FOREWORD

This book is based on the efforts of very many people. Its purpose is to support the efforts of the Government of Guyana to develop a National Protected Areas System in the country. Much of the information presented in the book is technical and scientific in nature, while some chapters synthesise what little is known on a particular subject. For those interested in the main objectives and results of the book reading Chapters 1 and 12 may suffice. Some basic information on Guyana's plant diversity is presented in Chapter 2. The other Chapters deal with certain aspects of plant diversity or typical regions in Guyana.

In the first place I would like to thank all the persons who contributed in raw data and words to this book. Their names can be found on top of the chapters and in the list of contributors below. Without their help this book would never have been written. On their and my behalf I would like to thank all those who have contributed otherwise to the successful completion of this book.

Thanks to the Guyana Natural Resources Agency, the Office of the President, the National Agricultural Research Institute, the University of Guyana, the Guyana Forestry Commission for their continuing support to the Tropenbos-Guyana Programme.

Thanks to the Environmental Protection Agency, the Guyana Forestry Commission and the Iwokrama International Centre for the Rainforest Conservation and Development for their support and co-operation through the several workshops we had in Guyana. Thanks also to the Tropenbos-Guyana Programme, notably George Walcott and Roderick Zagt, the Tropenbos Foundation and the Utrecht University, notably Thijs Pons and Wim Dijkman, for the support in Guyana and the Netherlands.

Thanks to all our colleagues who have produced and/or published materials that we needed so much to carry out the analyses, especially Roger de Milde, Derk de Groot and Ivan Welch for leaving behind such important forest inventory data, the Guyana Forestry Commission for permission to utilise these old and valuable datasets (Chapters 4, 5, 8), Romaine Too-Kong for the data input (Chapter 5) and Gavin Nicol to come up with even more data (Chapter 5), Barama and the Edinburgh Centre for Tropical Forests for raw plot data (Chapters 3, 8), CELOS, Suriname, for data of the Suriname FAO forest inventory (Chapter 4) and Bernard Fleury and Jean-Jaques de Granville for forest inventory data and literature of French Guiana (Chapter 4).

Thanks to Scott Mori (NYBG), Carol Kellof, Vicky Funk and Tom Hollowell of the Smithsonian Institution, Tinde van Andel and Claude Persaud for databases with specimen data (Chapter 6), André Chanderballi, Tobi Pennington, Mark Johnston, Scott Mori, Susan Fraser and Jan Lindeman for help with collection lists (Chapter 6), Ben ter Welle, Paul Maas, Ara Görts-van Rijn for botanical collection data

(Chapters 6 and 11), the Hydrometh Department for meteorological data (Chapters 5, 6 and 7).

Thanks to Nazeem Nasir of the Centre for the Study of Biodiversity for teaching how to link databases to Arcview and Joselyn Grimond of Iwokrama for digitising map data and other GIS tasks.

Many persons reviewed chapters. Thanks to (in alphabetical order): Tinde van Andel (Chapter 6), David Cassells (Chapters 5, 6), Wim Dijkman (Chapter 6), Renske Ek (Chapter 6), Nancy Garwood (Chapter 7), Jaboury Ghazoul (Chapter 7), David Hammond (Chapters 5, 6), Otto Huber (Chapter 10), Maarten Kappelle (Chapter 7), Valerie Kapos (Chapter 7), Paul Maas (Chapter 6), Scott Mori (Chapter 5), David Newbery (Chapter 3), Mark van Nieuwstadt (Chapter 3), Thijs Pons (Chapters 3 and 8), Mark Ritchie (Chapter 7), Kalle Ruokolainen (Chapter 3) Doug Sheil (Chapter 7), John Terborgh (Chapter 3), René Verburg (Chapter 3), George Walcott (Chapter 5), Graham Watkins (Chapter 6), Ivan Welch (Chapter 5), Ben ter Welle (Chapter 11), Marinus Werger (Chapters 3, 7), Tim Whitmore (Chapter 7), and last but not least Roderick Zagt who read and commented on all chapters and is almost the editor of the editor.

In the final stages Wanda Tammens did a thorough final check on lay-out and consistency of the book.

Country base-maps were obtained from ESRI Inc. (http://www.esri.com), digital data was further obtained from the USGS EROS Data Center (http://edcdaac.usgs.gov/1KM/comp10d.html, NOAA AVHRR NDVI data, and http://edcdaac.usgs.gov/gtopo30/gtopo30.html, Digital terrain model) and NASDA (JERS-1 radar satellite data).

The work that led to this book was financially supported by project "Conservation and Sustainable Use of Botanical Diversity in Guyana" (B7-6201/98-13/FOR) of the European Community, in Brussels, special thanks to Marjukka Mahonen of the Brussels Office and Maria Ralha of the EU Delegation in Guyana for their support in the start-up phase of the project.

I sincerely hope I have not forgotten anyone who has contributed to the completion of this book. This is not intentional, my apologies if this has happened.

This book was written to help in the planning of Protected Areas in Guyana. We hope that it fulfils a significant role in this process by generating the proper information and serving as an example for the analysis of other biological groups in Guyana. The readers and end-users will have to decide whether we have succeeded in reaching these goals.

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Utrecht
April 28, 2000

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1 INTRODUCTION

Hans ter Steege, Per Bertilsson, Roderick Zagt

The forest of Guyana, situated on the north-eastern edge of South America (Figure 2.1), has among the lowest deforestation rates of the world and these rates have been consistently low over the past decades (Lanly 1982, Luning 1987, Burgess 1993, Bryant *et al.* 1997). The low deforestation pressure on Guyana's forest can be attributed to its very low population of 732,000 people, mostly concentrated in the coastal area.

Guyana is at crossroads where utilisation, conservation and preservation of its forests are concerned. As a country with little industry but rich in natural resources, the Government of Guyana (GoG) has a need to exploit its natural resources for the development of the country and its people. The GoG has expressed its intention to do this in a sustainable manner (Chandarpal 1997, Ministry of Finance 1996). To effectuate this, large tracts of forest (approximately 4.5 million ha) have recently (1997) been designated as State Forest Lands and are available as exploratory concessions (no logging in the first two/three years). In addition, the granting of exploratory mining concessions is considered over large stretches of the country.

In 1994 Guyana ratified the Convention on Biological Diversity. To effectuate its Environmental Policy the Government, through an Environmental Protection Act, established the Environmental Protection Agency that will be responsible for the "effective management of the environment so as to ensure conservation, protection and sustainable use of its natural resources" (Persaud 1997). More recently a National Biodiversity Action Plan (NBAP) has been produced (EPA 1999), which has been subject to an extensive process of public consultation and approved by Cabinet. The NBAP is the overall framework for biodiversity related aspects such as wildlife management, bioprospecting and research as well as ex- and in-situ conservation. Implementation of the NBAP is ongoing and progress has been made for several of the components. Five additional geographical areas have been identified for immediate planning and implementation process leading to the establishment of these areas as protected areas (Stage I). Several other areas have been identified as stage II of the expansion of the NPAS. These require further studies and analysis in order to confirm their biodiversity and conservation values.

Guyana has established a National Protected Area System, which consists of:

1. Kaieteur National Park, which has recently been extended to approximately 630 km^2, ratified by the Executive President of Guyana in 1999.
2. Iwokrama International Centre for Rain Forest Conservation and Development. In 1989 Guyana donated 3600 km^2 of rain forest area to the 'International Community' in order to develop a conservation/wise utilisation programme (Kerr 1993), now legally embedded through the Iwokrama Act. Half of Iwokrama is designated to become protected wilderness area.

3. Reserve Forest Areas. A total of 16 separate areas with a total coverage of 77 km^2 of which the largest is Moraballi Forest Reserve.
4. Forest Reserve Mabura Hill, which is an area (18 km^2) set aside for research activities undertaken by the Tropenbos-Guyana Programme. The programme is a collaboration between the Governments of Guyana and the Netherlands to develop sound forest management (ter Steege *et al*. 1996).

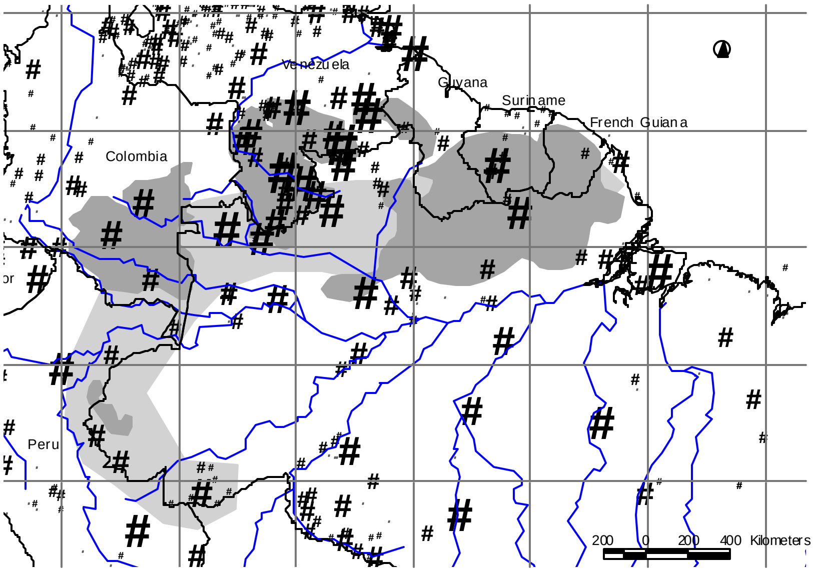

Figure 1.1 Protected areas in the Guiana Shield and adjacent areas based on the WCMC database of protected areas (IUCN categories I to V, IUCN 1994, http://www.wcmc.org.uk/protected areas/data/un_97_list.html). The size of the dots is comparable to the actual size of the protected areas. In areas where parks are close to each other some overlap may occur, underestimating the amount of protected area in that area (e.g. the Gran Sabana area in Venezuela). Light grey: 'Wilderness area' as suggested by McNeely *et al.* 1990 and IUCN 1994; dark grey: 'Frontier Forests' sensu WRI (Bryant et al. 1995).

The total extent of the present National Protected Area System in Guyana is approximately 2525 km^2, which represents just over 1% of the total area of the country. Although there are at present relatively few protected areas in Guyana, ample opportunities exist for the conservation of substantial biodiversity as the forest of Guyana is still quite intact over large areas (see above). In fact, the south of Guyana is part of one of the last 'Wilderness Areas' (McNeely *et al*. 1990, IUCN 1994, Figure 1.1) or 'Frontier Forests' (sensu Bryant *et al.* 1997, Figure 1.1) world-wide. However, there are also threats to Guyana's biodiversity of which logging and mining are perceived to be the greatest (Colchester 1997).

It is obvious, under the given circumstances, that data on which to base an expansion of NPAS have to be gathered quickly in order to make a 'best estimated guess' as to where the highest benefit can be expected from protected areas, with the least possible conflicts for development. Such a process is now being pursued as part of the implementation of the NBAP. One possible strategy is to utilise the existing knowledge of Guyana's biodiversity as gathered over the past century. A major constraint to be dealt with is the fact that much of the information, if not lost, is scattered over old archives and dispersed over foreign libraries and biological collections.

Despite the limited information on the distribution of forest types and species in Guyana, yet available, it is important that information present at this moment is made available for the process of planning protected areas. If information is not brought to policy makers at an early stage few opportunities may be left for an adequate delineation of a comprehensive set of protected areas.

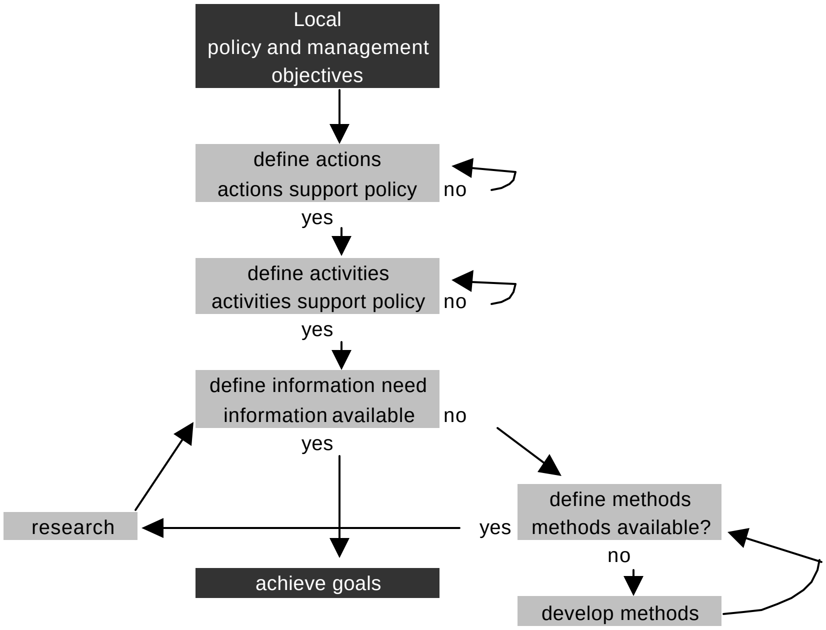

Figure 1.2 Schematic representation of an analytical process to determine information needed and to make information on biodiversity available (after Lammerts van Bueren and Duivenvoorden 1996). The various checkpoints for the process are indicated.

The process

In order to be able to contribute significantly to the process of selecting a comprehensive set of protected areas in Guyana we need to follow a process that is closely linked to the biodiversity objectives of Guyana as outlined in the National Biodiversity Action Plan. An example of such a process, is given in Figure 1.2 (Lammerts van Bueren and Duivenvoorden 1996).

The Government of Guyana stated the following policy objectives for a NPAS (Persaud 1997):

1. Preservation of viable examples of all natural ecosystems in Guyana
2. Protection of areas of particular biological significance
3. Contribution to key watersheds and provision of buffer zones to mitigate against the effects of climate change and natural hazards
4. Helping to maintain Guyana's cultural heritage
5. Provision of opportunities for education and training
6. Contribution to sustainable economic development through the provision of opportunities for nature-based tourism and recreation and for sustainable utilisation of natural resources
7. Provision of sustainable employment opportunities for remote communities through conservation services
8. Helping to meet the biodiversity conservation requirement of international reference standards for sustainable forest management needed to gain certification and market access for timber and forest products in high value consumer markets
9. Provision of future options by maintaining a broad pool of genetic resources

The actions and activities of the GoG are reflected in the National Biodiversity Action Plan (action), through which an expansion of protected areas and its infrastructure will be undertaken (activities).

As argued above the necessary knowledge base may be insufficient to make the best selection of areas to protect an as wide as possible array of Guyana's biodiversity. This book aims to contribute to the national knowledge base of plant diversity that should assist the GoG in reaching its objectives concerning the preservation and the sustainable use of forest resources in Guyana, specifically targeting objectives 1 and 2. A closer look at objectives 1 and 2 will enable us to define our information needs somewhat more precisely.

Objective 1: preservation of viable examples of all natural ecosystems in Guyana

To be able to contribute to the preservation of all ecosystems of Guyana we must first ask what those ecosystems are. Secondly, we must find out where they are. In this book forests will be the central focus and we will work a great deal with forest inventories to reveal the composition and distribution of different forest ecosystems at large and smaller scales in Guyana (Chapters 4, 5, 8). Botanical collections, which form a second readily available data source, are used to complement the forest inventory data (Chapter 6). In Chapters 10 and 11 emphasis will be given to the non-forests areas of the highlands and savannah areas of Guyana, respectively.

Objective 2: protection of areas of particular biological significance

The second objective strives to protect areas of ‘particular biological significance’. Obviously the question arises: what is particular biological significance? We propose to interpret this fivefold:

1. Forest types typical to Guyana and the adjacent areas (Guianas, Guiana Shield)
2. Areas with high levels of plant endemism
3. Areas with high levels of plant diversity
4. Areas with (high) occurrence of endangered species
5. Areas of outstanding natural beauty

To be able to assess what forests are typical for Guyana we need a regional perspective. In Chapters 3 and 4 we present this perspective by comparing the composition of a suite of forest plots well distributed over the Amazon and Guiana Shield areas (Chapter 3) and by assessing the forest composition of Guyana’s forests in comparison with that of its neighbouring countries (Chapter 4).

Distribution and abundance of endemics[1] will be discussed in Chapters 5 and 6. The forest inventory data in Chapter 5 provide us with relative abundance data of several species, whereas the botanical data of Chapter 6 provide us with more exact knowledge on the occurrence of several rare endemic species.

Using forest inventories and hectare plots, the tree diversity of forests can be computed numerically. This approach is taken in Chapters 4, 5 and 8. In Chapter 9 non-tree groups are included in such analyses. Botanical data are useful to achieve better estimates for regional species richness[2] (Chapter 6).

We have very little data on endangered plant species in Guyana. Arguably, species with small populations and/or ranges (such as narrowly distributed endemics) can be perceived to be endangered or vulnerable.

Outstanding natural beauty is obviously a very subjective measure. No data have been gathered but two regions, generally perceived to have great scenic value, are the Kanuku Mts. with surrounding savannah areas and the Pakaraima highlands with its grandiose sandstone table mountains.

We have not attempted to define diversity (see Box 1.1), or make a comprehensive list of all reasons for protecting biodiversity in Guyana or in general. This has been done comprehensively in a great number of publications. The main objective of this book is to contribute to the wish of the GoG to establish a protected areas system in Guyana by providing data, means of analyses and recommendations for protected areas and further research.

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[1] endemic: a species restricted to a particular area, which can be either a country or a habitat

[2] species richness = number of species

Box 1.1 What is Biodiversity?

Biodiversity or biological diversity in full has been defined as "*the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems*" UNEP (1992)

While this definition may appear clear we still need to ask ourselves if biodiversity is a property that can reasonably be measured. And, if it can be measured, what would be the most appropriate way to measure it. Harper & Hawksworth (1995) listed a number of questions that may help to clarify the problems faced:

1. Is biodiversity just the number of species in an area?
2. If biodiversity is more than the number of species, how can it be measured?
3. Are all species of equal weight?
4. Should a measure of biodiversity include infraspecific diversity?
5. Do some species contribute more than others to the biodiversity of an area?
6. Are there useful indicators of areas where biodiversity is high?
7. Can […] biodiversity […] be estimated by extrapolation?

A number of these questions will be tackled in the forthcoming chapters for the situation in Guyana. We are of the opinion (as are Harper & Hawksworth 1995), that biodiversity is more than just the number of species in the area and should include some information on how individuals are being distributed over the species. In most chapters we will use Fisher's α to describe α-diversity.

Three types of Biodiversity

Three levels of diversity are commonly used (Whittaker 1970)

1. α-diversity: The diversity of a point. More commonly used now for the diversity of a habitat. We will use α-diversity mainly for tree diversity in relatively small areas, such as one-hectare plots. A-diversity can be measured with the Shannon-Weaver index and Fisher's α.

2. β-diversity: Species turnover, the increase in species as one moves from one habitat to another. B-diversity can be measured with indices of complementarity such as Sorensen's index. Soil heterogeneity and altitudinal gradients often contribute greatly to β-diversity.

3. γ-diversity: Originally γ-diversity is defined as the multiplication of α-diversity and β-diversity but is somewhat synonymous to the number of species in a region (and here will be used as such).

2 A PERSPECTIVE ON GUYANA AND ITS PLANT RICHNESS

Hans ter Steege

Location

Guyana is situated on the north-eastern edge of South America between latitudes 1-9°N and longitudes 56-62°W (Figure 2.1). Guyana is part of the Guiana Shield, a massif of hard, mainly Proterozoic, rocks (Gibbs and Barron 1993), which together with the Brazilian and west African shield forms one of the oldest land surfaces of the earth.

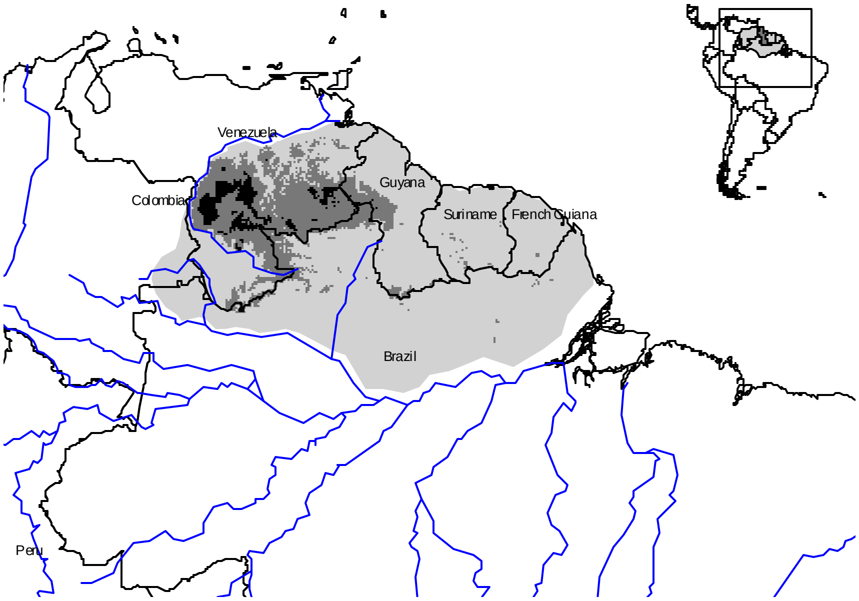

Figure 2.1 Guyana's position in S-America (inset) and on the Guiana Shield. Light grey: the approximate extent of the Guiana Shield; medium grey: areas over 500m altitude; dark grey: areas over 1500m altitude (both for Guiana Shield area only).

Climate

The climate in Guyana is strongly influenced by the movement of the Intertropical Convergence Zone (ICZ). There are two wet and two dry seasons but the dry season months have on average more than 100 mm of rain per month. A long wet season

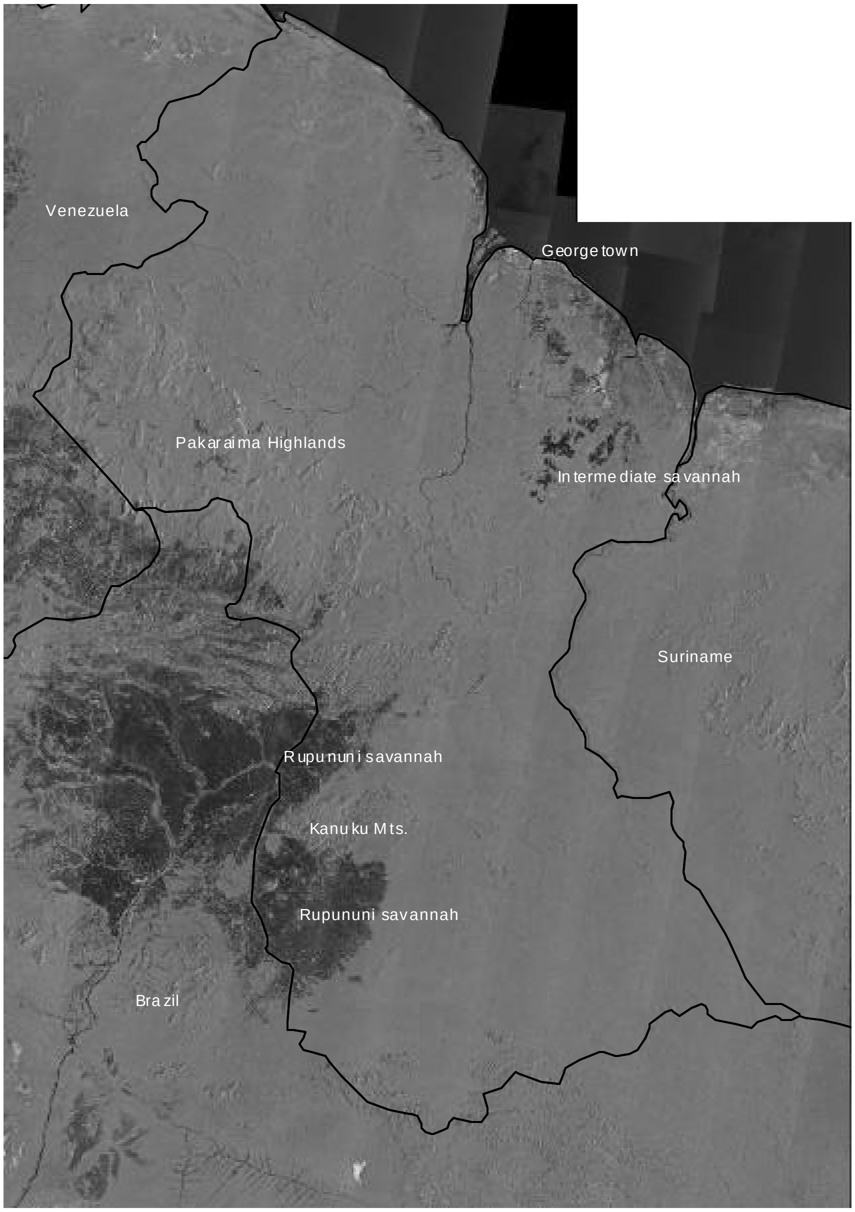

Figure 2.2 Main natural features of Guyana. Basemap JERS-1 radar satellite image (NASDA 1996). The medium grey areas have mainly forest cover, non-forest areas are dark or white. Note the slash and burn pattern just south across the border in Roraima State, Brazil.

occurs from May to August and a short wet season from December to February. Rainfall in Guyana is also strongly affected by the Pakaraima mountains in the west and the Wilhelmina mountains in Suriname, in the east. As easterly winds prevail, orographic uplift and subsequent condensation cause a high annual rainfall of 4400 mm on the eastern slopes of the mountains. The annual rainfall decreases to 1700 mm towards the east of the country, as this area and western Suriname lie on the leeward side of the Wilhelmina mountains. Year to year variation in rainfall is high (ter Steege and Persaud 1991, Jetten 1994).

The dry seasons are periods of lower cloud cover and thus have higher sunshine hours. On average the sunshine amounts to 45% of the total daytime (ter Steege 1994). Annual potential evapotranspiration (PET) amounts to 1350-1500 mm. Average daily temperature is 25.9°C and while the annual variation in daily average temperature is only about 2°C, the average diurnal variation is about 6°C. Warmest months are September and October, coldest are January and February (Persaud and Persaud 1993).

Landforms and vegetation

Four broad major landscape types have been identified in Guyana (Daniel and Hons 1984):

1. Young coastal plain in the north
2. White sands area in the north-central to eastern area
3. Pakaraima highlands in the west
4. Pre-Cambrium plateau in the north-west and south

Approximately 80-85% of Guyana's land area is covered with forest, including wet evergreen rain forest, dry evergreen forest, (semi-) deciduous forest and tall to low scrub. The major non-forest vegetation areas are found in the coastal areas, the intermediate savannah, the north and south Rupununi and in the Pakaraima highlands (Figure 2.2).

The Flora

In Guyana 5562 native flowering plant species have been collected (Boggan *et al.* 1997, Table 2.1). An estimated 25 species have been introduced into the wild (0.4%) but surely close to population centres more of such species are to be expected. Based on the low number of introduced species, we must consider the flora of the interior of Guyana largely intact and undisturbed. Based on their occurrence just across the border, a number of species is expected to be found in Guyana with greater collecting effort, while the status of several other species is uncertain. The total sums up to 5989 species, which are found in 1673 genera and 198 families. For non-flowering plants the collected number of species is: Liverworts 225; Mosses 232; Psilophyta 1; Clubworts and allies 48; Ferns 453 (Bogan *et al.* 1997).

Suriname and French Guiana have comparable, but lower, species numbers for flowering plants: 4156 in Suriname and 4474 in French Guiana, respectively. The total number of flowering plant species found in the three Guianas is 7493. Venezuelan Guayana, an area roughly similar in size to the three Guianas is considerably richer in species. Berry *et al*. (1995) attribute this to the larger expanse of montane habitat in the area but more intensive collecting cannot be excluded either.

Table 2.1 Number of flowering plants in the three Guianas (based on data from Boggan *et al*. 1997) and Venezuelan Guayana (Berry *et al*. 1995).

	Guyana	Suriname	Fr. Guiana	Total	Ven. Guayana
Native	5562	4156	4474	7493	8622
Introduced	25	26	26	26	100
Uncertain	402	261	354	829	
Total	5989	4443	4854	8348	8722
Area (km^2)	215,000	163,000	89,800	467,800	454,000

Composition of the Flora

Table 2.2 shows the families with more than 50 species in Guyana. Most of these are important neotropical families. Orchidaceae, Rubiaceae, Poaceae and Melastomataceae rank high in any checklist in the Neotropics (e.g. Gentry 1990). Chrysobalanaceae are considered typical for the Guiana lowlands, together with Lecythidaceae (just under 50 species)(Gentry 1990, Ek and ter Steege 1998). The two families are also important in that, world-wide, they have the major part of their diversity in the Neotropics. If all Legumes are considered in one family it would be the most species rich family in Guyana. Each of the three (sub-) families also rank high individually.

Table 2.2 Major plant families in Guyana – families with more than 50 species (based on data from Boggan *et al*. 1997).

family	# species	family	# species
Orchidaceae	523	Araceae	95
Rubiaceae	356	Bignoniaceae	95
Poaceae	325	Annonaceae	86
Melastomataceae	260	Lauraceae	86
Cyperaceae	239	Piperaceae	82
Caesalpiniaceae	224	Malpighiaceae	76
Fabaceae	223	Sapotaceae	72
Chrysobalanaceae	220	Sapindaceae	71
Asteraceae	160	Arecaceae	67
Euphorbiaceae	138	Malvaceae	62
Mimosaceae	138	Asclepiadaceae	62
Myrtaceae	133	Convolvulaceae	60
Clusiaceae	117	Ochnaceae	60
Bromeliaceae	116	Solanaceae	54
Apocynaceae	110	Moraceae	51

Table 2.3 Genera with more than 30 species in Guyana (based on data from Boggan *et al*. 1997).

Genus	# species	Genus	# species
Psychotria (Rubiaceae)	94	*Eugenia* (Myrtaceae)	41
Licania (Chrysobalanaceae)	92	*Panicum* (Poaceae)	41
Miconia (Melastomataceae)	76	*Inga* (Mimosaceae)	40
Rhynchospora (Cyperaceae)	56	*Myrcia* (Myrtaceae)	40
Paspalum (Poaceae)	51	*Hirtella* (Chrysobalanaceae)	38
Piper (Piperaceae)	51	*Ouratea* (Ochnaceae)	37
Maxillaria (Orchidaceae)	43	*Pouteria* (Sapotaceae)	36
Epidendrum (Orchidaceae)	43	*Passiflora* (Passifloraceae)	34
Cyperus (Cyperaceae)	42	*Swartzia* (Fabaceae)	34
Pleurothallis (Orchidaceae)	41	*Solanum* (Solanaceae)	32
Clusia (Guttiferae)	41	*Peperomia* (Piperaceae)	30

The most species rich genera are given in table 2.3. Several of these genera are also the most common ones at other sites, such as *Psychotria, Miconia, Piper, Peperomia, Pleurothallis, Epidendrum*. The high number of species *Licania* and *Swartzia* is typical for the lowlands rain forest of eastern Amazonia. Several genera that are very species rich in western Amazonian sites such as *Philodendron, Anthurium* and *Ficus* (Gentry 1990) are notably poorer in the Guianas. Due to the small amount of high montane area, compared to the Venezuelan part of the Guayana Highlands, Guyana is also lacking in genera typical of that area compared to bordering Venezuela (*Ilex, Navia, Xyris, Bonettia, Stegolepis*, Berry *et al*. 1995).

Endemism

There is no clear picture of the extent of plant endemism in Guyana. A preliminary unpublished list was produced by C.A. Persaud (pers. comm.), which contains 284 species, roughly 5% of the species. *Swartzia* and *Licania*, both genera with many restricted species, have the highest number on this list (see also chapter 6). Guyana is no phytogeographic entity in itself but part of the Guiana Shield area. Consequently, endemism is either caused by accident (restricted-range species) or if a habitat containing endemics is confined Guyana. Local endemism is often associated with such habitats as white sands, serpentine rock, swamps, igapo, varzea, rock outcrops and cloud forests (Gentry 1992). As such we can, for instance, expect concentrations of endemics in Guyana in the white sands area and Pakaraima highlands. In terms of conservation, endemism may also have to be defined more broadly in a Guiana Shield perspective. As many as 3763 species, 118 genera and 4 families of the plants of Venezuelan Guayana are endemic to this area (Berry *et al.* 1995) and also Guyana can contribute significantly to the preservation of such species.

The first law of biodiversity

Larger areas hold more species than smaller ones (see Figure 2.3). The relationship between the size of an area and the number of species it holds was recognised as early as 1859 (Rosenzweig 1995) and could be called the 'first law of biodiversity' (see Rosenzweig 1999). The relationship has conveniently been described by a power function since 1921 (Arrhenius 1921):

$S = cA^{z}$ or $\mathrm{Log}(S) = \mathrm{Log}(c) + z\mathrm{Log}(A)$

Where S is the number of species in the area, A is the size of the area, c and z are constants which vary slightly between areas.

A new mathematical framework for the species area curves was derived recently (Harte and Kinzig 1997, Harte *et al*. 1999a, 1999b). Within this new framework also an 'Exclusive Species-Area' curve emerges, as well as predictions to spatial turnover of species. It proves formally the intuitive notion that two areas that are further apart will have fewer species in common than those close by (Harte and Kinzig 1997, Harte *et al*. 1999a), which may be an important consideration for the selection of protected areas. Exclusive species are defined here as those species that occur exclusively in a sub-area (as compared to the number of species in the total area).

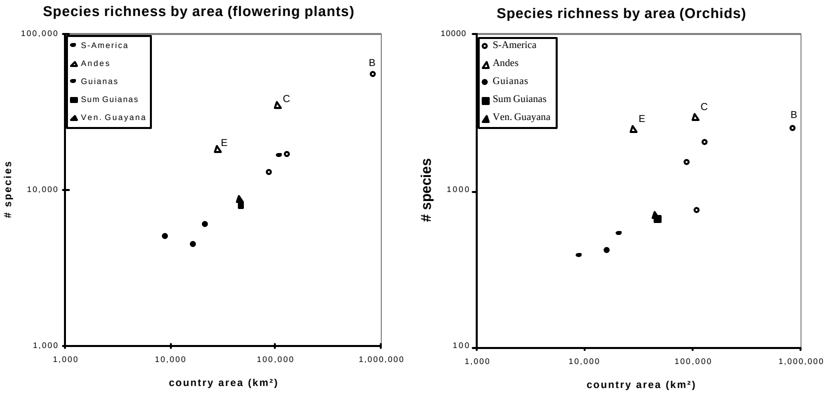

Figure 2.3 Species richness to area relationship for Amazonian countries. Data from Groombridge (1992), Boggan *et al*. (1997), Berry *et al*. (1995) and Dressler (1981). Area explains a large amount of total species richness found in a country. Compared to Brazil (B), with an estimated 55,000 flowering plants species (Groombridge 1992), the Guianas appear poor places. The greater total richness of Brazil, however, is largely explained by its larger size. Two countries with major Andean habitat (Ecuador, E and Colombia, C) have unexpected high species richness.

Larger areas harbour more species for a number of reasons:

1. They have more individuals
2. They have more habitats
3. They may include more independent biogeographic regions

Altitudinal variation also adds greatly to the species richness of an area as can be seen from the plant richness of Ecuador and Colombia, two countries with a major part of their country in montane habitat (Figure 2.3). Another good example is the orchid family. The small Guianas have low total richness, mainly explained by their small size (Figure 2.3). Ecuador and Colombia abound in species.

From the species area curve we can make a few preliminary predictions. Assume some 6000 plant species in Guyana, with a land area of 21,000,000 ha. Assume a z of 0.25 then it follows that c = 88.63 thus for Guyana:

$S = 88.63\ A^{0.25}$

With area in hectares. For restricted species it holds that (calculated according to Harte and Kinzig (1997)):

$S_{restricted} = 2.29 \cdot 10^{-16}\ A^{2.65}$

There are two large areas in Guyana with a protected status: Kaieteur National Park (KNP, 63,000 ha) and the Iwokrama forest (360,000). On the basis of the above equations we estimate that KNP should include some 1404 species, none of which are exclusive to the Park area and 1100 of which have been collected up till now (Kellof and Funk 1998). The total of Iwokrama is estimated to have 2171 species, again with no species unique to the area. Half of Iwokrama is to become ‘Wilderness Area’. Our estimate for that area is 1826 species. If the relation would hold all the way down an estimate for the richness of a one ha plot is 89 species (we will see in Chapter 9 that this is within the range found).

The Endemics-Area curve also shows that 90% of Guyana’s land area will hold roughly 4500 unique species (not found in the other 10% of Guyana). Such species will not be protected by a park system that encompasses the other 10%. Thus, also outside of protected areas conservation measures have to be in place to protect a substantial part of the country’s biodiversity. Secondary and managed forest could play an important role here.

3 A REGIONAL PERSPECTIVE: ANALYSIS OF AMAZONIAN FLORISTIC COMPOSITION AND DIVERSITY THAT INCLUDES THE GUIANA SHIELD[1]

Hans ter Steege, Daniel Sabatier, Hernan Castellanos, Tinde van Andel, Joost Duivenvoorden, Alexandre Adalardo de Oliveira, Renske Ek, Ramesh Lilwah, Paul Maas, Scott Mori

Introduction

Neotropical rain forests have been considered the most species rich forests that exist worldwide (Gentry 1988a, 1988b; Valencia *et al.* 1994). Very high α-diversities of trees, birds, butterflies, reptiles, amphibians and mammals (Gentry 1988a, and references therein) suggest that in particular western Amazonia has an almost unrivalled species diversity. Forests in the east of Amazonia and especially the Guianas are characterised by lower diversity when compared to western Amazonia, both in plants (ter Steege 1998a) and mammals (Voss and Emmons 1996, Kay *et al*. 1997). In terms of plant families, Bombacaceae, Meliaceae and Moraceae are richer in species in western Amazonia while Chrysobalanaceae and Lecythidaceae are relatively richer in species in the eastern Amazonia and the Guianas (Gentry 1990, Ek and ter Steege 1998). However, while some general patterns have been described, a comparison of tree species composition and tree diversity between Amazonia and the Guiana Shield has never been attempted. Below we briefly summarise the state of knowledge at present.

Floristic patterns

A first attempt to classify the forest types of Amazonia was made by Ducke and Black (1954). Later classifications were by e.g. Pires and Prance (1984) and Prance (1987). The classification of forests was based on climate, soil and physiognomy, with some account of species composition. A very thorough forest inventory has been carried out in Brazilian Amazonia (RADAMBRASIL 1968-1978, SUDAM 1974) but the data of these inventories have never become available in the literature (Rollet 1993). Thus, numerical comparisons over large areas remain scarce. Terborgh and Andresen (1998) produced an excellent first analysis of large-scale patterns in Amazonia, focusing on 'family-composition' gradients. Unfortunately, this analysis relied heavily on plots in western Amazonia. Data from the Guiana Shield but also from central Amazonia were scarce.

Diversity patterns

Until now most studies examining the patterns of plant diversity in the Neotropics have also relied heavily on plots in western Amazonia (Gentry 1988a, b; Phillips *et al*. 1994, Clinebell *et al*. 1995, Givnish 1999). In Western Amazonia species

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[1] This chapter has also been accepted in slightly different form by the *Journal of Tropical Ecology*.

richness is strongly correlated with total annual rainfall (Gentry 1988a, b), which is often considered a proximate estimate of ecosystem productivity (Gentry 1988a, b; Phillips *et al.* 1994, Clinebell *et al.* 1995). Rainfall shows stronger correlation with species richness than do soil fertility and soil toxicity factors (Clinebell *et al.* 1995). Givnish (1999) argued that by favouring natural enemies of plants (fungi and insects), higher rainfall would promote more density dependent mortality and hence higher diversity. Other studies have confirmed the rainfall-diversity correlation (Huston 1980 1994, Hall and Swaine 1976). In each of these studies fertility was negatively correlated with rainfall, complicating the search for single causal relationships. But the signals are also confusing. Phillips *et al*. (1994) did not find a strong link between rainfall and diversity, allegedly, because they did not include the climatic extremes (Clinebell *et al*. 1995). Because probably 90% of the Neotropical rain forests do not occur near 'climatic extremes', it appears that a model, as proposed by Clinebell *et al.* (1995), in which annual rainfall and periodicity are the most important factors, may not be sufficient in predicting species diversity over major areas of Amazonia (as will be further shown below).

Habitat diversity contributes significantly to regional species diversity. Species may differentiate along topographical differences and soil types (Guianas: e.g. Schulz 1960, ter Steege *et al.* 1993, ter Steege 1998a, Sabatier *et al*. 1997, W. Amazonia e.g. Tuomisto *et al.* 1995, Tuomisto and Ruokolainen 1997, Duivenvoorden and Lips 1995, 1998).

Historical events are also considered to have had a large influence on diversity. As an example, Pleistocene fluctuations may have led to contracting and expanding rain forests and through isolation of tree populations have contributed to speciation (Prance 1982, for recent reviews see Bush 1994, Haffer 1997). However, such hypotheses are notoriously difficult to test and often lead to circular reasoning (Tuomisto and Ruokolainen 1997) and in fact may have been based on collector-artefacts (Nelson *et al.* 1990). Other evidence suggests that many of the present day species may have evolved before the Pleistocene climate changes (see examples in Bush 1994, Kay *et al.* 1997).

The Guiana Shield

The number of floristic plots in the Guiana Shield area has risen steadily over the years and, combined with the relatively well-known flora, this has led to high quality data (Maas 1971, Comiskey *et al.* 1994, Johnston and Gillman 1995, Ek 1997; T. van Andel, unpublished data; Sabatier 1990; D. Sabatier and M.F. Prévost, unpublished data). The forest is generally species-poor (ter Steege 1998a) over the full rainfall range (2000-5000 mm y^{-1}). Including these plots of species-poor forests and several new plots from central and eastern Amazonia, occurring under rainfall regimes similar to the older studies in an analysis of species composition and diversity may greatly increase our understanding of causes of diversity in the Amazon.

In the present chapter we present an analysis of family-level floristic composition, comparing the Guianan forest block with that of Central and Western Amazonia. We also examine whether the rainfall-diversity hypothesis is capable of explaining woody species diversity in a dataset that includes the forests of the Guiana Shield and Eastern Amazonia.

Methods

Our analysis focuses on family-level floristic composition and diversity of 268 forest plots that are well distributed over Amazonia and the adjacent Guiana Shield (Figures 3.1, 3.3, Appendix 1). However, not the same information was available for all plots thus the floristic analyses and diversity analyses were carried out on different subsets of the data.

Floristic composition

Less than half of the plots have floristic information in the form of the number of individuals by species or only by family. To avoid over-representation of certain sites, the number of plots per forest type (TF, terra firme; FL, floodplain; PZ, podzol; SW, swamp; DF, dry forest) was reduced to two per site. In this case we selected the site with the lowest diversity (highest dominance) and the highest diversity (lowest dominance). While strictly speaking this may be considered pseudo-replication, plots closer to each other will in principle always be more similar due to spatial auto-correlation (and they should also be closer on a gradient when ordinated). We tested for spatial auto-correlation with Variowin 2.21 (Pannatier 1996) and Spatialstats (S-PLUS 2000, Mathsoft Inc. 1999).

For floristic analysis 105 plots were available (Appendix 1). Our first set of 48 plots was derived from Terborgh and Andresen (1998). We could duplicate the main results of Terborgh and Andresen (1998) by using the 16 most abundant families reported. The 16 families were Annonaceae, Arecaceae, Bombacaceae, Burseraceae, Chrysobalanaceae, Euphorbiaceae, Lauraceae, Lecythidaceae, Leguminosae, Meliaceae, Moraceae, Myristicaceae, Rubiaceae, Sapotaceae, Sterculiaceae and Violaceae. We concluded that these abundantly present families, which amounted to 65-96% of all individuals on the plots (Terborgh and Andresen 1998) dominated the analysis, and not unimportantly, neotropical rain forests.

To make the other plots comparable to the first set we used the same criteria as Terborgh and Andresen (1998): plot size at least 1 ha and only trees with DBH ≥10 cm were used. Such plots capture a fair amount of the local diversity (Laurance *et al.* 1998, but see Condit *et al.* 1998). The plots were truncated to 450 trees by randomly selecting 450 individuals and assigning these to their respective families (Note that only the 16 families mentioned were used for the ordinations below). We made a few exceptions to include plots of areas where no other data was available:

1. Three plots with fewer individuals: San Pedro, Venezuela, 443 ind. (Finol Urdaneto undated); Haut Camopi, French Guiana, 435 ind. (Sabatier and Prévost 1987); and Jaru, Rondônia, 442 ind. (Absy *et al.* 1987).
2. In the case of Saimadodyi, Venezuela (Lizarralde 1997) and El Tigre, Bolivia (Bergmans and Vroomans 1995) only average numbers per family were available for combined plots. Here we calculated the number of individuals per

family not by random selection but by converting the percentage of individuals to numbers within a sample of 450 trees.

3. Two plots were based on plotless tree samples along a line (within one forest type) rather than on a 1-ha plot basis (Mori and Boom 1987, Mori *et al.* 1989). In this case the first 450 trees sampled were used.

Species and genus information was not used in the analysis. This is an obvious drawback as evolution and competition take place at this level rather than at the family level. However, as Terborgh and Andresen (1998) pointed out, the data at species and genus level contains too much noise to produce interpretable results.

We recognised four main 'forest types': forests on ultisols and oxisols, so-called 'terra firme' forest (TF); forests on floodplains (FL); forests on white sand podzols or spodosols (PZ); and swamp forests (SW). Initially, the plots were assigned to eight regions: Western Amazonia (WA), Rondônia (RO), Central Amazonia (CA), Eastern Amazonia (EA), Guiana Shield (GS), Chocó, Central America and Atlantic Brazil.

Swamp plots (n = 2) were not included in the multivariate floristic analyses (see Terborgh and Andresen 1998). Because the floras from the Chocó area, Central America and the Atlantic forest are relatively separated geographically from the main large Amazonian forest mass and because we had only few plots in them, we also omitted the plots from these areas from the final analysis. The Rondônia plots resembled Western Amazonian plots most closely and because of their geographical proximity were added to WA.

The remaining data (94 plots) were analysed with principal component analysis and detrended correspondence analysis (MVSP 3.01, Kovach Computing Services) on the basis of the 16 major plant families. We compared the results of these ordinations also with multidimensional scaling (with both a correlation matrix and Euclidean distance matrix as input, Statistica 4.5, Statsoft, Inc. 1993) and chose the ordination that best separated the data spatially.

We also analysed the data of the TF plots (n = 70) and FL plots (n = 24) separately.

Diversity patterns

Almost all plots (258) have information on the number of individuals and number of species, which were used for the calculation of α-diversity (Appendix 1, Figure 3.3). Many of these plots were gathered from the literature but again a substantial portion of these plots comes from our own work.

Alpha-diversity was quantified with Fisher's α (Fisher *et al*. 1943, Taylor *et al*. 1976, Rosenzweig 1995) using all individuals and species per plot. Fisher's α, which is relatively insensitive to sample size, performs very well on data of forest plots (Leigh 1995, Condit *et al*. 1998). Using all plots for the calculation of α-diversity allows us to compare local differences of diversity with regional differences. Core Amazonian rain forest plots were defined as those occurring east of the Andes, between 8° S to 8° N, with rainfall ≥ 2000mm. This set includes the hyper-diverse plots of Peru and Ecuador but excludes the dry (deciduous) forest plots in Venezuela and Bolivia. Differences between regions and forests were analysed with ANOVA, post-hoc comparisons were carried out with Scheffé's tests.

We tested for spatial auto-correlation with Variowin 2.21 (Pannatier 1996) and Spatialstats (S-PLUS 2000, Mathsoft Inc. 1999).

Productivity

For just a few sites in the neotropics net primary productivity has been estimated on the basis of field measurements - San Carlos de Rio Negro and Reserva Ducke (Raich *et al*. 1991). We used one proxy estimate for productivity - rainfall (e.g. Gentry 1988a, b; Phillips *et al*. 1994, Clinebell *et al*. 1995), that shows good correlation with modelled net primary productivity (Raich *et al*. 1991). We analysed the relationship between α-diversity and rainfall for the complete data set (including low rainfall plots) and various subsets, based on region, edaphic condition and major soil type with regression analysis.

Maps were created with Arcview 3.1 (ESRI Inc.).

Results

Floristic patterns

The 16 families considered in the analyses made up 79% of the tree populations in the Amazonia, if we assume the plots to be representative for the area. Leguminosae dominate the neotropical forests. On average 16% of all individuals on the plots were Leguminosae (Table 3.1). In half of the forest regions and forest types Leguminosae is the most abundant family (Table 31). Leguminosae are especially abundant in the Guianas in floodplain forests (Table 3.1) and forests on white sand podzols (an average of 164 ind. in three 450-tree samples), and in fact, in the Guiana Shield in general (Table 3.1). Over the whole area considered the abundance of Leguminosae is twice as high as that of the next two most abundant families - Arecaceae and Lecythidaceae, with 9% and 8% respectively. These data also show that just three families amount to nearly one third of all trees in Amazonia. In forests on white sand podzols in the Guiana Shield (n = 3), Leguminosae and Bombacaceae are very abundant (163-165 and 72-130 ind. in 450-tree samples respectively). Arecaceae and Moraceae are most abundant in the terra firme forest of WA, as are Myristicaceae and Rubiaceae. Sapotaceae are most abundantly found in CA and Burseraceae in both CA and EA. Lecythidaceae and Chrysobalanaceae are most abundant in CA and GS. Arecaceae dominate the floodplain forests in both WA and EA (Table 3.1) and also the swamp forests in WA (data not shown) and GS (van Andel, unpublished data).

The DCA, PCA and MDS ordinations gave very similar results and the scores of the plots on the first axis were highly correlated ($r_{Pearson}$: DCA-PCA 0.983; DCA-MDS – 0.954). Because there are distinct floristic differences between TF and FL plots (Table 3.1) the results of the TF and FL ordination are discussed separately.

Table 3.1 Average number of individuals of sixteen major tree families in random samples of 450 trees on 1-ha plots in terra firme plots in four Amazonian regions. Abbreviations: WA western Amazonia, CA central Amazonia, EA east Amazonia, GS Guiana Shield. The families have been ordered according to their abundance from WA to GS. Differences in the small letters following the abundance indicate significant differences between regions. P-level indicates the level of significance as tested with one way ANOVA. Families that show a significant difference between regions are in bold.

terra firme forest	**WA**	**CA**	**EA**	**GS**	**p-level**
number of plots	21	10	11	28	
Arecaceae	51.7 a	13.1 b	10.9 b	10.0 b	0.000
Myristicaceae	28.7 a	14.6 ab	7.8 b	6.1 b	0.000
Moraceae	50.6 a	28.6 b	18.8 b	9.0 b	0.000
Rubiaceae	10.7 a	3.1 b	1.9 b	4.0 b	0.000
Violaceae	11.6	7.6	8.5	3.4	0.305
Sterculiaceae	11.7	3.9	11.5	5.0	0.320
Sapotaceae	21.3 b	59.8 a	31.7 b	28.3 b	0.000
Euphorbiaceae	21.3	11.8	29.7	16.8	0.104
Meliaceae	12.1	6.8	19.3	9.4	0.176
Burseraceae	19.3 b	35.2 a	41.5 a	21.0 b	0.007
Lauraceae	14.3	21.2	14.0	18.9	0.337
Bombacaceae	8.6	4.7	4.8	12.1	0.118
Annonaceae	10.9	9.6	13.3	16.4	0.194
Lecythidaceae	21.2 b	59.7 a	43.5 b	56.7 a	0.001
Leguminosae	49.3 b	55.9 ab	77.6 ab	94.6 a	0.001
Chrysobalanaceae	8.4 b	27.5 a	12.2 b	38.4 a	0.000

floodplain forest	**WA**	**CA**	**EA**	**GS**	**p-level**
number of plots	16	3	3	2	
Rubiaceae	10.1	10.7	0.0	0.0	0.185
Moraceae	34.1	33.0	4.3	0.0	0.087
Myristicaceae	25.4	28.0	3.0	3.0	0.087
Violaceae	5.4	4.3	0.0	1.5	0.789
Annonaceae	27.9	29.0	0.3	7.0	0.065
Sapotaceae	18.1	31.3	3.7	3.0	0.060
Sterculiaceae	9.5	6.0	7.7	2.5	0.514
Lauraceae	9.8 b	32.7 a	0.0 b	8.5 ab	0.008
Euphorbiaceae	20.8	33.3	21.0	9.5	0.604
Arecaceae	100.1 ab	17.3 b	181.7 a	0.0 b	0.008
Bombacaceae	22.8	7.0	16.0	14.0	0.676
Chrysobalanaceae	6.9	15.0	31.3	2.0	0.160
Burseraceae	3.0 b	11.3 a	19.3 a	6.5 a	0.002
Meliaceae	16.7	7.0	22.0	31.0	0.402
Lecythidaceae	4.8 b	43.0 a	16.7 ab	48.5 a	0.000
Leguminosae	44.8 b	49.0 b	83.0 b	236.0 a	0.000

The ordination with MDS produced the best separation of TF plots by area in a biplot (Figures 3.1, 3.2). Explained variance is approximately 27% for axis 1 and 11% for axis 2, based on PCA and DCA ordination. In this ordination (as in the others) the plots are ordered more or less in an north-east to south-west direction (Figure 3.1). Plots with a low score are found in the Guianas, EA and CA. Plots with a high score are mainly found in WA. However, the more central portion of WA has lower

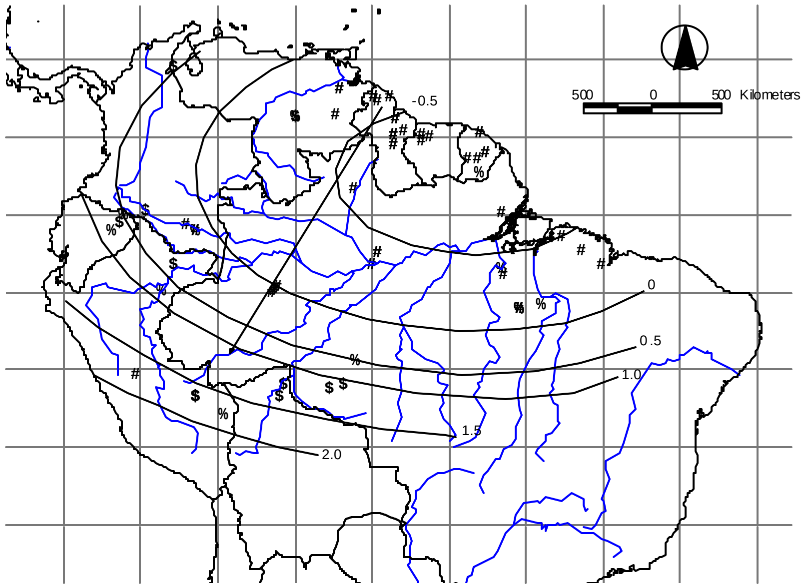


Figure 3.1 Location and plot score of 70 Amazonian TF plots used in a Multidimensional Scaling ordination based on the abundance of the 16 most dominant tree families. Scores are indicated in three classes: circles < 0, squares between 0 - 1, triangles > 1. Solid line: interpolated value = 0; broken line: interpolated value = 1. The elliptic lines are isoclines of a spatial quadratic regression (see text) on MDS plot scores. The arrow from Guyana to Peru indicates the direction of a linear spatial regression (see text) and the major direction of the spatial gradient described.

scores than the more southern and northern parts. Although a linear spatial regression explains the variation of MDS plots scores relatively well ($R = 0.699$, $p < 0.001$, Figure 1), a quadratic function explains the variation better ($R = 0.754$, $p < 0.001$). The linear component can be interpreted as the main gradient from Guyana-east Venezuela to Peru-Bolivia (Figure 3.1). The quadratic model shows anisotropy caused by the fact that the plots on the edge of western Amazonia and the Guiana Shield are more similar to the plots in the Guianas than the plots in Peru. Auto-correlation analysis of MDS plot scores results in an exponential variogram ($r = 0.81$, $p < 0.01$), suggesting that none of the plots are really spatially independent (no matter the distance) but rather are ordered on a gradient.

Families that show the strongest correlation with MDS axis 1 are (Table 3.2): Arecaceae, Myristicaceae and Moraceae, increasing in abundance from the Guianas towards western Amazonia, and Chrysobalanaceae (Figure 3.3a) and Lecythidaceae (Figure 3.3b) increasing towards the Guianas. Sapotaceae show an optimum in CA indicated by only a significant 2^{nd} order polynomial. Sterculiaceae and Violaceae show highest abundance at the two ends of the gradient but the significance is mainly caused by one point with very high abundance.

The gradient for the 24 FL was less 'method-independent' ($r_{Pearson}$: DCA-PCA -0.612; DCA-MDS 0.891). However, the explained variance (DCA) was still 41% for the first two axes together. Arecaceae, Lecythidaceae and Leguminosae had strongest correlation with the first axis. Because all FL plots in EA were also strongly dominated by Arecaceae, WA and EA plots were always close together in the bi-plots.

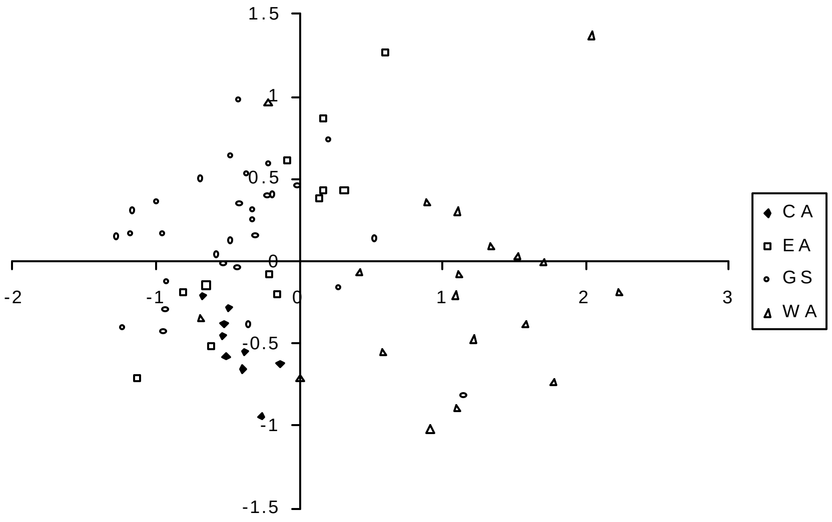


Figure 3.2 Ordination with Multidimensional Scaling of 70 Amazonian TF plots on the basis of their similarity in numbers of individuals in 16 major plant families. Similarity was calculated with correlation coefficients.

Diversity patterns

The range found in Fisher's α (in the complete dataset) was quite large - from 3.6 (GS: N = 395, S = 17) to 221.8 (CA: N = 769, S = 322). Plots with very high α-diversity (Fisher's α > 200) are found in a wide area from Western to Central Amazonia (Figure 3.3). These plots include the hyper-diverse plots in Peru (Gentry 1988a) and Ecuador (Valencia *et al.* 1994) but also in Brazil (Oliveira and Mori 1999, Amaral 1996). Most plots in Eastern Amazonia, the Guianas and other areas have much lower diversity, except for some plots in the Chocó (Faber-Langendoen and Gentry 1991) and French Guiana (Mori and Boom 1987). The variogram constructed for α-diversity of TF plots suggest autocorrelation up to 300 to 500 km but contains a substantial amount of noise at larger distances. For interpolation of TF diversity an interdistance-weighting up to 500 km is used in Figure 3.3.

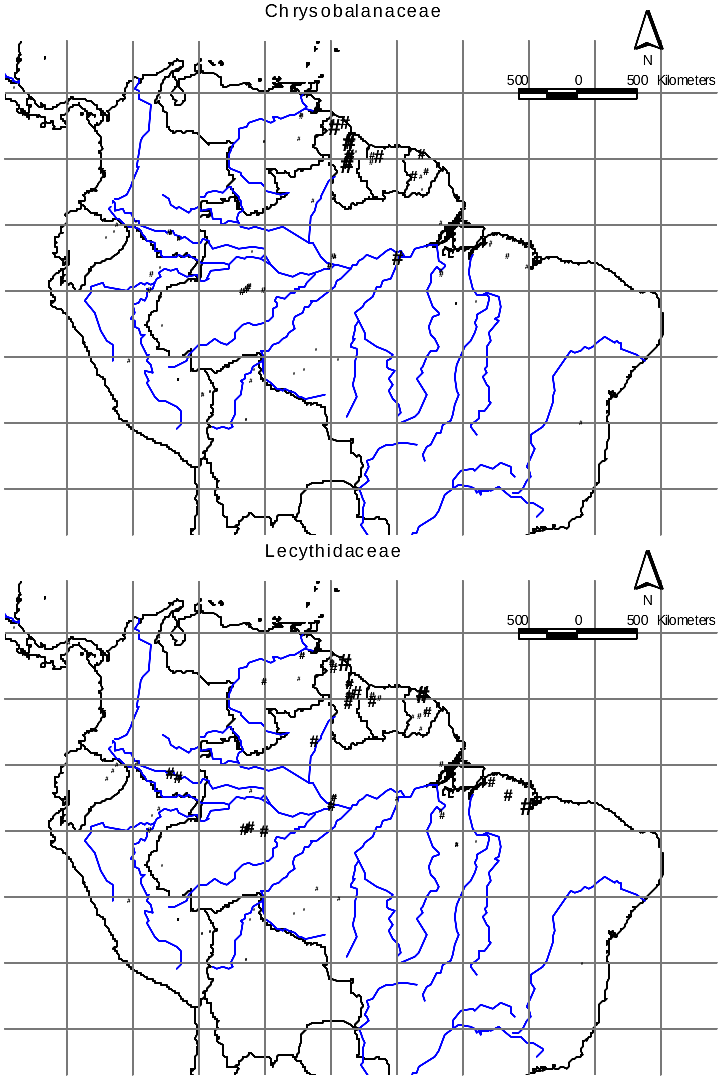


Figure 3.3 Abundance of Chrysobalanaceae and Lecythidaceae in the Neotropics. The size of the dots indicates the number of trees in a sample of 450 individuals. The range from smallest dot to largest dot is: Chrysobalanaceae (0-108); Lecythidaceae (0-145). Note that only data can be given for sampled sites. Empty map space does not indicate the absence of the family but rather the absence of plots.

Table 3.2 Coefficients of determination (r^2) of a multiple regression of the plot axis-score of the multidimensional scaling and family abundance on 70 TF plots in Amazonia and the Guiana Shield area. Significant regressions (with Bonferroni correction) are given in bold. With four families the 2^{nd} order polynomial is necessary to describe the relationship between axis and abundance well. Sapotaceae and Legumes show an optimum in the centre axis scores, Sterculiaceae and Violaceae a minimum.

Family	1st order	2nd order	sign.
Annonaceae	0.04	0.05	ns
Arecaceae	**0.74**	**0.78**	*
Bombacaceae	0.00	0.00	ns
Burseraceae	0.01	0.11	ns
Chrysobalanaceae	**0.39**	**0.55**	*
Euphorbiaceae	0.01	0.01	ns
Lauraceae	0.11	0.12	ns
Lecythidaceae	**0.58**	**0.68**	*
Leguminosae	0.06	**0.19**	*
Meliaceae	0.08	0.11	ns
Moraceae	**0.52**	**0.52**	*
Myristicaceae	**0.17**	**0.17**	*
Rubiaceae	0.13	0.14	ns
Sapotaceae	0.13	**0.18**	*
Sterculiaceae	0.09	**0.16**	*
Violaceae	0.13	**0.27**	*

Both region (WA+RO, CA, EA, GS) and forest type (only FL and TF tested) had a significant effect on Fisher's α (Regions: $F_{[3,137]} = 12.23$, $P < 0.001$; Forest type: $F_{[1,137]} = 23.24$, $P << 0.001$; No interaction $F_{[1,137]} = 1.45$, $P = 0.23$) when tested together for the for the core Amazonian plots (8° S – 8° N, rainfall > 2000 mm y^{-1}). Average α-diversity is highest in Central Amazonia followed closely by Western Amazonia (Table 3.3). The most diverse floodplain forests are found, on average, in Western Amazonia. The plots on the Guiana Shield and Eastern Amazonia have low diversities for terra firme and floodplain forest, as well as forest on white sand podzols and in swamps (as compared to WA and CA). Post-hoc comparison (Scheffé's test) shows that in terms of α-diversity there are two regions. CA and WA plots are not significantly different from each other and neither are EA and GS plots. Between the CA-WA on one hand and EA-GS on the other all combinations are significantly different. Thus, EA and GS plots have significantly lower diversity than WA and CA plots.

Swamp plots appear to have lowest diversity, while white sand podzols, have higher diversity than floodplains. Both were not tested statistically because of their low numbers.

The overall relationship between rainfall (complete range) and diversity (all plots in WA+RO, CA, EA and GS) was very weak (Figure 3.5). Rainfall explained approximately 8% of the variation in Fisher's α ($r = 0.279$, $p < 0.001$). Two very rich plots in WA have a large influence on the regression outcome and show very high Cook's distances (0.14, 0.15 vs. an average of 0.05) and can be considered statistical outliers. But even with omission of four plots with Fisher's α over 200 the

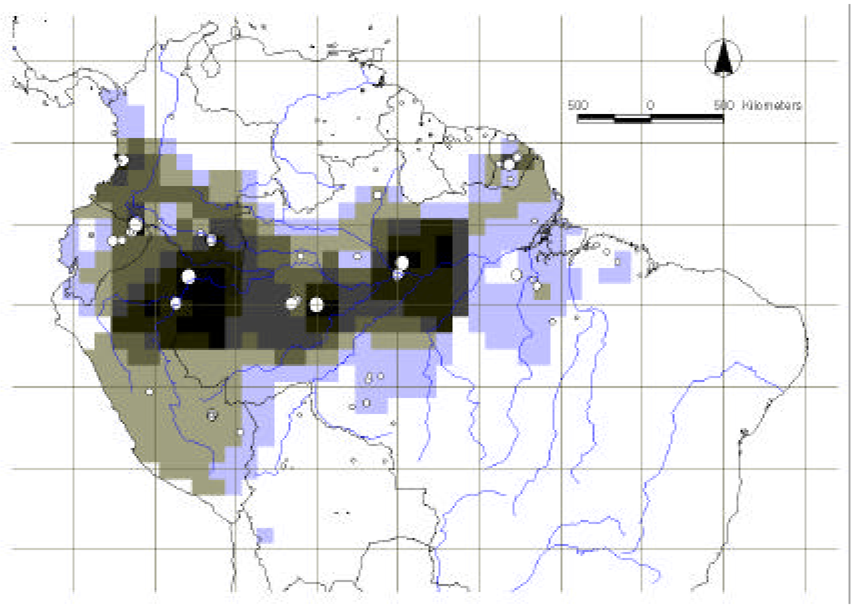


Figure 3.4 Location of 258 Amazonian plots used in the analysis of tree α-diversity. Dot size indicates the value of Fisher's α (in case of overlap only the highest will be visible). Grey-scales indicate interpolated values of Fisher's α (with interdistance weighting up to 500 km).

influence of rainfall is still significant ($r = 0.211$, $p < 0.01$). Both for TF and FL plots rainfall shows a significant correlation with Fisher's α ($r = 0.244$, $p < 0.01$; $r = 0.455$, $p < 0.01$). In the case of TF plots the relationship is no longer significant when the plots with annual rainfall below 2000 mm (in the dry regions of Bolivia and Venezuela) are removed ($r = 0.041$, $P > 0.05$). In WA + RO (ter Steege *et al.* accepted) rainfall has a significant correlation with Fisher's α for all plots ($r = 0.576$, $p < 0.001$). This is also the case for the all TF plots ($r = 0.568$, $p < 0.01$) when the two outlier plots are removed ($r = 0.391$, $p < 0.05$). There is no significant correlation when only plots with rainfall over 2000 mm are used ($r = 0.305$, $p > 0.05$). In CA (ter Steege *et al.* accepted) there is no significant correlation between rain and Fisher's α, when all plots or TF plots are analysed. There is a significant

Table 3.3 Average α-diversity for 1-ha plots in core Amazonian rain forest (8°S – 8°N, rainfall >2000 mm annually). Abbreviations: GS Guiana Shield, EA east Amazonia, CA central Amazonia, WA western Amazonia, TF terra firme, FL floodplain forest, PZ forest on white sand podzols, SW swamp forest. Maximum Fisher's-α per forest per region in parentheses. Letters indicate differences in average Fisher's-α between the regions as tested with post-hoc Scheffé's test ($p < 0.05$), p indicates significance for single-way ANOVA per forest type.

Forest	**WA**		**CA**		**EA**		**GS**		**p**
TF	124.5	(221.1) a	126.3	(221.8) a	56.0	(123.6) b	51.9	(155.5) b	< 0.001
FL	78.7	(131.7) a	46.1	(109.4) ab	20.8	(24.6) ab	16.7	(22.7) b	< 0.01
PZ	99.7	(142.2) a					24.3	(39.1) b	< 0.05
SW	33.7	(67.2)					7.5	(8.2)	n.s.

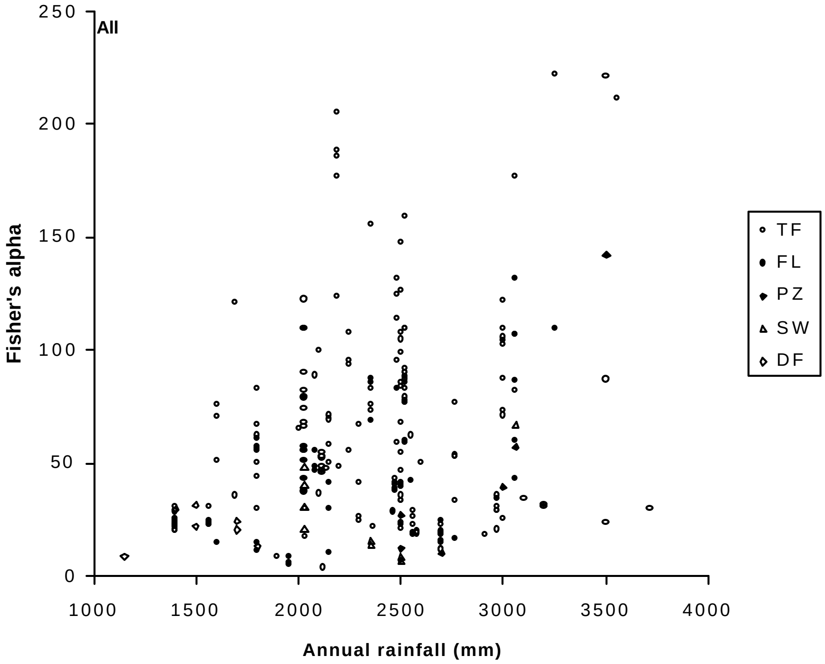


Figure 3.5 The relationship between annual rainfall (mm year $^{-1}$) and Fisher's α for (a) all plots in Western, Central, Eastern Amazonia and the Guiana Shield. Legend: TF, terra firme; FL, floodplain; PZ, podzol; SW, swamp; DF, dry forest.

correlation for the FL plots but this is caused by only one data point and considered doubtful. There is no significant relationship between rainfall and Fisher's α in EA for all plots, TF plots or FL plots (ter Steege *et al.* accepted). In the GS plots (ter Steege *et al.* accepted) there is a small significant correlation ($r = 0.257$, $p < 0.01$) between rainfall and Fisher's α, but not if the dry forest plots (rain < 1500 mm) in Venezuela are removed ($r = 0.138$, $p > 0.05$). The same is true when TF plots are analysed separately. The GS plots contain one clear outlier, Saül, with a Fisher's α of 155.5. Outliers in terms of rainfall are Rio Caura (3715 mm y^{-1}) and San Carlos (3500 mm y^{-1}), both with very low diversity.

The range in diversity (Fisher's α) within one area can be substantial but is remarkably stable in other areas (Appendix 1). A few examples for terra firme plots: Manaus 123.6 – 205.1 (n = 4); Nouragues 70.9 – 122.0 (n = 8); St Elie 58.9 – 109.8 (n = 16); Manu Pakitza 55.6 – 122.6 (n = 5); Mabura Hill 8.4 – 11.6 (n = 3). Central Guyana shows consistently low figures for α-diversity (Appendix 1), with species numbers almost always under 100 per ha. Similarly low values are found in Venezuelan Guayana lowland forests. Moving eastwards through Suriname to French Guiana diversity in the Guianas increases steadily. The sample with highest diversity in the Guianas is found near Saul, French Guiana with a Fisher's α of 155.5 (Appendix 1).

Discussion

In the neotropics a total of 292 plant families occur, 140 of which contain tree species (Maas and Westra 1993). Only 16 families out of this high number make up close to 80% of all the tree individuals that grow over 10 cm DBH. These few families dominate most Neotropical forest sites, confirming Gentry's (1990) observation that neotropical forests are floristically very similar. However similar though, there are clear large-scale patterns in the abundance of important tree families in lowland Amazonian forest. Leguminosae, Lecythidaceae and Chrysobalanaceae dominate in eastern Amazonia and Guiana Shield terra firme and floodplain forests. Palms, Moraceae and to a lesser extent Myristicaceae dominate the forests of western Amazonia. This result is in full agreement with Terborgh and Andresen (1998) and firmly establishes the unique composition of the flora on the Guiana Shield area as being one end of a floristic gradient. The patterns in abundance correspond to species richness in the families. Palms are also more species-rich on the plots in WA (see references in Appendix 1) and in WA as a whole (Kahn and de Granville 1992). Chrysobalanaceae (*Licania*) are not only common in the Guianas, they also attain high diversity there (Prance 1986). However, whereas Lecythidaceae are most abundant in Guyana, they have highest diversities in central Amazonia (Mori *et al*. in press).

If rainfall is not a good predictor of large-scale patterns in α-diversity in Amazonia, what is? We briefly discuss four possible causes, specifically comparing the Guiana Shield area with Central and Western Amazonia.

Primary productivity

Primary productivity is thought to have an important influence on species richness (e.g. Huston 1994, Rosenzweig 1995) and Phillips *et al*. (1994) found indeed that that the most productive sites in western Amazonia had the species highest diversity. A higher turnover, leading to escape from competitive conclusion could be the mechanism (Huston 1994, Phillips *et al.* 1994). Unfortunately, rainfall, seasonality, temperature and soil quality may all independently affect productivity.

Large scale differences in NPP, between WA, CA and GS appear to be non-existent (see Raich *et al*. 1991). Most soils in the Amazon basin are poor, rainfall ranges and temperatures are similar. However, the NPP as calculated by Raich *et al.* (1991) is based upon the FAO soil map of the world, which greatly underestimates the presence of ultisols in the western Amazon, which are all classified as oxisols (Richter and Babbar 1991). Based on the data we have, we cannot conclude that differences in productivity are the cause of differences in the large-scale diversity patterns over Amazonia.

Rainfall as a proxy estimate for productivity has been found to correlate strongly with diversity (a.o. Clinebell *et al.* 1995). We find rainfall to be a poor estimator for tree α-diversity, especially when only plots with rainfall over 2000 mm are taken into account, which would include most plots with rain forest. There is a difference in tree α-diversity between forests with very low rainfall, dry forests, and the forests with higher rainfall, rain forests. However, considering only rain forests, we cannot agree with Clinebell *et al*. (1995) that “Wet forests with an ample year-round moisture harbour the greatest number of woody plant species and should be a focus of conservation efforts”. Forest in central Amazonia with lower annual, more seasonal, precipitation, such as around Manaus can be just as species rich as the aseasonal very wet forests of western Amazonia and possibly several areas in between (Figure 3.4). On the other hand under a similarly large range in rainfall, tree α-diversity in the Guianas is consistently lower than that of CA or WA. In addition to that, such a simple model easily leads to overemphasis of just one measure of diversity as a tool of preservation and neglects phytogeographic differences and patterns of endemism (see below).

Ecosystem dynamics

Both intermediate disturbance hypothesis and dynamic equilibrium theory predict higher species richness with intermediate disturbances that delay or prevent competitive exclusion (Huston 1994). Higher turnover has indeed been reported from forests with higher diversity (Phillips *et al*. 1994). But more recently such high diversities have also been reported from forests with very low dynamics (Rankin *et al*. 1990, Oliveira 1997). Some community characteristics, related to shade tolerance such as an average large seed size (Hammond and Brown 1995) have been put forward as evidence that the Guianas suffer less large scale disturbances than WA. Also within Guyana a decline in α-diversity is correlated with an increase in average community seed size and wood density and a decrease in pioneers (ter Steege and Hammond, unpublished manuscript). This gradient in diversity has also been interpreted as a gradient in disturbance, possibly related to pre-historic Amerindian activities (ter Steege and Hammond, unpublished manuscript). If higher turnover should also lead to shorter generation periods this could also affect diversity at longer (evolutionary) time scales (Rohde 1992). Marzluff and Dial (1991) indeed found that short generation time (and the ability to colonise new resources) is associated with higher diversity.

Area

Area probably holds more influence over the origin and maintenance of diversity at large and small scales than currently appreciated. It may, for example, be largely responsible for the latitudinal gradient (Terborgh 1973, Rosenzweig 1995). Larger areas should have more species for four reasons - two pertaining speciation rates and two pertaining extinction rates (Rosenzweig 1995). Speciation rates in larger areas are higher because (a) larger areas are more likely to contain geographical barriers, important for allopatric speciation and (b) species with larger ranges have more genetic variation and seem to evolve faster. Extinction rates in large areas/populations are lower because (c) larger ranges lead to larger populations that are less likely to go extinct due to random population fluctuations and (d) larger ranges encompass more niche refugia, where populations may reside when large changes (e.g. climatic) occur.

Because species richness in smaller areas is also influenced by the size of the total area it belongs to, caused by sink-source relationships, or mass effects (Rosenzweig 1995, Zobel 1997), 1-ha plots in large forest tracts should have more species than those of smaller tracts. If we carefully consider the location of the Guianas in relation to the rest of Amazonia, a much larger area, three barriers exist between them. From the north to the south these are: the Llanos, the Guayana Highlands and the Transverse Dry Belt (Pires 1997). Eastern Amazonia is separated from Central Amazonia by the same Transverse Dry Belt in the west and is bordered on the south by dry deciduous forest. The mouth of the Amazon effectively separates Eastern Amazonia and the Guiana Shield areas. Also the river drainage system of the three Guianas is almost completely separated from the Amazon drainage (e.g. Rosales-Godoy *et al*. 1999). While the separation is by far not 'species-tight' only a pattern of this scale can explain the consistent differences in species diversity between Eastern Amazonia and the Guiana Shield on one hand and Central and Western Amazonia on the other hand.

Area may also help to explain why certain forest types are richer than others. Obvious conclusions sometimes force themselves upon us. We generally believe that floodplains and mangroves are poor places to live with severe physiological constraints imposed by perpetual waterlogging and regular submersion by the seawater, allegedly limiting the pool of species that can grow (e.g. Clinebell *et al*. 1995). But is this true? Mangroves and floodplains are also fringe habitats, small in area and heavily fragmented. Could this contribute to their low species richness? Thinking long-term and large-scale, most likely it does (Terborgh 1973, Rosenzweig 1995, see above arguments). We would be surprised that, if mangroves covered an area the size of Amazonia, they would as poor in species as they are now. In fact, where mangroves are more extensive (the Pacific) they are indeed much richer in species (Tomlinson 1986).

In the light of the above, it should not be surprising that the forest that covers most of the 'typical soils' of Amazonia (ultisols and oxisols) is also the richest, not only in CA and WA but also within the Guianan area. Floodplain forests, swamps and forests on white sands are much smaller in extent (Table 3.4) and more fragmented and for reasons stated above that should explain to some extent their lower species richness. White sand podzols cover only 2.8% of the Amazon basin and 7.9 % in Guyana (Table 3.4). Because of obvious ecological differences they harbour, despite their low species richness, a flora relatively rich in endemics (Huber 1995a, Lleras 1997; ter Steege 1998a, ter Steege *et al.* 2000a). Had the situation be reversed with most of Amazonia being white sand and just a few areas with ultisols/oxisols, undoubtedly the latter would have been far poorer in species (we probably would have attributed this to the 'obvious' aluminium toxicity of such soils). Floodplains are more species-rich where they cover larger areas in WA. Within that area they had even far greater extent in historical times (Rosales-Godoy *et al*. 1999).

Table 3.4 Percentage of soil types in four neotropical areas largely covered with rain forest. Oxisols and ultisols cover the majority of these areas and are particularly extensive in the Brazilian Amazon. Data: Guyana, Gross-Braun *et al*. 1965; Brazil, Richter and Babbar 1991; Colombia, Duivenvoorden and Lips 1998; Peru, Salo *et al*. 1986).

	Podzols	**FL**	**O/U**	**Lithosols**	**Total area (km2)**
Guyana	7.9	8.2	51.5	16.7	214,056
Brazilian Amazon	2.8	7.1	71.4	4.5	4,614,100
Colombian Amazon (p.p.)	4.1	14.3	72.7	8.2?	6,700
Peruvian Amazon	na	12	na	na	515,800

Endemics are most often found in small distinct habitats, often fragmented (‘ecological islands’), such as white sand areas, serpentine rock, cloud forests (Gentry 1992, Huber 1995a, Lleras 1997, ter Steege 1998a, ter Steege *et al.* 2000a). With the same reasoning mangrove-, floodplain- and swamp-restricted species could be considered ‘ecological endemics’. Because small habitat areas are likely to have fewer species (see above) we expect the relationship between endemism and diversity to be negative within a phytogeographic region. Between regions or continents, i.e. areas with a separate evolutionary history, the relationship is undoubtedly positive, the more species the more endemics.

Two factors, area and disturbance regime, may be responsible for a large part of the differences in α-diversity found between the Guiana Shield area and Eastern Amazonia as compared to Central and Western Amazonia. Very recently a third potential factor was added to this list: the ‘mid-domain effect’ (Colwell and Lees 2000). This model suggests that even without environmental gradients species richness should peak in the centre of a large biogeographic area and is based on the range-size distribution found in species.

The causes for gradient in family composition could be both ecological and historical (Terborgh and Andresen 1998). Arecaceae and Moraceae are very abundant and species-rich in Western Amazonia but they are not absent in the eastern areas. In several floodplain sites Arecaceae even dominate the forests in EA and the coastal swamps of the Guianas. Similarly, Chrysobalanaceae and Lecythidaceae are not absent from Western Amazonia but less abundant. But why are Moraceae more abundant and rich in species in WA and are Chrysobalanaceae, Lecythidaceae and Legumes more abundant in GS? We believe that the disturbance regime may be partly responsible (Hammond and Brown 1995, ter Steege and Hammond, unpublished manuscript). Higher dynamics may allow members of families with pioneer-like characteristics such as light wood, small seeds and short generation times (many Moraceae) to dominate over the slower growing species from the dense wooded and large-seeded families (Chrysobalanaceae, Lecythidaceae). In Guyana we found clear patterns of average community seed size, wood density and diversity (ter Steege and Hammond, unpublished manuscript). At larger scale the seed size spectrum of Guianan forest is also strikingly different from that of Western Amazonia (Hammond and Brown 1995). Fast growing species tend to have short generation times, which may promote species richness of such taxa (Marzluff and Dial 1991). This may be an additional cause for the high diversity in western Amazonia.

Appendix 1 Plots used in the floristic and diversity analyses of Chapter 3

Sites are ordered by country. Site and location are given in the first column. Np = number of plots used for α-diversity calculations at the site; α = average Fisher's α; α max = maximum Fisher's α found at the site; Nf = number of plots used in floristic analysis (because more forest types can be present at one site and sometimes plots are given general coordinates but are not close, more than one per site is possible.

Country/ Site/ coordinates	Np	a	a max	Nf	references
Bolivia					
Alto Ivón, 11°45' S, 66°02' W	1	30.2	30.2	1	Boom 1986
Amboró, 17°45' S, 63°44' W	1	20.7	20.7		Vargas 1995 in Smith & Killeen 1998
Rio Beni, 14°38' S, 66°18' W	2	12.9	14.8	2	Dallmeijer *et al*. 1996 and in Terborgh & Andresen 1998
Chimanes, 15°00' S, 66°30' W	1	24.2	24.2		de Aquila 1996 in Smith & Killeen 1998
El Tigre, 10°59' S, 65°43' W	4	23.5	24.5	1	Bergmans & Vroomans 1995
Noel Kempff, 14°35' S, 60°50' W	2	26.5	31.1		Saldias *et al*. 1994 in Smith & Killeen 1998
Perseverencia, 14°33' S, 62°45' W	1	29.4	29.4		Vargas *et al*. 1994 in Smith & Killeen 1998
Rio Beni, 14°22' S, 67°33' W	2	45.2	47.7		de Walt *et al*. 1999
Rio Maniqui, 14°30' S, 66°50' W	1	13.0	13.0		Palacios *et al*. 1991 in Ceron & Montalvo 1997
Serrania Pilón, 14°55' S, 67°05' W	1	62.2	62.2		Smith & Killeen 1998
St. Cruz de la Sierra, 17°47' S, 63°04' W	1	9.1	9.1		Paz 1991 in Silva *et al*. 1992
Brazil					
Altamira, 3°12' S, 52°45' W	2	78.2	121.0		Dantas & Muller 1979 in Campbell *et al*. 1986, Dantas *et al*. 1989 in Ferreira & Rankin 1998
Aripuana, 10°10' S, 59°27' W	1	0.0	0.0	1	Ayres 1981 in Terborgh & Andresen 1998
BDFFP, 3°08' S, 60°02' W	2	176.9	176.9	2	Ferreira & Rankin 1998, Rankin *et al*. 1990, Rankin *et al*. 1992
Belém, 1°30' S, 47°59' W	2	25.1	33.2	1	Black *et al*. 1950
Breves, 1°40' N, 50°09' W	1	76.8	76.8		Pires 1966 in Campbell *et al*. 1986
Camaipa, 0°10' N, 51°37' W	1	68.4	68.4	1	Mori *et al*. 1989
Capitão Poço, 1°44' S, 47°09' W	1	49.8	49.8		Dantas *et al*. 1980 in Campbell *et al*. 1986
Carajás, 6°00' S, 50°30' W	5	51.0	54.6	3	Salomão *et al*. 1988, Silva & Rosa 1989, Silva *et al*. in Silva & Rosa 1989, Silva *et al*. 1986
Castanhal, 1°20' S, 47°50' W	1	53.3	53.3	1	Pires *et al*. 1953

Country/ Site/ coordinates	Np	a	a max	Nf	references
Caxiuaña, 3°50' S, 51°30' W	4	88.2	107.7	1	Almeida *et al*. 1993
Costa do Marreção, 3°25' S, 60°46' W	1	28.3	28.3		Worbes *et al*. 1992
Guama, 1°20' S, 48°30' W	1	24.6	24.6	1	Pires & Koury 1958
Ilha de Maraca, 3°20' N, 61°20' W	3	30.6	41.4		Milliken & Ratter 1998, Thompson *et al*. 1992
Japura, 2°00' S, 66°00' W	4	59.8	88.8	1	Ayres 1981, Ayres 1993
Jarú, 9°19' S, 61°45' W	2	61.6	62.2		Absy *et al*. 1987
Jarú, 9°23' S, 61°03' W	2	56.0	56.7	1	Absy *et al*. 1987
Jarú, 9°37' S, 61°50' W	2	62.4	67.1		Absy *et al*. 1987
Jaú NP, 2°00' S, 62°30' W	7	47.0	71.0		Ferreira & Prance 1998b, Ferreira 1997
Manaus, 2°25' S, 59°44' W	3	193.0	205.1	3	de Oliviera & Mori 1999
Manaus-Itacoatiara, 3°08' S, 60°00' W	1	123.6	123.6		Prance 1990
Marabá, 5°45' S, 49°02' W	6	40.1	43.3	1	Salomão 1991
Maranhão, 3°10' S, 45°06' W	1	47.0	47.0	1	Balee 1986
Maré, 1°45' N, 61°15' W	1	100.2	100.2	1	Milliken 1998
Mucambo, 1°27' S, 48°27' W	1	53.0	53.0		Cain *et al.* 1956
Municipio Uná, 15°00' S, 41°00' W	1	85.5	85.5	1	Mori *et al*.1983
Rio Gelado, 6°00' S, 50°30' W	1	45.8	45.8	1	Silva *et al*. 1987
Rio Gurupi, 2°20' S, 46°30' W	1	67.3	67.3	1	Balee 1987
Rio Juruá, 4°40' S, 66°10' W	1	108.0	108.0	1	Silva *et al.* 1992
Rio Juruá, 4°47' S, 66°15' W	1	99.2	99.2	1	Silva *et al*. 1992
Rio Juruá, 4°50' S, 66°22' W	1	126.4	126.4	1	Silva *et al*. 1992
Rio Juruá, 4°57' S, 66°35' W	1	147.5	147.5	1	Silva *et al*. 1992
Rio Juruá, 7°38' S, 72°40' W	1	40.1	40.1	1	Campbell *et al*. 1992
Rio Tapajós, 2°31' S, 54°58' W	3	6.4	8.6	1	Ferreira & Prance 1998a
Rio Urucú, 5°00' S, 65°00' W	2	165.6	221.8	1	Amaral 1996, Peres 1994, Peres 1991 in Terborgh & Andresen 1998
Rio Xingú, 3°29' S, 51°40' W	4	53.0	75.8	1	Campbell *et al*. 1986
Rio Xingú, 4°45' S, 52°36' W	1	65.6	65.6		Balee & Campbell 1990

Country/ Site/ coordinates	**Np**	**a**	**a max**	**Nf**	**references**
Rondônia, 11°00' S, 61°57' W	1	82.5	82.5	1	Salomão & Lisboa 1988
Rondônia, 11°15' S, 62°50' W	2	39.8	50.2	1	Lisboa & Lisboa in Maciel & Lisboa 1989, Maciel & Lisboa 1989
Serra do Navio, 0°55' N, 52°01' W	2	36.1	36.9		Rodrigues 1963
Ubatuba, 23°27' S, 45°04' W	1	0.0	0.0	1	Silva & Filho 1982, in Terborgh & Andresen 1998
Vilheña, 12°15' S, 60°15' W	1	44.0	44.0		Santos in Salomão *et al.* 1988
Colombia					
Araracuara, 0°34' S, 72°08' W	5	76.9	131.7	5	Londoño Vega 1993, Urrego 1997
Araracuara, 1°00' S, 71°30' W	5	106.6	176.6	4	Duivenvoorden & Lips 1995
Bajo Calima, 3°55' N, 77°00' W	1	152.6	152.6		Faber-Langendoen & Gentry 1991
Carare, 6°35' N, 73°56' W	4	21.8	29.1		Vega 1968
El Amargal, 5°34' N, 77°31' W	1	62.1	62.1		Galeano *et al*. 1998
La Tagua, Solano, 0°12' N, 74°39' W	1	34.3	34.3	1	IGAC 1993
Costa Rica					
La Selva, 10°26' N, 84°00' W	3	39.8	44.5	1	Hartshorn 1983, Heany & Proctor 1990, Phillips *et al*. 1994
Ecuador					
Añangu, 0°32' S, 76°26' W	3	85.2	114.0	1	Balslev *et al*. 1987, 1998, Korning & Balslev 1994
Charco Vicente, 0°43' S, 78°53' W	1	48.5	48.5		Palacios *et al*. 1991 in Cerón & Montalvo 1997
Cuyabeno Reserve, 0°00' N, 76°10' W	1	211.0	211.0	1	Valencia *et al*.1994, 1998
Jatun Sacha, 1°04' S, 77°36' W	3	117.1	131.2		Neil *et al*. in Ceron & Montalvo 1997, Neil *et al*. in Valencia *et al.*1994
Rio Shiripuno, 1°01' S, 76°58' W	1	104.6	104.6	1	Ceron & Montalvo 1997
San Miguel Cayapás, 0°45' S, 78°56' W	1	39.2	39.2		Palacios *et al*. 1991 in Ceron & Montalvo 1997
French Guiana					
Haut Camopi, 2°43' N, 53°08' W	1	65.3	65.3	1	Sabatier & Prevost unpubl. data
Inini, 3°39' N, 53°49' W	2	85.0	86.2	1	Sabatier & Prevost unpubl. data
Nouragues, 4°05' N, 52°42' W	8	97.0	122.0	2	Sabatier & Prevost unpubl. data
Saül, 3°38' N, 53°12' W	1	155.5	155.5	1	Mori & Boom 1987
St Laurent, 5°30' N, 54°00' W	2	19.1	19.6		Gazel 1981
St. Élie, 5°18' N, 53°03' W	16	84.7	109.8	2	Sabatier & Prevost unpubl. data

Country/ Site/ coordinates	**Np**	**a**	**a max**	**Nf**	**references**
Guyana					
Asakata, 7°45' N, 59°05' W	1	6.7	6.7		van Andel, unpublished data
Barama, 7°44' N, 59°52' W	2	0.0	0.0	2	ECTF unpublished data
Iwokrama, 4°35' N, 58°43' W	4	19.9	23.5	3	Johnston & Gillman 1995
Kako, 5°44' N, 60°37' W	1	3.6	3.6		Ramdass *et al*. 1997
Kariako, 7°23' N, 59°43' W	1	7.1	7.1		van Andel, unpublished data
Kariako, 7°25' N, 59°44' W	1	33.8	33.8	1	van Andel, unpublished data
Kwakwani, 5°30' N, 58°00' W	2	23.4	29.3	1	Comiskey *et al*. 1994
Mabura Hill, 5°02' N, 58°48' W	1	18.7	18.7		Thomas, unpublished data
Mabura Hill, 5°13' N, 58°35' W	11	16.5	23.0	4	Ek & Zagt, unpublished data, Ek, unpublished data, Lilwah & ter Steege unpublished data, Thomas unpublished data, van Essen unpublished data.
Mabura Hill, 5°13' N, 58°43' W	1	11.9	11.9	1	Ek, unpublished data
Moraballi, 6°11' N, 58°33' W	6	22.4	28.9	5	Davis & Richards 1934 , Ramdass *et al*. 1997
Moruca, 7°36' N, 58°57' W	1	33.1	33.1	1	van Andel, unpublished data
Moruca, 7°41' N, 58°55' W	1	8.2	8.2		van Andel, unpublished data
St. Cuthberts, 6°22' N, 58°05' W	1	22.0	22.0		Ramdass *et al*. 1997
Mexico					
Los Tuxtlas, 18°35' N, 95°07' W	1	35.1	35.1		Bongers *et al*. 1988
Panama					
Barro Colorado Island, 9°09' N, 79°51' W	2	36.0	36.0	1	Condit *et al*. 1996
Peru					
Aguajal, 11°52' S, 71°21' W	1	47.9	47.9		Pitman *et al*. 1999
Barranco, 11°48' S, 71°28' W	1	109.7	109.7		Pitman *et al*. 1999
Barranco, 11°53' S, 71°23' W	1	74.2	74.2		Pitman *et al*. 1999
Cabeza de Mono, 10°20' S, 75°18' W	1	87.0	87.0	1	Gentry 1988a, Terborgh & Andresen 1998
Cuzco Amazonico, 12°35' S, 69°07' W	2	0.0	0.0	2	Nunez & Phillips in Terborgh & Andresen 1998
Jenaro Herrera, 4°54' S, 73°40' W	1	159.0	159.0	1	Spichiger 1996
Maizal, 11°48' S, 71°28' W	1	109.7	109.7		Pitman *et al*. 1999

Country/ Site/ coordinates	**Np**	**a**	**a max**	**Nf**	**references**
Manu, 11°45' S, 71°30' W	13	63.7	122.6	11	Dallmeijer *et al*. 1996 and in Terborgh & Andresen 1998, Gentry 1988a; Gentry & Terborgh 1990, Phillips *et al*. 1994, Terborgh & Andresen 1998, Pitman *et al*. 1999
Manu, 12°03' S, 71°10' W	1	40.8	40.8		Pitman *et al*. 1999.
Mishana, 3°47' S, 73°30' W	1	142.2	142.2	1	Gentry 1988a; Phillips *et al.* 1994; Gentry in Terborgh & Andresen 1998
Renacal, 11°52' S, 71°21' W	1	30.3	30.3		Pitman *et al*. 1999
Tambopata, 12°49' S, 69°43' W	8	62.9	87.3	2	Phillips *et al*. 1994, Stern 1998
Yanamomo, 3°16' S, 72°54' W	1	221.1	221.1	1	Gentry 1988a; Phillips *et al.* 1994; Gentry in Terborgh & Andresen 1998
Suriname					
Blanche Marie Falls, 4°45' N, 56°51' W	1	39.4	39.4	1	Maas 1971
Kamisa Falls, 5°06' N, 56°20' W	1	41.2	41.2	1	Maas 1971
Mapane, 5°26' N, 54°40' W	1	36.5	36.5		Schulz 1960
Paris Jacob Creek, 4°54' N, 56°57' W	2	43.4	46.9		Maas 1971
Snake Creek, 5°14' N, 56°48' W	1	54.6	54.6	1	Maas 1971
Tonka, 5°15' N, 55°42' W	1	48.8	48.8		Jonkers 1987
Winana Creek, 5°15' N, 57°04' W	2	31.3	35.5		Maas 1971
Venezuela					
Cerro Neblina, 0°50' N, 66°11' W	1	39.1	39.1		Gentry 1988a, Gentry & Terborgh 1990
El Buey, 8°14' N, 62°11' W	13	24.3	30.5	2	Castellanos unpubl. Data
Q. Delgadito, 8°49' N, 69°30' W	1	11.5	11.5		Stergios *et al*. 1998
Q. Iguez, 8°51' N, 69°12' W	1	13.4	13.4		Stergios *et al*. 1998
Rio Caura, 4°09' N, 63°44' W	1	18.2	18.2		Marin & Chaviel 1996
Rio Caura, 4°58' N, 64°47' W	1	30.0	30.0		Marin & Chaviel 1996
Rio Caura, 5°30' N, 64°00' W	1	25.3	25.3		Marin & Chaviel 1996
Rio Caura, 6°18' N, 64°29' W	1	20.7	20.7		Marin & Chaviel 1996
Rio Caura, 6°21' N, 64°59' W	5	31.7	35.7	2	Castellanos 1998, Castellanos unpubl. Data
Rio Portuguesa, 9°04' N, 69°37' W	1	11.5	11.5		Stergios *et al*. 1998
Saimadodyi, 9°37' N, 72°54' W	2	31.2	31.4	1	Lizarralde 1997
San Carlos, 1°56' N, 67°03' W	1	23.9	23.9		Uhl & Murphy 1981
San Pedro, 6°30' N, 62°23' W	1	8.6	8.6	1	Finol Urdaneta, undated

Table 4.1 Average densities (# trees/100 ha) of the most common genera in large-scale forest inventories in the Guiana Shield area. Areas and genera are ordered to enhance similarities and differences among them. For locations see Figure 4.1. Sources are given in text.

Genus (trees/100ha)	Essequibo-Demerara	Demerara-Mahaicony	Berbice-Courantyne	North West District	Cuyuni-Supenaam	Cuyuni-Mazaruni	Mazaruni-Essequibo	Pakaraima highland area	South Guyana: dry	South Guayna: wet	Kabalebo	Fallawatra	Pokigron	Nassau	Coastal French Guiana	Imataca	Roraima: submontane	Roraima: lowland	Roraima: dry	Tumucumaque: lowland	Tumucumaque: dry	Tumucumaque: submontane	Roraima: montane
Diospyros/Lissocarpa	12	27		11	7	11	15	16															
Dicymbe								651															
Pentaclethra	30	3		9	12	6	22	59								17			5				
Emmotum	22	34	20		4	2	3																
Chlorocardium	711	18	139	1	464	380	465	59	4	4													
Campsiandra	8	1	1																				
Clathrotropis (in Suriname with *Alexa, Ormosia*)	53			2	4	14	4	26			25	24	28	12		1							
Carapa	63	1	50	86	33	133	31	118	4	20	64	107	60	57	45	128				41			
Symphonia	8	4	11	43	6	9	15	13	4	8	30	14	21	51	101	6		3					
Eperua	774	267	395	25	379	545	909	316	54	448	593	590	711	539	893								
Dimorphandra	120	194	20				46	16	8	4	43	130			1					3			
Chaetocarpus	18	9	14	17	12	10	14	10	31	36	79	66	53	83		161							
Talisia	28	49	35	7	18	12	84	6			21	21	8	2		1							
Mora	719	67	692	553	612	593	593	303	245		114	294	67			1	10						
Catostemma	120	46	66	177	126	121	134	104	93	56	18	26	30	2	9	91							
Alexa	2		1	35	37	67	21	84		16					19	52	30	7		113			
Aldina						2	2	35										10					
Dipteryx	2	1	1				2	6		20	26	53	10	16	10	4							

Genus (trees/100ha)	ED	DM	BC	NW	CS	CM	ME	PM	SD	SW	Ka	Fa	Po	Na	FG	Im	Rs	Rl	Rd	Ts	Ts	Ts	Rm
Vouacapoua	134					3	8	4	16	20	62		141	107	69					69			
Swartzia	274	197	167	35	93	272	142	87	62	68	105	160	73	67	38		50	28	10	16		333	14
Sterculia	9	3	10	45	51	38	18	12	19	16	63	62	45	65	61	87		28		47	20	17	
Macrolobium (in Suriname with Crudia)	4	3	9	18	1	1	1	15		84	25	37	34	2	11							183	
Eschweilera	210	42	98	295	154	392	112	309	54	132	181	120	158	134	474	385		183		166	60	117	443
Laetia	6	1	9	9	4	6	3	6	12	8	18	18	22	8		9	10	35	5	31			
Ormosia	58	33	7	1	38	25	52	37	12	40	14	14	9	8	45	15	50	62	5	19	40		200
Peltogyne	21	2	10	6	21	9	19	8	31	12	16	12	10	18	5	50		55	815	9	40		
Virola	9	3	8	11	3	7	1	3	12	28	85	82	99	83	57	3	30	55	45	56			
Tabebuia	17	5	14	14	4	7	12	13	8	12	26	36	37	10	12	15	10	7	15	144	20	17	
Simarouba	5	2	5	6	5	4	4	5	23	16	27	23	44	16	27	24		10	20	22	20		29
Pterocarpus			5	27	27	32	15	33	12	132	58	45	67	49		9	10		5	19	40		
Pithecellobium	52	29	30	22	26	21	15	3	23	32	58	79	48	39	49	64	90	21	25	65	20	33	14
Parinari/Excellodendron	43	44	61	31	17	15	10	5	62	108	122	96	134	138		41	10	7	45	75	80	50	29
Ocotea	22	15	25	16	27	19	19	27	16	156	61	60	44	49	136	24	30	10	15	12	20	17	57
Manilkara	37	30	24	34	28	4	33	21	97	36	105	134	41	199	52	57		121	40	69	140	100	14
Licania	87	39	94	196	69	147	99	89	62	304	295	373	293	322	17	328	50	66	60	328	180	83	29
Lecythis	108	22	18	19	37	82	152	61	47	72	126	133	150	144		28	10	7	10	22	80	17	14
Jacaranda	9	4	5	7	5	6	6	18		8	22	25	15	30	12	3	40	41	20	13		17	114
Inga	23	9	21	46	39	33	20	49	66	56	100	106	102	89	23	136	60	107	25	100	20	117	271
Goupia	45	99	94	51	21	23	10	19	93	188	101	59	156	97	100	6	40	59	70	125	20	17	
Diplotropis	6	7	6	4	3	2	6	7	4	12	16	2	20	22	15	46	40	10	40	44			
Caryocar	22	2	4	3	2	1	7	12		20	40	28	36	41	42	6	20	10	20	47	20		57
Apeiba (may include some Annona)	12	4	2	13	13	12	8	13	4	16	40	37	49	26	15	31	20	31	45	6	60	17	14
Trattinickia	2	7	14	4	3	4	2	8	12	16	19	23	26	16			50	31	15	28		17	14

Genus (trees/100ha)	ED	DM	BC	NW	CS	CM	ME	PM	SD	SW	Ka	Fa	Po	Na	FG	Im	Rs	Rl	Rd	Ts	Ts	Ts	Rm
Terminalia	18	48	27	42	32	12	21	31	27	40	19	17	23	24	48	92	40	28	45	25	160		57
Tapirira	5	1	33	6	6	4	14	23	4		8	10	3	2	4	5	10	4		3	20	17	14
Schefflera	3	2	3	7	9	4	9	2	8	4	4	6	1	4		8	50	66	10	16	20		43
Pouteria	111	31	44	43	58	60	118	89	140	196	99	87	23	79	58	221	220	214	180	287	120	200	400
Chrysophyllum	13	3	9	32	47	8	6	45	12	44	34	10	2	36	135	8	20	28	20	35		150	57
Aspidosperma	98	101	229	69	77	24	78	17	23	8	17	11	9	20	13	298	20	34	35	28	40	200	57
Licaria	1		2	2	5	3	8	6	4	20	8	11	6	4			90	55	50	116	40	17	286
Elizabetha (may include some *Pithecellobium*)								24	43	28							70	52	5				71
Dinizia			3							24									80	69			
Vitex	3		9	5	3	5	1	7	16							14	40	14	15	6	60	50	
Hymenaea	7	2	6	2	3	2	1		8	4	5	2			12	4	40	48	45	38	20	50	
Sclerolobium	7	6	10	1	3	2	4	6	31	68	69	34	23	77	48	134	90	7	15	19			43
Saccoglottis	4	18	9	4	2	1	3				15	8	22	16	24	6		41	20	78	20	33	14
Protium	13		3	60	36	36	17	23		4	25	16	20	14		217	90	86	100	109			86
Couratari	4	2	7	11	8	8	8	19	101	24	138	89	114	136	47	39	30	69	50	22	60	67	
Cecropia	2	4			1	2	2	2		12	10	11	20			12	30	7		10			14
Bombax			3	1	2	3	2	1	16	8	22	10	28	30				7	15	6	20	17	
Pradosia	11		11	2			11	3	31	8	43	95	23	12		16	20	72	105	3		50	
Micropholis	1	7	4	3	1	1	2	9	12	12	65	52	77	43	96	7	30	55	5	103		17	186
Anacardium		1	4		1	2			31	12	8	12	6	12	8			14	20	13	60		
Vochysia	1	18	3					2	31	16	35	24	36	30	17	15		145	165	75	80	33	14
Tetragastris	1	1	5	5	3	3	1	7	31	32	191	253	196	176	37	68	40	79	20	41	60	67	43
Spondias			4	7		5			19	8	7	7	8	14		10	30	86	35	3			14
Parkia	2	6	12					4	19	104	43	43	52	34	34	30	10	7	10	35	20	17	14
Brosimum	1	3	2				2	2	39	56	17	13	14	14	12	2	30	28	15	28	20		14

Genus (trees/100ha)	ED	DM	BC	NW	CS	CM	ME	PM	SD	SW	Ka	Fa	Po	Na	FG	Im	Rs	Rl	Rd	Ts	Ts	Ts	Rm
Bagassa	1		1		2				27	4	6	5	5	6	2		20	10	10			17	
Minquartia								2	8	20	4	1	2	4				7	15	97	20		
Geissospermum	3	5	9					1	19	164	13	20	9	12			90	45	50	56	20	17	
Trichilia	1							2	51	36	6	8	6	6		3							
Lueheopsis	8						11	4		4	26	14	39	30									
Andira		2						2	4	12	38	37	18	34	49	5			5				
Pseudopiptadenia								7	12	68	45	47	61	45	108	41	40	51	50	156			
Guarea				1			1	1		4	18	24	18	2			80	14		16	20		
Sloanea							1	9	4		11		3	8		28	50	38	10	3	40		100
Pourouma	1	1	2					2	4	28	24	31	17	20			30	10	20	50	40	17	14
Nectandra		9								4	8				6	1	10	21		41			329
Bertholletia										12	1	2			10			10	20	3	80		
Qualea/Ruizterania											71	29	111	12	115	6		38	105	31	80	33	143
Croton											3		5	4		24	230	72	5	59			29
Caraipa											18	18	15	8	3			55		3		50	57
Erisma											14	5	20	10	12	154		3	5		20		
Martiodendron											20	15	29	26			10	35	10				
Copaifera										8	49		10	174		1	10	7		19		50	
Dicorynia											181		298	298	399								
Cynometra											2	4	1					3		13	540	317	
Labatia																	20	3		59	20		88
Dialium																	40	48	20	47	440		
Clarisia																17	40	17	45	16	20		
Cariniana																		35	25	100	40	50	171
Ragala																				3			229

4 A PRELIMINARY ANALYSIS OF LARGE-SCALE FOREST INVENTORY DATA OF THE GUIANA SHIELD

Hans ter Steege, Gerold Zondervan

Introduction

Large scale forest inventories have been carried out in all countries bordering Guyana (Fanshawe 1961, de Milde and de Groot 1970a-f, (Guyana); de Milde and Inglis 1974, Vink 1983 (Suriname); Rollet (1969a, Venezuela); Radambrasil (Leite *et al.* 1974, Veloso *et al.* 1975, Doi *et al.* 1975, (Brasil), see Figure 4.1 for locations) and allow us to study in more detail the composition of Guyana's forest in a regional perspective. There is very little available information on French Guiana, even though some large-scale inventories have been carried out (O.N.F. pers. comm.) Reports or data of the latter were not readily available. For the description of the forests on the southern peneplain we rely mainly on the forest inventories of Guyana and areas bordering the Guianas in Brazil.

The ten most abundant families (based on the average abundance over 24 large-scale forest inventories) are: Caesalpiniaceae (average 24.0%, range 4.9% - 45.3%), Lecythidaceae (9.9, 3.7 - 18.2), Papilionaceae (8.2, 3.5 - 16.5), Sapotaceae (7.9, 2.2 - 14.8), Chrysobalanaceae (7.3, 3.0 - 12.1), Lauraceae (5.3, 0.9 - 17.8), Mimosaceae

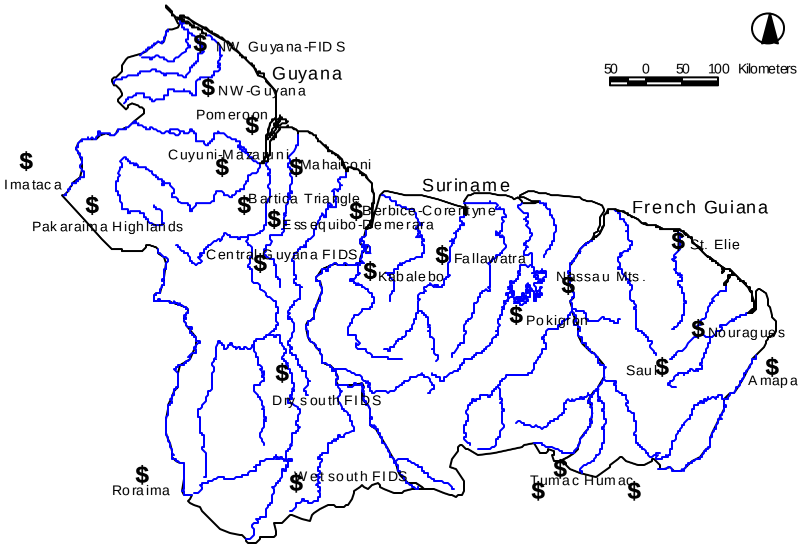


Figure 4.1 Location of large-scale forest inventories used in this Chapter. See text for sources.

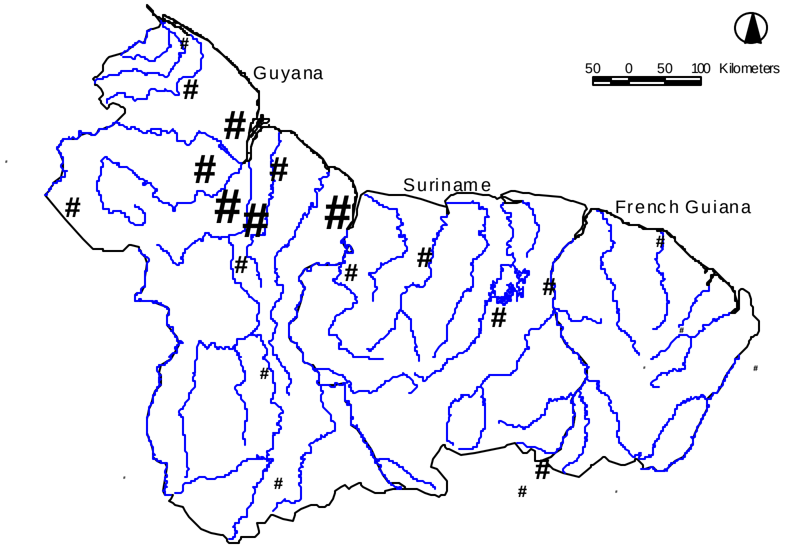


Figure 4.2 Regional dominance of Caesalpiniaceae expressed as the percentage of individuals in large-scale inventories in the Guiana Shield. The dot size indicates dominance and ranges from 9% (smallest) to 45% (largest).

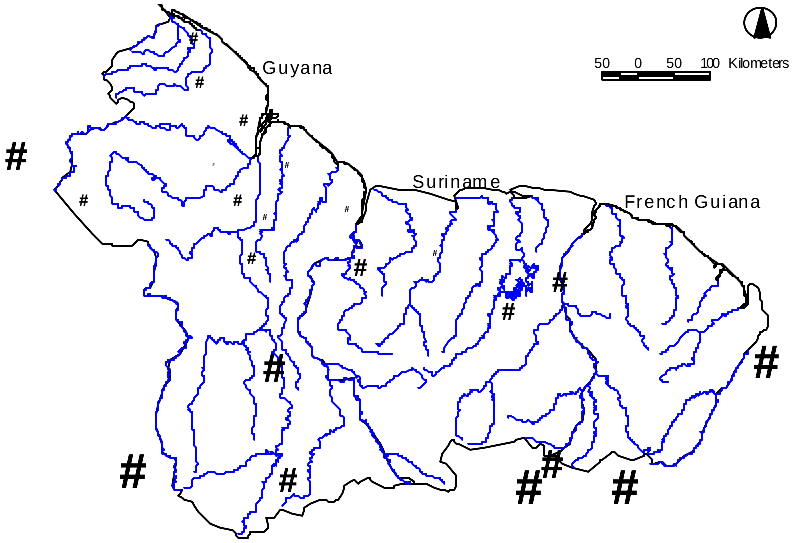


Figure 4.3 Regional abundance of Sapotaceae expressed as the percentage of individuals in large-scale inventories in the Guiana Shield. The dot size indicates abundance and ranges from 2% (smallest) to 15% (largest).

(5.1, 1.5 - 10.5), Apocynaceae (3.2, 0.7 - 9.0), Burseraceae (3.1, 0.4 - 7.5) and Bombacaceae (2.6, 0.3 - 7.9). These 10 families, out of a total of 73 found, account for 76.5% of all individuals. These 10 families are also among the most species-rich tree families in French Guiana (Sabatier and Prévost 1990). Other species-rich tree families that are not among the top ten abundant ones in the canopy of the forest are Annonaceae and Myrtaceae (mainly small trees) and Moraceae (low densities).

Caesalpiniaceae is the single most dominant tree family in the Guianas, with over 30% of all forest tree individuals over 40 cm in most of north and central Guyana (Figure 4.2). Caesalpiniaceae is the number one family in each of the large inventory areas in Guyana, Suriname and sub-coastal French Guiana. The high abundance of this tree family is caused by a large number of individuals of species in the genera *Eperua* in all three Guianas, *Dicymbe* in Guyana, *Mora* in Guyana and Suriname and *Dicorynia* and *Vouacapoua* in Suriname and French Guiana. Arguably, *Eperua falcata* is the most abundant tree species in the Guianas (Table 4.1).

Because Caesalpiniaceae can become extremely dominant locally, the abundance of most other families is negatively correlated with the abundance of Caesalpiniaceae (data not shown), except Lauraceae (*Chlorocardium rodiei*) and Bombacaceae (*Catostemma* spp.), which are also common to (co-) dominant in central and NW-Guyana (Chapters 3, 5). Families most negatively correlated with Caesalpiniaceae are Sapotaceae (Figure 4.3) and Mimosaceae. Because of the strong dominance of Caesalpiniaceae, their abundance greatly influences family diversity (Figure 4.4, r = 0.95, p < 0.001), with a minimum of family diversity (evenness) in central Guyana. The number of families present in large-scale inventories, however, is rather constant despite great changes in diversity and is thus not a good measure of diversity.

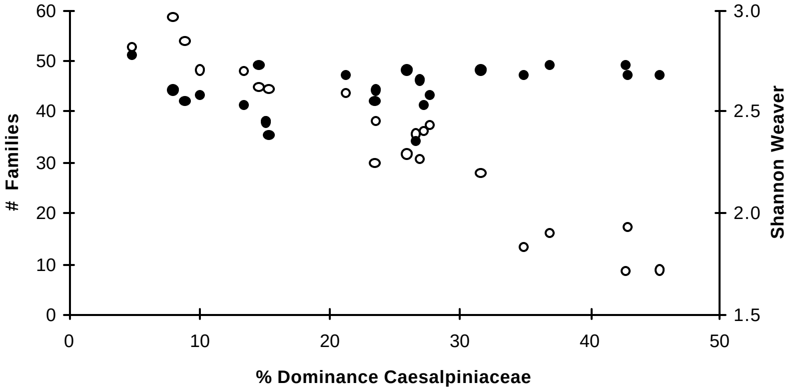


Figure 4.4 Number of families present (•) in large-scale forest inventories and the Shannon Weaver Index for family diversity (o) as a function of the dominance of Caesalpiniaceae in large-scale forest inventories in the Guiana Shield (see Figure 4.1 for locations).

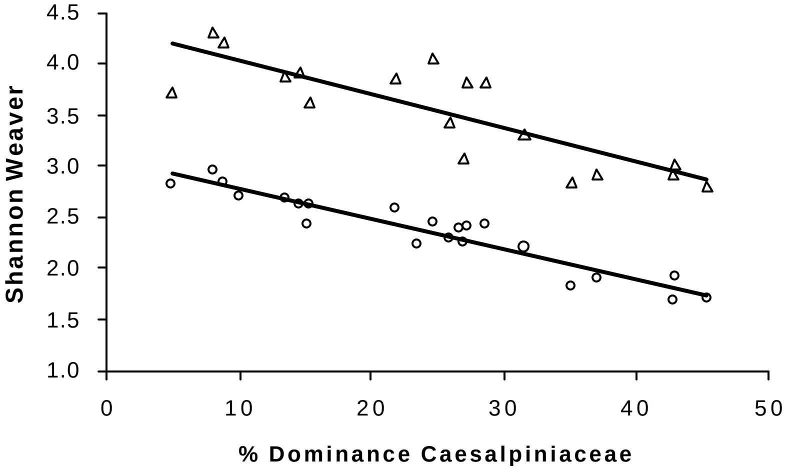


Figure 4.5 Shannon Weaver index of genera (Δ) and families (o) as a function of dominance of Caesalpiniaceae in large-scale forest inventories in the Guiana Shield (see Figure 4.1 for locations).

Dominance of Caesalpiniaceae also strongly affects the diversity of tree genera found in large-scale forest inventories (Figure 4.5, r = 0.84, $p < 0.001$). In fact, even the diversity of Caesalpiniaceae itself is (almost significantly) negatively correlated with its own dominance (r = 0.37, p = 0.08, data not shown). The main reason for this is that just four genera cause the large dominance of Caesalpiniaceae in Suriname and Guyana: *Eperua, Mora, Dicymbe* in Guyana and *Dicorynia* in Suriname.

Forests of the Guiana Shield

Table 4.1 presents the average composition of large forest areas in the Guiana Shield. A number of genera are clearly more abundant in Guyana than the surrounding countries and these include *Diospyros, Lissocarpa, Pentaclethra, Chlorocardium* and *Emmotum*. A few common genera appear to be characteristic for the forest of the three Guianas – they are much more common than in adjacent Brazil and Venezuela. These genera include *Carapa, Symphonia* (coastal), *Eperua, Mora, Talisia* and *Catostemma*. The southern parts of Guyana and Suriname have a higher proportion of species that may be considered long-lived pioneers (small seeds, light wood, wind or bird dispersal, see also Chapters 5 and 7). Such genera include: *Couratari, Sclerolobium, Jacaranda, Goupia, Cecropia* and *Parkia.* Genera such as *Lecythis, Eschweilera, Licania, Pithecellobium* and *Parinari* are abundant in all areas.

We suggest a preliminary division of the major forest regions in the Guianas to be as follows (Figure 4.6):

1. Forests in the coastal plain (Venezuela-Guyana-Suriname-French Guiana)
2. Forests in the North West District of Guyana and lowland Venezuelan Guyana
3. Forests on White Sands Formation (Guyana-Suriname-French Guiana)
4. Forests in the Pakaraima-Central Guayana Upland region (Guyana-Venezuela-Brazil)
5. Forests on the southern peneplain (Guyana-Suriname-French Guiana-Brazil)

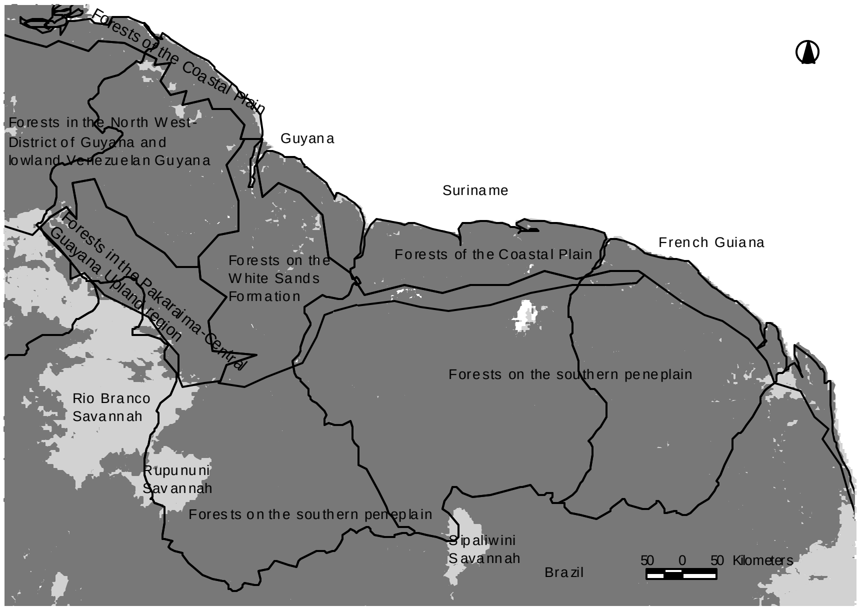


Figure 4.6 Forest regions of the Guiana Shield area as used in the text. Forested area is indicated by dark grey, non-forest areas by light grey, based on NOAA-AVHRR satellite images of September 1992 (http://edcdaac.usgs.gov/1KM/comp10d.html). Further information from Gross-Braun *et al.* (1965), Soterlac (http://www.isric.nl/Products.htm), Gibbs and Barron 1993, de Granville (1988).

These forest regions will be described in detail below.

1 Forests in the coastal plain (Venezuela-Guyana-Suriname-French Guiana)

The coastal zone of the Guianas forms part of the uninterrupted low and wet area that ranges from the Orinoco delta (Delta Amacuro) to the Amazon mouth. The area is for a large part covered with poorly drained (gleyic) soft clay and silt soils of alluvial and marine origin (Gross-Braun *et al.* 1965, de Milde and de Groot 1970c,f). Old beaches (ridges, ritsen in Suriname) occur parallel to the coast. Large areas with peat soils occur, especially in the north west region of Guyana. In eastern Guyana

and Suriname the presence of an old coastal plain, the Coropina formation of silty clays and sands is noteworthy (ibid.)

The distribution of forest types in the coastal plain is determined to a large extent by the proximity to the coast or riverbanks. Closer to the sea the sediments are more clayey and flooding duration often increases. Obviously, also salinity, which increases towards the sea, affects the zonation of vegetation types in the coastal area. Below we discuss this zonation from the coastal shore inwards.

There are no typical coastal genera among large trees (Table 4.1). Genera that have dominant species in this area such as *Virola, Iryanthera, Tabebuia, Pterocarpus* and *Macrolobium* also have (often vicariant) species common in the forest on the basement complex, except for the monotypic *Symphonia*.

Mangrove forests

Mangrove forests occur in a narrow belt of a few kilometres wide along the coast and along the banks of the lower reaches of rivers. The mangrove forest along the coast consists mainly of *Avicennia germinans* (Lindeman and Molenaar 1959, de Granville 1986), with occasional undergrowth of the salt fern, *Acrostichum aureum*. With increasing age of the stands, regeneration of *Avicennia* decreases and a low and open mangrove swamp is formed (Lindeman and Molenaar 1959, de Granville 1986). *Rhizophora* occupies the more exposed, soft silts in river mouths and shores. Where the water is distinctively brackish a third mangrove species can be found, *Laguncularia racemosa* (Lindeman and Molenaar 1959). Further inland mangrove species mix with *Euterpe oleracea* palms and such trees as *Pterocarpus officinalis* (Lindeman and Molenaar 1959, Huber 1995a, van Andel 2000) and is still further inland replaced by a mixture of *Pterocarpus officinalis* and *Pachira aquatica* (Fanshawe 1952, Lindeman and Molenaar 1959). Extensive (some 90,000 ha) and well preserved mangrove stands may still be present in Guyana's North West District and Pomeroon area (De Milde and de Groot 1970c,f, Welch 1975). Large tracts of mangrove forest are found also in the Delta Amacuro (4,200,000 ha, Pannier and Fraino Pannier 1989, cited in Huber 1995a) and towards the Amazon mouth in Amapá (Leite *et al.* 1974). *Avicennia* is used extensively as firewood and for tanning in populated areas and this practice has led to the decline of these forests in (eastern) Guyana and in Venezuela (Huber 1995a).

Permanently flooded palm marsh forest (coastal swamp forest)

In permanently flooded, flat plains in the present coastal zone a low (10-20 m tall) swamp forest is found. The soils are often poorly drained peat soils over coastal clay. The most extensive stands are found in the North West District of Guyana and the Orinoco delta in Venezuela (de Milde and de Groot 1970f, Huber 1995a). Characteristic species are *Symphonia globulifera, Tabebuia insignis/fluviatilis, Pterocarpus officinalis* and *Euterpe oleracea*. Species that can become locally dominant in this forest type in Guyana are *Pentaclethra macroloba, Vatairea guianensis, Pterocarpus officinalis* and *Virola surinamensis* (Welch 1975). *Manicaria saccifera* is commonly found as a narrow belt along rivers in Delta Amacuro, Guyana and western Suriname. *Iryanthera macrophylla* and *Tabebuia insignis* form extensive stands behind the *Manicaria* or *Mora excelsa* stands

(Fanshawe 1952). *Tabebuia, Virola* and *Symphonia* have been harvested to some extent in the Northwest District of Guyana (Welch 1975). Large-scale extraction of *Euterpe oleracea* is currently taking place (van Andel 2000). *Manicaria* is also in high demand as its entire leaves make very good roof thatch.

Seasonally flooded palm marsh and swamp forest

More inland the duration of flooding is less pronounced and forest composition is slightly different. Common species on peat soils are *Symphonia globulifera, Virola surinamensis, Iryanthera* spp., *Pterocarpus officinalis, Mora excelsa, Pachira aquatica, Manicaria saccifera* and *Euterpe oleracea* (Huber 1995a). Forest dominated by *Triplaris weigeltiana* is commonly found in Suriname (Lindeman and Molenaar 1959). In the *Triplaris* stands in Suriname species of the *Symphonia*-dominated forest are practically absent (Lindeman and Molenaar 1959). In the east of Guyana much land along the rivers was cultivated by the Dutch. Such old plantations are now also covered with *Triplaris weigeltiana* and *Cordia tetrandra* (Fanshawe 1952). These species are also commonly found on other disturbed or newly sedimented parts of the lower reaches of the rivers (Fanshawe 1952, ter Steege pers. obs.). Repetitive burning has led to large-scale herbaceous and grassy swamps, interspersed with *Mauritia* palms.

In Guyana *Mora excelsa* forms extensive stands along the rivers on alluvial silt up to the confluence of Rupununi and Rewa rivers (Chapter 5). *Mora* forest is low in height close to the coast but grows to magnificent stature more inland, with emergent individuals of over 60 m. Canopy associates of the *Mora* forest are *Carapa guianensis, Pterocarpus officinalis, Macrolobium bifolium, Eschweilera wachenheimii, E. sagotiana, Clathrotropis brachypetala, C. macrostachya, Eperua falcata, E. rubiginosa, Catostemma commune, C. fragrans, Pentaclethra macroloba, Vatairea guianensis, Symphonia globulifera, Terminalia dichotoma* and *Tabebuia insignis* (Fanshawe 1952). Several of the accompanying species are dominant in *Mora* forest in certain areas.

Forests on the old coastal plain: the ‘Coropina formation’

There is little specific information on the forests of the old coastal plain. *Nectandra rubra* is a species considered typical for this area in Guyana (I. Welch, pers. comm.). In Suriname *Parinari campestris* is common on old ridges (Lindeman 1953, Lindeman and Molenaar 1959, Theunissen 1980). Other common trees are *Tetragastris* spp., *Goupia glabra, Pouteria* spp., *Eschweilera* spp. and *Antonia ovata.* Marsh forest on silty clay in Suriname is not very different from Marsh forest of the young coastal plain with species such as: *Euterpe oleracea, Eschweilera* spp., *Parinari campestris, Carapa guianensis, Copaifera guianensis, Qualea caerulea* and *Pithecellobium jupunba* (Lindeman and Molenaar 1959, Theunissen 1980)

2 Forests in the Northwest District of Guyana and lowland Venezuelan Guayana

The upland forests in the north west of Guyana (and bordering Venezuela), are found both on soils developed on the crystalline shield, such as Granites and

Greenstones (Gibbs and Baron 1993) and on pockets of Plio-Pleistocene sediments (see Gross-Braun *et al*. 1965).

Rainforests of the Northwest District

The dry land forest of the Northwest District of Guyana and eastern Venezuela are characterised by a high abundance of *Eschweilera sagotiana, Alexa imperatricis, Catostemma commune, Licania* spp. and *Protium decandrum*. These species are found abundantly in almost every dry land forest type in this region (de Milde and de Groot 1970f, Huber 1995a, Barama Company Ltd. unpublished data). Most of these species belong to genera of the 'Lowland Guianas Dominants' of Table 4.1. Upland forests dominated by *Alexa, Eschweilera, Licania* and *Catostemma* continue far into Venezuela (Huber 1995a).

Poor mono-dominant stands of *M. gonggrijpii* are found on the (probably) more clayey soils between the Cuyuni and Mazaruni. *M. gonggrijpii* dominated stands are also found in the eastern parts of Venezuelan Guyana (Rollet 1969b, Finol Urdaneta undated).

Extraction of plywood species (mainly *Catostemma, Alexa* and *Mouriri*) has risen quite substantially over the last years in the area.

3 Forests on the White Sands Formation (Guyana-Suriname-French Guiana)

Extensive sediments have been deposited in the late Tertiary-Pleistocene in the Guianas. These sediments form the so-called White Sands Formation, in Guyana known as 'Berbice formation'. The formation is found from the Cuyuni-Waini waterdivide in Guyana to western French Guiana (Figure 4.6). It extends furthest inland in Guyana (Berbice-Corantyne waterdivide) and is over 2000 metres thick in the coastal area near the mouth of the Berbice river (Gibbs and Barron 1993). The formation gradually becomes less wide in Suriname and occupies only a small, narrow portion in coastal western French Guiana (ibid.). Soils in the Berbice formation consist of pure white sands to loamy sands. Dolerite intrusions (Dykes) are common in Guyana and are usually covered with lateritic soils. In creek valleys peat is commonly formed.

The forests are often dominated by a few or only one species (Davis and Richards 1934, Fanshawe 1952, ter Steege *et al.* 1993) and consequently have a low α-diversity (ter Steege 1998a, Chapters 5, 7, 8). The main forests in the region were classified as belonging to the *Eschweilera-Licania* association, which occurs on the brown sands and the *Eperua-Eperua* association on the white sands (Fanshawe 1952).

Genera typical of the Berbice formation are *Campsiandra, Emmotum, Dimorphandra, Chlorocardium, Talisia* and *Diospyros/Lissocarpa*, as are the typical lowland Guianas dominants (Table 4.1). There are gradual shifts in species composition from west to east (Table 4.1) but these also correspond with increased area of soils formed on the basement complex, included in the inventories in Suriname. The best examples of forests on the Berbice formation are found in central Guyana, in Table 4.1 exemplified by the Mazaruni-Essequibo, Essequibo-Demerara and Demerara-Mahaicony waterdivides. Palms are rare in the forests on the Berbice formation (Chapter 3). Most of the understorey palms belong to the genus *Bactris*. In swampy areas *Jessenia* and *Mauritia* may be dominant.

Rain forests on Pleistocene brown sands in central Guyana

In Guyana forests on the brown sands of the Berbice formation are almost invariably characterised by species of *Eschweilera* and *Licania*. Species, which may be locally dominant are *Eschweilera sagotiana, E. decolorans, E. confertiflora, Licania alba, L. majuscula, L. laxiflora, Chlorocardium rodiei, Mora gonggrijpii, Alexa imperatricis, Swartzia schomburgkii, S. leiocalycina, Catostemma commune, Eperua falcata, Pouteria guianensis, P. cladantha, Aspidosperma excelsum* and *Pentaclethra macroloba* (Fanshawe 1952). Mono-dominance is common in forests on brown sands in central Guyana and tends to get less in an eastward direction (see above). Mixed forests on brown sands have traditionally been the main targets for timber extraction in Guyana, with main emphasis on *Chlorocardium rodiei.*

Rain forests on Pleistocene brown sands in eastern Guyana, Suriname and French Guiana

Towards the east in Guyana and across the border in Suriname the species mix changes slightly and the more common species are *Goupia glabra, Swartzia leiocalycina, Aspidosperma excelsum, Manilkara bidentata, Terminalia amazonica, Parinari campestris, Vochysia surinamensis, Emmotum fagifolium, Humiria balsamifera, Catostemma fragrans, Hymenaea courbaril, Licania densiflora* and *Eperua falcata* (Fanshawe 1952, Maas 1971). In Guyana, this forest on light brown sands extends south towards the Kanuku mountains, where it grades into semi-evergreen forest of the Rupununi district (see below). Species common in these forests in Suriname are *Peltogyne* spp., *Loxopterygium sagotii, Platonia insignis, Vochysia* spp., *Protium* spp., *Aspidosperma marcgravianum* and *Andira inermis* (Lindeman and Molenaar 1959). In transition to forests on the basement complex, e.g in the Coesewijne and Wayombo areas, *Dicorynia guianensis, Nectandra rubra, Goupia glabra, Eperua falcata* and *Chaetocarpus schomburgkianus* are commonly found (Schulz 1960). Due to the occurrence of high value timber species, such as *Dicorynia, Nectandra* and *Goupia*, this area has been heavily exploited in Suriname. The Pleistocene sediments become a very narrow band in French Guiana. Gazel (1981) reports on the composition of a few plots near St. Laurent. Common species here are: *Eschweilera odora, Licania* spp., *Eperua falcata, Dicorynia guianensis, Virola melinonii, Iryanthera sagotiana* and *Goupia glabra*. As in the transition forest in Suriname species common on the basement complex (*Dicorynia, Virola, Iryanthera*) are more abundantly present here than in central Guyana.

Dry evergreen forest on white sands

Dry evergreen forest (Wallaba forest in Guyana, Savannah forest in Suriname) on bleached white sands (albic Arenosols) occurs from the Pakaraima escarpment (see below), through central Guyana and northern Suriname into a small narrow portion of French Guiana. The distribution of this forest type follows the Berbice-Zanderij formation very closely. The forest type can also be found on white sands with impeded drainage (gleyic Arenosols).

On the Pleistocene white sands *Eperua falcata* and *E. grandiflora* are strongly dominant and may form, alone or together, more than 60% of the canopy individuals (Fanshawe 1952). Common other species in the canopy layer are *Catostemma fragrans, C. altsonii, Licania buxifolia, Talisia squarrosa, Ormosia coutinhoi, Eschweilera corrugata, Aspidosperma excelsum, Terminalia amazonia, Chamaecrista adiantifolia, Chamaecrista apocouita, Swartzia* spp., *Dicymbe altsonii* (west Guyana only), *D. corymbosa* (ibid.), *Manilkara bidentata* (Pomeroon-Waini waterdivide) and *Pouteria* (Fanshawe 1952).

Forest dominated by *Dimorphandra conjugata* (Dakama forest) is common on the higher parts of waterdivides from central Guyana to western Suriname. This forest type is characterised by very high standing litter crop (up to 800 ton/ha, Cooper 1982) and is very fire prone. Other species, characteristic for Dakama forests, are *Eperua falcata, Talisia squarrosa, Emmotum fagifolium* and *Swartzia bannia* (Fanshawe 1952, Lindeman and Molenaar 1959). *Humiria balsamifera* (Muri) co-dominates the degraded Dakama forest (Dakama-Muri scrub) with *Dimorphandra*. Other common species in this scrub are *Swartzia bannia, Clusia fockeana, Licania incana, Bombax flaviflorum, Ocotea schomburgkiana, Trattinickia burserifolia, Ternstroemia punctata* and *Byrsonima crassifolia* (Lindeman and Molenaar 1959, Cooper 1982). In areas where fires are very regular, e.g. along the road from Soesdyke to Linden in Guyana, Dakama forest degrades into Muri-scrub and finally into unproductive grassland (pers. obs.).

Creek forest of the white sands formation

The White Sands Area has a gently rolling aspect with a drainage pattern of many small creeks. The water table in the heads of such creeks is perpetually high and often a swamp forest is found on a layer of peat soil (pegasse). Dominant species are *Jessenia bataua, Mauritia flexuosa, Tabebuia insignis, Clusia* spp., *Symphonia, Iryanthera, Couratari, Eperua falcata* and *Diospyros ierensis* (Fanshawe 1952, ter Steege *et al.* 1993, Chapter 5, 8). The forest is very open and a dense layer of herbs is found. This layer is often dominated by *Rapatea paludosa*. In the lower reaches of creeks a variety of soils is found ranging from redistributed sands to clays. Common tree species in these creek forests are *Mora excelsa, Eperua rubiginosa, E. falcata, Pterocarpus officinalis, Carapa* spp., *Inga* spp. and *Pentaclethra macroloba* in central Guyana (Chapter 8).

Rain forest and evergreen forest on laterite ridges

Throughout the Berbice formation Dolerite dykes penetrate through the sediments (Daniel and Hons 1984). These dykes, varying in heights between 100 to 400 m, are covered with lateritic soils of rocky, gravelly to clayey constitution (van Kekem *et al.* 1996). There is little quantitative information available on the forest composition on these soils (but see Chapters 5, 8). Common trees are *Eschweilera* spp., *Licania* spp., *Swartzia* spp., *Mora gonggrijpii* (Guyana), *Chlorocardium rodiei* (Guyana). On lateritic soils in central Guyana a local endemic, *Vouacapoua macropetala*, forms extensive stands with *Eschweilera sagotiana, Licania laxiflora, Sterculia rugosa, Poecilanthe hostmanii* and *Pentaclethra macroloba* (Chapter 8). On lateritic soils in Suriname its vicariant, *V. americana*, is often dominant (Schulz 1960).

On the rocky phase of laterite, which has low water retention capacity and consequently is characterised by periods of water shortage a low shrubby forest is found. Myrtaceae (*Eugenia* spp., *Calycolpes, Marlierea*) and Sapotaceae (*Ecclinusa, Manilkara*) dominate here (e.g. Chapter 8).

Because of the occurrence of steep slopes landslides are not uncommon on laterite ridges. Often liana forest is encountered on such landslides. Pioneers, such as *Cecropia* spp., *Schefflera morototonii, Jacaranda copaia* and *Pentaclethra macroloba* are also abundantly present on such sites in central Guyana (ter Steege pers. obs.).

4 Forests in the Pakaraima-Central Guayana Upland region (Guyana-Venezuela-Brazil)

The forests of the uplands of west central Guyana are part of the central Guayana province (Berry *et al.* 1995). The lowland forests of this region have been classified as belonging to the *Eschweilera-Dicymbe* association (Fanshawe 1952). The major soils in the region are shallow and rocky (Gross-Braun *et al.* 1965) having formed on steep volcanic mother material (basic and acidic) and on sandstone.

In Guyana, *Dicymbe*, which is practically restricted to the Guiana Shield (Berry *et al.* 1995), is the most characteristic genus for the lowland forests of this area (Table 4.1). *D. altsonii* and *D. corymbosa* are (absolutely) dominant over large stretches of forest from the Pakaraimas to the Essequibo (Fanshawe 1952, ter Steege 1998a). Genera, common to the southern upland region (crystalline shield), are common in the Pakaraimas as well (Table 4.1). *Podocarpus, Ragala, Micrandra* and a few other are characteristic for the montane forests in this area. These forests are the least known in Guyana but are also very small in extent. Most of our information is from bordering Venezuela and Brazil, where the areas with montane forests are much larger and also our knowledge is more advanced (Veloso *et al.* 1975, Huber 1995b, Chapter 10).

Lowland and lower montane forests of the Pakaraima uplands on brown sands

Dicymbe altsonii (endemic to Guyana) is the main characteristic and most common canopy species in the 'mixed forests' of the lowland eastern Pakaraima Mountains. *Dicymbe* may be absolutely dominant over large areas. Co-dominants are *Eperua falcata, Eschweilera sagotiana, E. potaroensis, Mora gonggrijpii, Alexa imperatricis, Licania laxiflora, Swartzia leiocalycina, Vouacapoua macropetala* and *Chlorocardium rodiei. Eschweilera potaroensis,* an endemic of this region, may be co-dominant in forests around the confluence of the Potaro and Essequibo Rivers (Chapters 5, 6).

Lowland and lower montane forests of the Pakaraima uplands on white sands

On the white sand derived from the weathering table mountains Legumes are a strongly dominant feature (Fanshawe 1952, Whitton 1962). The main dominant species are *Eperua falcata, Eperua grandiflora, Dicymbe altsonii, D. corymbosa* and *Dimorphandra davisii* (endemic to the Pakaraima Mts.). On isolated spots forest dominated by *Dimorphandra polyandra* is found (Fanshawe 1952). Several other species, associated with the white sands in Guyana (see below) are common in this region such as *Chamaecrista adiantifolia, Chamaecrista apoucouita, Talisia squarrosa* and *Ocotea schomburgkiana*. *Cunuria glabra* is widespread and dominant on poorly drained soils, along rivers, notably the Kako River (I. Welch, perscomm., see also Chapter 8), often together with *Dimorphandra macrostachya*. Forest with abundance of *D. macrostachya* is also found over large areas of the Gran Sabana in Venezuela (Hernández 1992, 1994, Huber 1995a). *Ormosia coutinhoi* is typical for the areas bordering swamps and *Aldina insignis* is found on the edges with *Mora excelsa* forest (Fanshawe 1952). Forests with *D. davisii, D. polyandra* and *D. cuprea* are characterised by thick litter layers, comparable to the forest of *D. conjugata*. Whitton (1962) reported that all *Dimorphandra* forest of the Pakaraimas showed signs of burning, with almost single dominance of *Dimorphandra* regenerating through clumping.

Dry submontane forests of the Pakaraima uplands

Xeromorphic woodland with *Dicymbe jenmanii* (endemic to the Kaieteur region), *Moronobea jenmanii, Humiria balsamifera, Chrysophyllum beardii, Tabebuia* spp., *Anthodiscus obovatus, Saccoglottis, Dimorphandra cuprea, Clusia* spp., *Oedimatopus, Archytaea, Bonettia, Didimopanax, Poecilandra retusa, Pradosia schomburgkiana, Pagamea guianensis* and *Chaetocarpus stipularis* is found on shallow soils. On areas with impeded drainage epiphytes of Araceae, Bromeliaceae, Cyclanthaceae and Rapateaceae cover the forest floor (Fanshawe 1952).

Much of this forest area is in a seral stage (scrub) recovering from fires (Fanshawe 1952). Such xeromorphic scrub vegetation is characterised by *Humiria balsamifera, Dimorphandra cuprea, Bonettia, Poecilandra retusa, Pradosia schomburgkiana, Pagamea guianensis* and *Chaetocarpus stipularis*.

Montane forests of the Pakaraima highlands

The montane forests (800-1500m) in Guyana are small in extent (see Chapter 10). In Venezuela just across the border montane forest is found with *Dimorphandra macrostachya, Byrsonima stipulacea, Sloanea pittieriana, Platycarpum rugosum, Enlicheria nilssonii, Sterigmapetalum guianense, Caryocar montanum, Moronobea ptaritepuiana* and *Podocarpus magnifolius* (Huber 1995a). It is very likely that elements of this forest also occur on the Guyanan slopes of Mt. Roraima. The only numerical data we have are from Brazil (Table 4.1, Veloso *et al.* 1975). The most abundant species in this area are *Micrandra lopesii, Nectandra rubra, Eschweilera odora, Elizabetha* sp., *Licaria canella, Micropholis guianensis, Ormosia flava, Caraipa grandiflora, Mezilaurus itauba* and *Cariniana micrantha*. Sapotaceae and Lauraceae, in general, are overwhelmingly abundant at higher elevations.

Upper montane forests of the Pakaraima highlands

Upper montane forests (1500-2000m) are only found on the high table mountains, such as Mts. Roraima, Ayanganna and Wokomung. Huber *et al.* (1995) and Huber (1995a) list: *Bonnetia tepuiensis, Schefflera, Podocarpus, Magnolia* and *Weinmannia*. The cloud forests are rich in cryptogamic and vascular epiphytes (Huber 1995a). The forest finally grades into tepui scrub (2200-2700m) with *Bonnetia roraimae, Schefflera, Clusia* and *Ilex*, which, in Guyana, is probably only found on Mts. Roraima and Ayanganna (Huber *et al.* 1995). On the Brazilian slopes of Mt. Roraima, Veloso *et al.* (1975) do not describe any forests with *Bonnetia*, but low scrubs with Melastomatataceae, Rubiaceae, *Ilex* and *Podocarpus steyermarkii.*

5 Forests on the southern peneplain (Guyana-Suriname-French Guiana-Brazil)

The forests in the southern regions of the Guianas are situated on soils developed on the crystalline shield, known as the 'Guiana peneplain' (Gross-Braun *et al.* 1965; Gibbs and Barron 1993). This peneplain extends from (east Colombia-) Venezuela, through the Guianas to Amapá (Brazil). These forests are among the least known in the Guianas, mainly due to their remote location. The few systematic inventories in the southern areas were carried out in Guyana (de Milde and de Groot 1970g, see also ter Steege 1998, Chapter 5) and further south just across the border in Brazil (Leite *et al.* 1974, Veloso *et al.* 1975, Doi *et al.* 1975). Several inventories were carried out on the crystalline shield in Suriname, near the coastal area. Thus, our knowledge in Suriname is restricted to the areas in the near interior. In French Guiana too, several inventories were carried out in the near interior (Fleury 1994). These data were unavailable but some incomplete summaries exist. Our knowledge of French Guiana is thus very restricted to a number of descriptive accounts (de Granville 1990, Sabatier and Prévost 1990) and a few detailed studies of relatively small areas (Mori and Boom 1987, Sabatier 1990).

The forests on the crystalline shield are more diverse than those of the white sands formation (Lindeman and Molenaar 1959, Fanshawe 1952, ter Steege 1998a, Chapter 5). Genera that are more common on the shield in south Guyana, Suriname, Brazil and Venezuela (Imataca) compared to central and north-west Guyana include (Table 4.1) *Anacardium, Andira, Bagassa, Cecropia, Couratari, Dipteryx, Geissospermum, Laetia, Micropholis, Parkia, Pourouma, Pseudopiptadenia, Qualea, Sclerolobium, Simarouba, Tetragastris, Virola* and *Vochysia*. Typical for Suriname (and French Guiana) are *Dicorynia, Andira, Dipteryx, Trichilia* and *Lueheopsis.* Further south still (Brazil) *Hymenolobium, Bertholletia, Cynometra, Dialium* and *Clarisia* become more abundant (Table 4.1). Several of these genera (and also of the non-mentioned genera) are comprised of species with medium to light wood and characteristic of late succession (Chapter 7).

Sub-coastal French Guiana and Brazil.

Six species: *Eperua falcata, Dicorynia guianensis, Eschweilera odora, Eschweilera amara, Chrysophyllum prieurii* and *Qualea albiflora* are responsible for 50% of the individuals in the forest of sub-coastal French Guiana (Fleury pers. comm, see Table 4.1). In Paracou, where intensive silvicultural studies are being carried out, the forest on the schist soils have an abundance of *Eperua, Licania, Parinari, Eschweilera, Dicorynia guianensis, Inga, Goupia glabra, Bocoa prouacencis, Symphonia globulifera, Qualea rosea, Ruizterania, Vouacapoua americana, Ocotea rubra* and *Virola* (Schmitt 1985, Bergonzini 1989). The most common taxa at the ECEREX station on the Piste de St. Elie, slightly more inland and in the Bonidoro schists area, (Lescure and Boulet 1985, Sabatier *et al.* 1997) on variably drained Ferralitic soils are Lecytidaceae (*Eschweilera*), Caesalpiniaceae (*Eperua*), Chrysobalanaceae (*Licania*) and Sapotaceae.

Just over the border in Brazil, in Amapá (Leite *et al.* 1974) *Eschweilera* is the most abundant genus followed by *Pouteria, Inga, Minquartia, Licania, Protium, Manilkara, Vouacapoua, Virola, Chrysophyllum, Vochysia, Pentaclethra, Qualea, Ocotea* and *Tachigali*. These genera together account for 50% of all individuals over 30 cm. Areas on the basement complex are characterised by *Dinizia excelsa, Manilkara, Minquartia, Pouteria, Protium, Tetragastris, Eschweilera, Couma, Iryanthera* and *Geissospermum sericeum*.

Dry to moist forests in the southern Guyana-Brazil border area

The North- and South-Rupununi savannah cover a fairly large part of the southern region. Dry (deciduous) forest types fringe these savannahs. Due to repeated burning of the savannah the forest edges in this region retreat further and further each year. Most of the dry forest stands show high presence of *Goupia glabra, Couratari, Sclerolobium, Parinari, Apeiba, Peltogyne, Catostemma, Spondias mombin* and *Anacardium giganteum* (Fanshawe 1952, ter Steege 1998a, Chapter 5). *Couratari guianensis, Terminalia dichotoma, Tetragastris panamensis* and *Licania* spp. form stands in the eastern part. These dry mixed forests extend far into Brazil (Veloso *et al.* 1975) and Venezuela (see Huber 1995a). Forests along the foothills of the Kanuku mountains are characterised by *Cordia alliodora, Centrolobium paraense, Apeiba schomburgkii, Acacia polyphylla, Pithecellobium* s.l., *Peltogyne pubescens, Manilkara* spp., *Cassia multijuga* and *Vitex* spp. (Fanshawe 1952, ter Steege 1998a). The first two species are sought after timber species within the local Amerindian communities. *Cochlospermum vitifolium* (and *orinocense*) is a conspicuous member of this forest. Similar forests with *Centrolobium, Cordia, Peltogyne, Vitex, Inga, Protium, Tetragastris, Parkia, Pseudopiptadenia, Spondias* and *Genipa* have also been found along the footslopes of the Acarai Mts. in Brazil (Veloso *et al.* 1975, Doi *et al.* 1975).

Inundated areas are characterised by *Orbignya* spp., *Maximiliana regia, Mauritia flexuosa* (Fanshawe 1952, Veloso *et al.* 1975). The latter is also a typical feature along creeks and depressions in the savannahs. Common trees are *Protium* spp., *Licania canella, Eschweilera* spp., *Macrolobium acaciifolium, Clathrotropis, Elizabetha, Simarouba, Inga* and *Couepia* (Veloso *et al.* 1975).

South of the Cuyuwini river to east of the New River the forest is characterised by a high presence of *Geissospermum sericeum*, *Eschweilera* cf. *pedicellata, Lecythis corrugata, Pouteria coriacea* and *Pourouma* spp. Several other taxa, characteristic of late secondary forest, have fairly high presence this region: *Parkia, Ficus, Sclerolobium, Trichilia, Parkia, Parinari* and *Goupia*. *Eperua rubiginosa, Pterocarpus* and *Macrolobium acaciifolium* are common in forests along the rivers in this area.

Moist forests on the basement complex in Suriname and French Guiana

Eperua falcata is the most abundant species in soils of the Zanderij formation and the soils on the basement complex in the near interior in Suriname. Other common species in these forests are *Dicorynia guianensis, Tetragastris altissima, Couratari* *stellata, Eschweilera odora, Iryanthera sagotiana, Virola melinonii, Parinari campestris, Mora gonggrijpii, Manilkara bidentata* and *Goupia glabra* (Schulz 1960). Other *Eschweilera* spp. and *Licania* spp. are also abundantly present. In comparison with the forests of the near interior of Guyana, Vochysiaceae, Myristicaceae, Mimosaceae, are more prominent in Suriname than in Guyana. There are clear trends from west to east: e.g. *Mora gonggrijpii* is not uncommon in certain areas in the west but is absent in the east, while *Dicorynia guianensis* increases in abundance toward the east. *Qualea rosea* is quite abundant in the somewhat drier sandier areas, whereas *Vouacapoua americana* in combination with *Eschweilera* spp. is characteristic of the lateritic hills (Schulz 1960). Comparable hill forest is found over large stretches in the further interior (e.g. Goliath creek, Stofbroekoe Mt., Voltz Mt.). On the higher portions of mountains Myrtaceae, Sapotaceae and lianas are conspicuous (Lindeman and Molenaar 1959, Schulz 1960). Liana forest is likely an indication of disturbance and species such as *Laetia procera* and *Goupia glabra* are common. No information could be found on the large mountain stretches in central to southern Suriname (a.o. Wilhelmina Mts., Eilerts de Haan Mts., Oranje Mts. but see below).

In Nouragues, central French Guiana, Lecythidaceae, Sapotaceae, Caesalpiniaceae, Chrysobalanaceae, Burseraceae are among the most common families (Poncy *et al.* 1998). The most abundant species in a 100-ha sample were *Vouacapoua americana, Eperua falcata, Bocoa prouacensis, Dicorynia guianensis, Sclerolobium, Pseudopiptadenia* and *Inga* spp. Large local differences were noted and *Tetragastris altissima* was extremely abundant in a forest area only 7 km away from the 100-ha sample. Granitic outcrops in the area are dominated by Myrtaceae (*Myrcia, Myrciaria, Eugenia*) with some *Eriotheca, Inga* spp., *Terminalia amazonica* and *Clusia* spp. Several species common on these rocks are also common in dry savannahs.

In Saül, *Tetragastris altissima* is by far the most abundant species, followed by *Quararibea turbinata, Protium apiculatum, Eschweilera coriacea, Virola michelii, Eperua falcata* and *Chimarris microcarpa* (Mori and Boom 1987). The leading families around Saül are Burseraceae (*Tetragastris altissima*), Sapotaceae, Lecythidaceae, Caesalpiniaceae and Mimosaceae. The terrain around Saül is relatively dissected with peaks of just over 400m.

Further down south close to the Brazilian border the forest at Trois Sauts, Oyapoque R., also shows a high abundance of Burseraceae (23% of all individuals, Sabatier 1990). Lecythidaceae are the second family, followed by Meliaceae, Mimosaceae and Lauraceae. Chrysobalanaceae and Caesalpiniaceae are 8th and 10th in rank respectively.

Forests south of the Brazilian border

It is reasonable to assume that the forest at the southern Suriname and French Guiana border will not be unlike the forest in bordering Brazil, which is dominated by *Licania* and *Pouteria* and with *Cynometra, Dialium, Protium, Eschweilera, Tabebuia* and *Manilkara* (Table 4.1). More easterly the forests are more dominated by *Eschweilera*, with *Vochysia*, *Manilkara*, *Tetragastris* and *Pouteria* (Table 4.1).

Submontane forest (200 - 600 m altitude) is found close to the border with Suriname and Guyana. Montane forest is found in the Acarai Mts from 600-800 m. Forests on the mountain tops are dominated by Myrtaceae and *Clusia* on Sierra do Acarai (Doi *et al*. 1975).

Conclusions

There are clear differences in forest composition over large areas in the three Guianas. Because several species have restricted ranges at the species level this is obvious but several large range species can be found nearly everywhere (e.g. *Goupia glabra*). There are also clear differences in composition at the genus and family level (Table 4.1).

Areas that stand out in terms of their forest composition are:

1. Forests in the sub-coastal Guianas, that may have the largest number of species/genera typical of the three Guianas
2. Forests on the Berbice Formation (Guyana mainly) with unique high dominance of Caesalpiniaceae and endemics (see also Chapters 5 and 6)
3. Forests of the Pakaraima highlands (see also Chapters 5 and 6)

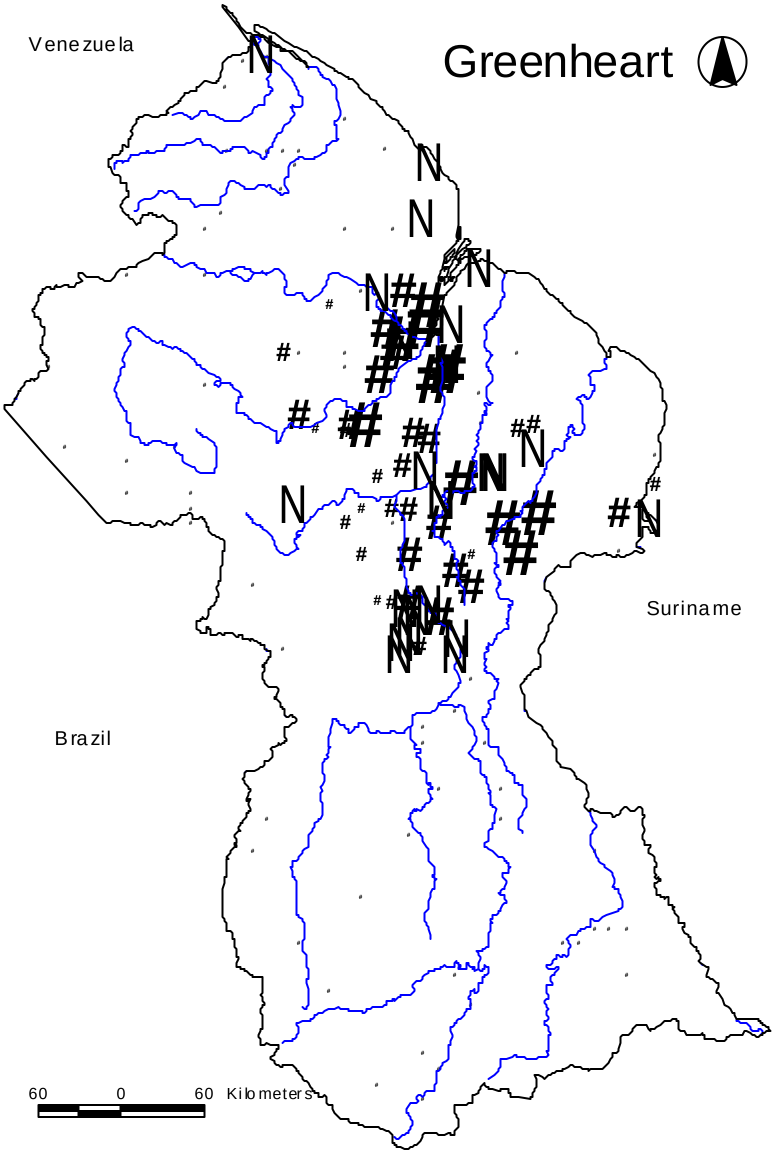
The forests in the southern areas of the Guianas are still the least known but probably show high similarity with those across the border in Brazil.

Appendix 2 Reconnaissance and valuations surveys used in Chapter 5

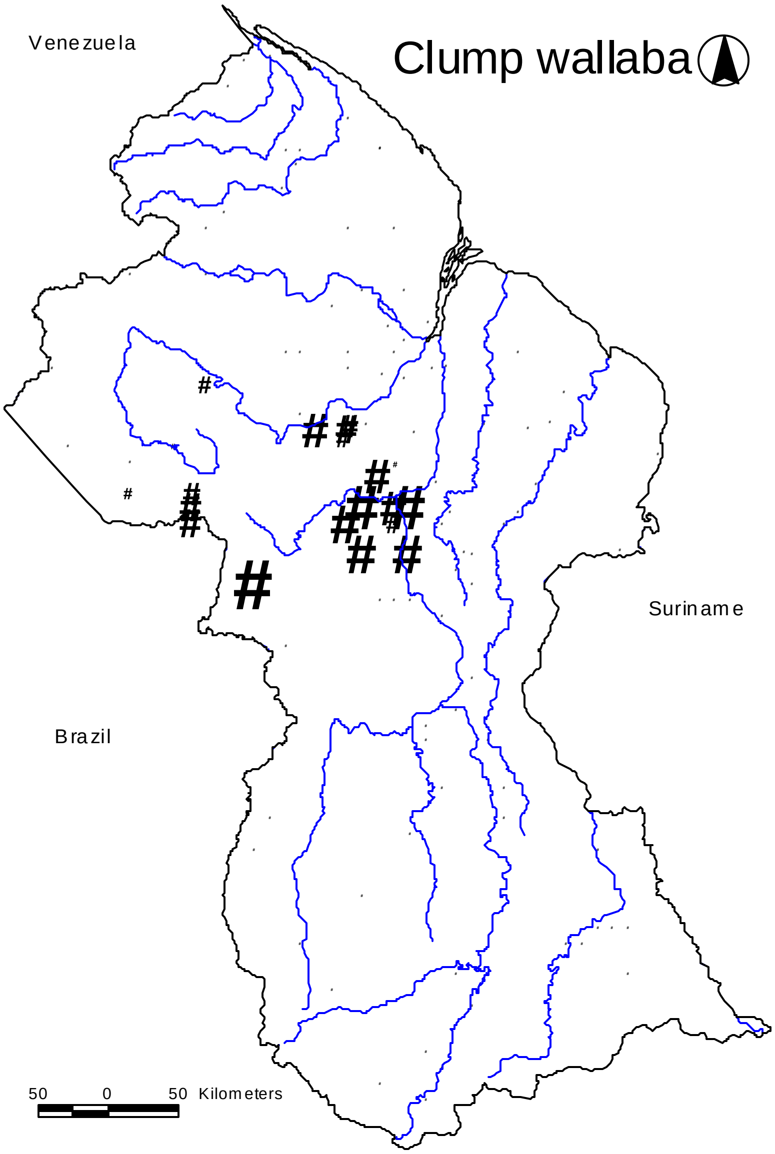
Valuation and Reconnaissance Surveys used in chapter 5. Source: GFC library, Fanshawe 1961.

GFC Nr.	Survey area	Year of survey	Area (km^2)
North West District			
2	Barima River	1927	515
3B/C	Barama River	1928	513
1A/B	Aruka-Yarakita Rivers	1929	311
26	Moruka Amerindian Reservation	1947	111
Cuyuni-Supenaam-Mazaruni			
5	Camaria-Cuyuni	1928 - 31	725
7	Kartabo Triangle	1929	306
4	Tinamu-Supenaam	1931	334
6	Arawak-Metope	1931	70
22	Upper Groete Creek	1944	135
24	Lower LB Mazaruni	1945	401
Bartica Triagle			
8	Mazaruni RB	1926	445
9	Ikuribisi LB Essequibo	1926	536
10	East Kaburi Plateau	1926	332
11A/B	Kaburi-Okuwa	1926	505
19	Moraballi-Arawai	1939	98
27	Bartica Potaro Rd. 55-90 mile	1947	1450
32	Issano Rd.	1952	596
Essequibo-Demerara-Mahacony			
15	Mahaicony River	1934	220
13	Demerara: Great Falls-Ekuk	1935	259
14	Itaburro Creek	1935	129
18	Tenabo-Demerara	1935	104
12	Demerara-Essequibo Divide	1937	223
16	Wiruni River	1938	186
20-21	Winiperu-Hariwa	1940	186
Berbice-Corentyne			
s.n.	Canje River	1914	233
23	Upper Corentyne River	1930	n.a.
23	Lower Corentyne River	1930	n.a.
17+A	Bebice River	1938	906

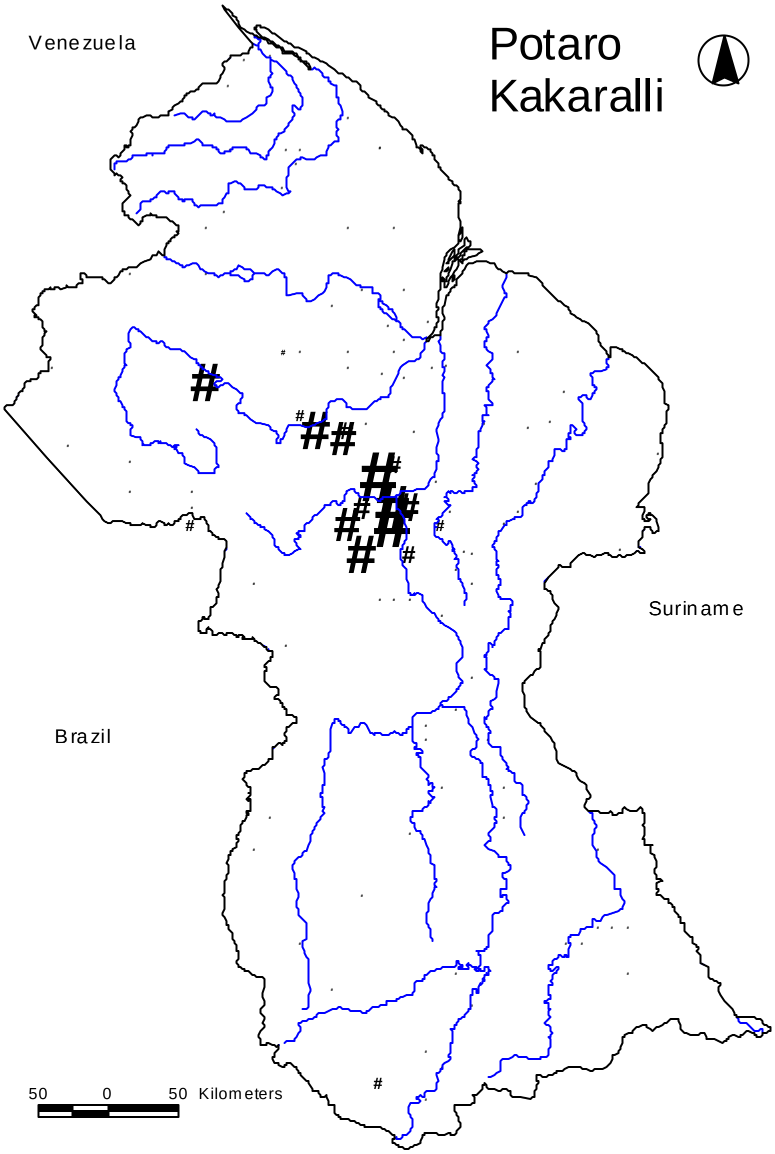
Appendix 3 Distribution maps of common endemics



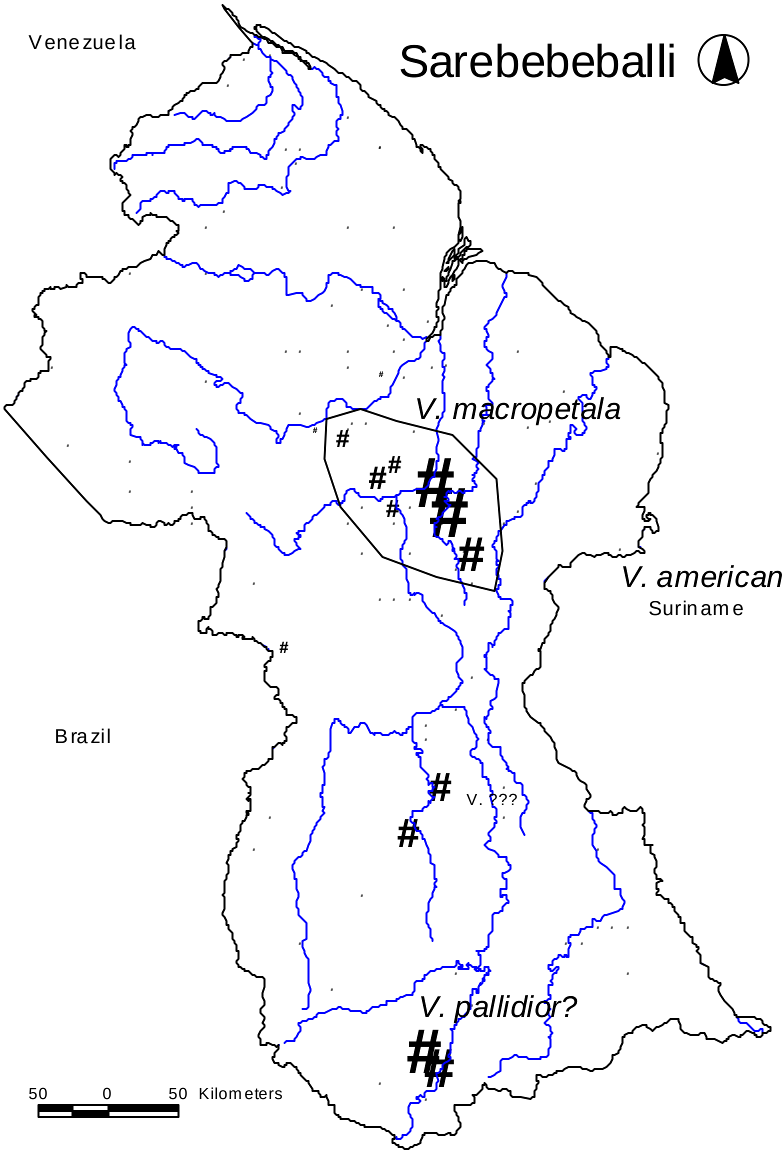
Map of abundance of *Chlorocardium rodiei* (Greenheart). The dot size is indicative for the relative contribution (in %) of *Chlorocardium* to the forest trees > 30 cm DBH. Dot size ranges from 0 – 22.3%. The crosses indicate botanical collections made of *Chlorocardium rodiei* in Guyana. One collection is known from Suriname (Maas 1971).



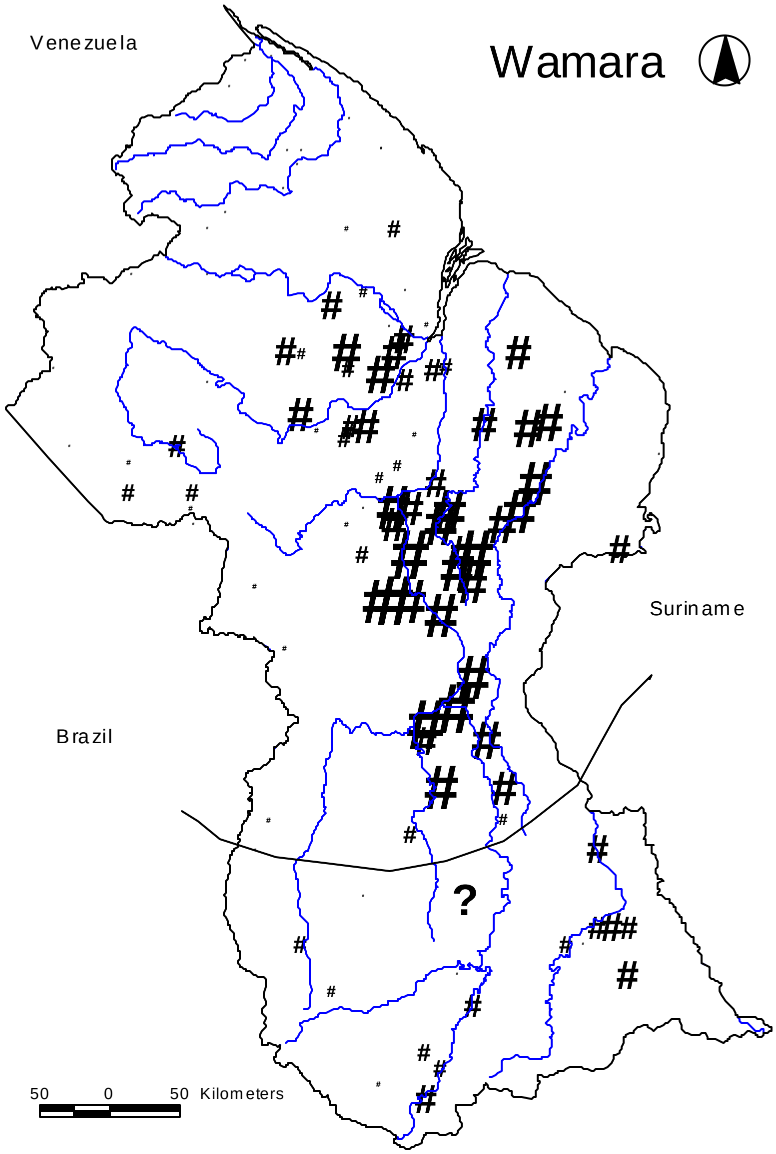
Map of abundance of *Dicymbe* (Clump wallaba). The dot size is indicative for the relative contribution (in %) of *Dicymbe* to the forest trees > 30 cm DBH. Dot size ranges from 0 – 47.8.



Map of abundance of *Eschweilera potaroensis* (Potaro kakaralli). The dot size is indicative for the relative contribution (in %) of *Dicymbe* to the forest trees > 30 cm DBH. Dot size ranges from 0 – 8.1. The dot in the south is no doubt a miss-classification.



Map of abundance of *Vouacapoua macropetala* (Sarebebeballi). The dot size is indicative for the relative contribution (in %) of *Dicymbe* to the forest trees > 30 cm DBH. Dot size ranges from 0 – 4.0. In Suriname the vicariant *V. americana* is found and in Brazil *V. pallidior*. Probably, the individuals found in south Guyana belong to the latter species.



Map of abundance of *Swartzia leiocalycina* (Wamara). The dot size is indicative for the relative contribution (in %) of *Dicymbe* to the forest trees > 30 cm DBH. Dot size ranges from 0 – 20.6. The individuals in the south are probably based on wrong identifications (Chapter 5).

5 THE USE OF NATIONAL FOREST INVENTORY DATA FOR A PROTECTED AREA STRATEGY IN GUYANA[1]

Hans ter Steege

Introduction

Forest inventories are largely neglected in the debate of national parks selection in Guyana (and probably elsewhere). More often botanical collections are used for this purpose. Also in Guyana a first attempt at resolving the lack of data supporting the selection of areas for protection has been made by using taxonomic collections as a basis for mapping biodiversity (The Centre for the Study of Biological Diversity 1995, Funk *et al.* 1999). However, such mapping tends to concentrate on collecting efforts more than biodiversity 'hot-spots' (Nelson *et al*. 1990) and this was also the case in Guyana where highest diversity was found around coastal Georgetown (ibid.). Furthermore, Guyana is still rather poorly collected, despite the collecting effort so far (Lindeman & Mori 1989, Ek 1990). For instance, *Swartzia leiocalycina*, a very common endemic in central Guyana was relatively recently only known from a few collections (Cowan & Lindeman 1989). As another example, *Eperua grandiflora*, a dominant of white sand forest in the three Guianas has no described seed in the Flora of the Guianas, due to poor or inadequate seed material (ibid.). Finally, much of the forest diversity is found in relatively poorly known groups (Lauraceae, Sapotaceae; Gentry 1992).

Lowland forests cover over 80% of the Guianas. Our present knowledge of its composition and structure, especially of the forests in the southern upland regions is very inaccurate. Some reviews of forest types in the Guianas have been produced (Fanshawe 1952 (Guyana), Lindeman & Molenaar 1959 (Suriname), de Granville 1986, 1988, 1990 (French Guiana, Guianas), Sabatier 1990 (French Guiana), Sabatier & Prévost 1990 (French Guiana), Huber 1995a (Venezuela)).

To fill some of the data gaps ter Steege (1998a) explored the use of a large-scale national forest inventory carried out in Guyana's forest from 1968 to 1970. In this chapter the data of several valuation and reconnaissance surveys carried out in Guyana from the 1920's until the 1960's is added to this analysis. These latter inventories fill gaps of the National Forest Inventory.

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[1] This paper is largely based on a previous publication: ter Steege (1998a). The use of forest inventory data for a National Protected Area Strategy in Guyana. *Biodiversity and Conservation* 7: 1457-1483.

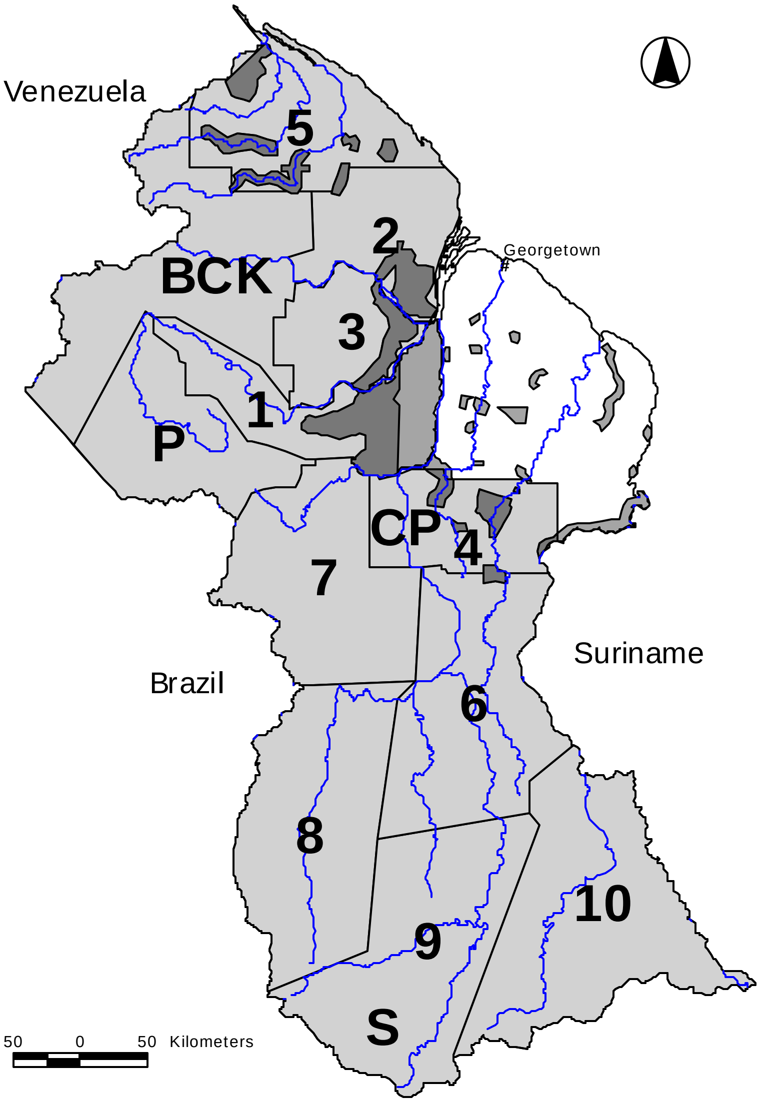

Figure 5.1 Guyana base map: map of the inventory zones of the Forest Industries Development Survey (FIDS, light grey areas). 1-5: ‘accessible’ forests zones; 6-10: ‘inaccessible’ forest zones; BCK: Barama, Cuyuni and Kako rivers drainage; S: South, Lumidpau to Akarai mountains; P: Pakaraima mountains; CP: Carl Persaud lease. Valuation and Reconnaissance Surveys Areas are in medium grey. Overlapping zones in dark grey.

In particular the inventory data are used to provide information on two points mentioned in Chapter 1:

1. Preservation of viable examples of all natural ecosystems in Guyana. Differences in species composition will be assessed at two levels:
    a) National forest regions, assuming that a comprehensive set of protected areas would include at least one site in each distinct region
    b) Forest types within regions and the relation between soil and forest type, to ensure that all forest types within a region are covered (as far as the data allow)

2. Protection of areas of particular biological significance, which can be interpreted to be areas with
    a) High species diversity: areas with high diversity allow protection of many species at a relatively small area investment
    b) High endemism. While endemism is not necessarily biologically meaningful, one can argue that certain endemics, due to restricted occurrence are vulnerable and in need of protection. However, restricted species straddling the order of two countries can be equally vulnerable

While it is clear that large-scale forest inventory data cannot provide all answers it will be shown that they can contribute significantly to the debate of National Parks selection in Guyana.

Materials and Methods

Forest Industries Development Survey

From 1966 to 1973 a large-scale forest reconnaissance survey was carried out in most of the forested areas of Guyana. The purpose of this inventory, co-funded by UNDP and FAO, was "*to assist the Government of Guyana in determining the extent and composition of accessible forest*" (de Milde & de Groot 1970a). At first only the accessible forest, close to the coast was included, subdivided into five zones. Later also the forest in the south was surveyed (de Milde & de Groot 1970g).

Field work for these surveys was carried out (Figure 5.1) in:

1. 1966: Barama, Cuyuni and Kako rivers drainage (zone BCK)
2. 1968: Lumidpau to Akarai mountains (zone S)
3. 1968 - to May 1969: 'Accessible' forests (zones 1 to 5)
4. 1969 - 1970: 'Inaccessible' Southern forests (zones 6 to 10)
5. 1971 and 1973: Pakaraima Mountains (zone P)
6. 1973: Carl Persaud lease (zone CP)

Sample plots were established, after extensive air-photo interpretation, along survey lines of 1.6 to 3.8 km long, starting from easily accessible points, such as air fields, rivers, roads, or forest savannah edges. Two to three plots were established per line. The location of the plots was planned in such a way that it was possible to collect data for the main forest types in a region. The plots were always laid out within one particular forest type and consisted of four, five or 10 circular sub-plots of 0.4047 ha (0.1 acre) each (de Milde & de Groot 1970a). The choice of the number of subplots was constant within a region based on commercial expectation and logistics of that particular region. Four subplots were enumerated in the accessible areas, except in the central part of Guyana (zone 4), where 10 subplots were enumerated. Five subplots were enumerated in the southern area (zone 6-10).

In each plot soil type, presence of rocks, topography, forest type, height of the highest tree (for each subplot), DBH (diameter at breast height or above the buttresses) and the vernacular name for all individuals over 30.5 cm (12 inch) DBH were recorded. Reports of these surveys were published in 1970 (de Milde & de Groot 1970a-g). The first report described the general set up of the survey in the accessible forests, five zones were described each in a separate volume and the southern area was covered by the last report. The reports are short and species were grouped according to their commercial potential at that time. Field forms of the survey, however, were still available at the Guyana Forestry Commission and were generously made available for this study. Unfortunately, data of zone 5 had been lost but after considerable searching, summary sheets for all zones were found and from these sheets at least the main information could be reconstructed for zone 5.

Plot data FIDS

In total 1029 plots of the FIDS were recovered. It proved impossible to locate all plots exactly, as almost all original field maps had been lost. However, field sheets often had some information of locality written on them and with this information, the date of recording and the name of the recorder, it was possible to find an approximate location (rounded to the nearest 10th of a degree) for most plots, except those in zone 5, for which all field data remained lost. To allow for multivariate analysis small, geographically close, plots were grouped. Plots in zone 5, where all location data was lacking, were grouped into three locations on the basis of their line number. This, finally, resulted in 77 locations.

Rainfall (monthly and yearly: Persaud 1994, Persaud & Persaud 1995), Pennman Evapotranspiration (PET, yearly: Persaud & Persaud 1993) and sunshine hours (yearly: Persaud 1982) were provided by the Hydro-Meteorological Service in Guyana. Soil data, extracted from the field forms, were classified as; peat, clay, loam, brown sand, laterite, rock and white sand. A few plots had no soil information and this was then classified as unknown.

Valuation and Reconnaissance Surveys

From 1926 to 1957 a large number of valuation and reconnaissance surveys were carried out in Guyana. These surveys were conducted throughout the near-coastal areas but deeper inland in the Bartica Triangle and lower along the Bartica-Potaro Rd. The level of inventory was between 0.5 and 2%, either in block or line surveys. Summaries of most of these surveys can be found in Fanshawe (1961). Not all data was present at the time of compilation and the areas used are listed in Appendix 2.

The summary tables of these surveys list all species recognised and their average number of stems over 40 cm (16”) per 1000 acres. These values were converted into stems per 1000 ha averaged over the complete survey area. The data of these inventories are not used in most of the diversity calculations below but serve mainly to increase the map coverage over Guyana for species occurrence and density data.

Species data

Scientific names were derived from the vernacular names, which are fairly constant in Guyana (Mennega *et al*. 1988), the main language in forestry being Arawak. However, there are a number of vernacular names that are used for more than one (not always closely related) species. Notably difficult are *Licania* spp., *Swartzia* spp. and Sapotaceae, all common and diverse taxa in the Guianas. Names were primarily extracted from Mennega *et al.* (1988) and several lists present in the library and herbarium of the Guyana Forestry Commission. A number of names in Akawaio, Wapisiana and Wai-wai languages could not be found but these were finally only a very small part of the total data set (in number of individuals). All these unknowns were treated, conservatively, as different species. A small but unknown number of Arawak vernacular names were used in the south for species different than those in the north (de Milde & de Groot 1970g). As no botanical collections were made and the species were not specified, this information could not be used.
Endemic status was treated in two ways:

1) 90% of the known distribution of the species or the **main** taxon indicated by a vernacular name is confined to Guyana: *Aldina* spp., *Chlorocardium rodiei, Dicymbe* spp., *Eschweilera potaroensis, Licania buxifolia* (Marishiballi), *Licania cuprea* (Konoko), *Maburea trinervis, Swartzia leiocalycina, Swartzia* spp. (Itikiboroballi) and *Vouacapoua macropetala.*
2) 90% of the known distribution of the species or the **main** taxon indicated by a vernacular name is confined to the Guiana Shield: *Alexa* spp., *Caryocar* spp., *Catostemma* spp., *Clathrotropis* spp., *Dimorphandra conjugata, Diospyros* & *Lissocarpa* spp., *Ecclinusa* spp., *Eperua* spp., *Eschweilera* spp., *Lecythis* spp., *Licania* spp., *Loxopterygium sagotii, Mora excelsa, M. gonggrijpii, Ormosia* spp., *Swartzia* spp. *and Trattinickia* spp.

Data Analysis

Exploratory data analysis was carried out with TWINSPAN (Hill 1979a, Oksanen & Minchin 1997) and DECORANA (Hill 1979b, see also Jongman *et al*. 1987, Oksanen & Minchin 1997). Analysis for all 1029 plots at the same time proved impossible as geographical and edaphic information interacted prohibitively. Thus first the 77 locations were classified TWINSPAN and subsequently plots within each cluster separately were classified. Analysis with both TWINSPAN and DECORANA was straightforward with default cut off levels and no downgrading of rare species.

For the 77 locations diversity was calculated using Fisher's α (Fischer *et al*. 1943, Taylor *et al*. 1976) and the Shannon-Weaver index (e.g. Huston 1994). Fisher's α is based on the log-normal relationship between individuals and species ranks and is relatively insensitive to sample size (Fisher *et al*. 1943, Leigh 1995). This measure was thus ideal in this case, where plot sizes were unequal.
Species and location characteristics were mapped with Arcview (Esri Inc. 1998) and geo-statistically analysed with PCraster (Dept. of Physical Geography, Utrecht University 1994, see also Burrough 1987).

The relationship between soil type and species occurrence was assessed by grouping all plots of similar soil type. Differences of occurrence per soil type were analysed, correcting for differences in total summed plot area per soil type, with chi-square tests or each species.

The relationship of diversity (Fisher's α) with rainfall, PET, length of dry season and sunshine hours was investigated with regression analysis (Statistica, Statsoft Inc. 1993). Regional effects on diversity and the effects of soil type on diversity were assessed with two -way Anova without replication.

Results

General

In 1029 plots, covering 212 ha, a total of 15,397 trees over 30.5 cm were measured. A total of 277 taxa was found, in 53 families. Caesalpiniaceae was the most abundant family, with 4571 individuals, followed by Lecythidaceae (1,766), Fabaceae (1663), Chrysobalanaceae (1,011), Sapotaceae (908), Mimosaceae (819), Lauraceae (553) and Bombacaceae (503). The most speciose families were Caesalpiniaceae (23 species), Papilionaceae (22), Lauraceae (19), Sapotaceae (19), Mimosaceae (15), Euphorbiaceae (15) and Lecythidaceae (15). Because of problems in identifying certain taxa, especially Chrysobalanaceae, Sapotaceae and Swartzia, the number of species in these taxa should be higher than reported here. The most abundant family in the data set was Caesalpiniaceae, which with 8% of all species amounted to nearly 30% of all individuals.

National forest regions

A cluster analysis of 77 locations with TWINSPAN resulted in five national forest regions, which were geographically well separated (Figure 5.2). Five plots were obvious outliers in the TWINSPAN and DECORANA analyses and were omitted for further analyses. There was considerable overlap in species composition between the five regions (Table 5.1) and a lack of distinction between the Central wet forests and the Pakaraima Mts. wet forest in the ordination bi-plot (Figure 5.3A).

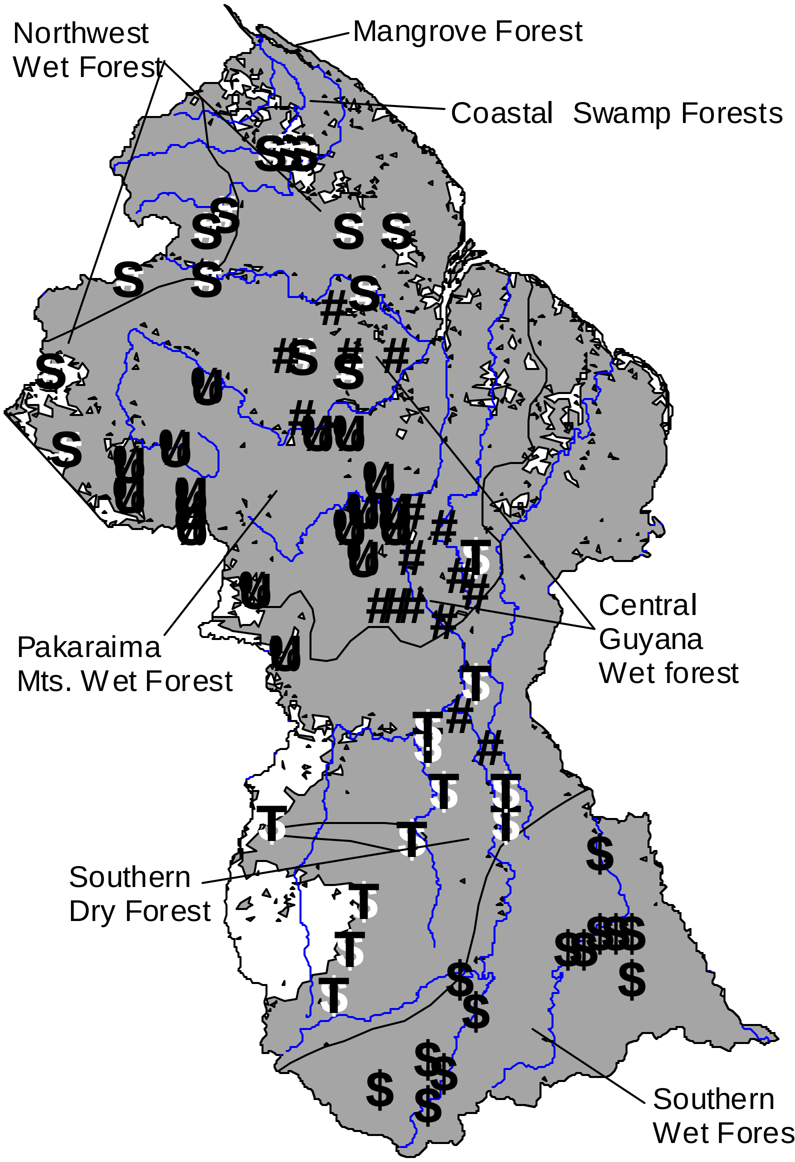

Figure 5.2 Geographical location of 72 forest locations in Guyana based on a standard (default parameters) TWINSPAN classification (Table 1 for details). TWINSPAN groups: ▲ Southern Wet Forests; Δ: Southern Dry Forests; ■ Pakaraimas Mts. Wet Forests; ● Central Guyana Wet Forest; O Northwest Guyana Wet Forests. Light grey areas: area under forest cover, based on NOAA-AVHRR satellite images of September 1992 (http://edcdaac.usgs.gov/1KM/comp10d.html). Thin lines: 2300 mm annual rainfall isohyeth (based on Persaud 1994, see Figure 6.3 for more information)

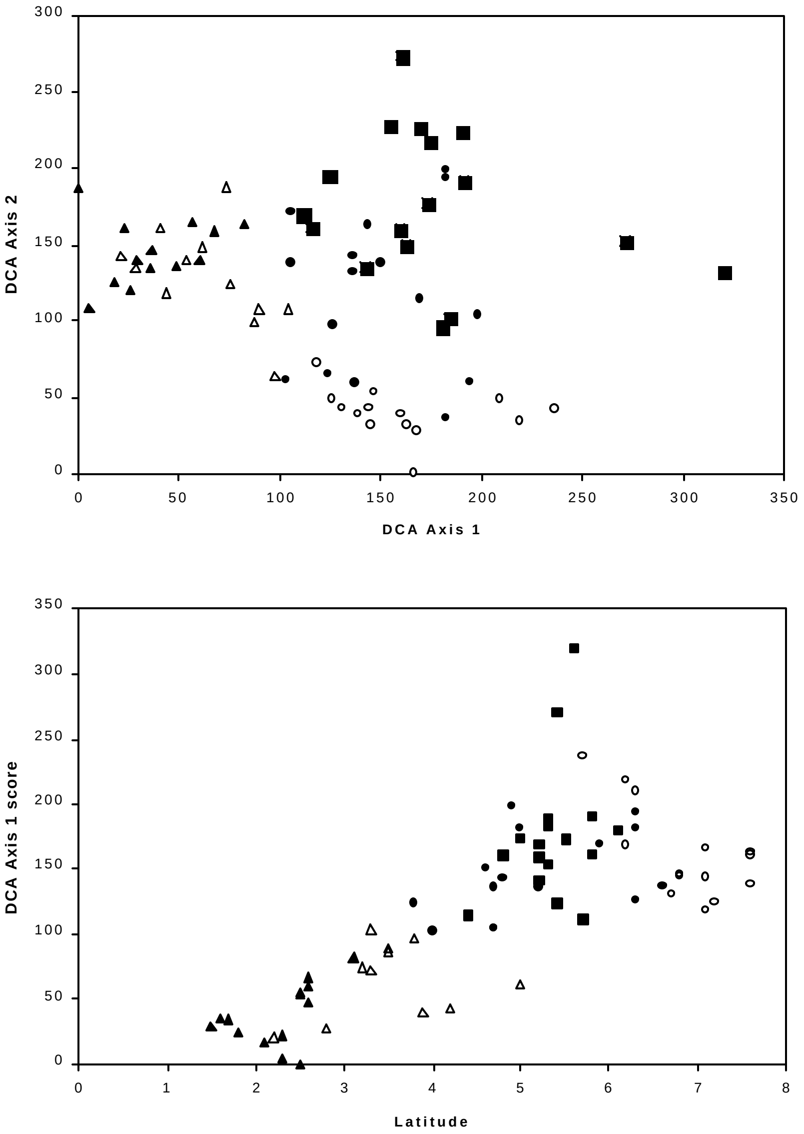

Figure 5.3 **A** Ordination bi-plot of a standard Detrended Correspondence Analysis of 72 forest locations (symbols as in Figure 2). Eigenvalue axis 1: 0.402. Eigenvalue axis 2: 0.289. There is good separation between the southern forest locations and the rest of the country. Axis 1 is interpreted as geographical gradient. **B**. Scatterplot of DCA axis 1 scores of 72 forest locations in Guyana against the latitude of the location.

Semivariance analysis of the DECORANA scores (data not shown) showed exponential increase of semivariance with distance, indicating that the locations form a gradient from north to south (Figure 5.3B). The first axis of the DCA (Eigenvalue 0.402) was, thus, interpreted as a geographical gradient in species composition. The second axis (Eigenvalue 0.289) separated mainly plots of the northwest from those of the central wet forest and the Pakaraima Mts.

Subsequent TWINSPAN classifications of plots per region revealed a number of forest types (or stands) for each forest region. These data are not shown separately but included in the description of the national forest regions below.

Five national forest regions were distinguished and they can be summarised as follows (Table 5.1):

1. **The Southern wet forests**, south of the Cuyuwini river to east of the New river. This forest region is characterised by a high presence of *Geissospermum sericeum, Eschweilera coriacea/decolorans, Pouteria coriacea* and *Pourouma spp.*. Several other taxa, characteristic of late secondary forest have fairly high presence in this region; *Parkia, Ficus, Sclerolobium, Trichilia, Parkia, Parinari* and *Goupia*. Also, species possibly associated with human activity are found here; *Spondias mombin, Bertholletia excelsa, Anacardium giganteum*. Although no species appears dominant, *Geissospermum sericeum* and *Eschweilera coriacea/decolorans* are the must abundant species, followed by *Licania, Eperua* and *Goupia*. Forest along the rivers in this area is characterised by presence of *Eperua* (*rubiginosa*), *Pterocarpus* and *Macrolobium* (prob. a*caciifolium*). In this region 192 species were found, 28 of which (15%) unique to this region in this data set.

2. **The Southern dry forests.** Most of the forest stands show high presence of *Goupia glabra, Couratari, Sclerolobium, Parinari* and *Catostemma*. *Spondias mombin* and *Anacardium giganteum* are found more often than in the wet southern forest. *Couratari guianensis, Terminalia dichotoma, Tetragastris panamensis* and *Licania* spp. form stands in the eastern part. In the northern part, along the Essequibo river, some *Mora excelsa* occur and some forest stands with *Swartzia leiocalycina* and those with *Mora gonggrijpii* occur. A few plots with stands of *Apeiba, Peltogyne* and *Spondias*, comparable to the dry deciduous forest of Venezuela (see Chapter 4), were also found. In this region 147 species were found, 6 of which (4%) unique to this region in this data set (but this region had a very low number of plots).

3. **The Pakaraima Mts. wet forest** is characterised by high presence of *Dicymbe altsonii* and *D. corymbosa* (species almost absent in other regions), *Chamaecrista adiantifolia, Chamaecrista apocouita, Ormosia coutinhoi*, the latter three white sand specialists and *Eschweilera potaroensis*, an endemic of this region. Other species with high presence are *Pentaclethra macroloba*,

Tapirira obtusa, Eperua spp. and *Carapa* spp. Forest types in the region include those highly dominated by *Dicymbe altsonii* and *D. corymbosa* (not together) with *Eperua falcata, Chlorocardium rodiei* and *Eschweilera potaroensis*; by *Eschweilera corrugata, Mora gonggrijpii* and *Swartzia leiocalycina*. Forest along rivers is often dominated by *Mora excelsa, Carapa* spp., *Pentaclethra macroloba* and *Alexa imperatricis*. White sands in the region are dominated by *Eperua* spp. and by a combination of *Aldina* and *Terminalia*. In the western part of this region forest stands with *Pithecellobium/Elizabetha* sp. and *Chrysophyllum sanguinolentum* and a large number of unknowns occur. These forests are likely to be quite similar to the forest described by Huber (1995a) across the border in Venezuela. In this region 208 species have been found, 32 of which (15%) were unique to this region in this data set.

4. **The Central Guyana wet forest**, situated on the sandy Berbice formation, is characterised by high abundance of commercial and often (near-) endemic species such as *Swartzia leiocalycina, Chlorocardium rodiei, Mora excelsa, M. gonggrijpii, Alexa imperatricis, A. leiopetala* and *Clathrotropis* spp. Forests in this region are often dominated by one of the above species, except for *Alexa* and *Clathrotropis* spp.. *Eschweilera* spp. and *Licania* spp. are common, but not dominant, in all forests in this region. *Mora excelsa* dominated forest is commonly found along the rivers often in association with *Carapa* spp.. Swamps with *Pterocarpus* and *Tabebuia insignis* are not uncommon in creek heads. Extensive forest stands dominated by *Eperua falcata* and *E. grandiflora* with *Swartzia leiocalycina* are found on the white sand soils of this region (the latter one occurring also on the lighter brown sands). *Vouacapoua macropetala*, a near endemic of this region is commonly found on lateritic soils in a small area south-west of Great Falls, Demerara river. A more detailed vegetation analysis of a small area within this region can be found in ter Steege *et al*. (1993). In this region 154 species were found, 5 of which (3%) unique to this region in this data set.

5. **The Northwest Guyana wet forest** is characterised by a high abundance and presence of *Alexa imperatricis, Protium decandrum, Eschweilera corrugata, Pentaclethra macroloba and Mora excelsa*. Extensive marsh forests of *Mora excelsa* with *Pterocarpus* and *Carapa* are found along the rivers. Mixed forest on dryer ground are dominated by a combination of *Eschweilera corrugata, Alexa imperatricis* or *E. corrugata, Licania* spp. and *Catostemma commune*. In the southern part of this region (the overlapping zone with region 4) large stands dominated by *Mora gonggrijpii* occur. The latter stands have very low species diversity. In this region 129 species were found, none of which unique to this region in this data set.

Table 5.1 Synoptic table of Guyana's national forest regions. Presence is calculated as percentage of locations in a region in which the species is present. Abundance (between brackets) is given in #trees/100 ha as average for the region. (Presented are those species having at least a presence of 50% in one area) Species with abundance > 85% or density over 200/100ha are shaded.

Forest region	**South Wet**		**South Dry**		**Pakar. Mts. Wet**		**Central Wet**		**Northw. Wet**	
No. of locations	13		12		17		16		14	
total plot area (ha)	25		25.7		60.4		50.4		23.6	
Species										
Parkia pendula	69	(56)			12	(3)				
Geissospermum argenteum/sericeum	100	(240)	33	(31)	6	(2)				
Pourouma guianensis/tomentosa	85	(104)	42	(27)	18	(12)	13	(4)		
Parkia ulei	54	(64)	42	(31)	24	(7)				
Anacardium giganteum	23	(12)	50	(27)			6	(4)		
Strychnos/Glycidendron	54	(32)	8	(4)	18	(8)	13	(4)		
Licania/Pouteria	54	(56)	42	(78)	18	(7)	19	(8)		
Licania 5spp.	77	(88)	50	(31)	18	(12)	13	(12)	14	(8)
Hevea pauciflora	54	(56)	8	(4)	47	(35)			7	(4)
Brosimum guianense	69	(76)	42	(58)	24	(7)	19	(10)	14	(8)
Pouteria coriacea	85	(128)	17	(23)	29	(15)	13	(6)	21	(13)
Sclerolobium guianense/micropetalum	77	(100)	75	(105)	41	(20)	38	(20)	7	(4)
Eschweilera coriacea/decolorans	100	(200)	8	(4)	65	(182)	13	(8)	21	(25)
Tetragastris panamensis	77	(68)	42	(70)	59	(33)	31	(14)	7	(4)
Pseudipiptadenia suaveolens	69	(84)	50	(35)	41	(25)	50	(18)		
Ormosia 6spp.	77	(60)	25	(23)	53	(35)	19	(10)	21	(13)
Macrolobium 3spp.	54	(112)	8	(4)	24	(23)	6	(4)	21	(25)
Lecythis holcogyne	62	(44)	75	(74)	53	(28)	31	(22)	14	(21)
Parinari/Excellodendron	85	(116)	83	(101)	41	(13)	38	(22)	29	(21)
Ocotea canaliculata	92	(128)			53	(30)	19	(6)	29	(21)
Virola spp.	31	(20)	50	(43)			31	(14)	7	(8)
Chamaecrista apoucouita	38	(44)	8	(4)	53	(46)	13	(12)	7	(4)
Pithecellobium/Elizabetha	46	(40)	67	(70)	71	(71)	44	(24)	7	(4)
Swartzia 9spp.	85	(160)	75	(58)	71	(78)	69	(46)	21	(21)
Trichilia rubra	54	(64)	50	(93)	29	(10)	38	(20)	29	(25)
Terminalia dichotoma	62	(52)	58	(74)	71	(73)	31	(14)	36	(34)
Pouteria filipes	77	(136)	75	(54)	18	(18)	56	(36)	50	(38)
Parinari excelsa	23	(24)	50	(27)	6	(2)	63	(22)		
Inga alba	77	(84)	83	(78)	59	(50)	63	(50)	50	(59)
Sloanea/Couepia 10spp.	69	(76)	25	(16)	76	(55)	25	(20)	43	(38)
Ocotea floribunda	77	(104)	50	(47)	59	(33)	56	(24)	43	(38)
Pouteria 3spp.	69	(92)	50	(70)	71	(45)	56	(30)	36	(42)
Manilkara bidentata	31	(28)	92	(128)	47	(35)	31	(14)	36	(38)
Vitex 5ssp.	15	(8)	58	(47)	18	(15)	19	(8)	21	(13)
Cordia 6spp.	23	(16)	25	(12)	53	(25)	19	(14)	14	(21)
Goupia glabra	92	(240)	75	(144)	76	(51)	81	(56)	57	(89)
Couratari 5spp.	38	(20)	92	(117)	71	(36)	44	(24)	43	(34)
Eperua grandiflora/jenmanii	85	(348)	25	(152)	65	(169)	56	(89)	50	(76)
Licania 6spp.	85	(208)	83	(109)	88	(71)	75	(73)	64	(135)
Aspidosperma/Casearia/Drypetes	54	(68)	67	(74)	35	(12)	44	(28)	50	(47)
Apeiba/Annona	46	(32)	42	(51)	59	(35)	38	(16)	36	(42)
Inga spp.	85	(84)	42	(54)	71	(91)	63	(50)	57	(148)
Pouteria guianensis	69	(96)	8	(4)	65	(48)	38	(32)	43	(38)

Table 5.1 (continued)

Forest region	**South Wet**		**South Dry**		**Pakar. Mts. Wet**		**Central Wet**		**Northw. Wet**	
Licania 3spp.	69	(160)	58	(43)	100	(124)	50	(95)	57	(144)
Lecythis corrugata	54	(44)	33	(31)	41	(20)	50	(18)	36	(25)
Jacaranda copaia	46	(28)	17	(16)	59	(43)	38	(16)	29	(21)
Mouriri 8spp.	54	(52)			18	(5)	13	(8)	43	(47)
Pterocarpus 4spp.	69	(140)	25	(19)	41	(63)	38	(52)	57	(102)
Chaetocarpus schomburgkianus/stipularis	62	(96)	67	(117)	53	(30)	63	(46)	57	(76)
Pouteria caimito/jenmanii	15	(12)	33	(27)	53	(31)	19	(14)	21	(13)
Catostemma 3spp.	92	(148)	75	(175)	82	(257)	100	(180)	79	(199)
Micropholis venulosa (melinonii?)	23	(20)	42	(62)	53	(31)	38	(20)	29	(17)
Peltogyne spp.	31	(20)	50	(39)	47	(23)	50	(26)	36	(25)
Moronobea coccinea	8	(12)			53	(33)	25	(10)		
Dicymbe altsonii					94	(475)	13	(85)		
Licania alba/majuscula	69	(168)	50	(93)	59	(58)	75	(127)	79	(220)
Ormosia coutinhoi					76	(50)	13	(8)		
Chamaecrista adiantifolia					65	(48)	13	(6)		
Eschweilera potaroensis	8	(4)			59	(205)	31	(22)		
Sterculia rugosa	23	(16)	50	(58)	53	(23)	50	(28)	43	(68)
Swartzia 3spp.	31	(44)	25	(12)	41	(27)	25	(8)	50	(42)
Carapa guianensis/procera	38	(44)	33	(51)	94	(215)	69	(129)	57	(85)
Lecythis zabucajo	38	(36)	8	(4)	53	(41)	50	(32)	50	(59)
Swartzia leiocalycina	8	(4)	50	(175)	47	(124)	100	(337)	21	(25)
Pithecellobium jupunba	15	(12)	33	(19)	35	(13)	81	(30)	29	(30)
Chlorocardium rodiei	8	(4)	8	(4)	47	(96)	81	(256)		
Eperua falcata	38	(284)	17	(16)	94	(278)	81	(220)	86	(148)
Eschweilera sagotiana/subglandulosa	23	(32)	58	(113)	94	(288)	100	(440)	100	(669)
Tapirira obtusa	8	(4)	17	(8)	82	(73)	19	(8)	57	(47)
Diospyros/Lissocarpa	23	(12)			59	(43)	44	(16)	57	(55)
Mora gonggrijpii			25	(78)	59	(136)	75	(250)	36	(182)
Clathrotropis brachypetala/macrocarpa			17	(19)	65	(61)	63	(52)	43	(42)
Mora excelsa			42	(198)	76	(214)	75	(392)	93	(355)
Protium 3spp.					82	(68)	63	(56)	71	(182)
Pentaclethra macroloba					88	(252)	56	(67)	79	(131)
Alexa ssp.	8	(16)			65	(129)	50	(103)	86	(635)
Unknown spp.	62	(120)	42	(23)	88	(197)	63	(56)	14	(21)

Two outlier plots fell within the coastal zone swamp and marsh forest zone, a clearly defined forest in the coastal zone of the Guianas (e.g. Fanshawe 1952, Lindeman & Molenaar 1959, de Milde & de Groot 1970c,f, see also Chapter 4).

6. The Northwest Guyana coastal swamp forests, characterised by *Virola surinamensis*, *Iryanthera lanceifolia*, *Pterocarpus officinalis*, *Tabebuia insignis* and *Symphonia globulifera*.
7. Coastal mangrove forest (de Milde & de Groot 1970c,f)

Relation species and soils

There is a clear preference of a number of tree species for certain soil types (Table 5.2.). Peat soils are characterised by a few species such as *Tabebuia insignis, Symphonia globulifera, Pterocarpus* and *Macrolobium*. *Virola surinamensis* and *Iryanthera lanceifolia* are also characteristic for these soils over extensive areas in the northwest, that were underrepresented in the survey. Soils of moderate hydrology (loam, brown sand, laterite) have the highest species diversity (Table 5.3.) and thus the highest number of species with preference for them. Clay soils are somewhat poorer and have uniquely high dominance of *Mora excelsa* and to a lesser extent of *Carapa* spp. Common species with a preference for excessively drained white sands are e.g. *Eperua falcata, E. grandiflora, Dicymbe altsonii, Chamaecrista adiantifolia* and *Ormosia coutinhoi*. The preference of certain dominant tree species gives rise to specific forest types on different soils. Within soil types there are smaller differences (Fanshawe 1952) and these are often attributable to small differences in soil hydrology based on the location on watersheds (ter Steege *et al*. 1993, Chapter 8).

Endemism

Species endemic to the three Guianas are, in Guyana, especially abundant in the central and northwest region (Figure 5.4), where they usually amount to more than 50% of all individuals > 30 cm in the forest. In forest just behind the coastal belt they may amount to as much as 80%. Species endemic to Guyana are more narrowly confined with maximum densities in an area surrounding the Potaro River basin and a small area to the east of that (Figure 5.5). These species include *Dicymbe altsonii, Chlorocardium rodiei, Vouacapoua macropetala, Eschweilera potaroensis and Swartzia leiocalycina*, the second and last being important timber species. Note that not all species are found abundantly in the same areas (Appendix 3). *Dicymbe*, is confined to the Pakaraima Mts. wet forest area, *Eschweilera potaroensis* to the area surrounding the confluence of the Potaro and Essequibo rivers, *Vouacapoua macropetala* and *Swartzia leiocalycina* to central Guyana and *Chlorocardium* to a slightly larger area around central Guyana .

Typical Guianan lowland genera such as *Licania, Swartzia, Lecythis* and *Eschweilera* were common throughout the lowland forest of Guyana. However, Lecythidaceae are more common (on an individual per community basis) in north and central Guyana (ter Steege 1998a), whereas *Swartzia* is more common in central to east Guyana (ter Steege 1998a). One would expect (given log-normal distribution of individuals among species within genera, see e.g. Nelson *et al.* 1990, Rankin *et al.* 1992) that where the higher taxa are more common, more species will be present (but see Chapter 6).

Table 5.2 Species preference for soil types in Guyana. No. Trees/10ha is given for those species that showed significant (chi square) preference for one or more soil types. The soils are ordered according to hydrology: from permanently wet to excessively drained. Important occurrences are shaded.

Soil type	**Peat**	**Clay**	**Loam**	**Brown sand**	**Laterite + rock**	**White sand**
Area (ha)	7.3	62.9	29.1	71.7	5.9	7.1
No. of plots	37	344	172	373	32	46
Species						
Tabebuia insignis/ (+stenocalyx)	33.8	1.3	1.3	0.7		1.4
Symphonia globulifera	52.8	2.3	1.3	1.4	1.7	2.7
Pterocarpus 4spp.	82.6	16.3	17.1	3.3		
Macrolobium 3spp.	24.4	5.9	6.3	0.3		
Mora excelsa	29.8	99.1	34.3	37.6	1.7	4.1
Carapa guianensis/procera	16.2	31.8	18.1	11.3	20.3	1.4
Protium 3spp.	5.4	8.6	9.6	5.0	6.8	1.4
Ecclinusa sanguinolenta		9.2	4.0	5.4	3.4	
Couratari guianensis		0.5	5.3	1.5		
Pentaclethra macroloba	1.4	20.4	25.7	12.2	8.4	2.7
Alexa ssp	2.7	32.4	50.5	16.7	5.1	12.3
Eschweilera coriacea/decolorans		11.9	22.4	7.7	6.8	1.4
Leatia/Casearia		0.6	4.3	3.3		
Pouteria guianensis		4.4	9.6	4.1	1.7	1.4
Licania alba/majuscula		12.7	20.1	17.0	5.1	2.7
Lecythis holcogyne		1.6	6.6	4.4	1.7	
Swartzia 3spp.		1.1	5.6	2.6	1.7	
Dicymbe corymbosa	8.1	14.9	33.3	13.8	11.8	12.3
Lecythis confertiflora		2.5	5.9	3.2	3.4	
Goupia glabra		7.0	12.2	15.6	6.8	
Swartzia leiocalycina		16.4	19.8	25.7	16.9	
Eschweilera sagotiana/subglandulosa	2.7	53.7	67.3	38.5	74.3	1.4
Pouteria speciosa		1.6	0.3	6.1		
Xylopia 5spp.		0.6	0.7	3.5		
Mora gonggrijpii		56.5	16.2	28.6	50.7	8.2
Eschweilera potaroensis		7.8	23.4	9.3	25.3	
Terminalia dichotoma	23.0	3.8	6.3	3.3	5.1	32.7
Chlorocardium rodiei	1.4	15.8	8.6	19.5	32.1	
Trichilia rubra		3.1	1.0	5.5	5.1	
Pseudopiptadenia suaveolens		2.0	1.0	5.4	3.4	
Sclerolobium guianense/micropetalum		2.3	3.0	6.8	3.4	1.4
Pouteria minutiflora		1.9	3.0	5.2	3.4	1.4
Ormosia 6spp.	1.4	2.7	3.0	2.3	10.1	1.4
Pouteria filipes	1.4	4.5	5.6	4.4	20.3	
Licania/Pouteria		0.6	0.7	5.1	3.4	
Dicymbe altsonii		46.3	75.5	34.5	62.5	102.1
Manilkara bidentata		2.5	8.2	5.2	16.9	4.1
Pouteria cladantha		2.8	0.3	1.1	13.5	
Aspidosperma excelsum	1.4	0.8	3.6	7.0	3.4	9.5

Iryanthera 4spp.	1.4	1.1	2.6	0.6		8.2
Eperua falcata	9.5	30.4	29.7	30.8	20.3	118.4
Tapirira marchandii		2.7	6.6	2.3	1.7	13.6
Chamaecrista adiantifolia	5.4	0.9	3.0	1.4	1.7	20.4

Table 5.2 (continued)

Soil type	**Peat**	**Clay**	**Loam**	**Brown sand**	**Laterite + rock**	**White sand**
*Eperua grandiflora/(jenmanii)**	19.0	21.4	13.2	20.9	10.1	119.8
Hevea pauciflora		1.7	4.0	1.2	5.1	8.2
Catostemma 3spp.	10.8	19.7	28.0	21.4	20.3	136.1
Parkia ulei		0.3	2.6	2.3		6.8
Talisia squarrosa/(furfuracea)		0.8	1.0	1.4	5.1	8.2
Pradosia schomburgkiana		0.6	2.6	1.9	5.1	17.7
Ormosia coutinhoi	1.4	0.8	2.3	1.4		34.0
Aldina insignis		0.9	2.3			70.8
Micrandra sp.		2.0				121.1

* The high occurrence on white sand is exclusively caused by *Eperua grandiflora* as *E. jenmanii* is a riverine species.

Species richness and diversity

Species diversity, expressed as Fisher's α ranged from 1 to 67.8, while the Shannon-Weaver index varied from 1.2 to 4.2 (and were well correlated, r=0.94, p<0.001). Species diversity was highest in the southern part of Guyana (Figure 5.6). As with the ordination scores, there was no apparent spatial scale at which the variance in diversity levels off (exponentially increasing semivariance with distance between points). Thus, as with the DCA scores, there existed a gradual change from south to north.

Species diversity showed no correlation with rainfall (r=0.08, p>0.487) but varied strongly with geographical location and soil type (ter Steege 1998a, Table 7.3). High α-diversity was found on intermediately moist soils, such as brown sand, loam and laterite, whereas potentially very dry soils, such as white sand and rock and very wet soils, such as peat, had lower diversity - a pattern consistent over Guyana with overall species richness and thus for each soil type increasing towards the south. Because different soil types have somewhat different forest composition (that is: poor soils are not a poor representation of rich soils, see Chapter 8), soil heterogeneity contributes to β-diversity in all national forest regions.

Discussion

The data show that there are large differences in forest composition and diversity over the study area. On the basis of TWINSPAN and DECORANA analyses five national forest regions could be distinguished in Guyana, that were well separated geographically. Two more national forest regions, not covered by the data here, but well documented elsewhere, were added. This is important information that can be fed into the discussion of a protected areas strategy for Guyana.

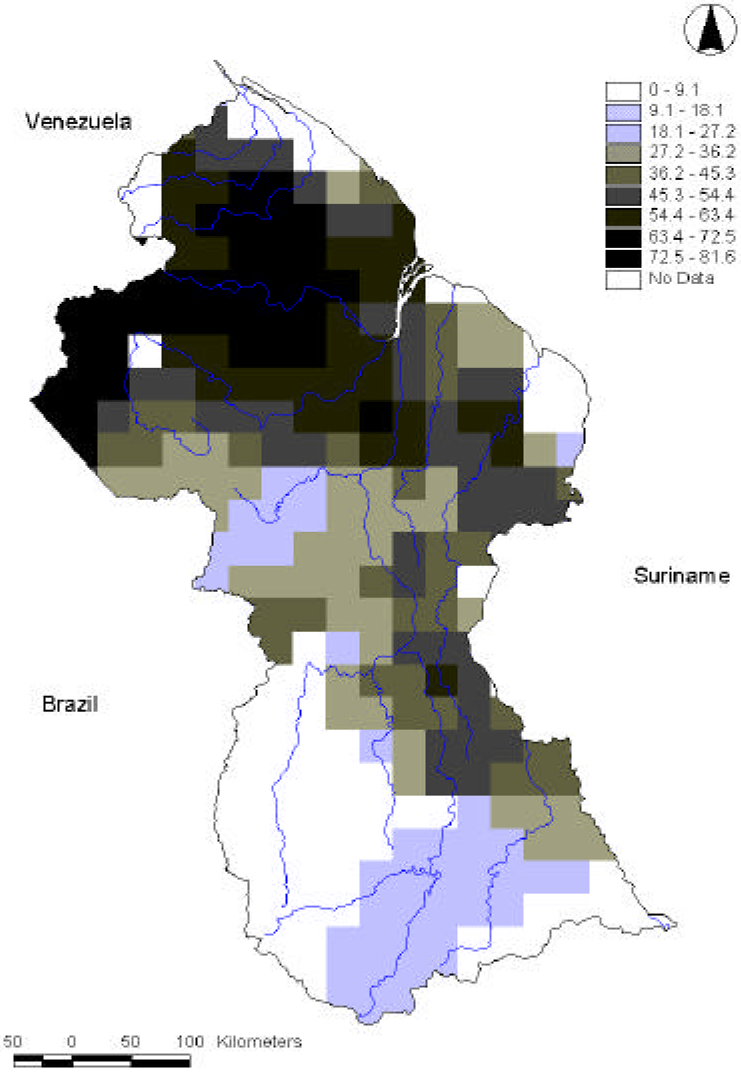

Figure 5.4 Map of abundance of individuals of species endemic to the three Guianas (excluding the species endemic to Guyana, which are in Figure 5.5), expressed as their percentage in the forest community. Data is interpolated at 0.25-degree grid level with spatial inter-distance weighting up to 50 km.

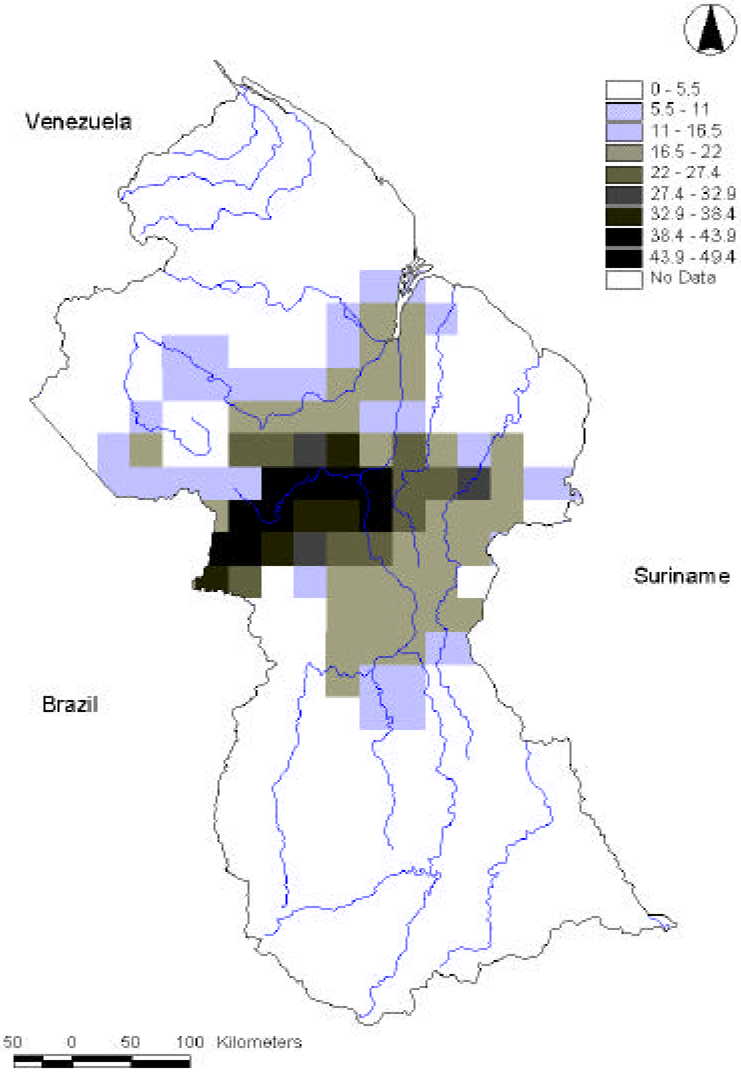

Figure 5.5 Map of abundance of individuals of species endemic to Guyana, expressed as their percentage in the forest community. Data is interpolated at 0.25-degree grid level with spatial inter-distance weighting up to 50 km.

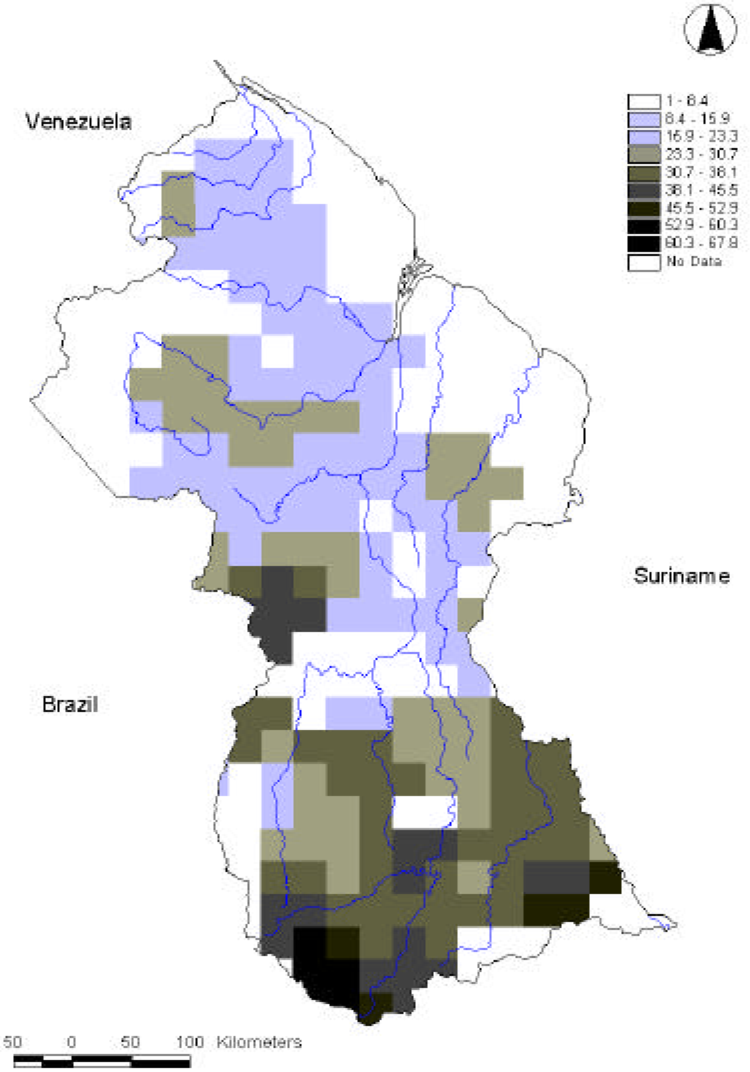

Figure 5.6 Alpha-diversity of FIDS locations in Guyana. There is a clear geographical increase in diversity from south to north. Data is interpolated at 0.25-degree grid level with spatial inter- distance weighting up to 50 km. Dots maps can be found in ter Steege (1998a) and Chapter 7 (Figure 7.2A).

The five national forest regions correspond well with our expectations as discussed below.

The southern forests are situated on soils developed on the crystalline shield, known as the 'Guiana peneplain' (Gross-Braun *et al.* 1965, Gibbs & Barron 1993). This peneplain extends from (east Colombia-) Venezuela, through the Guianas to Amapa (Brazil). These forests were among the least known in the Guianas (see also Chapter 4 for more information). The forests are similar in composition to forests in Venezuela (Rollet 1969), Suriname (unpublished FAO inventory data) and adjacent Brazil (Prance 1989, Chapter 4) on the crystalline shield. Genera that are more common on the shield in south Guyana, Venezuela and Suriname compared to central and northwest Guyana include: *Anacardium, Andira, Bagassa, Cecropia, Couratari, Dipteryx, Geissospermum, Laetia, Parkia, Pourouma, Sclerolobium, Simarouba, Tetragastris, Virola* and *Vochysia*. Several of these genera are comprised of species with medium to light wood and are characteristic of late succession. They are mainly wind or animal dispersed. *Geissospermum*, a genus typical of south Guyana may also be found in large parts of Amapa and was found to be dominant near the mouth of the Amazon (Mori *et al*. 1989) and very common in the forest near Manaus (Rankin-de Merona *et al*. 1992).

The forests of the Pakaraima Mts. are part of the central Guayana province (Berry *et al.* 1995). They were previously classified as belonging to the *Eschweilera-Dicymbe* association (Fanshawe 1952, Chapter 4). The major soils in the region are shallow and rocky (Gross-Braun *et al.* 1965) having formed on steep volcanic mother material (basic and acidic) and on sandstone. Because of the lack of tree spotters familiar with this area a larger number of species have been classified as unknowns in this area. The forest composition is thus likely to differ more from central Guyana than the results here show. It can be expected that the forest composition will be similar the forests just over the border in Venezuela (see Huber 1995b, Chapter 10).

The forests in the northwest of Guyana, are found both on soils developed on the crystalline shield (Granites and Greenstones, Gibbs & Baron 1993) and on pockets of Plio-Pleistocene sediments (see Gross-Braun *et al.* 1965). This mosaic is cause for the geographical overlap with forest of central Guyana. Upland forests dominated by *Alexa, Eschweilera, Licania* and *Catostemma* continue far into Venezuela (see Huber 1995a). The latter forests were classified by Fanshawe as the *Alexa imperatricis* faciation of the *Eschweilera-Licania* association. However, because of its lack of Legume dominants and high occurrence of *Alexa*, the northwest region is considered sufficiently different from central Guyana here to be classified as a forest region.

The coastal swamp forests are found in a band south of the coast on peat soils over alluvial and marine clays (Gross-Braun *et al.* 1965, de Milde & de Groot 1970c,f), whereas the mangrove forests are found in a narrow strip along the coast. This area extends from the mouth of the Amazon to the mouth of the Orinoco (Chapter 4).

Within national forest regions there are also large differences, especially between forests on different soils and this is supported by several studies (Davis & Richards 1934, Fanshawe 1952, ter Steege *et al.* 1993). Swampy peat soils and excessively drained white sands have a low diversity but a few specific species are apparently well adapted to the harsh conditions. Within soil types such as the brown sands and the white sands of the Berbice Formation gradients in species composition can be found from the wet lower sections of a watershed to the dryer upper parts (ter Steege *et al.* 1993). Thus soil heterogeneity affects tree composition at three levels, national, regional and local.

Large-scale differences are possibly due to differences in soil chemical status and fertility, leading to appreciable shifts in abundance of species. There were also large differences in α-diversity between the south and especially central Guyana. These differences were not well explained by rainfall differences, whereas soil types explained a good portion of the variation in diversity. The regional effect however was not entirely explained by soil type as all soils in the south had higher diversity than their counterparts in the north (Table 7.3). Two hypotheses can be put forward. First: the soils of the southern forest have developed on the crystalline shield and are richer than the soils formed on the very impoverished sediments. The latter soils allow only highly adapted species, such as members of the Leguminosae in general and those of the Caesalpiniaceae in particular to dominate.

Secondly, it has been argued (Hammond & Brown 1995, Chapter 7) that Guyana has experienced a very low rate of *large-scale* disturbances and that this, through competitive exclusion (cf. Huston 1994), has led to low diversity forests (see also Hart *et al.* 1989). In addition to low levels of natural disturbance, the central area of Guyana is thought to have been little used by pre-Colombian Amerindians (Evans & Meggers 1960). Thus, this area may have experienced the least environmental disturbance of all regions in Guyana (Chapter 7) and possibly Amazonia. In contrast, southern and northwestern forests of Guyana are known to have acted as important cultural centres prior to European arrival (Chapter 7). The forest soils around the Cuyuwini river have high presence of arrow points, charcoal and 'terra preta' (D. de Freitas pers. com.), petroglyphs (Dubelaar 1986) and other archaeological remains (Evans & Meggers 1960). Thus the high predominance of late successional species found there and human dispersed species may indicate high historical forest disturbance, whereas the area at present is almost uninhabited - present day Amerindian lands are mainly along the savannah-forest border (Chapter 7).

Because the inventories used were strategic low-level forest inventories the data have some inherent flaws. 1) Not all individuals were properly identified to the species level (and no reference collections were made to check identifications at a later stage). Specifically, some species in the southern region were identified by an Arawak name of a related species in the north, where it was thought to be a different species but unknown to the Arawak tree spotters (de Milde & de Groot 1970g). Thus the south is likely to be more different from central and north Guyana than can concluded now. The same is true for the forest in the Pakaraima Mts. 2) Absence of a species from a particular location in this inventory does not necessarily mean that the

species is absent in that region - the species could occur at such low densities that it is not picked up by a low-level inventory. For instance, *Geissospermum sericeum* was very prominent in the south and not found in central Guyana but it occurs regularly in the forests in central Guyana (pers. obs.). 3) Not all known forest types were well covered, including, for instance, the semi-deciduous *Centrolobium paraense* - *Cordia alliodora* forest (Fanshawe 1952) of the foothills of the Kanuku mountains in the south and the coastal swamp forests in the Northwest of Guyana.
Even with these flaws, I believe that the data are useful for defining macro-geographical patterns and are useful for the delimitation of (floristic) national forest regions in Guyana. This is supported by the fact that the regions make sense in a broader geographical perspective (see above and Chapters 4 & 6).

Six locations, on the outer edge of the geographical range of the study area, were considered outliers in the TWINSPAN and DECORANA analyses. These plots consist of two coastal swamp forest plots (forest region 6), two east Guyana plots and two 'savannah bush island' plots. For proper classification of these areas more information is needed.

Because the identifications of some taxa were not precise, diversity is almost certainly underestimated. All unknown vernacular names were treated as different species but individuals reported as unknown species were lumped. Such individuals are more abundant in the west-central region and to a lesser extent in the south. Thus, the west-central region is likely to be more diverse than presented here. However, because of the relative rarity of such species in the community I am confident that these unknowns would not greatly change the overall pattern in national forest regions.

Whereas central Guyana has a low α-diversity (Chapter 3, 4), it is endowed with a high occurrence of endemics, Lecythidaceae and Chrysobalanaceae, both families with high diversity in the Guianas (Gentry 1990, Berry *et al.* 1995, Mori & Prance 1993, Prance 1986, ter Steege *et al.* 1996). As for genera, *Licania* and *Swartzia* are notably diverse. Assuming log-normal distribution of individuals over taxa (see Nelson *et al*. 1990, Rankin-de Merona *et al.* 1992) it should be expected that central Guyana is rich in these 'Guianas-specific' taxa (Chapter 6).

The results presented here are based on large forest tree data alone. Thus, no conclusions on composition or diversity of non-forest areas, such as savannahs (see Chapter 11), the montane forests of the west of the country (Chapter 10), or even other plant groups within the forest (Chapter 9), can be made. However, as trees are a major structural component of the forest, their diversity will almost surely have an effect on the diversity of the 'many interstitial groups' (Huston 1994, Chapter 9).

Conclusions

There were two objectives formulated by the Guyana Government that were addressed with the data.

1. Preservation of viable examples of all natural ecosystems in Guyana

There are at least seven distinct national forest regions in Guyana. Any comprehensive protected areas system should thus include forest areas in all of these regions. Because habitat (read soil) differences are a significant source of β-diversity and as such are an important aspect of conservation (Tuomisto *et al.* 1995) in any protected area habitat diversity should be as large as possible. Because soils and forest correlate so well in Guyana, the use of the forest type maps (de Milde & de Groot 1970 a-f) and soil maps (e.g. Gross-Braun *et al.* 1965) should be used to accomplish this.
Below the major seven national forest regions are listed to show existing proposals of protected areas that would preserve significant forests areas within them (Figure 5.7, see also GNRA 1989, Hoosein 1996):

1. **South Wet**: New River Triangle; Cuyuwini-Kasykaitu; Konashen; Wakadanawa (Ramdass & Hannif 1990).
2. **South Dry**: the Kanuku mountains (Agriconsulting 1993, Parker *et al.* 1993), The southern half of Iwokrama consists of this type.
3. **Central Wet**: Iwokrama can preserve a bit of this forest region in its northern half (ter Steege 1998b); Forest Reserve Mabura Hill (some 1900 ha); Moraballi Forest Reserve (logged with experimental plots).
4. **Pakaraima Mts. Wet**: cabinet approved extension to 58,000 ha (in 1989!), WWF proposed 450,000 (Schuerholz 1991); Roraima Heritage Site (Ramdass & Hannif 1990)
5. **Northwest Wet**: Shell Beach Wildlife Sanctuary (Mangroves, Ramdass & Hanif 1990)
6. Swamp Forest: none
7. Mangrove Forest: see 5

Note that none of the proposals includes a significant portion of the forest from central or northwest Guyana, an area where the major concessions in Guyana are found and where rapid action would be needed if Guyana were to preserve some of this unique forest.

2. protection of areas of particular biological significance

The south of Guyana had highest diversity in the data set presented here. Since there are at present no concessions for timber or mining in the deep south selecting an area should pose not too many political obstacles.

Central Guyana (and the Northwest) have lowest diversity but a higher proportion of typical Guianan taxa and endemics. Furthermore, the low diversity could be the results of a long standing process of low disturbance and, as such, possibly unique to South America. Because central Guyana and the Northwest are the main timber concession areas, swift action to preserve a portion of this important area is needed.

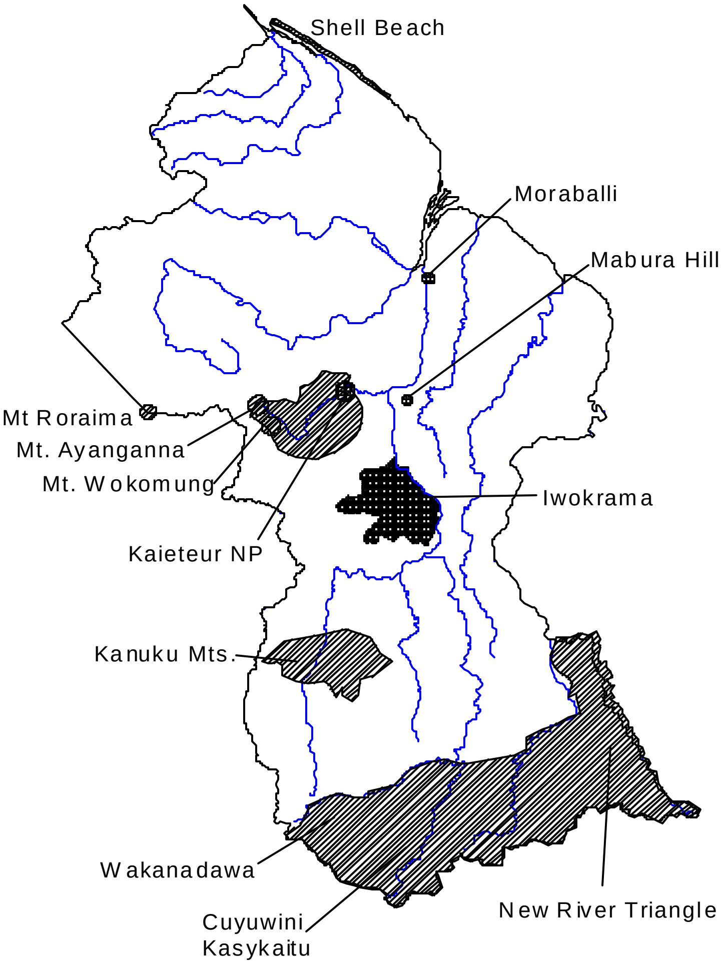

Figure 5.7 Map of 'Protected Areas' in Guyana and proposals that could conserve significant forest areas. Kaieteur (1.01 ha) is the only true National park at present. The Government of Guyana suggests to extend this to 58,000 ha (since 1989, see Chapter 12), shown here is WWF proposal of 450,000. Moraballi Forest Reserve is a logged Forest Reserve with experimental plots. Mabura Hill Forest Reserve (Tropenbos-Guyana) is a set of three research plots (appr. 32km^2), designated by the Guyana Forestry Commission as Research Plots. Iwokrama, 360,000 ha, is to set aside half of its area as a wilderness preserve. Without status are Mt. Roraima, Mt. Ayangana, Mt. Wokomung, New River Triangle, Cuyuwini-Kasykaitu, Konashen, Wakadanawa (Ramdass & Hannif 1990). Two proposals exist for the Kanuku Mountains

Again, it needs to be stressed that the forest inventory data only provides information on forest (and then not even all forest types). It should only add to the discussions of parks in Guyana. Decisions concerning savannahs in the south and northeast of the country cannot be made with these data. Other important areas, such as bird sanctuaries in the northeast, wetlands in the northwest, beaches for sea-turtle laying have to be made with specific data.

Also for good representation a regional perspective is necessary. For instance, Mount Roraima is quite unique from a Guyana point of view but is only a small portion of Pan-Tepui, which stretches far into Venezuela and may be relatively well preserved there (Huber 1995b, Figure 1.1, Chapter 10). Putting the forest vegetation in a regional perspective, however, reveals that Guyana has a lot to offer. It may have low diversity (and from a neo-tropical perspective the lowest priority, Chapter 3) but it may also be the least disturbed forest of South America. As such, the low diversity forests deserve a place in the natural history laboratory. Carefully comparing low diversity forest with high diversity forest will certainly give more insight in the process of maintaining diversity in tropical rain forests. This would thus aid in the fulfilment of number five of the Government's objectives.

6 CAN BOTANICAL COLLECTIONS ASSIST IN A NATIONAL PROTECTED AREA STRATEGY IN GUYANA? [1]

Hans ter Steege, Marion Jansen-Jacobs, Vijay Datadin

Introduction

In Chapter 5 (ter Steege 1998a) the use of large-scale forest inventory data is discussed in the light of the selection of National Parks in Guyana. Based on the forest inventory data five forest regions are described for those parts of Guyana covered by the inventories. Data from other sources (e.g. de Milde & de Groot 1970a, Fanshawe 1952) support the addition of at least two forest regions in the Northwest of Guyana, outside the inventory area. Whereas the forest inventory data allow us to specifically look at forest communities, the names of species are not always unique (ter Steege 1998a). Several botanical species may be included within one vernacular name (for Guyana: see Mennega *et al*. 1988). Thus, these forest inventories tend to underestimate diversity. Also, the same vernacular name was given to some tree species in the south, even when they were already known to be different from the species in the north with that same vernacular name (de Milde & de Groot 1970b). Thus, the differences between the northern and the southern forest regions may indeed be larger than described in Chapter 5.

Botanical collections refer to one particular species only. Moreover, they are permanent records and can always be checked again for proper identification. However, collections are clustered in areas with a high collecting effort. Consequently, areas with high 'species diversity' often coincide with well-collected areas (Nelson *et al.* 1990). Correcting for sampling errors these authors showed that most of the centres of high diversity in Amazonia (Conservation International 1990) should be considered sampling artefacts. Similarly, the 'hotspots' of diversity (Georgetown, Bartica, Kaieteur and Roraima) identified by a previous study in Guyana are also the best-collected sites and to a large extent sampling artefacts (The Centre for the Study of Biological Diversity 1995, Funk *et al.* 1999). The collecting density in the remainder of the country was too low to draw any conclusion as to the level at which this analysis was carried out.
Even if we assume that we can correct for sampling effort we have not corrected for the expertise and interest of a collector. Correcting for effort by applying a collecting-species curve, or using Fisher's α to correct for unequal sample sizes, assumes random sampling. Obviously, botanical collections are not random collections. For instance, around Mabura Hill, the five most abundant species (*Mora gonggrijpii, Eperua falcata, Chlorocardium rodiei, Dicymbe altsonii and Swartzia leiocalycina*) make up 43% of all individuals over 30 cm DBH (Welch & Bell 1971,

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[1] This paper has also been published as: ter Steege *et al*. (2000a). Can botanical collections assist in a National Protected Area Strategy in Guyana? *Biodiversity and Conservation* 9: 215-240.

raw data). These five species, however, account for only roughly 6% of all collections made of trees in the area (Ek & ter Steege 1998).

Once sufficient collections of species have been made, mapping potential distribution patterns using models may be used to estimate the potential distribution. Such analysis is based on the assumption that correlation with soil types and climatic variables are strong enough to predict the full range of a species. Good results have been obtained with DOMAIN (Carpenter *et al.* 1993). Whereas the algorithms should work well with relatively well collected (read sufficiently common) species in Guyana, they may not be suitable for the huge number of rare species that make up the bulk of the diversity of the forest.

We are thus faced with a problem. There is little time and money and incomplete data, which, in our opinion, has not been analysed correctly at present. Our main question is thus reflected in the title “Can botanical collections assist in a National Protected Area Strategy in Guyana?” and if so, how can they be used to describe differences in regional diversity and endemicity? Other questions are “How can we correct for unequal sample size when dealing with plant collections in Guyana?” and “At what spatial resolution can we look at the data?”.

To answer these questions we use botanical collections of a number of tree taxa, which are considered to be typical for the forests of the lowland Guianas, having both a high diversity and/or abundance in the area. Using simple GIS tools, we will examine the distribution patterns for the more common and endemic species in Guyana. We will compare the results those of a previous study (ter Steege 1998a, Chapter 5), focussing on the forest regions identified and on areas with high levels of endemicity. We will also try to assess the conservation potential of four previously proposed protected areas: Kaieteur National Park, the Iwokrama Forest, the Kanuku mountains and the New River Triangle-Akarai area.
We will show that, while botanical collections are difficult to use for the assessment of plant diversity, they can still contribute significantly to the selection of National Parks in Guyana.

Methods

Description of the taxa

In this study we use 5 taxonomic groups, which are considered to be typical for the lowland forests of the Guianas (see above). These groups are:

1. *Licania* (Chrysobalanaceae), a genus practically confined to the Neotropics, where it contains 183 species. In Guyana 61 species occur, 7 of which are endemic (Prance 1972, 1986, 1989).
2. *Eschweilera* and *Lecythis* (Lecythidaceae), genera with high diversity and abundance in the Neotropics. *Eschweilera* and *Lecythis* account for 84 species in the Neotropics, 27 of which occur in Guyana, 3 of which are endemic to Guyana (Mori & Prance 1993).
3. *Swartzia* (Fabaceae), a genus with at least 200 species in the Neotropics (Cowan 1968, Cowan & Lindeman 1989), 36 of which occur in Guyana, 10 of which are

endemic to Guyana. The species of *Swartzia* are often narrowly distributed (Koopowitz *et al*. 1994).

4. Lauraceae: the genera *Aiouea, Aniba, Chlorocardium, Endlicheria, Kubitzkia, Licaria, Mezilaurus, Nectandra, Ocotea, Rhodostemonodaphne* and *Sextonia*. The Lauraceae are a large pantropical family with over 800 species in the Neotropics (Kubitzki & Renner 1982, Rohwer 1986, Rohwer 1993). In Guyana one endemic species is found, whereas Guyana's main timber species, *Chlorocardium rodiei*, is practically confined to Guyana (ter Steege 1990).
5. Sapotaceae: *Pouteria* and related genera: *Chrysophyllum, Ecclinusa, Elaeoluma, Micropholis and Pradosia*. All the latter genera have exchanged species with *Pouteria*. The list includes all genera of major tree genera of the Sapotaceae, except *Ecclinusa* and *Manilkara*. There are 450 species of Sapotaceae in the Neotropics (Pennington 1990). Within the set of genera used 60 species occur in Guyana, 2 of which are endemic to the country.

Together these genera comprise over 250 species or 4% of the roughly 6000 flowering plant species in Guyana (Boggan *et al.* 1997). Because of their relatively high abundance (ter Steege 1998a, Chapter 5) they account for nearly 30% of all forest trees over 30cm DBH in Guyana (ter Steege 1998a, Chapter 4, 5).

Data collection

The data pertaining to the botanical collections were compiled from a number of sources. Firstly, lists of specimens from three Flora of the Guianas issues (Prance 1986, Cowan and Lindeman 1989, Mori & Prance 1993) were extracted. This provided us with a list of well-identified specimens but without collecting sites. Three herbaria in Guyana were searched for collections of the 5 groups mentioned. The "Accession Registers" of the Jonah Boyan Herbarium of the Guyana Forestry Commission proved invaluable for that task. The "Jenman Collection Books" of the Jenman Herbarium, University of Guyana served a similar purpose. The Botany Department of the Smithsonian Institution, Washington, kindly provided digital data from their extensive collections in Guyana (1986 - 1997). The Utrecht University Herbarium also holds a large Guyana collection (collection trips by: Stoffers *et al*. 1982, Maas *et al.* 1971 1979 1981 1988, Jansen-Jacobs *et al.* 1985 1987 1989 1991 1992 1994 1995 1997, ter Steege *et al.* 1985 1987-1992, Polak *et al.* 1990 - 1992, Ek *et al.* 1992-1997, Görts van Rijn *et al.* 1993, van Andel *et al.* 1994-1998). With collection lists of André Chanderballi of Missouri Botanical Garden, Pennington (1993), Johnston and Gilman (1995) and three Flora Neotropical volumes (Kubitzki & Renner 1982, Pennington 1990, Rohwer 1993) a final list was drawn up. Because the majority of the collections were identified by the respective specialists for the groups, we are confident that most identifications are correct.

The distribution area for all species was compiled from the floras used (see above). Species were classified as: 1) endemic to Guyana, 2) endemic to the three Guianas, 3) endemic to the Guiana Shield, 4) Amazonian, 5) occurring in a large part of South and Central America. The information was readily available for most species, except for a number of Lauraceae genera, for which no modern revisions exists.

Analysis

Regional (not α-!) diversity was quantified with Fisher's α (Fisher *et al*. 1943, Taylor *et al*. 1976), which is relatively insensitive to sample size (Leigh 1995, Rosenzweig 1995, Condit *et al.* 1998). Because sample sizes must not be too small to allow for a meaningful calculation, Fisher's α was first calculated for the 5 major forest regions identified by ter Steege (1998a, Chapter 5).

These areas are:
1. Northwest Guyana, including the coastal area west of the Essequibo River
2. Central Guyana, with omission of collections from Bartica Station, which were often nursery seedlings from seed material collected elsewhere (C.A. Persaud, pers. comm.)
3. the Pakaraima Mts.
4. the Dry South, forests surrounding the Rupununi Savannah
5. the Wet South, close to the southern border with Brazil

and
6. Northeast Guyana, for which forest inventory data was unavailable (ter Steege 1998a)

In addition, the data for smaller regions of particular interest were analysed:
1. Mabura Hill and surroundings, the field area of the Tropenbos-Guyana Programme in Central Guyana (ter Steege *et al.* 1996)
2. the Iwokrama Forest, field site of the Iwokrama Centre for Rain Forest Conservation and Development, also in Central Guyana (Kerr 1993)
3. Kaieteur Falls, a proposed national park in the Pakaraima Mts. (Schuerholz 1991)
4. Kanuku Mountains, a potential national park in the Dry South (Agriconsulting 1993, Parker *et al*. 1993)
5. Mt. Roraima, a potential national park in the Pakaraima Mts. (Ramdass & Hannif 1990)
6. Bartica-Potaro Road in central Guyana, an area in the White Sands Formation, on the edge of Central Guyana and the Pakaraima Mts., intensively collected by the former Forest Department.

To allow for further comparison plant collections per region were randomised 15 times and 15 random species-collection curves per region were constructed, the average of which was used for comparative purposes. To estimate local richness based on the plant collections, we fitted two models to the data. The first model is a non-asymptotic model (similar to the well-known species area curve):

$S_{(n)} = c * n^z$, where S is the number of species in a sample of n collections, with c and z being constants

The second model is an asymptotic model, assuming that there is a maximum number of species S_{max}, when most individuals in a restricted area have been collected (Colwell & Coddington 1995):

$S_{(n)} = (S_{max} * n)/(c + n)$, where c and n as above.

The data was also rarefacted by drawing 15 times 180 random collections from the set of each region. The number of species within these 'equal-sized' samples was compared. The analysis is based on the assumption that, even though botanical collecting is not a random process, the mechanism of acquiring species should be similar enough in large areas to allow for comparison within these samples.

Geostatistical analysis

Distribution areas of common species and endemics were compared with features known to cause differentiation in plant communities, such as rainfall, (monthly and yearly: Persaud 1994, Persaud and Persaud 1995), Pennman Evapotranspiration (PET, yearly: Persaud and Persaud 1993) and sunshine hours (yearly: Persaud 1982). The Hydro-Meteorological Service in Guyana kindly provided these reports.

During the analysis there were four problems:

1. there were considerable errors associated with the climate maps (Persaud 1994),
2. the soil map at 1:1,000,000 scale (Gross-Braun *et al.* 1965), provided too little detail between soil types that differ at very small scales (Jetten *et al*. 1993, Jetten 1994),
3. Coordinates of the collection sites were not always available and had to be estimated from descriptions on the herbarium labels (or collector trip reports, see Ek 1990)
4. Most species were rare and provided insufficient data for (statistical) analysis.

Thus, rather than utilising computer software to calculate the potential distribution patterns (Carpenter *et al.* 1993), we overlaid soil and climate maps with species distributions to come up with probable relationships. In most cases simple Chi-square test were used to assess if plant distributions were non-random with regard to abiotic factors (mainly rainfall and major soil type). To extract the collections per region studied the Access database was linked to a GIS (Arcview 3.1, ESRI Inc. 1998).

Results

Collections are not evenly distributed over the country (Figure 6.1). The south-eastern region has not received much attention (for geographical and geo-political reasons). Also the Cuyuni and Mazaruni basins are rather under-collected at present, due to the inaccessibility of these areas. Most collections, of the species selected, have been made in the forested area (see Figure 5.2), which is in agreement with the fact that most of the species are large forest dwelling trees. Some of the species occur in so-called 'bush-islands' in the southern savannahs.

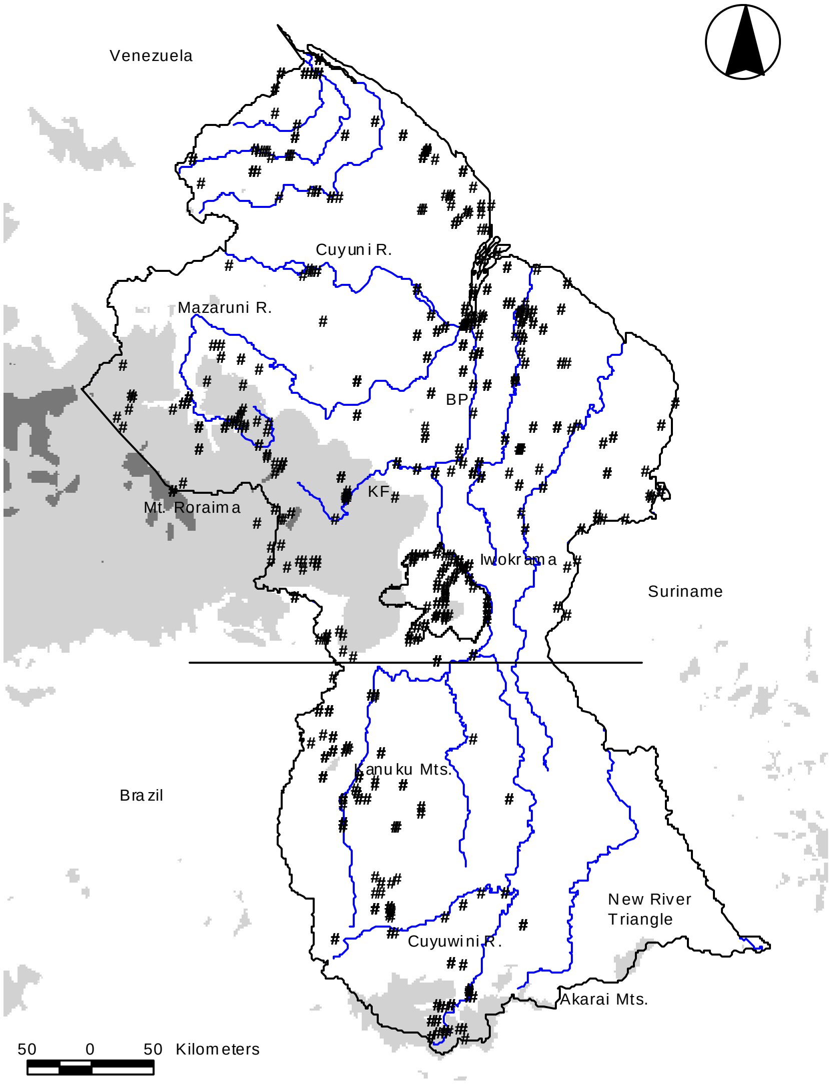

Figure 6.1 The distribution of 2268 collections of *Eschweilera, Lecythis, Licania, Swartzia, Ocotea* s.l., and *Pouteria* s.l. in Guyana. BP: Bartica-Potaro Road; KF: Kaieteur Falls. The horizontal line is the 4th parallel. Light grey: areas over 500m altitude, dark grey: areas over 1500m altitude (based on Digital Elevation Model of the USGS (http://edcwww.cr.usgs.gov/landdaac).

Species richness

A total of 2532 collections was retrieved, 2293 of which had been identified to the species level, with a total species number of 258. The largest genera are: *Licania* with 56 species, *Swartzia* (35), *Pouteria* (34) and *Ocotea* (25). Many species are rare (read: collected rarely): out of the 258 identified species, 61 are represented by only 1 collection, 26 by 2 and 42 by 3 to 4 collections. Together these species account for 50% of all species. Only 27 species are represented by 20 or more collections but they do account for 40% of all collections. Most species collected have an Amazonian distribution (37%, Table 6.1). A small part (9%) is endemic to Guyana and 7% are endemic to the 3 Guianas. Guiana Shield endemics constitute 24% of all species. Due to increased collecting several species have been added to the flora of Guyana, since the respective flora fascicles (see above) were written.

The breakdown by forest region (as defined by ter Steege 1998a) is as follows:

1. Northwest Guyana: A total of 385 collections, 344 of which identified. The most commonly collected species are: *Eschweilera wachenheimii* (18 collections), *Lecythis corrugata* (16), *Eschweilera sagotiana* (15), *Licania alba* (15), *Eschweilera decolorans* (14) and *Chrysophyllum argenteum* (12). This area has a very low percentage of endemics but a high percentage of Guiana Shield endemics (Table 6.1).
2. Central Guyana: 907 collections, 821 of which identified. The most commonly collected species are: *Chlorocardium rodiei* (38), *Licania alba* (23), *Licania heteromorpha* (23), *Eschweilera sagotiana* (23) and *Eschweilera pedicellata* (21). Endemics constitute just over 7% of the species list (Table 6.1) and are often collected *Chlorocardium* (38), *Licania cuprea* (14), *Swartzia leiocalycina* (12), *Swartzia xanthopetala* (11) and *Licania buxifolia* (11).
3. Northeast Guyana: 207 collections, 190 of which identified. The most commonly collected species are: *Licania incana* (23), *Ocotea schomburgkiana* (22), *Chlorocardium rodiei* (9), *Licania divaricata* (8) and *Lecythis corrugata* (7).
4. Pakaraima Mts.: 316 collections, 289 of which identified. The most commonly collected species are: *Licania incana* (23), *Licania heteromorpha* (10), *Eschweilera wachenheimii* (9), *Eschweilera coriacea* (8), *Licania lasseri* (8) and *Pouteria kaieteurensis* (6). Amazonian species are less common in this area of Guyana, which has a high proportion of endemics and Guiana Shield endemics (Table 6.1).
5. Dry South: 273 collections, 256 of which identified. The most commonly collected species are: *Eschweilera pedicellata* (24), *Pouteria surumuensis* (18), *Chrysophyllum argenteum* (15), *Swartzia dipetala* (12), *Licania apetala* (10), *Endlicheria reflectens* (10) and *Licania apetala* (10). The area is low in endemics (Table 6.1).
6. Wet South: 229 collections, 182 of which identified. The most commonly collected species are: *Eschweilera pedicellata* (15), *Licania leptostachya* (10), *Lecythis corrugata* (8), *Licania apetala* (7), *Pouteria cuspidata* (7) and *Eschweilera subglandulosa* (6). Endemics are few and the major part of the flora (55% and 62% of all collections) consists of species with an Amazonian distribution (Table 6.1).

Table 6.1 Floristic affinity (in percentage of total species) of 6 forest regions in Guyana: NWG Northwest Guyana, CG Central Guyana, NEG Northeast Guyana, PM Pakaraima Mts., DS Dry South, WS Wet South.

Status	**Total**	**NWG**	**CG**	**NEG**	**PM**	**DS**	**WS**
Endemic	8.9	2.3	7.2	9.1	9.4	1.5	3.5
3 Guianas	6.6	7.0	6.6	9.1	4.7	4.5	4.7
Guiana Shield	23.6	29.1	22.3	24.2	27.6	32.8	17.6
Amazonia	36.8	39.5	38.6	45.5	41.7	38.8	55.3
South Am.	7.0	14.0	9.0	7.6	9.4	11.9	5.9
Unknown	17.1	8.1	16.3	4.5	7.1	10.4	12.9

Licania, Eschweilera, Lecythis and *Swartzia* are most diverse in the central parts of Guyana (Table 6.2), especially in the Pakaraima Mts. Lauraceae and Sapotaceae are most diverse in the Pakaraima Mts. and the Wet South. Considering all taxa combined, the Pakaraima Mts. are more diverse than any other forest region in Guyana, with the Wet South and Central Guyana in second place. Low species richness typified the Dry South, the Northwest and Northeast. When calculating species richness values for smaller areas only a few areas have sufficiently large numbers of species. Two sites in Central Guyana, Mabura Hill and Iwokrama, have a regional diversity comparable to that of Central Guyana, in which they are situated (data not shown). The Kanuku Mts. show low diversity (data not shown), comparable to that of the Dry South, of which they are a part. Only the diversity of the area along the Bartica Potaro Rd., on the border of Central Guyana and the Pakaraima Mts., stands out. For *Licania, Eschweilera, Lecythis* and *Swartzia* Fisher's α is 37.0, only surpassed by that of the Pakaraima Mts. (Table 6.2).

Figure 6.2 shows the species-collection curves for the five main forest regions plus the east. The Pakaraima Mts. have the steepest species accumulation curve, whereas the Dry South is lowest in species accumulation per collecting effort. Rarefaction trials show the same results: the Pakaraima Mts. had an average of 98 species in the

Table 6.2 Species diversity of five forest regions in Guyana as calculated with Fisher's alpha. Abbreviations: n number of collections, S number of species. Abbreviations as Table 6.1.

	NWG	**CG**	**NEG**	**PH**	**DS**	**WS**
Eschweilera, Lecythis, Licania, Swartzia						
n	183	482	120	180	146	112
S	41	75	41	68	30	41
Fisher's α	16.4	24.9	22	39.2	11.4	23.3
x						
Ocotea s.l., *Pouteria* s.l.						
n	161	339	70	106	110	70
S	45	91	25	59	37	44
Fisher's α	20.7	40.8	13.9	54.8	19.6	50.8
X						
All taxa						
n	344	821	190	286	256	182
S	86	166	66	127	67	85
Fisher's α	36.8	62.2	35.9	88	29.5	62.1

15 random samples of 180 collections, followed by Central Guyana with 90, the Wet South with 84, Northwest Guyana with 66, Northeast Guyana with 65 and finally the Dry South with 58. These differences are highly significant (ANOVA on all data: $F_{[5,84]}$ =264, P << 0.001, Tukey's test: all regions have different number of species, except Northwest and Northeast Guyana).

The non-asymptotic model did not describe the data very well. Although the

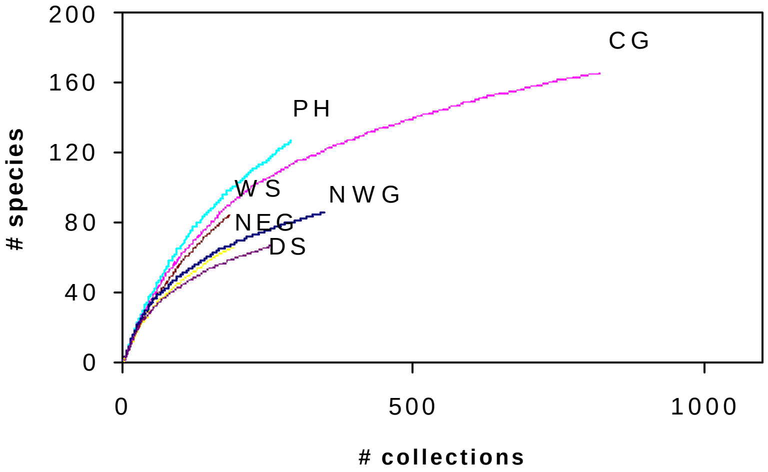

Figure 6.2 Species collection curves for 6 large regions in Guyana. Central Guyana is relatively well collected. A substantial increase in collecting effort may not increase its species list much (see text). Abbreviations: PH = Pakaraima Highlands, CG = Central Guyana, WS = Wet South, NWG = Northwest Guyana, NEG = Northeast Guyana, DS = Dry South.

coefficient of determination was fairly high (above 95% for all areas), the model did not describe the form of the curve closely, leading to overestimation of the species number at high collecting levels (data not shown). The asymptotic model had even higher coefficients of determination (Table 6.3) and followed the curves very closely in all cases. Table 6.3 lists some predictions for the number of species collected based on this model. The results are in close agreement with the above, with highest expected number of species in the Pakaraima Mts., followed closely by Central Guyana. The model also predicts that with a doubling of the collecting effort the number of species collected in Central Guyana will only rise from 166 to 183 species. The most substantial increases in species numbers are expected in the Wet South, where less than 50% of the expected species have been collected. The Pakaraima Mts. and Northeast Guyana are also relatively under-collected, with 55 and 59% of the expected species respectively.

Table 6.3 Observed (S) and expected ($S_{subscript}$) species richness of six forest regions in Guyana. Abbreviations: n number of plant collections, S number of species collected, S_n number of species estimated with asymptotic model (see text), S_{750} number of species expected with 750 collections, S_{1500} same with 1500 collections, S_{max} 95% confidence interval of the maximum number of species estimated for the region, S/S_{max} proportion of expected species that has been collected in the region, R^2 coefficient of determination for asymptotic model (see text), S_{end} estimated number of endemics (= S_{max} * % endemics of Table 6.1).

	Northwest	Central	Northeast	P Highlands	Dry South	Wet South
n	344	821	190	289	256	182
S	86	166	66	127	67	85
S_n	84	164	66	125	66	83
S_{750}	99	160	95	175	82	142
S_{1500}	106	183	103	199	87	160
S_{max}	115-116	214-215	111-113	231-233	92-94	181-185
S/S_{max}	.75	.76	.59	.55	.72	.46
S_{end}	3	15	10	22	1	6
R^2	0.998	0.999	0.999	0.9999	0.998	0.9999

Species distribution areas

Species distribution patterns are largely divided into two types: those of species with a major portion of their collections in northern Guyana and those of species with a major portion in the south. The boundary between north and south appears to be around the 4th parallel (data not shown). Figure 6.3 shows the distribution pattern of several species confined to the Northwest-central region of Guyana. The collections are almost completely confined to the area with an annual rainfall higher than 2200 mm. Figure 6.4 shows species with a southern distribution. These species occur significantly more below the parallel of 4°N within Guyana. Several of these species are confined (at least in Guyana) to the relatively dry forests surrounding the Rupununi savannahs. Several species within this data set are confined to the Pakaraima Mts. (above 500m altitude). Unfortunately, most have only been collected once. Figure 6.5 shows a few Pakaraima Mts. species, which have been collected at least a few times.

Endemism

Within the families surveyed 24 endemics were found: 10 species of *Swartzia*, 8 of *Licania*, 3 of *Eschweilera*, 2 of *Pouteria* and 1 of *Ocotea*. There are two areas with a concentration of endemics within the taxa selected in Guyana (Figure 6.6). The first area is situated in Central to Northeast Guyana with 14 endemics and is nearly completely confined to the White Sands (Berbice) Formation. The main concentration of endemics is in the northern part of the White Sands Formation in Guyana but some species have been collected as far south as the very southern edge of the White Sands Formation in the Iwokrama Forest (Figure 6.6, ter Steege 1998b). Several of the endemics of the White Sands Formation, such as *Licania cuprea* and *Swartzia eriocarpa,* range into the (white sands of the) Pakaraima Mts. A second concentration of endemics (7) is found in the headwaters of the Mazaruni and tributaries, including Mt. Roraima. Two of those endemics have a wider Pakaraima Mts. distribution, with *Swartzia tillettii* reaching the Iwokrama Mountains. Three *Swartzia* endemics have been found in the southern part of Guyana.

One, non-narrowly distributed, endemic, *Chlorocardium rodiei*, has a distribution that includes the White Sands Formation and Northwest Guyana. *Chlorocardium rodiei* has also been found on one locality in Suriname (and maybe one in Venezuela) but the centre of its distribution and the area where the species is abundant to co-dominant, is Central Guyana (ter Steege 1990, unpublished data).
Based on the percentage endemism in each region (Table 3.1) and the number of expected species in each region, Table 3.1 also lists the number of expected endemic species. This number is highest in the Pakaraima Mts. (22), followed by Central Guyana and Northeast Guyana. The Dry South has only one expected endemic species in the five taxonomic groups selected.

Discussion

The data of the botanical collections support to a large extent the results of ter Steege (1998a, Chapter 5). The strongest division in the data appears to be around the 4th parallel. This is also where a multivariate analysis of the forest inventories made its main division into southern forests and central-northern forests (ibid.). As suggested in figures 6.3 and 6.4 annual precipitation may play a role in this division (see also Davis 1941), as well as major geological features of the areas (Gross-Braun *et al*. 1965, ter Steege 1998a) and historical events (biogeography, see e.g. Whitmore & Prance 1987). As expected from a geographical point of view the Amazonian component increases from Central Guyana southward (Table 6.1). Davis (1941) already observed this trend. However, central and south Guianan forests still have a fair amount of species in common. Endemics are most prominent in the flora of central Guyana, where they are also most abundant (ter Steege 1998a).

Species Richness

Previous data suggested that South Guyana had higher tree α-diversity than Central and Northwest Guyana (ter Steege 1998a, Chapter 5). In terms of the regional species diversity of these areas the data show a different pattern (Table 6.2). Thus, while the forests in Central and Northwest Guyana have lower α-diversity (because they are dominated by a few species), at the regional level there are as many species as in the southern part. We suggest that the reason for this is a higher β-diversity in Central Guyana. Although many forests in Central Guyana are dominated by a few species, not all areas are dominated by the same species (see Davis & Richards 1934, ter Steege *et al.* 1993, Johnston & Gillman 1995, Comiskey *et al.* 1994, Ek 1997, de Jagher & Smeets 1997, Bröker & Huyskens 1998, Groenewegen & Smedema 1997, Chapter 8). Also the Central and Northeast Guyana are rich in habitat specialists. Forests on different soils have different species (ter Steege *et al*. 1993, ter Steege 1998a, Chapter 8). This implies that although the southern forests have higher α-diversity, they may be less heterogeneous at larger scales. For now, this remains to be tested.

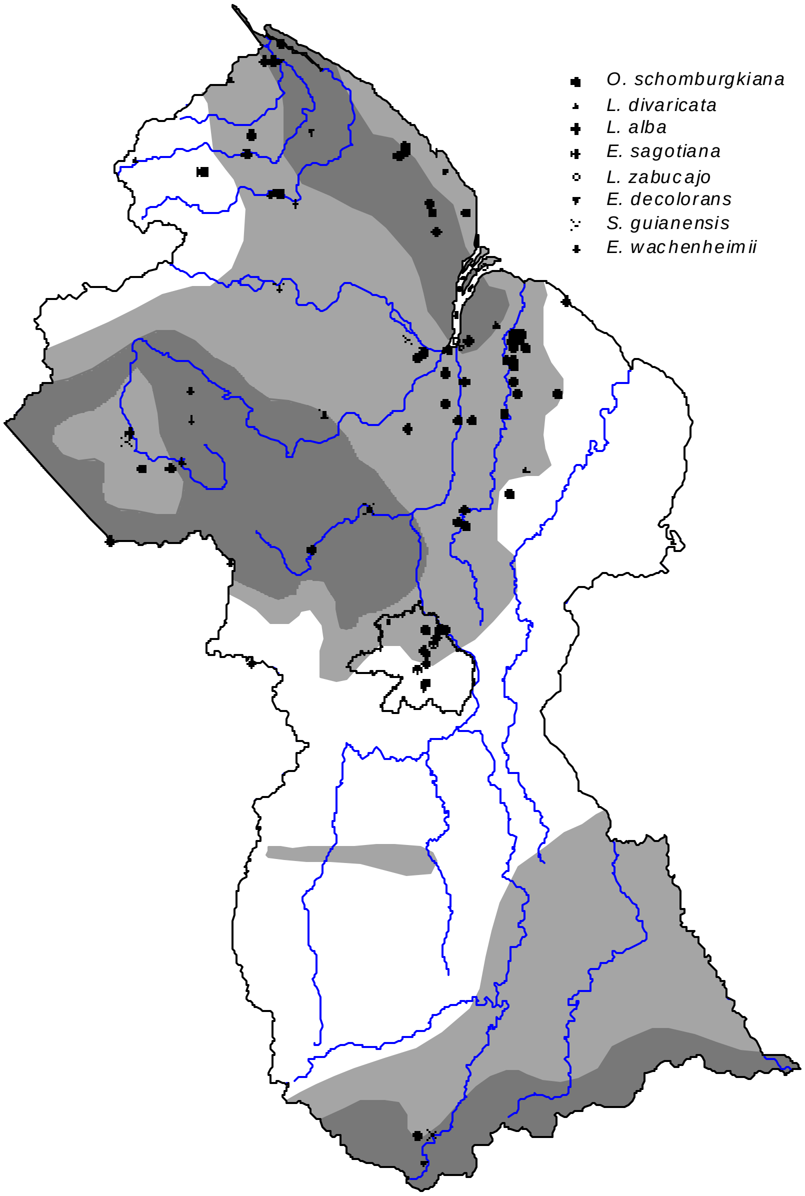

Figure 6.3 Distribution patterns of species with a 'Northwest-Central preference'. Grey shades: dark grey = annual rainfall > 2800 mm; light grey = annual rain between 2300 and 2800 mm; white = annual rain less than 2300 mm. Practically no records were found in the relatively dry zone (annual rainfall <2300 mm, sensu Persaud 1994) of Guyana. Within this zone there is a smaller band with annual rainfall under 2000 mm (Persaud 1994).

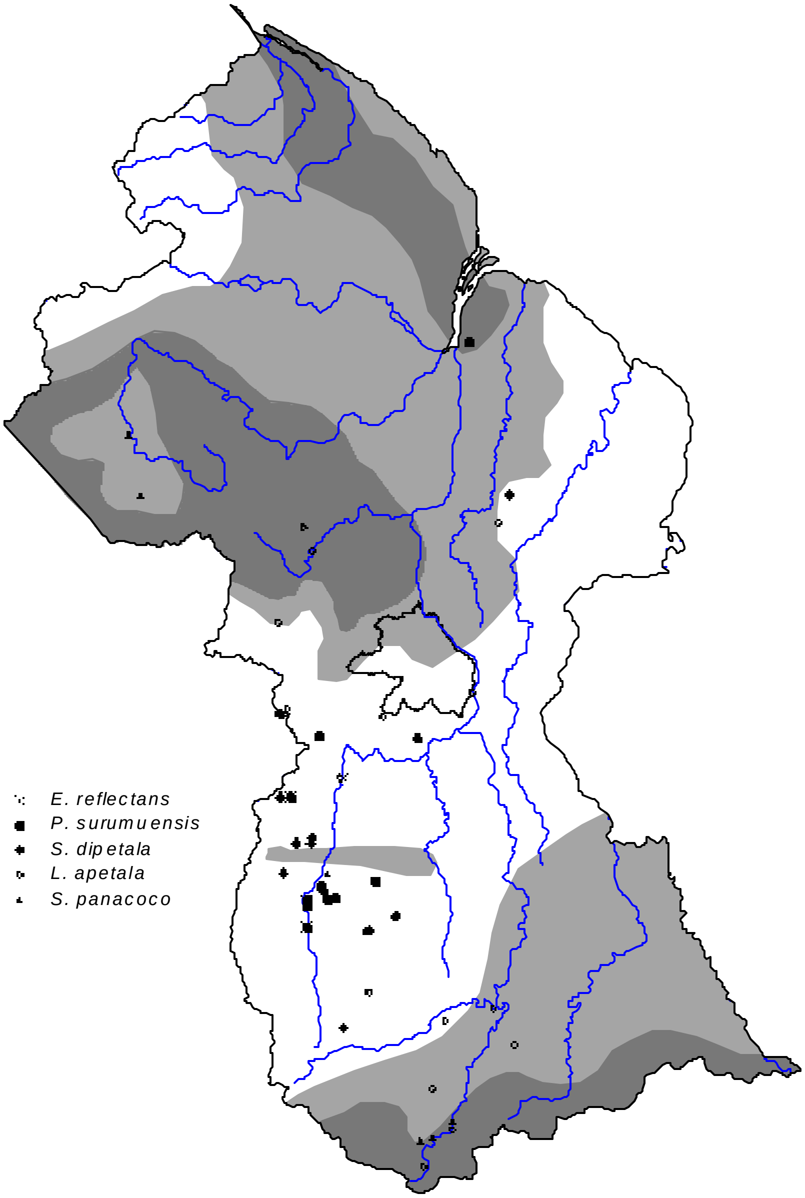

Figure 6.4 Distribution patterns of species with a 'southern preference'. Some of these species have also been collected in the Pakaraima Mts. area. Most of the collections fall within the dry area of Guyana. Grey shades as in Figure 6.3.

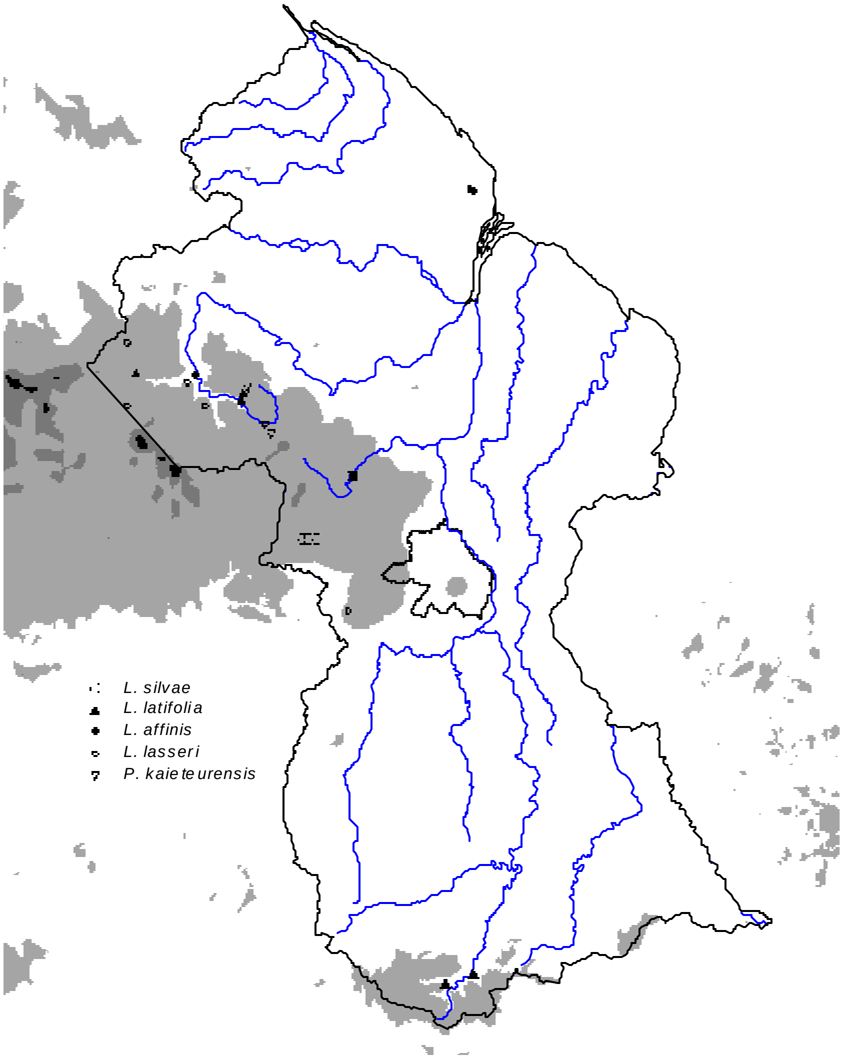

Figure 6.5 Distribution patterns of species with most of their collections in the Pakaraimas area. Shading: light grey = areas above 500 m (based on Digital Elevation Model, USGS (see Figure 6.1).

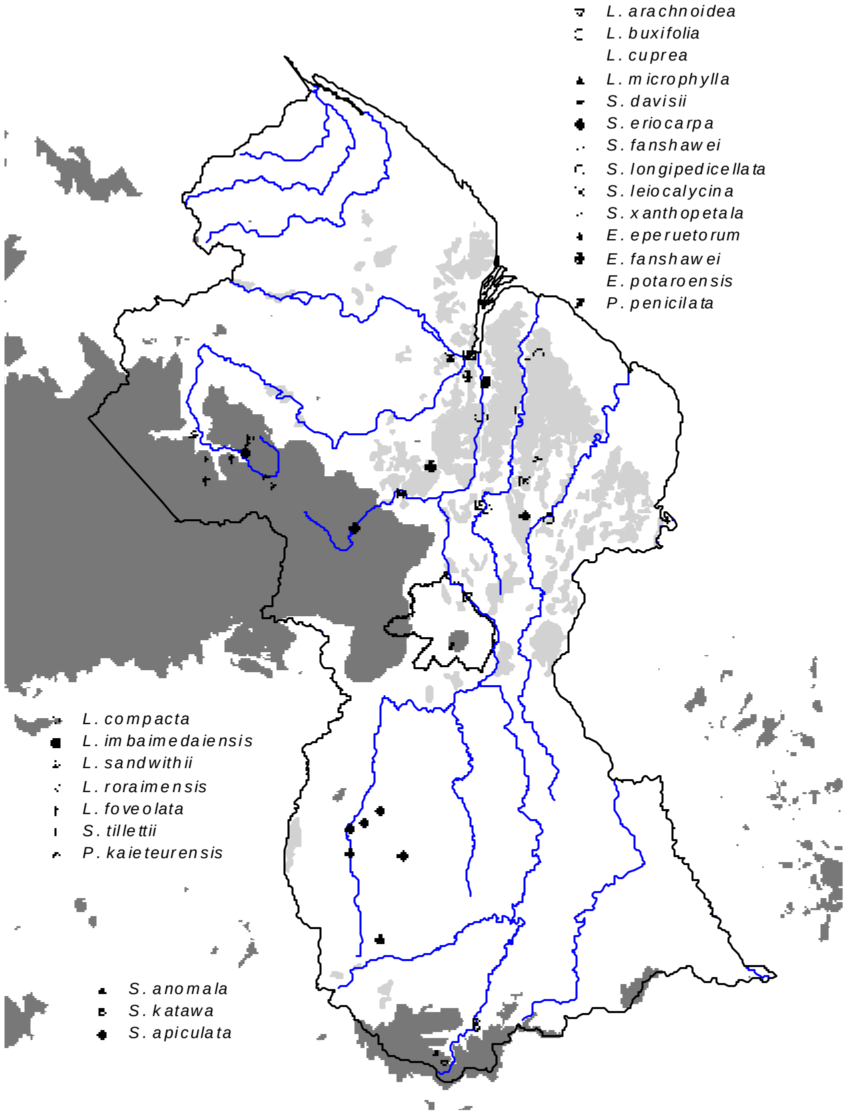

Figure 6.6 Distribution patterns of known endemics of *Eschweilera*, *Lecythis*, *Licania*, *Swartzia*, *Ocotea* s.l., and *Pouteria* s.l. in Guyana. There are two concentrations: the white sands area and the head of the Mazaruni - Mt. Roraima area. Presence of endemics in the Southeast is unknown due to the lack of collections in that area. Shading: dark grey = areas over 500m (see Figure 6.1); light grey = area with white sands of the Berbice Formation (after Gross-Braun *et al*. 1965).

How reliable are the regional species richness estimates? An asymptotic model was chosen to describe the number of species as a function of the number of collections. There were two reasons for this:

1. The model performed better than the log-log model of the general species area curve
2. A forest region has a distinct size and thus should have a distinct number of species - with continuous collecting the number of species found should not continue to grow indefinitely.

However, because the collections have not been made without bias, statistical comparison is troublesome. We believe (or hope) that because collecting has proceeded in a similar manner in all regions, that the data are comparable and that our projections are reasonable. This is strengthened by the fact that a check with the non-parametric 'Chao 1' index, based on the number of species with one and two individuals in a population (see Colwell and Coddington 1995) gives nearly identical estimates for the regional species richness (NWG 125, CG 218, NEG 120, PH 210, DS 91, WS 166, cf. Table 6.3).

Log-normal distribution of individuals over species predicts that if the numbers of individuals of a family increase in an area, the number of species will increase as well. One question asked in our previous publication was (ter Steege 1998a, Chapter 5): "If a genus is more abundant in an area will it be more species-rich there?" For *Swartzia* this would appear to be the case, the genus is both abundant (ter Steege 1998a) and species-rich (Table 6.2) in central and north-eastern Guyana. Lauraceae and Sapotaceae are more abundant in southern Guyana (ter Steege 1998a) and also have higher diversity in that area (Table 6.2) and this extends well into Brazil (Doi *et al.* 1975, Veloso *et al.* 1975). The species richness of these groups in the south is cause for a high part of the total diversity of the area (Table 6.2). However, while Lecythidaceae were most abundant in Northwest Guyana, they are certainly not most species-rich there.

Species distribution areas

The Pakaraima Mts. have a distinct flora (see also ter Steege 1998a). This is not unexpected as the higher altitude is cause for lower temperatures and the area is also characterised by very high rainfall (Persaud 1994). The sandy soils, originated in situ on the sandstones (Gibbs and Barron 1993), are somewhat comparable to the white sand soils of alluvial origin of Central Guyana and several genera/species are shared among them. Apart from the several species of *Licania* and *Swartzia*, other genera such as *Dicymbe* and *Dimorphandra* are common (to dominant) on these soils, with a few endemics too (Freitas da Silva 1986, Cowan & Lindeman 1989). Due to the altitudinal variation (500-3000m), habitat heterogeneity is large. This must be one of the main reasons for the high (expected) species richness for the area, as α-diversity may be quite low in forests on the poor soils of the Pakaraimas (Fanshawe 1952, ter Steege 1998a). We have no firm data to suggest which altitude may harbour the highest diversity in Guyana and that is in fact not possible with the set of typical lowland species by us here (cf. Berry *et al.* 1995). In Venezuelan

Guayana the highest species diversity in two large genera (*Bonnetia* and *Stegolepis*) was found around 1800-2000 m (Huber 1988, see Chapter 10). However, several species occur in rather small areas or are in fact endemic to one tepui (Huber 1988), thus contributing to a third biodiversity component - γ-diversity. To preserve a large proportion of the diversity of such genera, a single small area will not be sufficient. Berry *et al.* (1995) found 138 genera to be endemic to the Guiana Shield, 61 of which occur in Guyana. Most of these genera have a fairly wide altitudinal distribution. The main peak of generic diversity within this group is found around 1300 m altitude (Berry *et al.* 1995). However, out of the 61 genera, occurring in Guyana, only 8 are restricted to altitudes over 1000 m altitude but 14 below 500 m (more on this in Chapter 10).

The number of species collected in the Pakaraimas falls short of the expected number (Table 6.3), as in the other regions. Several species, known from Venezuelan Guayana, are expected to occur in the highlands of Guyana (e.g. Cowan & Lindeman 1989, Boggan *et al.* 1997), an area much better known (Berry *et al.* 1995, Huber 1995a). New species are still being described regularly (Prance 1995), such as *Licania imbaimadaiensis* (Prance 1992). On the other hand, species, now considered to be endemic to this area in Guyana, may well be found in the Venezuelan part as well.

The forests of the Dry South, a large part of which is formed by the Kanuku Mountains, of which just the few highest peaks are over 500m, have the lowest species richness of all forest regions in Guyana, based on the species set used. The dry seasonal climate, the rocky shallow soils, but also the smaller size of this area may all contribute to the low species estimate of this area. While there were very few endemics in the dry forests of south Guyana, species such as *Lecythis brancoensis, Lecythis schomburgkii* and *Pouteria surumuensis* are endemic to the Rupununi and Rio Branco savannahs of Guyana and bordering Brazil (Mori & Prance 1993, Pennington 1990, see Figure 2.2). The majority of the species in the Wet South have an Amazonian affinity, which is to be expected as a consequence of their proximity to the Brazilian Amazon. Still one quarter of the species found is Guiana Shield, Guianas, or Guyana endemic (Table 6.1). As was the case with the Pakaraima Mts., the species set chosen may not be a good indicator set for the richness of the forest of the Kanuku Mountains with their dry climate. In fact the area is very rich in *Clusia* (Clusiaceae), *Eugenia* (Myrtaceae) and other, often deciduous, species of Bombacaceae, Anacardiaceae and Leguminosae (Jansen-Jacobs, pers. obs.).

Endemism

Several species, and importantly, many endemics, are characteristic for the White Sands Formation in Guyana (Figure 6.6). Some of these are very abundant to co-dominant in *Eperua*-dominated forests on bleached, excessively drained, white sand, such as *Licania cuprea* and *Licania buxifolia* (Fanshawe 1952). Such species could be considered white sand specialists. There are more examples of such, often endemic, specialists: *Ecclinusa psilophylla* (Sapotaceae), *Dicymbe altsonii, Dicymbe corymbosa, Dicymbe jenmannii, Dimorphandra macrostachya, Dimorphandra cuprea, Dimorphandra davisii and Dimorphandra hohenkerkii* (all Caesalpiniaceae).

Because the largest areas of the White Sands Formation are found in Guyana, many white sand specialists are endemic to Guyana. In Suriname the composition of the forest on the White Sands Formation, a narrow belt there, is much more influenced by the forests of the Basement Complex nearby (Schulz 1960).

The occurrence of endemics is thought to be the result of three processes (Huston 1994):

1. In situ speciation
2. Failure to disperse/increase range
3. Survival and local accumulation over time

Whereas there is no a priori reason to suspect high speciation rates in the White Sands Formation, the large-seeded *Swartzia, Licania, Lecythis* and *Eschweilera* are less likely to be well-dispersed than several bird - and primate-dispersed groups, such as Lauraceae and Sapotaceae, which have very few endemics in the area. The low productivity of the sandy soils may also reduce gene flow and seed production (Huston 1994), contributing to restricted dispersal of genetic material. Specialisation to an endemic soil formation aids in the isolation and restricted spread.

Many areas with high endemism are characterised by low productivity (Huston 1994): "*the key to high levels of endemism seems to be the survival and accumulation of endemic species, which may be allowed by the low rates of competitive displacement found in low productivity environments*". Non-equilibrium as caused by frequent drought (common on white sand soils), fluctuating water tables (on some white sand soils) and/or fire (present, see Hammond & ter Steege 1998) may also prevent competitive equilibrium sensu Huston (1994, but see Chapter 7).

Not all endemics of Central Guyana are white sand specialists. Some occur on the lateritic hills within the Berbice formation area (see also Davis 1941). Important non-white sand (near-) endemics are *Chlorocardium rodiei, Vouacapoua americana, Mora gonggrijpii, Eschweilera potaroensis and Swartzia leiocalycina*. Several endemics are dominant. All six aforementioned, plus species of *Dicymbe* and *Dimorphandra*, may be dominant in parts of central and west Guyana (Fanshawe 1952, Whitton 1962, ter Steege 1998a).

Northwest Guyana has very few endemics. The majority of its species are Guiana Shield endemics or Amazonian species. This area is an integral part of the lowland forests that spread from NW-Guyana into lowland Venezuela Guayana (Huber 1995a, ter Steege 1998a) and possibly into eastern Colombia (see Duivenvoorden & Lips 1995).

Many Neotropical species are narrowly distributed, including most species of the taxa used for this analysis (see Koopowitz *et al*. 1994, Prance 1995). We could therefore expect more endemics in southern Guyana (3 according to Table 6.3) as the collecting effort increases.

A most likely scenario for National Parks in Guyana

Based on current initiatives (see Hoosein 1996, ter Steege 1998a, Chapter 5), a most likely scenario for National Parks will start with half of the Iwokrama Forest (180,000 ha), an extended Kaieteur National Park (Cabinet passed a bill March 1999, declaring an extended Kaieteur National Park of 62,700 ha) and possibly the Kanuku Mts. Such a scenario will not preserve areas in Northwest Guyana and the Wet South.

More disturbing is the lack of attention for the Berbice Formation in Central Guyana, an area with a large set of habitat specific endemics, which is under serious threat of over-exploitation, charcoal extraction, fires and agricultural conversion. The Iwokrama Forest, however, contains some of these species (ter Steege 1998b) and protection of the white sand areas in northern Iwokrama may be a significant contribution to the conservation of plant diversity in Guyana. The Iwokrama Forest also has a large area with basic volcanic rocks, where typical Central Guyana endemics such as *Swartzia leiocalycina* and *Vouacapoua macropetala* can be expected, as well as *Dicymbe altsonii*. The northern area also contains important Guianas-Guiana Shield elements such as *Mora excelsa, Mora gonggrijpii and Chlorocardium rodiei* (ter Steege 1998b), which are under considerable pressure from logging elsewhere.

One relatively small National Park (Kaieteur NP), with relatively low α-diversity in the Pakaraima Mts., may be insufficient to preserve a representative set of the large species richness in this heterogeneous area, which also harbours substantial endemism. Thus, to conserve a wide spectrum of such endemics, the full altitudinal range should be taken into account (Chapter 10). A large area with the major mountain islands may satisfy both of the above requirements in Guyana viz. Mts. Roraima, Ayanganna and Wokumong.

The Kanuku Mts. have been suggested to be an area of high species richness and endemicity (Ramdass & Haniff 1990, Agriconsulting 1993). Whereas animal surveys indeed show high richness for this area (Parker *et al.* 1993), our data for trees do not support high species richness nor high endemism. Because of its distinct character, being the major part of one forest region in Guyana (ter Steege 1998a), a conservation effort is still to be supported.

While much Forest Lands have been given into concession in Northwest Guyana (Guyana Forestry Commission, unpublished data) much land in the south is not under direct threat of large-scale timber extraction. In areas close to the national borders, conservation initiatives could be selected in collaboration with the bordering countries, Venezuela and Suriname and Brazil. In the south interesting possibilities for an extended wilderness area exist (Bryant *et al.* 1997, Chapter 1).

Botanical collections: yes or no?

General botanical collectors have been collecting for museums mainly, maximising their number of species per unit time. Specialists may collect their ‘own’ taxa very selectively. As an example, after André Chanderballi (of Missouri Botanical

Garden) collected Lauraceae in the Iwokrama Forest, the diversity of that group soared in the area. The high diversity of the Bartica-Potaro Road (but not its endemism), that was intensively collected by the very knowledgeable botanists of the Forest Department, may also have been caused by the extensive knowledge of the collectors. They probably did not collect too many sets of the same species. A species-collection curve may therefore overestimate diversity until an asymptote is reached. Because the densities of collections do not satisfactorily reflect the densities in the field, the data cannot be used for community diversity measurements but rather will yield an estimate of total species richness of an area (=γ-diversity). Because collecting densities are usually low, only large areas with sufficient numbers of collections can be taken into account. Other biases include the seasonal preference (dry season) for field collections (although the groups concerned have similar flowering and fruiting peaks: ter Steege & Persaud 1991). Certain groups may also be more difficult to collect than others are. Size and colour of flowers and fruits most certainly have an effect on their visibility (ter Steege & Persaud 1991).

Based on the number of species found and expected, the Northwest and Central Guyana are the best known areas with three quarters of the species expected actually collected. To achieve a similar level of coverage for the other four regions a substantial collecting effort is required. Based on the asymptotic model (see Table 6.3), we can estimate that some 1183 collections of these taxa have to be made to achieve this. Because the taxa comprise some 4% of the flora this translates into a total of over 25,000 additional general collections. After this we will have, in terms of numerical plant diversity, one single number for the species richness of 6 regions of Guyana. Therefore, general collecting does not appear to be a cost-effective way to quickly increase operational knowledge for a National Parks system in Guyana. For the completion of a thorough knowledge of the Flora of Guyana such work is obviously of importance but Flora projects operate at different time scales (e.g. Prance 1988) than required for a project like NPAS.

Conclusions

There are critical problems in using botanical collections for the assessment of diversity but we believe that with some caution collections can be used, to estimate species richness in relatively large areas (γ-diversity). In addition, if sufficient collections have been made, species distributions can be estimated. This, however, will never be possible for the bulk of diversity, which consists of rare to ultra-rare species.

The botanical collections of five important tree taxa show distinct regional patterns, supporting our previous classification of Guyana in several large forest regions (ter Steege 1998a, Chapter 5). Alpha-diversity and endemism, within the groups studied, are inversely related in Guyana. The areas with lowest α-diversity have highest endemism and possibly β-diversity.

A 'most likely' scenario for National Parks in the near future in Guyana includes half of the Iwokrama Forest to be designated as Wilderness Area, Kaieteur National Park (62,700 ha) and the Kanuku Mountains. Such a scenario does not include a major part of the areas of high tree endemism.

Many tree endemics in Guyana are habitat specialists. Their habitat, the Berbice formation, is under serious threat due to short-term logging leases (1 and 5 year leases), fire (Hammond & ter Steege 1998) and the poor nutrient status of the soil delaying recovery from large scale disturbances. This area is in serious need of planning if a part of Guyana's most typical flora is to be protected. The Iwokrama Forest has the potential to preserve at least a number of White Sands Endemics in the northern part but better inventories are necessary to be able to assess its full conservation potential of these endemics in Guyana (ter Steege 1998b, Chapter 5). Another possibility is the requirement of conservation areas within timber concessions. The Code of Practice for Forest Management of the Guyana Forestry Commission allows for such a measure.

With limited funds and time available for decision-making, research in support for a NPAS has to acquire results as cheap and fast as possible. We have argued that general collecting in areas where few collections have been made will not produce such results quickly and furthermore are difficult to interpret at small scales.

What sort of collecting needs to be done and where? Forest inventories give some sort of community-based diversity but names are often crude (ter Steege 1998a, Chapter 5). Including a botanist on such inventories would greatly enhance the value of its data and this is highly recommended. Plots studies (1 ha) or transect studies with botanical collecting of all species (or selected taxa) are also suitable to collect both numerical as well as qualitative data. Hectare plots have already been established in the Northwest (de Jagher & Smeets 1997, Bröker & Huyskens 1998, Groenewegen & Smedema 1997), central Guyana (Davis & Richards 1934, Comiskey *et al*. 1994, Johnston & Gillman 1995, Ek 1997) and the Pakaraimas (Ramdass *et al.* 1997). New plots could be established in the south, taking edaphic conditions into consideration and in the Pakaraimas taking both edaphic and altitudinal conditions into consideration.

There is a large body of existing botanical collections already available. We have shown that with caution they can contribute significantly to a discussion on the location of protected areas. Large sets of collections are present in Guyana (Jonah Boyan Herbarium, Forest Department Herbarium, Jenman Herbarium, Jenman Collection, the Centre for the Study of Biodiversity) and outside Guyana (Utrecht, Kew, Washington, New York). Most recent collections of Utrecht and Washington are already computerised. Combining these large data sets and including the Forest Department records, Jenman collections and eventually computerising all of Guyana's collections will be of great value, especially if freely accessible through the Internet.

Appendix 4 Species enumerated in the National Forest Inventory of Guyana and their characteristics.

WD = wood density in g cm^{-3}, SC is seed class in log_{10} steps [log classes: 1 = 10^{-5} – 10^{-4}, 2 = 10^{-4} - 10^{-4},…….8 = >100], PC is pioneer class, 1 is pioneer, 2 is long-lived pioneer, N is number of individuals in survey.

Family/species	WD	SC	PC	N
Anacardiaceae				
Anacardium giganteum	0.52	6	2	13
Astronium ulei	0.81	5		9
Loxopterygium sagotii	0.68	5	2	14
Spondias mombin	0.55	6	1	7
Tapirira guianensis	0.34	5	1	11
Tapirira obtusa	0.34	5	1	67
Annonaceae				
Ephedranthus/Oxandra	0.68	6		2
Rollinia exsucca	0.44	4	1	7
Unonopsis glaucopetala	0.72	5		19
Xylopia 3 spp.	0.68	4	1	31
Apocynaceae				
Ambelania acida	0.55	5		1
Aspidosperma decussatum	0.92	5		1
Aspidosperma excelsum	0.92	5		77
Aspidosperma/Casearia /Drypetes	0.91	5		70
Geissospermum 3 spp.	0.96	5		82
Himatanthus 2 spp.	0.68	5		17
Macoubea guianensis	0.48	5		2
Parahancornia fasciculata	0.59	5	2	28
Aquifoliaceae				
Ilex martiniana	0.63	5		5
Araliaceae				
Schefflera 2 spp.	0.51	4	1	18
Bignoniaceae				
Jacaranda copaia	0.43	3	1	55
Tabebuia 2 spp.	0.67	5		43
Tabebuia 2 spp.	1.04	5		16
Tabebuia sp.nov	1.04	5		10
Bombacaceae				
Catostemma 3 spp.	0.59	7		488
Ceiba pentandra	0.4	4	1	3
Rhodognaphalopsis/ Eriotheca 3 spp.	0.4	4	2	12
Boraginaceae				
Cordia 6 spp.	0.45	5	1	35
Cordia alliodora	0.56	3	1	7
Burseraceae				
Protium 3 spp.	0.64	6	2	135
Protium 4 spp.	0.72	5	2	27
Tetragastris 2 spp.	0.96	5	2	65
Trattinickia 2 spp.	0.5	5	1	36
Caryocaraceae				
Caryocar microcarpum	0.8	7		9
Caryocar nuciferum	0.88	7		26
Celastraceae				
Goupia glabra	0.84	2	1	200
Maytenus 5 spp.	0.88	5		12
Chrysobalanaceae				
Hirtella 16 spp.	0.92	5		11
Licania 2 spp.	1.03	7		272
Licania 6 spp.	1.03	7		228
Licania heteromorpha	1.03	6		50
Licania hypoleuca	1.12	7		47
Licania laxiflora	1.2	7		246
Licania/Pouteria	1.03	7		46
Parinari excelsa	0.89	6		25
Parinari/Exellodendron	0.89	7		86
Cochlospermaceae				
Cochlospermum orinocense	0.26	4	2	46
Combretaceae				
Terminalia amazonia	0.8	5		11
Terminalia dichotoma	0.84	5		111
Dichapetalaceae				
Hebepetalum humirifolium	1	3		15
Ebenaceae				
Diospyros dichroa	0.56	5		19
Diospyros ierensis	0.56	5		2
Diospyros/Lissocarpa	0.56	5		53
Eleocarpaceae				
Sloanea grandiflora	1	6		11
Sloanea schomburgkii	1	6		9
Sloanea/Couepia 15 spp.	1	6		76

Family/species	**WD**	**SC**	**PC**	**N**
Euphorbiaceae				
Alchorneopsis floribunda	0.48	5		1
Amanoa guianensis	0.94	6		1
Chaetocarpus schomburgkianus	0.83	5		124
Conceveiba/Aparisthmium guianensis	0.68	5		6
Hevea pauciflora	0.56	6		42
Hyeronima alchorneoides	0.8	4	2	17
Hyeronima oblonga	0.7	4		9
Mabea piriri	0.7	4		6
Maprounea guianensis	0.65	4	1	3
Micrandra sp.	0.75	4		102
Pera/Simaba	0.64	4		32
Pogonophora schomburgkiana	0.97	4		1
Sandwithia guianensis	0.86	5		2
Sapium 2ssp.	0.48	4		7
Flacourtiaceae				
Laetia procera	0.64	3	1	41
Guttiferae				
Clusia spp.	0.65	4		2
Moronobea coccinea	0.96	5		32
Rheedia 3 spp.	0.85	4		1
Symphonia globulifera	0.72	6		71
Tovomita 4 spp.	0.92	6		5
Vismia 7 spp.	0.58	3	1	7
Hugoniaceae				
Hebepetalum humiriifolium	1	4		4
Humiriaceae				
Humiria balsamifera	0.95	5		8
Humiriastrum obovatum	0.84	5		11
Saccoglotis 2 spp.	0.96	6		28
Icacinaceae				
Emmotum fagifolium	0.84	5		7
Lauraceae				
Aniba	0.64	6	2	1
Aniba 3 spp.	0.64	6	2	16
Aniba canellila	1.2	6		1
Aniba excelsa	0.64	6	2	3
Chlorocardium rodiei	1.05	7		288
Enlicheria/Licaria/Ocotea	0.6	6	2	4
Lauraceae indet	0.75	6	2	1
Licaria canella	1.05	5		26
Nectandra rubra	0.66	6		1
Nectandra/Ocotea 4 spp.	0.56	6	2	7
Ocotea aciphylla	0.64	6	2	8
Ocotea canaliculata	0.48	6	2	63
Ocotea floribunda	0.38	6	2	87
Ocotea glomerata	0.75	5		2
Ocotea leucoxylon	0.55	6	2	19
Ocotea oblonga	0.42	5	2	4
Ocotea spp.	0.48	6	2	1
Ocotea tomentella	0.54	6	2	21
Lecythidaceae				
Bertholletia excelsa	0.67	6	2	5
Couratari 5 spp.	0.62	5	2	83
Couratari guianensis	0.62	5	2	30
Eschweilera 2 spp.	1.07	6		880
Eschweilera alata	1.12	6		7
Eschweilera coriacea /decolorans	1	6		207
Eschweilera parviflora	1.11	6		1
Eschweilera potaroensis	1	6		208
Eschweilera wachenheimii	1	6		58
Lecythidaceae spp.	1.12	6		40
Lecythis confertiflora	0.92	6		63
Lecythis corrugata	0.9	6		52
Lecythis holcogyne	0.92	6		64
Lecythis zabucajo	1.02	6		67
Leguminosae (C)				
Aldina insignis	0.83	7		65
Cassia cowanii	0.72	5		15
Chamaecrista adiantifolia	0.8	5		45
Chamaecrista apoucouita	1.1	5		50
Copaifera 2 spp.	0.83	5		11
Dialium/Mikania /Swartzia/Tabebuia	1	5		4
Dicymbe altsonii	0.88	7		906
Dicymbe corymbosa	0.88	7		318
Dimorphandra davisii	1	7		28
Dimorphandra polyandra	0.88	5		2
Dinizia excelsa	1.15	5		6
Eperua 2 spp.	0.92	7		440
Eperua falcata	0.86	6		621
Eperua spp.	0.92	7		19
Hymenaea 2 spp.	0.88	6		6
Macrolobium 2 spp.	0.8	6		79
Mora excelsa	0.99	8		1035
Mora gonggrijpii	1.03	8		653
Peltogyne spp.	0.84	5		74
Sclerolobium 2 spp.	0.68	5	1	78
Senna multijuga	0.69	5		1
Vouacapoua macropetala	0.92	6		23
Leguminosae (M)				
Acacia polyphylla	0.74	5		10
Inga alba	0.64	5	2	125
Inga graciliflora	0.67	5	2	7
Inga lateriflora	0.67	5	2	8
Inga melinonis	0.67	5	2	1
Inga spp.	0.67	5	2	168

Family/species	**WD**	**SC**	**PC**	**N**
Inga/Pithecellobium	1.12	5		29
Parkia pendula	0.48	4	2	16
Parkia ulei	0.4	5	2	32
Pentaclethra macroloba	0.8	6		306
Pithecellobium FD4555	0.74	5	2	9
Pithecellobium jupunba	0.64	5	2	41
Pithecellobium/Elizabetha	0.8	5		98
Pseudopiptadenia suaveolens	0.59	5		58
Leguminosae (P)				
Acosmium nitens	0.96	5		3
Acosmium praeclarum	0.79	5		12
Alexa imperatricis	0.64	6	2	497
Andira 2 spp.	0.87	7		13
Clathrotropis 2 spp.	1.1	7		93
Clathrotropis/Licania/Spiranthera	1	7		26
Diplotropis purpurea	0.91	5		39
Dipteryx 2 spp.	1.07	6		16
Hymenolobium sp. nov.	0.75	5		28
Lonchocarpus hedyosmus	0.91	5		1
Lonchocarpus latifolius	0.91	5		1
Ormosia 2 spp.	0.7	6		54
Ormosia coutinhoi	0.62	7		48
Platymiscium/Dulacia	0.98	6		9
Pterocarpus 4 spp.	0.52	6	2	258
Swartzia 3 spp.	0.72	6		46
Swartzia 3 spp.	0.89	6		9
Swartzia 9 spp.	0.89	6		134
Swartzia bannia	1.29	6		2
Swartzia leiocalycina	1.06	7		368
Vatairea guianensis	0.74	7		6
Loganiaceae				
Antonia ovata	0.56	5		1
Glycidendron amazonicum	0.84	5		17
Malpighiaceae				
Byrsonima 2 spp.	0.88	6		6
Byrsonima spicata	0.61	5		6
Byrsonima stipulacea	0.88	5		17
Melastomataceae				
Miconia guianensis	0.7	1	1	1
Mouriri 7 spp.	1.04	5		32
Meliaceae				
Carapa 2 spp.	0.67	7	2	367
Cedrela fissilis	0.51	4	2	8
Cedrela odorata	0.36	4	2	5
Guarea guidonia	0.64	5		4
Trichilia rubra	0.68	5		66
Monimiaceae				
Siparuna 2 spp.	0.83	4		2
Moraceae				
Bagassa guianensis	0.8	5		12
Brosimum guianense	1.17	5		45
Brosimum rubescens	0.92	5		21
Cecropia 5 spp.	0.44	2	1	25
Ficus 21 spp.	0.48	2	1	14
Helicostylis tomemtosa	0.76	5		6
Pourouma 2 spp.	0.44	5	1	45
Trymatococcus paraensis	0.88	6		4
Myristicaceae				
Iryanthera 3 spp.	0.59	6		26
Virola 3 spp.	0.46	6	2	46
Myrtaceae				
Calycolpus/Myrcia/Myrciaria/Plinia	0.88	7		11
Eugenia 2 spp.	0.92	5		11
Eugenia patrisii	1	5		2
Marlieria schomburgkiana	1.07	5		1
Nyctaginaceae				
Neea/Pisonia	0.87	4		13
Ochnaceae				
Cespedesia spathulata	0.84	7		2
Poecilandra retusa	0.98	5		1
Olacaceae				
Chaunochiton kappleri	0.6	5		10
Heisteria 2 spp.	0.85	5		1
Maburea trinervis	0.95	7		12
Minquartia guianensis	0.83	5		20
Proteaceae				
Panopsis sessilifolia	0.6	6		4
Quiinaceae				
Quiina albiflora	1.1	5		1
Rubiaceae				
Duroia eriopila	0.92	5		1
Genipa americana	0.76	4		1
Guettarda acreana	1.01	5		6
Rutaceae				
Hortia regia	0.91	5		1
Zanthoxylum apiculatum	0.51	3		3
Sapindaceae				
Matayba/Vouarana	0.9	5		6
Talisia 2 spp.	1.02	5		27
Talisia elephantipes	0.54	4	1	1

Family/species	**WD**	**SC**	**PC**	**N**
Sapotaceae				
Chrysophyllum pomiferum	0.95	6		62
Chrysophyllum sanguinolentum	0.88	6		114
Ecclinusa psilophylla	0.88	5		2
Manilkara bidentata	1.1	6		95
Manilkara huberi	1.1	6		16
Micropholis venulosa	0.92	5		54
Pouteria 2 spp.	1.17	5		42
Pouteria 3 spp.	0.88	5		98
Pouteria caimito	0.7	6		10
Pouteria cladantha	1.2	5		35
Pouteria coriacea	1.04	6		62
Pouteria filipes	1.12	6		91
Pouteria grandis	1.08	6		19
Pouteria guianensis	1.17	6		89
Pouteria sp.	0.67	6		17
Pouteria speciosa	0.7	8		55
Pouteria torta	1.17	6		2
Pradosia schomburgkiana	1	5		45
Simaroubaceae				
Simarouba amara	0.41	4	1	37
Sterculiaceae				
Sterculia pruriens	0.48	6	2	25
Sterculia rugosa	0.48	6	2	65
Theobroma sp.	0.55	6		2
Theaceae				
Ternstroemia 3 spp.	0.8	5		1
Tiliaceae				
Apeiba/Annona	0.38	3	1	78
Lueheopsis rugosa	0.64	3	1	6
Ulmaceae				
Ampelocera edentula	0.8	6		3
Verbenaceae				
Vitex 4 spp.	0.67	5		43
Vochysiaceae				
Vochysia 9 spp.	0.6	4	1	29

7 AN ANALYSIS AT THE ECOSYSTEM LEVEL: COMMUNITY CHARACTERISTICS, DIVERSITY AND DISTURBANCE[1]

Hans ter Steege, David Hammond

Introduction

Generally speaking, tropical rain forests are characterised by high tree species richness. High rainfall and geographical variation in soil properties have been suggested as explanations for this phenomenon (Richards 1952, Gentry 1988, Connell and Lowman 1989, Tuomisto *et al.* 1995). However, not all tropical forest communities show particularly high tree α-diversity (Richards 1952, Connell and Lowman 1989, Hart *et al.* 1989, ter Steege 1998a, Chapters 3, 5). Low diversity, in extreme cases leading to mono-dominance, has been attributed to adverse moisture or nutrient properties of the soil (Richards 1952, Connell and Lowman 1989, Hart *et al.* 1989) but could also be the result of competitive exclusion due to environmental stability (Huston 1994, Hammond and Brown 1995). Low tree diversity is typical of forests in central Guyana (e.g. Richards 1952, Fanshawe 1952, ter Steege *et al.* 1993, Johnston and Gillman 1995). It has been linked, via seed size, to the relatively infrequent occurrence of larger-scale disturbances (Hammond and Brown 1995), which are more common at other neotropical forest sites (Boucher 1990, Horn and Sanford 1992, Bush and Colinvaux 1994, Zimmerman *et al.* 1996, Saldarriaga and West 1986, Nelson *et al.* 1994, Salo *et al.* 1986, Lugo and Scatena 1997).

Disturbance regimes

It has been long recognised that plant communities are not just random assemblages of species. Certain assembly rules underlie the communities as we see them (e.g. Keddy 1992, Grime 1993). Keddy (1992) defined assembly rules as filters acting on a regional set of species. Such environmental filters remove species from the regional set, which are unsuited to a specified set of conditions. Possible filters include changes in climatic conditions, biotic interactions, and disturbance regimes. Episodic disturbances which alter canopy cover, such as shifting cultivation, hurricanes, fires, landslides, phytopathogen epidemics, and dynamic fluvial processes, directly or indirectly affect all tree species in a forest stand and may drive tree communities towards character convergence (e.g. see Lugo and Scatena 1997). Species unsuited to survival and growth in these highly dynamic environments are slowly filtered out of the regional assembly. In forests subject to repeated large-scale disturbances at a wide range of scales, selection should place a premium on trees, which are able to reproduce at an early age. Frequent canopy disturbance and an increased likelihood of suffering a terminal injury, would diminish the

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[1] This paper has also been submitted to *Ecology*.

reproductive success of individuals maturing late. Similarly, if a forest community is only subject to relatively small-scale minor disturbances, such as tree or branch-fall gaps, then certain species characteristics in this community should show greater convergence towards those states which convey the greatest fitness under low disturbance conditions (Hammond and Brown 1995).

Seed size, establishment and dispersal

To deal with these different growth and reproductive strategies, trees have traditionally been divided into pioneer and climax species (e.g. Huston and Smith 1987, Swaine and Whitmore 1988). During early stages of succession, fast growth and high sapling establishment are considered important characteristics for success, whereas shade tolerance is more important during later stages (Huston and Smith 1987). Similarly, low disturbance conditions would favour shade tolerance, mostly achieved through large seed reserves (Hart *et al.* 1989, Hammond and Brown 1995). Whereas size and residence time determine success of seedlings in the understorey and small gaps in central Guyanan forests, the ability to increase relative growth rate (RGR) under high light conditions determines to a large extent success in large gaps (Boot 1996, ter Steege and Hammond 1996). Because larger seeds produce larger seedlings with greater structural mass, RGR in seedlings of a similar (young) age is negatively correlated with seed size (ter Steege 1994). Data from other studies support this trend (Osunkoya *et al*. 1994, Kitajima 1994). In the functional classification of trees, seed size also plays a prominent role in the distinguishing of groups (e.g. Brzeziecki and Kienast 1994, Grime *et al.* 1997). Thus seed size may be one reasonable estimator of the place of a species in the continuum of regeneration strategies.

Seeds are dispersed by a variety of mechanisms and dispersal is important in helping seeds to escape heavy mortality near the parent tree (Howe and Smallwood 1982). The adaptation to a particular mechanism, however, can constrain other seed attributes, such as size. Dispersal explained over 30% of the variation in seed mass near Mabura Hill, Guyana (Hammond and Brown 1995). Most of this variation is not found at the species level: only 22% of the variation in seed size is accounted for by species included in the Flora of the Guianas, the remainder explained at the genus (53%) and family levels (25%, Casper *et al*. 1992). Most species within a genus are dispersed by the same dispersal mechanism (only 4% variation explained at species level), and are either all dry or fleshy, dehiscent or indehiscent (Casper *et al*. 1992). This obviously also reflects our way of classifying species. The highest species richness is found in genera associated with vertebrate dispersers: e.g. *Psychotria, Miconia, Ocotea* (birds), *Piper, Solanum, Ficus* (bats), *Licania, Swartzia* (bats and rodents), *Protium, Pouteria* (Primates) (Charles-Dominique 1993). We have no *a-priori* hypothesis of how dispersal should be related to larger spatial and temporal scales of disturbance in a rain forest. However, wind-dispersed seeds may tend to arrive first in large gaps (Schupp *et al.* 1989), followed by bird, bat and rodent dispersed seeds. Autochorous and barochorous species, due to their larger average seed size, are expected to arrive last or least in large openings (see also Foster *et al.*

1986). Thus wind, bird, bat and primate dispersed-species may be expected to be more common than gravity or rodent-dispersed species in forests which repeatedly experience extensive canopy fragmentation over the course of centuries or millennia (Hammond and Brown 1995). The latter species may regenerate more through the presence of a shade-tolerant seedling bank present at the time of gap formation. Their large seed size, and hence large seedling size, is beneficial in this respect (Boot 1996, ter Steege and Hammond 1996).

Wood density and growth rates

Like large seed size, large stem size and long lifespan typify climax species (Huston and Smith 1987) and maximum height and diameter have been found to be important characters when grouping both temperate (Brzeziecki and Kienast 1994) and tropical (Favrichon 1994) trees. We showed earlier (ter Steege and Hammond 1996) that increasing disturbance rates should disproportionately limit recruitment in slower-growing species. Individuals that reside in smaller size classes for longer periods, due to slow growth, are more likely to be incidentally involved in treefall events (see also Clarke and Clarke 1991). Data on the maximum intrinsic growth rates of most tropical trees is lacking. This ‘information gap’ complicates any effort to understand the relationship between long-term growth and long-term fluctuations in external conditions. There is evidence to suggest, however, that high growth rates in tropical trees are associated with low wood density (Favrichon 1994, Suzuki 1999, ter Steege unpublished data). The advantages given to fast-growing trees in a highly disturbed environment suggests that wood density, as a measure of long-term growth performance, may also be a proximate measure of disturbance sensitivity.

In this paper we examine the landscape-scale spatial pattern in tropical canopy tree diversity in Guyana and its relationship with tree and plot attributes over an area of 15 million ha, spanning from 1°30’ to 8°12’N. There is considerable spatial variation in community-level averages of disturbance-sensitive attributes in these forests and these are strongly associated with variation in α-diversity. We submit that this pattern may be explained in terms of regional differences in the disturbance history of the forests in Guyana.

Methods

From 1966 to 1973 a low-level strategic reconnaissance survey was carried out with FAO/UNDP funding to "to assist the Government of Guyana in determining the extent and composition of accessible forest" (de Milde and de Groot 1970a). The survey consisted of 1,029 plots, covering nearly the entire country, and amounting to 243 ha of enumerated forest (ter Steege 1998a, Chapter 5). Because the exact location of each plot could not be reliably reconstructed from the survey archives, the plots were grouped into 77 sites, each consisting of a constellation of plots that were within a few km of each other. Multivariate analysis showed that these 77 sites gave a good indication of the regional tree flora (ter Steege 1998a, Chapter 5).

We constructed a relational database containing the main raw field data (plot number, species, DBH), plot data (including location, soil, rainfall, and potential evapotranspiration and species-specific data. Species-specific data consisted of:

1. Seed size (Hammond and Brown 1995, Hammond *et al*. 1996, van Roosmalen 1985). Seed weight was classified in $\log_{10}$-classes to account for the range in seed size found in Guyanan forests (10^{-5} to 10^{2} g dry weight, see Hammond and Brown 1995, Hammond *et al.* 1996). The log-classes also account to some extent for the high variability in seed size within a species, which in some large seeded-species can range from 10 to 240 g (ter Steege 1990, 1994).
2. Dispersal type (ibid.), classified as primate, bird, bat, rodent, wind, water, and unassisted. We allowed more than one dispersal type per species, as this frequently is the case.
3. Wood density, which is the specific gravity at 12% moisture content, or air-dry timber (Fanshawe 1961, Détienne and Jaquet 1982, Vink 1983, Favrichon 1994, Gérard *et al*. 1996),
4. Endemic status (Davis 1941, Polak 1992), an endemic being defined as a species with more than 90% of its known distribution in Guyana.
5. Pioneer status. Pioneers and long-lived pioneers *sensu* Favrichon (1994) and Finegan (1996).

Alpha-diversity per site was calculated with Fischer's α, because of its independence of sample size (Fisher *et al*. 1943, Taylor *et al.* 1976, Leigh 1995, Rosenzweig 1995). Dominance was defined as the percentage of individuals attributable to the most common species (i.e. with rank one). Because dominance was thought to be linked to disturbance, we defined the percentage of (long-lived) pioneers as "the percentage of individuals of pioneer species among all individuals minus the individuals of the most abundant (= dominant) species. This was done to avoid obvious pseudo-correlation.

The relationship of diversity (Fischer's α) with rainfall (monthly and yearly: Persaud 1994; Persaud and Persaud 1995), Potential Evapotranspiration (PET, yearly: Persaud and Persaud 1993), length of dry season, and sunshine hours (yearly: Persaud 1982) was investigated with regression analysis (Statistica, Statsoft Inc. 1993). Regional effects on diversity and the effects of soil type on diversity were assessed with ANOVA. Because there was no replication and an unbalanced design, the ANOVA was carried out with the GLM module of Systat 8.0 as a model I, 2-way without replication (Wilkinson 1998).

We examined the relationship between the plot and species attributes by carrying out a Principal Component Analysis (PCA) for 72 sites. Seed size and wood density were log-transformed and percentages of soil type per site and percentage of individuals per dispersal type per site were arcsine transformed. Five sites were identified as gross statistical outliers in a multivariate vegetation analysis (ter Steege 1998a) and omitted from the PCA undertaken here. For each soil type the percentage of plots on that soil type was calculated per geographical site. For the PCA these percentages were arcsine transformed.

Results

In total 15,397 trees over 30.5 cm DBH were found on the plots. They comprised 251 identified taxa in 53 families (ter Steege 1998a) and 17 unknowns**.** The most abundant family in the sample was Caesalpiniaceae, which accounted for 8% of all species and nearly 30% of all individuals. There were clear differences in the forest composition from south to north and 5 forest regions were earlier distinguished (ter Steege 1998a, Chapter 5).

The wood density, seed size and dispersal mode were available for 243 tree species (Appendix 3). Average wood density ranged from 0.26 to 1.29 g cm^{-3}. Seed size ranged from just over 10 micrograms to 120 g or 8 orders of magnitude. Seed size and wood density showed a weak positive correlation ($r^2 = 0.11$, $P < 0.001$, Figure 7.1). Wood density and seed size were not equally distributed over dispersal types and/or taxa (Tables 7.1 and 7.2). Dispersal type had an effect on seed size but not on wood density (Table 7.1). Wind, bird and bat-dispersed species had the smallest seeds. Primates and rodents can handle larger food items and seed sizes of species

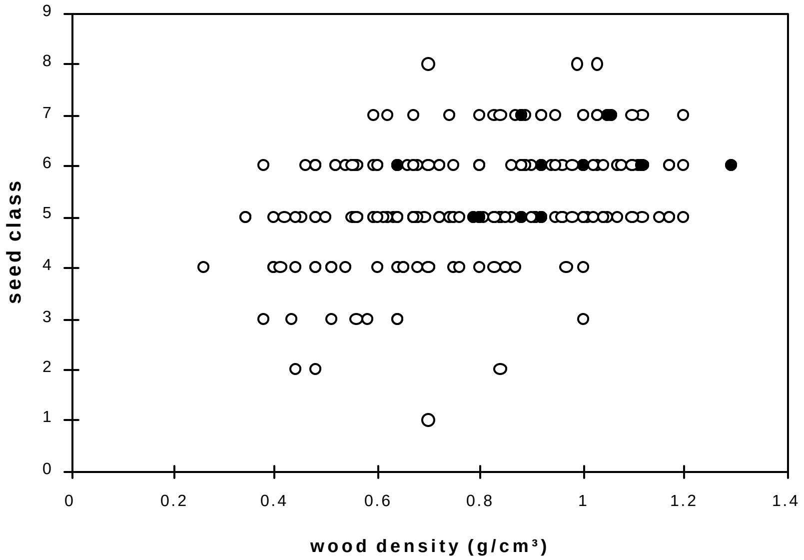

Figure 7.1 Seed size (log classes: 1 = $10^{-5} – 10^{-4}$, 2 = 10^{-4} - 10^{-4},…….8 = >100) and wood density (g/cm^3) for 250 species found in the National Forest Inventory in Guyana. There is a significant correlation between seed class and wood density ($r^2 = 0.11$, $P < 0.001$). Solid circles are species endemic to Guyana.

dispersed by them were larger. Seeds that are not dispersed by animals, wind or water were largest on average.

Table 7.1 Average wood density (g/cm^3) and seed size class per dispersal type. The range is given between brackets.

Dispersal	**Wood density**	**Seed size**
Wind	0.74 (0.34 – 1.2)	0.07 (10-3 – 10)
Birds	0.74 (0.34 – 1.20)	0.09 (10-5 – 10)
Bats	0.89 (0.44 – 1.29)	0.9 (10-4 – 10)
Water	0.70 (0.36 – 0.99)	0.2 (10-3 – 100)
Primates	0.80 (0.34 – 1.29)	0.25 (10-4 – 100)
Rodents	0.89 (0.4 – 1.29)	1.73 (10-2 – 10)
Unassisted	0.87 (0.62 – 1.10)	2.68 (10-1 – 100)

Several of the most common tree taxa in Guyana are characterised by large seeds (see also Hammond and Brown 1995) and dense wood. The Lauraceae encompasses a large variation in wood density (Table 7.2) and contrasting regeneration pathways. Within the Legumes, Mimosaceae have the lowest wood density and smallest seeds, whereas Caesalpiniaceae have the densest wood and largest seeds (Table 7.2). Guianan endemics are among the species with the heaviest wood (all over 0.75 g cm^{-3}) and largest seeds (Figure 7.1). The most common species in the survey were characterised by large seeds (data not shown).

Table 7.2 Average wood density (g/cm^3) and seed size class for some of the most important taxa in Guyana. The range is given between brackets.

Taxon	**Wood density**	**Seed size**
Licania	1.03 (0.96 – 1.12)	7.2 (1 – 10)
Lecythis/Eschweilera	1.01 (0.90 – 1.12)	1
Swartzia	0.97 (0.72 – 1.29)	1.6 (1 – 10)
Pouteria s.l.	0.97 (0.67 – 1.17)	0.63 (0.1 – 100)
Lauraceae	0.70 (0.38 – 1.12)	5.8 (0.1 – 10)
Mimosaceae	0.69 (0.4 – 1.12)	0.1 (0.01 – 1)
Fabaceae	0.86 (0.49 – 1.29)	1 (0.1 – 10)
Caesalpiniaceae	0.88 (0.68 – 1.15)	1 (0.1 – 100)

Species diversity, as expressed by Fischer's α, was highest in the southern part of the country and declined along a gradient towards the north ($r^2 = 0.469$; $P < 0.01$, Figure 7.2A, 7.3A). Total annual rainfall was a poor estimator of diversity on the 77 sites ($r^2 = 0.01$, $P = 0.48$) and PET did not explain any significant variation in diversity ($r^2 = 0.02$, $P = 0.28$) either. All other climatic parameters tested, viz. length of dry season, difference between rain and PET and total annual sunshine, showed a strong correlation with rainfall and did not explain significant variation in diversity.

Mesic soil types, such as brown sand and loam (Ferralsols (FAO)), clay (Fluvisols) and laterite (Leptosols) had higher tree diversity than more xeric soils, such as rock and white sand (Albic Arenosols), or hydric soil types, such as peat soils (Histosols) (Table 7.3). This relationship was consistent throughout the country.

The southern sites, however, were generally more species-rich than the northern sites (Table 7.3).

Table 7.3 Canopy tree diversity, expressed as Fischer's α, for five TWINSPAN forest regions in Guyana (Chapter 5) and per major soil class within that region. Fisher's α was calculated with the total number of species and total number of individuals in each cell. nwwf = north west wet forest, cgwf = central Guyana wet forest, plwf = Pakaraima central lowland wet forest, swf = southern wet forest, sdf = southern dry forest. Soils FAO: brown sand = ferralic Arenosol/Haplic Ferralsol, clay = mainly dystric fluvisol, laterite = Leptosol/Cambisol, loam = Ferralsol, pegasse = Histosol, white sand = albic Arenosol. (Adapted from ter Steege 1998a). Anova was carried out with GLM module of Systat 5.1 as a model I, 2-way without replication. ANOVA results; Soil $F_{[7,22]} = 7.87$ $P < 0.001$; Region: $F_{[4,22]} = 4.93$, $P < 0.005$.

Soil Group	drainage	nwwf	cgwf	plwf	sdf	swf	All
Brown sand	good	28.8	33.4	38.9	42	46.9	47.8
Clay	good-poor	26.4	29.6	38.6	37.8	40.9	43.7
Laterite	good-poor	16.6	29.9	23.2	x	51.8	48.2
Loam	good	25.4	9.8	39.3	36.7	46.4	45
Pegasse	waterlogged	5.6	6.5	16.9	x	18.8	21.4
Rock	excessive	x	x	20.1	8.5	x	26.3
White sand	excessive	5.3	4	16.6	9.5	7.8	23.3
Unknown	x	x	10.9	34.7	46.5	13.1	43.8
All	x	30	35	41.4	43.6	52.2	47.6

Community averages of species attributes, weighted by the abundance of each species (i.e. averaged by the number of individuals of each species, rather than number of species alone), showed distinct spatial variation when all plots were mapped onto a countrywide grid (Figure 7.2). A high average (and median) seed weight (Figure 7.2C) was most typical of tree communities in central Guyana while most individuals in the south had a median seed weight that was 1-2 orders of magnitude smaller than communities in the central region. Average wood density (Figure 7.2B) of the forest communities in the south was also less than in central or northwestern sites. Bird-dispersed trees were especially common in the forest communities in the southern parts of Guyana, where 36% of the species on average were bird dispersed, compared to 14-19% in the rest of the country (Figure 7.2E). This was also the case, to a lesser extent, for primate-dispersed trees, with an average of 68% of the species in the south being dispersed by primates, compared to 40-50% in the other parts of the country (Figure 7.2F). Rodent-dispersed trees were more abundant in central Guyana, accounting for 60% of all individuals, compared to 50% in the north west and 40% in the south of the country (Figure 7.2G). Trees with seeds dispersed by gravity or water typified both central and northwestern areas (41 and 43% respectively, Figure 7.2H) and were relatively uncommon in the southern plots (13% of individuals).

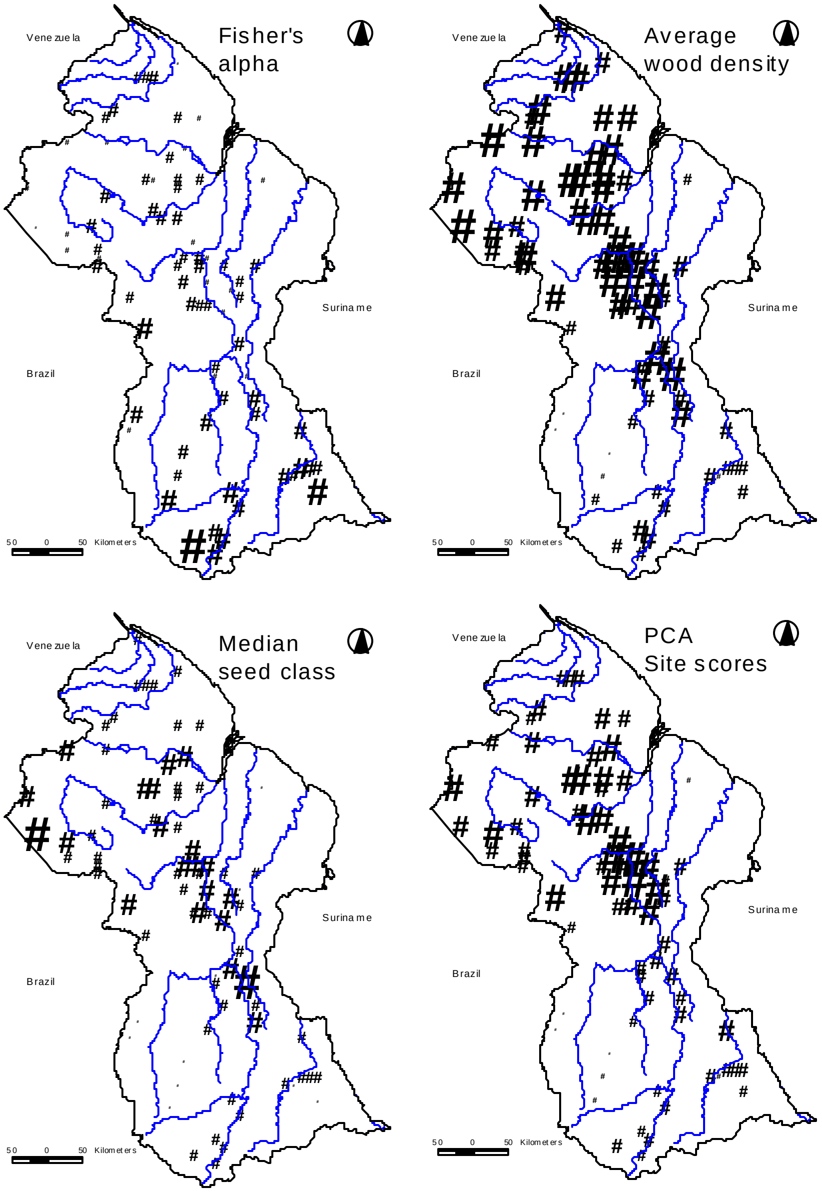

Figure 7.2 Maps of community characteristics of Guyana's rain forest. The diameter of the circle is a reflection of the value of the characteristic at a location. For each characteristic the value range is given between brackets. **A** Fischer's α: 1 to 68, see also Figure 7.3A. **B** Average wood density of the forest: 0.61 to 0.98. **C** Median seed weight of the forest: 1 to 100, 3 logarithmic classes. **D** PCA axis 1 score of forest sites: -1.91 to 1.93, see also Figure 7.3B.

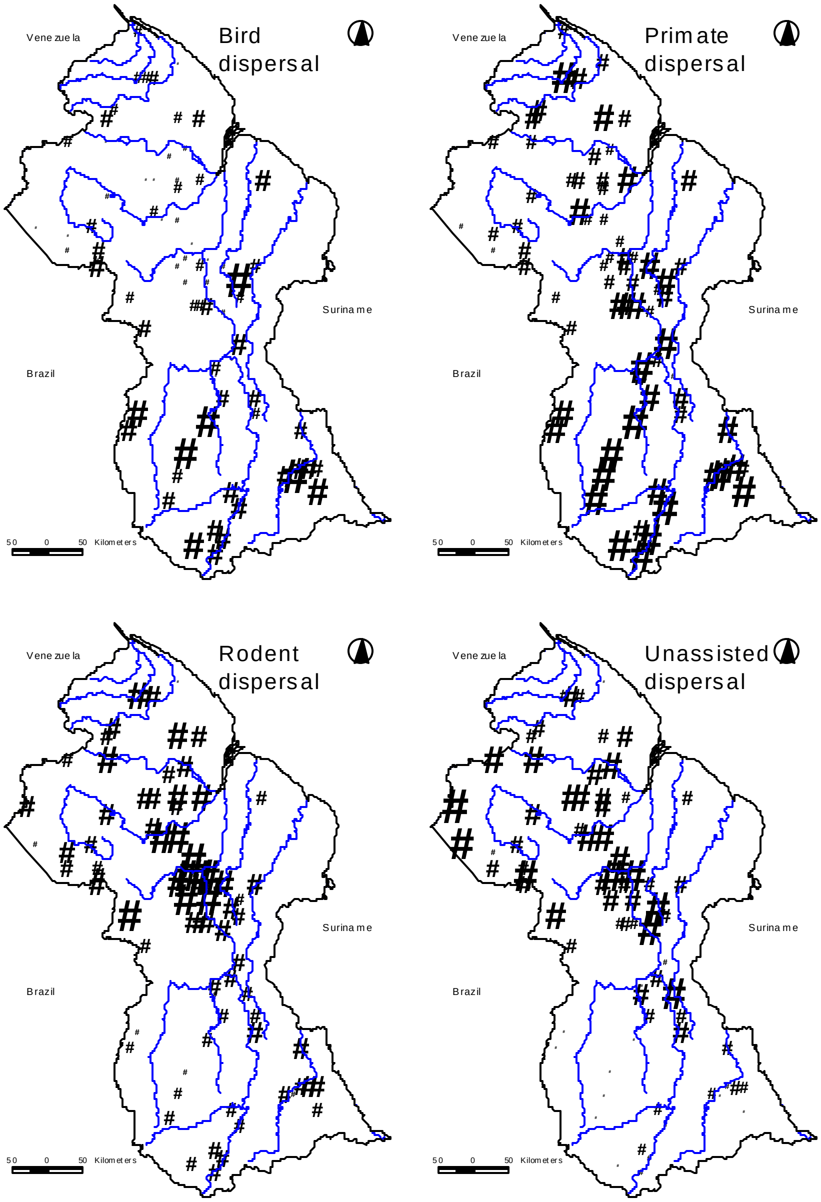

Figure 7.2 (continued) Percentage of individuals in the forest community **E** dispersed by birds: 4 to 53, **F** dispersed by primates: 18 to 83, **G** dispersed by rodents: 0 to 87, and **H** with unassisted dispersal: 0 to 74.

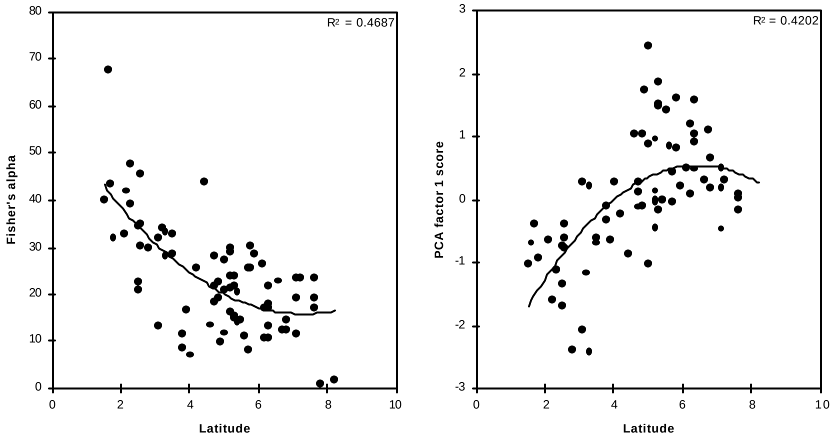

Figure 7.3 Scatterplots of community characteristics versus latitude. Regressions are 2nd degree polynomials r^2 and P given between brackets. **A** (left) Fischer's α decreased from the south to the north in Guyana $r^2 = 0.469$; $P < 0.0001$. All values over 30 were found below 2 degrees latitude. **B** (right) PCA axis 1 scores were highest in central Guyana, from 5 degrees to 6 and a half degrees north latitude $r^2 = 0.420$; $P < 0.0001$.

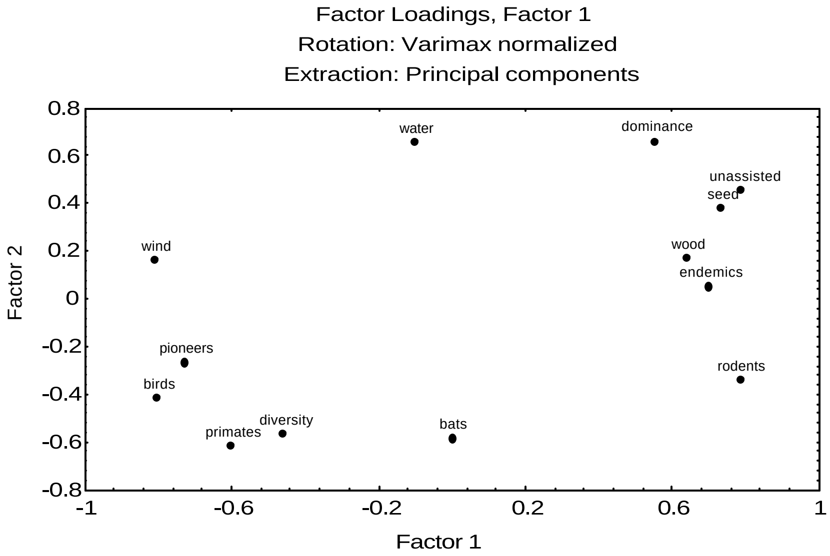

Figure 7.4 Factor loadings of community characteristics of Guyana's rain forest based on Principal Component Analysis Varimax normalized rotation. Axis one has an eigenvalue of 6.19 and explains 47.6% of all variance, axis two, with an eigenvalue of 1.78, 13.7%. Total explained variance is 61.3%. Axis one can be interpreted as an axis of disturbance vs. non-disturbance in Guyana's forest, with characteristics of low disturbance aggregated at the right of the diagram high wood density, high seed

The results of the Principal Component Analysis are shown in Figure 7.4. Initially, climatic data, soil data and tree species attributes were included in the PCA. Both annual rainfall and the difference between rainfall and PET had no significant direct correlation with diversity (see above) and their inclusion or exclusion did not alter the PCA results (communality of rainfall with axis 1, 0.42). Thus, rainfall data were excluded from the final PCA. There was considerable variation in tree diversity among soil types (Table 7.1). However, soil type also had no effect on the PCA (communalities of soil variables with PCA axis 1 varied from -0.37 to 0.45) and did not correlate well (most r's were between -0.2 and 0.2) with any of the community characteristics when analysed per site. Soil information was therefore also removed from the analysis.

The first axis of the PCA (Figure 7.4) shows that large seed size, high wood density, and dispersal by rodents were associated, while on the other hand low seed size, low wood density, primate and bird dispersal were associated. To understand how diversity and disturbance were related to the PCA axes, we superimposed α-diversity (Fisher's α), the percentage of (long-lived) pioneers, the frequency of dominant species, and the abundance of endemics of each site onto the existing PCA variable set. The inclusion of these three site-characteristics did not change the PCA with regard to the data already included.

The subsequent analysis revealed (Figure 7.4) that α-diversity and a high occurrence of pioneer species were related to small seed size, low wood density and primate and bird dispersal, that is to say, they grouped with the characteristics on the left side of PCA axis 1. Dominance grouped well with characteristics on the right side of PCA axis 1. There were no real clusters within the sites but rather the sites form a continuous gradient with the main variance distributed over axis 1 (Figure 7.3).

Interestingly, a strong positive correlation exists between dominance and seed weight ($r^2 = 0.40$, $P<0.01$, ter Steege and Hammond submitted), whereas dominance is negatively correlated with the percentage of pioneers and primate and bird-dispersed species. While seed size and wood density had a correlation coefficient of 0.33 by species, the correlation for these characteristics according to site was 0.52. Geographically, the plots with the highest PCA axis 1 scores (0 to 1.7), being those sites with high wood density, large seeds and a high degree of dominance, were situated in central and Northwest Guyana (Figure 7.2D, 7.3B). Most sites below 4°N have a negative score on the first PCA axis, whereas most sites above 4°N have a positive score.

Discussion

Explaining spatial variation in canopy tree diversity

Soil effects - There exists a clear gradient of α-diversity of canopy trees across Guyana (Figure 7.2A). Traditionally soils in Guyana have been classified as brown sands (sandy loam to loamy sands), white sands, peat, laterite, and clay. Regional differences in the occurrence of these soil types did not explain any significant variation in regional diversity. However, as was shown previously (ter Steege 1998a, Chapter 5), the underlying geology, or the soil parent material is very different for the five regions discussed in Guyana. The sites in the southern part of Guyana on soils derived from the crystalline shield have a higher α-diversity than sites on soils developed on the Berbice formation or Sandstone formation of the Pakaraimas. The plots in the north west of Guyana, also on soils derived from the basement complex, are somewhat intermediate. At a more local level, differences in soil type may cause a high β (between habitat)-diversity in Guyana (Fanshawe 1952, ter Steege *et al.* 1993) as elsewhere (Gentry 1988a, Tuomisto *et al*. 1995). In our data set, a tight relation between vegetation and soil also existed across the entire country, giving rise to distinct forest types on different soil types (ter Steege 1998a, Chapter 5). Mesic soil types had higher tree diversity than more xeric or hydric types (Table 7.1). This relationship was consistent over the country, the southern sites, however, being generally more species-rich than the northern sites (Table 7.1). Within forest types, α-diversity is further influenced by edaphic properties, mainly along soil water gradients (Fanshawe 1952, ter Steege *et al.* 1993, ter Steege 1994). Thus, soils influence diversity at nested spatial scales.

Results presented here and in earlier studies would suggest that variation in α-diversity in Guyana is affected by:

1. Macro-scale differences in soil parent material
2. Meso-scale changes in the edaphic quality of the soil
3. Micro-scale hydrological variation within soil types

while β-diversity:

1. Increases when different soil types have different tree communities (though often with considerable overlap in composition)
2. May cause higher α-diversity in adjacent communities due to continuous sinking of species (Rosenzweig 1995)

The weakness of correlations between the analysed species attributes and soil and rainfall characteristics of the plots suggests that seed size, wood density and dispersal type are not strongly influenced by variation in soil properties. This agrees with the result of a previous study carried out in central Guyana (Hammond and Brown 1995).

Rainfall effects
Yearly rainfall was a poor estimator of diversity. We conclude that geographical variation in rainfall is not important in explaining spatial patterns in tree diversity at the scale studied, even though annual rainfall at the sample plots varies from 1650 to

3550 mm. This is in sharp contrast with Gentry (1988b), who considered rainfall to be of the highest importance for α-diversity (but see Chapter 3).

The gradient in diversity we detect over a large area from 1 degree to 8 degrees north in Guyana, should not be confused with the latitudinal gradient in diversity that is apparent when moving from the tropics to the temperate and boreal areas. This latitudinal gradient is largely the product of changes occurring from 60 degrees to 20 degrees. Within the tropics, this gradient largely disappears, mainly because all areas within the tropics are subject to similar annual amounts of incoming radiation (Rosenzweig 1995).

Tree attributes

Diversity is strongly correlated with other community characteristics, such as dominance, pioneer abundance, seed size, and wood density as shown in the PCA analysis. Plots with a high score on this axis had low canopy tree diversity, often verging on mono-dominance, as well as a high average seed weight and wood density. Rodent, gravity or water-dispersed species and relatively high endemism also characterised these plots. The plots also had a high occurrence of typical Guyanan taxa such as Lecythidaceae and Chrysobalanaceae (ter Steege 1998a, Chapter 5). In contrast, plots with low scores on PCA 1 were mainly situated in the south of Guyana. These plots were characterised by a highly diverse set of trees with small seeds, typically dispersed by birds and primates, and stems with relatively low wood density.

Competitive exclusion and spatial character convergence

Relatively low disturbance, as we think is normal for central Guyana, results in a stable forest in which mainly small gaps occur. The forest composition seen today is largely a reflection of competitive exclusion, as predicted by the Dynamic Equilibrium Hypothesis (Huston 1994). Shade tolerance of seedlings is expected under such conditions (Huston and Smith 1987, Huston 1994, Hammond and Brown 1995) and can be achieved through large seeds (Hammond and Brown 1995). In small gaps, a large seedling, being the result of a large seed, may be more important then a high relative growth rate in determining establishment success (Boot 1996, ter Steege and Hammond 1996). If disturbance increases, mostly leading to larger and more frequent gap-forming events, more opportunities are created for canopy tree species whose relatively small seeds can be transported to greater distances and can achieve much greater relative growth rates than those of large-seeded species (Boot 1996, ter Steege and Hammond 1996). Also, we showed with a very simple model (ter Steege and Hammond 1996), that species with dense wood, and hence lower growth, and recruitment rates, are more affected by an increase in disturbance than faster growing species. Thus, we interpret the first PCA axis as an axis of disturbance.

Many canopy trees typically referred to as pioneers are expected to have low to medium-density wood and small seeds and those classified as climax species are expected to have dense wood and large seeds (Swaine and Whitmore 1988). Yet, the correlation between wood density and seed size in our data set is weak (but significant). Grime *et al*. (1997) suggests that "*Patterns of evolutionary specialisation in attributes of the mature plant do not vary in parallel with those of the regenerative phase*". This may not be surprising, on second thought, when we realise that growth and mortality in seedlings is much more strongly dependent on gap dynamics (cf. Boot 1996). For saplings and subadults random mortality, caused by debris, is also an important factor (Clark and Clark 1991). Wood density may be a more variable character in evolutionary terms. Seed size must be more constrained by mode of dispersal. In the flora of the three Guianas, species accounted only for a very small percentage of the variation in fruit types – i.e. species within a genus usually have the same fruit type (Casper *et al*. 1992) and seed size (Kelly 1995, this study). Kelly (1995), however, argued that seed size was much more under control of dispersal type (birds vs. mammals) than of successional ecology.

Geographically, the plots with the highest PCA axis 1 scores (0 to 1.7) were situated in central Guyana (Figure 7.1D, 7.2B). The fact that these areas are characterised by species-poor forests is interesting as these areas are thought to have been little used by pre-Colombian Amerindians (Evans and Meggers 1960, Dubelaar 1986), now recognised as having had a widespread role in shaping present forest composition and species distributions in the neotropics (Bush and Colinvaux 1994, Saldarriaga and West 1986, Bush *et al*. 1989, Meggers 1994). This region may have experienced the least environmental disturbance of all regions in Guyana, and possibly Amazonia (Chapter 3), whereas the southern and northwestern forests of Guyana are known to have been important inhabitation centres prior to European arrival (see Evans and Meggers 1960, Dubelaar 1986).

We believe that these landscape-scale results support the idea that the absence of large-scale disturbance in rain forest ultimately can lead to low tree diversity (Hart *et al.* 1989, Huston 1994). Species with characteristics adapted to low disturbance ultimately converge in space and time as other species with fewer of these adaptations are competitively disadvantaged and therefore are no longer afforded sufficient establishment opportunities to maintain local populations. We further believe that large seed size, a characteristic limiting dispersability and supporting seedling establishment and persistence in low-light conditions (Hammond and Brown 1995) is directly associated with competitive superiority in low disturbance environments and drives the approach towards mono-dominance. Interestingly, the percentage of long lived pioneers in the plots was negatively correlated with dominance, further suggesting that large disturbance events in low-diversity forests in Guyana are infrequent enough to suppress widespread colonisation of pioneers. It is important to note here that none of the most dominant species are considered (long-lived) pioneers and show mostly self-replacing population structures (ter Steege *et al*. 1993). In contrast, southernmost regions are typified by characteristics such as small seed size and high dispersability (via birds and primates) which are normally associated with superior colonising ability.

Analysis of community (life history) characteristics and diversity on this spatial scale may help to define protected areas in Guyana and other countries, for which such data exist. Diversity alone may be insufficient to make correct choices if the processes that maintain diversity are unknown. Assessing diversity by botanical collections alone may also lead to incorrect choices (Nelson 1990, ter Steege *et al*. 2000a, Chapter 6). Interestingly, the forests that seem least important for preservation from a diversity viewpoint may indeed be the most characteristic of Guyana, given the relatively large proportion of trees in these areas which are locally abundant, but have restricted distributions (see also ter Steege *et al*. 2000a, Chapter 6). These forests may experience the most drastic change to poorly-designed logging practices due to character convergence among tree species locked in a competitive environment which is not driven by frequent disturbance. As this area is also in the heart of the forestry concession belt of Guyana, quick action to preserve a vestige of these forests is urgently needed.

8 DIVERSITY AT DIFFERENT SCALES: A COMPARISON OF LARGE-SCALE FOREST INVENTORIES AND SMALLER PLOTS

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Introduction

In Chapters 4 and 5 (ter Steege 1998a), the use of forest inventories to describe forest regions in Guyana was discussed. It was shown that forest inventories greatly assist in the description of forest regions at several levels. However, because of the large-scale nature of the inventories, the sampling intensity was low and in addition to that species identifications were mostly incomplete.

One objective of this chapter is to determine how well the Forest Industries Development Surveys (FIDS; de Milde and de Groot 1970a-g) describe the forest composition and tree diversity in a region – that is, at smaller scales. A second objective is to determine to what extent soil heterogeneity at smaller scales contributes to overall diversity. Altitudinal zonation, another local determinant of species diversity, is described in more detail in Chapter 10.

For the comparison at different scales we make use of inventory data from smaller areas in Central Guyana and the Northwest District of Guyana. In Central Guyana regional inventories were carried out: the Great Falls Inventory (Welch and Bell 1971), and two management level inventories: the Waraputa Inventory (ter Steege *et al.* 1993), and the Inventory of the Forest Reserve Mabura Hill (ter Steege *et al.* 2000b).

In addition to that a large number of 'hectare' plots have now been established in Guyana (Figure 8.1, Table 8.1), the earliest dating back to 1933 (Davis and Richards 1933, 1934). Most plots have been laid out in the central portion of Guyana (ibid, Comiskey *et al.* 1994, Johnston and Gillman 1995, Ek 1997, Ramdass *et al.* 1997, Thomas 1999, van Essen 1999, van der Hout 1999). In the Northwest District a large number of PSP's have been laid out by Barama Company Ltd. and ECTF (Barama Company unpublished data) and van Andel (2000). Finally plots have been established in the Pakaraima Highlands (Ramdass *et al.* 1997, Boom pers. comm.).

Whereas the forest inventories allow us to examine the forest composition on several different soil types, the hectare plots give no doubt the best estimates for local tree α-diversity.

In the following a brief comparison is made between the results of the FIDS and the inventories at smaller scales. A comparison is also made between the diversities as suggested by the FIDS for regions in Guyana and those from other forest inventories and hectare plots. In the last section the effect of habitat heterogeneity as caused by soil types is discussed at various scales.

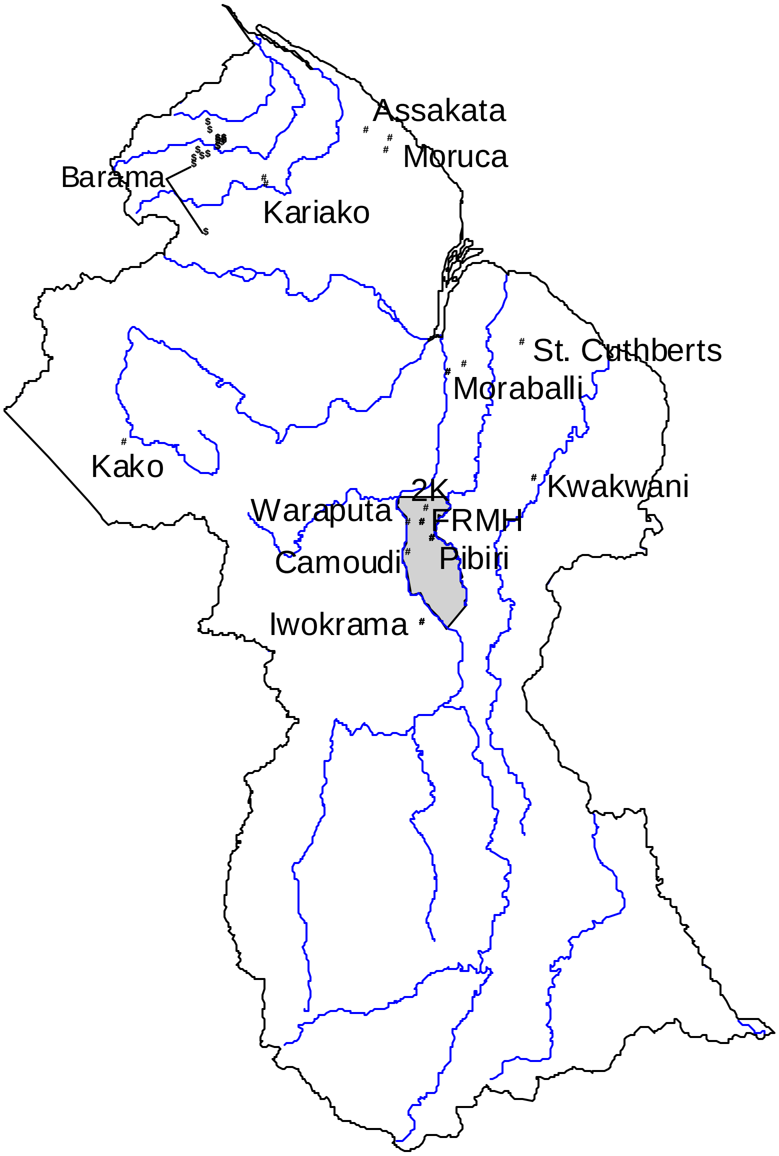

Figure 8.1 Locations of botanical hectare plots in Guyana (dots), PSP's of Barama Company Ltd. (triangles), and the Great Falls Inventory area (light grey shade).

Comparison of forest composition at different scales

Northwest District

According to the FIDS the forest of the Northwest District of Guyana is characterised by a high abundance and presence of *Alexa imperatricis, Protium decandrum*, *Eschweilera spp.*, *Pentaclethra macroloba*, and *Mora excelsa*. Mixed forests on well-drained soils are dominated by a combination of *Eschweilera corrugata*, *Alexa imperatricis* or *E. corrugata, Licania* spp. and *Catostemma commune*. In the southern part of this region (the overlapping zone with region 4, Figure 5.2) large stands dominated by *Mora gonggrijpii* occur.

In the vicinity of Port Kaituma 51 one-hectare plots were established (Barama Company Ltd. and ECTF unpublished data). The 10 most common species (DBH ≥ 20 cm) of these plots are given in Table 8.1.

Table 8.1 Abundance, range and presence of the most common species (DBH 20 cm) on 51 one-hectare permanent sample plots in the Barama area, Northwest District Guyana.

Species	Average (# ind./ha)	Range (# ind./ha)	Presence (%)
Eschweilera spp.	52	0-90	98
Licania/Couepia	31	0-95	98
Alexa imperatricis	26	0-54	98
Pentaclethra macroloba	15	0-65	80
Catostemma commune	13	0-37	96
Protium decandrum	13	0-26	98
Inga spp.	9	0-23	98
Sterculia spp.	5	0-25	98
Licania cf *heteromorpha*	3	0-12	84
Pouteria cf. *minutiflora*	3	0-43	80
Carapa guianensis	3	0-11	90

The presence of these species on the plots is high. All species are present in over 80% of the plots, while six are present in as much as 98% of the plots. However, as shown by the minimum and maximum trees per hectare, the numbers per plot differ substantially for each species.

Most of these species were also encountered in two botanical plots (trees with DBH ≥ 10 cm) that have been established in this area (van Andel 2000, Table 8.2):

1. **Kariako**: *Couepia parillo* (89 ind.), *Eschweilera wachenheimii* (45), *Alexa imperatricis* (43), *Protium decandrum* (17), *Licania alba* (16), *Catostemma commune* (15), *Unonopsis glaucopetala* (15), *Eschweilera pedicellata* (14), *Neea* cf. *constricta (14), Inga rubiginosa* (12, Fisher's α = 29.0)
2. **Moruca**: *Eschweilera* cf. *sagotiana* (62), *Eschweilera wachenheimii* (60), *Licania alba* (49), *Eschweilera decolorans* (28), *Licania heteromorpha* (24), *Tovomita* cf. *schomburgkii* (17), *Alexa imperatricis* (15), *Pentaclethra macroloba* (14), *Licania* sp. (13), *Pouteria* cf. *durlandii* (11, Fisher's α = 40.5)

Extensive marsh forests of *Mora excelsa* with *Pterocarpus* and *Carapa* are found along the rivers (Chapter 5). One 1-hectare plot was established in such a marsh forest (van Andel 2000). *Mora excelsa* (182 ind./ha) is strongly dominant, followed in abundance by: *Pterocarpus officinalis* (27), *Eschweilera wachenheimii* (21), *Zygia latifolia* (16), and *Pentaclethra macroloba* (15).

Two plots were laid out in swamp forests (van Andel 2000). One of these plots (Asakata) was strongly dominated by *Euterpe oleracea* (124 ind./ha). *Pentaclethra macroloba* (116), *Symphonia globulifera* (65), *Eperua falcata* (49), *Euterpe precatoria* (45), and *Tabebuia insignis* (40) were abundantly present. The second swamp plot (Moruca) was dominated by: *Symphonia globulifera* (81), *Tabebuia insignis* (77), *Diospyros guianensis* (69), *Humiriastrum obovatum* (56), and *Macrosamanea pubiramea* (54).

Central Guyana

The most common species in central Guyana, as suggested by the FIDS are (in order of abundance): *Chlorocardium rodiei, Mora gonggrijpii, Dicymbe altsonii, Swartzia leiocalycina*, *Eschweilera* spp., *Mora excelsa, Catostemma* spp., *Carapa* spp. and *Licania* spp.. A total of 154 species was found in a sample of 1340 individual trees over 30 cm DBH. The FIDS made a fair estimate of the most common species. As a comparison the most common species in the Great Falls Inventory (12,349 trees, Welch and Bell 1971, ter Steege *et al*. 2000b) were (in order of abundance): *Mora gonggrijpii, Eperua falcata, Chlorocardium rodiei, Dicymbe altsonii, Swartzia leiocalycina, Eschweilera sagotiana, Eschweilera* spp., *Eperua grandiflora, Carapa guianensis, Catostemma* spp.. Obviously, in this larger sample more species were found (183).

The forest composition is not constant over the Mabura Hill Concession area. The northern part of the Great Falls Inventory area is dominated by *Dicymbe altsonii* and *Eperua rubiginosa* (ter Steege *et al*. 1993, 2000b), two species not occurring in the southern part, where *Mora gonggrijpii* is the most abundant species. Also *Eperua grandiflora* does not occur in the most southern portion of the GFI area. It is also apparently absent from the Iwokrama forest (ter Steege 1998b). Finally, *Vouacapoua macropetala*, which is dominant on the laterite soils of the Mabura Ridge and eastern Akaiwanna Mts., is very uncommon in the central Akaiwanna Mts. (ter Steege *et al*. 2000b).

As in the Barama area the forest composition may show substantial variation at local level as shown by data from 15 2-hectare plots in the Pibiri research area (Table 8.2).

Conclusions

In both areas, NW-Guyana and central Guyana, intensifying the inventory effort increases the number of species found. Thus, species not found with the FIDS in central Guyana need not be totally absent (Chapter 5). *Geissospermum,* a genus typical for the southern forests (Chapter 5), was not found by the FIDS in central Guyana. However, in the more detailed inventories (Mabura Hill Forest Reserve and Pibiri area) the species was found several times.

Table 8.2 Abundance and presence of the most common species (DBH ≥ 20 cm) on 15 one-hectare plots in the Pibiri area, Central Guyana (van der Hout 1999).

Species	Average (# ind./ha)	Range (# ind./ha)	Presence (%)
Chlorocardium rodiei	39	24-73	100
Lecythis confertiflora	25	11-43	100
Catostemma fragrans	17	6-37	100
Mora gonggrijpii	8	0-70	33
Carapa guianensis	7	0-28	67
Eperua falcata	6	0-24	73
Licania canescens	6	0-19	87
Licania alba/ L. majuscula	6	0-15	80
Swartzia leiocalycina	6	0-16	87
Eschweilera sagotiana	6	0-52	33
Eschweilera coriacea/decolorans	4	0-16	53
Vouacapoua macropetala	4	0-45	27

Despite its low intensity the FIDS estimated the relative abundance of the most dominant species in the Northwest District and Central Guyana quite well. We conclude that the FIDS can be used (as done in Chapter 5) to describe forest regions in Guyana.

Comparison of diversity at different scales

Alpha-diversity in Guyana peaks in the southern regions and is lowest in the central portion (Figures 5.6, 7.3A). While quite a few plots have been established in the Central and Northwest portion of Guyana no botanical plots have been laid out in the southern part. Consequently, it is not possible to assess the validity of the results of the FIDS survey with regard to the differences in α-diversity between regions.

Hectare plots offer a standard means of estimating α-diversity for trees (see also Chapter 3). On average a one-hectare sample of trees over 10 cm DBH will result in some 400 to 500 individuals, which is sufficient for an estimate of Fisher's α. Several of such hectare plots exist in central Guyana, many of recent date (Davis and Richards 1933, 1934, Comiskey *et al.* 1994, Johnston and Gillman 1995, Ek 1997, Thomas 1999, van Essen 1999, van der Hout 1999). Alpha-diversity of most, if not all, of these plots in Guyana is low (Table 8.3), as was discussed in also Chapter 3. The richest plot in Guyana was found in the NW-District (van Andel 2000, Table 8.3). The plot with the lowest diversity was found in the Pakaraima Highlands (Table 8.3) and is almost completely dominated by *Micrandra glabra* .

The plots in central Guyana have an average Fisher's α of 19.4, ranging from 11 to 23. This means that with tree densities (DBH > 10 cm) from 300 to 500 stems/ha, a 1-hectare plot in central Guyana will contain roughly between 55 and 65 species. Within the Great Falls Inventory area there is a slight (but significant) difference between the α-diversity of plots south of the Akaiwanna Mts. and those north of it ($F_{[1,18]} = 76.84$, $P = 0.01$). On average, the plots in the southern portion have 10 species more per hectare.

Table 8.3 Hectare plots in Guyana. The plots are ordered by soil/forest type within regions. Abbreviations: For = forest type: mi mixed forest, mo mora forest, sw swamp forest, wa wallaba forest, cu cunuria forest; Soil, Fr Ferralsol, FlD dystric Fluvisol, Hs Histosol, Ara albic Arenosol, Lpd dystric Leptosol; Plot size (ha), DBHmin (cm), 20/10 based on different sample sizes for trees 10 cm (0.25 ha) and trees 20 cm (1 ha). N number of individuals; S number of species in sample; α Fisher's α. FRMH, Forest Reserve Mabura Hill.

Site	For	Soil	Lat.	Long.	Plot size	DBH min	N	S	a	Reference
Northwest District										
Kariako	mi	Fr	7°22' N	59°42' W	1	10	496	92	33.8	van Andel 2000
Moruca	mi	Fr	7°39' N	58°55' W	1	10	550	95	33.1	van Andel 2000
Kariako	mo	Fld	7°22' N	59°42' W	1	10	314	27	7.1	van Andel 2000
Asakata	sw	Hs	7°45' N	59°05' W	1	10	663	31	6.7	van Andel 2000
Moruca	sw		7°39' N	58°55' W	1	10	963	39	8.2	van Andel 2000
Central Guyana										
Iwokrama	wa	Ara	4°35' N	58°43' W	1	10	742	50	12.1	Johnston and Gillman 1995
FRMH	wa	Ara	5°13' N	58°35' W	2.3	10	1455	52	10.5	Thomas unpubl.
Moraballi	wa	Ara	6°14' N	58°27' W	1	10	495	63	19.1	Ramdass *et al*. 1997
Moraballi	wa	Ara	6°11' N	58°33' W	1.5	10	919	74	19.0	Davis and Richards 1934
St. Cuthberts	wa	Ara	6°22' N	58°05' W	1	10	534	71	22.0	Ramdass *et al*. 1997
Iwokrama	mo	Fld	4°35' N	58°43' W	1	10	375	64	22.2	Johnston and Gillman 1995
FRMH	mo	Fld	5°13' N	58°35' W	2.3	10	1124	77	18.7	Thomas 1999
Moraballi	mo	Fld	6°11' N	58°33' W	1.5	10	462	60	18.4	Davis and Richards 1934
Iwokrama	mi	Fr	4°35' N	58°43' W	1	10	477	67	21.2	Johnston and Gillman 1995
Iwokrama	mi	Fr	4°35' N	58°43' W	1	10	459	71	23.5	Johnston and Gillman 1995
2K	mi	Fr	5°18' N	58°41' W	1	20/10	318	62	23.0	Ek, unpubl.
Camoudi	mi	Fr	5°02' N	58°48' W	2.3	10	1124	77	18.7	Thomas, unpubl.
FRMH	mi	Fr	5°13' N	58°35' W	1	10	555	51	13.7	Ek and Zagt, unpubl.
FRMH	mi	Fr	5°13' N	58°35' W	1	10	453	52	15.2	Ek and Zagt, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	233	41	14.4	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	243	45	16.2	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	260	49	17.9	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	265	51	18.8	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	270	53	19.7	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	228	50	19.8	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	275	55	20.7	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	312	58	21.0	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	334	60	21.3	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	295	58	21.6	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	215	52	21.8	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	268	57	22.2	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	288	60	23.1	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	1	20/10	243	57	23.5	van der Hout, unpubl.
Pibiri	mi	Fr	5°07' N	58°30' W	2	20/11	275	44	14.8	van der Hout, unpubl.
Waraputa	mi	Fr	5°13' N	58°48' W	1	20/10	336	47	14.9	Ek, unpubl.
Moraballi	mi	Fr	6°11' N	58°33' W	1.5	10	460	69	22.5	Davis and Richards 1934
Moraballi	mi	Fr	6°11' N	58°33' W	1.5	10	773	90	26.4	Davis and Richards 1934
Moraballi	mi	Fr	6°11' N	58°33' W	1.5	10	644	91	28.9	Davis and Richards 1934
FRMH	mi	Lpd	5°13' N	58°35' W	1.5	10	577	57	15.7	van Essen, unpubl.
FRMH	mi	Lpd	5°13' N	58°35' W	1.5	10	631	65	18.2	van Essen, unpubl.
FRMH	mi	Lpd	5°13' N	58°35' W	2.3	10	957	67	19.4	Thomas, unpubl.
East Guyana										
Kwakwani	mi	Fr	5°30' N	58°00' W	1	10	493	59	17.5	Comiskey *et al*. 1994
Kwakwani	mi	Fr	5°30' N	58°00' W	1	10	504	85	29.3	Comiskey *et al*. 1994
Pakaraima Highlands										
Kako	cu	Lit	5°44' N	60°37' W	1	10	395	17	3.6	Ramdass *et al*. 1997

Ferralsols and Leptosols have higher α-diversity (21.3, 17.8) than albic Arenosols (16.5) but this difference is not significant ($F_{[3,36]} = 1.39$, $P = 0.260$). Very high and low diversity plots may be found very closely together. For instance in the Northwest District (Table 8.1), plots along the rivers have strikingly lower diversity than plots in mixed forest on well-drained soils.

It is not possible to calculate Fisher's α for single plots using forest inventory data, as there are usually too few trees to calculate the statistic. In chapters 4 and 5 plots were lumped on the basis of proximity or soil type (within a region). Table 8.4 shows that the Fisher's α calculated for such combinations of plots is almost always higher than the Fisher's α of 1-hectare plots. We conclude that the underestimation of α-diversity made by forest inventories by sometimes lumping several species into one vernacular name (see Chapter 5) is more than compensated for by the contraction of distant plots.

Table 8.4 Fisher's α calculated for soil types at different scales in central Guyana. FIDS: data from table 5.3; GFI: Great Falls Inventory, data from ter Steege *et al*. (2000b) based on contraction of all plots in soil groups; Waraputa: data ter Steege *et al.* (1993) contraction of all plots on one soil type; FRMH: Forest Reserve Mabura Hill (ter Steege *et al*. 2000b), based on line samples of roughly 0.5 to 1 ha; ha plots, average from table 8.3.

Soil type	**FIDS**	**GFI**	**Waraputa**	**FRMH**	**Ha plots**
Brown sand (Ferralsols, ferralic Arenosol)	33.4	23.3	25.1	21.9	19.8
Clay (dystric Fluvisol)	29.6	25.5		18.7	19.9
Laterite (dystric Leptosol, xanthic Ferralsol)	29.9	27.0	13.4	23.9	17.8
Loam (ferralic Arenosol)		28.6	13.0	30.8	19.8
Pegasse (fibric and terric Histosol)		15.9	13.4	12.6	
White sand (albic Arenosol)		15.1	12.5	12.6	16.5

Forests on white sand have low or lowest Fisher's α in all inventories compared in Table 8.4. Low values are also found on swamp soils (Pegasse). Although most plots along the rivers (with low diversity) are found on clay soils, not all plots on clay soils show low diversity. The question remaining now is "if particular soil types have lower diversity than others, do they just have a sub-set of the richer soils or do they have different species adapted to the different soil conditions"? This question will be tackled below.

Soil heterogeneity and b -diversity

In Chapter 5 (Table 5.2) it was shown that soil heterogeneity increases β-diversity, as many species have significant preference for a particular soil type in the dataset of the National Forest Inventory. Increasingly, the importance of soil types for forest composition has become clear in the Neotropics (e.g. Davis and Richards 1934, Fanshawe 1957, Ogden 1960, Lescure and Boulet 1985, ter Steege *et al.* 1993, Duivenvoorden and Lips 1995, Tuomisto *et al.* 1995, Sabatier *et al.* 1997, Clark *et al.* 1999).

Table 8.5 Common species with non-random distribution (X^2, $p < 0.05$) over soil types in Forest Reserve Mabura Hill, central Guyana (Lilwah and ter Steege unpublished data). Ara, albic Arenosol; Arg, gleyic Arenosol; Hs, Histosol; Fld, dystric Fluvisol; Arf, ferralic Arenosol; Frx, xanthic Ferralsol; Lpd, dystric Leptosol. Numbers in the columns represent the percentage of 750 individuals selected randomly from each soil type (this 750 is determined by the smallest number of individuals that could be selected from all soil types). The sum of each table row adds up to 100%.

Species	**Ara**	**Arg**	**Hs**	**Fld**	**Arf**	**Frx**	**Lpd**
Licania cuprea	87	0	0	0	4	4	4
Tovomita grata	89	4	4	0	4	0	0
Duroia eriopila	79	13	0	0	8	0	0
Aspidosperma excelsum	43	14	5	0	29	10	0
Chrysophyllum sanguinolentum	55	21	13	0	8	1	1
Swartzia benthamiana	21	25	0	13	17	13	13
Eperua grandiflora	58	28	13	0	1	0	0
Licania buxifolia	51	10	27	0	6	0	6
Eperua falcata	32	25	18	5	11	4	5
Aniba kappleri	38	36	24	0	0	2	0
Catostemma fragrans	22	29	25	10	8	3	3
Talisia squarrosa	33	20	40	0	3	3	0
Ormosia coutinhoi	25	43	33	0	0	0	0
Chamaecrista adiantifolia	5	66	14	7	3	5	0
Cupania scrobiculata	14	18	32	5	23	9	0
Clusia fockeana	30	10	60	0	0	0	0
Tapura guianensis	4	34	23	9	21	4	6
Hevea pauciflora	0	53	30	17	0	0	0
Licania laxiflora	0	64	36	0	0	0	0
Diospyros ierensis	10	16	58	13	0	3	0
Iryanthera sagotiana	0	26	57	15	2	0	0
Aniba excelsa	0	12	52	12	24	0	0
Marlierea schomburgkiana	0	15	70	10	0	0	5
Licania densiflora	0	15	79	3	0	0	3
Tabebuia insignis	1	13	82	2	1	1	0
Symphonia globulifera	0	9	82	0	0	0	9
Senna multijuga	2	0	54	0	0	6	38
Jessenia bataua	0	3	97	0	0	0	0
Pera bicolor	15	25	0	13	35	5	8
Swartzia oblanceolata	24	7	6	19	30	11	4
Dicymbe altsonii	21	4	11	7	48	10	0
Sandwithia guyanensis	2	17	19	11	20	30	2
Oxandra asbeckii	0	32	1	6	25	26	9
Calycolpus goetheanus	23	7	0	10	17	7	37
Eperua rubiginosa	0	21	0	74	5	0	0
Mora excelsa	0	9	0	72	9	7	3
Carapa guianensis	0	3	0	71	3	11	11
Chaemaecrista apoucouita	3	11	1	25	27	24	9
Guatteria atra	0	4	8	23	42	23	0
Pentaclethra macroloba	0	7	3	28	4	34	25
Eschweilera sagotiana	0	1	0	40	33	18	8
Licania heteromorpha	0	3	0	0	82	6	9
Chlorocardium rodiei	0	12	0	2	47	28	12
Mora gonggrijpii	0	1	2	18	33	38	8
Clathrotropis brachypetala	0	0	2	11	23	33	32
Paypayrola longifolia	0	5	0	23	36	23	14
Guatteria sandwithii	3	0	3	0	25	11	58
Sloanea guianensis	0	0	0	13	29	19	39
Unonopsis glaucopetala	0	0	0	25	28	31	16

Table 8.5. Continued.

Species	Ara	Arg	Hs	Fld	Arf	Frx	Lpd
Lecythis confertiflora	0	0	0	8	50	22	20
Maburea triner vis	0	0	0	13	34	26	27
Sterculia rugosa	8	0	0	1	0	10	81
Marlierea cuprea	0	10	1	2	3	29	55
Poecilanthe hostmanii	0	3	0	9	13	25	50
Swartzia leiocalycina	1	0	0	18	12	46	22
Vouacapoua macropetala	0	0	1	10	5	48	36
Trichilia rubra	0	0	0	0	0	5	95
Cassipourea lasiocalyx	0	0	0	0	5	34	61
Eschweilera wachenheimii	0	0	0	23	1	59	17

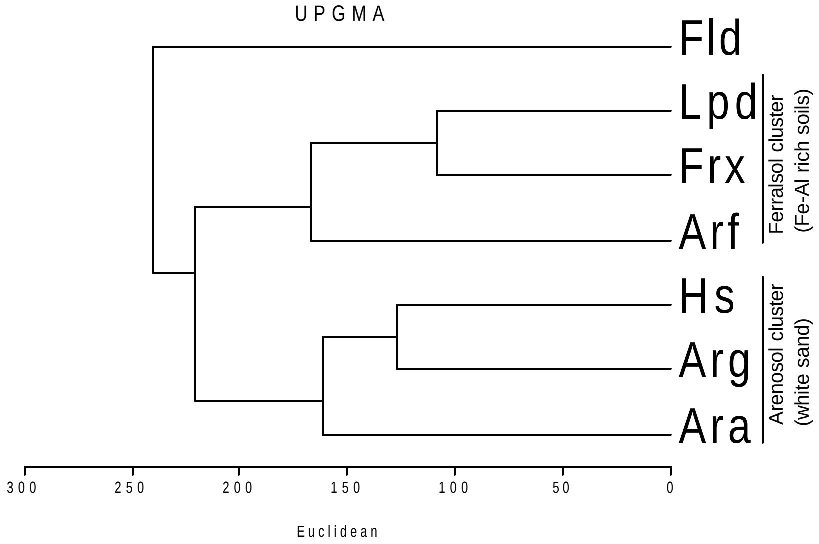

Figure 8.2 Clustering (Unweighted Pair-Group Method using arithmetic Averages with Euclidean distances (UPGMA), MVSP 3.1) of soil types based on the species composition of 750 random individuals from each soil type. Abbreviations as in Table 8.5.

The pattern of habitat preferences found nation-wide is also found at smaller scales for instance at concession level (ter Steege *et al.* 2000b) and for the Forest Reserve Mabura Hill (Table 8.5). As in the National data set, strong habitat specificity is found in species with preference for white sands or peat soils, suggesting that these soils differ substantially in their chemical and/or physical characteristics to support 'niche differentiation'.

Table 8.5 also shows that species composition on albic Arenosol is more comparable to that of gleyic Arenosol and Histosols than to that of ferralic Arenosol, xanthic Ferralsol, and dystric Leptosol. A cluster analysis of soil types on the basis of a random sample of 750 individuals from each soil type confirms this observation (Figure 8.2).

On the basis of species composition the soil types grouped in two main clusters (Figure 8.2). The first cluster consists of all soils on white sands, either wet (Arg, Hs) or dry (Ara) and will be referred to as the ‘Arenosol cluster’. The second group consists of soils with high Al and Fe content, sandy (Arf), clayey (Frx) or lateritic (Lpd) and will be referred to as the ‘Ferralsol cluster’. Apparently chemical content of the soil is more important than water status. The differences in tree composition between the soil clusters are large. A random selection of 8600 individuals (the maximum possible from both clusters) from the Arenosol cluster and a similar number from the Ferralsol cluster group contains 238 species. Half of these occur significantly more on either one of the two soil clusters (cf Table 8.5). Fifty-five percent of these species are found more on the Ferralsol cluster. The most common of these are: *Vouacapoua macropetala, Marlierea cuprea, Sterculia rugosa, Poecilanthe hostmanii, Pentaclethra macroloba, Swartzia leiocalycina, Maburea trinervis, Mora gonggrijpii, Chaemaecrista apoucouita, Cassipourea lasiocalyx* and *Eschweilera wachenheimii*. Forty six percent are found more on the Arenosol cluster. These species include: *Eperua grandiflora, Eperua falcata, Catostemma fragrans, Licania buxifolia, Chrysophyllum sanguinolentum, Dicymbe altsonii, Tovomita grata, Talisia squarrosa, Ormosia coutinhoi, Tapura guianensis, Duroia eriopila, Aniba kappleri* and *Licania cuprea*. Twenty-eight species are found exclusively on the Ferralsol cluster (the most common being *Maburea trinervis, Cassipourea lasiocalyx, Trichilia rubra* and *Ampelocera edentula*) and eight on the Arenosol cluster.

Within the Ferralsol cluster only a minority of the species show distinct preference (41 or 23%, based on a sample of 1574 individuals, containing 178 species) for either the Leptosol-Xanthic Ferralsol combination or the ferralic Arenosol. Species that prefer Leptosol-Xanthic Ferralsol combination to the ferralic Arenosol are: *Vouacapoua macropetala, Marlierea cuprea, Sterculia rugosa, Poecilanthe hostmanii, Pentaclethra macroloba, Swartzia leiocalycina* and *Cassipourea lasiocalyx*. Most of the species that are found preferably on the ferralic Arenosol within the Ferralsol cluster are species that show preference for the Arenosol cluster in the total dataset.

Within the Arenosol cluster there is a gradient from wetter to dryer areas on the watershed (Figure 8.3). The gradient in species composition is steepest at the swamp edge (change from Histosol to albic Arenosol). Similar gradients have been described in all the Guianas (Davis and Richards 1933, 1934, Schulz 1960, Ogden 1960, Lescure and Boulet, 1985, Barthes 1988, 1991, ter Steege *et al*. 1993, Sabatier *et al.* 1997). In most cases tree species behave similarly over large areas. As an example, the preference of *Eperua falcata* for both very dry and very wet soil conditions has been noted in each of the Guianas (Schulz 1960, Lescure and Boulet 1985, Barthes 1991, ter Steege *et al.* 1993, Figure 8.3).

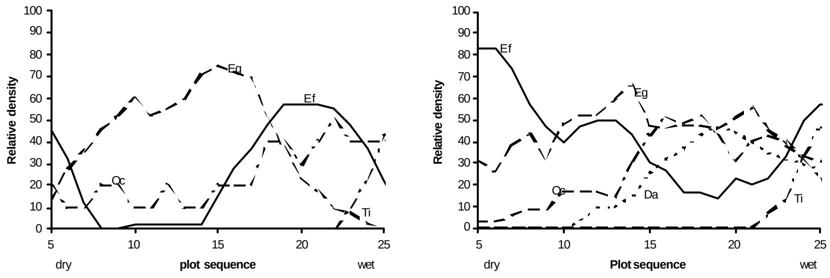

Figure 8.3 Gradient of moving-average (5 plots) of relative density (based on the highest density of each individual species found) of a number of common species on two different transects, both spanning a hydrological gradient in different creek gullies on a white sand watershed. Swamp plots are on the right part of the graph and the dry plots of the watershed are on the left. Abbreviations: Ef *Eperua falcata*; Eg *Eperua grandiflora*; Oc *Ormosia coutinhoi*; Da *Dicymbe altsonii*; Ti *Tabebuia insignis*.

In addition to hydrology, differences in soil within the Arenosol cluster also contribute significantly to β-diversity. When comparing species composition on albic Arenosol (dry conditions) with the combination of gleyic Arenosol and Histosol (based on a sample of 1845 individuals, containing 135 species), approximately 30 percent of the species show a significant preference for one of the soil types. Most of these (60%) show preference for the wet soils and are typical swamp species such as *Tabebuia insignis, Eperua rubiginosa, Iryanthera sagotiana, Licania laxiflora, Jessenia bataua, Hevea pauciflora, Mauritia flexuosa, Symphonia globulifera*. Species with preference for the dryer parts are the typical white sand species such as *Eperua falcata, Talisia squarrosa, Swartzia oblanceolata, Eperua grandiflora, Dicymbe altsonii, Chrysophyllum sanguinolentum, Licania buxifolia*. Certain species prefer the edges of the swamps e.g. *Ormosia coutinhoi* and *Dicymbe altsonii* (Figure 8.3).

What causes differences and gradients in forest composition?

There are critical differences in floristic composition between soil types. This suggests that adaptations exist that are based on differences in soil characteristics. Below we discuss three of such differences that may be involved in segregation of species over soil types and hydrological gradients:

1. Soil water relations
2. Soil fertility
3. Soil acidity and Al-toxicity

Soil water relations

The differences in forest composition between white sand and brown sand are often attributed to water availability (ter Steege *et al*. 1993, Whitmore 1990). White sand soils are routinely classified as excessively drained soils in Guyana. The higher clay content in brown sand soils is certainly cause for slightly more beneficial water retention characteristics of these soils. According to a water balance model only white sands experience drought in excess of the permanent wilting point but only after considerable periods without rain (Jetten 1994). The large differences soil water between Histosols and Gleysols, where groundwater is often close to the surface, as compared to the albic Arenosol are most likely cause for differences in composition. Data on long-term water use efficiency (ter Steege, unpublished data) further suggest that even within soil types species may segregate a watershed on the basis of water availability (see also Figure 8.3). Experiments have shown that differences in tolerance to drought (or flooding) within one genus may lead to separation along soil hydrological gradients (*Mora*, ter Steege 1994, *Eperua*, ter Steege, unpublished data). However, both on white sand soils and on brown sand soils a gradient in species is observed from the valley bottoms to the upper parts of the watersheds (ter Steege *et al*. 1993). These gradients consist largely of different species between the soil types. Thus, differences in water availability are not likely the cause for the main differences in composition between the two major soil-forest combinations in the Forest Reserve Mabura Hill. The hydrological conditions along the gradients may still be different between the soil types, e.g. in the temporal dynamics of drought

Soil fertility

White sands, which practically consist of pure quartz, are regarded as the poorest soils possible. This is certainly true for total nutrients (Raaimakers 1994, Brouwer 1995, van Kekem *et al.* 1995). However, available nutrients do not differ too much between the two soils, probably because of the strong adsorption of nutrients to the Al-Fe-Sequioxides in brown sands (Raaimakers 1994). This may suggest that nutrients are not likely to play a big role in determining differences in forest composition (Whitmore 1990). However, there are strong indications that nutrients may be more limiting on white sands than on brown sands. Productivity, if properly estimated through fine leaf litter fall, is lower on white sands than on either floodplains or brown sands. Litter fall averages for soils in Amazonia based on references in Proctor (1984), Duivenvoorden and Lips (1995), Brouwer (1996) and Thomas (1999) were: brown sands (n = 22, 8.6 ton ha^{-1} y^{-1}), floodplains (n = 8, 8.1 ton ha^{-1} y^{-1}) and white sands (n = 11, 6. 6 ton ha^{-1} y^{-1}). The differences are significant (ANOVA all groups: Fs = 9.1, $p < 0.001$), attributable to a lower litter production on white sands. There is also a significant difference in nitrogen content of the litter between those sites (% N in litter on brown sands: 1.47%, on white sands: 0.95%; $F_{[1,28]} = 27.49$, $P<0.001$, references as above). Consequently, the total turnover of litter nitrogen is also strongly different between these soils (N turnover in litter on brown sands: 125.3 kg/ha; on white sands: 62.6 kg/ha; $F_{[1,28]} = 38.27$, $P<0.001$, based on data from references above). Phosphorous concentrations in litter are not significantly different between soil types (data not shown), suggesting that nitrogen may be more limiting on white sands than is phosphorous.

Plants show a variety of adaptations to nutrient limitations. Among these mycorrhiza, N-fixing nodules, and “cluster-roots” (a.k.a. proteoid roots) are best known and clearly adaptive under low availability of certain nutrients. There are also clearly defined mycorrhiza types differing in their characteristics. For instance, ectomycorrhizal roots have access to other (more) phosphorous pools than VA-mycorrhizal and non-mycorrhizal roots (Lambers *et al.* 1998).

Associations with microbionts are not randomly distributed over the plant kingdom. Nodulation is mainly almost exclusively in Legumes. Even within the Legumes there are differences. Fabaceae and Mimosaceae have much higher incidence of nodulation than Caesalpiniaceae (Corby 1981). Mycorrhizal associations are also dependent on taxonomy to some extent. The majority of species show association with VA-mycorrhiza. Families such as Dipterocarpaceae, Myrtaceae, and within the Legumes Caesalpiniaceae often have an association with ectomycorrhiza (Alexander 1989).

It should be clear that with such a variety of adaptations within and among plant taxa, nutrient availability will not be similar for all species on similar or different soil and this may have consequences for their occurrence. Legumes show a variety of adaptations to nutrient stress and their high abundance on the nutrient poor soils in the Guianas (see Chapter 4, Figure 4.2) may be attributable to that.

Soil acidity and Al-toxicity

Both a low pH and high Aluminium concentrations may lead to toxicity problems in plants (e.g. Marschner 1991). In temperate areas Al has been suggested to control the distribution of plants species (Falkengren-Grerup *et al.* 1995 and references therein). In the tropical agriculture Al-toxicity is also a well-known problem. However, in tropical forest species, only in *Eperua grandiflora* a correlation between soil Al and abundance has been shown (ter Steege 1990, but see Chenery 1947).

Whereas Al-saturation is very low on most white sands (never over 20%, mostly 0%), it is very high on both Ferralsols (mostly over 30% and up to 100%) and Leptosols (50 – 100%, van Kekem *et al*. 1996). The Al-saturation levels of Leptosols are considered toxic to most crops (van Kekem *et al*. 1996). The pH of the soils under normal forested conditions are never very low (mostly over 4.5, Brouwer 1995) and acute toxicity is not expected under these circumstances. Still, Al-concentrations may be high enough to affect the rooting depth of species (Marschner 1991, Kingsbury and Kellman 1997). Also, Al may interfere with the uptake of specific cations, such as Ca, and induce nutrient deficiencies (Huang *et al*. 1996, Lambers *et al.* 1998).

In tree fall gaps on brown sands the pH may become quite low and the Al level may rise considerably (Brouwer 1995). In gaps several pioneer species with a tolerance for high Al concentrations are found. Such species are commonly found in Rubiaceae, Melastomataceae, and Celastraceae (Chenery 1947, 1951, Chenery and Sporne 1976) and can accumulate large quantities of Al in their leave tissue (Chenery 1951, for Guyana: Alexander and ter Steege unpubl. data). Thus, in gaps tolerance to Al may be crucial for the establishment of species and determine future forest composition.

We conclude that soil chemical differences are most likely the main cause for the large differences in forest composition between white sands on one hand and the Fe-Al rich soils on the other hand. The data further suggest that within soil, soil water relations are important for the segregation of species along gradients.

Implications for NPAS

At large scale the Forest Industries Development Surveys gives a fair estimation of the dominant tree species of a region and can be used to classify broad forest regions. At smaller scales several 'soil type – forest type' combinations exists. Such heterogeneity contributes substantially to the β-diversity of an area. Soil chemical differences and taxon-specific adaptations probably play a major role in determining forest composition in central Guyana and likely other parts in Guyana. In selecting potential protected areas it is therefore imperative that due consideration is given to the occurrence of:

1. Combinations of soil and forest types
2. Overall soil heterogeneity
3. Specific soil types

9 A COMPARISON OF DIVERSITY PATTERNS OF TREE AND NON-TREE GROUPS

Hans ter Steege, Renske Ek, Tinde van Andel

Introduction

In the previous chapters we have discussed plant diversity patterns in Guyana focussing on trees. Because over 90% of Guyana is covered by forest and forest like vegetation (Chapter 2) and more than 95% of the forest biomass in Guyana is formed by trees (ter Steege 1998b) this emphasis covers the major structural component of the forest. However, woody standing species make up about half of the total forest species richness. The question that will be addressed in this chapter is: are forests that are rich in trees also rich in other life forms, such as lianas, shrubs, herbs, epiphytes, or cryptogamic plants. In other words can tree diversity be used as an indicator for total plant diversity in rain forests? The use of indicator taxa is fraught with difficulties (Kerr 1997). Also in Guyana the species-richness in common families is not positively correlated with each other in all cases (Chapter 5). Hence, the richness of one family can not simply be taken as an estimate for the richness of another family. Still, the use of indicator taxa is widely discussed and potentially useful and in this chapter we will explore if sufficient data exist to support the use of tree diversity as an indicator for diversity of other plant groups[1].

There are only very few forest sites where the total diversity of all plant forms has been documented: Guyana (Davis & Richards 1933, 1934, Ek 1997, van Andel 2000), Costa Rica (Whitmore *et al.* 1986), Ecuador (Gentry & Dodson 1987, Balslev *et al*. 1998), Colombia (Galeano et al. 1998, Duivenvoorden & Lips 1995), and French Guiana (Bordenave 1996). Most of our information is therefore based upon knowledge from the Guyana Shield. These datasets will be used in the following analysis.

Smaller trees

Because woody species account for over 50% of all species, total plant diversity is to a large extent dependent on tree diversity. In all studies the diversity (or species-richness) of the trees with DBH ≥ 10 cm corresponded well with the diversity (or species-richness) of the smaller trees (for Colombia see Table 9.1). Partly this is caused by the fact that many of the smaller trees are seedlings of the overstory trees. Because smaller trees are much more numerous, the understory is in fact much more species-rich than the overstory of the forest (e.g. Duivenvoorden & Lips 1995, Balslev *et al*. 1998). The higher number of species in the understory is higher for a

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[1] At the landscape level there exists an obvious relation between species richness of different groups. Trees are negatively correlated with herbs and shrubs when forests are compared to savannahs and shrub-lands. Such differences will not be discussed here. Chapter 10 will briefly touch upon the shrub-lands of the Pakaraima highlands, whereas Chapter 11 will discuss the typical species composition and diversity of the southern savannah areas.

large part because the sample sizes are often larger. For instance, in Cuyabeno, the higher numbers can explain most, if not all, of the differences. Balslev *et al.* (1998) found 307 species over 10cm DBH in one hectare of forest in Cuyabeno, Ecuador (Appendix 1). They found 473 species between 5cm and 10cm DBH and within the trees smaller than 5 cm, 464 species. Accounting for the differences in stem number, Fisher's α is hardly different for the different size classes (226.6, 230.8, 211.0 respectively). Similar results were obtained when comparing different size classes in a large 50-ha plot in dry tropical forest on Barro Colorado Island (Leigh 1996).

Table 9.1 Correlation between species numbers of plant life forms on ten 0.1 ha plots in the Colombian Amazon. Data from Duivenvoorden & Lips (1995). Small climbers DBH < 2.5 cm, large climbers DBH ≥ 2.5 cm, small trees DBH < 2.5 cm, medium trees 2.5 ≤ DBH < 10 cm, large trees DBH ≥ 10 cm.

Lifeform	**Herbs**	**Epiphytes**	**Shrubs**	**Small climbers**	**Large climbers**	**Small trees**	**Medium trees**	**Large trees**
Herbs	1							
Epiphytes	0.50	1						
Shrubs	0.46	0.61	1					
Small climbers	0.53	0.31	0.28	1				
Medium climbers	0.57	0.20	0.18	0.89	1			
Small trees	0.54	0.50	0.49	0.90	0. 70	1		
Medium trees	0.47	0.33	0.29	0.85	0.71	0.94	1	
Large trees	0.46	0.21	0.08	0.65	0.69	0.60	0.73	1

Lianas

Lianas are to a large extent dependent on trees for their support. Without large trees large lianas are unlikely to occur. There is no a-priory reason, however, to suspect that tree diversity directly influences liana diversity. Still, tree diversity predicts the liana diversity relatively well both in Colombia (Table 9.1) and Central Guyana (Figure 9.1), the only sites for which multiple plot data exists.

At this scale, possibly, the diversity (or species richness) of lianas and trees are controlled by the same processes. Although lianas are almost fully dependent on trees for their support, they attain roughly similar crown sizes and may have similar life span. Lianas are often wind dispersed but in Guyana a large proportion of the large 'climax'-forest lianas (e.g. of the Celastraceae) are animal dispersed and have relatively large seeds. Thus, also in their dispersal and regeneration behaviour they may have a fair amount of overlap. Lianas are known to flourish in large gaps, but often the species involved are weedy ones and not the species found in the forest plots used in this analysis. Fisher's α of lianas in the 15 Pibiri plots ranged from 10.56 to 19.39, an almost identical range as that of the trees (11.49 – 18.14). But although the numbers of species were positively correlated (Figure 9.1), the relationship between Fisher's α of lianas and trees was poor ($r^2 = 0.10$, $p = 0.24$), as were the numbers of individuals of lianas and trees ($r^2 = 0.01$, $p = 0.74$).

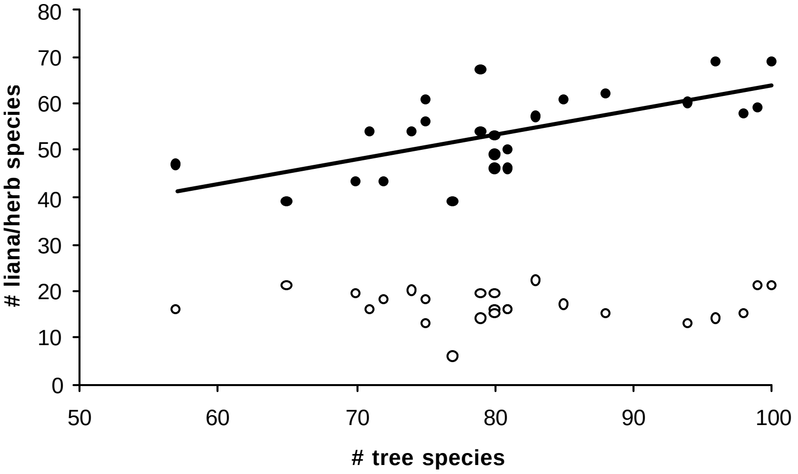

Figure 9.1 Species richness of large trees in 1-ha plots in central Guyana predicts the number of liana species plus or minus 10 species (filled circle, $r^2 = 0.44$, $p < 0.001$) but not herb species richness (open circles, $r^2 = 0.00$, $p = 0.97$). Data of 24 one-ha plots from Ek (1997).

Shrubs and herbs

The diversity and species richness of herbs and shrubs is rather constant within 24 plots in Central Guyana, where tree diversity ranges largely (Ek 1997). Hence tree richness, which varied considerable within those plots, is a poor estimator for herb species richness (Figure 9.1). The same is true for the 10 smaller plots in Colombia (Table 9.1). The low species richness per ha is surprising as the number of individuals of herbs can easily reach 10,000 per ha (Poulsen & Balslev 1991, Ek 1997, van Andel 2000). Total plot size for herbs in Guyana was only 0.04-0.25 ha) ha. Thus, the low number of species in Guyana is also a reflection of the small area sampled. Assuming a constant Fisher's α for the plots it can be estimated that only between 50 and 60% of all herb species, present in one ha, were actually recorded in these plots. The total number of herb species per ha would then range between 21 and 38 species. The latter is equal to the total number of herbs found in all plots combined in Mabura (R. Ek unpubl. data).

The low species numbers thus indicate a very low α-diversity for herbs in these forest plots. Low species richness of herbs, despite the high number of individuals, seem to be the norm for forest understories in the Guiana Shield (Davis & Richards 1934, Duivenvoorden & Lips 1995, Ek 1997, Bordenave 1996, van Andel 2000). In western Amazonia the species richness of herbs may be considerably higher (Balslev *et al.* 1998, see also Gentry 1990). However, compared to the diversity of the woody understory (seedlings, shrubs, understory trees) the diversity of herbs is strikingly low all over the Neotropics (Figure 9.2).

So what keeps the diversity of herbs so low despite their large numbers? Competitive exclusion is unlikely. Even though the densities may be high, herbs are mostly so small that competitive exclusion does not seem probable. Possibly a very low population growth/productivity compared to the disturbance of their populations may be the key (Huston 1994). A more favourable ratio between productivity and competition for herbs is found in savannah vegetation where competition, due to the high density of herbs, is much higher but species richness is much higher as well.

Herbs and shrubs, like trees (Chapter 8) segregate spatially along water availability gradients and among soil types (van der Werff 1992, Tuomisto & Ruokolainen 1993, Tuomisto and Poulsen 1996, Ruokolainen *et al.* 1997 Tuomisto *et al.* 1998). Thus, the total herb richness of a larger area will increase if the soil heterogeneity increases – i.e. when more soil types are included but at a different rate than for trees.

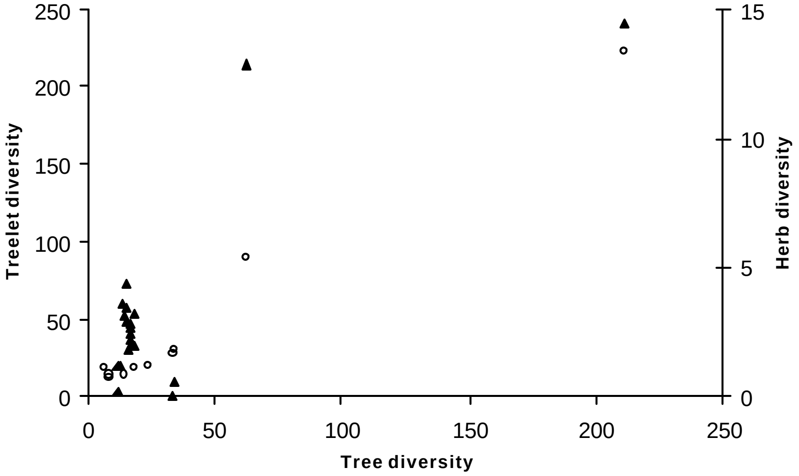

Figure 9.2 Diversity (Fisher's α) of small trees (filled circles) and herbs (triangles) in the understory of forest plots in the Neotropics as a function of large tree diversity (data from sources in the text).

Vascular epiphytes

Epiphytes, by definition, are dependent on trees for their support. Epiphytes are mostly living in a hard environment with highly fluctuating water availability, high light intensities and low nutrient availability and posses several adaptations to cope with their environment. World-wide, epiphytes account for approximately 10% of all species (Kress 1986). In Guyana the families that contribute most to the epiphyte richness are Orchidaceae, Bromeliaceae, Araceae and Ferns.

Because tree diversity for epiphytes can be interpreted as habitat diversity it is expected that there is a clear link between tree and epiphyte diversity. The data from Colombia (Table 9.1), however, suggest a low correlation between the number of tree species and epiphyte species.

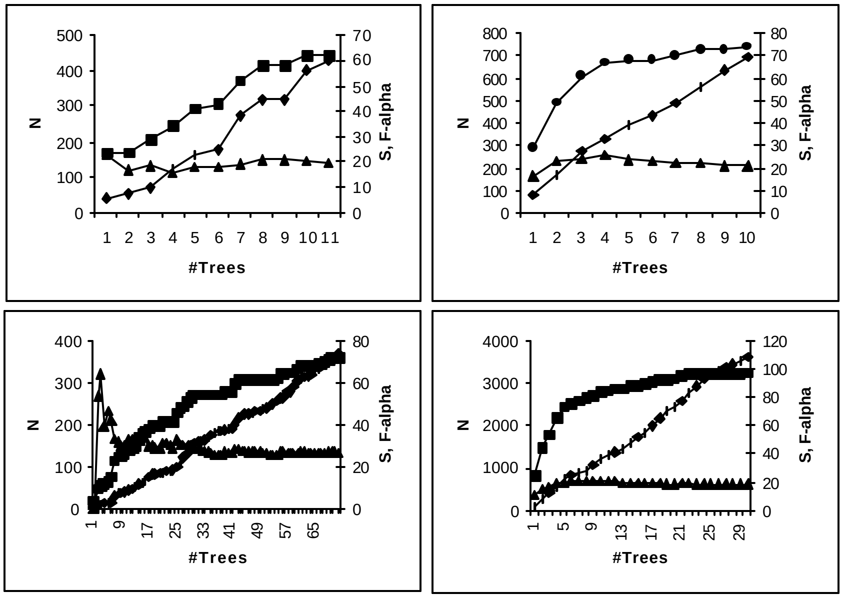

Figure 9.3 Epiphyte numbers (N, ♦), and species (S, ■) observed in plots on trees in four forest plots. Upper left, Wallaba forest; upper right, Mora forest, lower left Greenheart forest, lower right mixed forest in Saül, French Guiana. Fisher's α (▲) is nearly identical for all forests.

Trees can function as differential habitat if host-specificity of epiphytic species exists. In Guyana this has been suggested for a few species occurring on either *Eperua falcata* or *E. grandiflora*. However, the number of species for which this could be shown was very small (ter Steege & Cornelissen 1990). Still, not all trees are equally good hosts. Epiphyte numbers (read individuals) increase linearly with the number of trees sampled (Figure 9.3). At the same time the number of species levels off at some stage. There is a clear difference in the average numbers per tree on different species. Trees in Saül, French Guiana, have far more individuals observed in plots than *Eperua* or *Mora* trees in Guyana. The numbers are not completely comparable because all epiphytes of logged trees in Greenheart forest (Pibiri) were counted, while only small plots were sampled in the other forests. From Figure 9.3 we can conclude that Greenheart is a very inhospitable tree to epiphytes, most likely due to its strongly flaking bark (but bark chemistry can not be ruled out).

Interestingly, Fishers α is quite similar for all forest types and even slightly higher for Greenheart (Figure 9.3). This suggests that the dominance – diversity or species to individuals relationships are similar for these forests. Thus although epiphyte densities may differ widely among trees it appears that diversity is still regulated by a similar mechanism. It has been suggested that epiphytes rarely compete for space (Huston 1994) and that their diversity should be positively correlated with biomass. The data above show that when the number of individuals per tree increase (increase in biomass), the species-richness increases but the diversity as measured with Fisher's α does not.

Because differences between hosts in terms of epiphyte abundance may be the main determinant of epiphyte richness of a forest area, the relationship between tree diversity and epiphyte diversity is expected to be low. Forests with good hosts have more individuals and hence more species of epiphytes but this is not a-priori related to the tree diversity. There is no a-priori reason to classify trees in good and bad hosts but large adult size and large horizontal branches are both prerequisites for high epiphyte densities on trees.

There are some differences in epiphyte composition between forest types with Orchids and Bromeliads being more dominant in the drier forest, whereas Ferns and Aroids are more dominant in the wetter forests (Ek 1997). However, over large areas epiphyte composition may be rather comparable. A large number of epiphytes were common between the Guyana and French Guiana sites. Similarly, the epiphyte flora of Wallaba forest is quite comparable to that of Campina forest close to Manaus (Braga 1977).

Non-vascular epiphytes (mosses, liverworts, lichens)
Cryptograms (mosses, liverworts and lichens) are among the least studied plants in the tropics. This may be partly because as much as half of the species occur in the canopy of the forest (Gradstein *et al.* 1990). While the tropics are far richer in vascular plant species than most temperate areas, this is not the case for mosses, liverworts and lichens (Wolf 1993). In the three Guianas 375 species of liverworts and 234 mosses have been collected (Gradstein *et al.* 1990). The British Isles, for example, have over 1000 species, when both groups are added (Wolf 1993). Bryophytes (mosses and liverworts) have very efficient dispersal through small spores. Eighty percent of all species found in the Guianas are rather widespread in South America and the level of endemism is very small – less than 2.5% in the Guianas (Gradstein *et al*. 1990).

Non-vascular epiphytes are rather commonly found on trees in the forest and on a sample as small as 5 trees more than 75% of the expected flora is already encountered (Montfoort & Ek 1989, Gradstein *et al*. 1990). Samples of just a few trees also harbour a significant portion of the nation's cryptogamic flora (Table 9.2). In Saül 154 species were found on 28 trees, which amounts to 25% of the total species richness found in the three Guianas. On five trees in mixed forest in Guyana 88 species were found, which is nearly 20% of the total number of species found in Guyana (Chapter 2). Hence a small number of trees already captures a very significant portion of the cryptogamic species richness.

As with vascular epiphytes the non-vascular epiphytes show a clear zonation in trees (Cornelissen & ter Steege 1989, Montfoort & Ek 1989). In the Wallaba forest of Mabura Hill 43% of the species show some form of host preference for either *Eperua grandiflora* or *E. falcata*. This is most strongly found in mosses, which have a preference for *E. grandiflora*, while macro lichens seem to have a preference for *E. falcata* (Cornelissen & ter Steege 1989). In Saül host specificity was suspected but could not statistically be supported. Trees with more species generally have more cover (higher number of individuals) as well, which complicates the comparison.

Bark structure (establishment, moisture) and chemistry are likely factors influencing cryptogamic abundance among tree species.

Table 9.2 Numbers of species of cryptograms found on trees in different forests in the Neotropics. Data from Guyana (Cornelissen & ter Steege 1989), Suriname (Florschütz de Waard & Becker 1987), French Guiana (Montfoort & Ek 1989), Brazil (Lobato Lisboa 1976), Colombia (Wolf 1993).

Location	# Trees	Mosses	Liverworts	Macro-lichens
Guyana				
Wallaba forest	11	28	72	33
Mixed Forest	5	28	60	88
Suriname				
Marsh forest	unknown	49	74	na
Mixed forest	unknown	41	58	na
Wallaba forest	unknown	26	47	na
French Guiana				
Mixed forest	4	43	61	21
Mixed Forest	28	66	88	209
Brazil				
Campina	29	12	22	na
Colombia				
Lower montane forest (1500m)	4	22	36	49
Middle montane forest (2550m)	4	33	102	51
Upper montane forest (3510m)	4	19	63	37

The cryptogamic communities found in Guyana (Richards 1984, Cornelissen & ter Steege 1989) may be widespread in Guianas (see Florschütz de Waard & Becker 1987, Montfoort & Ek 1989). Still there are considerable differences in species richness between forest types (Table 9.2, Florschütz de Waard & Becker 1987, Cornelissen & Gradstein 1990). The lowest species numbers are found in dry forests in Guyana, Suriname and Brazil (Table 9.2). Species numbers found in montane forests (Wolf 1993) are comparable to those of the lowlands (Table 9.2), although especially liverworts are more species-rich in the middle montane forest site. Because there is considerable species turn-over over an altitudinal gradient (Wolf 1993), the total species richness of mountainous areas is likely higher than that of the lowlands and several species are restricted to high altitude areas. Hence, the Pakaraimas are likely to have a distinct floristic high altitude element, which is small, however (17 ssp., Gradstein *et al*. 1990).

Conclusions

Diversity (Fisher's α or species richness) of large trees (DBH ≥ 10 cm) is a good indicator of the diversity of smaller size classes of trees and a relatively good indicator for the diversity of lianas.

In Guyana tree diversity is not a good indicator for the diversity of shrubs and non-woody taxa such as herbs, epiphytes, and cryptograms. Small areas may already preserve substantial species-richness of these groups.

At very large scales tree diversity and herb diversity in forest plots are related but there are too few plots available for hard conclusions

All groups show to some extent differentiation to habitat/soil types, underscoring the importance of inclusion of soil heterogeneity in a Protected Area System.

10 FLORA, VEGETATION, ENDEMISM AND ALTITUDINAL GRADIENTS IN THE GUAYANA HIGHLAND AREA: A BRIEF OVERVIEW[1]

Hans ter Steege

Introduction

The Pakaraima Mts. is a region with high species richness and high endemism in Guyana (Chapter 6). Tree α-diversity, however, may be quite low (Chapter 4, Fanshawe 1952, Whitton 1962, Berry *et al.* 1995), due to high dominance of some taxa, such as *Dicymbe, Eperua,* and *Dimorphandra* . It was suggested that altitudinal zonation and isolation in mountainous areas must have contributed to the high overall species richness, compared to other regions in Guyana (Chapter 6). While little is known on the flora of this region in Guyana, we can draw on a large knowledge base built up in adjacent Venezuelan Guayana to gain some insight in the vegetation and potential richness of this region.

The Guayana floristic region can be subdivided in four provinces (Berry *et al*. 1995), of which the Eastern Guayana Province has been the subject of most of this book, as it includes the lowland forests of Guyana. The Guayana Uplands (Figure 10.1) form the Central and part of the Western province of the Guayana region, as defined by Berry *et al.* (1995). The Central Guayana Province, which consist mainly of (sub-) montane forest and shrublands from 300-1500 m altitude (Berry *et al*. 1995), extends into western Guyana (Pakaraimas and Iwokrama Mts.) with an outlier in Suriname (Tafelberg). The Guayana Highlands correspond to the Pantepui Province, which consists of the high mountain ecosystems above 1500 m (Berry *et al*. 1995), and is found almost exclusively in Venezuela but small pockets are found in Guyana (Mts. Ayangana, Wokomung, and Roraima) and northern Brazil.

The flora

The Guayana Highlands have a rich flora (Huber 1997). Venezuelan Guayana, an area roughly equal in size to the Guianas, is richer in species with 9411 reported vascular plant species (Berry *et al.* 1995) compared to the Guianas, where 7088 species have been collected (Boggan *et al.* 1997). Berry *et al.* attributed the higher number of species to the higher altitudinal variation of Venezuelan Guayana (see below).

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[1] The information of this chapter is based almost entirely on the information given in Huber 1988, 1995a and Berry *et al* 1995. It presents a very brief synthesis. The reader is referred to the afore mentioned sources for further information

A number of families are more species-rich in the Guayana Highlands compared to the lowlands. Given the difference in altitude this is not surprising and many of such families are those that are ecologically adapted to (open) mountain ecosystems, such as Rapateaceae, Ericaceae, Xyridaceae. Among the woody families Araliaceae (*Schefflera*) and Aquifoliaceae (*Ilex*) are prominent (Berry *et al.* 1995).

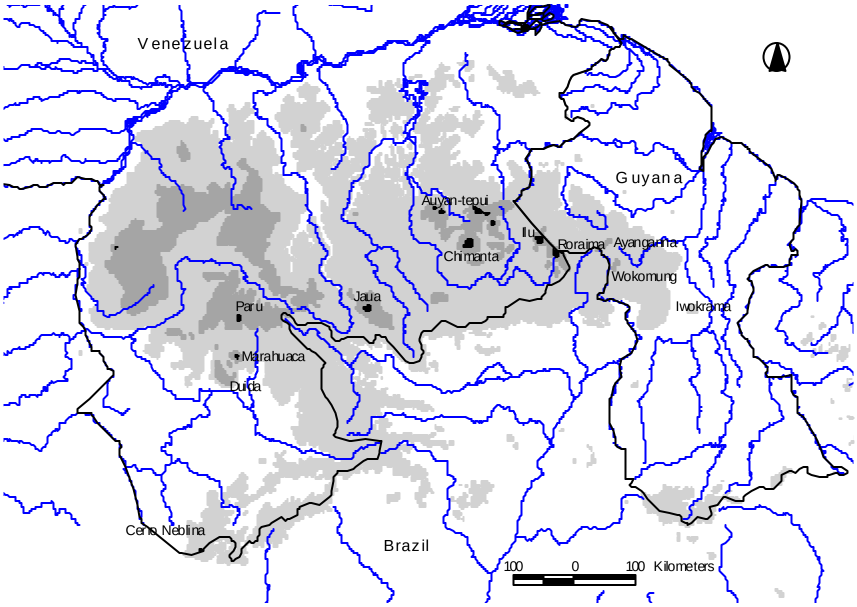

Figure 10.1 The Guayana Highlands, showing the principal mountain systems. The three major mountain systems in Guyana are Roraima, Ayanganna and Wokomung. The Iwokrama Mts. are an isolated part of these highlands. Grey shades: light grey areas are the uplands over 500 m altitude; dark grey are the highlands over 1500 m; black are areas over 2500 m (based on Digital Elevation Model of the USGS (http://edcwww.cr.usgs.gov/landdaac).

Lowland and upland vegetation of the Pakaraima Mts.

The vegetation of the Guayana Highlands, including the Pakaraima Mts., is greatly influenced by variation in altitude and isolation caused by the rugged landscape (Huber 1995a, 1997). There are also very sharp gradients in rainfall with as little as 1700 mm y^{-1} in the south-eastern Pakaraimas (bordering the north Rupununi Savannah) to as much as 4000 mm y^{-1} on the high mountain sides facing the north-eastern trade winds (Persaud 1994). Differences in soil types (see Gross-Braun *et al*. 1965) also contribute to the heterogeneity of this area.

The forest types of this area were discussed in some detail in Chapters 4 and 5. Here we briefly recapitulate the most important features.

Lowland forests (0 – 500 m)

The lowland forests of the Pakaraima Mts. area can broadly be classified into two groups (Fanshawe 1952): rain forest on brown sands derived from intrusive volcanic rocks and rain forest on the sandstones and sediments of the Kaieteurian series (white sands). The lowlands of the Pakaraima region border with three major national forest regions (Chapter 4) and there is most likely a smooth gradient between them.

The lowland forests of the northern part of the Pakaraima Mts. grade into the wet forests of the Northwest of the country (Chapter 5) and are mainly dominated by *Eschweilera, Licania, Alexa* and *Mora gonggrijpii* (Chapters 4, 5, Fanshawe 1952, Huber 1995a). In the eastern parts, bordering the wet central forests, *Dicymbe* is one of the most striking components. *Dicymbe*, which is almost entirely a Guiana Shield genus (Berry *et al.* 1995), spreads eastwards into central Guyana (Chapter 4) but remains within the 2700 mm y^{-1} isohyeth (ter Steege unpubl. data). This area and especially the drainage basin of the Potaro river has very high abundance of species endemic to Guyana (Chapters 4, 5). In the southern part, where annual rainfall is much lower, dry deciduous forests with *Cordia* and *Centrolobium* can be found (Fanshawe 1952).

On the white sands typical Wallaba forest is found dominated by *Eperua falcata* and *E. grandiflora* (see Chapter 4 for more details).

Lowland (and upland) savannahs

Lowland savannahs, dominated by the grasses *Trachypogon* and *Axonopus* and the shrubs *Curatella* and *Byrsonima* are found mainly in the southern parts where the Pakaraima Mts. border the Rupununi and Rio Branco savannahs and are also scattered throughout the western part of the region (Fanshawe 1952, Huber *et al*. 1995, Chapter 11). At slightly higher altitude *Echinolaena* and *Bulbostylis* are also typical (Fanshawe 1952, Huber *et al.* 1995). Savannahs on white sands have more sedges and also include more genera typical of the alpine meadows (Fanshawe 1952, see below).

Montane or upland forests (500 - 1500 m)

Montane or upland forests (500-1500 m) cover only a very small area in Guyana and their composition remains largely unknown (but see Veloso *et al.* 1975, Huber 1995a). Sapotaceae and Lauraceae, in general, are overwhelmingly abundant at higher elevations (e.g. Table 4.1).

Legumes, such as *Eperua falcata, Eperua grandiflora, Dicymbe altsonii, D. corymbosa* and *Dimorphandra davisii*, dominate the white sands derived from the weathering table mountains (Fanshawe 1952, Whitton 1962, Chapter 4). *Micrandra glabra* is widespread and dominant on poorly drained soils, along rivers, notably the Kako R. (I. Welch pers. comm., FIDS unpubl. data), often together with *Dimorphandra macrostachya*. Fires are common in this area (Hammond and ter Steege 1998) and much of this forest is in a seral stage (*Humiria* and *Dimorphandra* scrub) recovering from fires (Fanshawe 1952, Chapter 4).

Pantepui (Highlands)

Pantepui is defined as that part of the Guiana Shield that is over 1500 m altitude (Berry *et al*. 1995). There are four main vegetation formations that make up Pantepui (Huber 1997):

1. Upper montane forests
2. Tepui scrubs
3. Alpine meadows
4. Open rock vegetation

Upper montane forests (1500 – 2000 m)

In Guyana upper montane forest are only found on the three highest table mountains - Mts. Roraima, Ayanganna, and Wokomung. Typical highland genera such as *Bonnetia, Schefflera, Podocarpus, Magnolia*, and *Weinmannia* are found here (Veloso *et al.* 1975, Huber *et al.* 1995, Huber 1995a). The cloud forests are rich in cryptogamic and vascular epiphytes and have a dense and rich undergrowth (Huber 1995a).

Tepui scrub (2200 – 2700 m)

At higher altitudes the forest finally grades into tepui scrub which, in Guyana, is only found on Mts. Roraima and Ayanganna (Huber *et al*. 1995). Most characteristic genera are *Bonnetia, Schefflera, Clusia*, and *Ilex* (Veloso *et al.* 1975, Huber *et al.* 1995, Huber 1995a). The Tepui scrub is the formation with the highest diversity in the Guayana Highlands with different scrub types found on almost all large tepuis (Huber 1997).

Alpine meadows (c. (950) – 1500 – 2500 m)

The alpine meadows are also a very rich and distinct formation within the Guayana Highlands (Huber 1997). In Guyana it is only found in the upper reaches of the Kamarang R., Mt. Holitipu and Lamotai Mt., both along the lower Kamarang R. Grasses are usually not dominant (Huber 1995a). Their ecological niche is taken up by *Stegolepis* spp. (Rapateaceae). Other common genera include *Abolboda, Xyris, Orectanthe, Chalepophyllum, Lagenocarpus* and *Brocchinia* (Huber 1995a).

Open rock vegetation

The high summits of tepuis are mostly bare but small pockets of vegetation are present. Apart from cyanobacteria and lichens, which are often the first visible pioneers, Bromeliaceae, such as *Lindmania, Navia* and *Brocchinia*, are typical (Huber 1995a). A recent study of 33 of such vegetation ‘islands’ on Mt. Roraima (Michelangeli 2000) found 40 species, of which *Bonettia*, Poaceae and Rapateacea had highest cover. Orchidaceae were the most species rich, with 7 species.

Rock vegetation is also found at lower altitudes, often in small areas. *Vellozia* is a characteristic plant of such patches (Fanshawe 1952). Although too small to be mapped effectively, apparently significant stretches occur close to Mt. Ayanganna (Fanshawe 1952). Rock vegetation is also commonly found on rocky outcrops in the savannah and this type will be discussed in more detail in Chapter 11.

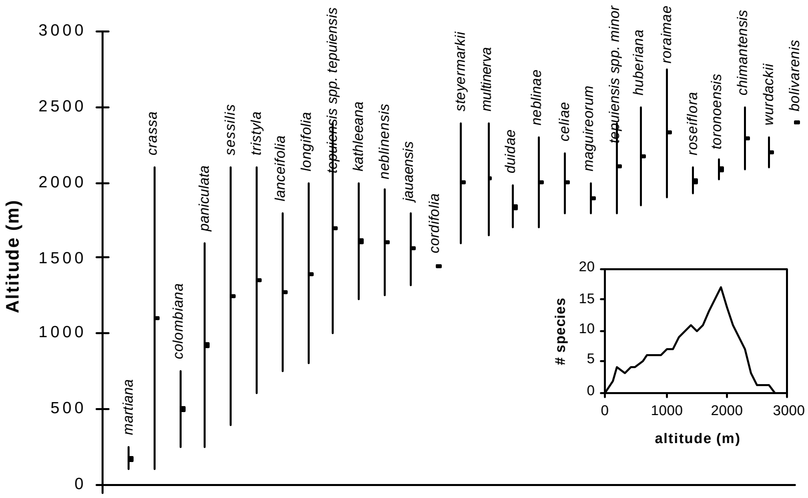

Figure 10.2 Altitudinal distribution of species of *Bonnetia* in Venezuelan Guayana (Huber 1988). The inset shows the number of species found at each altitude.

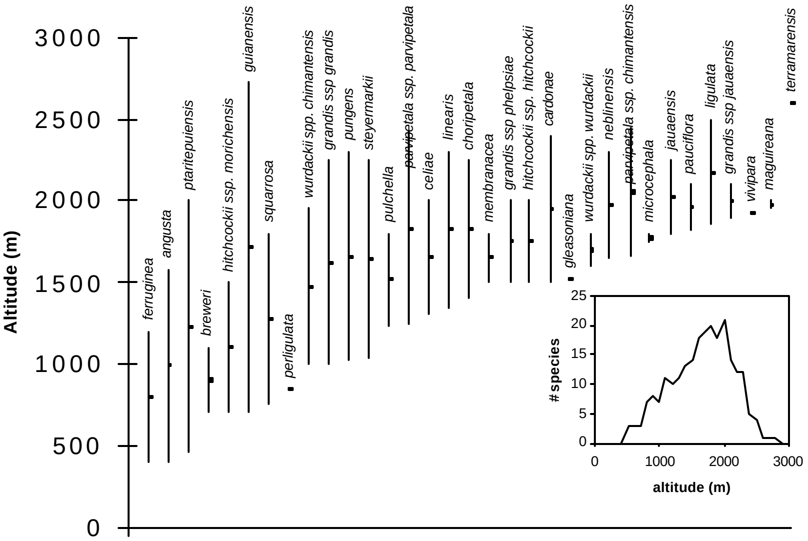

Figure 10.3 Altitudinal distribution of species of *Stegolepis* in Venezuelan Guayana (Huber 1988). The inset shows the number of species found at each altitude.

Altitudinal zonation

As is discussed above altitudinal variation in the Pakaraima Highlands, which ranges from below 500 m to close to 3000 m, adds substantially to habitat heterogeneity. Even with a set of lowland taxa the region showed very high species-richness (γ-diversity, Chapter 6). We have no firm data to suggest which altitude may harbour the highest diversity in Guyana and that is not even be possible with the set of typical lowland species used in Chapter 6 (cf. Berry *et al.* 1995). In Venezuelan Guayana the highest species diversity in two large genera (*Bonnetia* and *Stegolepis*) was found around 1800-2000 m altitude (Figures 10.2, 10.3). These two genera represent the major dominant herbaceous (*Stegolepis*) and woody (*Bonnetia*) element of Pantepui (Huber 1988).

Several species occur in rather small areas or are in fact endemic to one tepui (Huber 1988), thus also contributing to the third biodiversity component - γ-diversity.

Endemism

The Guayana Highlands region has high levels of endemism – as much as 40% of its species are endemic to the Guiana Shield area (Berry *et al.* 1995). In Venezuelan Guayana 1270 species are considered endemics of the area (Berry *et al.* 1995), which is just over 13% of the total flora. Similarly, the Pakaraima Mts. area is the area with highest endemism (9.4 %) in Guyana (Chapter 6). The concentration of endemic taxa is especially high at higher altitudes - Pantepui accounts for just 1% of the Guayana Highlands area but holds 766 species that are endemic to the Guayana Highlands (36% of the total number of endemic species and 23 of the 34 endemic genera) (Berry *et al.* 1995). Pantepui is probably one of the main centres of endemism in the neotropics (Huber 1997).

In Guyana, the area between the Kako River, the head of the Mazaruni River, and Mt. Roraima is an area with high endemism (Chapter 6). Because the drainages of the Mazaruni and Cuyuni Rivers are relatively undercollected compared to the Roraima area this may be an artefact of sampling intensity. However, also at the Guiana Shield level the Roraima-Ilu chain is one of the five concentration areas for endemics in the region (Huber 1997) and the eastern Pantepui subdivision (Huber 1988) is the also the largest centre of endemism for *Bonnetia* and *Stegolepis*. This subdivision includes major tepuis like Auyan-Tepui, Chimana, Ila and Roraima.

Berry *et al.* (1995) found 138 genera to be endemic to the Guiana Shield, 61 of which occur in Guyana. Most of the genera have a fairly wide altitudinal distribution (Figure 10.4). The main peak of generic diversity is found around 1300 m altitude (Figure 10.4 inset). However, out of the 61 genera, 8 are restricted to altitudes over 1000 m altitude, and 14 below 500 m. Ten genera are fully restricted to Guyana: *Gynocraterium, Thysanostemon, Boyania, Maguireanthus, Ochtephilus, Tryssophyton, Maburea, Whittonia, Potarophytum, Windsorina* (Berry *et al.* 1995).

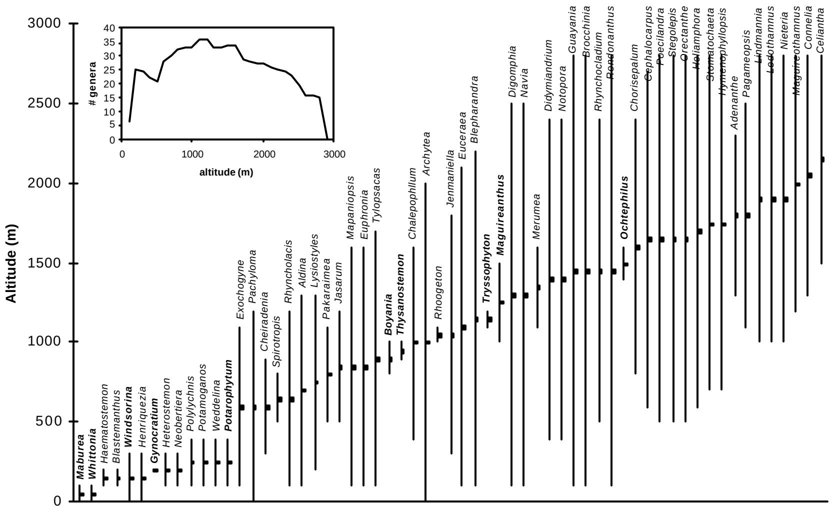

Figure 10.4 Altitudinal distribution of 61 genera, endemic to the Guiana Shield area and occurring in Guyana (data from Berry *et al*., 1995). The genera are ordered based on an increasing 'geometric mean' (horizontal line) of their altitudinal range. The first 14 genera are confined to altitudes below 500m. **Inset**: The number of genera present as a function of altitude. Genera endemic to Guyana are given in bold. **Note!** This is a regional average: not all genera will generally be present at one single site.

Conclusions and some implications for conservation

The Guayana Highlands are one of the important centres of plant diversity and endemism in the neotropics. The Pakaraima Mts. Region in Guyana has very high regional species-richness and the highest level of endemism of the country. A concentration of endemic species was observed in the Upper Mazaruni-Kako-Roraima area, making it the second most important area for endemism in Guyana, after the Berbice Formation area in central Guyana (Chapter 6). However, more rigorous collecting may change the levels of endemism substantially.

Endemic species are very abundant in the Potaro R. basin (Chapter 5), which forms a part of the lowlands (0-500 m) and uplands (500-1500 m) of this region. Although this area has relatively low α-diversity, its high abundance of endemic species is of great conservation value.

Altitudinal variation adds greatly to the diversity at the family, generic (Figure 10.4) and species (Figures 10.2 and 10.3) level. It is therefore important that not only the high altitude areas are preserved, even though the data may suggest that they harbour the greatest concentration of typical species. In addition to that single high mountains often have a set of unique species, not found on other mountains.

Thus, to preserve a large proportion of the plant diversity in this region, a single small area will not be sufficient. Rather, the full altitudinal range *and a substantial geographical range* should be taken into account. A large area with the major 'mountain islands' may satisfy both of the above requirements in Guyana viz. Mts. Roraima, Ayanganna, and Wokomung

Substantial parts of the Guayana Highlands have been conserved in Venezuelan Guayana (Huber 1995b, 1997). The inclusion of the Upper Mazaruni-Kako-Roraima area in the already protected parts of Venezuelan Guayana will help to protect one of the major regions of endemism and species richness in the Guiana Shield, the Guyanan Highlands and Guyana.

Although substantial collecting has been carried out in the area no synthesis on the botanical data is easily made at present. To gain further insight in the vegetation and flora of the region a further analysis of collections made in the area and ecological and botanical field studies are very necessary.

Appendix 5 Collecting trips of the Utrecht Herbarium in Southwest Guyana from 1979 to 1997.

Year	Details of expedition
1979	P.J.M. Maas *et al*., N Rupununi (Manari), Kanuku Mts. (Moco moco), S Rupununi (Mountain Point), 407 records.
1982	A.L. Stoffers *et al*., N Rupununi (Lethem), S Rupununi (Aishalton), Marudi Mts., 359 records.
1985	M.J. Jansen-Jacobs *et al*., Kanuku Mts. (Puwib R.), S Rupununi (Sandcreek, Mountain Point, Mt. Shiriri), 501 records.
1987	M.J. Jansen-Jacobs *et al*., N Rupununi (Lethem, Nappi), Kanuku Mts. (Mt. Nappi, Jordan Falls, Bank of Guyana), 641 records.
1988	P.J.M. Maas *et al*., N Rupununi (Karanambo, Mt. Makarapan), 539 records.
1989	M.J. Jansen-Jacobs *et al*., Upper Essequibo Region (Gunn's, Kamoa R.), 535 records.
1991	M.J. Jansen-Jacobs *et al*., Eastern Kanuku Mts. (NE of Warimure), S Rupununi (Dadanawa), Upper Essequibo Region (Cuyuwini R.), 499 records.
1992	M.J. Jansen-Jacobs *et al*., S Rupununi (Dadanawa, Kusad Mts.), Upper Essequibo Region (Cuyuwini R.), 614 records.
1992	A.R.A. Görts-van Rijn *et al*., N Rupununi (Karanambo), S Rupununi (Dadanawa), 161 records.
1994	M.J. Jansen-Jacobs *et al*., Eastern Kanuku Mts. (Crabwood Cr., Two-Head Mt.), S Rupununi (Shea, Kwitaro R.), 619 records.
1995	M.J. Jansen-Jacobs *et al*., N Rupununi (Manari, Karanambo), Kanuku Mts. (Moco moco, Crabwood Cr.), S Rupununi (Dadanawa, Mountain Point, Mt. Shiriri, Shea, Jerome's Place), 1207
1997	M.J. Jansen-Jacobs *et al*., S Rupununi (Dadanawa, Shea, Miliawau R., Wakadanawa), 251 records.

Documents concerning these trips have been published by the Utrecht Herbarium (Listed in chronological order of the expedition (as above)):

Jansen-Jacobs, M.J., Gradstein S.R., and ter Welle, B.J.H. (1985). *Botanical exploration in Guyana, 1985*. Institute of Systematic Botany, University of Utrecht.

Jansen-Jacobs, M.J. and ter Welle, B.J.H. (1989). *Botanical exploration in Guyana, 1985. Annex: identifications*. Institute of Systematic Botany, University of Utrecht.

ter Welle, B.J.H., Jansen-Jacobs, M. J., Görts van Rijn, A.R.A. and Ek, R.C. (1987). *Botanical exploration in the northern part of the western Kanuku mountains (Guyana) 1987*. Institute of Systematic Botany, University of Utrecht.

Jansen-Jacobs, M.J., ter Welle, B.J.H., (1990). *Botanical exploration in the northern part of the western Kanuku mountains (Guyana) 1987. Annex: identifications*. Institute of Systematic Botany, University of Utrecht.

Maas, P.J.M, Koek-Noorman, J., Lall, H., ter Welle, B.J.H. and Westra, L.Y.Th. (1988). *Botanical exploration in the northern part of the Rupununi savanna and in the Mabura Hill area (Guyana) 1988*. Institute of Systematic Botany, University of Utrecht.

Maas, P.J.M. and Westra, L.Y.Th. (1990). *Botanical exploration in the northern part of the Rupununi savanna and in the Mabura Hill area (Guyana) 1988. Appendix: identifications*. Institute of Systematic Botany, University of Utrecht.

ter Welle, B.J.H., Jansen-Jacobs, M.J. and Nic Lughadha, E.M. (1989). *Botanical exploration in the Wai-wai area of southern Guyana 1989*. Institute of Systematic Botany, University of Utrecht.

Jansen-Jacobs, M.J. and ter Welle, B.J.H. (1992). *Botanical exploration in the Wai-wai area of southern Guyana 1989. Annex: identifications*. Herbarium, University of Utrecht.

ter Welle, B.J.H. and Jansen-Jacobs, M.J. (1991). *Botanical exploration in Guyana - Rupununi district 1991*. Herbarium, University of Utrecht.

Jansen-Jacobs, M.J. and ter Welle, B.J.H. (1994). *Botanical exploration in Guyana - Rupununi district 1991.*

Annex: identifications. Herbarium, University of Utrecht.

ter Welle, B.J.H., Jansen-Jacobs, M.J. and Sipman, H.J.M (1993). *Botanical exploration in Guyana - Rupununi district and Kuyuwini river 1992*. Herbarium , Utrecht University.

Jansen-Jacobs, M.J. and ter Welle, B.J.H. (1994). *Botanical exploration in Guyana - Rupununi district and Kuyuwini river 1992. Annex: identifications*. Herbarium , Utrecht University.

Görts-van Rijn, A.R.A., van den Wollenberg, L.J.W. and Florschütz-de Waard, J. (1994). *Botanical exploration in Guyana 1992*. Herbarium, Utrecht University.

Görts-van Rijn, A.R.A., van den Wollenberg, L.J.W. and Florschütz-de Waard, J. (1996). *Botanical exploration in Guyana 1992. Annex: identifications*. Herbarium, Utrecht University.

ter Welle, B.J.H., Jansen-Jacobs, M.J., Chanderbali, A. and Raghoenandan, U. (1994). *Botanical exploration in Guyana - Eastern Kanuku mountains/Crabwood creek 1994*. Herbarium , Utrecht University.

Jansen-Jacobs, M.J. and ter Welle, B.J.H. (1996). *Botanical exploration in Guyana - Eastern Kanuku mountains/Crabwood creek 1994. Annex: identifications*. Herbarium , Utrecht University.

ter Welle, B.J.H. and Jansen-Jacobs, M.J. (1995). *Botanical exploration in Guyana - North and South Rupununi savanna and Kanuku mountains 1995*. Herbarium , Utrecht University.

Jansen-Jacobs, M.J. (1998). *Botanical exploration in Guyana - North and South Rupununi savanna and Kanuku mountains 1995. Annex: identifications*. Herbarium , Utrecht University.

Jansen-Jacobs, M.J. (1998). *Botanical exploration in Guyana – South Rupununi Savanna 1997*. Herbarium, Utrecht University.

Jansen-Jacobs, M.J. (1999). *Botanical exploration in Guyana – South Rupununi Savanna 1997. Annex: identifications*. Herbarium , Utrecht University.

ter Welle, B.J.H., Jansen-Jacobs, M.J. and Haripersaud, P.P. (2000). *Botanical exploration in Guyana – Corona Falls (Rewa River) towards Essequibo River 1999*. Herbarium , Utrecht University.

11 SOUTHWEST GUYANA: A COMPLEX MOSAIC OF SAVANNAHS AND FORESTS

Marion Jansen-Jacobs, Hans ter Steege

Introduction

In the southern part of Guyana the largest savannah area of the country is found: the Rupununi Savannah (Figure 11.1), which covers approximately 13,000 km^2 (Daniel and Hons 1984). The Kanuku Mts., a mainly forested mountain range, divides the Rupununi Savannah in a northern and southern part. The Rupununi Savannah is in fact an extension of the larger Rio Branco Savannahs of Brazil (see Figure 2.1). Phytogeographically the area belongs to the Amazon Region and not to the Eastern Guayana Province of the Guayana Region, such as the rest of Guyana (Berry *et al.* 1995, see also Chapter 10). As was suggested in Chapter 6 the approximate boundary may be around 4° N, just north of the savannah area.

There are several publications on the vegetation in Southwest Guyana (Schomburgk 1847, 1848, Davis 1936, Myers 1936, Smith 1939, Fanshawe 1952, Eden 1964, 1973; Goodland 1966, Anonymous 1966) but no clear synthesis. Southwest Guyana differs substantially from central and north Guyana in terms of climate, geomorphology and population. Because these factors are important for the understanding of the vegetation they are briefly discussed below.

Climate

In contrast to central and north Guyana, with two dry and two wet seasons, the Rupununi area experiences only one wet and one dry season (Persaud 1994). The annual rainfall in the Rupununi Savannah is between 1500-2000 mm y^{-1}, of which ca. 70-80 % falls during the wet season from May-August (Persaud 1994). The savannah areas also have the highest amount of sunshine hours of the country (8 h day^{-1}, Persaud 1982). The mean annual daily temperature is 27.5 ° C (Persaud and Persaud 1993). Rainfall increases towards the south because of the orographic uplift caused by the Acarai Mts. (Persaud 1994, see also Figures 6.3, 6.4). The drainage system of the Rupununi Savannahs is unable to carry a high volume of surface runoff. As a result most rivers flood in the wet season. In a few places ground water drainage is impeded by clay, and ponds and lakes persist for several months (Hills 1969).

Geomorphology and soils

Geomorphologically SW Guyana belongs to the Precambrian Lowlands (Daniel and Hons 1984), which derives its name from the underlying Precambrian crystalline basement rocks. These rocks are exposed in the Kanuku Mts. and over a wide area in the South Rupununi Savannah. In the North Rupununi Savannah the Precambrian rocks are covered by the sedimentary rocks of the Takutu Formation (Sinha 1968).

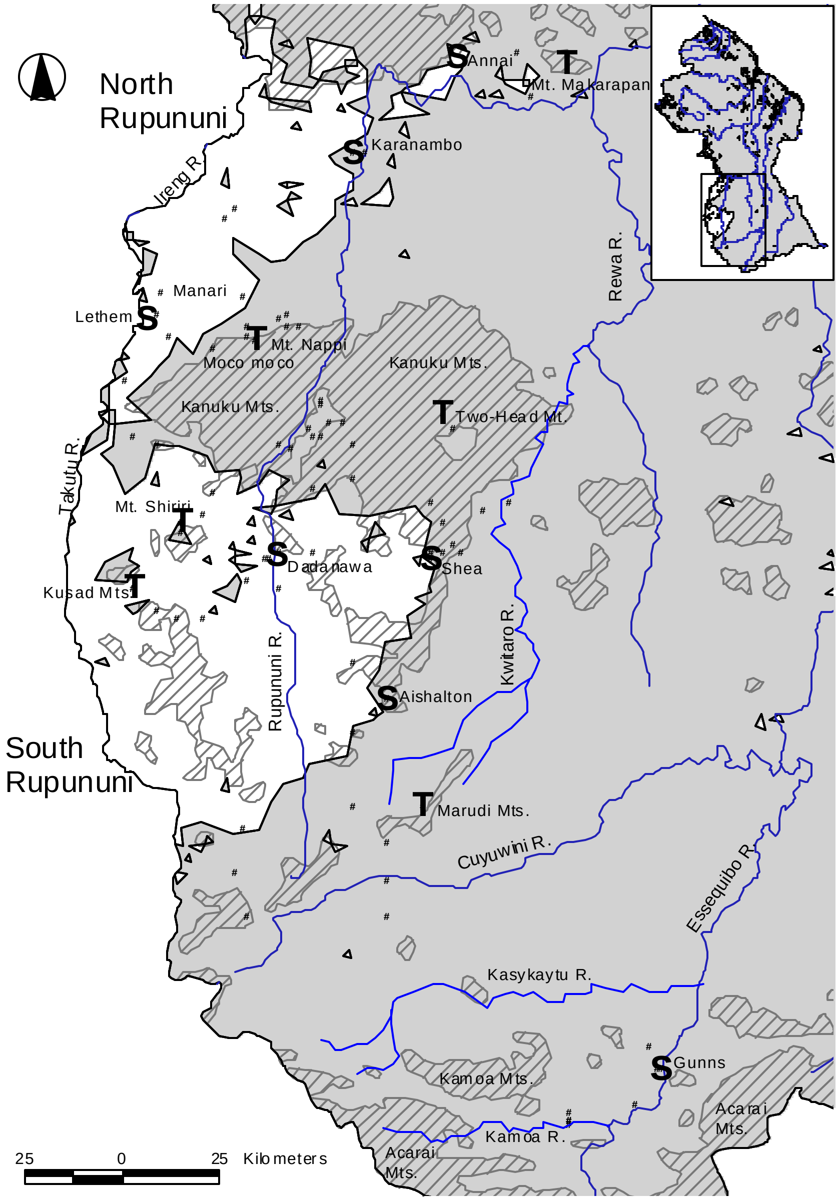

Figure 11.1 North and South Rupununi Savannahs and important locations. Black dots: collecting locations of the Utrecht Herbarium. Important mountains are indicated by a triangle, important villages by a circle. The inset shows the location of the Rupununi in Guyana. Savannah area is indicated by white. Forest cover is indicated by light grey (based on NOAA-AVHRR satellite images, September 1992 (http://edcdaac.usgs.gov/1KM/comp10d.html)). The main rocky soils are indicated by dark grey hatching (after Gross-Braun *et al*. 1965).

The landscape of the North Rupununi Savannah is gently undulating. Domes and ridges with porous laterite on top are mostly forested, in-between seasonally waterlogged flats with sandy clay are found (Daniel and Hons 1984, Sinha 1968, Eden 1973). The Kanuku Mts. are a large outcrop of granite. The slopes have a thin layer of sandy-clayey lithosol and are covered with forest. In the south Rupununi Savannah the granitic bedrock is close to the surface. It is visible as inselbergs - summits of the bedrock that dominate the landscape (Frost 1968, Eden 1973). The slopes of the higher inselbergs are steep and strewn with boulders. The thin sandy soil that develops on the slopes supports a moderately thick forest. The pediments have thin soil with lateritic tendencies (Daniel and Hons 1984). In the depressions, “groundwater laterites” are formed which act as a partially impermeable layer (Frost 1968). In general the soils of the Rupununi Savannah are highly acidic and poor in nutrients (Goodland 1966).

Population

Several Amerindians tribes, amounting to some 15,000 people (B.J.H. ter Welle, pers. comm.), inhabit the Rupununi area. The main tribes are the Macushi who mainly live in the North Rupununi Savannah; the Wapishiana who live in the South Rupununi Savannah and the Wai-Wai who live around Gunn’s near the border with Brazil in the far south. The largest villages are Annai, Lethem and Aishalton. In the savannah a number of large cattle ranches have been established, such as Karanambo, Pirara, Manari and Dadanawa.

Savannah fires

The vegetation of the Rupununi Savannahs is mostly burned once a year to promote the growth of pasture grasses for the cattle but also to keep vegetation around dwellings short. Hence, fire is usually of human origin, but it may also have natural causes (Hills 1969). Due to lack of combustible material, the total area burned by one single fire is usually not large. Fire is important in the maintenance of savannahs - it enables fire-resistant plants (pyrophytes) to grow and increase in numbers. One of the widespread species of sparse woody plants in the Rupununi Savannah is the fire-resistant treelet *Curatella americana*, with a thick corky bark and xerophytic leaves. Importantly, fires are a direct threat to bush-islands and forest at the savannah edge and notable decreases of forest cover appear to have occurred on the forested mountains over the last decades (B.J.H. ter Welle pers. comm., M.J. Jansen-Jacobs pers.obs., H. ter Steege pers. obs.). Especially during severe El Niño years, such as the 1997-1998 event, fires may cause substantial damage to forest in and around the savannah (Hammond and ter Steege 1998).

Flora of Southwest Guyana

The floristic composition of SW Guyana is known to some extent as a result of activities of botanical collectors since the 19th century, notably Robert Schomburgk between 1835-1843, Richard Schomburgk in 1840-44, A.C. Smith in 1937-38, G. Wilson-Browne in 1948, and R.J.A. Goodland in 1963 (Ek 1990).

Since 1979 the Utrecht Herbarium conducts systematical botanical explorations of the southern part of Guyana in the framework of the ‘Flora of the Guianas’ project (Appendix 5). The explorations resulted in a database of 6333 specimens of vascular plants from this area. The aim of this chapter is to describe the floristic composition of the northern and southern Rupununi and the forests surrounding them on the basis of this database and to shed light on the position/significance of the flora of the Rupununi Savannah in Guyana.

The 6333 records of vascular plants in SW-Guyana represent 3618 species belonging to 150 families, 65% of all species collected in Guyana so far (see Table 2.1). The families, best represented in terms of species are: Fabaceae (131 species), Rubiaceae (131), Poaceae (124), Pteridophyta (111), Cyperaceae (107), Orchidaceae (90), Melastomataceae (89), Caesalpiniaceae (72), Euphorbiaceae (70), Mimosaceae (52) and Asteraceae (51). The most species-rich genera are: *Miconia* (28), *Psychotria* (26), *Rhynchospora* (26), *Piper* (24), *Utricularia* (24) and *Polygala* (21). The largest number of species (1165) was found in the South Rupununi Savannah (2281 collections), against 713 species from the North Rupununi Savannah (1149 collections). The difference is partly due to the more intensive collecting activity in the South Savannah, but probably also to the presence of the inselbergs in the South Savannah (a random sample of 1149 collections yields 764 species). Comparing those two samples from the two areas shows that of a total of 1203 species only 23% were common to the North and South Rupununi, 40% has been collected only in the South Rupununi and 36 % only in the North Rupununi. Thus, the two areas are either severely under-collected or substantially different in floristic terms. In the Kanuku Mountains, 929 species were found/collected (1644 collections). It is expected that many more species will be recorded in the future once collecting of the taller, inaccessible trees progresses. In the Upper Essequibo Region 813 species were collected (1249 collections). This number will also increase with increased collecting effort, as the area is still very much ‘under-collected’ (Chapter 6).

Vegetation types of the Savannah area

The main savannah area is divided by the Kanuku Mountains in the North and South Rupununi Savannah. The border between the, mostly forested, Kanuku Mountains and the savannah area is not sharp. In this zone, mostly at lower altitudes, some small savannahs pockets surrounded by forest exist. The southern border of the Rupununi Savannah is situated more or less around the Cuyuwini River. Here, the savannah landscape is interrupted by bush islands, which gradually coalesce into the extensive Amazonian forest of South Guyana.

Savannah

Fanshawe (1952) classified the fire-climax savannah vegetation as the *Curatella-Byrsonima* association, with contains characteristic species such as: *Curatella americana, Byrsonima crassifolia, Byrsonima coccolobifolia, Antonia ovata,* *Palicourea rigida*, *Tibouchina aspera* and *Amasonia campestris*. The main grasses belong to the genera *Trachypogon, Paspalum, Axonopus* and *Andropogon* and the main sedges to the genera *Rhynchospora* and *Bulbostylis* (Myers 1936, Fanshawe 1952, Jansen-Jacobs pers. obs.). Table 11.2 shows the most remarkable savannah herbs, growing on dryer places. Some species tend to appear and flower only after substantial rain, such as the herbs: *Schultesia benthamiana*, *Schiekia orinocensis*, *Polygala* spp., *Abolboda pulchella* and the bulbous herbs: *Curculigo scorzonerifolia*, *Alophia drummondii* and *Cipura paludosa*. In other herbs flowering is induced by fire. These species often have a subterraneous woody stem, such as: *Byrsonima verbascifolia*, *Clitoria guianensis*, and *Cissampelos ovalifolia*. In the whole savannah area the parasite *Cassytha filiformis* is common.

Table 11.2 Non-grass and –sedge species most commonly collected in the open savannah vegetation in South Guyana. N. Rup, Northern Rupununi; S. Rup, Southern Rupununi; K. Mts., Kanuku Mts., Up. Ess, Upper Essequibo region.

Family	**Genus**	**Species**	**N. Rup.**	**S. Rup.**	**K. Mts.**	**Up. Ess.**
Amaryllidaceae	*Curculigo*	*scorzonerifolia*	1	4		
Caesalpiniaceae	*Chamaecrista*	*hispidula*	4	4		
Convolvulaceae	*Merremia*	*aturensis*	4	5	1	
Fabaceae	*Clitoria*	*guianensis*	2	2	1	
Fabaceae	*Indigofera*	*lespedezioides*	2	7		
Fabaceae	*Macroptilium*	*longepedunculatum*	3	1		
Gentianaceae	*Schultesia*	*benthamiana*	2	9		
Haemodoraceae	*Schiekia*	*orinocensis*	3	2		
Iridaceae	*Alophia*	*drummondii*	2	1		
Iridaceae	*Cipura*	*paludosa*	4	1	1	
Lythraceae	*Cuphea*	*antisyphilitica*	2	6	1	4
Orchidaceae	*Galeandra*	*stylomisantha*	1	4		
Polygalaceae	*Polygala*	*longicaulis*	4	4		
Polygalaceae	*Polygala*	*trichosperma*	6	4		
Rubiaceae	*Diodia*	*apiculata*	3	5		
Rubiaceae	*Perama*	*hirsuta*	3	6		2
Rubiaceae	*Sipanea*	*pratensis*	6	1	2	4
Scrophulariaceae	*Buchnera*	*rosea*	5	3		
Sterculiaceae	*Waltheria*	*indica*	2		1	
Turneraceae	*Turnera*	*guianensis*	4	3	2	
Verbenaceae	*Lippia*	*origanoides*	5	4	1	
Xyridaceae	*Abolboda*	*pulchella*	2	3		1

Bush islands

Small forest patches, locally called 'bush islands', are found commonly within the savannah. The bush-islands vary in size, the larger ones are found on the more elevated places in the landscape and sometimes are rocky. The latter type of bush-island is more frequent in the South than in the North Rupununi Savannah. Common woody species of the bush-islands in the savannah vegetation are listed in Table 11.3. The height of the trees in larger bush-islands is not more than 10 m. Several tree species, which are common in bush-islands, also occur in the more open savannah area as solitary trees:

Himatanthus articulatus, *Curatella americana*, *Humiria balsamifera*, *Byrsonima* spp., *Palicourea rigida*, *Tocoyena neglecta* and *Vitex schomburgkiana*. *Curatella americana*, the most common woody plant in the savannah area, has only been collected a few times. Table 11.3 shows that there are more records of woody species from the South than from the North Rupununi Savannah.

Table 11.3 Species most often collected in the 'bush islands' of the Rupununi Savannahs. Abbreviations as in Table 11.2.

Family	Genus	Species	N. Rup.	S. Rup.	K. Mts.	Up. Ess.
Annonaceae	*Annona*	sp. nov.		4		
Annonaceae	*Guatteria*	*schomburgkiana*	2	2	2	
Annonaceae	*Xylopia*	*aromatica*	1	2	1	
Apocynaceae	*Himatanthus*	*articulatus*	2	4	5	2
Boraginaceae	*Cordia*	*curassavica*		3		1
Caesalpiniaceae	*Cassia*	*moschata*	1	4	1	
Caesalpiniaceae	*Peltogyne*	*paniculata*		5	1	
Caesalpiniaceae	*Senna*	*multijuga*		6	3	
Chrysobalanaceae	*Hirtella*	*racemosa*	4	2	6	6
Cochlospermaceae	*Cochlospermum*	*vitifolium*		7		
Connaraceae	*Rourea*	*grosourdyana*	1	4		
Dilleniaceae	*Curatella*	*americana*	1	2		
Erythroxylaceae	*Erythroxylum*	*suberosum*	2	2	1	
Fabaceae	*Centrolobium*	*paraense*		2		
Fabaceae	*Clitoria*	*brachycalyx*	1	3		
Fabaceae	*Platymiscium*	*trinitatis*		6		
Flacourtiaceae	*Casearia*	*sylvestris*	2	1	4	
Humiriaceae	*Humiria*	*balsamifera*	2	3	1	1
Malpighiaceae	*Byrsonima*	*coccolobifolia*	1	4		
Malpighiaceae	*Byrsonima*	*crassifolia*	2	5	1	2
Malpighiaceae	*Byrsonima*	*schomburgkiana*	3	7	2	1
Mimosaceae	*Pithecellobium*	*roseum*	1	3		
Myrtaceae	*Eugenia*	*punicifolia*	5	4	3	1
Polygalaceae	*Securidaca*	*diversifolia*		5	1	
Rubiaceae	*Isertia*	*parviflora*	3	4	5	2
Rubiaceae	*Palicourea*	*rigida*	3	1		
Rubiaceae	*Tocoyena*	*neglecta*	2	2		
Rutaceae	*Zanthoxylum*	*caribaeum*		5		
Sapindaceae	*Cupania*	*hirsuta*	1	3	4	1
Sapotaceae	*Pouteria*	*surumuensis*	2	5	4	
Verbenaceae	*Lantana*	*canescens*		3		
Verbenaceae	*Vitex*	*schomburgkiana*	1	3		

Rocks

The South Rupununi Savannah in particular has many places with bare rock . These rocks can vary from small flat plates to large outcrops, up to 50-80 m high. On such rocks typical 'rock vegetation' occurs in the small patches wherever some soil substrate is present. The species present on the smallest rock plates are: *Cereus hexagonus*, *Melocactus smithii*, *Cnidoscolus urens*, *Cyrtopodium glutiniferum* and *Portulaca sedifolia*. On more extended rocks *Furcraea foetida* is found too, as are woody species such as *Cyrtocarpa velutinifolium*, *Clusia* spp., *Mimosa brachycarpoides*, *Bredemeyera floribunda* and *Cestrum latifolium*. The commonest species of the rock vegetation are listed in Table 11.4. On the slopes of Shea Rock and Mt. Shiriri, well-known rocky outcrops in the South Rupununi Savannah, mats formed by *Pepinia* *geyskesii*, and on places with running water *Sinningia incarnata* and *Anemia* species occur.

Bare rock is also found on the highest peaks (ca. 800-900 m) of some mountains (primarily the Kanuku Mts. and Mt. Makarapan). Woody elements here are a.o. *Clusia palmicida, Erythroxylum mucronatum* and *Myrcia sylvatica*.

Table 11.4 Species most often collected on rock outcrops in the Rupununi Savannahs. Abbreviations as in Table 11.2.

Family	Genus	Species	N. Rup.	S. Rup.	K. Mts.	Up. Ess.
Agavaceae	*Furcraea*	*foetida*		1		
Anacardiaceae	*Cyrtocarpa*	*velutinifolia*		2	1	
Apocynaceae	*Stemmadenia*	*grandiflora*		4	1	
Bromeliaceae	*Pepinia*	*geyskesii*	1	1		
Cactaceae	*Cereus*	*hexagonus*	1	1		
Cactaceae	*Melocactus*	*smithii*		3		
Dioscoreaceae	*Dioscorea*	*manicorensis*		4		
Euphorbiaceae	*Cnidoscolus*	*urens*		2	1	
Gesneriaceae	*Sinningia*	*incarnata*		3		
Melastomataceae	*Miconia*	*rufescens*	1	3		
Mimosaceae	*Mimosa*	*brachycarpoides*		2		
Moraceae	*Ficus*	*mathewsii*		3	1	1
Orchidaceae	*Cyrtopodium*	*glutiniferum*		2		
Polygalaceae	*Bredemeyera*	*floribunda*		3	1	
Portulacaceae	*Portulaca*	*sedifolia*		7		
Pteridophyta	*Anemia*	*ferruginea*		3	1	
Pteridophyta	*Doryopteris*	*collina*		3		
Solanaceae	*Cestrum*	*latifolium*		2	4	
Turneraceae	*Turnera*	*odorata*		7	2	

Wet savannah and ponds

Ponds are a common feature of the Rupununi Savannahs. They are fully extended in the wet season and dry up gradually in the dry period, although some have water the year round. Except of real aquatic plants, of which the common ones are listed in Table 11.6, there exists a broad variety of plants adapted to wet and dry circumstances. These plants, nearly all herbaceous, are mostly in flower when the ponds are drying up and the soil is still muddy. The more general species are listed in Table 11.5, as the species of the wet savannah. Some genera, or even families, are represented with several species in the wet savannah, such as *Cyperaceae, Eriocaulaceae, Aeschynomene, Utricularia, Acisanthera, Sauvagesia, Ludwigia, Polygala, Bacopa* and *Xyris*.

Oxbow lakes and ponds near Karanambo

Some ponds in the surroundings of Karanambo are isolated parts of the meandering Rupununi R., so-called oxbow lakes. The water level in these ponds varies with the level of the river. The vegetation along the ponds has much in common with the forest along the Rupununi R. but remarkable is the abundance here of *Cordia grandiflora, Bothriospora corymbosa, Chomelia angustifolia*, and *Simaba orinocensis*. The famous *Victoria amazonica* is common in the aquatic vegetation of the ponds. Eight other real aquatic plants have been collected here, of which *Polygonum acuminatum* and

Eichhornia azurea have not been recorded from other ponds in the area.

Table 11.5 Species most often collected in the wet savannahs of the Rupununi Savannahs. Abbreviations as in Table 11.2.

Family	**Genus**	**Species**	**N. Rup.**	**S. Rup.**	**K. Mts.**	**Up. Ess.**
Burmanniaceae	*Burmannia*	*bicolor*	1	5		1
Caesalpiniaceae	*Chamaecrista*	*diphylla*	3	3		
Campanulaceae	*Lobelia*	*aquatica*		5		
Cyperaceae	*Lagenocarpus*	*rigidus*	5	1		2
Droseraceae	*Drosera*	*sessilifolia*	2	6		
Eriocaulaceae	*Eriocaulon*	*tenuifolium*		7		3
Eriocaulaceae	*Philodice*	*hoffmannseggii*	1	5		
Eriocaulaceae	*Syngonanthus*	*simplex*	2	5		2
Euphorbiaceae	*Phyllanthus*	*caroliniensis*	1	4	1	
Fabaceae	*Aeschynomene*	*paniculata*	3	6		
Gentianaceae	*Irlbachia*	*caerulescens*	1	6		1
Gentianaceae	*Schultesia*	*brachyptera*	4	3		1
Hydrophyllaceae	*Hydrolea*	*spinosa*	2	6		1
Labiatae	*Hyptis*	*atrorubens*	2	2		2
Lentibulariaceae	*Utricularia*	*amethystina*	1	2		3
Lentibulariaceae	*Utricularia*	*foliosa*	2	4		
Lentibulariaceae	*Utricularia*	*gibba*		4		
Lentibulariaceae	*Utricularia*	*simulans*	4	5		1
Malvaceae	*Pavonia*	*angustifolia*	5	5		
Malvaceae	*Peltaea*	*trinervis*		10		
Malvaceae	*Sida*	*linifolia*	3	3	1	
Mayacaceae	*Mayaca*	*fluviatilis*	1	5		
Melastomataceae	*Acisanthera*	*uniflora*	4	3		
Melastomataceae	*Comolia*	*villosa*	2	7		2
Melastomataceae	*Rhynchanthera*	*serrulata*		5		
Ochnaceae	*Sauvagesia*	*sprengelii*	4	4		2
Onagraceae	*Ludwigia*	*octovalvis*	4	2	2	
Polygalaceae	*Polygala*	*timoutou*	2	10		1
Rubiaceae	*Limnosipanea*	*schomburgkii*		3		1
Scrophulariaceae	*Agalinis*	*hispidula*	4	3		1
Scrophulariaceae	*Bacopa*	*sessiliflora*	3	4		
Sterculiaceae	*Byttneria*	*genistella*	1	5		
Sterculiaceae	*Melochia*	*villosa*	3	3		
Verbenaceae	*Stachytarpheta*	*angustifolia*	3	1		
Xyridaceae	*Xyris*	*jupicai*	5	4		1
Xyridaceae	*Xyris*	*savanensis*	2	7		1

Rivers and creeks

The main river system in southern Guyana belongs to the Essequibo drainage basin, including the Rupununi R. that drains most of the Rupununi Savannahs. The Takutu R. and Ireng R., which drain the westernmost parts of the savannah, are part of the Amazon basin. The water-divide between these drainage systems lies in north-south direction in the Rupununi area. When the Savannah is flooded waters from both river basins merge.

Table 11.6 Species most often collected in the ponds of the Rupununi Savannahs. Abbreviations as in Table 11.2.

Family	**Genus**	**Species**	**N. Rup.**	**S. Rup.**	**K. Mts.**	**Up. Ess.**
Alismataceae	*Echinodorus*	*subalatus*		6		
Alismataceae	*Sagittaria*	*rhombifolia*	2	4		
Cabombaceae	*Cabomba*	*furcata*		4		
Euphorbiaceae	*Caperonia*	*castaneifolia*	2	3		
Euphorbiaceae	*Phyllanthus*	*stipulatus*	1	7	1	2
Mimosaceae	*Neptunia*	*plena*	2	1		
Lentibulariaceae	*Utricularia*	*myriocista*	5	3		1
Marantaceae	*Thalia*	*geniculata*		5		
Menyanthaceae	*Nymphoides*	*indica*	3	5		
Onagraceae	*Ludwigia*	*inclinata*	1	3		
Onagraceae	*Ludwigia*	*sedoides*	3	2		
Pontederiaceae	*Eichhornia*	*diversifolia*		5	1	
Pontederiaceae	*Pontederia*	*subovata*		2		
Scrophulariaceae	*Benjaminia*	*reflexa*	5	7		

The rivers in the savannah area are bordered by gallery forest, which is inundated during part of the year. The height of the vegetation mostly does not exceed 10 m. The forest along the river and larger creeks in the Kanuku Mts. is somewhat higher, 15-20 m. Trees species such as *Caryocar microcarpum*, *Macrolobium acaciifolium*, *Senna latifolia*, *Zygia cataractae* and *Genipa spruceana* occur along all the rivers in S-Guyana. Common liana species are *Cydista aequinoctialis* and *Memora schomburgkii*. *Mauritia flexuosa* is the most common tree along rivers and creeks. In the open savannah *Mauritia* is a dominating element in the landscape. Some woody species are present only along the rivers in savannah area, such as *Faramea crassifolia*, *Genipa americana*, *Rosenbergiodendron densiflorum*, *Waltheria involucrata*, and *Clerodendrum aculeatum*; others are confined to the wetter environment of the Kanuku Mts. and Upper Essequibo Region, such as *Duguetia quitarensis*, *Licania leptostachya*, *Zygia inaequalis*, and *Mouriri acutiflora* . Some species tend to a more northern distribution, such as *Lecythis schomburgkiana*, *Pouteria glomerata*, *Crateva tapia*, and *Chomelia angustifolia*; others to a more southern distribution, such as *Alchornea schomburgkii*, *Andira surinamensis*, *Etaballia dubia*, and *Swartzia panacoco*.

The Rupununi Savannahs in a regional context

It is remarkable that species that are dominant in the Rupununi Savannahs such as *Curatella americana*, *Byrsonima crassifolia*, and *Palicourea rigida* occur in all savannahs in northern South America, but most of the other species are less widespread. Genera are often similar, but the species differ. Comparable savannahs are the Gran Sabana in Venezuela (Huber 1995a), the Rio Branco Savannah in Brazil (see Takeuchi 1960, Milliken & Ratter 1998) and the Sipaliwini Savannah in Suriname (van Donselaar 1969). Also the Intermediate Savannah, although on the Berbice Formation, shares most of the common species with the Rupununi savannahs (see e.g. Fanshawe 1952).

Forests of Southwest Guyana

The forest in Southwest Guyana is found on the slopes of the Kanuku Mts., the Marudi Mts. and in the Upper Essequibo Region (see also Chapter 5). The forest is mostly between 20 and 30 m high with canopy trees reaching 40 m. In the transition zone between the savannah and the wet forest the vegetation possesses a species composition that is comparable to that of bush-islands but the trees are lower and mostly semi-deciduous (see also Chapters 4 and 5).
Commonly collected species in the undergrowth are shrubs-treelets such as *Cymbopetalum brasiliense*, *Tabernaemontana* spp., *Geonoma* spp., *Psychotria* spp., *Clavija lancifolia*, and *Rinorea* spp. and herbs such as: *Dichorisandra hexandra, Calyptrocarya glomerulata, Calathea elliptica, Heliconia hirsuta, Piper* spp. and *Adiantum latifolium.* Most of the tree species collected in the wet forests are medium-sized with a height between 15-25 m, such as: *Anaxagorea acuminata*, *Duguetia calycina, Duguetia macrocalyx, Schefflera morototoni, Jacaranda copaia, Protium tenuifolium, Tapura guianensis, Casearia commersoniana, Eschweilera pedicellata*, and *Duroia eriopila*. To the largest trees belong: *Anacardium giganteum, Ceiba pentandra, Catostemma fragrans, Parkia* spp., *Bagassa guianensis*, and *Manilkara bidentata*. Canopy trees, in general are poorly represented in the collections. This makes it difficult to compare the collection lists of South Guyana with North and Central Guyana, where tree species were abundantly collected (but see Chapters 4 and 5).

Cloud forest

On the higher tops of the Kanuku Mts., which can be between 700 and 960 m altitude and on top of Mt. Makarapan, between 750-800 m altitude, cloud forest exists. To the species found in this very wet area belong: *Couepia canomensis, Stelestylis stylaris, Sphyrospermum cordifolium, Rhodostemonodaphne scandens, Marcgraviastrum pendulum, Cybianthus detergens*, and *Cybianthus roraimae*.

Conclusions

The savannah region of Southern Guyana contributes a very distinct floristic element to Guyana's plant species-richness. The composition of the flora differs substantially at the species, genus and family level. The Intermediate Savannah, on the Berbice Formation, shares many of its common species with the southern savannahs but a complete floristic inventory was not possible at present.

The Southern Rupununi has a, for Guyana, unique rock vegetation that is quite vulnerable to disturbance.

Fire is important in the maintenance of low savannah vegetation. Recurrent fire, however, is one of the most important threats to the forests surrounding the savannahs but possibly also for the herbaceous savannah itself. Protection of this unique area should therefore include strict fire management.

The forests of the Kanuku Mts. differ substantially in their composition from the forests in central and south Guyana. At present we have very little quantitative and qualitative data to make a good comparison, however.

The savannahs with their forest edges, and surrounding mountains are one of the most impressive landscapes in Guyana.

Implications for conservation:

Because of its unique contribution to the flora of Guyana and its unique landscape, the savannahs in southern Guyana have considerable conservation potential. The south Rupununi Savannah may be the least disturbed, a fact already noted by (Myers 1936).

There are considerable potential conflicts between utilisation and conservation in the savannah area, due to the relatively high concentration of people living and utilising the area. Conservation in this area will have to be achieved by finding a good balance between protection and utilisation by the people living in it. While it may be relatively easy to preserve the vastness or impressiveness of the landscape, protection of the unique flora may be more difficult. Recurrent fire is considered one of the most important threats of the savannah system, although paradoxically, it may also be necessary for the maintenance of that same savannah. The effect of fire on the savannah ecosystem and its surrounding forests should therefore be considered an important issue.

Fire is also a threat to the forests surrounding the savannahs and considerable changes have already taken place at the forest-savannah interface. Here, stricter fire control measures should be put into place, if these forests are to be protected.

The rock vegetation in the south Rupununi Savannah is quite vulnerable to disturbance. Although this unique vegetation type may be little endangered at present, increased visits to rocky areas may damage the vegetation beyond the capacity to recover. Hence, in order to protect this vegetation somewhat stricter rules are necessary.

The Kanuku Mts. are an impressive part of the southern landscape and have forests not found in abundance elsewhere in Guyana, such as dry deciduous forests (see also Chapter 5). Together with the slightly wetter forests in the east, which continue towards the south, some of the least disturbed forests can be found. Possible the best wilderness protection opportunities exist in an area from the eastern Kanuku Mts. towards the east and south.

12 PLANT DIVERSITY IN GUYANA: IMPLICATIONS FOR THE ESTABLISHMENT OF A PROTECTED AREAS SYSTEM

Hans ter Steege, Roderick Zagt, Per Bertilsson, James Singh

Introduction

As a signatory to the Convention on Biological Diversity (ratified in 1994), the Government of Guyana is committed to the conservation of biodiversity within the context of sustainable development. The Environmental Protection Agency is mandated with the implementation of a strategy to conserve the Nation's biodiversity. The development of a National Protected Areas System is an important component of this strategy. Currently, Guyana has two larger protected areas (Kaieteur NP, *c*. 63,000 ha and Iwokrama, 180,000 ha). Compared to its neighbours the total number and area of protected areas is still very small (Figure 12.1).

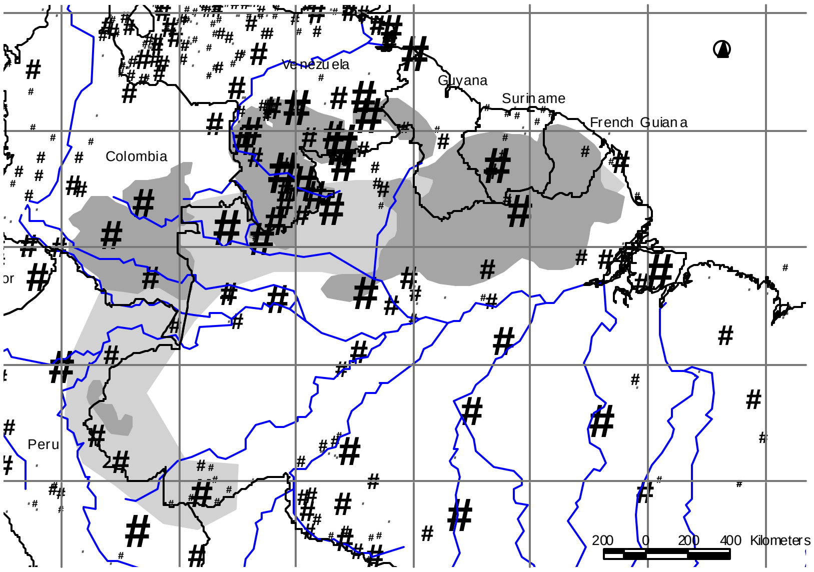

Figure 12.1 Protected areas in the Guiana shield and proximity, based on the WCMC database (http://www.wcmc.org.uk/protected areas/data/un_97_list.html)). The size of the dots corresponds with the actual size of the reserve. Light grey: 'Wilderness area' as suggested by McNeely et al. 1990 and IUCN 1994; dark grey: 'Frontier Forests' sensu WRI (Bryant et al. 1995).

A well-developed National Protected Areas System should be based on a careful analysis of a number of criteria and be compatible with development objectives (Chapter 1). The Government of Guyana stated the following policy objectives for a NPAS (Persaud 1997).

1. Preservation of viable examples of all natural ecosystems in Guyana.
2. Protection of areas of particular biological significance.
3. Contribution to key watersheds and provision of buffer zones to mitigate against the effects of climate change and natural hazards.
4. Helping to maintain Guyana's cultural heritage.
5. Provision of opportunities for education and training.
6. Contribution to sustainable economic development through the provision of opportunities for nature-based tourism and recreation, and for sustainable utilisation of natural resources.
7. Provision of sustainable employment opportunities for remote communities through conservation services.
8. Helping to meet the biodiversity conservation requirement of international reference standards for sustainable forest management needed to gain certification and market access for timber and forest products in high value consumer markets.
9. Provision of future options by maintaining a broad pool of genetic resources.

Presently, all the data to support the selection of an optimum system of protected areas is not available. However, the urgency of conservation of Guyana's biodiversity can't wait until all the data have been collected. Therefore, this chapter attempts to interpret old and existing botanical data from different sources, analysed in previous chapters, in the light of the needs of planning for a protected areas system.

The strategy for collecting the data needed to select protected areas (to be considered in the context of comprehensive land-use planning) can be summarised as follows:

1. What are the objectives of the protected areas system (locally or globally)?
2. What information is required to fulfil these objectives?
3. What information is currently available?
4. Which are the most cost-effective ways to collect additional information?
5. Gather and interpret information
6. Rank and prioritise information,
7. Disseminate information to stakeholders in the decision-making process
8. Decide and implement

Two objectives that were summarised above will be examined in some detail in this chapter:

Objective 1: "Preservation of viable examples of all natural ecosystems in Guyana". To be able to contribute to the preservation of all ecosystems of Guyana we must ask what and where those ecosystems are. Concentrating on forest ecosystems, we will present data from forest inventories and herbarium collections to answer these questions.

Objective 2: “Protection of areas of particular biological significance”. Here, the question arises: what is “particular biological significance”? We have interpreted this threefold:

1. Forest types typical to Guyana and the closely adjacent areas (Guianas, Guiana Shield)
2. Areas with high endemicity
3. Areas with high (bio)diversity

We acknowledge that there are many more criteria important to identify protected areas, even within the already limited area of forest trees that is the topic of this chapter.

What is typical to the forests of Guyana in comparison with other Neotropical forests?

Guyana is largely covered by forests (Figures 2.2, 4.6, 5.2) and many of these are still intact. This fact by itself is significant in a time that most of the world’s tropical rainforests are under pressure. However, intactness is only one criterion for designing a system of protected areas. Another criterion would be to protect species and ecosystems, which are typically Guyanese. A wider perspective is required to place Guyana in a Neotropical context.

To this end the forest composition of 258 plots of 1 ha scattered over the Neotropics was examined in Chapter 3. The first remarkable conclusion is that Guyana’s forests, while species-rich compared to temperate forests, are poor[1] compared to forests in Western and Central Amazonia (Figure 12.2). Tree α-diversity generally seems to drop when moving from west to east through the Amazon basin, with the poorest plots in the peripheral areas in the North, far South and East.

Several families are better represented in Eastern Amazonia and the Guianas than in Western Amazonia, and vice versa. Chrysobalanaceae (Kauta’s etc.), Lecythidaceae (Kakaralli’s), and Leguminosae are examples of such families (Figure 3.3). Palms are a striking example of the reverse pattern. Guyana is unique in its high abundance of Caesalpiniaceae, a subfamily of the Leguminosae (Chapter 4; Figure 12.3). Well-known members of this family are the Wallaba’s (*Eperua* spp.) and Mora’s (*Mora* spp.). Their high abundance frequently leads to monodominance – forest communities strongly dominated by a single species.

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[1] Poor when expressed on the scale of 1 ha plots. The total number of species in the entire country depends also on other factors, such as geographic variation (see Chapter 2).

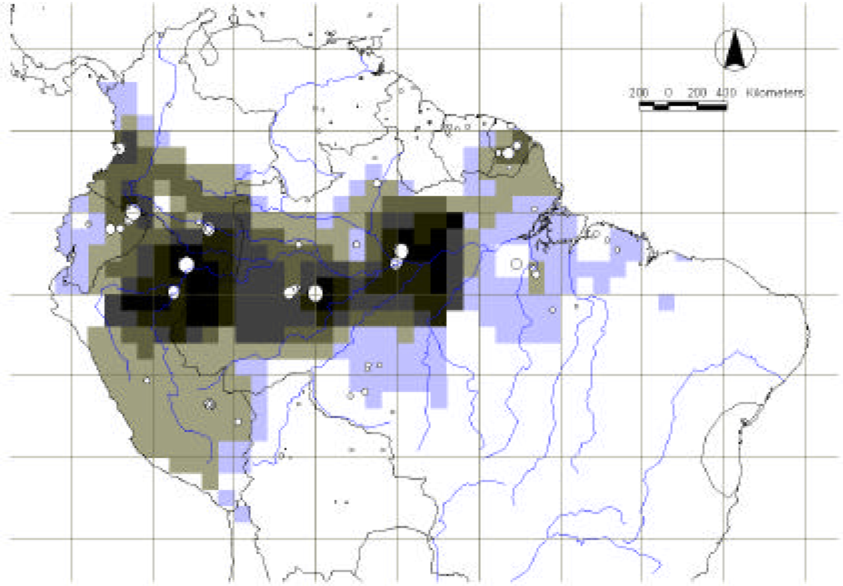

Figure 12.2 Location of 258 amazonian plots used in the analysis of tree α-diversity. Dot size indicates the value of Fisher's α (in case of overlap only the highest will be visible). Grey-scales indicate interpolated values of Fisher's α (with interdistance weighting up to 500 km).

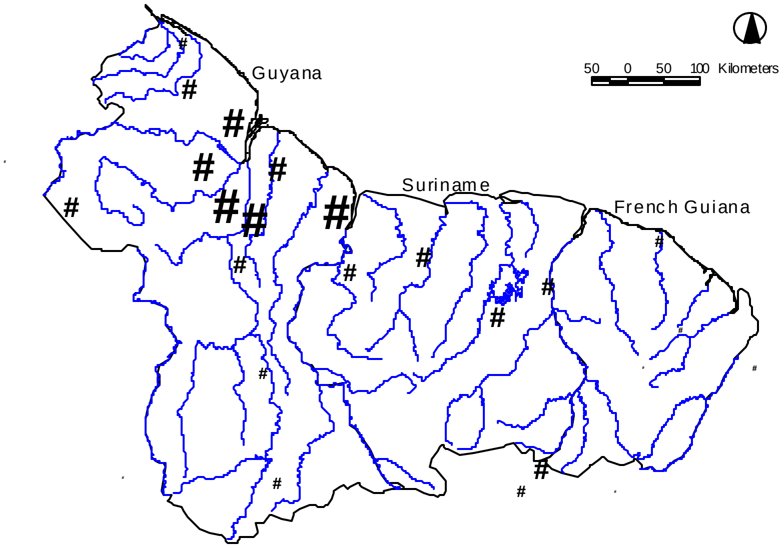

Figure 12.3 Regional dominance of Caesalpiniaceae expressed as the percentage of individuals in large-scale inventories in the Guiana Shield. The dot size indicates dominance and ranges from 9% (smallest) to 45% (largest).

The total flora of Guyana comprises almost 6,000 species (Boggan 1997), compared to 4,100 in Surinam and 4,400 in French Guiana. While this may appear much less than the 55,000 species found in Brazil, this is mainly an effect of the much smaller area of these countries (Chapter 2, Figure 2.3). It is not well known what percentage of the flora is confined to Guyana (endemics). A preliminary list by C.A. Persaud included 284 endemics or 5% of the total flora. However, further exploration may add new species to this list and remove others. See also below for a further discussion of endemism.

Guyana's forests are:

- *Relatively intact over large areas;*
- *Relatively species-poor by neotropical standards;*
- *Characterised by mono-dominant forest communities;*
- *Rich in members of the Caesalpiniaceae, Chrysobalanaceae and Lecytidaceae.*

What is the variation in forest types in Guyana?

On the basis of an analysis of large-scale forest inventory data (see Chapter 5) one can conclude that there is substantial geographic variation in the composition of the forest within Guyana. From these, seven identifiable forest regions were described (Chapter 5, Figure 12.4), while an eighth region was added on the basis of other data (Chapter 6).

In the south there are two regions that are distinguished on the basis of annual rainfall: the wet and the dry southern forest. These regions have a high affinity with true Amazonian forests in Brazil and Surinam (Chapter 6), and contain a high abundance of late secondary and pioneer species (Chapter 7). The Central Guyanan forests occupy the sandy soils of the Berbice Formation. These forests are characterised by slow-growing hardwoods with very large seeds (Chapter 7). This region also has a high abundance of commercial species. The Pakaraima Mts. consist of a large variety of vegetation types, many at higher altitudes. In the Northwest, a forest is found that is fairly similar to the Central forests. However, the lower abundance of Leguminosae sets it apart from the central forests. In the low-lying areas of the Northwest swampy forest on clay soils is found, while the mangroves in the salt and brackish coastal zone are radically different from all other forest types. The sampling was poor in the north-eastern region, so this region could not be classified on the basis of large-scale forest inventories (Chapter 5). However, other data sources suggest that this forest region has much in common with the central forest on the Berbice Formation (Chapter 6) but is somewhat intermediate between this and the more seasonal forests of the south (Chapter 4).

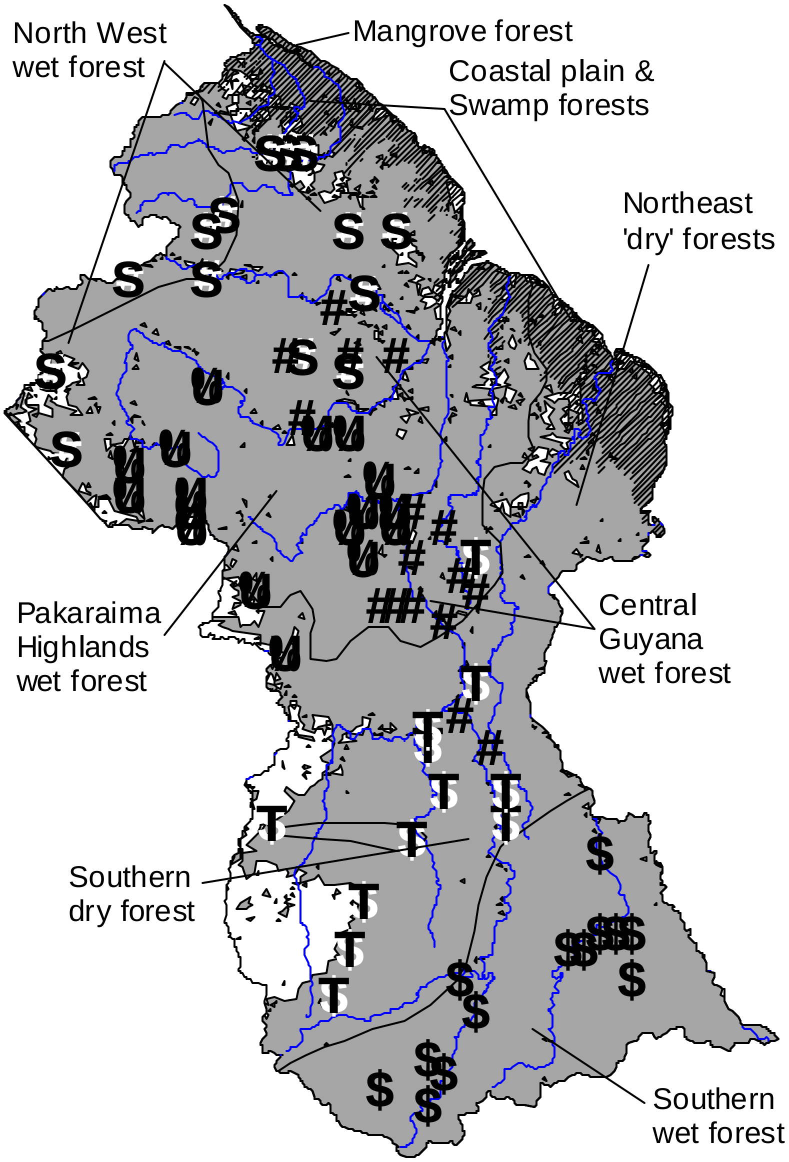

Figure 12.4 Forest regions in Guyana (see Chapter 5 for details): ▲ Southern wet forests; △: Southern dry forests; ■ Pakaraima Mts. wet forests; ● Central Guyana Wet Forest; O North-West Guyana wet forests. Light grey areas: area under forest cover, based on NOAA-AVHRR satellite images of September 1992 (http://edcdaac.usgs.gov/1KM/comp10d.html). White areas are non-forest areas (savannah, open swamp, low scrub a.o.). Thin lines: 2300 mm annual rainfall isohyeth (based on Persaud 1994, see also Figure 6.3). The coastal plain (after Gross -Braun *et al*. 1965) with mangroves, swamps and swamp forests is hatched.

The forest regions generally merge smoothly into one another and few species are restricted to a single region. A main zone of transition appears to be present around 4^o N Latitude (Chapter 6). This transverse belt through Guyana is interpreted as a relatively dry zone, and forests to the north of it are distinctly different from the more Amazonian forests that are found south of it. Many species either occur north or south of this line (Chapter 6).

The main non-forest areas (white in figure 12.4) are found in the south of Guyana (Rupununi Savannahs, Chapter 11), in the Northeast (the Intermediate Savannah), the Northwest (open swamps) and in the Pakaraima Mts. region (savannahs, meadows and scrubs, Chapter 10).

At many scales, nationally, within the forest regions and even between neighbouring forests, there is variation in soil type that contributes to large differences in forest composition. The Wallaba forests of north and central Guyana are a striking example of the influence of soil type on forest composition and forest structure. Within soil types one can distinguish dryer and wetter variants, depending on the position on the hydrological gradient.

- *Eight forest regions can be distinguished in Guyana, based on differences in the composition and abundance of large tree species.*
- *In each region, variation in soil, hydrology and altitude contribute to increased tree diversity.*

Differences in diversity between the forest regions

The forest regions do not only differ in species composition, but also in tree diversity. In general, forest inventories show that the forests in the south have higher tree diversity than those in the north, especially those in Northwest and Central Guyana (Chapter 5, Figure 5.6).

Possible causes of the observed differences between the forest regions are:

1. Parent geology, leading to differences in the chemical composition of the soil. Southern forests grow on the soils derived from the crystalline base shield, while northern forests generally developed in impoverished sediments. This allows for the high abundance of specialised species from the Leguminosae family (Chapters 4, 5).
2. Diversity is influenced by the dynamics of the forests, both large scale (e.g. hurricanes) and small scale (tree falls). In the Guyanese context, areas with historically low levels of forest dynamics are poor, while diversity is higher in areas with higher levels of dynamics (Chapter 7). While all Guyanese forests experience low levels of dynamics, this seems to be even more the case in Central Guyana. In the South and the Northwest there is historical evidence of higher human populations, which may have contributed to higher dynamics and

therefore higher levels of diversity (Chapter 7). It is not clear what contributes to the low diversity of North-western forests.

The low α-diversity in Central Guyanan forests (but also in some other forest types) is strongly related to the tendency of some of its species to dominate the vegetation. This is a special feature of Guyanese forests. Wallaba forest, Mora forest, Clump Wallaba forest are just a few examples of forests where one or two species represent a very high percentage of the total number of stems and/or basal area. In many cases these species are characterised by large seeds that are dispersed by rodents or by gravity (in the case of Mora by water) (Chapter 7). Most belong to the family of Caesalpiniaceae (Leguminosae). In the more diverse southern forests such dominant species are a much rarer phenomenon, and many species have small seeds that are dispersed by birds and primates (Chapter 7).
A slightly different pattern of diversity emerges when the species-richness of herbarium collections[2] is calculated per region (γ-diversity) (Chapter 6). The Pakaraima Mts. stand out as the most species-rich region, while Central Guyana and the wet south have a similar diversity. The dry south (Kanuku Mts.) is very poor in species of taxa selected in Chapter 6 but more comparable when all taxa are taken into account (Chapter 11).

Comparing the results of these two methods gives insight into the patterns of tree diversity. The southern forests are diverse due to a relatively high number of species on small spatial scales (high α-diversity). The forests of the Pakaraima Mts. are also very diverse, but small areas of forests there are often poor or even very poor (in extreme cases single species dominate the vegetation for up to 95%! Chapter 8). Its high γ-diversity is derived from a high diversity of habitat types which each contribute new species to the regional species pool (high β-diversity). Thanks to the variation in soil types and the altitudinal gradients unknown to other areas in Guyana, a high regional (as opposed to local) diversity is observed here. Similarly, in central Guyana α-diversity is low, but there is a high diversity of soil types and therefore fairly high β-diversity.

- Guyana's forests show a gradient in diversity from north (species-poor) to south (species rich)
- "Point diversity" is highest in Southern Guyana.
- "Regional diversity" is highest in the Pakaraima's, followed by the Central Guyana and the wet Southern Forest Region.

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[2] This was done for a number of "typical", selected taxa: *Lecythis* and *Eschweilera* (Lecythidaceae), *Licania* (Chrysobalanaceae), *Swartzia* (Fabaceae), *Ocotea* (with all other tree genera, Lauraceae) and *Pouteria* (with related tree genera, Sapotaceae). Together these genera comprise over 250 species or 5% of the roughly 5000 vascular plant species in Guyana; they account for nearly 30% of all forest trees over 30cm DBH in Guyana (Chapters 5 and 6).

The occurrence and abundance of endemics in Guyana

The occurrence of endemic species[3] adds significantly to the conservation value of a forest. Therefore it is important to consider the distribution of endemic species in the country. We examined two aspects of endemic species occurrence: abundance (Chapter 5) and species distribution (Chapter 6). The data from large-scale forest inventories provide a quantitative estimate of the abundance of species, and thus it is possible to calculate the total abundance of endemic species (Chapter 5). However, many taxa with the same vernacular name actually consist of two to even more than ten different botanical species, some of which may be endemic and others not. Only carefully collected and identified botanical specimens provide evidence about a species' identity. From these botanical data, which are stored in herbaria worldwide, distribution maps can be compiled. These are botanically more correct but less "complete" than inventory data[4]. This exercise was carried out for a selection of families and genera that were considered abundant or diverse in Guyana and in which a large number of endemics was expected[2] (Chapter 6).

Abundance of endemics

Forests with a high abundance of true Guyanan endemic species are found in the Pakaraima Mts. and in the central Guyanan forest regions, particularly in the Potaro River basin (Figure 12.5). Southern, the north-western and north-eastern regions show low abundances of true Guyanan endemics. The picture is different if the endemics of the three Guianas are considered. These species also occur in the neighbouring countries but not elsewhere in the Neotropics. Species such as Mora (*Mora excelsa*), Black Kakaralli (*Eschweilera sagotiana*) and the Wallaba's (*Eperua* spp.) contribute to a high abundance of such species in the Northwest and the white sand forests (Figure 12.6). Several endemic species are very common and some are of commercial importance (Table 12.1), while others are rare and are only known from very small areas (many of the *Swartzia's* belong to this category).

Two concentration areas of endemic species

The actual distribution of most but the best-known endemics is better judged from herbarium collections than from forest inventories. Among the selected groups of trees, about 10% of the total number of species was endemic. There are two major concentrations of endemics in these groups. The first area is situated in Central Guyana with 14 endemics and is nearly completely confined to the White Sands (Berbice) Formation (Chapter 6, Figure 6.6). A second concentration of endemics (7) is found in the headwaters of the Mazaruni and tributaries, including Mt. Roraima, with some species reaching as far east as the Iwokrama Mountains (Figure 6.6).

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[3] Endemics are defined here as species of which >95% of all individuals is estimated to occur within the borders of Guyana. We make distinction between true Guyana endemics, confined to Guyana, and Guianan endemics, species that are limited to the Guiana Shield region (Chapter 5)

[4] Botanical collections are generally available from much fewer locations and provide no quantitative information about the relative abundance of the species.

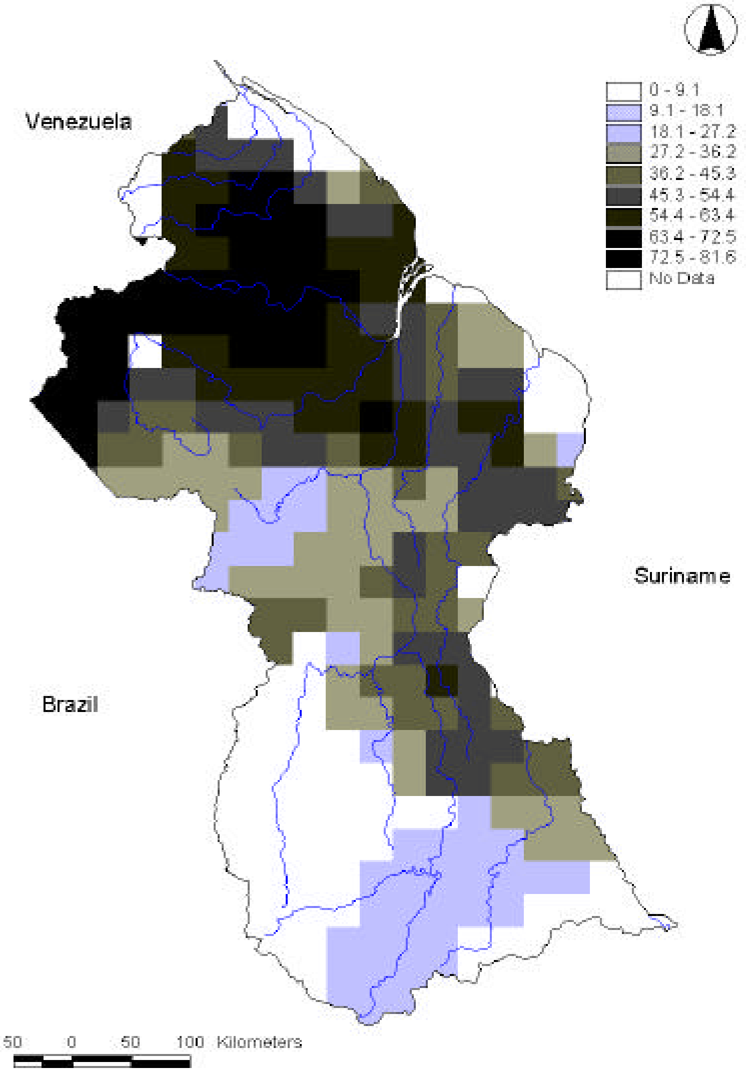


Figure 12.5 Map of abundance of individuals of species endemic to the three Guianas (excluding the species endemic to Guyana, which are in Figure 12.6), expressed as their percentage abundance in the forest community. Data is interpolated at 0.25-degree grid level with spatial inter- distance weighting up to 50 km.

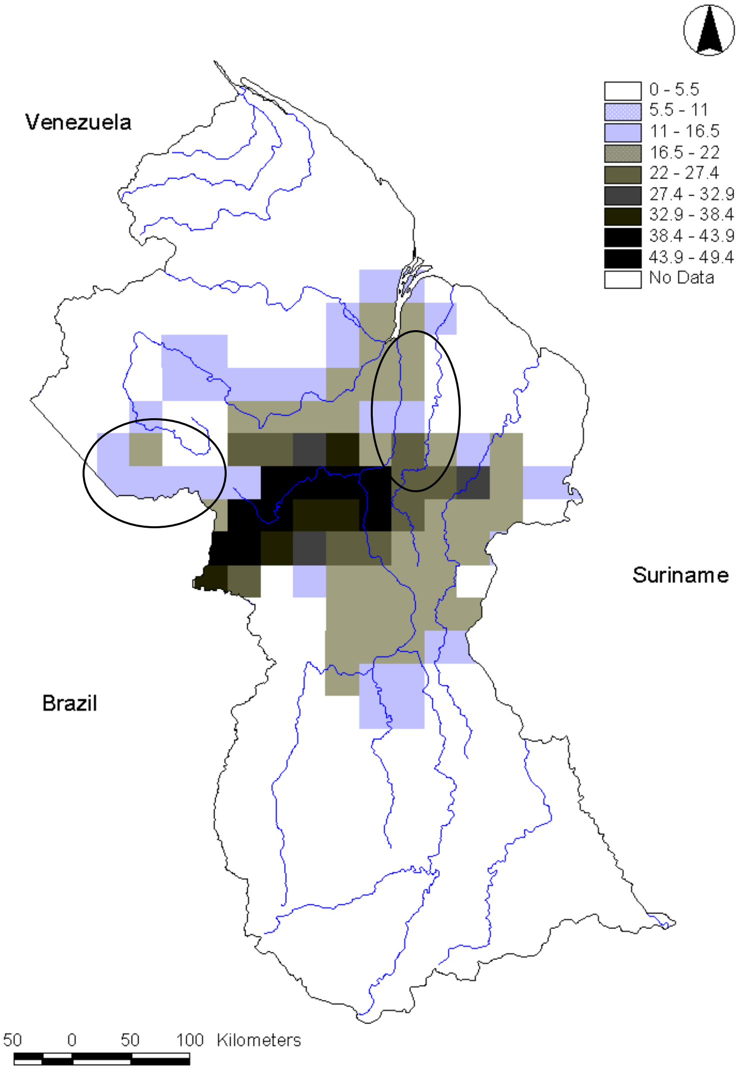


Figure 12.6 Map of abundance of individuals of true Guyanan endemics, expressed as their percentage abundance in the forest community. Data is interpolated at 0.25-degree grid level with spatial inter- distance weighting up to 50 km. The two main centres of species diversity of endemics (Chapter 6) are indicated by black ellipses (Upper Mazaruni R. - Kako R and Potaro basin – Upper Demerara).

Table 12.1 Examples of well-known and abundant endemic species of Guyana and the Guiana Shield

Vernacular name	Botanical name	Commercial species
True Guyanan Endemics		
Greenheart	*Chlorocardium rodiei*	Yes
Wamara	*Swartzia leiocalycina*	Yes
Sarabebeballi	*Vouacapoua macropetala*	No
Konoko	*Licania cuprea*	No
Marishiballi	*Licania buxifolia*	No
Guiana Shield Endemics		
Mora	*Mora excelsa*	Yes
Morabukea	*Mora gonggrijpii*	Yes
Soft Wallaba	*Eperua falcata*	Yes
Ituri Wallaba	*Eperua grandiflora*	Yes
Baromalli	*Catostemma fragrans/commune*	Yes
Black Kakaralli	*Eschweilera sagotiana*	No

A small number of endemics occurs in the deep south, but this may be an underestimate caused by the relative scarcity of collections in that area.

The best-known endemic of Guyana is Greenheart (*Chlorocardium rodiei*), which has a fairly wide distribution in the centre and north-western portions of the country, associated with the poor sandy soils of the Berbice formation. The high incidence of endemics in this area, particularly the white sands, suggests that most endemics in Guyana are habitat specialists (Chapter 6). Their occurrence is restricted because their habitat is restricted, but where the habitat occurs, they may be very common. Other endemics are confined to the higher altitudes of the Pakaraima Mts. region, which again represents a special habitat that is rare. Evidently there are many more endemics in Guyana in families that were not examined for this study. Their distribution is currently poorly known.

- *The abundance of endemic species is very high in the Central Guyana and Pakaraima Mts. Forest Regions.*
- *High species richness among endemics of selected taxa is concentrated in Central Guyana and the headwaters of the Mazaruni.*
- *Many endemics are habitat specialists of the white sand formation;*
- *Some endemics may be very common in their restricted range.*

Conclusions and recommendations for policy

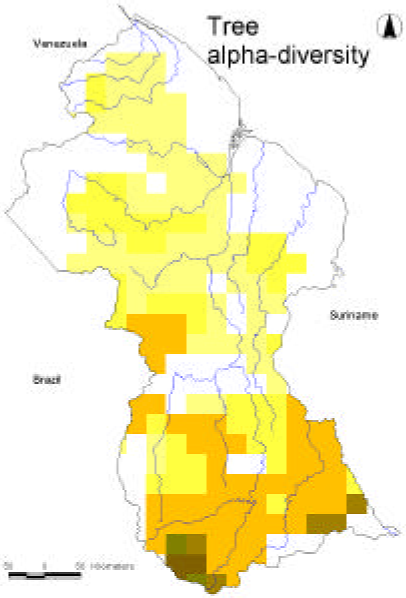
The results presented here and of related studies provide important information that may assist in the decision making process for protected areas. It reveals differences in the tree component of the forests between various regions in Guyana and identifies where important concentrations of endemic species can be found.

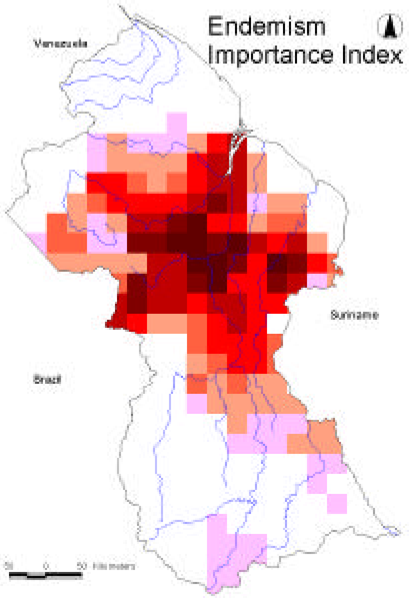
Where, then, would forest areas of special importance be found in Guyana from the viewpoint of our two objectives, "Preservation of viable examples of all natural ecosystems in Guyana" and "Protection of areas of particular biological significance"? The approach chosen does not permit the precise delineation of specific areas, but rather zones of importance that should guide a comprehensive conservation strategy.

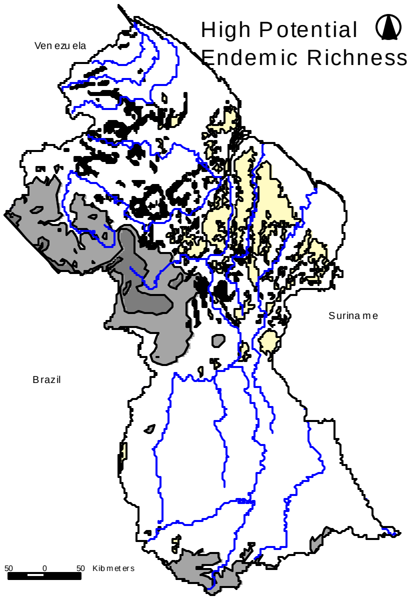
Several main conclusions emerge from the work and should be kept in mind when formulating policy:

1. Guyana's forests are poor by Neotropical standards, but rich for several families of trees (Chapter 3). Two outstanding features of Guyana's forests are the occurrence of monodominance and the high abundance of Caesalpiniaceae (Chapters 3, 4, 5 and 7).
2. Eight forest regions can be distinguished in Guyana, based on differences in the composition and abundance of large tree species.
3. Many of Guyana's forests (particularly in Central Guyana) seem to have evolved under conditions of low disturbance (Chapter 7).
4. Within regions, variation in soil types, hydrological gradients (Chapter 8) and altitudinal gradients (Chapter 10), contribute greatly to β-diversity and consequently γ-diversity
5. There are two main centres of endemism (Chapter 6): Berbice Formation and the Pakaraima Mts. region. Guyana has special responsibilities for these species, which occur nowhere else.
6. Endemics dominate forest vegetations in the Potaro River basin and adjacent Upper Demerara (Chapter 5). The entire area between Mazaruni and Berbice, south to the Rupununi River may be considered as an area with high abundance of these species.
7. Guiana Shield endemics are most common in the Northwest and Lower and Upper Berbice.
8. Many endemics are high value timber species.

Based on these considerations it is possible to construct maps of areas of high conservation significance for Guyana (Figure 12.7). These should be used together with the observation that eight main forest regions exist (Figure 12.7D). Tree α-diversity is shown in Figure 12.7A. We defined an Endemism Importance Index, which is based on the proportion of Guianas endemics (which occur mainly in three countries and to a lesser extent in five) plus 5 times the proportion of true Guyanan endemics. As expected from figures 12.4 and 12.5, the central portion of Guyana has the maximum score for this index (Figure 12.7B). White sands of the Berbice formation, Lateritic hills and high altitude areas are habitats where a high richness of endemic species can be expected (Chapters 5 and 6). These habitats are mapped in Figure 12.7C.


Tree
alpha-diversity
Venezuela
Suriname
Brazil
50 0 50 Kilometers


Endemism
Importance Index
Venezuela
Suriname
Brazil
50 0 50 Kilometers


High Potential
Endemic Richness
Venezuela
Suriname
Brazil
50 0 50 Kilometers

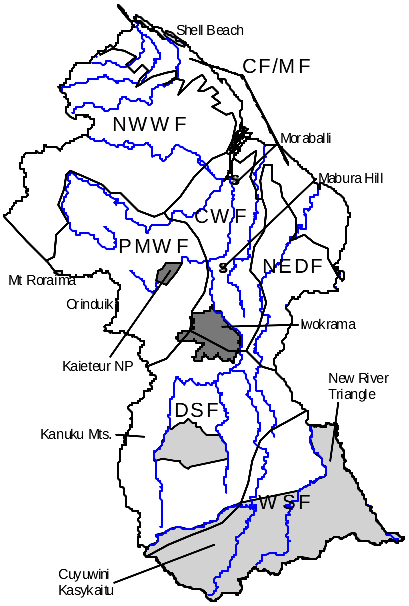

Shell Beach
CF/MF
NWWF
Moraballi
Mabura Hill
CWF
PMWF
NEDF
Mt Roraima
Orinduik
Iwokrama
Kaieteur NP
New River
Triangle
DSF
Kanuku Mts.
EWSF
Cuyuwini
Kasykaitu

Figure 12.7 A: Map of tree α-diversity in Guyana (Figure 5.6); B: combined Guianas and Guyana endemism based on the proportion of Guianas endemics plus 5 times the proportion of true Guyanan endemics; C: the occurrence of habitat with potential high endemic richness (light grey: white sands of the Berbice formation (Chapter 6); black: Lateritic hills (Chapter 6); medium greys: high altitude areas (Chapter 10); D: Proposed parks in Guyana based on EPA workshop, December 1999 (light grey). The size of the protected areas has not been established as yet, except for Kaieteur NP and Iwokrama (dark grey) and two forest reserves (dark grey dots). Forest zones (based on Chapters 5 and 6) are indicated by black lines: NWWF Northwest Wet Forest, CWF Central Guyana Wet Forest, NEDF Northeast Dry Forest; PMF Pakaraima Mts. Wet Forest, DSF South Guyana Dry Forest, WSF South Guyana Wet Forest.

In 1999 several important steps have been taken to start implementing a protected areas strategy, such as the extension of the Kaieteur NP and the prioritisation of five additional areas where multi-stakeholder planning committees are engaged in a process to establish of protected areas. These areas are indicated in Figure 12.7D. Comparison with the other maps (and Figures 12.1, 12.4, 12.5 and 12.6) shows that these proposed areas preserve[5]

1. Examples of Southern Wet Forests with high tree α-diversity and wilderness value. (Cuyuwini/Kasykaitu proposed park)
2. Examples of Southern Dry Forests with high tree α-diversity, low to medium γ-diversity and high scenic and wilderness value. (Kanuku Mountains proposed park, Iwokrama Forest)
3. Examples of Pakaraima Forests, with low tree α-diversity but high β- and γ-diversity and high endemic species richness. (Kaieteur NP and Roraima proposed park)
4. Examples of Mangrove Forests (Shell Beach proposed park)

But do not preserve:

5. Examples of Northwest Upland Forests, with medium to low tree α-diversity but very high abundance of Guiana shield endemism.
6. Examples of Northwest Coastal (Swamp) Forests.
7. Examples of Berbice Formation Forests, with low tree α-diversity, medium to high β-diversity and high abundance and richness in Guyana endemics, although Iwokrama will preserve some of these forests.

Further elaboration of the protected areas system, whether in the current selection of sites or in new areas, should take the following conclusions from the present research into consideration:

1. Protected areas should aim at conserving representative examples of all eight Forest Regions in Guyana, so the current list should be extended.
2. There is a unique opportunity to preserve relatively large tracts of intact forests in Guyana, particularly in the South.

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[5] In addition to these forest areas an example of the Rupununi Savannah would be conserved in the Orinduik proposed park.

3. In areas with relatively low α-diversity but high β-diversity (Central Guyana, Pakaraima Mts. area) care should be taken to include a comprehensive range of habitat types in each individual protected area.
4. The long-term protection of the forest of Central and Northwest Guyana requires the maintenance of the conditions of low disturbance under which they have evolved
5. The management of forest concessions and other large-scale land uses should support the objectives of biodiversity conservation. This implies specific attention for biodiversity planning in the management, backed by a regulatory framework.

Recommendations on reconciling land-uses

The above analysis largely ignores the existence of other land uses and objectives, such as resource extraction, agriculture and the presence of Amerindian Lands. In many areas in the country strict forms of conservation will be difficult to implement. However, strict protection is not always required to achieve biodiversity objectives – many forms of land use are compatible with a certain level of biodiversity protection.

Strict protection, allowing only certain forms of non-consumptive co-utilisation of land, may be required to conserve certain ecosystems and species that would disappear if the area would be brought under other land use:

1. If species (or species on which they depend) require large and uninterrupted expanses of habitat. In the case of trees this may apply to species with relatively rare habitat requirements or species with pollinators or dispersers with a large home-range or habitat requirements only found in large expanses of habitat.
2. If there is a large discrepancy between the level of disturbance required to maintain the ecosystem and the level of disturbance introduced by other forms of land use. Many species and habitat types may accept certain levels of disturbance, but others depend on an ensemble of conditions only found in deep forest or disturbance rates that are much lower than in forests managed for timber or disturbed by other forms of use.
3. To protect ecologically sensitive, scenic or sacred areas.
4. To protect undisturbed reference systems for the study of impacts of land use and the effects of change.
5. To address other functions of protected areas, such as watershed protection etc.

The success of conservation of biodiversity outside strict reserves will depend on our ability to reconcile the objectives of conservation and other uses. Some land-uses are incompatible with conservation, while other land uses still allow the occurrence of substantial levels of biodiversity. One may think of forest operations where logging is carried out at low intensities and utilising methodologies that minimise impacts. Even within areas designated for other purposes biodiversity conservation may take on an important role in management. Indeed, the long-term viability of many resource extraction activities depends on the maintenance of

healthy and functioning ecosystems: forestry, non-timber forest products extraction, hunting and trapping, fishing, etc. The maintenance of high levels of biodiversity in areas managed for other land uses may be critical for the ability to successfully achieve the objectives of nearby protected areas.
It is critical that objectives of biodiversity conservation will become an explicit component of the management of such areas, even if the main purpose of management is different. First and foremost in this respect will be an adequate land use policy, implemented by an effectively functioning National Land Use Committee. This will increase the ability of the Authorities to adequately weigh long-term planned policy objectives with shorter term unplanned investment opportunities.

The Guyana Forestry Commission, through its Code of Practice for Forest Operations (GFC 1998) can contribute significantly to this process, as most of Guyana's forests of Northwest, Central and Northeast Guyana are under some form of forest concession. The Code of Practice contains clear guiding principles and objectives for conservation through concession Biodiversity Reserves. It is extremely important that the local Biodiversity Reserves are chosen within the framework of a national strategy. Hence the GFC should be fully involved in the implementation of the objectives of NPAS.

The Environmental Protection Agency has the mandate to enforce biodiversity considerations through the Environmental Impact Assessment procedure and the Environmental Permit. The EIA obligation exists for a wide range of development initiatives, including new forest and mining concessions.

In some instances it may be impossible to identify suitable areas for conservation that are large enough to maintain critical ecosystem processes. The forests of the Berbice Formation present a challenge in this respect. The area is the centre for forestry and mining activities, while agricultural use is on the rise. These forests are home to many endemic species, and their presence seems to be the consequence of a very little dynamic ecosystem. Utilisation and fire (another important feature of the area) increase dynamics and therefore change the characteristics of the system. This area will require creative solutions if conservation objectives are to be met.

Another challenge is presented by the high significance of the Potaro Basin for true Guyanan endemics (Figure 12.6). The middle reaches are now protected in the extended Kaieteur National Park, but the lower reaches are one of the main centres of small and medium scale mining activity in the country. Even though the impact of mining might be largest on the aquatic environment, land ecosystems also undergo significant modification resulting from the use of high suction pressure pumps to wash away hill slopes. The scale of the individual mines may be small, but the number of operations is large. It is unknown to what extent tree biodiversity is affected or even threatened by these activities. It seems certain that there is significant direct and indirect impact on wildlife. Therefore it appears to be critical that mining is conducted in a context of regional planning that includes biodiversity considerations (e.g. allowing for conservation zones), and that the individual operations minimise impacts.

Recommendations for further research

1. The interpretation of these data requires some caution. They reflect the lack of comprehensive and systematic biodiversity surveys in Guyana. As most of the forest inventories were not designed to sample botanical diversity but timber resources, they lack detail where small trees and non-tree plants are concerned. In Chapter 9 it was shown that diversity of small trees and, to some extent, liana's, is reasonably well predicted by large tree diversity, but that is not the case for other plant groups. Species identification in the field is difficult for several important groups, so many species are not recognised in forest inventories. Furthermore, it was observed above that many endemic species are specialists of habitats which may be small and scattered and therefore not detected (or even actively excluded) by forest inventories. Non-forest areas are evidently not represented in forest inventories (but see Chapters 10 and 11).

   Nevertheless, we are confident that the large quantity of data and large-scale, standardised approach of the inventories provide a systematic overview of patterns in forest composition across the country, unhampered by large differences in "collectors bias" (Chapter 5).
   Therefore, as far as forests are concerned, these data provide a firm framework for policy decisions. Further research may focus on completing the database of existing data, and to fill in gaps where these are lacking. Both the Utrecht Herbarium and the Smithsonian already have substantial digital databases. Important other collections can be found in Guyana in the Jenmann Herbarium (mainly the Jenmann collections) and the Forestry Herbarium (FD collections) and outside Guyana in New York, and Kew.

   Additional inventory and collection should concentrate on areas outside the currently proposed protected areas and outside the best known areas, mainly in the South Guyana (all areas south of 4 °N and east of the Essequibo R., Rewa R. and Kwitaro R. basin and Upper Berbice R.), the Pakaraima Mts., including the middle Mazaruni basin and the Cuyuni R. basin.
   A national clearinghouse for biological collections and related databases linked to Geographical Information Systems should be established. The Biodiversity Centre appears well positioned to perform this role.
2. The identification of endemic species should also be approached with caution. Endemics are often only by-products of the incomplete collection of tropical countries. Taxonomic review may reveal new endemics or remove others. In spite of this, certain observed patterns are robust and probably reliable. The heavy concentration of endemics in the Pakaraima Mts. and on the Berbice Formation is not a pattern that will change substantially with advancing exploration of taxonomic knowledge. Many endemics share important

ecological features, which suggests that the conditions are apparently present to "produce" such species in a certain area (Chapters 6 and 7).

The analysis of endemic species was based on a limited number of taxa (even though they represented a large proportion of the trees in the forest). Considering the importance of endemics for conservation policy, an effort should be raised to identify the remaining species, and to construct maps of endemism on the basis of all herbarium specimens and reliable field records.

3. Many conservation objectives will have to be met in areas, which have another landuse. There is need for studies on the compatibility of these landuses with biodiversity, with the purpose to develop ways to mitigate (mutual) negative impacts. The Tropenbos-Guyana Programme has already done considerable work on the impact of logging on the forest environment and biodiversity, but the nature of this type of study is complex and long-term.

4. Presently there are few other groups but forest trees for which a similar analysis is possible, due to the absence of large scale inventories and the difficulties inherent to, e.g., faunal research. Evidently there is a separate need to analyse patterns of faunal and non-tree floral data. An alternative approach would be to assess to what extent the forest regions postulated in this study are supported by the other groups of organisms. If so, one may cautiously assume that important proportions of Guyana's biodiversity are conserved when focusing on these regions. In addition, areas should be identified for biological phenomena that are restricted in area (such as nesting grounds, rare habitats, etc.).

Finally…

Guyana possesses unique opportunities for the conservation of the plants, animals and ecosystems that have become rare or even extinct in many parts of the tropics. Two main agencies with a major role to play in biodiversity conservation, the Environmental Protection Agency and the Guyana Forestry Commission are in the process of policy formulation and capacity building that has already contributed to a much improved environment and a broadly supported framework for biodiversity planning. Other agencies such as the Guyana Geology and Mines Commission are starting to see similar changes. The Iwokrama International Centre for Rain Forest Conservation and Development provides a unique and highly publicised test case for developing land-use options that embrace the principles of biodiversity conservation. There is a high and increasing interest from international organisations for the Guianas. This clear national and international interest provides opportunities that can and must be used to safeguard the national biodiversity patrimony for the benefit of present and future generations. We hope that this book will contribute to this goal.

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