CHAPTER 4

THE LOWLAND HIGH RAINFOREST:
STRUCTURE AND TREE SPECIES DIVERSITY

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1. Introduction

Diversity studies provide data useful to the basic knowledge of biodiversity as well as a baseline for many other research fields. Forest dynamics, descriptive and functional ecology, conservation and sustainable development projects, need such data that are still few for neotropical forests, and especially so for French Guiana. Data from previous studies in this region come from 'Piste de Saint-Elie' (Sabatier & Prévost 1990b, Prévost & Sabatier 1996) and Saül (Oldeman 1974, Mori & Boom 1987). The research program at Nouragues aims to study forest dynamics and natural regeneration processes in the forest, including seed dispersal by vertebrates. The establishment of the station as a permanent research site has provided opportunity as well as appropriate conditions to undertake such studies, and to add one more piece to the jigsaw (Milliken 1998). The first surveys of floristic and tree diversity at Nouragues were based on preliminary results from 1989 (Sabatier & Prévost 1990a) and 1995 (Poncy *et al.* 1998).

In this chapter we present the tree diversity, as presently known, based on various inventories carried out on plots in lowland, old-growth *terra firme* dense rainforest. The particular type of low forest that covers the foothills, slopes or top of the inselberg is treated elsewhere in this volume (Larpin, Chapter 5).

Moreover, as floristic data were gathered (by two of us, D. Sabatier and M. Prévost) from several neighbouring one- hectare plots within the study area, some features of the variation of floristic diversity at the local scale will be presented. Such amounts of data from the same place are still rare, and they help to enhance our basic floristic knowledge. Further accurate analyses should help our understanding of the correlations between compositional patterns and local environmental factors. A first attempt was made by Prévost and Sabatier (1996), using the data collected at 'Piste de Saint-Elie', to suggest correlations between variations of species diversity and other parameters involved in forest dynamics, especially soil characteristics.

2. Methods

2.1 THE 'SAUT PARARÉ' SITE

Ecological studies of trees in the area of 'Saut Pararé' were initiated in 1978 by the MNHN. The first was carried out on the border of the river Arataye, close to the rapids called 'Sauts Pararé' (Maury & Poncy 1986). A rectangle of 200 x 300 m, including 6 contiguous one-ha plots, was delineated in an area with uneven topography. It lies on hills with steep slopes and talwegs and includes little flat land, and no flooded ground. The forest was high, with a relatively open understorey, disturbed in some places by recent tree fall gaps. The tree inventory took place in several stages. The first one, carried out in 1978, consisted in numbering and mapping all trees with DBH ≥ 30cm. Later (1983-88) the inventory was continued in order to include all trees with DBH ≥ 10cm and to provide botanical identifications. By late 1985, the inventory itself (numbering, labelling, mapping) included 5 of the 6 one-ha plots. 2674 trees in total were inventoried. DBH was measured with a tape, or estimated above buttresses or stilt roots. As part of the first inventory in 1978, most trees with DBH ≥ 30cm were given a local name (of the *aluku* language). When available, these names help identification at least at the family level. Subsequently, botanical specimens were collected from most trees with DBH ≥ 10cm on the same five hectares, by climbing the trees. Two methods are used to climb the trees, depending on tree size and overall conditions: climbing spikes enable climbing the tree itself; harnesses for speleologists can be used to climb a rope previously installed between the ground and the biggest branches of a tall tree, and with this method, the climber is generally able to collect specimens from several trees around. Vouchers were deposited at the Cayenne herbarium, with duplicates in Paris and, if needed, sent to specialists. Identifications of the vouchers were conducted by the late eighties; sofar 1520 trees have been named, most for them at the species level (1149) and half of the total (1339 out of 2674) at the generic level. A reinventory was carried out in 1995, aiming to collect data about dynamics (growth and mortality).

2.2 THE INSELBERG SITE

The Nouragues area lies 7 km away from the 'Sauts Pararé' plot. A botanical and structural study of the forest was first carried out on five one-hectare transect-like plots (500 x 20 m) where all trees ≥ 10cm DBH were recorded in 1988/89 (Fig. 1, plots 1-5) (Sabatier & Prévost 1990a). Some of these plots were part of a 100-ha study area of the station, gridded in 1-ha quadrats. A comprehensive inventory of trees in this area was initiated in 1992, aiming at numbering, labelling, mapping all trees of DBH ≥ 30cm. The inventory also included all stems of DBH ≥ 10cm on 22 of these quadrats. Twelve of them formed a 12-ha area of the so-called 'Petit-Plateau' where forest dynamics have been studied (van der Meer *et al.* 1994, Van der Meer & Bongers 1996a, 1996b).

   The botanical study of canopy trees (DBH ≥ 30cm) was carried out in a 9 x 1-ha strip of contiguous plots within this area (Poncy *et al.* 1998) and on the five plots mentioned above. Moreover, two additional plots were recorded by D. Sabatier and M.-F. Prévost in 1994

(Fig. 1, plots 6-7), also 1 hectare in area, but with a different shape (40 x 250 m). The botanical record on plot 7 was 80% completed[1].

Thus, the floristic knowledge of the trees at Nouragues presented in this chapter is based on data collected from 15.8 hectares of forest, with two distinct data sets recorded at
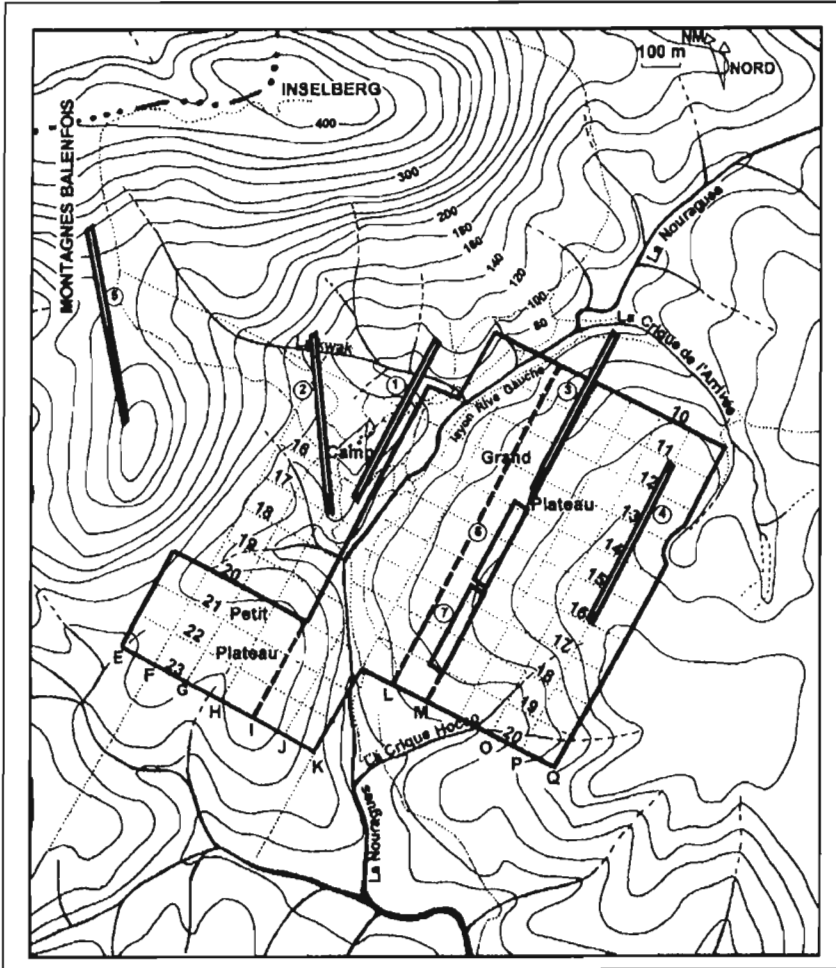

Figure 1. Map of the study area of the Inselberg site

two different scales: firstly, a survey of all trees with DHB ≥ 30 cm on a 10-hectares area; secondly, a study of trees with DBH ≥ 10 cm over 7 transect-like plots each of one-hectare (Fig. 1). Comparative data on specific diversity on these 7 plots, gathered by D. Sabatier

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[1] This plot will not be deleted from this study because it includes a particular forest type, with many lianas. It will be taken into account only when pertinent, due to the lack of floristical data.

and M.-F. Prévost, will be presented in a separate paper, and only preliminary comments are given here.

Identifications were partly obtained in the field (based on habit, bark, leaves observed in the crown and collected from the ground), especially for the species that were common or recognised without any doubt. Local names provided by two Surinamese of the Saramaca ethnic group helped preliminary identifications, most often at a generic level. Collection of vouchers was done when needed for identification, and when climbing was possible. Vouchers were deposited in Cayenne (CAY, herbier de Guyane) and Brunoy (Laboratoire d'Ecologie, MNHN), and some duplicates were sent to specialists. Seven trees remain totally unidentified, and 10% of the total were given only a family or a genus name. Botanical names follow the Checklist of the vascular plants of the Guianas (Boggan *et al.* 1997)[2].

Floristic data are managed in Brunoy, using a multifile database (floristic checklist, tree inventory, reference collections); the database for herbarium specimens is related to the main database of the Cayenne Herbarium ('AUBLET': Hoff *et al.* 1989), now part of the integrated system of forest research databases in French Guiana, named 'ARLEQUIN.

3. Results[3]

3.1 PARARE SITE

Structure and dynamics

The first inventory in 1978 recorded 777 trees of DBH ≥ 30 cm on 6ha (Maury & Poncy 1986) while the overall inventory (trees ≥ 10cm DBH) covered 2674 trees.

Densities (Tab. 1) range from 108 to 137 per hectare for the canopy trees (≥ 30 cm) and from 474 to 652 for all trees (≥ 10 cm). As a result of the reinventory conducted on 5 of the plots in 1995, mortality and recruitment of trees in the area can be estimated. The relative mortality for all trees with DBH ≥ 10cm after 10 years ranges from 9% to 14% in each plot, with a mean of 11.9 (Tab. 1). Similarly, the recruitment (in growth into the DBH ≥ 10 cm

TABLE 1. Density, mortality and recruitment of trees on 5 hectares at 'Pararé site', between 1983 and 1995 (percentage into bracket)

	DBH cm	1	2	3	4	5	total 5 ha
Density (1985)	≥ 30	115	116	125	136	127	619
	≥ 10	490	474	652	537	521	2674
Mortality (1985-95)	≥ 30	18	18	13	8	12	69
		(15.7)	*(15.5)*	*(10.4)*	*(5.9)*	*(9.4)*	*(9.2)*
	≥ 10	71	64	68	48	66	317
		(14.5)	*(13.5)*	*(10.4)*	*(9)*	*(12.7)*	*(11.9)*
Recruitment (1985-95)		62	82	56	34	41	275
		(12.7)	*(17.3)*	*(8.6)*	*(6.3)*	*(7.9)*	*(10.3)*

[2] Authorships of scientific names are not included in this chapter, they are available in the floristic list (see appendix).
[3] Further analyses of the data (especially completing voucher identifications) are currently in progress, in order to write a detailed study of this site.

size class) varies from 6.3% to 17.2%, with a mean of 10.3%. Based on these values, the mean mortality per year reached 1.19%. For the same lower DBH limit (10 cm), Spichiger*et al.* (1996) and Rankin-de Merona *et al.* (1990) found very similar percentages in Peru (Jenaro Herrera, 1.14%) and in Central Amazonia (1.13%) respectively, while Uhl (1982, cited by Rankin-de Merona, *l.c.*) gives 2.93% in Venezuelan Amazonia. In their study of mortality in forests in Venezuela, Carey *et al.* (1994) consider annual mortality rates (that range from 0.5% to 3.3%) to be random, 'quite variable from plot to plot and from year to year', and not related to the type of life zone or initial biomass.

Floristic composition and diversity of trees
Half of the trees with a DBH ≥ 10 cm inventoried on the 5 plots have yielded floristic information, since 1336 out of 2674 trees were given at least a family name. Because the data set was considered not complete enough to allow quantitative analysis, only a qualitative overview is given below.

Based on the inventory of the biggest trees (DHB≥ 30cm) in the 6 ha sample (Maury & Poncy 1986), the most abundant family is Burseraceae (15% of the trees), then Lecythidaceae, Moraceae, Sapotaceae and Mimosaceae. When all trees are considered (DBH ≥ 10 cm), 46 families are represented. The highest number of trees is again in Burseraceae, but Meliaceae come out as the second most abundant family, then Sapotaceae, Lecythidaceae, Myristicaceae and Euphorbiaceae.

In total, 215 tree species were identified. This number clearly underestimates the real number of species present on the plots and the remaining unidentified trees are likely to belong to additional, unrecognised species.

The most abundant identified canopy species (DBH ≥ 30 cm) belonging to the leading families mentioned above, are *Protium sagotianum, Tetragastris altissima, T. panamensis* in Burseraceae and *Eschweilera coriacea, Lecythis persistens, L. poiteaui* in Lecythidaceae. The importance of Moraceae and Mimosaceae is due to their specific diversity (Moraceae, 16 species with *Brosimum rufescens* among the most abundant; Mimosaceae: 17 species, including 13 *Inga* species). Sapotaceae has the highest number of species (25), three of them are rather abundant: *Chrysophyllum sanguinolentum, Pouteria gonggrijpii, Pradosia ptychandra*. Other abundant species belong to additional families (*Dicorynia guianensis*, Caesalpiniaceae; *Carapa procera*, Meliaceae; *Virola michelii*, Myristicaceae; *Minquartia guianensis*, Olacaceae).

With respect to medium-size and understorey trees (DBH ≥ 10 cm), 20 species were represented by 10 trees or more. A few belong to families already mentioned (*Protium apiculatum*, Burseraceae; *Pseudolmedia laevis, Trymatococcus oligandrus*, Moraceae), while some additional important species in this patch of forest are *Unonopsis rufescens* (Annonaceae), *Thyrsodium spruceanum* (Anacardiaceae), *Quararibea turbinata* (possibly a synonym of *Q. duckei*, Bombacaceae), *Licania densiflora* (Chrysobalanaceae), *Tovomita cephalostigma, T. choisyana* (Clusiaceae), *Conceveiba guianensis, Drypetes variabilis, Mabea piriri* (Euphorbiaceae), *Ocotea rubra, Nectandra pisi* (Lauraceae), *Guarea silvatica, Trichilia septentrionalis* (Meliaceae), *Siparuna cuspidata* (Monimiaceae), *Eugenia coffeifolia* (Myrtaceae), *Iryanthera sagotiana* (Myristicaceae) and *Theobroma subincanum* (Sterculiaceae).

3.2 INSELBERG SITE

Structure and physiognomy

An analysis of structural data by Poncy *et al.* (1998) recognised the occurrence of physiognomically different forest zones in the Nouragues area. High mature forest with a fairly open understorey, can be divided into two subsets according to canopy height, the first with an average canopy height estimated at 30-35 m, and the second at 20-25 m. Low forest with many lianas was also subdivided into two zones: the first one with average canopy height of 12 m, few stems reaching 30 cmDBH (see below), many trees overloaded with lianas, and a dense understorey; the second one dominated by lianas, and imbricated liana stems at ground level making the understorey extremely difficult to penetrate. The last type consists of patches of swamp forest dominated by *Euterpe olacea* palms.

Densities for trees ≥ 30cm DBH ranged from 64 to 125 stems/ha for the 44 1-ha plots inventoried up to 1995 (Poncy *et al.* 1998). The variation reflects the forest types described above. Densities < 100 stems/ha indicate either a strong recent perturbation (large gap) or the presence of liana forest in the plot considered. For trees ≥10 cm DBH, densities range from 468 to 681 stems per ha on the 29 plots for which data are available (see also Table 4.4, for 7 plots). All plots but one have fewer than 600 trees. Such numbers accord well with other records from Amazonian *terra firme* forests (review by Spichiger *et al.* 1996, Matos & Amaral 1999), but are lower than those of Mori and Boom (1987) (619 trees/ha at Saül, ca 100 km), Gentry (1988) (ca/600 stems/ha), Rankin-de Merona *et al.* (1990) (600-700 stems/ha), Rankin-de Merona *et al.* (1992) (637 stems/ha). Very high densities (ca 2000 stems/ha or more) are mentioned in Northwestern Amazonian swamp forests (Duivenvoorden & Lips 1995).

The distribution of size classes based on stem diameters was given by Poncy *et al.* (1998) with respect to two forest types: 77% and 88% of trees below DBH 30 cm occur respectively in high forest and in forest with liana-forest patches, while the percentage of trees over 30 cm was lower in the liana forest. In the high forest, 12.2% of the trees are greater than 40 cm in DBH, and 2.2 % greater than 80 cm, *vs* 16.7% and 3.1%, respectively, on La Fumée Mountain near Saül, (Mori & Boom 1987).

Total basal areas, ranging from 30 to 45.3 m²/ha, are generally higher than those recorded in other Amazonian forests outside French Guiana (e.g. Valencia *et al.* 1994, Rankin-de Merona *et al.* 1990, Spichiger *et al.* 1996) but lower than the estimation of 53m²/ha, based on point-centred quadrat sampling by Mori and Boom (1987) in the vicinity of Saül, French Guiana.

Floristic composition

The data gathered to date, both from tree-inventories and sporadically records within the study area, have contributed to the floristic knowledge of the area. The different forest patches vary to some extent in their structure, age, and also in the families or the species that dominate each of them. The total number of tree species recorded over the inventoried area reaches 550, belonging to 63 families (see floristic list, appendix 1). *Eschweilera coriacea*, *Vouacapoua americana* and *Eperua falcata* are by far the most abundant species, but no species dominates the whole study area.

Families

The Family Importance Value (FIV) is an index now widely used to evaluate floristic composition at the family level, and it combines species richness, density and dominance[4] (Mori *et al.* 1983). For canopy trees (DBH ≥ 30cm), the highest values on the 9-ha studied initially (see figure 20.11 *in* Poncy *et al.* 1998) were for Caesalpiniaceae, Sapotaceae, Mimosaceae, Lecythidaceae, Burseraceae, Chrysobalanaceae and Lauraceae. Among the 33 families of Dicotyledons[5] recorded, 50% of the trees belonged to five families, with legumes (Caesalpiniaceae + Mimosaceae) totalling 26% ; Sapotaceae, Burseraceae and Lecythidaceae being the next most abundant. The high value for Caesalpiniaceae was mainly due to the great abundance of two species, *Eperua falcata* and *Vouacapoua americana*. The whole Leguminosae complex accounts for 31% of the identified species. For other families, high numbers of species were also responsible for high values.
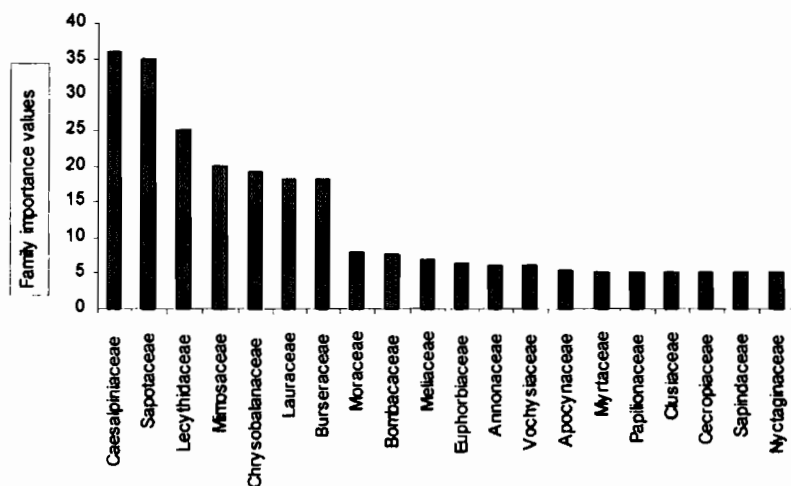

Figure 2. Family importance values for the most important families of trees on the Nouragues study site

Figure 2 shows the FIV pattern based on our 7 other plots, for all trees with DBH ≥ 10cm. The total 3714 trees recorded were assessed to 58 families (7 trees remain unidentified). This figure shows that the forest is markedly dominated by seven families with FIV > 15. They total ca 40% of the species and 50% of the trees. The four leading families are the same as in the canopy inventory sample (DBH ≥ 30 cm) (Poncy *et al.* 1998.), *i.e.* Caesalpiniaceae, Sapotaceae, Mimosaceae, Lecythidaceae. Again, the Leguminosae-complex, totalling 5% of the identified species and 18% of the trees, is important, although slightly less so than in the canopy inventory.

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[4] FIV = (relative number of species + relative density + relative basal area)100
[5] In this paper, Leguminosae are considered as a suprafamilial taxon, including 3 separate families: Fabaceae, Caesalpiniaceae, Mimosaceae.

TABLE 2. The large trees of the Nouragues forest (DBH ≥ 70cm, height ≥ 40 m)

Family	Species
Apocynaceae	*Aspidosperma marcgravianum, A. oblongum, Geissospermum laevis*
Bignoniaceae	*Tabebuia serratifolia*
Bombacaceae	*Ceiba pentandra*
Boraginaceae	*Cordia goeldiana*
Burseraceae	*Protium apiculatum, P. araguense, P. demerarense, Tetragastris altissima*
Caesalpiniaceae	*Dicorynia guianensis, Dimorphandra pullei*
	Eperua falcata, E. grandiflora, Hymenaea courbaril, Peltogyne venosa Swartzia polyphylla, S. arborescens, Tachigali aff. albiflora, Vouacapou americana
Caryocaraceae	*Caryocar glabrum*
Cecropiaceae	*Pourouma bicolor, P. tomentosa*
Celastraceae	*Goupia glabra*
Chrysobalanaceae	*Licania alba, L. majuscula, Parinari excelsa*
Combretaceae	*Buchenavia grandis, Terminalia guyanensis*
Fabaceae	*Lonchocarpus aff. heptaphyllus, Dipteryx odorata, Dussia discolor*
Lauraceae	*Ocotea rubra*
Lecythidaceae	*Couratari guianensis, Eschweilera coriacea*
	Lecythis persistens, L. zabucajo
Meliaceae	*Carapa procera, Guarea sp.*
Mimosaceae	*Abarema jupunba, Balizia pedicellaris, Enterolobium oldemanii, Inga alba, Parkia nitida, P. pendula P. velutina, Pseudopiptadenia psilostachya, Zygia racemosa*
Moraceae	*Brosimum guianense, Bagassa guyanensis, Ficus nymphaeifolia*
Myristicaceae	*Virola michelii, V. kwatae, V. surinamensis*
Olacaceae	*Minquartia guianensis*
Rhamnaceae	*Ziziphus cinnamomum*
Rubiaceae	*Chimarrhis turbinata*
Sapotaceae	*Chrysophyllum lucentifolium, C. pomiferum, C. sanguinolentum, Micropholis melinoniana, M. guyanensis, Pouteria guianensis, P. gonggrijpii, P. glomerata, P. melanopoda, P. laevigata, Manilkara bidentata, M. huberi*
Sterculiaceae	*Sterculia pruriens*
Tiliaceae	*Apeiba petoumo*
Vochysiaceae	*Erisma uncinatum, Qualea rosea*

Among the 21 most important families listed in Fig. 2 (those with FIV > 4), 16 are also found in the canopy inventory (Poncy *et al.* 1998). The differences can be explained because the sample includes small to medium-sized trees, and the families that include many understorey or middle-size species and/or trees then come out among the highest FIV: Euphorbiaceae, Annonaceae, Sapindaceae, Chrysobalanaceae and Moraceae. Bombacaceae is the most striking example, because of the local abundance of a single species, *Quararibea turbinata*. The abundance of palms is a major physiognomical feature of the understorey in this forest, but since only the biggest individuals are captured in the inventory, the FIV for Arecaceae is only 3.2.

TABLE 3. Comparative importance (Family Importance Value) of the families in the 7 plots (plots 1-6 are 1 ha, plot 7 is 0.8 ha in size) for families with FIV > 10).

1	2	3	4	5	6	7
Caesalpiniace 73.4	Sapotaceae 48.8	Sapotaceae 50.4	Burseraceae 37.0	Sapotaceae 52.2	Mimosaceae 42.8	Mimosaceae 42.0
Lecythidacea 43.5	Caesalpiniaceae 45.2	Caesalpiniacea 40.9	Caesalpiniaceae 31.3	Chrysobalanaceae 36.1	Lecythidaceae 29.5	Bombacaceae 33.1
Sapotaceae 32.8	Lecythidaceae 31.1	Lecythidaceae 36.1	Chrysobalanacea 28.1	Caesalpiniaceae 27.4	Caesalpiniaceae 27.4	Sapotaceae 24.8
Burseraceae 17.9	Chrysobalanacea 24.8	Mimosaceae 18.4	Sapotaceae 27.8	Clusiaceae 20.1	Burseraceae 22.5	Lecythidaceae 24.0
Chrysobalanac ae 13.2	Burseraceae 12.4	Burseraceae 15.2	Lauraceae 18.3	Lauraceae 20.1	Sapotaceae 22.3	Meliaceae 18.7
Mimosaceae 12.6	Mimosaceae 11.7	Lauraceae 12.8	Annonaceae 16.1	Lecythidaceae 14.1	Lauraceae 17.4	Caesalpiniacea 14.0
	Lauraceae 10.7		Lecythidaceae 14.1	Fabaceae 13.4	Vochysiaceae 10..3	Nyctaginaceae 13.8
	Apocynaceae 10.7		Mimosaceae 10.4	Mimosaceae 10.4		Lauraceae 13.1
			Vochysiaceae 12.1	Myrtaceae 10.1		Moraceae 10.9
						Cecropiaceae 10..3
						Burseraceae 10.2

Differences in FIV are also due to local heterogeneity, since two different sets of plots are considered. With respect to the most important families, Table 3 shows the differences between plots within the study area (see also Sabatier & Prévost 1990a, for a preliminary analysis of 5 out of the 7 plots). Caesalpiniaceae and Sapotaceae are always present among the 5 major families per plot; other families with FIV > 10, that occur on all plots, include Lecythidaceae and Mimosaceae, while Lauraceae and Burseraceae occur on 6 plots, and Chrysobalanaceae on 4 plots. Vochysiaceae have a high FIV in 2 plots, while Annonaceae, Apocynaceae, Bombacaceae, Cecropiaceae, Fabaceae, Meliaceae, Moraceae and Nyctaginaceae do so only in one plot. Plot 5 is unusual with Clusiaceae and Myrtaceae coming out in the group of leading families. The second rank for Bombacaceae in plot 7 is due to the local abundance of *Quararibea turbinata*; the importance of Nyctaginaceae, Moraceae and Cecropiaceae also contribute to the distinctive pattern of this area. The occurrence on all plots of a number of families with at least middle Family Importance Value (3-10) contributes to homogeneity at this level: Anacardiaceae, Annonaceae, Apocynaceae, Icacinaceae, Meliaceae, Myristicaceae, Sapindaceae, Sterculiaceae, Tiliaceae. On the contrary, a number of families with low FIV are found only on one or two plots. They include mainly the less species rich families, like Aquifoliaceae, Erythroxylaceae, Lacistemataceae, Linaceae, Proteaceae, Quiinaceae, Rhizophoraceae, Rutaceae, Styracaceae and Theaceae.

Species composition

The total number of woody species recorded on the 16 hectares includes 541 trees and a few large lianas.

As part of the botanical identification of mature canopy trees (DBH≥ 30 cm) completed on 9 one-ha plots (100 x 900 m), 145 species were identified (Poncy *et al.* 1998). The species number per hectare ranged from 39 to 87. The 25 most abundant species (with 10 trees or more on the 9 hectares) represent ca. 20 % of the total. In addition to the three very abundant species mentioned above (*Eperua falcata, Vouacapoua americana, Eschweilera coriacea*), they include several members of the Leguminosae complex (*Swartzia polyphylla, Dicorynia guianensis, Sclerolobium melinonii, Sclerolobium* aff. *paraense, Tachigali* cf. *albiflora, Pseudopiptadenia psilostachya),* Sapotaceae (*Pouteria guianensis, P. gonggrijpii, Chrysophyllum lucentifolium, Manilkara bidentata, M. huberi, Micropholis guianensis),* Burseraceae *(Tetragastris altissima, Protium opacum, P.* aff. *demerarense),* Chrysobalanaceae *(Licania canescens, L. membranacea),* Lecythidaceae *(Lecythis persistens subsp. aurantiaca),* Myristicaceae (*Virola michelii, V. kwatae),* Rubiaceae (*Guettarda acreana*) and Nyctaginaceae (*Neea* aff. *floribunda).*

Not as abundant but rather frequent (present in more than half of the complete set of 16 studied plots) are *Poraqueiba guianensis, Dendrobangia boliviana* (Icacinaceae), *Qualea rosea* (Vochysiaceae), as well as several mimosoids *(Inga alba, I. huberi, I. rubiginosa, Abarema jupunba, Parkia nitida).*

In order to give another view of tree species composition, we listed the species of biggest trees, on the basis of DBH ≥ 70 cm and/or estimated height > 40 m, throughout the 15.8 hectares. They are often emergent trees dominating the canopy that averages ca 30mhigh. The species list comprises 75 species that fall into 25 families (Table 2).

With respect to medium-sized and understorey trees (trees with 10≤ DBH ≤ 30 cm on 7 non-contiguous plots, 6.8 ha), the most abundant species include: *Andira coriacea, Apeiba glabra, Bocoa prouacensis, Conceveiba guianensis, Coussarea racemosa, Duguetia surinamensis, Eugenia coffeifolia, Eschweilera grandiflora, E. micrantha, E. pedicellata, Gustavia hexapetala, Iryanthera sagotiana, Lecythis idatimon, L. poiteaui, Licania alba, L. canescens, Pourouma minor, Pouteria decorticans, Protium opacum ssp. rabelianum, P. sagotianum* and *Quararibea duckei.* Less abundant but frequently recorded are: *Mabea piriri, Swartzia polyphylla, Tovomita choisyana, Theobroma subincanum, Xylopia nitida.* Some other species are locally abundant but restricted to reduced areas, e.g. *Duroia genipoides, Eschweilera collina, Micropholis longipedicellata, Ocotea aciphylla, Oxandra asbeckii, Quiina oiapocensis, Siparuna cristata, Swartzia guianensis, Trichilia pallida, Unonopsis rufescens.* Similarly, *Guarea gomma* and *G. kunthiana* occur only in the forest with lianas (plot 7), as does *Inga acreana.* Rubiaceae, like *Capirona surinamensis* or *Guettarda acreana,* have striking smooth, peeling green or white bark that locally marks the physiognomy of the understorey.

Some taxa are important at the genus level but not at the species level, each species remaining poor in number of individuals, especially *Inga,* with at least 12 individuals per ha, and *Aspidosperma, Eschweilera, Lecythis, Pourouma, Pouteria, Licania, Ocotea, Talisia, Protium* and *Swartzia.* The commonest palm species scored is *Astrocaryum sciophilum* which is present on all but one plot, with a maximum density of 27 individuals per plot. Another abundant palm is *Jessenia bataua,* while *Oenocarpus bacaba* is rather frequent, and *Maximiliana maripa* is locally frequent in the western part of the study area.

Finally, 85 species were recorded only once, some of them being rare. While some are small-sized trees with only rare individuals reaching 10cm DBH (*Erythroxylum ligustrinum, Amphirrhox longifolia, Ouratea candollei, Posoqueria longifolia...*), others are known to be generally common species, but often with very low densities, and might be only locally rare (*Bagassa guianensis, Laetia procera, Macoubea guianensis, Swartzia panacoco...*). However, most are likely to be truly rare species in French Guiana (for instance, *Ephedranthus guianensis, Ilex* sp., *Kubitzkia mezii, Lacistema grandifolium, Licania rodriguesii, Ternstroemia dentata...*).

Patterns of specific diversity

Comparative data on specific diversity on these 7 plots are presented Table 4. In the 6 plots where botanical identification was completed, the number of species ranges from 171 to 217 per hectare. Values for the number of trees per plot are rather similar from plot to plot, as found by Duivenvoorden (1996) in NW Amazonia, based on the number of species in proportion to the number of trees. Here we use the reverse ratio (individual/species) as did Spichiger *et al.* (1996). In our plots, this ratio is rather similar for 5 of the six plots (2.6-2.9), and it is never as low as in the plot studied at Jenaro Herrera (Spichiger *et al.* 1996). This is consistent with the current assumption that the highest species richness is encountered in western Amazonia (Gentry 1988, Balslev *et al.* 1989, Valencia *et al.* 1994, Duivenvoorden 1994).
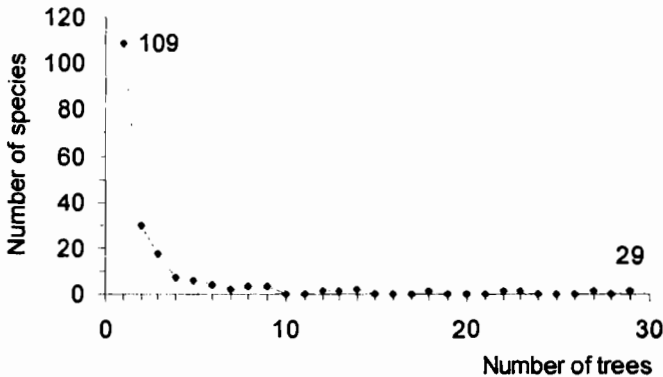

Figure 3. Species abundance distribution in plot 4

Species abundance in the plots was scored at two levels (Table 4): density ≥ 5 trees/ha and density ≥ 10 trees/ha, the latter considered as « abundant species ». More than half of the trees belong to a species having a minimum density of 5, on all plots but one. This figure (illustrated for plot 4 in Fig. 3) reflects the general pattern of species diversity in tropical rainforest, *i.e.* the relative abundance of a few species, and the scarcity of most species represented by less than 5 trees per hectare. This pattern is less marked in the plot at Jenaro Herrera, where there are lower percentages of abundant species (Table 4).

TABLE 4. Differential features of tree diversity measured on 7 one-ha plots, for all trees with DBH ≥ 10cm   (JH = Jenaro Herrera: data of Spichiger et al. 1996 bring one point of comparison). * Identification was completed on 0.8 ha on plot 7

	1	2	3	4	5	6	7	JH
STRUCTURE								
Number of trees	468	575	471	539	681	504	489	504
Basal area (m²)	35.5	40.1	35.9	45.3	32.0	30.7	26.3	23.6
DIVERSITY								
Families with FIV ≥ 10	6	8	6	9	9	7	11*	12
Number of species	179	217	180	188	171	172	143*	227
Ratio nb trees / nb species	2.6	2.6	2.6	2.9	4.0	2.9	3.4	2.2
Abundant species (≥ 10 trees)								
Number of species	5	11	7	9	19	8	6*	5
% total number of species	2.8	5.0	4.0	4.8	11.0	4.7	4.2	2.2
Number of trees	142	175	125	172	313	145	174*	68
% total number trees	30.5	30.4	26.5	32.0	46.0	28.8	35.6	13.4
Species with ≥ 5 trees								
Number	20	31	21	26	42	24	25*	24
% total number of species	11.2	14.3	12	14	24.5	14	17.5	10.6
Number of trees	237	292	210	291	464	252	302*	178
% total number of trees	50.6	50.8	44.6	54.0	68.1	50.1	62.0	35.3
Species with a single tree								
Number	108	128	98	105	78	108	72*	125
% total number species	60.0	59.0	54.5	56.0	46.0	63.0	50.3	55.0

A general pattern similar to that of plot 4 would be obtained from our other plots, but the extreme values clearly make a difference. The highest number of trees per plot for the most abundant species varies from 25 (4.3%; plot 2) to 66 (14.1%; plot 1), and to 77 (for 0.8 ha) on plot 7 (15.7%), while the number of species with a single tree per hectare varies from 78 (plot 5) to 127 (plot 2). Indeed, the proportion of species with a single tree per hectare is over 50% in all plots but one, which is strikingly high.

Plot 5 clearly exhibits a different pattern compared to the other plots, since it is less species rich, despite a higher density (Table 4), as is also shown by the higher percentage of abundant species and lower percentage of 'single' species. This pattern is indicative of the particular forest type that occurs on the slope at the foothill of the inselberg (Fig. 1, plot 5), which is transitional between the high dense forest (plots 1-4, 6) and the low forests of the inselberg, described by Larpin (1993) and Poncy et al. (1998).

Contrasting with the overall distribution of species abundance (Fig. 3), qualitative differences affect the floristic composition from plot to plot. Evidence for this is given by an analysis of the occurrence of the species in the 7 plots (Fig. 4). Only four species occur in all 7 plots, while 257 occur in only one plot. The occurrence of about 100 species in more than 3 plots (less than 20 % of the total number of species recorded) suggests strong floristic heterogeneity at the local scale. The abundant species (i.e., in the present study, those with more that 10 individuals on a plot, see Table 4) seem to contribute to this heterogeneity. Throughout the 7 plots, 31 species were recorded as abundant (≥ 10 trees) at least in one plot (Table 5). Only one is abundant in 4 plots (Eschweilera coriacea); another

Lecythidaceae (*Lecythis persistens* subsp. *persistens*) occurs with more that 10 trees in 3 plots; no other species is abundant in more than 2 plots. Thus, no species is abundant throughout the whole area.
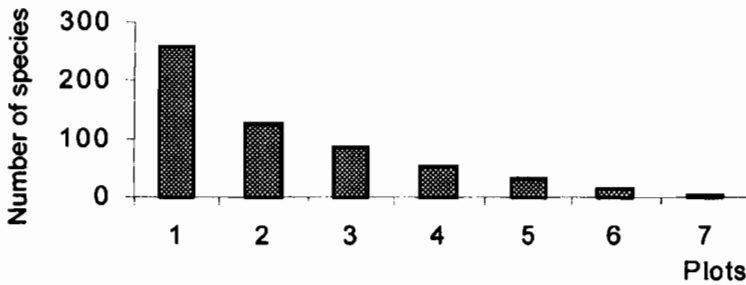

Figure 4. Species frequencies distribution

4. Discussion

4.1 THE DIVERSITY OF NEOTROPICAL FORESTS

Forest tree diversity has been worked on intensively over the last 20 years in the neotropics, especially in Central and Western Amazonia (Gentry 1988). The first results were summarised by Duivenvoorden (1995, 1996), Phillips *et al.* (1994), Spichiger *et al.* (1996), Richards (1996), Ek & van der Hout (1997), but few data were available from French Guiana. Our analyses show that the pattern of species richness and floristic composition at Nouragues is similar to that described from several inventories conducted in the Central Amazon region near Manaus (summarised by Rankin-de-Merona *et al.* 1992, see also Matos & Amaral 1999). As mentioned above, species richness is lower than in western Amazonia where the highest values have been recorded (Foster, 1990, Balée *et al.* 1989, Valencia *et al.* 1994, Spichiger *et al.* 1996, Duivenvoorden 1995, 1996).

Comparing the geographic distributions for a set of species, Mori (1991) recognised a distinct floristic ' province' as part of the large Amazonian biogeographic area. Recent studies in the nearby forests of Guyana (Comiskey *et al.* 1994, Johnston & Gillman 1995, Ek & Ter Steege 1997, Ek & Van den Hout 1997) have shown that these forests are species-poor and/or dominated by single species, such as Greenhart (*Chlorocardium rodiei*). In spite of some floristic affinity, for instance with respect to the dominant families (Leguminosae and Lecythidaceae in the large size-classes; Annonaceae and Bombacaceae in the smaller size-classes), major differences are apparent when species abundance are compared. At Kurupukari, Central Guyana (Johnston & Gillman 1995), 25% of species were represented by a single tree per hectare, while the percentage at Nouragues was 46% to 60%, and two to six species accounted for 50% of the trees at Kurupukari, while at Nouragues this was 20 to 30%. Ek (1997) surveyed the theories that may explain species richness in rainforests, including refuge theory and the stability–time hypothesis. She discussed the particular case of the Guianas and the assumption by Hammond and Brown (1995), that the Nouragues area shows a pattern of disturbance intermediate between that

at Saül (most disturbed site), and Mabura Hill (least disturbed), based on the proportion of large-seeded families. However, Mori and Boom (1987) suggested that the forest at Saül has not undergone major disturbance, based on the high proportion of large trees compared with records from elsewhere. Using the same criterion would suggest that the forest at Nouragues was more disturbed (see below).

TABLE 5. The most abundant species (≥ 10 trees) in each of 7 plots at Nouragues. Number of trees are given in brackets.

Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7
Eperua falcata (66)	Lecythis persistens (16)	Eschweilera coriacea (26)	Eperua falcata (29)	Brosimum guianense (31)	Quararibea turbinata (30)	Quararibea turbinata (77)
Eschweilera coriacea (30)	Licania membranacea (11)	Lecythis persistens (22)	Astrocaryum sciophilum (27)	Bocoa prouacensis (28)	Eschweilera coriacea (24)	Neea aff. floribunda (34)
Lecythis idatimon (18)	Eperua grandiflora (11)	Quararibea turbinata (20)	Licania membranacea (23)	Maytenus sp. (25)	Lecythis persistens (19)	Eschweilera coriacea (31)
Lecythis persistens (15)	Eschweilera micrantha (13)	Vouacapoua americana (17)	Licania kunthiana (22)	Ocotea aciphylla (22)	Sclerolobium paraense (17)	Apeiba glabra (11)
Vouacapoua americana (13)	Bocoa prouacensis (12)	Pouteria gonggrijpii (15)	Qualea rosea (18)	Licania laxiflora (20)	Pourouma minor (16)	Guarea kunthiana (11)
		Eperua falcata (14)	Unonopsis rufescens (14)	Manilkara bidentata (19)	Poraqueiba guianensis (15)	Trichilia surinamensis (10)
			Licania canescens (14)	Duroia genipoides (15)	Pouteria gonggrijpii (13)	
			Trichilia pallida (13)	Coussarea racemosa (15)	Inga huberi (11)	
			Eschweilera grandiflora (12)	Andira coriace (15)		
			Micropholis longipedicellata (11)	Astronium ulei (11)		

4.2 FLORISTIC COMPOSITION AND ITS VARIATION AT THE LOCAL SCALE

Two interesting patterns are discussed here below. Firstly, patches of high lowland forest with similar structure and species richness may show important variation in their floristic composition, even at the family level. While at Inselberg site the forest is dominated by Caesalpiniaceae and Sapotaceae, Burseraceae is the most important family at Pararé site, only a few kilometres away. One species, *Tetragastris altissima*, is abundant here, as it is around Saül (Mori & Boom 1987), while *Vouacapoua americana* (Caesalpiniaceae) is absent, in contrast to Nouragues. These differences are consistent with the two main forest types recognised in central French Guiana by Sabatier and Prévost (1990b); each

characterised by its dominant family, either Burseraceae or Caesalpiniaceae. Secondly, at a very local scale within the study site of Nouragues, the tree species composition is rather homogeneous at the family level but not at the species level. Some species are abundant but none dominates the whole area. Most species are neither abundant nor frequent, since only a few of them occur in all seven plots where trees with DBH $\geq$ 10 cm were scored, while most are found only in one or two plots. Variations of species richness also account for heterogeneity at the β-level. Two of the seven plots are less species rich than the remaining five, one of which (plot 5) is located at the base of the inselberg. Its particular structure and floristic composition reflect the transition between the high humid forests and the low forests found there (Larpin 1993, Poncy *et al.* 1998). Plot 7 is mainly situated in a forest dominated by lianas, and such liana-forest patches occur from place to place in French Guiana as well as in other areas of Amazonia. Their origin and dynamics remain controversial, although they are often considered to be of anthropogenic origin (Balée & Campbell 1990). This hypothesis was supported by Poncy *et al.* 1998, since evidence of previous human occupation, such as polishers, earthenware pieces and charcoal (Tardy 1998) has been found at several sites in the Inselberg site.

However, other factors might also be responsible for structural and floristic heterogeneity, including the occurrence of this liana forest. Sabatier and Prévost (1990b) favoured an edaphic origin, and according to preliminary pedological data reported by Poncy *et al.* 1998, a close association can be expected between liana forest and soil type. Moreover, as described by Grimaldi and Riéra (Chapter 2), the two parts of the study area, on either side of the river Nouragues, lie on different geological substrates and soils, and this might influence the distribution of some species. To the east of the river, the substrate is metamorphic rocks in the series 'Paramaca', called 'Roches vertes' by the local people and covered with clayey soil; the slope is gentle and ends on the 'Grand Plateau'. To the west, granite and crystalline rocks of the series 'Caraibe' are partly covered with sandy clay soil; its steeper slopes form the foothill of the inselberg. Most studies carried out in French Guiana (Lescure & Boulet 1985, Sabatier *et al.* 1997) and elsewhere (Duivenvoorden & Lips 1995) emphasise the importance of both topography and soil structure and composition (that determine hydrology and drainage) on species richness and on the distribution of tree species. Preliminary data observations from the forest plots at Nouragues on variation in floristic composition in relation to soil (Sabatier & Prévost 1990a,b) suggest that the relationship is complex. Climate changes in the recent past are also hypothesised to have influenced the distribution patterns of tree species. These changes are currently being studied using analyses of charcoals (Tardy 1998), of patterns of distribution of tree species that have low recolonisation rates and/or slow growth (Charles-Dominique, Chapter 7) and of the succession of pollen and seeds captured in the sediments (Ledru *et al.* 1997).

Other major topics of ecological research in the Nouragues area include the role of animals, especially vertebrates, as seed dispersers, and the dynamics of tree-fall gaps. As mentioned before by Sabatier and Prévost (1990b), both of these have effects at a small scale and may influence species composition and local variations within it at the Nouragues study site.

Further studies in tree diversity should include analyses for the whole site, based on the trees censused so far over the study area. Condit *et al.* (1996) consider 50-ha as a sufficiently large area for accurately characterising tropical tree communities. In addition,

more detailed small-scale analyses, based on comparison of 1-ha or smaller plots would be valuable. Plot-shape could be taken into account, since plots of three different shapes were used in the present study. Recent work in Brazil (Laurance *et al.* 1998), however, showed that plot shape has only minor effects on estimates of tree-diversity. The general results presented in this chapter thus give a good overview on structure and diversity of the high rainforest at Nouragues.

NOURAGUES

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