, 2004; 2006). Other trade offs, where adaptations to the slow growth on white sands cause either detrimental effects or a diminished competitive advantage on brown sands could also be operative.

Concluding remarks

Of the factors that could contribute to the environmental filter between forests on brown and white sands, soil nutrient status is currently the only convincing candidate to explain, on its own account a continuous and strong filter that is already operative at the seedling stage. White sands seem to be more N and P limited than brown sands. In some cases, the lower soil moisture content in the upper white sand layer may affect seedling survival, and this could contribute to the observed floristic differences between brown and white sand forests. Adaptations to slower growth on white sands may also inflict trade-offs for tree species growth on other soil types. To what extent the other factors discussed in this paper are involved in such trade-offs remains less clear at this point in time.

Next page: *Dimorphandra* cf. *multiflora*, rainforest on slope of Brownsberg, Suriname



Chapter 3

Tree Diversity Patterns in the Guianas

Olaf Bánki, Daniel Sabatier, Jean-François Molino, Terry Henkel, Hernan Castellanos, Hans ter Steege, Raquel Thomas, and Marinus Werger

Abstract

A study on the biogeographical patterns in tree diversity in the Guianas, involving 156 forest plots and six forest types, revealed clear floristic differences, a longitudinal gradient in tree alpha-diversity, and an equal role of environmental conditions and geographical distance in determining forest composition. Species composition was also found to follow geological patterns. Plant attributes in the Guianan forests revealed a spectrum of covariation with on the one hand dry fruits and large seeds with high wood densities, and on the other fleshy fruits with smaller seeds and lower wood densities. We discuss to what extent this spectrum in covariation in plant attributes could be related to different functional strategies of trees in the forests of the Guianas.

Introduction

One of the basic questions in tropical forest ecology is what drives tree species occurrence and abundance in tropical rainforests. In recent years, research on large scale forest plot datasets in the Neotropics have started to unravel biogeographical patterns and their possible underlying processes (Condit *et al.*, 2002; ter Steege *et al.*, 2006). Several of the current ecological processes that are thought to drive patterns in tropical forest composition and diversity are: 1) seasonality and soil fertility, 2) intermediate disturbances, 3) dispersal limitation, and 4) density dependant mortality (Bongers *et al.*, 2009; Condit *et al.*, 2002; Connell, 1978; Engelbrecht *et al.*, 2007; Givnish, 1999; Janzen, 1970; Malhi *et al.*, 2004; Molino & Sabatier, 2001; Phillips *et al.*, 2009; Quesada *et al.*, 2009a; ter Steege *et al.*, 2003). Historical processes, such as paleo-climatic and geological events, and landscape features such as topography may also have their imprint on current diversity patterns and gradients in forest composition (Stropp *et al.*, 2009; Valencia *et al.*, 2004). Forest composition could also be

merely a random draw of species from a metacommunity or regional species pool, as is assumed by dynamical neutral community models (Bell, 2001; Hubbell, 2001). These neutral models have spurred discussions on the relative role of habitat, geographical distance, dispersal limitation, and historical processes on species composition (Chave & Leigh, 2002; Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Ruokolainen *et al.*, 2002; Tuomisto *et al.*, 2003; Chapter 4).

In Amazonia, the families and genera represented by canopy trees differ substantially between geographical regions, and their dominance can be partly explained by plant functional traits (Fyllas *et al.*, 2009; ter Steege *et al.*, 2006; Terborgh & Andresen, 1998). Habitat differentiation (including precipitation), geographical distance and dispersal limitation are the probable causes of the high beta-diversity, the rate of change in species composition over landscapes, in tropical lowland rainforests of Panama and Western Amazonia (Condit *et al.*, 2002). In Panama, beta-diversity is high due to habitat differentiation, while the lowland tropical rainforest of Peru and Ecuador may show a rather uniform composition over large geographical areas (Condit *et al.*, 2002; Pitman *et al.*, 1999; 2001). However, in the lowland forest of Panama geographical distance still 'statistically explained' more variation in species composition (22-27%) than did environmental conditions (10-12%), and the interaction between the two accounted for 13 to 18% of variation in species composition (Chust *et al.*, 2006). In South-East Peru, the tree floristic variation was mostly explained by abiotic habitat conditions (40%), with geographical distance representing only 10% of the variation (Phillips *et al.*, 2003). These differences between areas, based on large scale plot studies, clearly show that floristic variation in composition in different geographical regions within one continent of tropical rainforests correlate to different degrees with different factors.

The Guiana Shield forms a separate floristic biogeographical region within Amazonia (Lindeman & Mori, 1989). The Guianas reportedly have low tree alpha-diversity compared to Western Amazonia, and a relatively high endemism and habitat specificity of tree species (Davis, 1941; ter Steege *et al.*, 2000a). The lowland rainforests in the Guiana Shield are also dominated by species with substantial higher wood densities and larger seeds compared to Western Amazonian forests (ter Steege *et al.*, 2006). Both patterns in seed mass and wood density suggest long-term low disturbances in the Guiana Shield compared to Western Amazonia (ter Steege *et al.*, 2006). Climatic differences in terms of precipitation and seasonality are not strong in the Guianas, and their explanatory power, especially in our research areas is not high (Haripersaud, 2009). The

Guiana Shield itself is of Precambrian origin, and the soils are old, leached and rather nutrient poor (Gibbs & Barron, 1993; Quesada *et al.*, 2009b; van Kekem *et al.*, 1996). In the Guianas the landscape is formed by a mosaic of different soil types that alternate with each other at short distances. Gradients in forest composition partly respond to these differences in soil types, and species composition is suggested to follow geological patterns (Davis & Richards, 1933; 1934; Lindeman & Moolenaar, 1959; Schulz, 1960). Forest inventories on a genus level in the Guianas indeed showed that tree genera may follow geological patterns, contrasting between the sandy soils of central Guyana and the soils of the Guiana Shield basement complex in Suriname and French Guiana (ter Steege & Zondervan, 2000). Testing and quantification of environmental, and geographical responses in variation of forest composition at a species level within the Guianas has been lacking so far.

Here we perform the first biogeographic assessment on a species level of 156 mostly 1-ha plots in the Guianas, spanning a gradient of c. 1400 km from Venezuela to French Guiana (see Figure 1.1). This large scale plot dataset contains terra firme lowland tropical rainforest on brown sands and laterite clays, flood plain forest, forest on bauxite plateaus (between 500-700 meter above sea level), swamp forest, savannah forest (a xerophytic low statured forest type on hard rock and rocky outcrops), and white sand forests. We pose the following research questions:

- What are the roles of geographical distance and environmental differentiation on the species composition of trees over the Guianas?
- Are there families, genera, and species that can be considered indicators for certain forest types?
- How do plant attributes and diversity covary, and what do possible covariations tell us about the functioning of the Guianan forests?

Methods

Our dataset contains 156 (mainly 1-ha) plots with 86346 individual trees \geq 10 cm diameter at breast height representing 1744 (morpho-)species. The plots are situated in six different forest types in Venezuela, Guyana, Suriname, and French Guiana and span a maximum distance of 1400 km (see supplementary Table S3.1 for plot meta data). The core of the database is formed by 61 1-ha plots across Guyana and Suriname mostly inventoried and identified on a (morpho-) species level by the first author. Other parts of the dataset consist of approximately 32 1-ha plots inventoried in French Guiana by Daniel Sabatier et al., a dataset of 15 1-ha plots from Venezuela by Hernan Castellanos, and 9 plots inventoried by Terry Henkel in Guyana. The remainder of the plot data originated from the work of well respected botanical researchers and institutes (see Table S3.1 for plot ownership). Where possible, the names of the species in the different inventories were standardized and corrected for synonymy. Apart from the datasets inventoried by the same researchers, the collections of the different plots were not matched. Still, ordinations on a genus and species level, gave similar results, lending support that a preliminary analyses on a species level with robust results is feasible. Most morphospecies were excluded from the analyses except when clearly coded in the large datasets of O.S. Bánki (for Guyana and Suriname) and Daniel Sabatier (for French Guiana).

Floristic patterns in the data were explored with ordinations in PC-ORD (McCune & Mefford, 1999). A DCA (Detrended Correspondance Analysis) gave similar results as an NMDS (Non-linear Multi Dimensional Scaling) with relative Sørensen as floristic distance measure, and 250 runs with randomized and real data. Only the DCA results are shown in this paper. To disentangle the role of environment and geographical distance on the tree species composition, we performed variation partitioning with Rda and PCNM (Borcard & Legendre, 2002; Legendre, 2007). Data were Hellinger transformed (Legendre & Gallagher, 2001), and the significance level was tested with Anovas of 200 permutations. The analyses were conducted in Vegan version 1.16-32 in R (<http://vegan.r-forge.r-project.org>). Plots were either divided according to the six different forest types, or the lowland tropical rainforest dataset was split into four countries resulting in 9 different forest groups. The Guyana lowland tropical rainforest plots of Kwakwani plot 1, Mapenna Savanna on the brown sands and Simuni Creek on the penepain of the Guiana Shield Basement Complex (see Table S3.1) were treated as belonging to the Suriname group because of floristic similarities. Species indicator analyses were conducted to establish whether tree species

were significantly linked to a certain forest group (Dufrene & Legendre, 1997). As floristic distance measure we used relative Sørensen, and data were reshuffled by 10.000 permutations (McCune & Mefford, 1999). Indicator analyses were run with both classifications into six and nine forest groups, and with 156 and 146 plots. The latter was performed since the flood plain, savannah, and swamp forests contained only a small number of plots per group. This could result in a biased result of the indicator analyses as the chance that a species occurs in every plot is higher in a small compared to a large plot dataset. To avoid this bias, indicator analyses were also performed without the flood plain, savannah, and swamp forests totaling an analysis with 146 plots.

We used a dataset on plant attributes (ter Steege *et al.*, 2006) to study if functional characteristics of tree species (abundances) were associated with the different forest types and groups. This dataset contained information on the wood density, seed mass, and fruit characteristics of tree species, as well as the species ability to fix nitrogen, and accumulate aluminum. Plant attributes were correlated with the DCA axes, with Fisher's alpha (a measure for the diversity of a plot), and with each other. Statistical analyses were performed in SPSS (SPSS-Inc., 1989-2007).

Results

Gradients in floristic composition and tree diversity

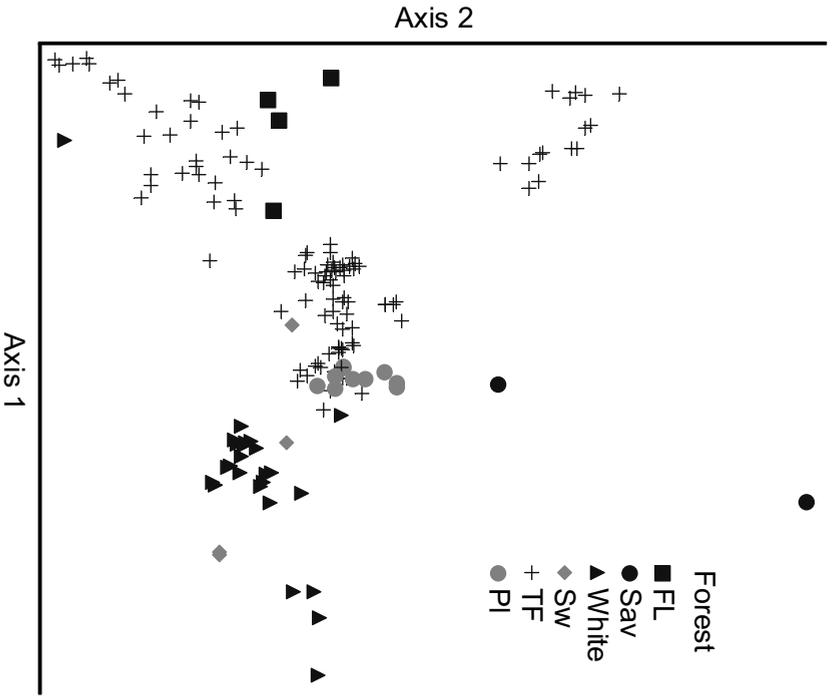
Plots originating from the flood plain, savannah, swamp, and white sand forests types were separated from the lowland tropical rainforest groups, and the plots in forests on bauxite plateaus (Figure 3.1A). Especially the white sands were clearly separated from all other forest plots. Still, the white sand forests of Guyana and Suriname showed floristic differences from one another. Forests growing on the brown sands and laterite soils of Central Guyana grouped together, and were separated from forests on the brown sands and laterite soils in Suriname and French Guiana (the Guiana Shield basement complex). The plots from Venezuela were also separated on the basis of their species composition. In total, from the DCA analyses nine forest groups could be discerned: flood plain, savannah, swamp, white sand, and bauxite plateau forests and the lowland tropical rainforests in Venezuela, Guyana, Suriname, and French Guiana (Figure 3.1A, B).

Fisher's alpha of plots differed significantly along a longitudinal gradient increasing in both the lowland tropical rainforests and the forests on bauxite plateaus from Venezuela towards French Guiana (ANOVA, $F_{[132, 23]} = 23.98$, $P < 0.001$, Figure 3.2A). Between the nine forest groups, the number of individuals, the number of species and Fisher's alpha of 1-ha plots differed significantly (Kruskal Wallis, $P < 0.001$, Figure 3.2A,B, Table S3.1). In the lowland tropical rainforest of Guyana Fisher's alpha was significantly lower than those of all the other lowland tropical rainforest plots and of the forests on bauxite plateaus (Mann-Whitney, $P < 0.05$). The white sand forest plots showed a reverse trend in Fisher's alpha, not increasing from East to West, but with a tendency of a lower Fisher's alpha in Suriname. Fisher's alpha of the swamp, and white sand forests were significantly lower than those of all the other forest plots (Mann-Whitney, $P < 0.05$), with lowest average Fisher's alpha in the swamp forest (excluding the savannah plots from the analysis). The swamp and white sand forest also had the lowest number of species, and the highest number of individuals per 1-ha plot (Mann-Whitney, $P < 0.05$).

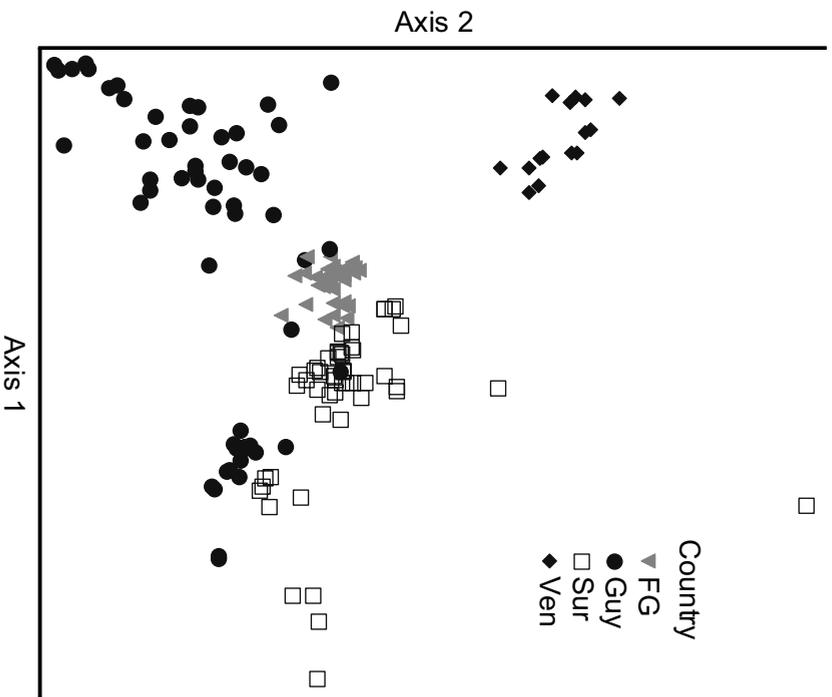
Figure 3.1

On the next page the ordination of the Detrended Correspondence Analyses (DCA) of 156 1-ha plots in the Guianas is shown with plots labeled according to forest type (**A**), and country (**B**). The forest types (**A**) consist of: flood plain forest (**FL**), savannah forest (**Sav**), forest on white sand (**White**), swamp forests (**Sw**), terra firme forests on brown sands to lateritic clays (**TF**), and forests on bauxite plateaus (**PI**). The countries (**B**) consist of: French Guiana (**FG**), Guyana (**Guy**), Suriname (**Sur**), and Venezuela (**Ven**).

A



B



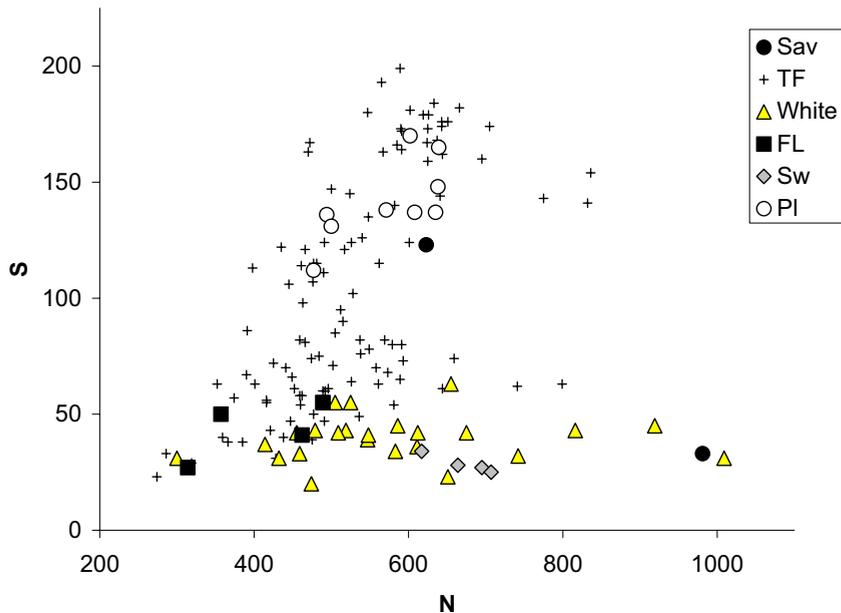
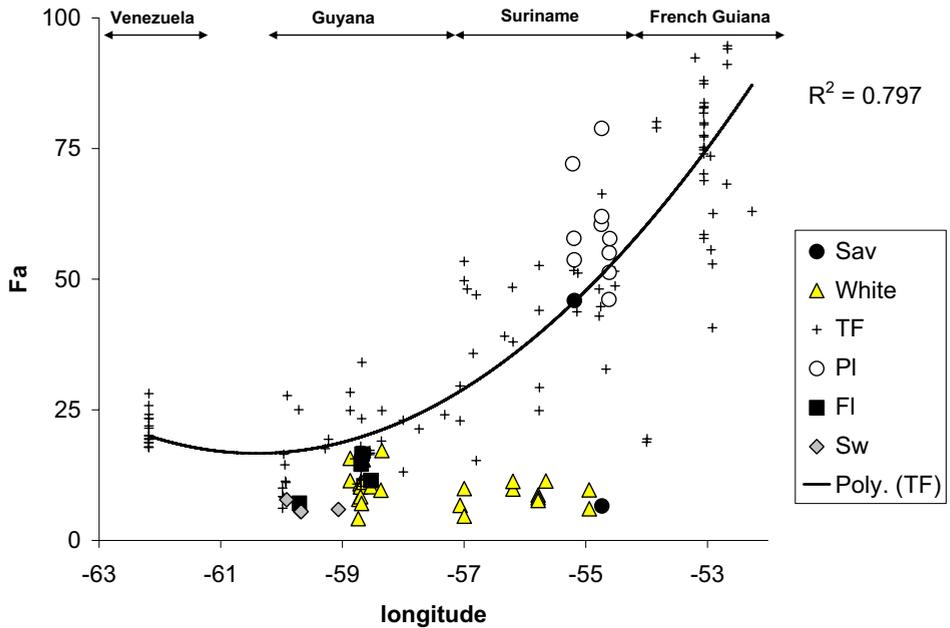


Figure 3.2

Above the Fishers alpha (F_a) versus longitude (**A**) and the number of species (S) versus number of individuals (N) per 1-ha plot (**B**) for the forest types are given. The forest types consist of: flood plain (**FI**), plateau (**PI**), savannah (**Sav**), white sand (**White**), and swamp forests (**Sw**), and the terra firme forests (**TF**) in Venezuela, Guyana, Suriname, and French Guiana.

Variation in composition expressed by environmental differentiation and geographical distance

The results of the RDA variation partitioning with PCNM showed that species, genus, and family composition was affected by both environmental conditions and geographical distance on a more or less equal basis. The amount of variation in species, genus, and family composition on account of environmental categories (the nine forest groups) ranged between 16 and 19 %. The amount of variation in species, genus, and family composition represented by geographical distance (41 PCNM vectors) ranged between 14 and 17 %. Between 12 and 16 % of the variation was shared by both the effect of environment and geographical distance. The total amount of variation in composition represented by the RDA variation partitioning ranged between 44 and 49 % (ANOVA, $P < 0.005$). In all cases, the use of nine forest groups as environmental categories over the six forest groups (where tropical lowland rainforest is treated as one forest group) improved the total amount of variation explained.

Tree indicator families, genera, and species of the forest groups

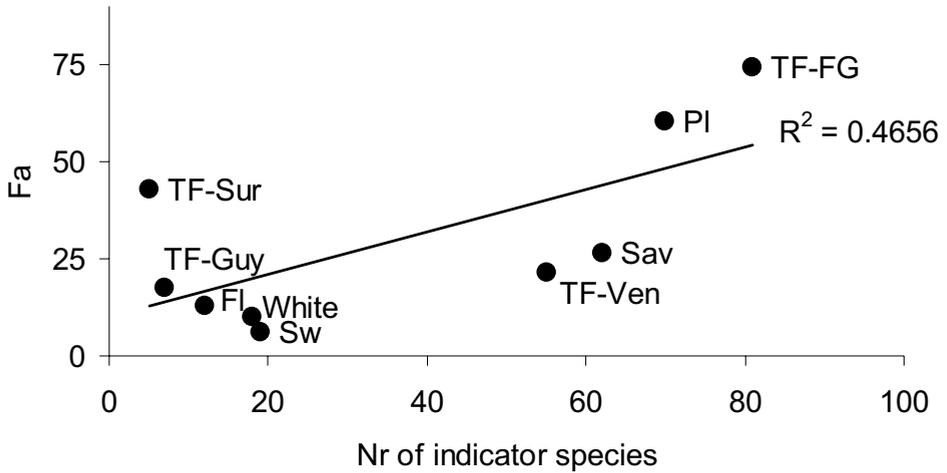
The indicator analyses of all the 156 plots, and of the 146 plots, excluding the flood plain, savannah, and swamp forests, showed that almost all the nine forest groups had significant indicator species, genera, and families ($P < 0.05$). Both the tropical lowland rainforest of Guyana and Suriname had very low numbers of indicator species, genera, and families (none for Guyana) with very low dominance in the forest groups. Fisher's alpha was in most cases positively correlated with the number of indicator taxa in the nine forest groups. The dominance of these indicators taxa was negatively correlated with the Fisher's alpha of forest groups. The lowland tropical rainforest in French Guiana and the bauxite plateau forests, with the highest Fisher's alpha, had the most indicator taxa but these taxa had low dominance in the forests. The flood plain, savannah, swamp, and white sand forests, with low Fisher's alpha, had relatively few indicator taxa but these taxa had high dominance in the forests. Lower tree alpha-diversity in forest groups apparently means fewer indicators, but these indicators may often have high dominance (Figure 3.3A,B).

For each of the nine forest groups we list below some of the significant indicator taxa with a high to relatively high dominance within the forest group.

The flood plain forests had a high dominance of Fabaceae (58 % of all individuals), especially because of *Mora excelsa* and *Pentaclethra maculosa*, and the genera *Pterocarpus*, and *Clathrotropis*. The savannah forest showed a high dominance of Euphorbiaceae (30 % of all individuals) mostly due to *Micrandra brownsbergensis* and *Croton argyrophyloides*, and showed also high dominance in Ochnaceae (*Elvasia elvasioides*, *Ouratea*), Rubiaceae (*Guettarda acreana*), Myrtaceae, Combretaceae (*Terminalia*), and the genus *Ecclinusa*. The swamp forests had high dominance of Arecaceae (25% of all individuals, e.g. *Euterpe oleracea*), Bignoniaceae (*Tabebuia insignis*), Clusiaceae (*Symphonia globulifera*), Myristicaceae (*Iryanthera lancifolia*), Ebenaceae (*Diospyros guianensis*), Anacardiaceae (*Tapirira*), and the genus *Hydrochorea*. The white sand forests also had a high dominance of Fabaceae (39% of all individuals) mostly due to *Eperua falcata*, *Eperua grandiflora*, and *Swartzia bannia*. Other families with high dominance were Chrysobalanaceae (*Licania buxifolia*, *Licania incana*), Malvaceae (*Catostemma fragrans*), and to a lesser extent Sapindaceae (*Talisia squarosa*, *Matayba*), Clusiaceae (*Clusia fockeana*), and the species *Ocotea schomburgkiana*. The bauxite plateau forests had Vochysiaceae (5% dominance of all individuals, e.g. *Qualea rosea*), Nyctaginaceae, the genus *Pouteria*, and *Elizabetha princeps* as striking elements. These forests also had substantial overlap with the savannah forests in the relative dominance of Myrtaceae (7% of all individuals), Rubiaceae, and *Micrandra brownsbergensis*. The lowland tropical rainforest in Venezuela had Picodendraceae (4% of all individuals) and Boraginaceae (*Cordia*) as striking elements, but also high dominance of Sapotaceae (12% of all individuals, e.g. *Ecclinusa*), Euphorbiaceae (*Croton matourensis*, *Piranhea longepedunculata*, *Chaetocarpus schomburgkianus*), Meliaceae, and the genera *Aspidosperma*, *Protium*, *Pentaclethra* and to a lesser extent *Enterolobium schomburgkii*. The lowland tropical rainforest of Guyana had no significant indicator families, but a high dominance of *Eschweilera sagotiana* (11% of all individuals), *Chlorocardium rodiei*, *Mora gongrijpii*, and *Licania laxiflora*. Other striking features were *Dicymbe corymbosa*, *Maburea trinervis*, *Licania heteromorpha*, and a very high dominance of the genus *Eschweilera* (16% of all individuals). The lowland tropical rainforest of Suriname had only few indicators with very low dominance. Some taxa with relatively high dominance were the Burseraceae (6% of all individuals, e.g. *Tetragastris*), and *Lecythis corrugata* (5% of all individuals). In French Guiana the lowland tropical rainforests had high dominance of Lecythidaceae (19% of all individuals) especially due to the genus *Lecythis*, and the species *Lecythis idatimon*, *Lecythis persistens*, and *Eschweilera*

micrantha. Other features with some dominance were the tree families Myristicaceae, Annonaceae and Arecaceae.

A



B

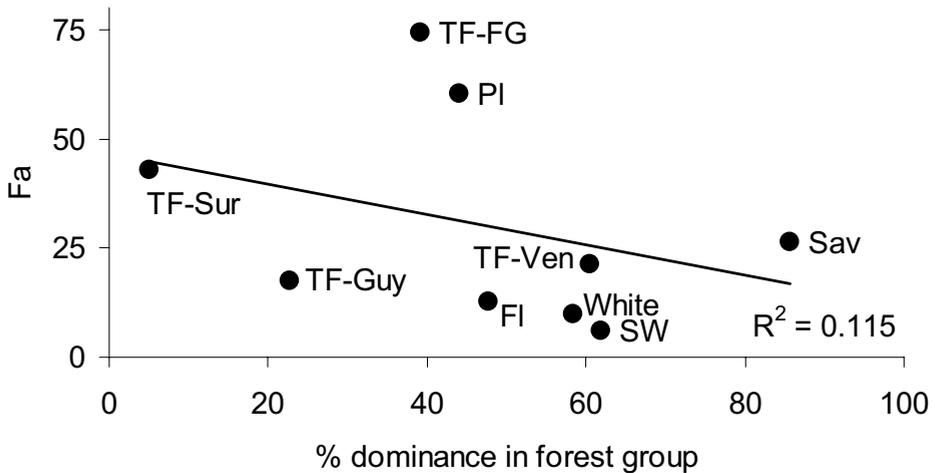


Figure 3.3

Above the number of indicator species in a forest group versus the Fisher's alpha (**Fa**) of the forest group is given (**A**). Also the dominance of these indicator species within a forest group is presented in relation to the Fisher's alpha in the forest group (**B**). The forest types consist of: flood plain forests (**FI**), plateau forests (**PI**), savannah forests (**Sav**), swamp forests (**Sw**), white sand forests (**White**), and the terra firme (**TF**) forests of French Guiana (**FG**), Guyana (**Guy**), Suriname (**Sur**), and Venezuela (**Ven**).

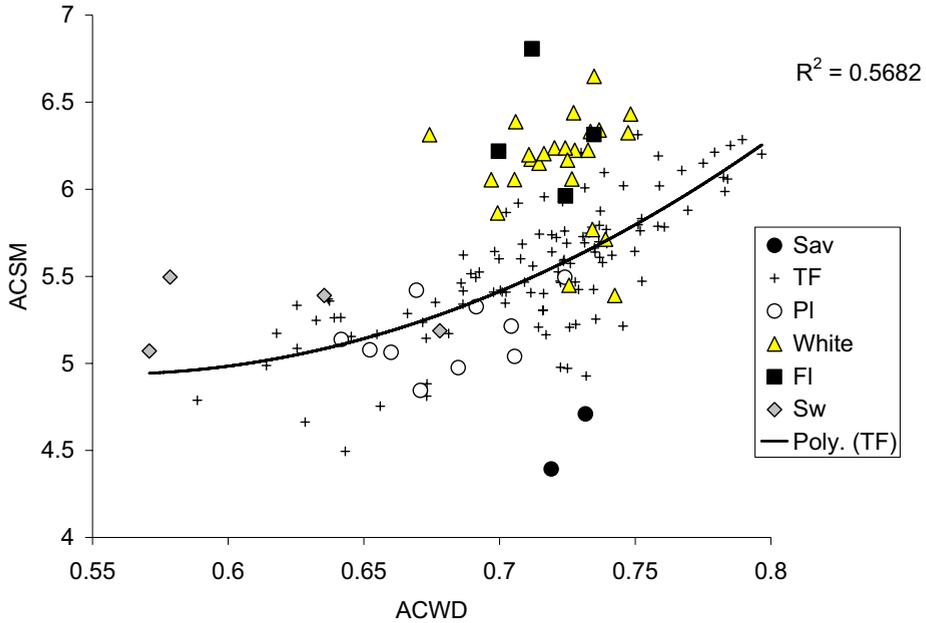


Figure 3.4

Above the relation between the averaged community wood density (**ACWD**) and the averaged community seed mass (**ACSM**) is given between forest types. The forest types consist of: flood plain forests (**FI**), plateau forests (**PI**), savannah forests (**Sav**), swamp forests (**Sw**), white sand forests (**White**), and the terra firme forests (**TF**) in Venezuela, Guyana, Suriname, and French Guiana. Averaged community seed mass in the flood plain and the white sand forests is higher in comparison to the terra firme forests (trendline). The savannah forests are clearly below this trendline. The swamp forests have a rather low averaged community wood density.

Wood density, seed mass, and fruit characteristics

Forest groups differed significantly in their community averaged wood density and seed mass (relativised number of individuals within a class, ANOVA, $F_{[8, 147]} = 11.46 \text{ \& } 38.06, P < 0.000$). Community averaged wood density and seed mass were also highly correlated over the forest groups (Figure 3.4). The lowland rainforests in Guyana had together with the flood plain, savannah, white sand, and lowland forests in French Guiana the highest community averaged wood density. The lowest community averaged wood density was found in the swamp forests, although this was not significantly lower than in the bauxite plateau, savannah, and the lowland forests of Venezuela (Scheffe, $P < 0.05$). The white sand had the highest community averaged seed mass compared to all other forest groups, except for the flood plain and the lowland forests in Guyana.

In the white sand forests over 50% of the individuals belonged to the higher seed mass classes. The savannah forests had the lowest community averaged seed mass, but not significantly different from the bauxite plateau, swamp, and lowland forests of Venezuela (Scheffe, $P < 0.05$).

Forest groups also differed significantly in their species averaged wood density and seed mass (relativised number of species within a class, ANOVA, $F_{[8, 147]} = 5.65$ & 20.87 , $P < 0.001$). Species averaged wood density and seed mass were correlated as well over the forest groups (Figure 3.5). The swamp forests had significantly lower species averaged wood density compared to the white sand forests and the lowland forests in French Guiana, Guyana, and Venezuela. All other species averaged wood densities between forest groups were not significant. The forests in the lowland of Guyana had significantly higher species averaged seed mass compared to all other forest groups, except for the flood plain and the white sand forests. The lowland forests of Venezuela had significantly lower species averaged seed mass compared to all other forest groups, except for the savannah and bauxite plateau forests (Scheffe, $P < 0.05$).

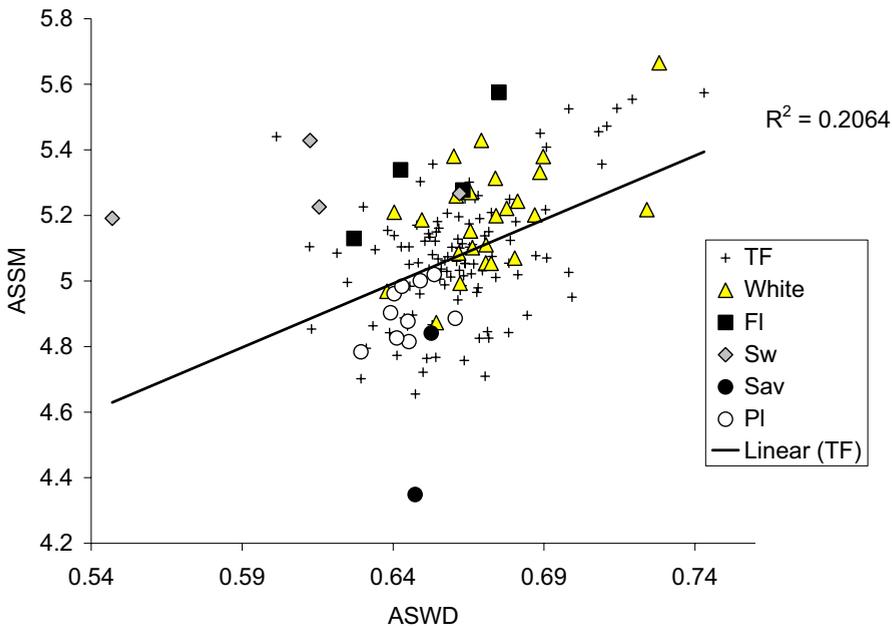


Figure 3.5

Above the relation between the averaged species wood density (**ASWD**) and the averaged species seed mass (**ASSM**) is given. The forests types consist of: flood plain forests (**FI**), plateau forests (**PI**), savannah forests (**Sav**), swamp forests (**Sw**), white sand forests (**White**), and the terra firme forests (**TF**) in Venezuela, Guyana, Suriname, and French Guiana. The species averaged seed mass of the flood plain and swamp forests are clearly above the trendline of the terra firme forests. The swamp forests also have low wood densities on a species average.

The percentage of individuals with fleshy fruits within a forest group differed significantly between the nine forest groups (Kruskal-Wallis, $P < 0.000$). Trees with fleshy fruits were especially abundant in the lowland rainforests of Suriname and French Guiana (Mann-Whitney, $P < 0.05$). The relation between the percentage of the individuals with fleshy fruits within a forest group, and community averaged seed mass was more or less stable between seed mass classes 4.5 to 6 (see Figure 3.6). Beyond seed mass class 6 there was a steep drop in the percentage of the individuals with fleshy fruits. The percentage fleshy fruits was also correlated with tree alpha-diversity (Figure 3.7). But the relationship is mostly caused by those forests types with seeds mass class beyond 6, as the relation between tree alpha-diversity and community averaged seed mass shows (Figure 3.8). Community averaged wood density did not correlate well with either percentage of fleshy fruits or tree alpha-diversity. The white sand forests had, together with the flood plain and savannah forests, the lowest percentage of individuals with fleshy fruits (Mann-Whitney, $P < 0.05$). White sand forest, flood plain forests, and some of the lowland rainforests on sandy soils in Central and Northwest Guyana had large dry seeds, and were among the forests with the lowest tree alpha-diversities in the Guianas.

The percentage of individuals belonging to pioneer species, defined as having a seed mass class below 4 and a wood density class below 6, differed between the nine forest groups (ANOVA, $F_{[8, 147]} = 2.96$, $P < 0.004$). A posthoc test revealed only a significant difference between the white sand forest and the forest on bauxite plateaus, and not between any other combination of the nine forest groups (Bonferroni, $P < 0.001$).

Other plant functional traits

There is a significant difference between the nine forest groups in the percentage of individuals of N₂-fixing species (Kruskal-Wallis, $p < 0.000$). The flood plain forest had by far the highest percentage of individuals belonging to N₂-fixing species. The savannah forest, white sand forest, and the lowland tropical rainforests of Suriname and French Guiana had rather low percentages of individuals belonging to N₂-fixing species. The percentages of individuals belonging to N₂-fixing species did not show significant differences between soil types.

Between the nine forest groups the percentage of individuals of species that could be classified as aluminum accumulators differed significantly (Kruskal-Wallis, $p < 0.000$). Swamp forests (9% of the individuals), forest on bauxite

plateaus, and the lowland tropical rainforest of Suriname had significantly higher percentages of individuals known to be aluminum accumulators. Flood plain forest, savannah forest, white sand forest, and the lowland tropical rainforest of Venezuela had rather low percentages of individuals.

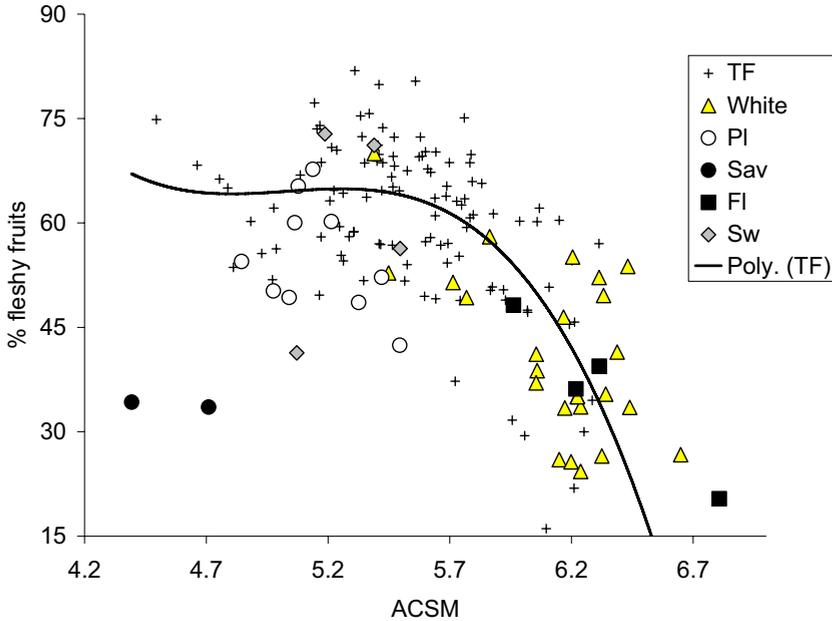


Figure 3.6

Above the relation between the averaged community seed mass (**ACSM**) and the averaged dominance (%) of individual trees with fleshy fruit within the forest types is given. The forest types consist of: flood plain forests (**FI**), plateau forests (**PI**), savannah forests (**Sav**), swamp forests (**Sw**), white sand forests (**White**), and the terra firme forests (**TF**) in Venezuela, Guyana, Suriname, and French Guiana. The flood plain and white sand forests as well as some terra firme forest plots on sandy and laterite soils in Guyana have a tendency for high community averaged seed mass and relatively dry fruits. The savannah forests combine relatively low community averaged seed mass with relatively dry fruits.

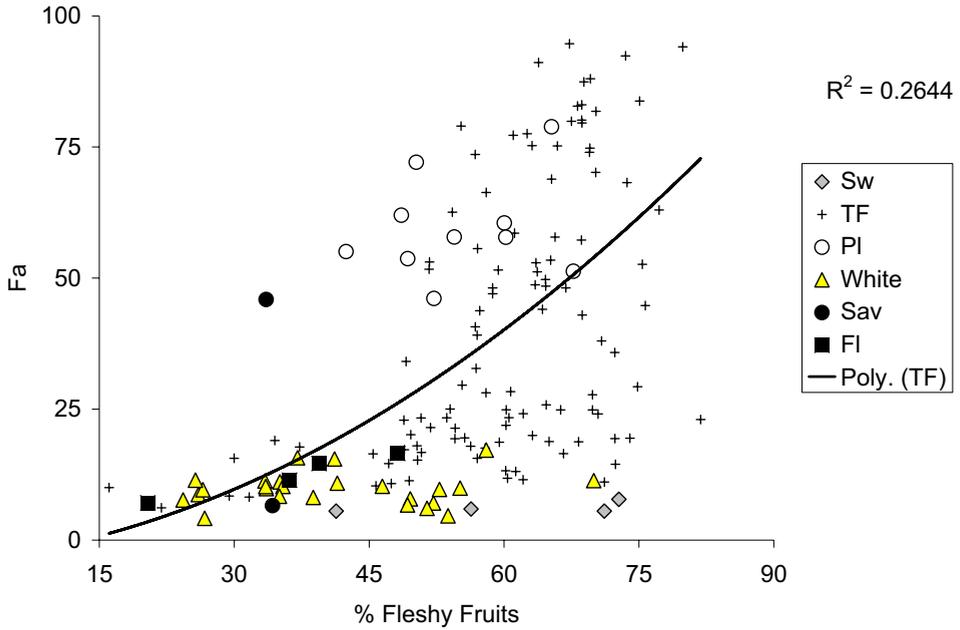


Figure 3.7
Fisher's alpha (F_α) seems to be positively related to the averaged dominance (%) of individual trees with fleshy fruit within the forest types (see Figure 3.6 for notes on legend).

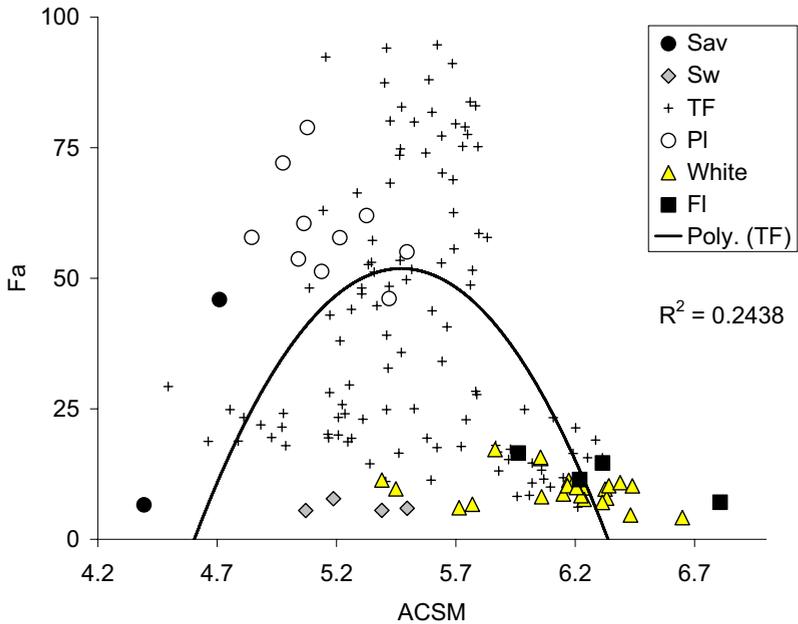


Figure 3.8
The relation between Fisher's alpha (F_α) and averaged community seed mass (ACSM) is mostly caused by the flood plain, white sand forests, and some terra firme forests in Guyana.

Discussion

Forest composition and diversity

Forest composition changes dramatically from place to place in the Guianas. Marked floristic differences were found between the white sand, flood plain, savannah, and swamp forests. All these forests had low alpha-diversities, and were dominated by a small set of common species. These forest types also strongly differed floristically from the lowland rainforests plots, and the forests on bauxite plateaus. Still, the flood plain forests in Guyana showed overlap in species composition with the lowland forests in Guyana on brown sands and laterite soils. This was further shown by the increase of indicator taxa for the lowland rainforests in Guyana, with the exclusion of the flood plain forests from the indicator analyses. Such floristic overlap was also found elsewhere in Amazonia between the varzea and terra firme forests (Pitman *et al.*, 1999; Pitman *et al.*, 2001; Terborgh & Andresen, 1998; Wittmann *et al.*, 2006).

Clear floristic differences were also found between the lowland rainforests, and these differences were combined with a longitudinal gradient in tree alpha-diversity from Venezuela to French Guiana (ter Steege *et al.*, 2003). The lowland forests of Guyana differed in species composition and in having a lower alpha-diversity from the forests on the peneplains of the Guiana Shield basement complex. Although the brown sands in Guyana and Suriname both have the same geological origin (the Berbice/Zanderij formation), the forest composition and tree alpha-diversity differed significantly between the countries. Possibly the brown sands forests in Suriname receive a species influx from the more species rich forests of the Guiana Shield basement complex. Within the lowland forests on the peneplains of the Guiana Shield basement complex, forest composition of the plots in Venezuela differed significantly from the lowland forests in French Guiana, and Suriname. The bauxite plateau plots were floristically very close to the lowland forests in Suriname, but still showed differences in species composition with these lowland forests. Thus, in the lowland forests tree species composition and tree diversity follow geological patterns in the Guianas. This confirms earlier findings from forest inventories at a genus level, and suggestions from smaller plot datasets in Guyana and Suriname (Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Lindeman & Moolenaar, 1959; Maas, 1971; Schulz, 1960; ter Steege & Zondervan, 2000).

Given these clear floristic patterns between forest types, there was an equal role of environment and geographical distances in explaining the variation in forest composition in the Guianas. In the white sand, flood plain, savannah, and swamp forests, forest composition changed substantially over geographical distances. The same could be observed in lowland forests, and in the bauxite plateau forests. Geographical distance had a most prominent effect in the Guyana lowland plots. Forest composition of plots from the Pakaraima Mountains, including the floristically distinct *Dicymbe* forest (Henkel, 2003), was different from the forest composition of plots in Central Guyana and the Northwest district of Guyana.

Wood density, seed mass, fruit characteristics and functioning of forests

Forest types in the Guianas showed clear differences in plant attributes, especially in wood density, seed mass, and the occurrence of fleshy fruits. In our data set community averaged wood density and to a lesser extent species averaged wood density was positively correlated with seed mass, corresponding to patterns found at the scale of the whole Amazon (ter Steege et al. 2006). We also showed a covariation between community averaged seed size and the percentage of trees with fleshy fruits within a forest group. The question is what these covariation patterns in the forest compositions tell us about the functioning of these forests?

The percentage fleshy fruits in our forest groups suddenly made a steep drop above a certain threshold in seed mass (> seed mass class 6). Large seeds apparently also mean drier and less fleshy fruits. Such covariation of seed and fruit characteristics should have an effect on the mode of dispersal of trees within the forest groups (Coomes & Grubb, 2003; Hammond & Brown, 1995; ter Steege & Hammond, 2001). It may also reflect strategies where large seeds produce superior survivors (large investment in seedling survival) and small seeds superior colonizers (large investment in dispersal), but such trade-offs are only thought to operate under conditions with strong asymmetric competition (Coomes & Grubb, 2003). Based on the covariation in the percentage of fleshy fruits and seed mass we can observe a spectrum in covariation also involving wood density and to a lesser extent tree alpha-diversity. At the ends of this spectrum in our dataset, we can observe two suites of traits: 1) one represented by the white sand, flood plain, and lowland forests of Guyana, especially in forests on the sandy soils and some laterite soils in Central and Northwest Guyana, with high dominance of trees with large seeds in dry fruits combined

with high wood densities, and low tree alpha-diversities, and 2) another represented by the bauxite plateau forests in Suriname and the lowland forests of Venezuela with high dominance of trees and species with smaller seeds in fleshy fruits combined with relatively low community averaged wood density, and higher tree alpha-diversities. Earlier studies in Guyana showed a strong correlation between community averaged wood density and seed mass with tree alpha-diversity (ter Steege & Hammond, 2001). This pattern was confirmed at the scale of the Amazon and coupled with the lower soil fertility in the Guiana Shield compared to Western Amazonia (ter Steege *et al.*, 2006). Our results do not show such a strong relation with tree alpha-diversity nor soil fertility over the Guianas, as the lowland forests in French Guiana with highest tree alpha-diversity fall in the middle of the spectrum in covariation between traits (see below).

At the first end of our proposed spectrum, some of the lowland forests of Guyana, the flood plain, and the white sand forests had the highest dominance of trees and species with dry fruits with large seeds compared to the other forest groups. These forests also had high dominance of trees and species with high wood density. In the Guyana lowland forests most brown sandy soils and some laterite soils in Central and Northwest Guyana carried forests with high wood density and a high occurrence of dry fruits with large seeds. In both the lowland forests of Guyana and the white sand forests the high wood density may reflect slow growth conditions due to low soil fertility, especially on the (white) sandy soils, but may also be associated with dryer conditions (Brouwer, 1996; Chave *et al.*, 2009; Malhi *et al.*, 2004; Quesada *et al.*, 2009b; van Kekem *et al.*, 1996). However, wood densities did not differ significantly between the lowland forests in Guyana and the white sand forests. Moreover, wood density can also be constrained in its variation to environmental conditions due to phylogenetic relatedness of species, as is shown by the constancy of wood density values within tree genera (Chave *et al.*, 2009; Chave *et al.*, 2006b). Similarly, though the larger seeds in the lowland forests of Guyana and in the white sand forests may reflect strategies to enhance seedling survival (e.g. protection against hazards, dry spells), and adaptations to shaded conditions, this probably only partly explains this pattern (Coomes & Grubb, 2003; Hammond & Brown, 1995).

In the white sand forests the community and species averaged wood densities did not go below the 0.63 wood density class. Most other forest types did show lower wood density classes either on a community or species average. Several of the most dominant tree species on the white sands with dry fruits and large seeds have unassisted dispersal modes, like ballistic and gravity dispersal

(e.g. *Eperua*, *Catostemma*), although rodent dispersal could also occur (e.g. Chrysobalanaceae, Hammond & Brown, 1995; ter Steege & Hammond, 2001). However, looking solely at species level, the white sand forests carry more species with fleshy fruits than species with dry fruits (data not shown). This seems in agreement with earlier findings in white sand forests of the Upper Rio Negro (Prance, 1996). Nevertheless, our data of the white sand forests in the Guianas do not support the view that long distance dispersal between forest patches is high, as a result of a high occurrence of tree species with bird dispersal (Prance, 1996). It is more likely that due to the ballistic dispersal mode of several white sand dominants, fronts of these tree species proceed slowly in historic and geographical terms over the landscape.

In the flood plain forests high wood density and large seeds are not likely to be an adaptation to low nutrient availability, as the flood plain habitat is considered to be more fertile than the surrounding terra firme soil types (van Kekem *et al.*, 1996). Possibly the large seeds also enhance seedling survival in these forests, but the reasons for improved seedling survival by large seeds could be different than for the species in the white sand forests and the lowland forests of Guyana (see Coomes and Grubb 2003). Large seeds may also be an adaptation to the flooding conditions as this could provide the seedlings with a head start before the seasonal floods arise again (Hammond & Brown, 1995; Parolin, 2000). Larger seeds in the flood plain forests may also be an adaptation to an unassisted dispersal mode through water, by increasing the buoyancy of the seeds (Parolin, 2000). The advantage of high wood density in the flood plain forests is unclear. Possible environmental explanations for the high wood density could be that it provides mechanical strength and resistance to wood decay and embolism in respect to the fluctuating wet and dry conditions in the flood plains (see also Chave *et al.*, 2009).

At the other end of our proposed spectrum, the bauxite plateau forests in Suriname and the lowland forests of Venezuela combine high dominance of trees and species with fleshy fruits and small seeds with a relatively low community averaged wood density. This coincides with a strategy for superior colonizers. The bauxite plateau forests are standing on laterite soils. Here the soil undersurface can be relatively deep with clayey soils, but also shallow due to the hard ferrobauxite crust (Chapter 5). Suitable growing conditions could be patchy for large forest trees. It is also possible that the forests are more prone to wind disturbances due to a relatively shallow rooting depth. But at the moment there is no evidence of higher forest dynamics at the plateaus in comparison to the lowlands. Soil and environmental conditions in the plots of the lowland forests of

Venezuela may be comparable to the forests on the bauxite plateaus in Suriname. The high dominance and occurrence of tree species with small fleshy seeds in both forest types would suggest a tendency for an animal dispersal mode, such as by birds, primates, and other mammals, and suggests high investment in dispersal.

The savannah forests occupy a separate position in the fleshy fruit and seed mass spectrum. This forest type combined a relatively high community averaged wood density, but relatively low species averaged wood density, with a high occurrence of small seeds in dry fruits. The variation in these functional traits could be typical for xerophytic forests in South America, where higher wood density could be seen as an adaptation to dryer environmental conditions (see Chave *et al.*, 2006b). High abundance of dry fruits with small seeds suggests a tendency for unassisted dispersal modes, like wind dispersal, and a lesser dependency on animal dispersal in these forests.

Swamp forests combined low wood density with a high dominance of trees with small seeds and moderate to high amount of fleshy fruits. Species averaged seed mass was, however, relatively high in comparison to the other forest groups. Why swamp forests show lower averaged wood densities than the flood plain forests remains largely unclear, although the high occurrence of palms could be affecting the wood density values. The high occurrence of fleshy fruits with small seeds suggest a tendency for more animal dispersal, such as bird and bat dispersal, in these forests.

The lowland forests of Suriname and French Guiana take up an intermediate position in the spectrum of covariation between percentage of fleshy fruits, seed mass, and wood density. Both lowland forests did not differ significantly from each other in these functional traits. The lowland forest of French Guiana had a slight tendency towards the first end of the spectrum. In wood density there were no significant differences with the flood plain forests, white sands forests, and tropical lowland forests of Guyana. The higher dominance and occurrence of smaller seeds in fleshy fruits was significantly different from these forests. The lowland forests of Suriname had a slight tendency towards the second end of the spectrum. Dominance of trees, not species, with lower wood density was significantly higher in the lowland forests of Suriname compared to those in Guyana. The Suriname lowland forests also had comparable sizes of seeds with amongst others the bauxite plateau forests and the lowland forests in Venezuela. The number of species with larger seeds was significantly higher compared to these forests. Both the Suriname and French

Guianan lowland forests had the highest percentage of fleshy fruits, making them especially suitable for all types of animal dispersal modes.

Intermediate disturbances and forest types

Our results do not support a strong role for intermediate disturbances in regulating diversity patterns in the forests in the Guianas, as found in other studies (Molino & Sabatier, 2001; ter Steege & Hammond, 2001; but see Bongers *et al.* 2009). The only significant pattern in smaller seeds (seed mass class < 4) combined with lighter woods (wood density class < 6) was found between the white sand and the bauxite plateau forests. In general the occurrence of pioneers is very low in the Guianas compared to other Amazonian forests (see ter Steege *et al.*, 2006). Moreover, our plot data showed very little occurrences of pioneer species on white sands, a possible effect of poor growth conditions (Chapter 2).

Nodulation and Aluminum accumulation

Patterns in the dominance of *Rhizobium* nodulators and aluminum accumulators were weak across forests and soil types. The high dominance of nodulators in the flood plain forests may be partly caused by the high dominance of *Mora excelsa*, although high dominance of nodulators has also been reported in other flood plain forests in the Guianas and in Amazonia (Koponen *et al.*, 2003). Our study does not support views that nodulation is an adaptation to less fertile soils, as the dominance of nodulators in the forests on the brown sandy soils and the white sands was very low. This corresponds to earlier findings at a regional scale, where the dominance of nodulators was higher in Western than Eastern Amazonia, along a decreasing gradient in soil fertility (ter Steege *et al.*, 2006). The aluminum accumulators were in general very low in dominance and corresponded only weakly to soil types. This despite the fact that soil types in the Guianas are thought to differ considerably in aluminum content and availability, especially at the bauxite plateaus (Bakker & Lanjouw, 1949; Brouwer, 1996; van Kekem *et al.*, 1996).

Concluding remarks

In the Guianas forest types showed clear floristic differences, both due to environmental conditions and geographical distance. Forest types also showed covariation in several plant attributes, such as wood density, seed size, and the percentage of fleshy fruits. These plant attributes mostly showed weak correlations with tree alpha-diversity and soil fertility across the Guianas. Between forests groups a spectrum of covariation is observed, that shows dry fruits with large seeds and high wood densities on the one hand, and fleshy fruits with small seeds and lower wood densities on the other. This spectrum in covariation of plant attributes can be interpreted as a trade-off between large investment in survival as opposed to large investment in dispersal. Such trade-offs are only thought to occur under strong asymmetric competition (Coomes & Grubb 2003). To what extent this is found to operate in the different forest types in the Guianas remains largely untested.

Next page above: white sand forest at 24 Miles Reserve, Guyana
Next page below: brown sand forest at Mabura Hill, Guyana



Chapter 4

Inferring asymmetric environmental filtering in tropical forest trees

Olaf S. Bánki, Franck Jabot, Jérôme Chave, and Hans ter Steege

Abstract

In spite of recent advances using developments of the neutral theory of biodiversity, we are still deficient in our understanding on how local diversity is shaped by regional diversity. Tropical forests growing on white sands have a woody flora distinctive of the forests on brown sands, and cover only 3% of the total Amazon rainforest. Here we use the largest paired plot data set of rainforest on brown and white sands, to infer the parameters of general tree community models. We provide strong evidence that asymmetric environmental filtering and a lower regional diversity are causal for the lower diversity found in white sand forests compared with neighboring brown sand forests. White sand forests are not necessarily more dispersal limited than forests on brown sands. However, evident changes in species abundance patterns in the white sand forests occur under similar climatic and soil conditions along geographical distances. Our study makes clear that striking biogeographical patterns in the rainforests of the Guianas remain unexplained.

Introduction

The determinants of species composition and abundances with geographical distance in tropical rainforests remain uncertain and debated (Condit *et al.*, 2002; Tuomisto *et al.*, 2003). The neutral theory proposes the simplified view that changes in species composition are only due to isolation by distance caused by a limited dispersal ability of plant species. In Hubbell's (2001) neutral model all individuals have equivalent birth, death, and dispersal rates, local community size is fixed, and the chance of occupying a vacant spot is proportional to the abundance of a species. There is no speciation in the local community, but any species can become a member of the local community through immigration from a metacommunity (Alonso *et al.*, 2006; Leibold *et al.*,

2004). This metacommunity is governed by neutral dynamics in speciation and extinction rates. The neutral theory could potentially offer new insights into the assemblage of ecological communities, by stressing stochastic events and placing local and regional community dynamics in an analytical framework (Alonso *et al.*, 2006). In contrast, one possible outcome of niche theory suggests that ecological communities are an assemblage of ecologically similar species, which are adapted to local environmental conditions. Other species not present in the community have been filtered out by the environment even if they have dispersed into the community. Hence species turnover mostly depends on environmental factors (Chave, 2004; McGill *et al.*, 2006b).

The Guianas are an ideal natural setting to study community assembly processes because of the high amount of habitat specificity expressed in striking differences in community composition between soil types (ter Steege *et al.*, 2000a). The Northern parts of the Guianas have little climatic differences (Haripersaud, 2009), but the laterite and brown sands soils of Central Guyana show noticeable differences in species composition in respect to the laterite and brown sands soils of the Guiana Shield basement complex in Suriname (Fanshawe, 1952; Lindeman & Moolenaar, 1959; Schulz, 1960; Chapter 3). Tree alpha-diversity, in our case the diversity of a 1-ha plot, is thought to increase from the West towards the East of the Guianas (ter Steege *et al.*, 2003; 2006, Chapter 3). Nevertheless, clearest differences are found between white sands and the other soil types in the Guianas, and the white sands across the Guianas are thought to be similar at least in the most dominating species (Davis & Richards, 1933; 1934; Schulz, 1960). Forests on white sand have a distinct species composition, share less species with adjacent soil types than forests on these soil types do between each other, and are less species rich (Davis & Richards, 1934; Fine *et al.*, 2004). These white sands offer a unique opportunity to study environmental filtering. Forests on white sand cover only 3% of the total Amazon rainforest (c. 8% of the rainforest in Guyana), and space itself may influence diversity (ter Steege *et al.*, 2000b). The regional flora of forests on white sands may contain in general less species than forests on brown sands (Anderson, 1981). Everything else being equal, this would lower the alpha-diversity observed in local communities on white sands (Ricklefs, 2004). If area controls the regional diversity of white sand forests, the smaller white sand area in Suriname should have a lower regional diversity compared to the white sand area in Guyana. White sand forests can be viewed as isolated islands connected through long distance dispersal, and could therefore be more dispersal limited than forests on brown sands (Prance, 1996). Lastly, the harsh environmental

conditions of the white sand with its low levels of total nutrients for plants may cause deterring growth conditions for trees and other plants, and this may lead to different species pools between the brown and white sand forest (Fine *et al.*, 2004; 2006; Chapter 2).

Recent developments in the neutral theory have made the relationship between a local community and a metacommunity mathematically tractable (Etienne, 2005; Etienne & Alonso, 2005; Etienne & Olff, 2004). This means that from species abundance data in local communities the regional diversity (θ) of the metacommunity and the immigration rate (m) from the metacommunity into the local community can be estimated. Because, neutral dynamics are assumed in the metacommunity every individual of any species has the same chance of entering a local community. In Jabot *et al.* (2008) the metacommunity is not described by the neutral regional diversity number, but by the regional species abundances through summing all the local species abundances. The fact that the metacommunity is not strictly neutral enables the estimation of the immigration rate between a metacommunity and various local communities all with different immigration rates. Moreover, a species may be present or absent in a local community not only because of dispersal limitation, but also because of environmental filtering. The immigration rate from the metacommunity into any local community i , m_i , may be interpreted as a result of both dispersal limitation and post-dispersal environmental filtering (establishment limitation) (Jabot *et al.*, 2008, see Figure 4.1).

To tackle the different hypotheses trying to explain the low diversity found in white sand forests we used a generalized version of the Jabot *et al.* (2008) model. In this model the recruitment limitation (dispersal limitation and post-dispersal environmental filtering) can be inferred from two objectively constructed regional species pools (see Figure 4.1). For species abundance data we inventoried 38 1-ha plots in mature forests on white and brown sands over ca. 450 km in Guyana and Suriname. Our model approach is a first step towards a consistent reconciliation of neutral and niche processes.

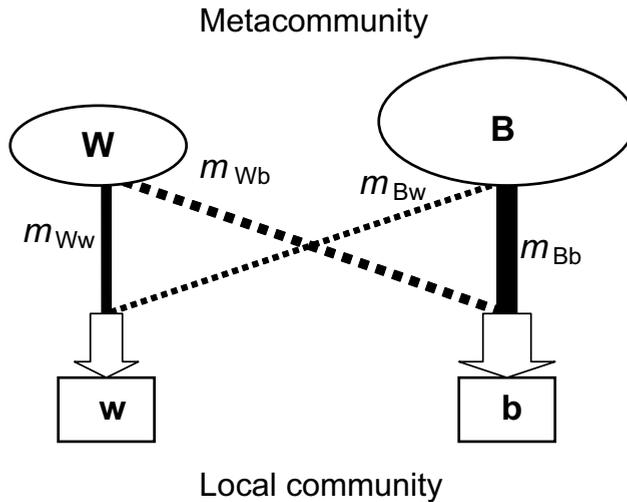


Figure 4.1

Extended neutral framework, where neutral dynamics are assumed in the local community but not in the metacommunity. The circles with capitals W (white) and B (brown) reflect the regional species pools, and the squares with normal caption w (white) and b (brown) represent the plots. The m is the immigration rate from the regional species pool into the plots. The solid lines represent the dispersal limitation from the white sand regional species pool into the white sand plots (MWw), and from the brown sand regional species pool into the brown sand plots (MBb). The dashed lines correspond to post-dispersal environmental filtering (plus some dispersal limitation) from the white sand regional species pool into the brown sand plots (MWb), and from the brown sand regional species pool into the white sand plots (MBw). The results of our analysis are reflected in this figure as the smallest circle corresponds to the lowest regional diversity, the thinnest solid line to the highest amount of dispersal limitation, and the thinnest dashed line to the most severe post-dispersal environmental filtering.

Methods

Plot inventories

In 2003, 2005, and 2006 38 1-ha plots were established predominantly by the first author in pairs in tropical forest on well drained white and brown sands in Guyana and Suriname over a distance of approximately 450 km (see supplementary Table S4.1). Plots were placed in high primary non-inundated forest. All trees ≥ 10 cm dbh (diameter at breast height) were pre-identified with the aid of the current best tree-spotters in the Guianas, Mr. Aaron Braithwaith (Guyana) and Mr. Frits van Troon (Suriname). Plant collections of trees were

identified to (morpho-) species level in the National Herbarium of the Netherlands.

Gradients in the species abundance data were explored with non-metric multidimensional scaling in PC-Ord 5.0 (MjM software, 1995-2005), by using 250 runs of randomized and real data, and relative Sørensen as floristic distance measure. Data were first investigated with 6 dimensions, and eventually with 2 dimensions as stress was reduced below 20% (see Figure S4.1). We performed species indicator analysis (Dufrene & Legendre, 1997) with PC-Ord 5.0 (MjM software, 1995-2005), and randomized the species abundance data 5000 times, to investigate if certain species portrayed a high fidelity to either brown or white sands and had a high frequency in plots on one of the soil types.

The model approach

We developed a stochastic community model which generalizes Hubbell's neutral model (Hubbell, 2001). In this model, there are two regional pools each one containing the flora associated either with brown (B) or white sands (W, Figure 4.1). Each plot is connected to the two pools with different immigration rates, and immigration between local communities is assumed not to occur (Figure 4.1). We assumed that white sand (respectively brown sand) species migrate into a white sand site (w) at a rate m_{Ww} (respectively m_{Bw}) and into a brown sand site (b) at a rate m_{Wb} (respectively m_{Bb}). Once this immigration from the two pools is performed, the local dynamics is assumed to be neutral for mathematical tractability. We develop a maximum-likelihood method to infer the immigration rates from two regional species pools in each plot based on the pooled species abundances in the 38 1-ha plots (Jabot *et al.*, 2008; see under likelihood computation). Assuming a given partition of species into the two pools, the likelihood approach yields an estimate for the four immigration parameters (see Figure 4.1) and a maximum likelihood (ML). With Markov Chain Monte Carlo (MCMC, see below) searches, we assessed the best partition, the one having the largest likelihood value (ML) (Burnham & Anderson, 2002), of the species into two species pools. In this way, for any partition of the species into two pools, we not only obtain an estimate for immigration rates from these two pools in each plot, but also a measure – the likelihood – of the goodness of fit of the data with this model. This enables the two species pools to be constructed objectively as being the partition of the species which leads to the best fit – the highest likelihood – of the data. With the Akaike information criterion (Burnham & Anderson, 2002) we evaluated the performance of models with one regional

species pool with models of two regional species pools. We also assessed the regional diversity (θ) of the regional species pools by using constrained MCMC's, such that a singleton remains on its original soil type, and by using the Ewen's formula (Etienne, 2009, see equation 1; Ewens, 1972).

Likelihood computation

The likelihood function was found by extending the function earlier developed for a one group model (Jabot *et al.*, 2008). If immigration in a local community comes from two different groups of species G_1 and G_2 with scaled immigration rates $I^{(1)}$ and $I^{(2)}$ respectively, and with relative abundances of species j in G_1 and G_2 denoted by $\chi_j^{(1)}$ and $\chi_j^{(2)}$ respectively, then the model is equivalent to a one group model (Jabot *et al.*, 2008) with relative abundance of species j given by:

$$I^{(1)}\chi_j^{(1)} + I^{(2)}\chi_j^{(2)} / (I^{(1)} + I^{(2)}), \text{ and scaled immigration rate } I^{(1)} + I^{(2)}.$$

Consequently, the formula for a two-group model

$$\text{is: } L = \prod_{i=1}^D \frac{J_i!}{\prod_{j=1}^S n_{ij}!} \frac{\prod_{j=1}^S (I_i^{(1)}\chi_j^{(1)} + I_i^{(2)}\chi_j^{(2)})^{n_{ij}}}{(I_i^{(1)} + I_i^{(2)})^{J_i}}$$

We only considered groups that partition the species list, which means that a species cannot belong to the two groups simultaneously. Hence $\chi_j^{(1)}=0$ or $\chi_j^{(1)}=\chi_j$. We used the approximation that pooled local species abundances in the total dataset are proportional to the regional abundances χ_j . We also explored an alternative approximation where χ_j is proportional to the frequency of occurrence of species j in the plots. Results with the last approximation (χ_j proportional to frequency of occurrence of species j in the plots) are reported in the main text, since this approximation leads to larger likelihood values. Similar results were obtained with the other approximation, and those are reported in the annexes.

MCMC search (Metropolis-Hastings algorithm)

We launched a Markov Chain Monte Carlo (MCMC) search of the best partition of the species into two groups, the one having the largest likelihood

value. We used a Metropolis-Hastings algorithm, which consists in starting from a random partition of the species into two groups, jumping from one partition to another, computing the likelihood ratio of this new partition compared to the previous one, and accept the move with probability $P = \min(1, \text{likelihood ratio})$. The jumping function in the space of all the partitions consisted in swapping one species from one group to the other with all the individuals belonging to this species. We launched 100 independent MCMC runs of 10000 steps (10000 jumps in the space of partitions). This length of the MCMC was found to be sufficient to reach the area of largest likelihood in the partition space.

The calculation of the regional diversity of the species pools may be affected by the equal division of the singletons and very rare species between these groups during the MCMC searches. To obtain a more realistic value of regional diversity we constrained the MCMC such that each singleton remained on its original soil.

Selection of the best two regional species pool models

Since the space of all the partitions was too vast to be exhaustively explored (it is of size 2^5), the partition that we found to be optimal cannot be considered as the global optimum. However, if all the MCMC searches converged towards similar partitions (which were the case in our analyses) then the optimal partition found by this approach could be reasonably considered close to the global optimum. We checked the robustness of our results by using other partitions of high likelihood (but smaller than the largest one that we found). To do this, we selected all partitions that had an Akaike weight greater than 5% compared to the best partition found (Burnham & Anderson, 2002). If the results found with these other partitions were similar to what we found with the best partition, then it is reasonable to consider that the globally optimal partition would lead to similar results. For each pair of partitions retained with the Akaike weight criterion explained above, we computed the correlation between the $m_i^{(1)}$ parameters in each plot, and the $m_i^{(2)}$ parameters. In all cases, we found R^2 values above 99%.

Results

Plot inventory data

In the 38 1-ha plots we encountered 19684 individual trees and 524 species in total of which 132 on white sands (see Table S4.1 for plot meta data). Forests on white sands ($n = 21$ plots) had significantly more individuals ($P < 0.003$, on average 571 compared to 452 on brown sand), lower number of species ($P < 0.001$, on average 41 compared to 84 on brown sand), and lower values of Fisher's alpha a measure for tree alpha-diversity ($P < 0.001$, on average 10.3 compared to 31.8 on brown sand). Forests in Guyana ($n = 20$ plots) contained significantly less species ($P < 0.001$, on average 54 compared to 67 in Suriname) and lower alpha-diversity ($P < 0.001$, on average 16.4 compared to 23.8 in Suriname). There was also a significant interaction effect between country and soil ($P < 0.001$), where forests on brown sand in Suriname had a significantly higher number of species and Fischer's alpha compared to Guyana, while this pattern was the reverse for forests on white sands in Suriname compared to Guyana (see Remarks S4.1).

A non-metric multidimensional scaling analysis revealed that there were two main axes explaining the gradient in floristic distance. One was explained chiefly by East-West geographical distance, separating the Guyana from the Suriname plots, and the second partitioned forest plots on brown and white sands (Figure 4.2). There is a small set of species dominating the white sand forests in the Guianas. The number of indicator species for forests on white sands (24) was lower compared to forests on brown sands (96). In Suriname, the indicator species for white sand forests (9) was much lower compared to the number found in Guyana (27). While the number of indicator species for forests on brown sands in Suriname (65) was much higher than the number found in Guyana (37, see Table S4.2).

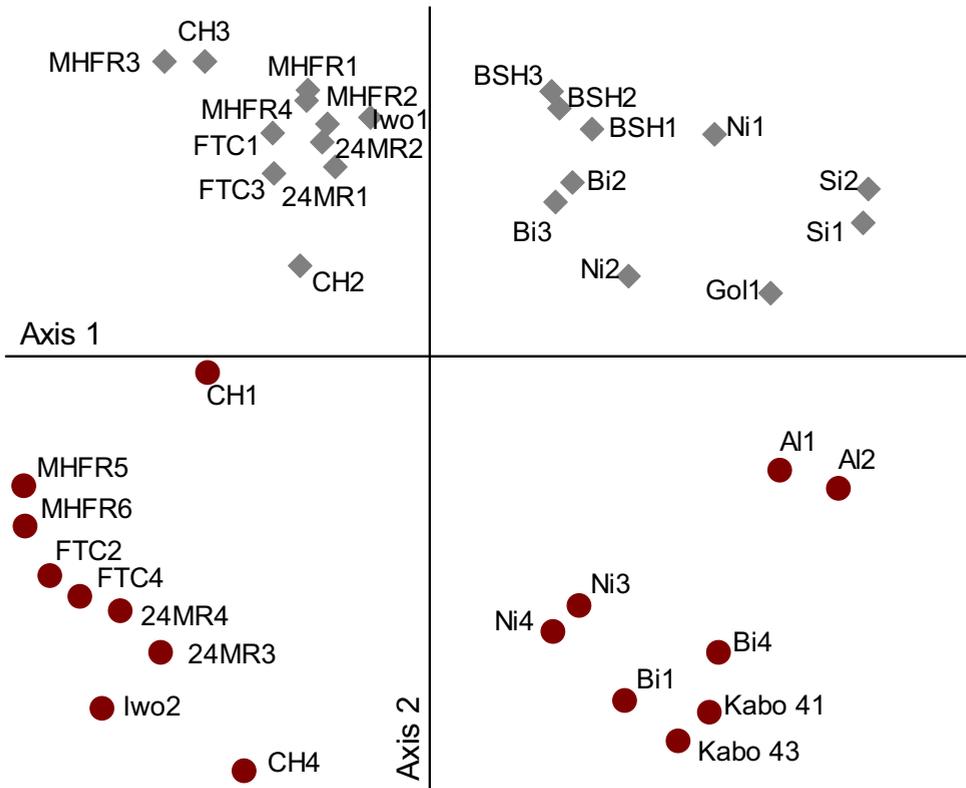


Figure 4.2

Non-metric multidimensional scaling based on 38 paired plots. The circles (brown) represent the plots in forests on brown sand, and the diamonds (grey) represent the plots in forests on white sand. The first axis separates the plots according to geographical distance, between the Guyana and Suriname plots. The second axis separates the plots according to soil type between brown and white sand plots (see Figure S4.1 for screeplot).

The model approach

The first partitioning of the full dataset by MCMC searches showed that the separation between the Guyana and the Suriname plots (geographical distance) was indeed the strongest floristic gradient in the data. In all cases models with two regional species pools (corresponding to the Guyana and Suriname floristic groups) were significantly improving the fit of the data compared to a model with a single regional species pool (Figure 4.3, see also Figure S4.2).

We repeated the MCMC searches for the best partitioning in the Guyana and Suriname datasets separately. In both the Suriname and Guyana datasets,

we found the best-fit partitions to correspond to a model with two regional species pools (associated with the brown and white sand floristic groups), and this two-pool model outperformed a single-pool model of community dynamics (Figure 4.3, see also Figure S4.2). The latter result is firmly confirming the role of environmental filtering between forests on brown and white sands.

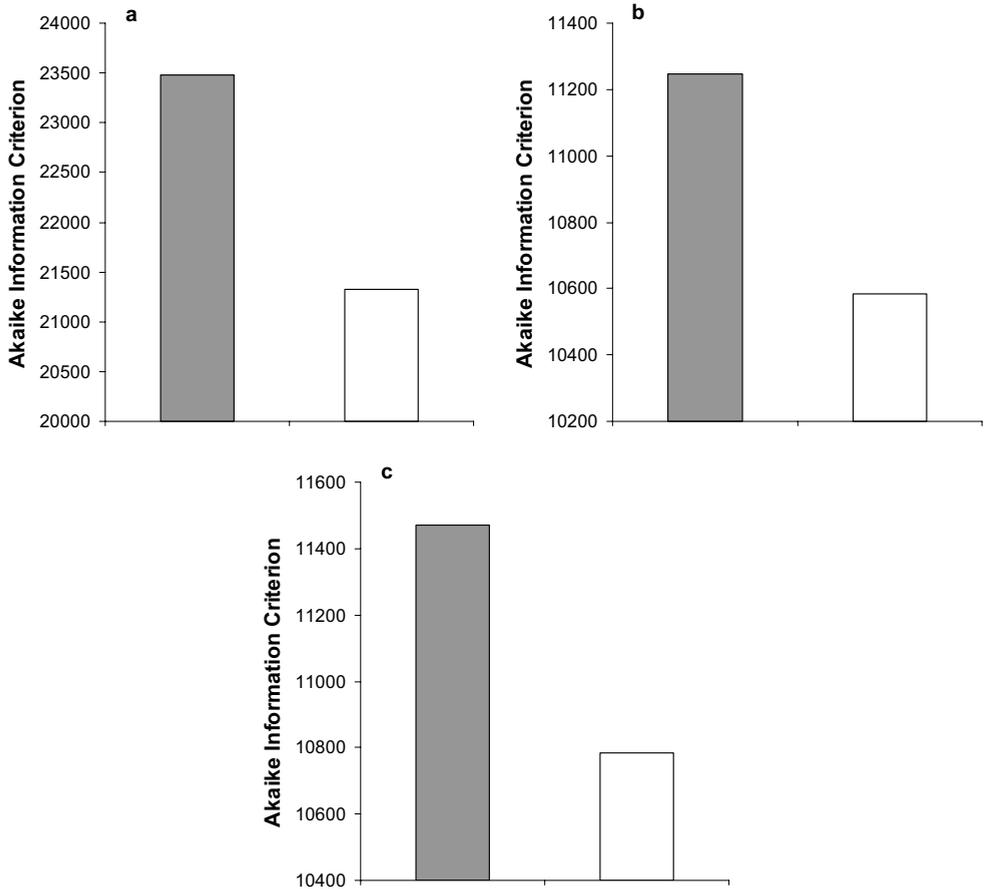


Figure 4.3

Comparison of model results of one and two regional species pools. **a**, Floristic separation into Guyana and Suriname regional species pools (white column, Akaike weight 1) outperforms a single regional pool (grey column, Akaike weight $< e^{-1078}$), based on 17 retained partitions out of 7 different MCMC searches. **b**, Separation into a brown and white sand regional species pool (white column, Akaike weight 1) outperforms a single Guyana regional species pool (grey column, Akaike weight $< e^{-331}$), based on 9 retained partitions out of 4 different MCMC searches. **c**, Separation into a brown and white sand regional species pool (white column, Akaike weight 1) outperforms a single Suriname regional species pool (grey column, Akaike weight $< e^{-343}$), based on 8 retained partitions out of 2 different MCMC searches.

Hypotheses on the low diversity of white sand forest

The regional diversities (θ) of the white sand regional species pools in both Guyana and Suriname were found to be less diverse than the brown sand regional species pools ($W_\theta < B_\theta$). In addition, the regional diversity of the white sand regional species pool in Suriname was lower compared to the regional diversity of the white sand regional species pool in Guyana. These results confirm our hypothesis that the lower diversity of white sand forests is partly due to a lower regional diversity of the flora associated to this soil type (Figure 4.1, Table 4.1).

Table 4.1 Regional diversity (theta) of the brown and white sand regional species pools. Below the theta's associated with the brown and white sand regional pool are given per country for each of the two approximations of regional abundances. Also the results of the likelihood ratio tests are given.

Guyana	Theta brown	Theta white	P value
<i>Model "frequency of occurrence in plots":</i>	35.3	19.9	
○ theta brown > theta white			p<0.001
○ theta white < theta brown			p<0.001
<i>Model "sum of local abundances":</i>	38.3	17.2	
○ theta brown > theta white			p<0.001
○ theta white < theta brown			p<0.001
Suriname	Theta brown	Theta white	P value
<i>Model "frequency of occurrence in plots":</i>	62.9	12.9	
○ theta brown > theta white			p<0.001
○ theta white < theta brown			p<0.001
<i>Model "sum of local abundances":</i>	65.9	11.1	
○ theta brown > theta white			p<0.001
○ theta white < theta brown			p<0.001

Being very different in species composition from other soil types, white sands may be more dispersal limited. At the level of the Guianas we found that the white sand plots were indeed more dispersal limited from the Guianas white sand regional pool than the brown sand plots were from the Guianas brown sand regional species pool ($m_{Ww} < m_{Bb}$, Figure 4.1, Table 4.2). This significant relation was mainly caused by the Suriname white sands plots, which were very dispersal limited from the Suriname white sand regional species pool (Table 4.2). In these Suriname white sand plots, other common species were dominating the forests at each site, causing high beta-diversity. Some of these common species on white sands in Suriname did not dominate or occur in the Guyana white sand plots. In Guyana, white sands forests were not significantly more dispersal limited compared to the Guyana brown sand forests (Table 4.2). Most white sand plots at various sites in Guyana shared several common species. Those plots that

did not contain large abundances of the most common species *Eperua falcata* had lower m -values from the Guyana white sand regional species pool. The Guyana white sand plots had a significantly higher m from the Guianas white sand regional species pool compared to the Suriname white sand plots (m_{Ww} in Guyana > m_{Ww} in Suriname, Table 4.2). This shows that the beta-diversity in the Guyana white sand forests was less. The Guyana white sand plots also contributed more to the abundance patterns of the most common species in the Guianas white sand regional species pool. We found no significant correlation between the m -values and the distance of the Suriname white sand plots from Guyana.

Table 4.2 Amount of dispersal limitation from regional species pool to the plots. The m from the regional brown sand pool into the brown sand plots is greater than the m from the regional white sand pool into the white sand plots.

Guyana	Anova
Model "frequency of occurrence in plots":	F _{18, 4.41} = 9.1906, p < 0,01
Model "sum of local abundances":	F _{18, 4.41} = 0.0631, p < 0,9
Suriname	Anova
Model "frequency of occurrence in plots":	F _{16, 4.49} = 30.782, p < 0,001
Model "sum of local abundances":	F _{16, 4.49} = 26.49, p < 0,001

We found that recruitment limitation was more intense for brown sand species in white sand plots than for white sand species in brown sand plots (m_{Bw} < m_{Wb} , Figure 4.1, Table 4.3). This relation was found to be significant on the level of the Guianas, as well as in Guyana and Suriname separately. More species could enter the brown sands from the white sand forest than vice versa, although our plot data also revealed a set of species in the white sand forests that did not enter the brown sands forests at all.

Table 4.3 Amount of dispersal limitation from the regional species pool into the plots attributed to post-dispersal environmental filtering. The m from the regional brown sand pool into the white sand plots is lower than the m from the regional white sand pool into the brown sand plots.

Guyana	Anova
Model "frequency of occurrence in plots":	F _{18, 4.41} = 38.11, p < 0,001
Model "sum of local abundances":	F _{18, 4.41} = 22.538, p < 0,001
Suriname	Anova
Model "frequency of occurrence in plots":	F _{16, 4.49} = 74.326, p < 0,001
Model "sum of local abundances":	F _{16, 4.49} = 21.666, p < 0,001

Discussion

Both forests on brown and white sands in the Guianas show large influences of biogeographical distributions in tree species abundances along geographical distances. For the brown sands this is not unexpected, and it confirms earlier findings reporting that the brown sands forests of Central Guyana differ in species composition from forests of the Guiana Shield basement complex in Suriname (Fanshawe, 1952; Lindeman & Moolenaar, 1959; Schulz, 1960; Chapter 3). Species from the basement complex are likely to disperse into the brown sand forests in Suriname, causing the Fisher's alpha of these forests to increase from Guyana to Suriname (see also ter Steege *et al.*, 2003; 2006). For the white sand forests the separation between the Guyana and Suriname plots is less expected, since these forests were thought to be quite similar in species composition (Davis & Richards, 1933; 1934; Schulz, 1960). As soil and climatic differences are similar between Guyana and Suriname, this beta-diversity is not controlled by habitat heterogeneity caused by these (current) environmental conditions. Only the Suriname white sand plots are more dispersal limited compared to the brown sands, while the Guyana white sands are not. This does not support the view that white sand forests are necessarily more dispersal limited, due to their patchy distribution. It is less clear, what causes the high beta-diversity on white sands in Suriname. The fact that the Suriname white sand forests have lower regional diversity, lower Fisher's alpha, and less common species compared to Guyana, could influence this pattern.

Our analyses suggest that forests on brown and white sands draw their different species from different regional species pools. Here environmental filtering plays a major role. The fact that this filtering is asymmetric is most likely the result of the more strenuous environmental conditions of the white sand. White sands are thought to be more nutrient poor, N- and P-limited, and because of that have a lower productivity (Cuevas & Medina, 1986; 1988; Chapter 2). These environmental conditions may strongly constrain the species composition in the forests on white sand (Fine *et al.*, 2004; 2006).

Our results and those of others (Haripersaud, 2009; ter Steege & Zondervan, 2000) show that there are strong biogeographical patterns in the Guianas forest flora. The different compositions of the white and brown sand forests might well be attributed to environmental filtering. However, also the brown sand forest flora and species abundances in Guyana differs somewhat from that in Suriname, as do the white sand forest flora's in these two areas,

while the climatic and soil conditions in Guyana and Suriname do not seem to differ much.

Our analysis based on a neutral-like model does not suggest a straight forward explanation for this biogeographical pattern. On the other hand, the similarity in ecological conditions suggests that a niche-based modeling also might have little explanatory power. Our study makes clear that part of the striking biogeographical patterns in the Guianas remain unexplained. Neither the neutral, nor the niche modeling approaches seem capable of unraveling these unexplained biogeographical patterns, but genetical and phylogeographic analyses could prove more promising tools.

Next page: low savannah moss forest on the plateau of the Lely Mountains, Suriname



Chapter 5

An assessment of tree diversity for nature conservation on bauxite mountains in Northeastern Suriname

Olaf S. Bánki, Hans ter Steege, Kenneth Tjon, and Fenneke van der Vegte

Abstract

The way we perceive how the diversity and composition of tropical forests is generated and maintained, is relevant for conservation decision-making processes. Knowledge whether the similarity in species composition in tropical rainforests at distances is the result of environmental conditions or of geographical distance may lead to different conservation approaches. Here we use a quantitative approach to establish conservation values in terms of tree diversity of bauxite mountains in Northeastern Suriname. These mountains are all destined for open-pit mining for aluminum ore, and may constitute a rare and endangered landscape type. We found that both environmental conditions and geographical distance determine the similarity between forest plots, the influence of environmental conditions being larger. Several indicator species, genera and families for the plateaus were found. However, forest composition on the plateaus is also partly a random draw of species from the lowlands, and each of the mountains has its own specific species composition. On the plateaus genera and families of trees occur that are typical for dry savannah-like conditions with soils with high aluminum contents. These conditions are not common in Suriname. The plateaus also have the highest tree alpha-diversity currently found in Suriname.

Introduction

The causes of beta-diversity in tropical forests, the changes in species composition over distances, are currently hotly debated (Condit *et al.*, 2002; Hubbell, 2001; Tuomisto *et al.*, 2003). This debate places ecology at the heart of conservation biology. It has long been argued that environmental conditions shape species composition, as ecological communities consist of the best competitors for limited resources (Chase, 2005; Tilman, 2004). The introduction

of neutral community models in ecology has challenged this view (Bell, 2000; Hubbell, 2001), though so far there is limited support for neutrality (Chave, 2004; McGill *et al.*, 2006b). Neutral community models assume that species composition changes randomly over geographical distances with dispersal limitation (spatially clumped species) as the main driving process of beta-diversity (Alonso *et al.*, 2006; Hubbell, 2001). This places this diversity in a historical context (Ricklefs, 2006). Evidence is mounting that distance decay in similarity (in terms of species composition) between sites is occurring in different organisms, suggesting it could be a general pattern for ecological communities (Nekola & White, 1999; Soininen *et al.*, 2007). Knowledge whether species composition in tropical forest changes because of geographical distance or because of environmental (such as soil mediated) gradients may lead to different conservation and ecosystem management approaches. If species composition changes rapidly over distance gradients, capturing a wide variety in species composition would require large areas of forests or alternatively many evenly spaced areas with some form of connectivity between forest patches. In case species composition is more controlled by environmental conditions, including geographical distances in a conservation design becomes less important. Choosing between sites with similar environmental conditions would be defensible in these circumstances.

The laterite-bauxite mountains in Northeastern Suriname form a large distinct geological formation, locally called the Brokolonko formation (Figure 5.1). These mountains together cover less than 0.5 % of the Surinamese land surface. On the plateaus a ferro-bauxite cap is found that dates back to the Oligocene, some 26 to 34 Million years ago (Gibbs & Barron, 1993). Soils are shallow with laterite gravel, rock outcrops and boulders, with low water retention, and high aluminum saturation (Bakker & Lanjouw, 1949; Schulz, 1960; Teunissen, 2005). On the plateaus the following main vegetation types can be observed: high terra firme tropical rain forest on laterite plateaus, high marsh forest on laterite plateaus, savannah (moss) forest on rocky outcrops, vegetation in and near rocky creek beds, high terra firme tropical rainforest on slopes, and disturbed or secondary forests (this study, Lindeman & Moolenaar, 1959; Teunissen, 2005). The mountains are all destined for open pit mining for aluminum ore (bauxite). Soils of the slopes are mostly deeper and clayey, becoming more loamy and sandy in the lowlands (Schulz, 1960; Teunissen, 2005). As these mountains are part of the greenstone belt, threats also come from the lowlands where (often illegal) mining activities for gold and diamonds are taking place. Given their size

and typical soils these mountains may constitute a rare and endangered landscape type for Suriname.

In this paper we assess the conservation values of these bauxite mountains in terms of tree diversity by posing the following questions: 1) is species composition of trees on the plateaus a random draw from the surrounding lowlands as neutral theory with limited dispersal would predict? 2) to what extent is the similarity between sites affected by geographical distance and by habitat type? 3) are some species confined to or indicators for these bauxite plateaus? To answer these questions, we designed a plot study in the lowlands, on the mid-slopes, and on the plateaus of three major bauxite mountains: the Brownsberg, the Lely Mountains and the Nassau Mountains (the plateaus lying each between 500-700 m altitude above sea level).

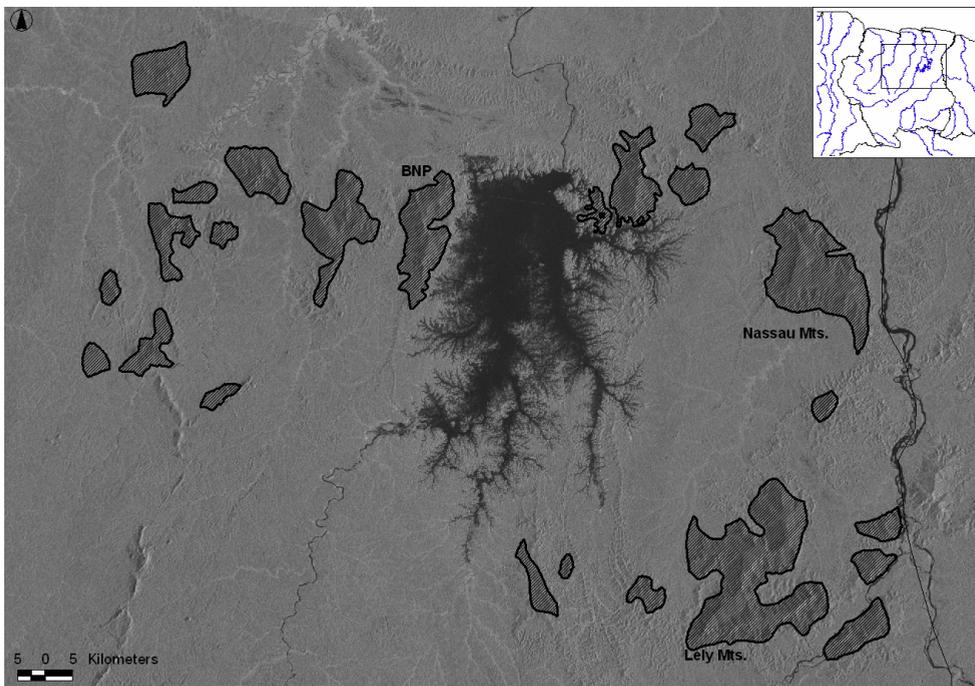


Figure 5.1

Bauxite caps (Brokolonko landscape) of Northeastern Suriname as indicated by the 1977 soil map (CBL 1977). Indicated with names are the Brownsberg (BNP), the Lely Mountains, and the Nassau Mountains.

Methods

Plot inventory

Between 2003 and 2005, 22 1-ha plots and one 0.5-ha plot were established in the lowlands, on the mid-slopes, and on the plateaus of the Brownsberg (9 plots), the Lely Mts. (8 plots), and the Nassau Mts. (6 plots). Plots were randomly placed in high terra firme tropical rain forest, without avoiding natural disturbances. On the Brownsberg and the Lely Mts. two 1-ha plots were placed in lower savannah forest on the plateaus. On the Nassau Mts. no plots were established on the mid-slopes (see supplementary Table S5.1 for plot meta-data). All trees ≥ 10 cm dbh (diameter at breast height) were pre-identified in the field with the help of Frits van Troon, Suriname's most able tree-spotter. Vouchers were made for each new species encountered. Plants were identified to (morpho-) species level in the National Herbarium of the Netherlands. Specimens were deposited in the National Herbarium of the Netherlands, and in the National Herbarium of Suriname.

Data Analysis

To analyze the tree community structure we used abundance data of all species, genera, and families. The species were also separated into common species (more than 25 individuals across all plots) and rare species (less than 25 individuals across all plots). We used Fisher's alpha as a measure of local tree diversity, since it is relatively independent of sample size (Fisher *et al.*, 1943; Taylor *et al.*, 1976). Differences in Fisher's alpha (F_α), species number (S) and number of individual trees (N) per plot were tested between habitat groups and separately between sites (Brownsberg, Lely Mts., and Nassau Mts.) with the nonparametric Kruskal-Wallis test, and a post hoc Mann Whitney-U test (SPSS-Inc., 1989-2003). The plots N2P and L5S (see Table S5.1) were excluded from the tests because of aberrant values for N , S or F_α .

Patterns in floristic differences between plots were explored with Nonmetric Multidimensional scaling (McCune & Grace, 2002; McCune & Mefford, 1999). Plots were divided into 0.5 ha for the ordination. This made sizes equal for all plots, and allowed us to separate plots with savannah forest, as a few mixed forest plots also contained close to 0.5 ha of savannah forest. The amount

of runs for real and randomized data was set at 250. We explored the data with two dimensions and used Relative Sørensen as the floristic distance measure.

The two research questions whether species composition of the plateaus is a random draw from the lowlands, and the effect of geographical distance and habitat type on similarities were assessed with (partial) Mantel tests. The hypothesis that geographical distance had a significant effect on the similarity between plots was tested with a simple Mantel test on the 20 1-ha plots and one 0.5 ha plot. The savannah forest (plot B9S and L5S) was excluded from the tests, as it differs in composition from the other plateau plots, and there were too few plots to fully characterize this forest. Relative Sørensen was used for floristic distances (1-similarity) between plots. Euclidean distance, calculated from the UTM coordinates (in metres), was used for the geographic distance matrix between plots. Both the simple Mantel and the partial Mantel tests were run with 9999 permutations. The total amount of variation explained by distance was calculated by squaring the standard Mantel statistic r . The effect of habitat on the similarity between plots while controlling for geographical distance was tested with a partial Mantel test (zt Software; Bonnet & Peer, 2002). The total variation explained by habitat was calculated by the formula $b^2 \cdot (1 - a^2)$, where a is the standard Mantel statistic for geographical distance and b the standard Mantel statistic for habitat, controlled for geographical distance. The lowland, mid-slope and plateau were used as categorical variables for habitat. The simple and partial Mantel tests were first performed with plots of the lowland and plateaus, and in second instance with the inclusion of the mid-slope plots.

The indicator value of species, genera, and families for the lowland and plateau plots was determined with indicator analysis (Dufrene & Legendre, 1997). The mid-slope was excluded from the test, because it is intermediate in species composition between the lowlands and the plateaus. The savannah forest plots were also excluded, since these forests differ a lot in species composition from the other plateau forest plots. For every set 9999 randomization runs were used in the Monte Carlo significance tests (McCune & Grace, 2002; McCune & Mefford, 1999).

Results

Plot inventories

We found 13,241 individual trees with a dbh ≥ 10 cm in the 23 plots. In total 605 (morpho-)species were encountered. Of these we identified 303 to species level which represented 70 % of all individuals. The other 302 remained assigned to morpho-species (162 identified at the genus level, 131 at the family level, and nine remained unidentified). In all plots we found 211 genera and 61 plant families. The ten most common species in order of abundance were: *Lecythis corrugata*, *Eperua falcata*, *Micrandra brownsbergensis*, *Eschweilera sp.OSB167_263*, *Elvasia elvasioides*, *Croton argyrophyloides*, *Qualea rosea*, *Astrocaryum sciophilum*, *Quararibea duckei*, and *Bocoa prouacensis* (for nomenclature see Funk *et al.*, 2007). These species represented 23 % of all individuals in the plot database. Tree alpha-diversity differed significantly between the lowlands, the mid-slopes and the plateaus (Kruskal Wallis, $p = 0.013$; Table S5.1). Largest differences were found between the lowlands and the plateaus (Mann Whitney U, $p = 0.005$). The highest tree alpha-diversity was found on the plateaus.

In the ordination with all species data, the plots were ordered from the lowlands to the plateaus to the savannah forests plots on the first axis. We interpret this as a gradient from mesophytic to more xerophytic conditions. The first axis represented 47 % of the variation in floristic distances. On the second axis, representing 23 % of the variation, geographical distance separates the plots (Figure 5.2). A similar pattern was shown in ordinations with the common species, genera, and family data, and also with the exclusion of the two savannah forest plots (B9S & L5S).

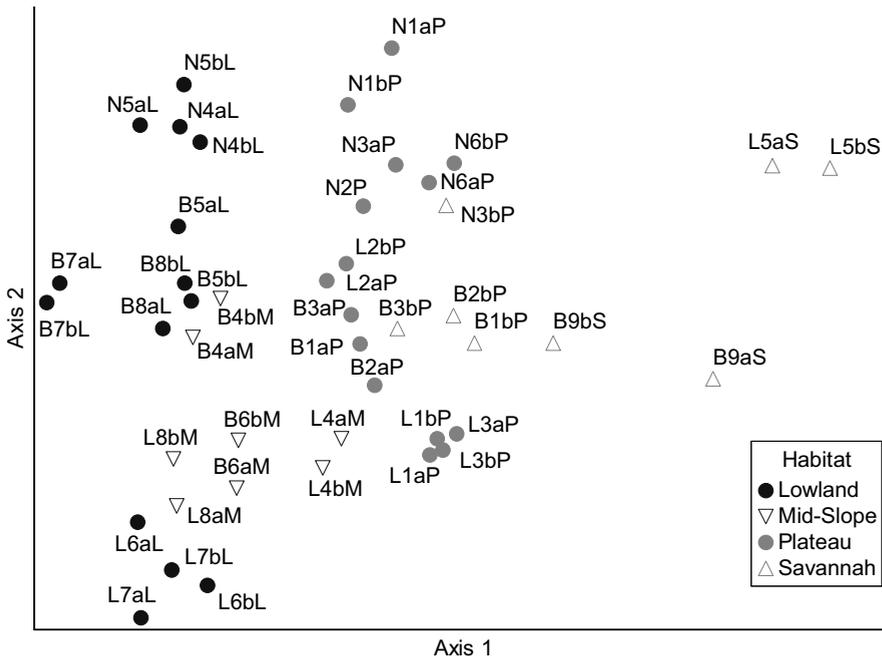


Figure 5.2

NMS ordination bi-plot showing the floristic distances between all 0.5 ha sub-plots in the study with all species data. The first letter of the plot name consists of each mountain (B = Brownsberg, L = Lely, N = Nassau), followed by plot number, followed by a or b indicating 0.5 ha plot halves, and followed by habitat type (L = lowland, M = mid-slope, P = plateau, S = savannah forest). On the first axis plots are separated by habitat type and on the second axis by geographical distance.

Similarity, geographical distance, and habitat

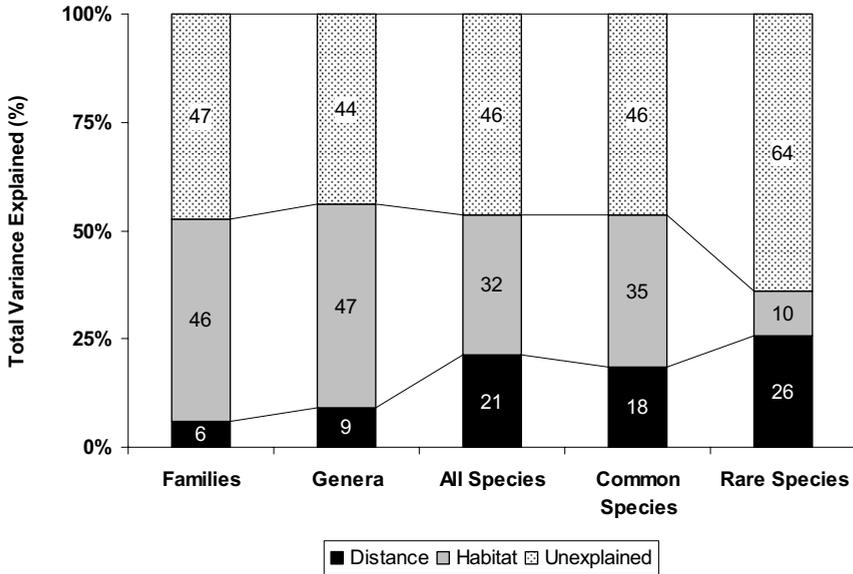
Geographical distance had a significant effect on the similarity between plots of the lowlands and plateaus in all test combinations ($p < 0.01$). The variation in similarity explained by geographical distance was highest in the rare species, followed by all species data, and the common species. In the genera and family data, geographical distance explained a substantial lower amount of variation in similarity (see Figure 5.3A). Habitat also had a significant and even stronger effect on the similarity between plots after the effect of geographical distance was removed ($p < 0.001$). The similarity between plots of the same habitat type (lowland or plateau) differed significantly from the similarity between plots of different habitat types. Habitat explained more of the variation in similarity in the genus and family data than that of all species, and the

common species data (Figure 5.3A). In the rare species, the variation in similarity explained by habitat was substantially lower (Figure 5.3A). The total variation in similarity explained by both geographical distance and habitat ranged between 53 and 56 % (disregarding the rare species), with habitat contributing stongest in all cases. The inclusion of the mid-slope plots gave similar results, with small differences in the amount of variation in similarity explained by geographical distance and habitat (see Figure 5.3B). These differences in the variation explained, were caused by the addition of new species and genera of the mid-slope plots, and the fact that the species composition of these plots was intermediate between the lowlands and plateaus. Tests, that controlled for habitat type first and then for geographical distance, with or without the mid-slope plots, rendered similar results (data not shown).

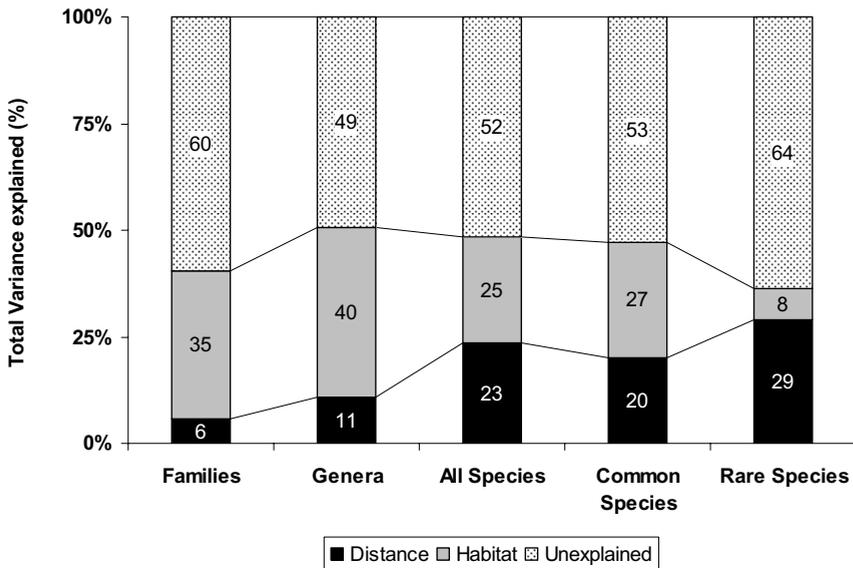
Indicator analysis

Of the total species in the lowland and plateau plots 9.4% had a significant indicator value ($p < 0.05$) for either the lowland or the plateaus (supplementary Table S5.2). The ten most common indicator species for the plateaus were: *Micrandra brownsbergensis*, *Qualea rosea*, *Nyctaginaceae OSB_427*, *Neea floribunda*, *Mabea piriri*, *Pouteria OSB_376*, *Jacaranda copaia*, *Inga OSB_130*, *Ruitzerania albiflora*, and *Sterculia OSB_276_554* (for nomenclature see Funk *et al.*, 2007). Of the genera 17.7% had an indicator value for either the lowland or the plateaus. The ten most common indicator genera were: *Pouteria*, *Inga*, *Micrandra*, *Qualea*, *Mabea*, *Neea*, *Ocotea*, *Sterculia*, *Jacaranda*, and *Terminalia*. Of the families 26.2% had a significant indicator value for either the lowland or the plateaus. The eight indicator families for the plateaus were: Sapotaceae, Vochysiaceae, Nyctaginaceae, Bignoniaceae, Melastomataceae, Combretaceae, Siparunaceae, and Cardiopteridaceae. The individuals of the lowland indicator species contributed more to the individuals of the plateaus (4.1%), than the individuals of the plateau indicator species contributed to the individuals of the lowlands (2.6%, Table S5.2). Except for genera this pattern was supported in the data with common species and families.

A)



A)

**Figure 5.3**

Total variance explained by habitat and geographical distance obtained through simple and partial Mantel tests: **A)** with the inclusion of the lowland and plateau plots, **B)** with the inclusion of the lowland, mid-slope, and plateau plots. Per factor the percentage of total variance is given in each column.

Discussion

Our results show that the similarity in species composition between plots of the bauxite mountains in Northeast Suriname are both the result of habitat and geographical distance. This pattern is consistent with numerous other studies in Western Amazonia and Panama (Chust *et al.*, 2006; Condit *et al.*, 2002; Pitman *et al.*, 2001; Pitman *et al.*, 2002; Tuomisto *et al.*, 2003), although the causes and the influences of environmental conditions and geographical distance on the similarities between forest plots may differ between areas. This result emphasizes that conservation planning should integrate the specific influences of environmental conditions and geographical distances for the area under consideration for protection or for extraction of mineral resources.

In the case of the bauxite mountains, habitat explained most variation in similarity between plots, and several indicator taxa were found for the plateaus. In another dataset we showed that the results of the indicator analyses, especially the number of individuals of indicator species in the non-indicator habitat, could indicate whether environmental filtering might be asymmetric (Chapter 4). The fact that the individuals of plateau indicator species make up less of the total amount of individuals found in the lowlands than vice versa, suggests that asymmetric environmental filtering also occurs here. This supports a view that some species that are associated with the plateaus are confined to these habitats, and the mountains partly function as isolated islands for these species. However, the amount of indicator taxa found for the lowlands and the plateaus is relatively low. In addition, the three mountains each have their specific species and species composition changes along geographical distances. In fact, most of the common species, families and genera occurred in both the lowlands and the plateaus, and at more than one site (Brownsberg, Lely or Nassau). This suggests that species on the plateaus and in the lowlands partly belong to the same metacommunity. Environmental conditions on the plateau could be similar to the lowlands, especially when the soils are deeper. Where the soil is rocky and the ferro-bauxite cap appears at the surface the species composition changes instantly and the lower savannah forest occurs (this study, Lindeman & Moolenaar, 1959). These soil conditions may alternate with each other at short distances even within a 1-ha plot, creating a mosaic of higher and lower forests. We therefore hypothesize that the soil depth on top of the ferro-bauxite cap is affecting the forest stature and composition, and similar patterns can be observed in the lowlands at places where soils are shallow and the parent rock comes close to the surface.

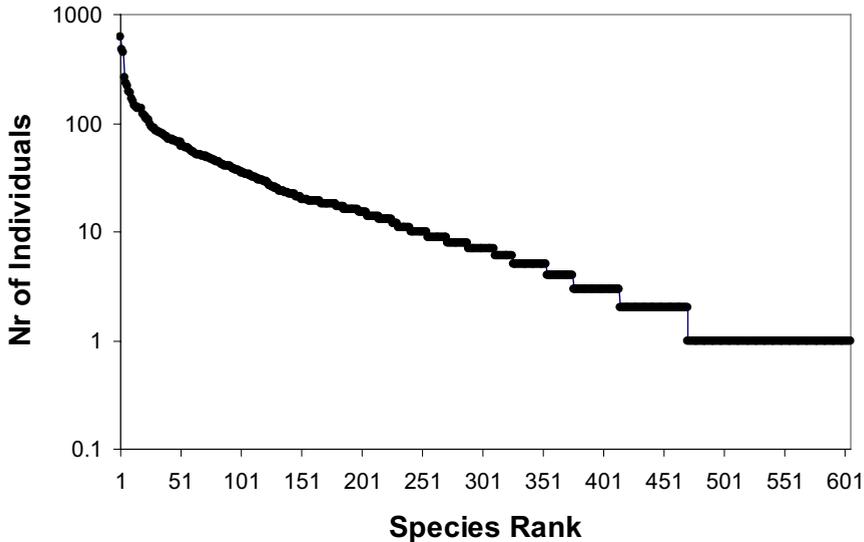


Figure 5.4

The species of the total database of 23 1-ha plots are ranked according to their abundances. On the left the common species are plotted, and on the right the rare species.

Conservation value

We did not find evidence for the occurrence of endemic tree species for the three plateaus. Most common species with a significant indicator value within our study have a geographical distribution extending outside Suriname (checked with the checklist of the plants of the Guianas, Funk *et al.*, 2007). It is however possible that such tree species are associated with bauxite plateaus across the Guianas, as is suggested for other plant taxa (de Granville, 1991). The majority of the species occur only in very low abundances (Figure 5.4) which is consistent with the predictions of neutral community models (Hubbell *et al.*, 2008). Their rarity, however, makes it impossible to test whether or not these species have a significant preference for either the lowland or the plateaus.

A unique feature of the plateaus is that several indicator genera and families are typical for dry savannah soils with high aluminum levels (Chenery, 1955; Chenery & Sporne, 1976; Haridasan, 1982; Haridasan & Monteiro de Araújo, 1988; Jansen *et al.*, 2000; Jansen *et al.*, 2004; Jansen *et al.*, 2002). These conditions are not very common in Suriname.

The high tree alpha-diversity on the plateau is to be expected if the floristic composition is a combination of a flora associated with the plateaus and

a flora originating from the lowlands. The savannah forest, which can have a very low alpha-diversity (Table S5.1), is very different from the high tropical rain forest. We currently lack the data to assess the conservation value of this forest type, but potentially it might be high. There are several types of savannah forest ranging from dry forest to forest covered with dense moss and epiphytic vegetation (e.g. bromeliads and orchids). This latter type is a kind of cloud forest at lower altitudinal levels (de Granville, 1991).

The bauxite mountains of Northeastern Suriname currently have the highest tree alpha-diversity found in Suriname (ter Steege *et al.*, 2003; ter Steege *et al.*, 2006). There are species that are specific for the plateaus, especially in the savannah forest. Based on these characters the forest types of the plateaus deserve some form of protection, especially since all the plateaus in Northeastern Suriname are destined for open pit mining. The plateaus and part of the slopes of the Brownsberg are already included in the Brownsberg Nature Park. The Lely Mountains and Nassau Mountains are so far without any protection. As the three mountains are quite dissimilar from each other in species composition, we argue that it is recommendable to at least protect parts of all three mountains and parts of their surrounding lowland forests.

Next page: *Swartzia grandifolia* in low forests on white sand, Alberga road, Suriname



Chapter 6 Summary and conclusions

Recent years have seen a fierce debate about the causes of beta-diversity, the change in species composition over landscapes, in tropical rainforests (Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Pitman *et al.*, 1999; 2001; Ruokolainen *et al.*, 2002; Tuomisto *et al.*, 2003). Much of this debate has been revived through the introduction of neutral models that predict that species composition changes randomly over landscapes with dispersal limitation as the driving ecological process, extending ideas of Gleason portrayed in the early 1900's (Bell, 2000; 2001; Gleason, 1922; 1926; Hubbell, 1997; 2001). In these neutral models all individuals of all species have the same chance of death, birth, dispersal, and speciation, and species are thought to be ecologically equivalent (Hubbell, 2005). These neutral models predict several diversity patterns found in ecological communities pretty well, and in doing so challenge niche differentiation theory (see Figure 6.1, Chave, 2004). In this study we investigated what we can learn from the interaction between local and regional diversity in the forests in the Guianas. We inventoried approximately 38 1-ha plots paired in forests on brown and white sands in Guyana and Suriname, and approximately 23 1-ha plots in the lowlands, on the slopes, and on the plateaus of bauxite mountains in Northeastern Suriname. These forest plots were combined with earlier available forest plot data, totaling a database of 156 mostly 1-ha plots in six different forest types.

Forest composition and tree diversity in the Guianas

The Guianas beg to disagree with a neutral community structure, as forest composition and diversity evidently responds to the mosaic of different soil types (Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Lindeman & Moolenaar, 1959; Maas, 1971; Schulz, 1960; ter Steege *et al.*, 1993). Our results of the first biogeographical study on a species level involving 156 forest plots in the Guianas showed that forest composition changed dramatically from place to place (Chapter 3). Several forest types, including flood plain, swamp, savannah and white sand forests had low alpha-diversities and were dominated by only a small suite of common species. These forests showed very clear floristic differences from the lowland tropical rainforests in the Guianas, and the bauxite plateau forests in Suriname. The lowland tropical rainforests in the Guianas, including the bauxite plateau forests in Suriname, showed a longitudinal gradient in tree

alpha-diversity increasing from Venezuela to French Guiana (ter Steege *et al.*, 2003). This means that relative to the number of individuals, the number of species that are encountered in 1-ha plots is increasing. The increase was mostly due to the addition of tree species with only one to few individuals per plot. In Guyana, the tropical lowland forests were the exception to the rule with the lowest average tree alpha-diversity found in the lowland forests of the Guianas. These lowland tropical forests in Guyana were also floristically different from all the other lowland forests of the Guiana Shield basement complex in French Guiana, Suriname, and Venezuela. In the forests of the Guiana Shield basement complex the lowland forests of Venezuela were floristically separated from the forests in French Guiana and Suriname. In general, forest composition followed geological patterns in the Guianas. These floristic patterns correspond well with earlier findings and suggestions from forests inventories on a generic level and from smaller forests plot datasets (Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Lindeman & Moolenaar, 1959; Maas, 1971; Schulz, 1960; ter Steege & Zondervan, 2000).

Wood density, seed mass, and fleshy fruits

In Chapter 3 we also investigated how plant attributes and diversity covary, and what possible covariations tell us about the functioning of the Guianan forests. Between nine forest groups we observed significant differences in several plant attributes of tree species in the Guianan forests. Comparisons of plant attributes between forest groups revealed a spectrum in covariation involving the percentage of fleshy fruits and seed mass, and also involving wood density and to a lesser extent tree alpha-diversity. At the two ends of this spectrum we observed two suites of traits: 1) one represented by the white sand, flood plain, and lowland forests of Guyana, especially the forests on the sandy soils and some laterite soils in Central and Northwest Guyana, with a high dominance of trees with large seeds in dry fruits combined with high wood densities, and low tree alpha-diversities, and 2) represented by the bauxite plateau forests in Suriname and the lowland forests of Venezuela with a high dominance of trees and species with smaller seeds in fleshy fruits combined with relatively low community averaged wood density, and higher tree alpha-diversities. Our results do not show such a strong relation of this spectrum in covariation with tree alpha-diversity nor soil fertility over the Guianas (ter Steege & Hammond, 2001), as the lowland forests in French Guiana, with highest tree alpha-diversity, fall in the middle of the spectrum in covariation between traits.

Covariation of seed and fruit characteristics should have an effect on the mode of dispersal of trees within the forest groups. It may also reflect strategies where large seeds produce superior survivors (large investment in seedling survival) and small seeds superior colonizers (large investment in dispersal), but such trade-offs are only thought to operate under conditions of strong asymmetric competition (Coomes & Grubb, 2003; Hammond & Brown, 1995; ter Steege & Hammond, 2001)

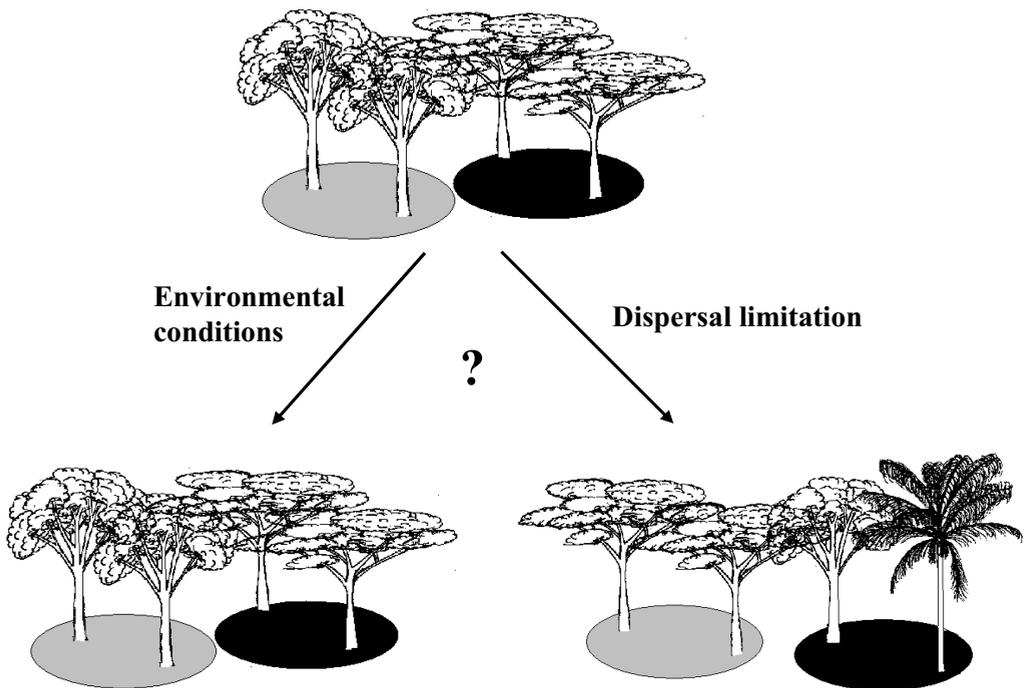


Figure 6.1

There are two opposing views on the build up of ecological communities.

The neutral perspective: ecological communities have open membership (any species can enter), are shaped by ecological drift (random birth, death, dispersal and speciation) and are in dynamic equilibrium (constantly changing in composition also at geographical distances e.g. through dispersal limitation).

The niche differentiation perspective: ecological communities have limited membership, are shaped by best competitors for limited resources, and can reach stable equilibrium (species are associated with certain environmental conditions).

Local and regional diversity in brown and white sand forests

In spite of recent advances using developments of the neutral theory of biodiversity, we are deficient in our understanding on how local diversity is shaped by regional diversity (Etienne, 2005; Etienne & Alonso, 2005; Etienne & Olff, 2004; Jabot *et al.*, 2008). We used advancements of the neutral theory to evaluate, with neutral-like dynamical community models, different hypotheses on the low diversity of the white sand forest. With a neutral-like model (Jabot *et al.*, 2008) the recruitment limitation (dispersal limitation and post-dispersal environmental filtering) could be inferred from two objectively constructed regional species pools. For abundance data we used the largest paired plot dataset of 38 1-ha plots in forests on brown and white sands. Through MCMC searches (Markov Chain Monte Carlo with Metropolis-Hastings algorithm), species were separated with all their individuals in two regional pools. Models where the regional pools corresponded with the floristic groups of Guyana and Suriname had the highest likelihood. Forest plots were thus first separated by geographical distance. Within Guyana and Suriname floristic groups that corresponded with the brown and white sands had the highest likelihood. This confirmed the role of environment in shaping the forest composition, and shows that forests on white and brown sands draw their species from different regional species pools. We provide strong evidence that asymmetric environmental filtering and a lower regional diversity influence the lower diversity found in white sand forests compared with neighboring brown sand forests. White sand forests were not necessarily more dispersal limited than brown sand forests, as suggested by earlier studies (Prance, 1996). Still within the white sand forests apparent changes in species abundance patterns occurred along geographical distances. Thus, we showed that a gradient in beta-diversity could occur in forests under similar climatic and soil conditions. Our results also suggest that tree alpha-diversity (Fisher's alpha) and the regional diversity of white sands areas could be controlled by the size of the white sand area, acting on the size of the regional species pool (Anderson, 1981; ter Steege *et al.*, 2000b). It would be interesting to make comparisons with the white sand forests in the Upper Rio Negro as the total extent of the white sand area there is larger than in both Guyana and Suriname. If the size of the white sand area is influencing the Fischer's alpha and regional diversity in white sand areas, we would expect higher diversity values in the Upper Rio Negro. Another interesting comparison would be to investigate whether the environmental filtering is of the same order in the Upper Rio Negro. Overall, our results indicate that there are striking biogeographical patterns in

the rainforests of the Guianas left unexplained by (current) environmental conditions.

What drives the difference in composition between brown and white sands forests?

In Chapter 4 we showed that an asymmetrical environmental filter was operating between the brown and white sand forests. With an asymmetrical environmental filter we mean that establishment and growth conditions are more difficult and severe on the white sand. More species are able to cross from the white to the brown sands than visa versa (Chapter 4). What biotic or abiotic factor constitutes this environmental filter is less clear (Chapter 2). Based on our field observations we hypothesize that a strong and continuously operating environmental filter must act already at the seedling stage. We discussed, amongst others, the role of water availability, light availability, nutrient availability and total nutrients of the soils. Interestingly, available nutrients in brown and white sands did not seem to differ much (Klinge *et al.*, 1977; van Kekem *et al.*, 1996). Also, only a few studies on foliar nutrients of mature trees showed significant differences between brown and white sands, and only for foliar N (Brouwer, 1996; Perreijn, 2002; Reich *et al.*, 1994). However, white sands had evidently lower total soil nutrients than brown sands, and we discussed to what extent trees could draw upon these nutrients (Brouwer, 1996; Quesada *et al.*, 2009b; Raaimakers, 1994). We used a database of leaf litter fall to show that productivity in terms of leaf and total small litter fall was a factor 1.35 lower in forests on white sands. Our results also indicated that white sands seemed to be more N- and P-limited than brown sands (e.g. Coomes, 1997; Cuevas & Medina, 1988; Raaimakers, 1994). Of the factors that could contribute to the environmental filter between forests on brown and white sands, soil nutrient status was currently the only convincing candidate to explain on its own account a continuous and strong filter that is already operative at the seedling stage. In some cases, the lower soil moisture content in the upper white sand layer may affect seedling survival, and this could contribute to the observed floristic differences between brown and white sand forests. Adaptations to slower growth on white sands may also inflict trade-offs for growth of tree species on other soil types (Fine *et al.*, 2004). To what extent other factors were involved in such trade-offs remains less clear at this point in time.

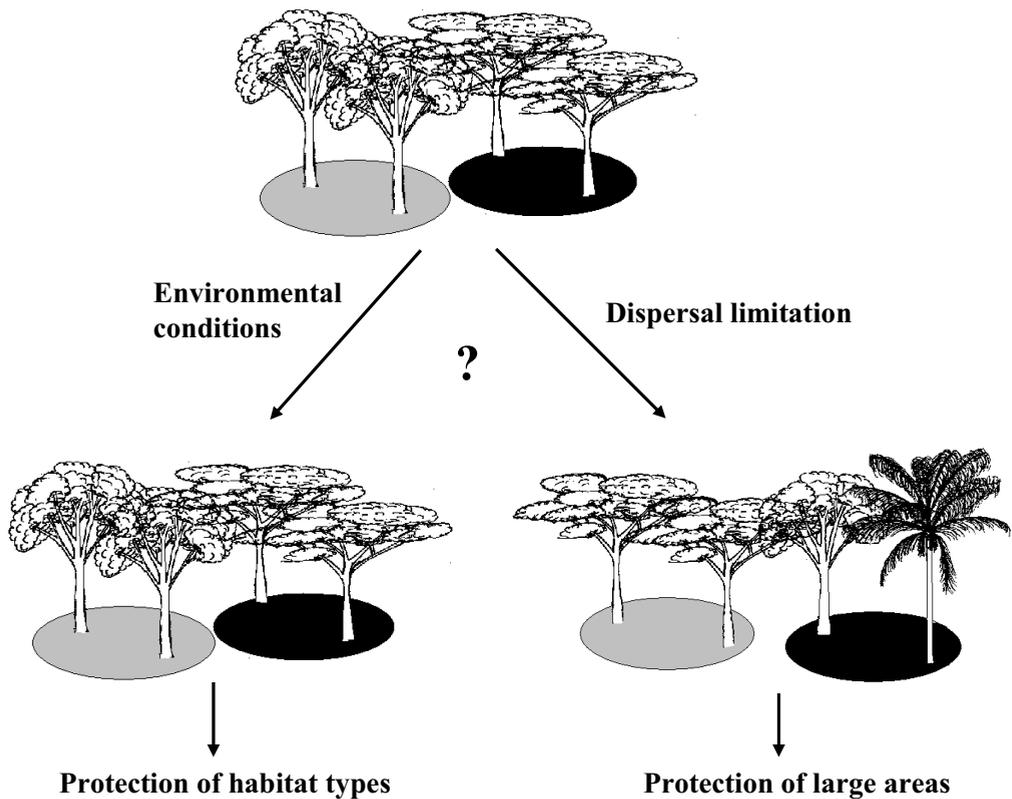


Figure 6.2.

Different views on the build up of ecological communities may lead to different conservation approaches:

The neutral perspective: If species composition changes rapidly over distance gradients (e.g. due to dispersal limitation), capturing a wide variety in species composition would require large areas of forests or alternatively many evenly spaced areas with some form of connectivity between forest patches.

The niche differentiation perspective: In case species composition is more controlled by environmental conditions, including geographical distances in a conservation design becomes less important. Choosing between sites with similar environmental conditions would be defensible in these circumstances

Neutral theory and its predictions for conservation

We used the predictions of the neutral theory to discuss the conservation value of forests on bauxite mountains in Northeastern Suriname (Chapter 5). These mountains are all destined for open-pit mining for aluminum ore, and may constitute a rare and endangered landscape type. Knowledge whether species

composition in tropical forest changes because of geographical distance or because of environmental (such as soil mediated) gradients may lead to different conservation and ecosystem management approaches (see Figure 6.2). To assess the conservation value in terms of tree diversity on these bauxite mountains, we designed a plot study of 23 1-ha plots on the plateaus, slopes, and in the lowlands. We found that both environmental conditions and geographical distance determined the similarity between forest plots, the influence of environmental conditions being larger. However, forest composition on the plateaus was also partly a random draw of species from the lowlands, and each of the mountains had its own specific species composition. On the plateaus genera and families of trees occurred that are typical for dry savannah-like conditions with soils with high aluminum contents. These conditions are not common in Suriname. In fact, the savannah forests could have the highest conservation value, but we lack data to evaluate this at this moment. Tree species composition may show an edaphic effect in response to the, at times, shallow soil surface on top of the hard ferro-bauxite crust. The plateaus also had the highest tree alpha-diversity currently found in Suriname. Considering that the bauxite plateau forests had different floristic elements, especially in relation to the savannah forests, compared to the lowland forests, we recommended that at least parts of these plateaus should be considered for conservation.

On the role of environment and geographical distance

In spite of clear floristic differences between six forest types (dataset of 156 plots), there is an equal role of environmental conditions and geographical distance in explaining forest composition in the Guianas (Chapter 3). Our results show that only under 'extreme' environmental conditions, forest composition clearly responds to soil-mediated habitat differences. Examples are the white sands (Chapters 2, 3, and 4), and those instances where species composition and forest physiognomy (e.g. in the savannah forest) are affected by a shallow soil because of a hard bed-rock undersurface (Chapter 5, see also Beard, 1944). Forest composition is also clearly responding to environmental conditions operating in swamp and flood plain forests (Chapter 3). Despite clear soil differences (e.g. in available nutrients) between brown sands and laterite soils (Quesada *et al.*, 2009b; van Kekem *et al.*, 1996), there is a substantial amount of floristic overlap (Chapters 3, and 5). Forests on brown sands and laterite soils floristically group together in the Guianas (Chapter 3). Nevertheless, under those conditions, where clear floristic differences are found, this is mostly caused by a

small set of common species with high dominance, at least in the low diversity forests (Chapters 3, 4, and 5). This raises the question why not all tree species are clearly responding to soil-mediated habitat differences?

One of the interesting aspects of the neutral theory by Hubbell (2001) is the assumption that intraspecific variability in response to environmental conditions exceeds interspecific variability (Chave, 2004). We still know very little about the variation in responses to environmental conditions within tropical trees species. Moreover, soil conditions and nutrients may fluctuate extensively in tropical soils at very short distances, and this could affect the resources available to individual trees on similar soils (Jetten, 1994). Probably one of the most likely explanations is that tree species can handle a wide variation in environmental conditions, or as Gleason (1926, page 8) put it: "*Nor are plants in general, apart from these few restricted species, limited to a very narrow range of environmental demands*". On average mature tropical trees can reach ages between 200 and 300 years, with some individuals of several species reaching up to 600 years (Fichtler *et al.*, 2003; Metcalf *et al.*, 2009; Worbes, 2002). Therefore, trees cannot really afford to be too specialized as they will encounter many changes over time.

Forest composition in the Guianas also changed considerably along geographical distance (Chapters 3, 4, and 5). Nonetheless, this does not necessarily have to mean that forest composition fluctuates randomly over the landscape (see also Clark, 2009). A decay in similarity over geographical distances between ecological communities is found in other studies as well, and could very well be an intrinsic pattern in various organisms (Morlon *et al.*, 2008; Nekola & White, 1999; Soininen *et al.*, 2007). In the forests of the Guianas changes in forest composition could indicate a considerable role for historical processes and contingencies. The exact role of dispersal limitation, whether historic or contemporary, still needs to be assessed, and we need to better match all the collections of the plots in the Guianas for this assessment. We showed in the white sands forests that forest composition could also change under similar climatic and soil conditions (Chapter 4). In the Guianan forests the distance-decay was not only due to the introduction of new species, but also the result of new combinations of species and different abundances of species. Our findings are in agreement with Morlon *et al.* (2008) who developed a general framework for the distance-decay of similarity in ecological communities. Again the common species dictate the pattern, and the rare species are of lesser importance (Lennon *et al.*, 2004; Morlon *et al.*, 2008).

Sampling the rainforest

One of the most arduous challenges for ecologists/naturalists is how to sample the composition of vast areas of tropical rainforests, and evaluate their uniqueness in comparison to other areas. In this study the forest plots represented the local communities (Chapter 3, 4, and 5). Asking whether a species dispersed into a local community, is the same as asking whether our samples reflect the species and their abundances well in an area? The general pattern in our data was that there are few common species and many rare species (see also Hubbell *et al.*, 2008 for the scale of the Amazon forests). The common species dictated the tree species composition and diversity patterns. Often in the low tree alpha-diversity forests this was caused by a small set of common species. In the higher tree alpha-diversity forests the number of common species responsible for the diversity patterns was higher, but their species abundances were much lower (Chapter 3, 4, and 5). This pattern of abundances and number of common and rare species most likely affects the total amount of variation in forest composition explained. The question is if this is a result of the sample size and/or the number of samples?

Making bigger plots than 1-ha plots is an option, and in some cases like in Western Amazonia this will boost-up the signal of the most common species (Pitman, 2000). This will also inevitably enlarge the tail of rare species. In some of our research areas, this will also raise the amount of habitat heterogeneity and possibly beta-diversity in the plots by including other soil conditions, creeks and streams, etc. Despite the large number of plots we used, it probably is still too small a sample. This especially counts for the bauxite mountains in Northeastern Suriname, where the number of plots are sufficient for a general recommendation on the conservation value of the plateau forests, but not a tailored recommendation for each separate bauxite mountain.

Our plot data set in the Guianas showed that most species were rare species. These rare species are a huge challenge for ecologists (see also Haripersaud, 2009; Ricklefs, 2000). Potentially these rare species can provide more information about the different forest types, and could increase the total amount of variation in composition explained. The question is how to achieve this? Since the rare species can hardly be evaluated on statistical grounds, community dynamical models that can predict the amount of rare species in different areas become very much needed (Harte, 2003). Rare species are also the first to disappear if there are major disturbances in the area (these could be

natural disturbances, but also man-made), and could have a conservation value but this is difficult to assess (Chapter 5, see also Harte, 2003).

With respect to our assessment of the conservation value of the forests on the bauxite mountains in Northeastern Suriname, our experience is that species collections can be very informative about an area. But a list of tree species without abundances can rarely be the sole basis for conservation approaches in tropical rainforests. This is of course unless a dataset with wider scale is involved and that database is evaluated with niche modeling (Haripersaud, 2009; Raes, 2009). Nevertheless, on the long run species collections of an area may better reflect the species present than plots will, as an example from Mabura Hill showed (Haripersaud, 2009). On the other hand, quantitative data on species abundances can give an insight into the ecological processes that are operating in an area. Species abundance data can also aid in assessing which areas should be set aside for conservation on the basis of complementarity (Chapter 5).

The future research framework

The debate that has been raised by the neutral theory on the structure of ecological communities, its predictions on beta-diversity, and speciation have been fruitful (Beeravolu *et al.*, 2009). Yet, the neutral theory has some serious weaknesses, concerning not in the least the neutrality assumption itself (Clark, 2009). Another weakness is that the metacommunity is assumed to be panmictic; every individual of every species has the same chance of entering a local community (but see O'Dwyer & Green, 2010 for new developments). However, the neutral theory has also spurred advancements in metacommunity analysis and likelihood computation, and made a start with the fusing of ecological and population genetical theory. New research should use these advancements, rather than to focus on the testing of neutrality alone.

A research framework that is focused on the interaction between a metacommunity and several local communities is worthwhile to pursue. There are currently at least three questions on the metacommunity that need answering:

1. What is the size and extent of the metacommunity; where does it end?
2. How to construct a metacommunity based on abundance data; in such a way that it is independently collected from the samples that are actually tested?

3. How to include a spatial component into the metacommunity concept to allow for a better understanding of what controls beta-diversity?

Answering these three questions would bring metacommunity analysis in the realm of forest management. With respect to the first question, Ricklefs (2008) has proposed a research agenda to leave the concept of the ecological community and focus more on populations. It is clear that we need to draft regional species pools with evolutionary and functional meaning (see also McGill 2008). In respect to the third question, we are in need of dynamical spatially explicit community models to better predict and model beta-diversity. This could mean that models have to be build from scratch again (Hubbell personal communication).

Concluding

Can the neutral theory explain the community composition in the Guiana Shield forests? The answer is no, it cannot. Floristics and covariation in plant attributes in various forest types of the Guianas show evident differences between tree species, yielding little support for a neutral view. Most patterns are caused by small sets of common species that may dominate the forests, especially where the alpha-diversity of the forests is low. There are, however, striking biogeographical patterns in the rainforests of the Guianas that remain unexplained by (current) environmental conditions. Other techniques, such as genetic and phylogeographic assessments could aid in unraveling these unexplained biogeographical patterns. Theoretical advancements within the framework of neutral theory could nonetheless aid in investigating the interaction between local and regional diversity.

Next page: research teams that contributed to the forest data set of this thesis in Suriname



Nederlandse samenvatting

In de afgelopen jaren is er een stevig debat ontstaan over de oorzaken van beta-diversiteit, dat is de veranderingen in soortensamenstelling over landschappen, in tropische regenwouden (Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Pitman *et al.*, 1999; 2001; Ruokolainen *et al.*, 2002; Tuomisto *et al.*, 2003). De introductie van neutrale modellen heeft dit debat nieuw leven ingeblazen (Bell, 2000; 2001; Gleason, 1922; 1926; Hubbell, 1997; 2001). Die modellen borduren voort op ideeën die Gleason in het begin van de 20^e eeuw uitte, en voorspellen dat de soortensamenstelling willekeurig over een landschap fluctueert, waarbij als ecologisch drijvend proces alleen beperkingen in de verspreiding van een soort een rol speelt en niet de natuurlijke omgevingsfactoren. Deze neutrale modellen stellen, dat alle individuen van alle soorten dezelfde kans op sterfte, geboorte, verspreiding en soortvorming hebben en gaan er van uit dat de soorten ecologisch equivalent zijn (Hubbell, 2005). De niche-differentiatie theorie komt onder druk te staan, doordat de voorspellingen van neutrale modellen ten aanzien van biodiversiteitspatronen overeenkomsten vertonen met patronen die in ecologische gemeenschappen gevonden worden (zie Figuur 6.1, Chave, 2004). In deze studie wordt onderzocht wat wij van de interactie tussen lokale en regionale diversiteit in de bossen van de Guianas kunnen leren. Hiervoor zijn er 38 1-ha proefvlakken in bos op zowel wit- als bruinzandgronden in Guyana en Suriname geïnventariseerd, als mede om en nabij de 23 1-ha proefvlakken in de bossen in de laaglanden, op de hellingen en op de plateaus van bauxiet bergen in het Noordoosten van Suriname. In combinatie met gegevens van bosopnamen die reeds eerder door anderen zijn geïnventariseerd, leverde dit in totaal een dataset van 156 meerendeel 1-ha proefvlakken in zes verschillende bostypen op.

Bossamenstelling en boomdiversiteit in de Guianas

De bossen in de Guianas lijken niet in overeenstemming met een neutrale gemeenschapsstructuur, aangezien zowel bossamenstelling als diversiteit overduidelijk met het mozaïek aan verschillende bodemsoorten correleren (Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Lindeman & Moolenaar, 1959; Maas, 1971; Schulz, 1960; ter Steege *et al.*, 1993). De eerste biogeografische studie op soortsniveau aan de hand van 156 proefvlakken laat zien, dat de bossamenstelling in de Guianas dramatisch van plaats tot plaats verandert

(Hoofdstuk 3). Enkele bostypen, waaronder vloedbossen, moerasbossen, savannebossen en witzandbossen, vertonen een lage alpha-diversiteit en worden gedomineerd door een kleine groep van algemene soorten. Er zijn duidelijke floristische verschillen tussen deze bossen en de bossen in de laaglanden in de Guianas en de bossen op bauxietplateaus in Suriname. De laaglandbossen in de Guianas, inclusief de bossen op bauxietplateaus in Suriname, vertonen volgens hun lengtegraadpositie een gradient in boom alpha-diversiteit die van Venezuela tot Frans Guiana toeneemt (ter Steege *et al.*, 2003). Volgens deze gradient neemt het aantal soorten, in verhouding tot het aantal individuen, in 1-ha proefvlakken toe, met name door boomsoorten met slechts enkele individuen per proefvlak. De laaglandbossen in Guyana vormen met een lage gemiddelde boom alpha-diversiteit een uitzondering. Dit is ook zichtbaar in de floristiek, die verschilt van alle laaglandbossen op het Guyana Schild 'basement' complex in Frans Guyana, Suriname en Venezuela. Van de bossen op het Guyana Schild 'basement' complex verschillen de bossen in Venezuela floristisch van de bossen in Frans Guiana en Suriname. De bossamenstelling volgt over het algemeen de geologische patronen in de Guianas. Deze floristische patronen komen goed overeen met eerdere bevindingen en suggesties betreffende bosinventarisaties op een genus niveau en van kleinere datasets van bosproefvlakken (Davis & Richards, 1933; 1934; Fanshawe, 1952; 1954; Lindeman & Moolenaar, 1959; Maas, 1971; Schulz, 1960; ter Steege & Zondervan, 2000).

Houtdichtheid, zaadmassa en vlezige vruchten

Hoofdstuk 3 laat ook zien hoe bepaalde planteneigenschappen covariëren met de diversiteit en wat deze covariaties ons vertellen over het functioneren van de bossen in de Guianas. Negen bosgroepen in de Guianas vertonen significante verschillen in planteneigenschappen van boomsoorten. Vergelijkingen van planteneigenschappen tussen deze bosgroepen tonen een spectrum in covariatie in de patronen van voorkomen van vlezige vruchten en de zwaarte van zaadmassa, alsook de houtdichtheid en in mindere mate de boom alpha-diversiteit. Aan de uiteinden van dit spectrum zijn twee groepen van eigenschappen te zien: 1) één die vertegenwoordigd wordt door de witzandbossen, de vloedbossen en de laaglandbossen van Guyana, met name de bossen op zandige gronden en enkele op laterietgronden in Centraal en het Noordwesten van Guyana; ze hebben een hoge dominantie van bomen met zware zaden en droge vruchten in combinatie met relatief hoge gemiddelde houtdichtheden en een lage boom alpha-diversiteit, en 2) één die

vertegenwoordigd wordt door de bossen op bauxietplateaus in Suriname en de laaglandbossen in Venezuela; ze hebben een hoge dominantie van bomen met lichte zaden in vlezig vruchten in combinatie met relatief lage gemiddelde houtdichtheden en een hoge boom alpha-diversiteit. Onze resultaten laten geen sterke relatie van dit spectrum in covariatie met boom alpha-diversiteit zien en ook niet met de bodemvruchtbaarheid in de Guianas (ter Steege & Hammond, 2001), aangezien de laaglandbossen in Frans Guiana, met de hoogste boom alpha-diversiteit, in het midden van het spectrum in covariatie van planteneigenschappen vallen.

Covariatie in zaad- en vruchtkenmerken hebben mogelijk een effect op de wijze van verspreiding van bomen in de bosgroepen. Het zou ook kunnen wijzen op strategieën in welke grote zaden door superieure overlevers (grote investering in de overleving van zaailingen) geproduceerd worden en kleine zaden door superieure kolonistoren (grote investering in verspreiding). Zulke compromissen ('trade-offs') worden alleen verondersteld operationeel te zijn in gevallen van sterk assymmetrische concurrentie (Coomes & Grubb, 2003; Hammond & Brown, 1995; ter Steege & Hammond, 2001).

Lokale en regionale diversiteit in bruin- en witzandbossen

Hoewel recentelijk de ontwikkelingen in de neutrale theorie van biodiversiteit enige vooruitgang hebben geboekt, is er nog steeds een groot gebrek aan kennis over hoe lokale diversiteit wordt vormgegeven door regionale diversiteit en vice versa (Etienne, 2005; Etienne & Alonso, 2005; Etienne & Olff, 2004; Jabot *et al.*, 2008). Het gebruik van progressie in de neutrale theorie stelt ons in staat door middel van min of meer neutrale dynamische gemeenschapsmodellen de verschillende hypothesen ten aanzien van de lage diversiteit in witzandbossen te evalueren (Hoofdstuk 4). Met een min of meer neutraal model (Jabot *et al.*, 2008) kan de limitatie in reclutering (limitatie in verspreiding en post-verspreidingsfiltering door natuurlijke omstandigheden) van twee onafhankelijk geconstrueerde regionale soortengroepen afgeleid worden. Hiervoor hebben wij gebruik gemaakt van gegevens van het voorkomen van soorten in de op dit moment grootste dataset van 38 gepaarde proefvlakken van 1 ha in bossen op bruin- en witzandgronden. Door middel van MCMC-trekkingen (Markov Chain Monte Carlo met Metropolis-Hastings algoritme) zijn soorten met al hun individuen gescheiden in twee regionale soortengroepen. Onze resultaten laten zien dat in de modellen met de hoogste waarschijnlijkheid deze de regionale soortengroepen overeenkomen met de floristische groepen van Guyana

en Suriname. De 38 proefvlakken worden dus als eerste floristisch gescheiden door geografische afstand. De resultaten van nieuwe MCMC-trekkingen binnen de Guyana en Suriname datasets laten zien dat in de modellen met de hoogste waarschijnlijkheid de regionale soortengroepen overeenkomen met de floristische groepen van bruin- en witzandgronden. Dit bevestigt dat natuurlijke omgevingsfactoren een belangrijke rol spelen in het vormgeven van de bossamenstelling en toont aan dat bossen op wit en bruin zand hun soorten betrekken uit verschillende regionale soortengroepen. Wij leveren sterk bewijs, dat assymetrische filtering door natuurlijke omstandigheden en een lagere regionale diversiteit, in belangrijke mate de lage diversiteit van bossen op wit zand in vergelijking tot aangrenzende bossen op bruin zand bepalen. De soorten van bossen op wit zand zijn niet per definitie meer gelimiteerd in hun verspreiding dan bossen op bruin zand, zoals eerder in andere studies gesuggereerd is (Prance, 1996). Toch zijn er in de witzandbossen echter wel duidelijke veranderingen waar te nemen in het voorkomen van soorten over geografische afstanden. Met andere woorden, wij laten zien dat er wel degelijk een gradient in beta-diversiteit kan ontstaan in bossen onder gelijksoortige klimatologische en bodemomstandigheden. Onze resultaten suggeren ook dat boom alpha-diversiteit (Fisher's alpha) en de regionale diversiteit van witzandgebieden door de grootte van het witzandgebied bepaald kan worden en dat dat op haar beurt weer de grootte van de regionale soortengroep beïnvloedt (Anderson, 1981; ter Steege *et al.*, 2000b). Het zou interessant zijn deze resultaten eens te vergelijken met bossen op de witzandgronden van de boven Rio Negro, aangezien de totale oppervlakte van het witzandgebied aldaar veel groter is dan in zowel Guyana als Suriname. Indien de grootte van het witzandgebied de Fisher's Alpha en de regionale diversiteit ervan beïnvloedt, dan verwachten wij hogere diversiteitswaarden in de boven Rio Negro. Een andere interessante vergelijking zou zijn om te bestuderen of de filtering door natuurlijke omstandigheden in wit- en bruinzandbossen van een zelfde orde is in de boven Rio Negro. Alles bij elkaar laten onze resultaten zien dat er opvallende biogeografische patronen in de regenwouden van de Guianas zijn, die aan de hand van (huidige) natuurlijke omgevingsfactoren niet verklaard kunnen worden.

Wat veroorzaakt het verschil in samenstelling tussen bruin- en witzandbossen?

In Hoofdstuk 4 laten wij zien dat er een assymmetrische filtering door natuurlijke omgevingsfactoren tussen bruin- en witzandbossen bestaat. Met assymmetrische filtering door natuurlijke omgevingsfactoren bedoelen wij dat de vestigings- en groeiomstandigheden moeilijker en veeleisender zijn op het witte zand. Meer soorten zijn in staat van bossen op witzand naar bossen op bruinzand te migreren, dan vice versa (Hoofdstuk 4). Welke biotische en/of abiotische factoren het filter vormen is minder duidelijk (Hoofdstuk 2). Wij stellen, gebaseerd op onze veld observaties, dat een sterk en continu werkend filter van natuurlijke omgevingsfactoren reeds operatief is op het zaailingstadium. Vanuit dit licht bezien, bediscussiëren wij onder andere de rol van de beschikbaarheid van water, licht, nutriënten en de totale nutriënteninhoud in de bodems. Opvallend is dat de beschikbare nutriënten in bruin- en witzandgronden nauwelijks lijken te verschillen (Klinge *et al.*, 1977; van Kekem *et al.*, 1996). Daarnaast, laten slechts enkele studies significante verschillen in bladnutriënten van volwassen bomen op bruin- en witzandgronden zien, en dan alleen voor N in het blad (Brouwer, 1996; Perreijn, 2002; Reich *et al.*, 1994). Witzandgronden hebben daarentegen overduidelijk een lagere totale hoeveelheid bodemnutriënten dan bruinzandgronden, maar het is de vraag in hoeverre bomen beschikking hebben over deze nutriënten (Brouwer, 1996; Quesada *et al.*, 2009b; Raaimakers, 1994). De hoeveelheid nutriënten in gevallen blad laat zien dat productiviteit, gedefinieerd in termen van gevallen blad en kleine boomresten, een factor 1.35 lager is in de bossen op het witte zand. De beschikbare data suggereren ook dat de witzandgronden sterker N- en P-gelimiteerd zijn dan bruinzandgronden (o.a. Coomes, 1997; Cuevas & Medina, 1988; Raaimakers, 1994). Van alle factoren die kunnen bijdragen aan het filter van natuurlijke omgevingsfactoren tussen bossen op bruin- en witzandgronden is de nutriëntenstatus van de bodem op het moment de enige overtuigende kandidaat om een continu en sterk filter te verklaren dat al operatief is op het zaailingstadium. In sommige gevallen zou de lage bodemvochtigheid in de bovenste laag van de witte zanden de overleving van zaailingen kunnen beïnvloeden en dit zou aan de waargenomen floristische verschillen tussen bossen op bruin- en witzandgronden kunnen bijdragen. Aanpassingen aan een langzamere groei op de witte zanden zou ook kunnen leiden tot compromissen ('trade-offs') in de groei in vergelijking met soorten op andere bodemsoorten

(Fine *et al.*, 2004). In hoeverre andere factoren een rol kunnen spelen in dergelijke compromissen ('trade-offs') blijft vooralsnog onduidelijk.

De neutrale theorie en haar voorspellingen ten aanzien van natuurbescherming

Aan de hand van voorspellingen van de neutrale theorie bediscussiëren wij de natuurbeschermingswaarde van de bossen op de bauxietbergen in het Noordoosten van Suriname (Hoofdstuk 5). Deze bergen zijn allen bestemd voor 'open-pit' mijnbouw voor de grondstoffen van aluminium en behoren mogelijk tot een zeldzaam en bedreigd landschapstype. Kennis in hoeverre bossamenstelling in tropische bossen verandert met geografische afstand of volgens gradienten in natuurlijke omgevingsfactoren (waaronder bodembepalende factoren) kan leiden tot verschillende benaderingen in de natuurbescherming en het ecosysteembeheer van gebieden (zie Figuur 6.2). Voor het bepalen van de natuurbeschermingswaarden in termen van de boomdiversiteit van de bossen op de bauxietbergen hebben wij een proefvlakstudie uitgevoerd aan ca. 23 1-ha plots in de laaglanden, op de hellingen en op de plateaus van drie bauxietbergen. Zowel natuurlijke omgevingsfactoren alsmede geografische afstand bepalen de similariteit tussen bosproefvlakken, hoewel de invloed van natuurlijke omgevingsfactoren groter is. Daarentegen, is de soortensamenstelling op de plateaus ook gedeeltelijk een willekeurige greep uit de soorten van de laaglandbossen en heeft elke berg een eigen specifieke soortensamenstelling. Op de plateaus komen genera en families voor die typisch zijn voor droge savanneachtige omstandigheden en bodems die een hoog aluminiumgehalte bevatten. Deze omstandigheden zijn niet algemeen in Suriname. Sterker nog, de savannebossen hebben mogelijk de hoogste natuurbeschermingswaarde, maar het ontbreekt nog aan data om dit vooralsnog nauwkeurig te evalueren. De boomsoortensamenstelling kan een edafische response vertonen al naargelang de bodem ondieper wordt en de harde korst van ferro-bauxiet aan de oppervlakte komt. De bossen op de plateaus hebben op het moment de hoogste boom alpha-diversiteit die er in Suriname gevonden is. In ogenschouw nemend dat de bossen op de bauxietplateaus floristisch verschillen van de laaglandbossen, met name de savannebossen, raadden wij aan ten minste delen van elk van deze plateaus voor natuurbescherming in overweging te nemen.

Concluderend

Op de vraag of de neutrale theorie de gemeenschapssamenstelling van bossen op het Guyana Schild kan verklaren, kan slechts negatief geantwoord worden. De floristiek, alsook de covariatie in planteneigenschappen in verschillende bostypen in de Guianas, laten duidelijke verschillen in boomsoorten zien, wat nauwelijks een neutraal perspectief op de bossen ondersteunt. De meeste patronen worden veroorzaakt door een kleine groep van algemene soorten, die de bossen kunnen domineren, met name daar waar de bossen een lage boom alpha-diversiteit hebben. Er zijn daarentegen overduidelijke biogeografische patronen in de regenwouden van de Guianas die door de (huidige) natuurlijke omgevingsfactoren onverklaard blijven. Andere onderzoekstechnieken, waaronder genetische en fylogeografische bepalingen, kunnen helpen om de onderliggende oorzaken van deze onverklaarde biogeografische patronen te ontrafelen. Theoretische vooruitgang in het kader van de neutral theorie kan desalniettemin helpen de interactie tussen lokale en regionale diversiteit verder te onderzoeken.

Supplementary Information

Table S3.1 Plot meta data of 156 plots in six forest types in the Guianas.

Forest*	Country	Site	Soil**	N	S	Fa	Latitude	Longitude	ha	data owner
FL	Guyana	Iwokrama Mora forest	Clay	357	50	16.53	4.646644	-58.6777	1.0	(Johnston & Gillman, 1995)
FL	Guyana	Mabura Hill Forest Reserve	Clay	1124	63	14.62	5.16592	-58.6927	2.3	(Thomas, 2001)
FL	Guyana	Moraballi mora forest	Clay	462	41	11.46	6.18333	-58.532	1.5	(Davis & Richards, 1934)
FL	Guyana	North West mora forest	Clay	314	27	7.10	7.38333	-59.7077	1.0	(van Andel, 2001)
LF	French Guiana	Antenne North Ridge	Lep	619	179	92.37	3.63333	-53.2	PCQ	(Mori & Boom, 1987)
LF	French Guiana	BAFOG 1	Fer	2364	87	18.81	5.5	-54	4.0	(Gazel, 1983)
LF	French Guiana	BAFOG 2	Fer	2315	90	19.43	5.5	-53.991	4.0	(Gazel, 1983)
LF	French Guiana	Crique & Mt. Plomb 1	Lep	500	147	73.57	5	-52.95	1.0	Sabatier et al. ***
LF	French Guiana	Crique & Mt. Plomb 2	Lep	836	154	55.62	5	-52.941	1.0	Sabatier et al. ***
LF	French Guiana	INI1, Inini	Lep	625	173	80.13	3.564495	-53.8364	1.0	Sabatier et al. ***
LF	French Guiana	INI2, Inini	Lep	643	174	78.98	3.564381	-53.8352	1.0	Sabatier et al. ***
LF	French Guiana	Nouragues 1	Lep	470	163	91.12	4.097574	-52.6748	1.0	Sabatier et al. ***
LF	French Guiana	Nouragues 2	Lep	589	199	108.28	4.099251	-52.6769	1.0	Sabatier et al. ***
LF	French Guiana	Nouragues 3	Lep	472	167	94.09	4.098001	-52.6697	1.0	Sabatier et al. ***
LF	French Guiana	Nouragues 4	Lep	547	180	94.69	4.094792	-52.6689	1.0	Sabatier et al. ***
LF	French Guiana	Nouragues 5	Lep	695	160	68.21	4.09917	-52.6814	1.0	Sabatier et al. ***
LF	French Guiana	Paracou 1	Fer	332	101	52.91	5.33333	-52.9167	0.5	Sabatier et al. ***
LF	French Guiana	Paracou 2	Fer	282	103	62.57	5.33333	-52.9077	0.5	Sabatier et al. ***
LF	French Guiana	Paracou 3	Fer	338	88	40.70	5.342339	-52.9167	0.5	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 10B	Lep	565	193	104.51	5.298106	-53.0626	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 1B	Lep	626	179	83.77	5.297175	-53.0546	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 2B	Lep	590	173	83.03	5.297289	-53.0555	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 2C	Lep	651	176	79.58	5.298176	-53.0554	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 3B	Lep	567	163	77.24	5.297377	-53.0564	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 3C	Lep	625	159	68.87	5.298263	-53.0563	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 4B	Lep	641	144	57.81	5.297482	-53.0573	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 5B	Lep	582	140	58.56	5.297579	-53.0582	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 6B	Lep	585	166	77.55	5.297684	-53.0591	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 6F	Lep	705	174	74.00	5.301212	-53.0586	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 6G	Lep	666	182	82.80	5.302116	-53.0585	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 6H	Lep	633	184	87.41	5.303021	-53.0584	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 6I	Lep	624	167	74.77	5.303916	-53.0583	1.0	Sabatier et al. ***

LF	French Guiana	Piste Saint Ely 6J	Lep	602	181	88.03	5.304811	-53.0582	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 7B	Lep	644	162	70.16	5.297799	-53.06	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 8B	Lep	637	178	75.20	5.297895	-53.0609	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely 9B	Lep	591	172	81.80	5.297992	-53.0618	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely P	Lep	643	176	79.92	5.292115	-53.0563	1.0	Sabatier et al. ***
LF	French Guiana	Piste Saint Ely R	Lep	591	164	75.25	5.291632	-53.0548	1.0	Sabatier et al. ***
LF	French Guiana	Tresor	Lep	435	122	62.98	4.6	-52.2667	1.0	Sabatier et al. ***
LF	Guyana	107 mi Bartica-Potaro road	Lep	651	43	10.79	5.49	-58.76	1.5	(Fanshawe, 1954)
LF	Guyana	24 mi Reserve Bartica-Potaro	Fer	391	86	34.08	6.147551	-58.6793	1.0	Bánki ***
LF	Guyana	24 mi Reserve Bartica-Potaro	Fer	390	67	23.30	6.147537	-58.6839	1.0	Bánki ***
LF	Guyana	Camoudi	Fer	1124	66	15.61	5.03333	-58.8	2.3	(Thomas, 2001)
LF	Guyana	Charabaru	FAS	452	61	19.00	4.949981	-58.359	1.0	ter Steege & Bánki ***
LF	Guyana	Charabaru	FAS	484	75	24.84	4.922867	-58.3499	1.0	ter Steege & Bánki ***
LF	Guyana	D1, Upper Ireng River	Fer	274	23	6.16	5.08333	-59.9833	1.0	(Henkel, 2003)
LF	Guyana	D2, Upper Ireng River	Fer	286	33	10.02	5.105853	-59.9833	1.0	(Henkel, 2003)
LF	Guyana	D3, Upper Potaro River	Fer	319	29	8.21	5.369816	-59.9653	1.0	(Henkel, 2003)
LF	Guyana	D4, Upper Potaro River	Fer	366	38	11.33	5.365312	-59.9833	1.0	(Henkel, 2003)
LF	Guyana	D5, Upper Potaro River	Fer	428	31	8.41	5.38333	-59.9833	1.0	(Henkel, 2003)
LF	Guyana	Forest Training Centre	Lep	466	81	28.33	6.627913	-58.8726	1.0	Bánki ***
LF	Guyana	Forest Training Centre	Lep	425	72	24.87	6.627913	-58.8726	1.0	Bánki ***
LF	Guyana	Iwokrama	Fer	449	66	21.34	4.52	-57.74	1.0	Bánki ***
LF	Guyana	Iwokrama Mixed forest	Fer	459	58	17.99	4.642283	-58.6989	1.0	(Johnston & Gillman, 1995)
LF	Guyana	Iwokrama Mixed forest 2	Fer	477	50	14.60	4.646553	-58.6937	1.0	(Johnston & Gillman, 1995)
LF	Guyana	Kwakwani 1	FAS	502	71	23.00	5.5	-58	1.0	(Comiskey et al., 1994)
LF	Guyana	Kwakwani 2	FAS	491	47	13.09	5.500901	-57.9991	1.0	(Comiskey et al., 1994)
LF	Guyana	M1, Upper Potaro River	Fer	581	54	16.50	5.365312	-59.9653	1.0	(Henkel, 2003)
LF	Guyana	M2, Upper Potaro River	Fer	475	39	11.08	5.351798	-59.9293	1.0	(Henkel, 2003)
LF	Guyana	M3, Upper Potaro River	Fer	536	49	14.46	5.351798	-59.9473	1.0	(Henkel, 2003)
LF	Guyana	Mabura Hill Forest Reserve	FAS	447	47	13.25	5.173202	-58.6933	1.0	Bánki ***
LF	Guyana	Mabura Hill Forest Reserve	FAS	359	40	11.53	5.173915	-58.6939	1.0	Bánki ***
LF	Guyana	Mabura Hill Forest Reserve	Lep	577	41	10.35	5.156057	-58.6966	1.5	van Essen ***
LF	Guyana	Mabura Hill Forest Reserve	Lep	631	46	11.80	5.157866	-58.6966	1.5	van Essen ***
LF	Guyana	Mabura Hill Forest Reserve	Lep	957	64	15.62	5.164071	-58.6857	2.3	(Thomas, 2001)
LF	Guyana	Mapenna savanna Corantyne	FAS	264	58	24.06	5.35	-57.3167	0.7	(Fanshawe, 1954)
LF	Guyana	Moraballi greenheart forest	Fer	799	63	16.72	6.18333	-58.541	1.5	(Davis & Richards, 1934)

LF	Guyana	Moraballi mixed forest	Fer	644	61	17.24	6.18333	-58.55	1.5	(Davis & Richards, 1934)
LF	Guyana	Moraballi Morabukea forest	Clay	460	54	16.43	6.192339	-58.55	1.5	(Davis & Richards, 1934)
LF	Guyana	Moruca Indian Reservation	Lep	842	73	19.36	7.65	-59.23	2.1	(Fanshawe, 1954)
LF	Guyana	North West Barama River	Lep	474	74	25.01	7.38333	-59.7167	1.0	(van Andel, 2003)
LF	Guyana	North West Moruca	Lep	537	82	27.73	7.68333	-59.9077	1.0	(van Andel, 2003)
LF	Guyana	Simuni Creek, Rupununi R.	Fer	741	62	17.56	3.76667	-59.2833	1.1	(Fanshawe, 1954)
LF	Suriname	Blanche Marie, K	Lep	614	101	35.79	4.75	-56.85	1.2	(Maas, 1971)
LF	Suriname	Celos Kabo plots	Fer	445	106	44.03	5.341851	-55.7669	1.0	Bánki ***
LF	Suriname	Celos Kabo plots	Fer	398	113	52.62	5.341851	-55.7669	1.0	Bánki ***
LF	Suriname	In the vicinity of Bitagron	FAS	461	114	48.45	5.072969	-56.2057	1.0	Bánki ***
LF	Suriname	In the vicinity of Bitagron	FAS	463	98	38.00	5.085185	-56.1947	1.0	Bánki ***
LF	Suriname	Kamisa, H	Fer	528	102	39.10	5.1	-56.3333	0.9	(Maas, 1971)
LF	Suriname	Lowland of Brownsberg	Fer	540	126	51.69	4.986662	-55.1954	1.0	Bánki & ter Steege ***
LF	Suriname	Lowland of Brownsberg	Lep	526	124	51.18	4.922977	-55.1296	1.0	Bánki & ter Steege ***
LF	Suriname	Lowland of Brownsberg	Lep	562	115	43.77	4.932314	-55.1444	1.0	Bánki & ter Steege ***
LF	Suriname	Lowland of Lely Mts	Lep	477	115	48.12	4.261756	-54.78	1.0	Bánki & ter Steege ***
LF	Suriname	Lowland of Lely Mts	Lep	476	107	42.94	4.270133	-54.7788	1.0	Bánki & ter Steege ***
LF	Suriname	lowland of Nassau Mts	FAS	775	143	51.53	4.929832	-54.5235	1.0	Bánki & ter Steege ***
LF	Suriname	lowland of Nassau Mts	FAS	832	141	48.71	4.934286	-54.5157	1.0	Bánki & ter Steege ***
LF	Suriname	Paris Jacob, G1	Fer	601	124	48.12	4.9	-56.9491	0.9	(Maas, 1971)
LF	Suriname	Road to Alberga	FAS	549	78	24.84	5.341851	-55.7669	1.0	Bánki ***
LF	Suriname	Road to Alberga	FAS	505	85	29.26	5.340174	-55.7604	1.0	Bánki ***
LF	Suriname	Slope of Brownsberg	Lep	466	121	53.05	4.971844	-55.1764	1.0	Bánki & ter Steege ***
LF	Suriname	Slope of Brownsberg	Lep	548	135	57.24	4.942494	-55.1767	1.0	Bánki & ter Steege ***
LF	Suriname	Slope of Lely Mts	Lep	524	145	66.33	4.248045	-54.7344	1.0	Bánki & ter Steege ***
LF	Suriname	Slope of Lely Mts	Lep	490	111	44.74	4.266763	-54.7548	1.0	Bánki & ter Steege ***
LF	Suriname	Snake creek, B	Fer	262	44	15.27	5.23333	-56.8	0.5	(Maas, 1971)
LF	Suriname	Snake creek, F 3	Fer	601	122	47.00	5.23333	-56.7991	1.3	(Maas, 1971)
LF	Suriname	Suhoza	Lep	515	90	32.77	5.487794	-54.6667	1.0	Schulz & Linderman ***
LF	Suriname	Vicinity of Nickerie River	FAS	517	121	49.73	4.993621	-56.9984	1.0	Bánki ***
LF	Suriname	Vicinity of Nickerie River	FAS	491	124	53.41	4.99543	-56.9984	1.0	Bánki ***
LF	Suriname	Winana, E II	Fer	459	82	29.56	5.25	-57.0649	0.9	(Maas, 1971)
LF	Venezuela	El Buey 1	Lep	538	76	25.80	8.23333	-62.1833	1.0	Castellanos et al. ***
LF	Venezuela	El Buey 10	Lep	593	73	23.33	8.235132	-62.1824	1.0	Castellanos et al. ***
LF	Venezuela	El Buey 11	Lep	374	57	19.34	8.235132	-62.1815	1.0	Castellanos et al. ***

LF	Venezuela	El Buey 12	Lep	558	70	21.91	8.235132	-62.1806	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 13	Lep	462	51	17.92	8.236033	-62.1833	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 14	Lep	496	61	18.67	8.236033	-62.1824	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 15	Lep	416	56	17.78	8.236303	-62.1826	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 2	Lep	569	82	28.10	8.233333	-62.1824	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 3	Lep	441	70	24.13	8.233333	-62.1815	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 4	Lep	573	68	21.47	8.233333	-62.1806	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 5	Lep	561	63	19.50	8.234231	-62.1833	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 6	Lep	659	74	23.35	8.234231	-62.1824	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 7	Lep	526	64	20.10	8.234231	-62.1815	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 8	Lep	589	65	19.96	8.234231	-62.1806	1.0	Castellanos et al.	***
LF	Venezuela	El Buey 9	Lep	492	60	18.75	8.235132	-62.1833	1.0	Castellanos et al.	***
PI	Suriname	Plateau of Brownsberg	Lep	639	165	72.09	4.928819	-55.2155	1.0	Bánki & ter Steege	***
PI	Suriname	Plateau of Brownsberg	Lep	571	138	57.83	4.932323	-55.1938	1.0	Bánki & ter Steege	***
PI	Suriname	Plateau of Brownsberg	Lep	635	137	53.69	4.946632	-55.1886	1.0	Bánki & ter Steege	***
PI	Suriname	Plateau of Lely Mts	Lep	638	148	60.50	4.269247	-54.745	1.0	Bánki & ter Steege	***
PI	Suriname	Plateau of Lely Mts	Lep	494	136	62.00	4.260005	-54.7379	1.0	Bánki & ter Steege	***
PI	Suriname	Plateau of Lely Mts	Lep	602	170	78.86	4.273211	-54.7373	1.0	Bánki & ter Steege	***
PI	Suriname	plateau of Nassau Mts	Lep	477	112	46.12	4.784255	-54.618	1.0	Bánki & ter Steege	***
PI	Suriname	plateau of Nassau Mts	Lep	257	92	51.30	4.815264	-54.612	0.6	Bánki & ter Steege	***
PI	Suriname	plateau of Nassau Mts	Lep	500	131	57.78	4.815659	-54.6034	1.0	Bánki & ter Steege	***
PI	Suriname	plateau of Nassau Mts	Lep	608	137	55.05	4.827287	-54.6122	1.0	Bánki & ter Steege	***
Sav	Suriname	On plateau of Lely Mts	Lep	981	33	6.59	4.252401	-54.7342	1.0	Bánki & ter Steege	***
Sav	Suriname	Plateau of Brownsberg	Lep	623	123	45.91	4.947098	-55.1872	1.0	Bánki & ter Steege	***
Sw	Guyana	Assakata	His	664	28	5.93	7.733333	-59.0667	1.0	Bánki	***
Sw	Guyana	Barima River	Clay	1033	29	5.54	7.83	-59.69	1.5	(van Andel, 2003)	
Sw	Guyana	Kaituma River 12 mi of mouth	His	1050	29	5.52	8.16	-59.68	1.5	(Fanshawe, 1954)	
Sw	Guyana	Moruca	His	617	34	7.79	7.683333	-59.9167	1.0	(Fanshawe, 1954)	
White	Guyana	24 mi Reserve Bartica-Potaro	WS	525	55	15.48	6.147614	-58.6595	1.0	(van Andel, 2001)	
White	Guyana	24 mi Reserve Bartica-Potaro	WS	519	43	11.13	6.147608	-58.6613	1.0	Bánki	***
White	Guyana	90 mi Bartica-Potaro road	WS	704	21	4.16	5.55	-58.74	1.5	(Fanshawe, 1954)	
White	Guyana	Charabaru	WS	655	63	17.18	4.949999	-58.35	1.0	ter Steege & Bánki	***
White	Guyana	Charabaru	WS	547	39	9.61	4.949962	-58.368	1.0	ter Steege & Bánki	***
White	Guyana	Forest Training Centre	WS	479	43	11.44	6.627913	-58.8726	1.0	Bánki	***
White	Guyana	Forest Training Centre	WS	505	55	15.71	6.627913	-58.8726	1.0	Bánki	***

White	Guyana	Iwokrama	WS	583	34	7.87	4.61	-58.73	1.0	Bánki ***
White	Guyana	Iwokrama White sand forest	WS	742	32	7.07	4.653397	-58.6862	1.0	(Johnston & Gillman, 1995)
White	Guyana	Mabura Hill Forest Reserve	WS	548	41	10.26	5.17887	-58.7039	1.0	Bánki ***
White	Guyana	Mabura Hill Forest Reserve	WS	509	42	10.86	5.163928	-58.7121	1.0	Bánki ***
White	Guyana	Mabura Hill Forest Reserve	WS	611	36	8.36	5.182604	-58.7008	1.0	Bánki ***
White	Guyana	Mabura Hill Forest Reserve	WS	612	42	10.22	5.179161	-58.7035	2.3	Bánki ***
White	Guyana	Moraballi white sand forest	WS	919	45	10.27	6.192339	-58.532	1.5	(Davis & Richards, 1934)
White	Suriname	In the vicinity of Bitagron	WS	455	42	11.29	5.082935	-56.1966	1.0	Bánki ***
White	Suriname	In the vicinity of Bitagron	WS	414	37	9.83	5.082926	-56.197	1.0	Bánki ***
White	Suriname	Kabo	WS	459	33	8.15	5.142045	-55.7835	1.0	Bánki ***
White	Suriname	Kabo	WS	300	31	8.68	5.145084	-55.7836	1.0	Bánki ***
White	Suriname	Kabo	WS	432	31	7.65	5.145084	-55.7827	1.0	Bánki ***
White	Suriname	Road to Goliath	WS	586	45	11.36	5.222496	-55.6548	1.0	Bánki ***
White	Suriname	Simonskreek	WS	816	43	9.67	5.318871	-54.9422	1.0	Bánki ***
White	Suriname	Simonskreek	WS	1009	31	6.05	5.315116	-54.9411	1.0	Bánki ***
White	Suriname	Vicinity of Nickerie River	WS	651	23	4.65	4.982765	-56.9984	1.0	Bánki ***
White	Suriname	Vicinity of Nickerie River	WS	675	42	9.92	4.984574	-56.9984	1.0	Bánki ***
White	Suriname	Winana, A I, II	WS	274	25	6.70	5.25	-57.0667	0.5	(Maas, 1971)
White	Suriname	Winana, E I	Fer	352	63	22.89	5.25	-57.0658	0.7	(Maas, 1971)

* Forest groups consist of: flood plain forest (FI), lowland rainforest (LF), bauxite plateau forest (PI), savannah forest (Sav), swamp forest (Sw), white sand forest (White); ** Soil categories: clay soils (Clay), ferralic arenosols (FAS), ferralsols (Fer), histosols (His), leptosols (Lep), white sands (WS); *** unpublished data

Table S4.1 Plot meta data of 38 paired 1-ha plots in the Guianas. N is the number of individuals, S is the number of species, and Fa is the Fishers alpha of the plots. With a two-way Anova (SPSS 16.0.1) we established a significant difference in N, S, and Fa between soil types ($p < 0.006$), a significant difference in S and Fa between countries ($p < 0.001$), and a significant difference in S and Fa in the interaction between soil type and country ($p < 0.001$).

Plot	N	S	Fa	Soil	Country	Lat	Long	dimension
24MR1	525	55	15.48	white	Guyana	6.14761	-58.65947	100 x 100m
24MR2	519	43	11.12	white	Guyana	6.14761	-58.66128	100 x 100m
24MR3	391	86	34.07	brown	Guyana	6.14755	-58.67935	100 x 100m
24MR4	390	67	23.29	brown	Guyana	6.14754	-58.68387	100 x 100m
CH1	452	61	19	brown	Guyana	4.94998	-58.35902	250 x 40m
CH2	655	63	17.18	white	Guyana	4.95000	-58.35000	250 x 40m
CH3	547	39	9.6	white	Guyana	4.94996	-58.36804	250 x 40m
CH4	484	75	24.83	brown	Guyana	4.92287	-58.34995	250 x 40m
FTC1	479	43	11.44	white	Guyana	6.26025	-58.78356	100 x 100m
FTC2	466	81	28.32	brown	Guyana	6.26926	-58.79262	100 x 100m
FTC3	505	55	15.71	white	Guyana	6.27827	-58.80169	100 x 100m
FTC4	425	72	24.86	brown	Guyana	6.28728	-58.81076	250 x 40m
lwo1	583	34	7.87	white	Guyana	4.61000	-58.73000	100 x 100m
lwo2	449	66	21.33	brown	Guyana	4.52000	-57.74000	100 x 100m
MHFR1	548	41	10.25	white	Guyana	5.17887	-58.70394	100 x 100m
MHFR2	509	42	10.85	white	Guyana	5.16393	-58.71214	100 x 100m
MHFR3	611	36	8.36	white	Guyana	5.18260	-58.70084	100 x 100m
MHFR4	612	42	10.22	white	Guyana	5.17916	-58.70355	100 x 100m
MHFR5	447	47	13.24	brown	Guyana	5.17320	-58.69335	100 x 100m
MHFR6	359	40	11.52	brown	Guyana	5.17391	-58.69388	100 x 100m
AI1	549	78	24.84	brown	Suriname	5.34185	-55.76689	250 x 40m
AI2	505	85	29.26	brown	Suriname	5.34017	-55.76039	250 x 40m
BI1	461	114	48.45	brown	Suriname	5.07297	-56.20573	250 x 40m
BI2	455	42	11.28	white	Suriname	5.08293	-56.19659	250 x 40m
BI3	414	37	9.83	white	Suriname	5.08293	-56.19696	250 x 40m
BI4	463	98	37.99	brown	Suriname	5.08519	-56.19470	250 x 40m
BSH1	459	33	8.15	white	Suriname	5.14205	-55.78351	250 x 40m
BSH2	402	36	9.57	white	Suriname	5.14508	-55.78362	250 x 40m
BSH3	432	31	7.65	white	Suriname	5.14508	-55.78272	250 x 40m

Golf	586	45	11:35	white	Suriname	5.22250	-55.65478	250 x 40m
Kabo 41	445	106	44.02	brown	Suriname	5.25018	-55.77990	100 x 100m
Kabo 43	398	113	52.61	brown	Suriname	5.25470	-55.77538	100 x 100m
Ni1	651	23	4.64	white	Suriname	4.98276	-56.99839	250 x 40m
Ni2	675	42	9.91	white	Suriname	4.98457	-56.99839	250 x 40m
Ni3	517	121	49.72	brown	Suriname	4.99362	-56.99839	250 x 40m
Ni4	491	124	53.4	brown	Suriname	4.99543	-56.99839	250 x 40m
Si1	816	43	9.66	white	Suriname	5.31887	-54.94222	250 x 40m
Si2	1009	31	6.05	white	Suriname	5.31512	-54.94115	250 x 40m

Table S4.2 Results of the species indicator analyses on the species and their abundances in 38 paired plots. S stands for species, and N for individuals. Species can become indicators ($p < 0.05$) if they occur with a substantial amount of individuals in several plots on one soil type. Non-indicator species did not reach significance, because they either occur in similar amounts on the two soil types or occur in either too few amounts and/or too few plots on one soil type. We considered rare species, those that have less than 4 individuals and occur in less than four plots on each soil type. For this reason these species could not reach significance in the species indicator analyses. **a**, Results of the species indicator analysis for all plots. **b**, Results of the species indicator analysis for 20 plots in Guyana. **c**, Results of the species indicator analysis for 18 plots in Suriname. There is a two third decrease in indicator species in the forests on white sands in Suriname, compared to the total amount of indicator species for white sand forests in Guyana. Several indicator species on white sands in Guyana occur in Suriname in similar amounts on brown and white sand (data not shown). The double amount of brown sand indicator species is found in Suriname, compared to Guyana.

	<i>indicator S</i>	<i>Non-indicator S</i>	<i>Rare S</i>	<i>Total S</i>		<i>indicator N</i>	<i>Non-indicator N</i>	<i>Rare N</i>	<i>Total N brown</i>	<i>Total N white</i>	<i>% spill over</i>
a											
S brown sand	96	56	240	392							
S white sand	24	55	53	132							
N brown sand	3923	1040	1582	6545							
(N white sand)	85 (0.7%)	416 (3.5%)	112 (0.9%)		613	5.2					
N white sand	7340	3208	729		11277						
(N brown sand)	363 (4.7%)	760 (9.9%)	24 (0.2%)	1147		14.9					
b											
S brown sand	37	28	118	183							
S white sand	27	28	40	95							
N brown sand	2159	295	947	3401							
(N white sand)	46 (0.8%)	165 (2.7%)	98 (1.6%)		309	5.1					
N white sand	4871	650	263		5784						
(N brown sand)	257 (6.7%)	199 (5.2%)	6 (0.16%)	462		12.0					

	<i>indicator S</i>	<i>Non-indicator S</i>	<i>Rare S</i>	<i>Total S</i>		
S brown sand	65	27	176	268		
S white sand	9	26	26	61		
	<i>indicator N</i>	<i>Non-indicator N</i>	<i>Rare N</i>	<i>Total N brown</i>	<i>Total N white</i>	<i>% spill over</i>
N brown sand	1542	802	1076	3420		
(N white sand)	24 (0.4%)	376 (6.5%)	111 (1.9%)		511	8.8
N white sand	3054	1742	490		5286	
(N brown sand)	125 (3.3%)	267 (7.0%)	17 (0.4%)	409		10.7
				3829	5797	

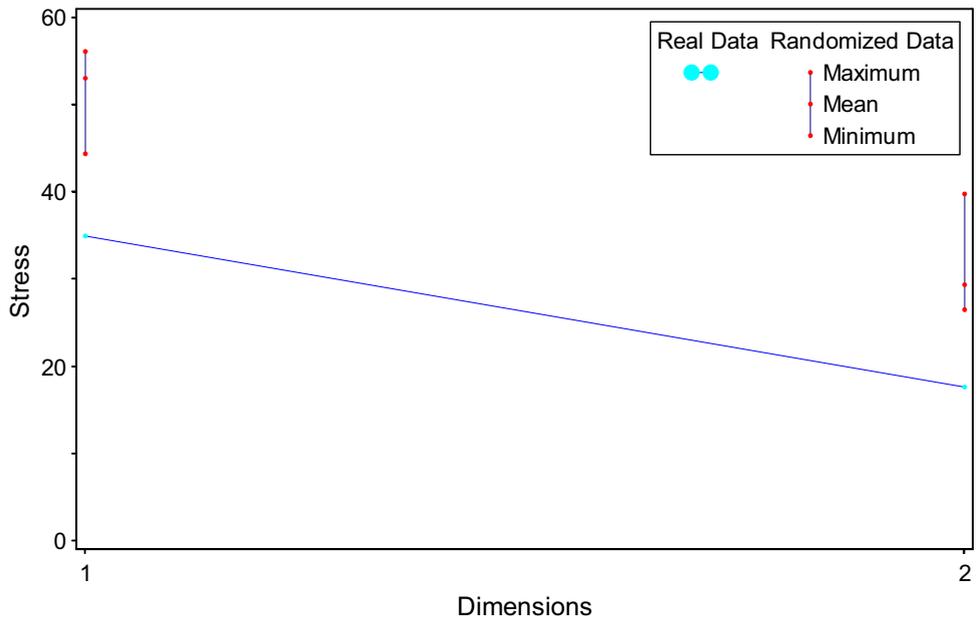


Figure S4.1

Screeplot associated with the non-metric multidimensional scaling shown in Figure 2. With 2 dimensions the amount of stress falls below the 20%, and an additional third dimension only adds 11% of variation. The amount of variation that is represented by axis 1 in Figure 2 was 34.7 %, and 34 % for axis 2. The orthogonality between axes 1 and 2 is 99.6 % ($r=0.062$).

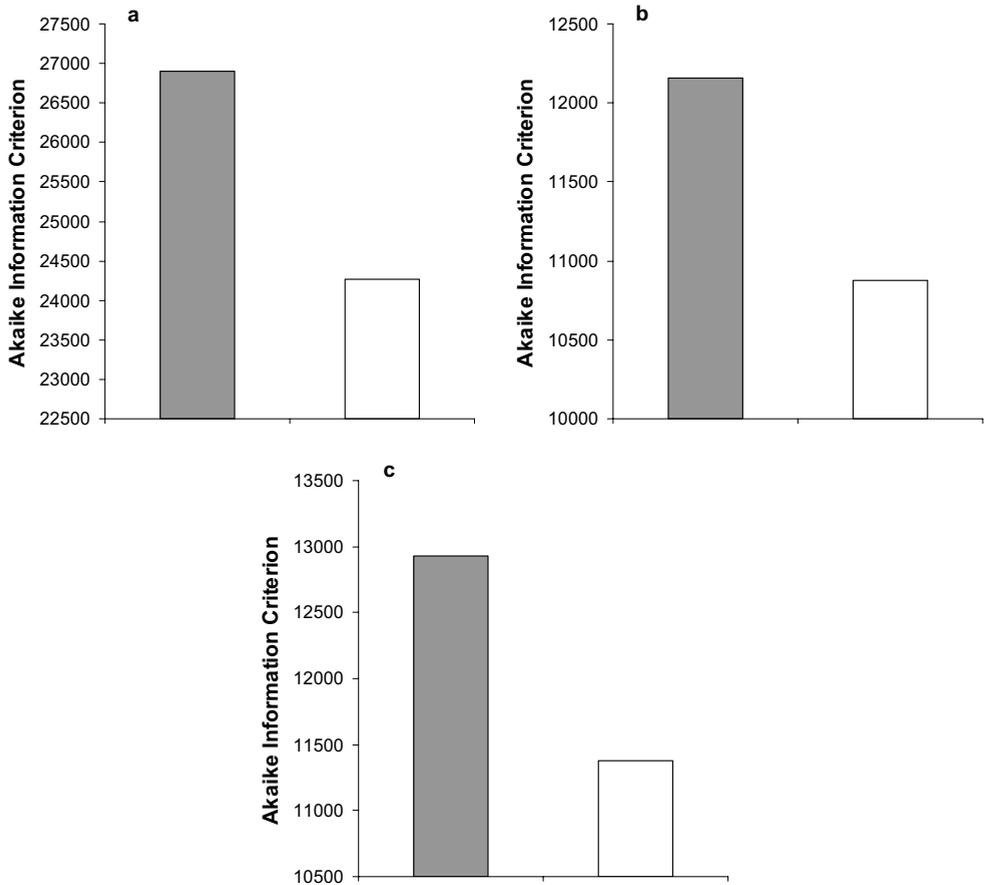


Figure S4.2

Comparison of model results of one and two regional species pools (approximation regional abundances = sum of local abundances). **a**, Floristic separation into Guyana and Suriname regional species pools (white column, Akaike weight 1) outperforms a single regional pool (grey column, Akaike weight $< e^{-1313}$), based on 37 retained partitions out of 9 different MCMC searches. **b**, Separation into a brown and white sand regional species pool (white column, Akaike weight 1) outperforms a single Guyana regional species pool (grey column, Akaike weight $< e^{-642}$), based on 19 retained partitions out of 4 different MCMC searches. **c**, Separation into a brown and white sand regional species pool (white column, Akaike weight 1) outperforms a single Suriname regional species pool (grey column, Akaike weight $< e^{-774}$), based on 25 retained partitions out of 7 different MCMC searches.

Table S5.1 Plot meta-data. Plot name starts with a letter for each mountain (B = Brownsberg, L = Lely, N = Nassau), followed by plot number, followed by habitat type (L = lowland, M = mid-slope, P = plateau, S = savannah forest). Easting and Northing = UTM coordinates in zone 21N, Altitude in m ASL (above sea level), Dimensions in m x m. S = number of species, N = number of individuals, Fa = Fisher's alpha.

Plot name	Easting	Northing	Altitude	Dimensions	S	N	Fa
B1P	545061	697876	c. 500	100 x 100	165	639	72.1
B2P	545455	700277	c. 500	100 x 100	138	571	57.8
B3P	547039	700849	c. 500	100 x 100	137	635	53.7
B4M	549831	702197	c. 350	100 x 100	121	466	53.1
B5L	551464	700083	c. 100	100 x 100	126	540	51.7
B6M	546585	702175	c. 350	100 x 100	135	548	57.2
B7L	544441	707401	c. 100	100 x 100	124	526	51.2
B8L	545469	705755	c. 100	500 x 20	115	562	43.8
B9S	546456	700480	c. 500	100 x 100	123	623	45.9
L1P	472256	750297	670	100 x 100	149	638	61.2
L2P	471236	751090	c. 600	100 x 100	136	494	62.0
L3P	472697	751155	670	100 x 100	170	602	78.9
L4M	469914	751482	430	100 x 100	145	524	66.3
L5S	470396	751497	500	250 x 40	33	981	6.6
L6L	471416	746418	135	250 x 40	115	477	48.1
L7L	472343	746542	135	250 x 40	107	476	42.9
L8M	471978	749208	420	250 x 40	111	490	44.7
N1P	529275	764217	c. 500	500 x 20	112	477	46.1
N2P	532708	764867	c. 500	250 x 20	92	257	51.3
N3P	532755	765819	c. 500	100 x 100	131	500	57.8
N4L	545419	774643	c. 50	500 x 20	143	775	51.5
N5L	545915	775512	c. 50	500 x 20	141	832	48.7
N6P	534038	764840	c. 500	100 x 100	137	608	55.1

Table S5.2 Below the results are given of the indicator analyses with all species (a), common species (b), genus (c), and family (d) data. Indicator taxa are those with a significant indicator value ($p < 0.05$). The rare taxa have less than 4 individuals and occur in less than 4 plots, so significance can never be reached in the test. The amount of spill over of individuals on the other habitat type is also given. For example 220 individuals of the indicator species for the lowlands occur also on the plateau. These individuals make up 4.1 % of the total individuals found on the plateaus.

a Species	indicator	non-indicator	rare	Total S	Total N plateau	% spill over
Lowland S	25 (4.7%)	78 (14.7%)	125 (23.5%)	228		
Plateau S	25 (4.7%)	122 (23.0%)	156 (29.4%)	303		
Lowland N (spill over on plateau N)	1324 (31.6%)	1550 (37.0%)	577 (13.8%)	3451 (82.4%)	1201	22.2%
Plateau N (spill over into lowland N)	220 (4.1%) 1208 (22.3%) 107 (2.6%)	906 (16.7%) 2460 (45.4%) 609 (14.4%)	75 (1.4%) 552 (10.2%) 21 (0.5%)	737	4220 (77.8%)	17.6%
b Common species	indicator	non-indicator	rare	Total S		
Lowland S	17 (13.7%)	30 (24.2%)	6 (4.8%)	53		
Plateau S	21 (16.9%)	43 (34.7)	7 (5.6%)	71		
Lowland N (spill over on plateau N)	1245 (38.4%)	1051 (32.4%)	365 (11.3%)	2661 (82.1%)	938	23.4%
Plateau N (spill over into lowland N)	218 (5.4%) 1190 (29.7%) 121 (3.7%)	717 (17.9%) 1587 (39.6%) 458 (14.1%)	3 (0.1%) 289 (7.2%) 0	579	3066 (76.6%)	17.9%

c Genera		<i>indicator</i>	<i>non-indicator</i>	<i>rare</i>	<i>Total G</i>		
Lowland G		15 (7.4%)	48 (23.6%)	36 (17.7%)	99		
Plateau G		21 (10.3%)	56 (27.6%)	27 (13.3%)	104		
Lowland N (spill over on plateau N)		<i>indicator</i> 1138 (29.9%)	<i>non-indicator</i> 1469 (38.6%)	<i>rare</i> 398 (10.6%)	<i>Total N lowland</i> 3005 (79.0%)	<i>Total N plateau</i>	<i>% spill over</i>
Plateau N (spill over into lowland N)		267 (6.0%)	1076 (24.2%)	33 (0.7%)	1376	1376	31.0%
		1640 (36.9%)	1378 (31.0%)	47 (1.1%)	3065 (69.0%)	3065 (69.0%)	
		297 (7.8%)	499 (13.1%)	4 (0.1%)	800		21.0%
d Families		<i>indicator</i>	<i>non-indicator</i>	<i>rare</i>	<i>Total F</i>		
Lowland F		8 (13.1%)	14 (23.0%)	8 (13.1%)	30		
Plateau F		8 (13.1%)	19 (31.1%)	4 (6.6%)	31		
Lowland N (spill over on plateau N)		<i>indicator</i> 1583 (37.8%)	<i>non-indicator</i> 1737 (41.5%)	<i>rare</i> 20 (0.5%)	<i>Total N lowland</i> 3340 (79.8%)	<i>Total N plateau</i>	<i>% spill over</i>
Plateau N (spill over into lowland N)		1051 (19.4%)	1621 (29.9%)	5 (0.1%)	2677	2677	49.4%
		1195 (22.0%)	1537 (28.4%)	12 (0.2%)	2744 (50.6%)	2744 (50.6%)	
		231 (5.5%)	615 (14.7%)	2 (0.1%)	848		20.2%

Remarks S4.1

The following remarks are about the significantly lower Fishers alpha on white sands in Suriname compared to the white sand plots of Guyana. The Si1 and Si2 plots in Suriname have the highest numbers of individuals found in an 1-ha plot on white sand. This could affect the analysis. If the Si1 and Si2 plots are removed from the analysis the Fishers alpha of the Suriname white sand plots is just not significantly lower, probably due to the low sample size. However, the number of species and also the Fishers alpha of the Si1 and Si2 plots fall within the variation found in white sand plots. So there is no reason not to use the plots for the analysis. We corrected for the high numbers of individuals, by either taken the first six hundred individuals or drawing 600 individuals randomly from the two plots. The Fishers alpha in Si1 was only slightly lowered when the first six hundred individuals were chosen, but the Fishers alpha remained comparable to the original value when six hundred individuals were drawn randomly. For the Si2 plot the Fishers alpha was slightly lowered in all cases but never lower than the Fishers alpha found in Ni1. In all cases where we adjusted for the higher number of individuals of the Si plots, the Fishers alpha of the Suriname white sands plots was significantly lower compared to Guyana.

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Next page left above: Frits van Troon Suriname's most able tree spotter and field botanist

Next page right above: Aaron Braithwaite one of Guyana's finest tree spotters

Next page below: forest plot research team at Iwokrama, Guyana



Curriculum Vitae

As a little boy I often roamed the forests surrounding Soest (the Netherlands), until I knew these forests by heart. Stories from my family and from Surinamese people at my mothers work at the 'Stichting voor Welzijnsbehartiging van Surinamers in de Provincie Utrecht', made me dream of adventurous travels to the tropics. With hindsight it was logical that I chose to study biology at the University of Amsterdam, and specialized myself in tropical plant ecology and botany. In 1997 I made my first visit to the tropics and inventoried secondary forests in Araracuara, Colombia. From 1997 to 1998 I studied the taxonomy, tree architecture, and forest regeneration in the genus *Vismia* on abandoned agricultural fields of Amerindians in Guyana. After I finished my studies in 1998 I shortly worked at the Ministry of Foreign Affairs of the Netherlands as a consultant. In 2000 I assisted Prof. Dr. Paul Maas at the Herbarium of the Netherlands – Utrecht branch with a course on Neotropical Flora, and prepared a similar course for Guyana. Later that year I started working for the Netherlands Committee for IUCN. Here I worked as the secretary of the Dutch Working Group on Ecology and Development and as a Biodiversity and Policy Officer on influencing the Dutch Government in taking up more ecology and sustainable thinking in their international policies. For IUCN/NL I reviewed the UNEP-Global Programme of Action for the Protection of the Marine Environment from land-based activities. I made several missions to Guyana and Suriname for the Guiana Shield Programme, and was a Non-Timber Forest Product facilitator at the 2002 Conservation Priority Setting Workshop in Paramaribo, Suriname. In my spare time I started to organize field trips to inventory plant diversity in Suriname for the National Herbarium of the Netherlands – Utrecht branch. This led to field trips to: the Raleigh Vallen and Volzberg in 2002, the Nassau Mts. and the Brownsberg in 2003, and the Lely Mts. in 2004. Eventually this also led to the study described in this thesis.

At the moment I am working at the University of Amsterdam for the LifeWatch project, a European preparatory project to construct a novel and integrated infrastructure for biodiversity and ecosystem research (www.lifewatch.nl). I am a member of the Dutch Working Group on Ecology and Development, and the IUCN Commission on Ecosystem Management. For an updated CV see <http://nl.linkedin.com/in/olafbanski>

Next page: research teams that contributed to the forest dataset for this thesis in Guyana

