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 and ECTF (Barama Company unpublished data) and van Andel (2000).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.

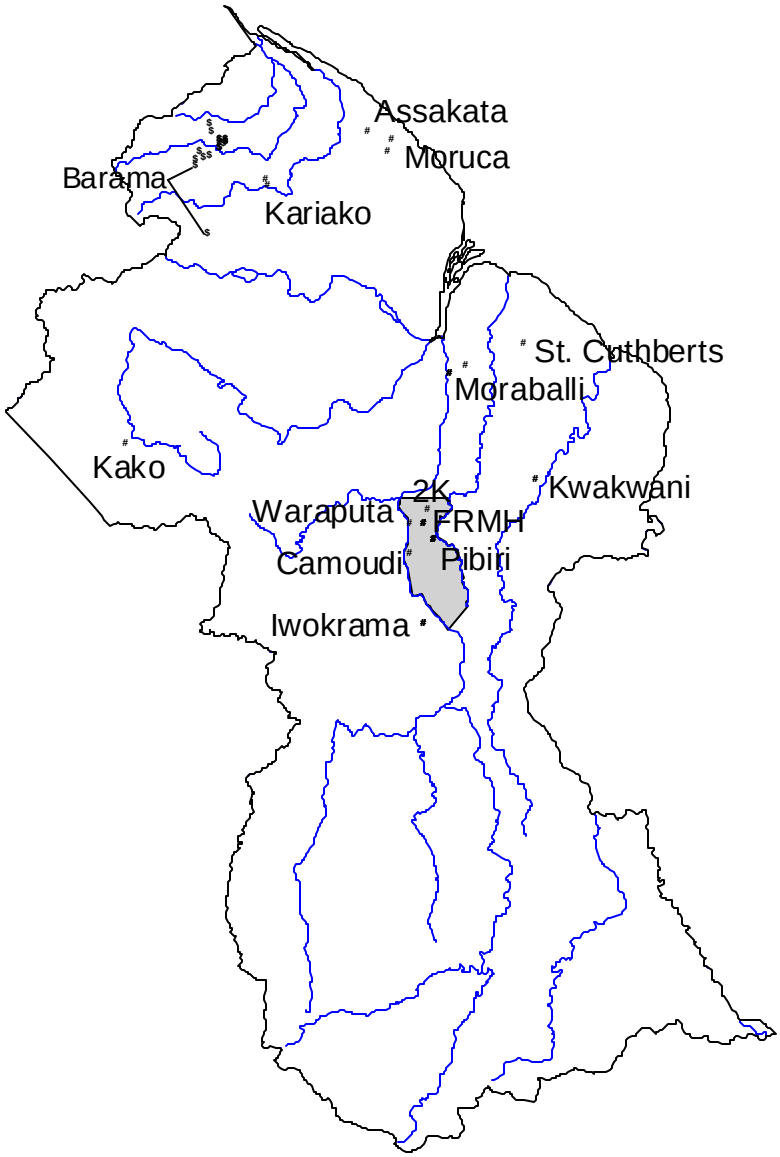

Figure 8.1 Locations of botanical hectare plots in Guyana (dots), PSP's of Barama Company Ltd. (triangles), and the Great Falls Inventory area (light grey shade).

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 Baraama 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 cununa 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	α	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

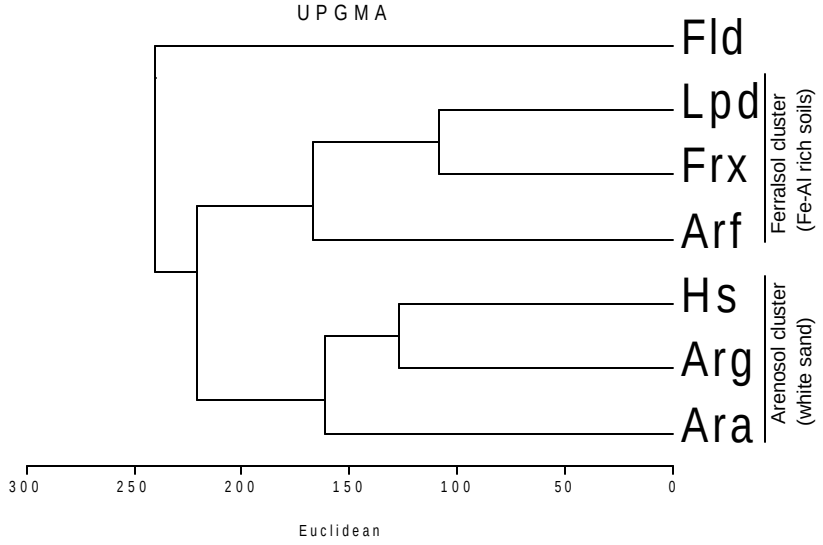

Figure 8.2 Clustering (Unweighted Pair-Group Method using arithmetic Averages with Euclidean distances (UPGMA), MVSP 3.1) of soil types based on the species composition of 750 random individuals from each soil type. Abbreviations as in Table 8.5.

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).

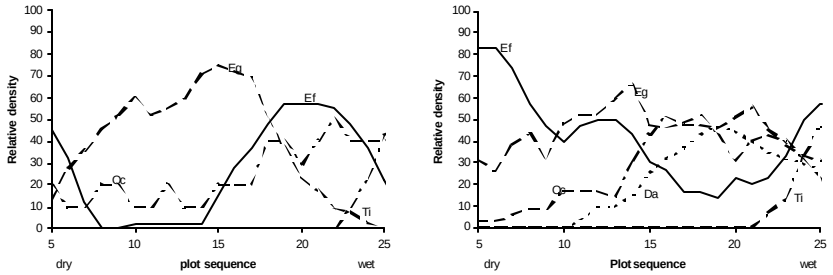

Figure 8.3 Gradient of moving-average (5 plots) of relative density (based on the highest density of each individual species found) of a number of common species on two different transects, both spanning a hydrological gradient in different creek gullies on a white sand watershed. Swamp plots are on 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