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

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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,

[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.

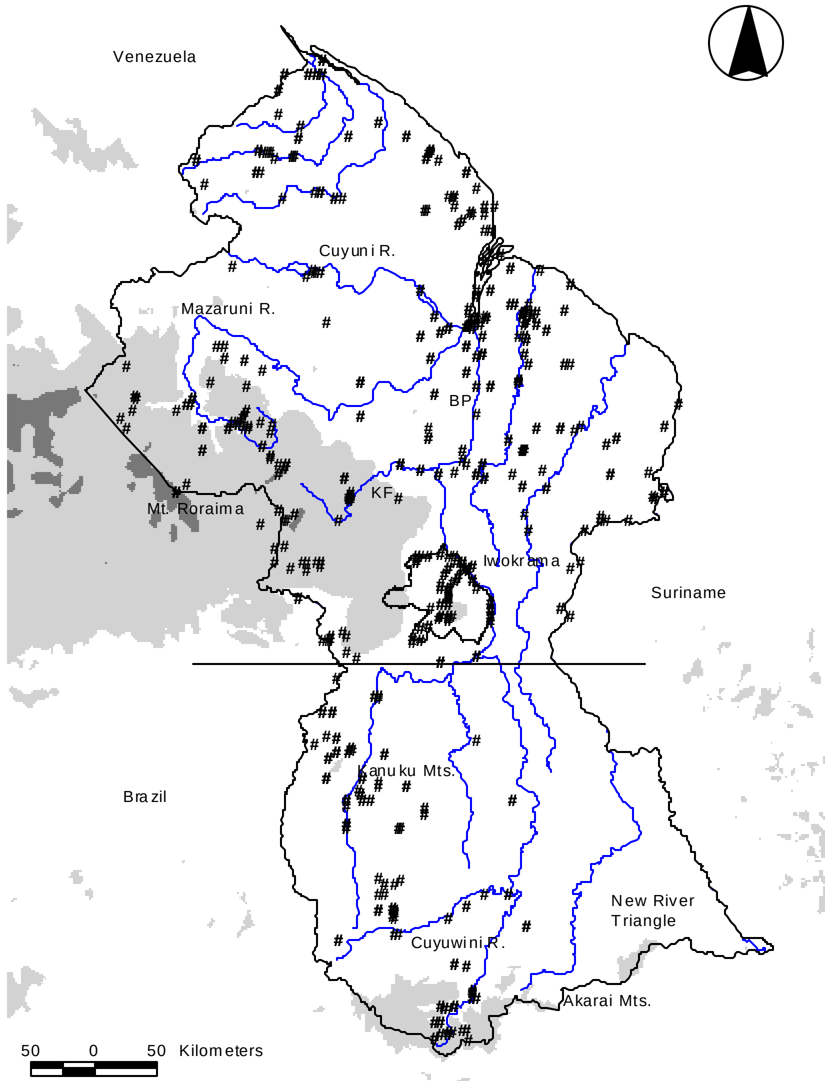

Figure 6.1 The distribution of 2268 collections of *Eschweilera*, *Lecythis*, *Licania*, *Swartzia*, *Ocotea* s.l., and *Pouteria* s.l. in Guyana. BP: Bartica-Potaro Road; KF: Kaieteur Falls. The horizontal line is the 4th parallel. Light grey: areas over 500m altitude, dark grey: areas over 1500m altitude (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

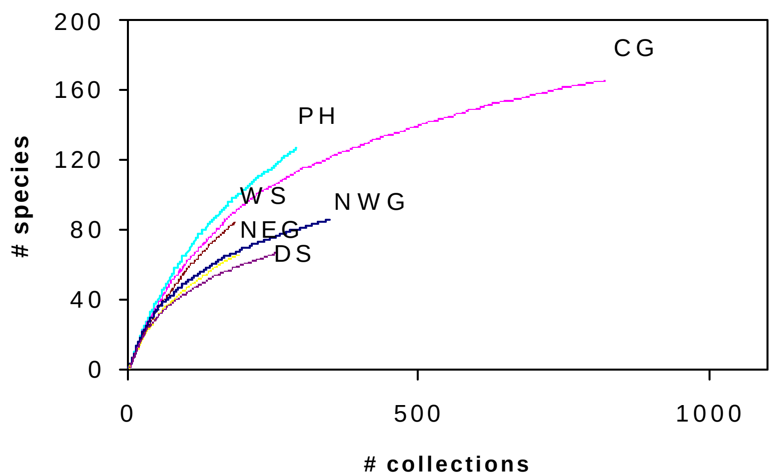

Figure 6.2 Species collection curves for 6 large regions in Guyana. Central Guyana is relatively well collected. A substantial increase in collecting effort may not increase its species list much (see text). Abbreviations: PH = Pakaraima Highlands, CG = Central Guyana, WS = Wet South, NWG = Northwest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

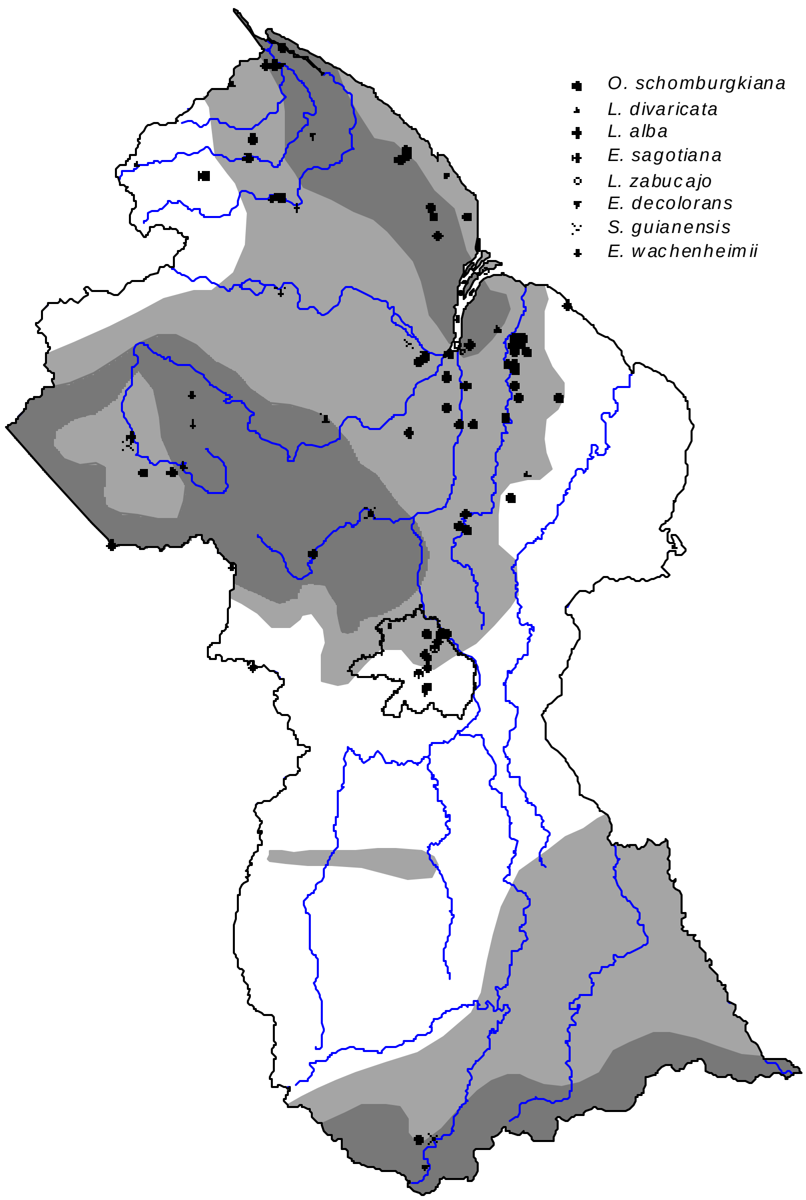

Figure 6.3 Distribution patterns of species with a 'Northwest-Central preference'. Grey shades: dark grey = annual rainfall > 2800 mm; light grey = annual rain between 2300 and 2800 mm; white = annual rain less than 2300 mm. Practically no records were found in the relatively dry zone (annual rainfall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

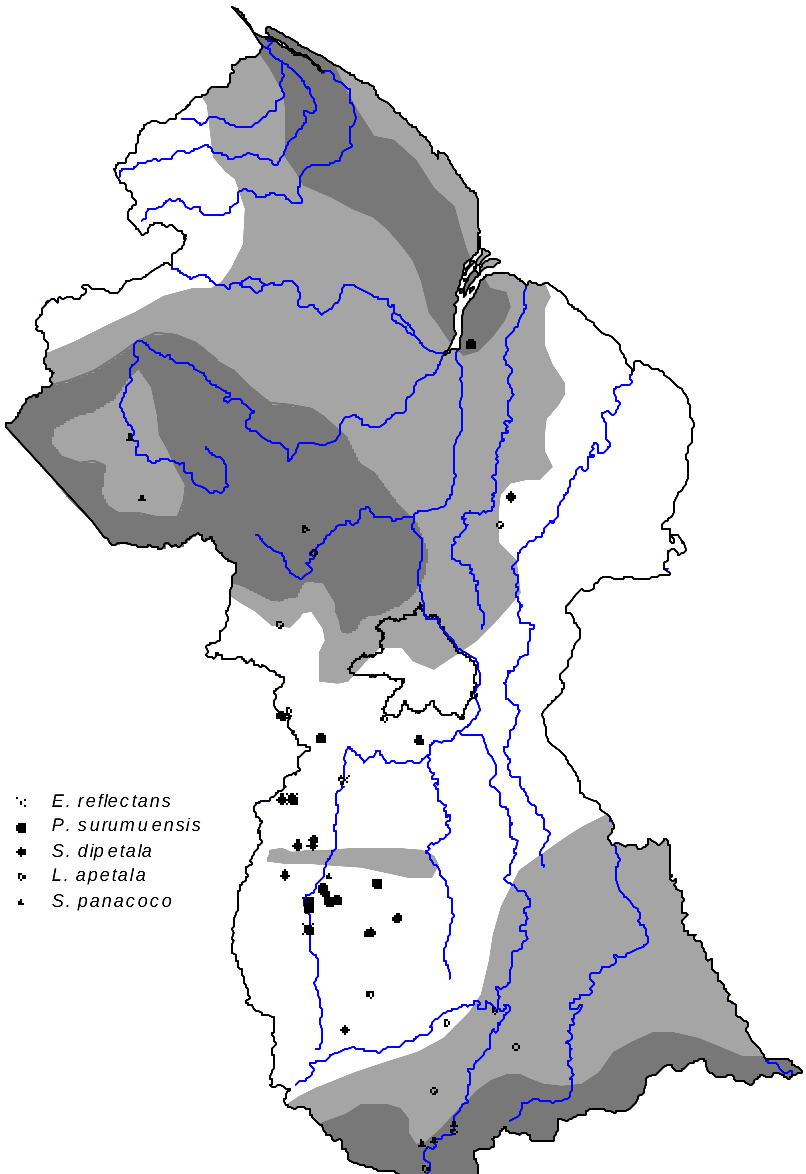

Figure 6.4 Distribution patterns of species with a 'southern preference'. Some of these species have also been collected in the Pakaraima Mts. area. Most of the collections fall within the dry area of Guyana. Grey shades as in Figure 6.3.

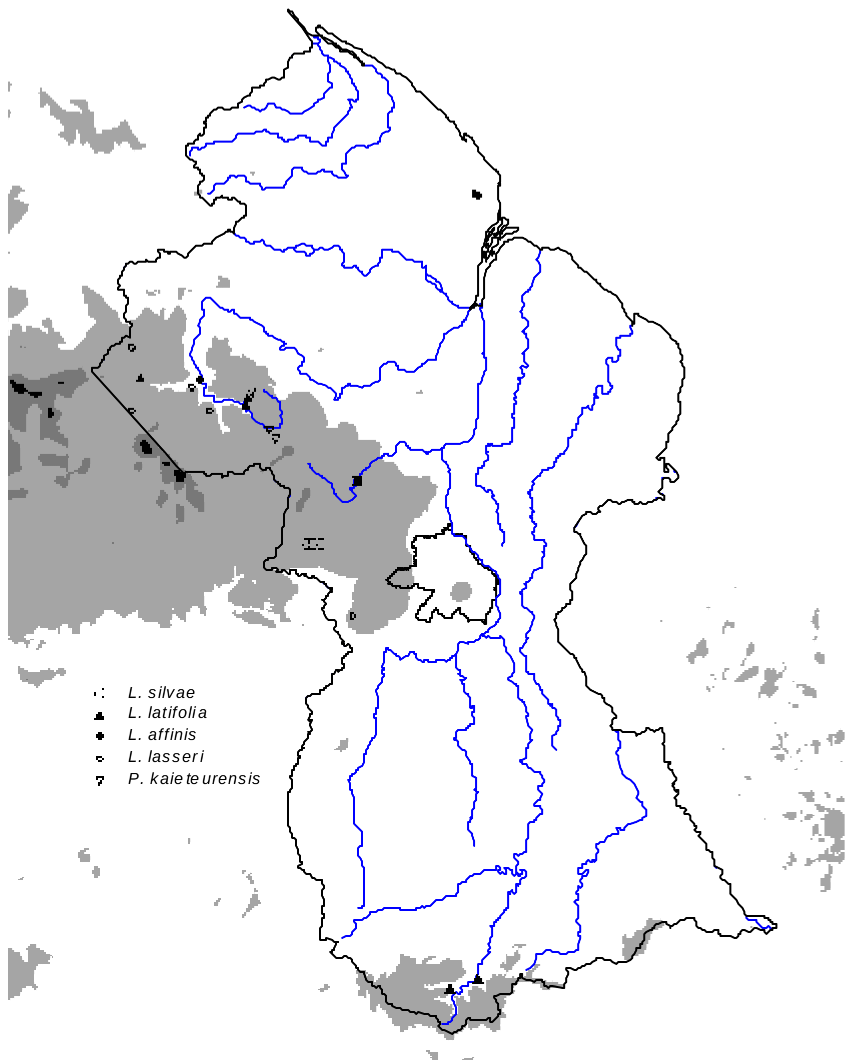

Figure 6.5 Distribution patterns of species with most of their collections in the Pakaraimas area. Shading: light grey = areas above 500 m (based on Digital Elevation Model, USGS (see Figure 6.1).

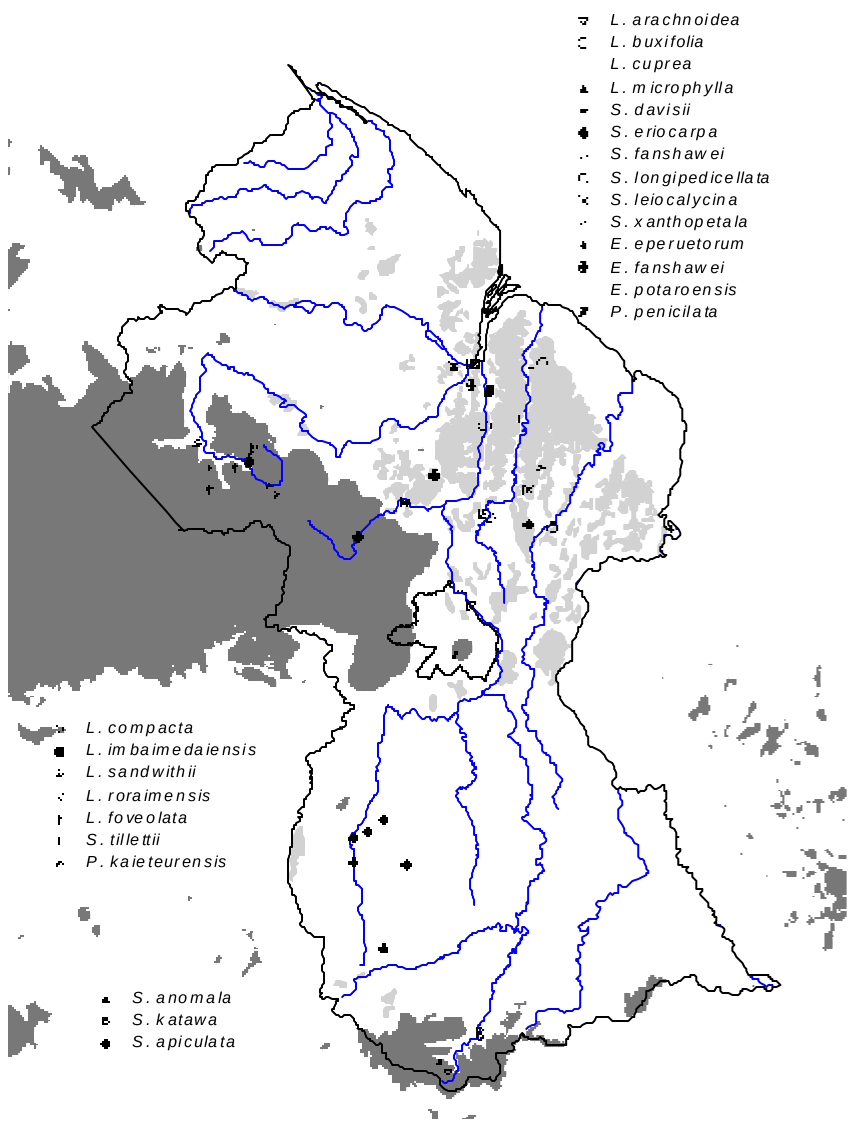

Figure 6.6 Distribution patterns of known endemics of *Eschweilera*, *Lecythis*, *Licania*, *Swartzia*, *Ocotea* s.l., and *Pouteria* s.l. in Guyana. There are two concentrations: the white sands area and the head of the Mazaruni - Mt. Roraima area. Presence of endemics in the Southeast is unknown due 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.