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CHAPTER 21

MEASUREMENT OF SPECIES RICHNESS
OF VASCULAR PLANTS IN A NEOTROPICAL
RAIN FOREST IN FRENCH GUIANA

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and Michel Hoff

INTRODUCTION

Current field work on the floristic composition of rain forests in French Guiana is focused on three main approaches: general floristic inventories, providing essential baseline information on botanical composition with taxonomic data (de Granville *et al.*, 1991; Cremers and Hoff, 1994; Hoff, 1994); taxonomic inventories of particular families, genera, and species (Allorge *et al.*, 1980; Poncy, 1985; Mori *et al.*, 1987; de Granville, 1990; Cremers and Hoff, 1994; Plumel, 1994); and quantified forest plots (Puig and Lescure, 1981; Riera, 1983; Mori *et al.*, 1987; Sabatier and Prévost, 1989, 1990). In most cases, this work examines trees ≥ 10 or 25 cm in diameter at breast height (dbh). Thus far, little information has been available on small-scale composition and spatial distribution of vascular plants, whose individuals are usually ≤ 10 or 25 cm dbh. Extensive data on floristic richness for all vascular plants in French Guiana have been recorded on a grid system of squares measuring 15° latitude $\times$ 15° longitude (de Granville *et al.* In press), using the AUBLET botanical database (Hoff *et al.*, 1989), but plot-scale, species-richness data analyses about vascular plants were lacking for quantifying biodiversity at the station level.

The aim of this paper is to present and analyze vascular-plant plot data recently gathered in the Sinamary River drainage basin and to compare them with larger scale floristic information from the same region. Field research in French Guiana was conducted in the forest surrounding the Sinamary River, which was partly flooded by the recent construction of a hydroelectric dam. The dam, operated by Electricité de France (EDF), is situated at the Petit Saut site 50 km south of the Atlantic Coast and one hour by road from Kourou. The dam basin occupies 310 km² of the 6200 km² total surface of the drainage basin. The flooding that followed the beginning of the operation at the dam primarily had impacts on riparian and swamp forest, although adjacent foothill *terra firme* forest was also affected as the water rose to 35 m above the original stream level at the Petit Saut site.

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Botanical collections in the Sinamary River area started as early as 1762, with Aublet's expeditions, followed by the work of Leblond (1787 to 1789) and Leprieur (1837 to 1839). However, the specimens left by these early collectors could not be used in the present work because the locality information was not accurate enough. Using the herbarium material available in the Cayenne Herbarium, all of the more recent botanical collections from the area with adequate locality data were recorded on the AUBLET database. The names of the collectors and the numbers of specimens for which data were captured are as follows: P. Berthet (73), F. Billet and B. Jadin (191), B. Bordenave (845), G. Cremers (155), G. Deward (294), J. J. de Granville (701), F. Hallé (57), M. Hoff (1879), J. P. Lescure (62), D. Loubry (810), S.A. Mori *et al.*, (315), R.A.A. Oldeman (360) P.A. Scheffer (123), M.F. Prévost (138), D. Sabatier (178), and O. Tostain (61).

METHODS

Regional botanical collections

The data used for the analysis of regional-scale floristic richness were derived from specimens identified to species level from previous botanical collections made in the river drainage basin, divided into seven collection areas from the lower to the upper part of the river (Figure 21.1). Riparian and swamp forest as well as open riverside vegetation were amply investigated by earlier botanists. Several additional inventories were conducted in terra firme forest surrounding the river course, which has been explored to a lesser extent than the other forests. The qualitative information provided by these collections does not, however, give an indication of the actual surface area sampled.

Regional-scale collections as well as vascular-plant, species-richness plot data were categorized according to several criteria. First was ecological formation, which included: i) well-drained, lowland *terra firme* forest (slope and crest in dense forest); ii) forest on hydromorphic soil (flooded, swamp, and riparian forest); and iii) open riparian vegetation.

Second was life form. Each specimen was assigned to one of the following mutually exclusive life-form classes: herb (H) – self-supporting herbaceous plant; shrub (S) – self-supporting woody plant with basal branching, less than 3 m in height; tree (T) – self-supporting woody plant without basal branching, more than 3 m in height; herbaceous climber (C) – ground-rooted, non-self-supporting herbaceous plant (referred to as vines in the text); woody liana (L) – ground-rooted, non-self-supporting woody plant (referred to as liana in the text); epiphyte (E) – non-ground-rooted (during the whole life cycle), non-self-supporting plant; and parasitic plant (P).

Third were taxa. All specimens with sufficient locality information for analyzing floristic richness were identified to species level and deposited at the Cayenne Herbarium.

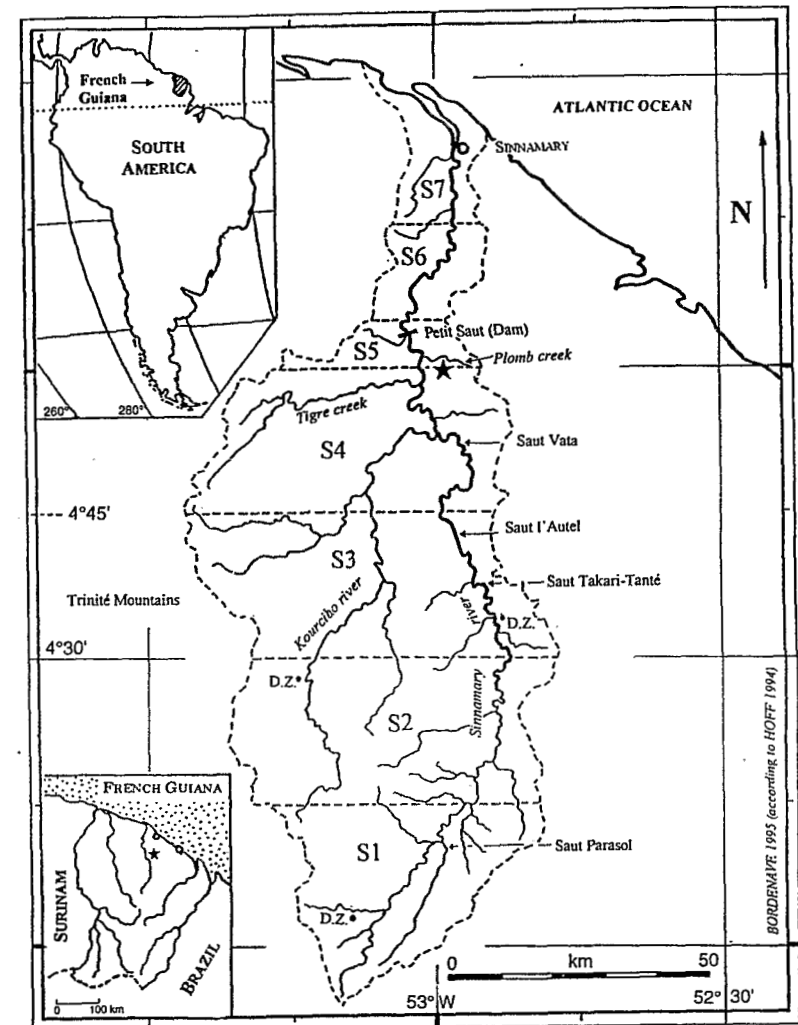


Figure 21.1 The Sinamary River drainage basin, French Guiana, divided into seven botanical collecting zones (* = vascular-plant species-diversity plots)

Vascular-plant species-diversity plots

As part of this project, all vascular plants (pteridophytes and phanerogams) were sampled in five 100-m² plots established in primary terra firme rain forest. A destructive sampling method (total cutting) was used in anticipation of the flooding of the dam's reservoir area. The site, in the area to be flooded, was upstream from Plomb Creek at less than 40 m above sea level and was accessible by motor boat (Figure 21.1). Plots were delimited in contiguous alignment, using a decameter tape and a compass, in a topologically homogenous, well-drained terra firme forest on gentle (20%) slope. The average height of the canopy was 35 m.

Every plant rooted within the plot was counted, except for saplings and juvenile trees < 5 cm dbh. On host trees with crowns reaching beyond the plot boundaries, all vines and lianas with roots located inside the plot were counted. In addition, all epiphytes on these trees were counted. However, epiphytes on branches overhanging the plots but borne on trees rooted outside the plots were excluded to equilibrate the sampling method. In each plot, understory plants were collected first. Trees, vines and lianas were individually marked and later felled. Trunk and crowns were carefully inspected for vines, lianas, epiphytes, and parasitic plants, but the dislocation of some tree forks induced a certain error because some small epiphytes and vines were crushed or became inaccessible.

Individuals of each species were enumerated, except for very abundant colonies of epiphytes, whose populations were estimated. One voucher specimen for each species was kept for each plot. All specimens were brought to the Herbarium of the Muséum National d'Histoire Naturelle in Paris for identification.

Information on each sample (taxon, height, dbh, number of individuals/plot or subplot, life form, phenological and morphological data, host tree number for epiphytes, vines and lianas, vernacular names and uses, etc.) was entered into the AUBLET database. Dbh was measured at 1.30 m above the ground for woody, ground-rooted plants. For acaulescent plants, dbh was recorded as zero. The dbh for small plants with stems (e.g. small palms and shrubs) was measured in the middle of the main axis.

RESULTS AND DISCUSSION

Large-scale floristic richness from previous studies

Analysis of information in the AUBLET database indicated that 1203 species were identified from the Sinamary River area, out of the more than 5100 vascular-plant species currently known in French Guiana. Of the 1203 species, 861 were dicotyledons, 216 monocotyledons, and 126 fern species. A total of 654 species came from well-drained *terra firme* forest, 806 from forest on hydromorphic ground, and 108 from open riparian vegetation. Table 21.1 shows the distribution of species by life form for the three different vegetation types.

Measurement of species richness of vascular plants

Table 21.1 Distribution of species by life form in three vegetation types found in the Sinamary River area (% = percent of total species in each life form)

Life form	Terra firme forest		Flooded forest		Open vegetation	
		%		%		%
Tree	322	45.7	320	36.5	18	15.7
Shrub	119	16.9	144	16.0	26	21.6
Herb	122	17.3	175	19.4	51	43.3
Epiphyte	84	11.9	148	16.4	11	9.6
Liana	43	6.1	98	10.9	7	6.1
Vine	15	2.1	17	1.9	2	1.7
Total	654	100	806	100	108	100

The number of species gathered in terra firme forest (654) compared with that for forest on hydromorphic ground (806), does not accurately represent the proportion of species that actually occurs in each of these vegetation types. Recent studies in Amazonia forest show a generally higher species diversity on well-drained soil than on flooded soil (Campbell *et al.*, 1986; Balslev *et al.*, 1987; Phillips *et al.*, 1994). The results obtained in the present study are probably an artifact of intense collecting in more accessible areas (flat swamp forest and the foothills) along the river rather than in the forests on slopes and crests, which cover a large surface (larger than the surface covered by the flooded soils) in the drainage basin. The difference between the number of species found in these two forest types is particularly striking for climbing and epiphytic species. For the vines and lianas, only 58 species were collected in *terra firme* forest (42 species were found in a single plot of 500 m²) versus 115 in flooded forest. Notwithstanding structural variations in species distribution, this difference can be partly explained by the difficulty of collecting fertile epiphytes and lianas in the understory. These life forms are easier to locate and gather from the river.

The number of specimens and species collected in each of the seven sectors delimited in the Sinamary River basin is presented in Figure 21.2, along with cumulative species- and family-area curves. Sector S5 appeared to be much richer in species than sector S6; the number of species encountered for the first time was more than twice as much in S5 than in S6. It should be noted that the Petit Saut site where the dam was constructed is located in S5 and was broadly prospected during a two-month exploration with the Radeau des Cimes (Bordenave, 1990).

The cumulated species-area curve shows an inflection from sector S5, where 700 km² were previously sampled. More than 400 species were found in the four upstream areas (sectors S4, S3, S2, and S1). The curves appear to approach an asymptote in S1. Although large areas surrounding the river are still unexplored, a substantial portion of the vascular plant species present in the region seems to have been collected.

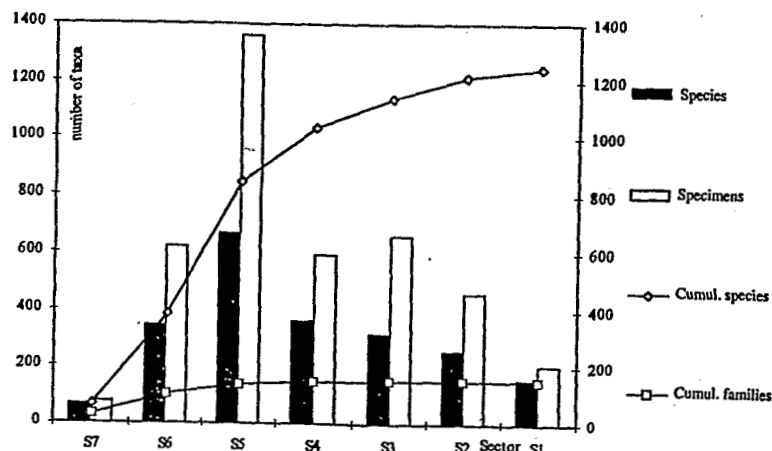


Figure 21.2 The number of specimens and species represented by available collections from seven successive sectors of the Sinamary River basin and the cumulative totals for species and families

Figure 21.3 shows the species-area curve for each life form. The epiphyte curve dipped in S6 but emerges in S5, as if the lack of collections in S6 were counterbalanced by the more extensive exploration in S5.

Figure 21.4 shows cumulative species listed for each of the main families and groups: Araceae, Arecaceae, Chrysobalanaceae, Lecythidaceae, Leguminosae (Caesalpiniaceae, Fabaceae, and Mimosaceae), Melastomataceae, Orchidaceae, Pteridophytes (all families), and Sapotaceae. Unlike the other taxa, Pteridophyte species showed no saturation (i.e. no apparent inflection in the cumulative curve). The progression between S5 and S4 was reduced with an increase of new species from S4 to S3. Since this group was carefully collected and thoroughly identified, the results obtained may indicate two different floristic zones – the lower basin and the upper basin, the second being geographically closer to the center of French Guiana. The transition would therefore be located somewhere around Saut l'Autel and Saut Takari Tanté (Figure 21.1). Further floristic assessment is necessary to confirm this hypothesis.

Species richness resulting from the present project

In the 500 m² plot (divided into five quadrats, all equal in size) that was examined for this study, 480 specimens were collected, representing 203 species, 120 genera, and 55 families. Among these samples, 123 species, 73 genera, and 35 families of dicotyledons, 59 species, 35 genera, and 9 families of monocotyledons, and 21 species, 12 genera, and 11 families of pteridophytes were enumerated. Of the species preliminarily identified as 203 morpho-species, a total of 152 (75%) were identified accurately to the species level, while 27

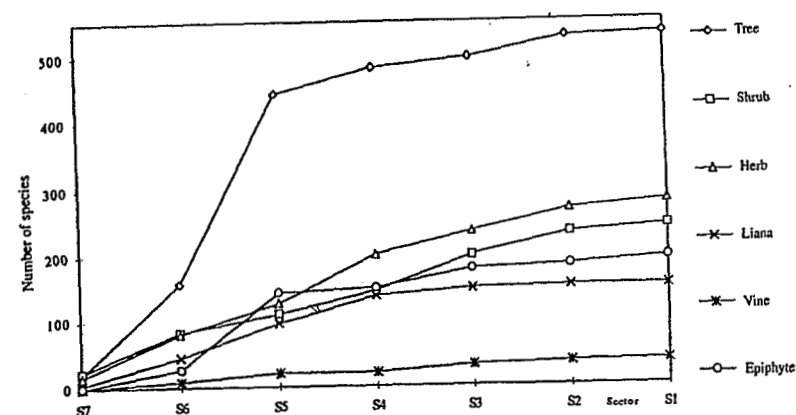


Figure 21.3 Cumulative species-area curve by life for all available collections from the Sinamary River basin

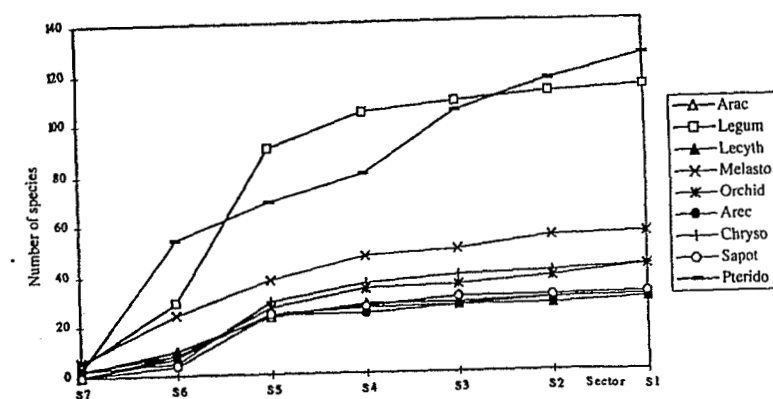


Figure 21.4 Cumulative species-area curve by main families for all available collections from the Sinamary River basin

(13%) could only be assigned to genus. An additional 16 species (7%) could be identified only to family, and 8 species of dicotyledons remain unidentified. A list of the species is available from the lead author.

Number of species per life form

Data on species distribution by life form are presented in Table 21.2. The percentage of species by life form in the study plots as compared to the total number of known species of the same life form in *terra firme* forest is also given.

The relatively large proportion of liana species present in the 500-m² plot, when compared with the total number collected in the *terra firme* forest in the

Table 21.2 Species richness by life form in a 500-m² plot and proportion of life form in this plot compared with percentage of all known species from *terra firme* forest in the Sinamary River Basin

Life form	# of species	% of species by life form	% of total known species in <i>terra firme</i> forest
Tree	58	28.6	18
Shrub	35	17.2	30
Herb	34	16.7	28
Epiphyte	33	16.3	37
Liana	31	15.3	72
Vine	11	5.4	73
Parasite	1	0.5	—
Total	203	100.0%	30.8%

entire river basin, probably reflects an underestimation of this life form in regional botanical collections. Note that unidentified vouchers from sterile collections were not taken into account for the regional-scale analysis. Conversely, morpho-species recognized as distinct taxa were counted in the plots, even though they were not identified to species level.

Cumulative species- and family-area curves

Cumulative species-area curves were calculated for the sample of 203 vascular plant species collected in the five plots, following the chronological order in which they were sampled. Figure 21.5 shows the cumulative total species. The curve tends to stabilize from plot p3 and increases slightly in p5, indicating a shift in floristic composition at this level. Two explanations come to mind. First is a change in soil features in plot p5 from plots p1 through p4; the relationship between soil type and plant distribution has been documented in French Guiana forest (Lescure and Boulet, 1985). Second is a difference in age with regard to the sylvigenetic cycle (Oldeman, 1974). The family-area curve is also presented in Figure 21.5. An inflection can be seen at the second plot, and the slope decreases in plots p4 and p5.

Figure 21.6 shows the species progression by life form. Curves for ground-rooted vascular plants (trees, shrubs, herbs, and lianas) are consistent with the results presented in Figure 21.5, with a slight increase in new species found in plot p4. Epiphytes and vines showed stabilization of species number from plot p3. This was not surprising for epiphytic species because pedological and soil hydrological factors appear to have no direct effect on their distribution (Benzing, 1987), thus supporting the first explanation noted above – that pedological variation occurs between the first four plots and plot p5. If a difference in the sylvigenetic cycle were present in plot p5, on the other hand, it would have influenced the epiphytic species composition.

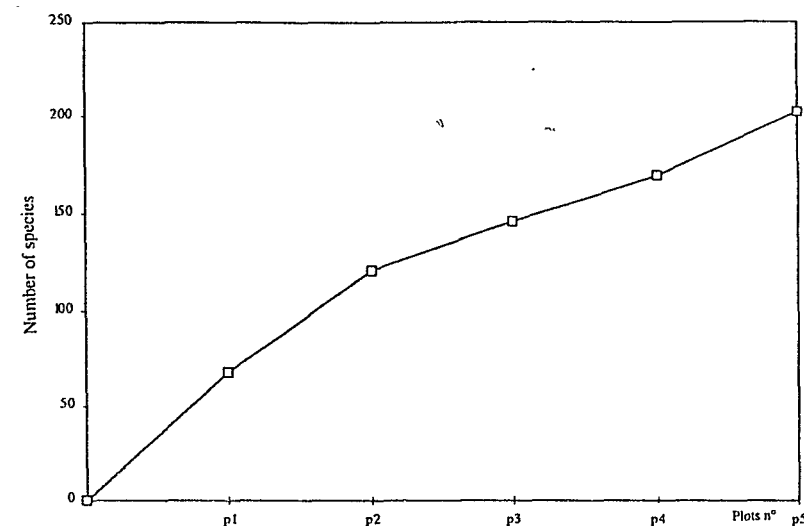


Figure 21.5 Cumulative species-area curve for all vascular-plant species in five plots (each 100 m² in size)

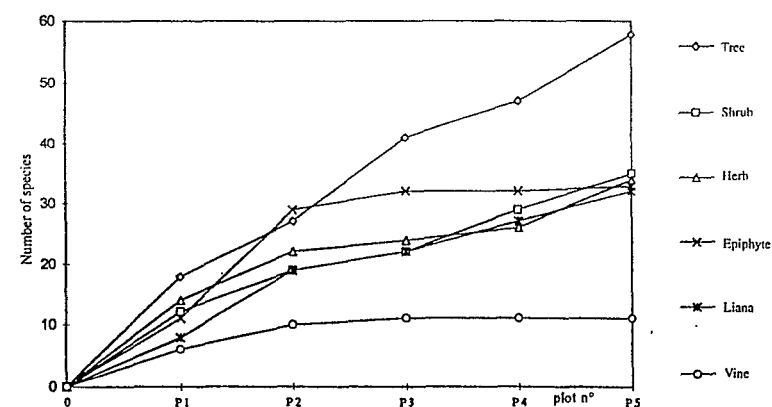


Figure 21.6 Cumulative species-area curves by life form in five plots (each 100 m² in size)

Figure 21.7 shows species area curves for the dominant families: Araceae, Arecaceae, Chrysobalanaceae, Leguminosae (Caesalpiniaceae, Fabaceae, and Mimosaceae), Lecythidaceae, Orchidaceae, Pteridophytes, and Sapotaceae. As for the life-form curves (Figure 21.6), the main herbaceous families (Araceae, Orchidaceae, and Fern) and palms showed a saturation of species encountered in the study area, although a slight progression occurred at plot p5 for Arecaceae

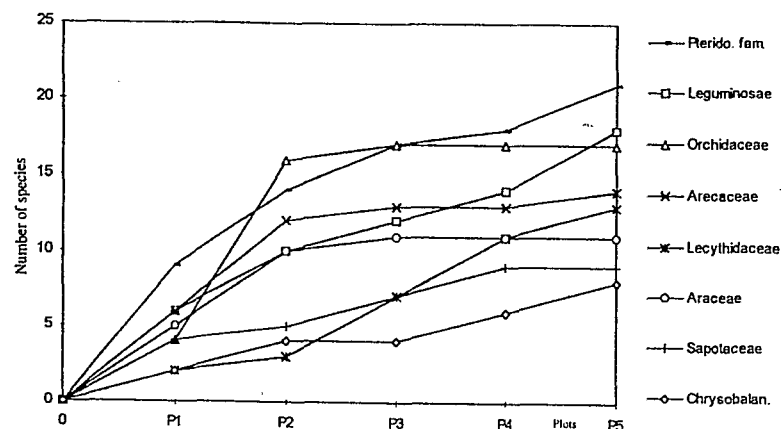


Figure 21.7 Cumulative species-area curves for main families in five plots (each 100 m² in size)

and Pteridophytes, again possibly because of pedological variation. Here, too, a greater uniformity of species of epiphytic families occurred compared with the main terrestrial families of plants (palms excepted).

Life-form species distribution at different sampling scales

The progression of species richness for each life form (Figure 21.5) and cumulative curves show the distribution of species by life forms (Figure 21.6) for the five plots studied. The sequence in which the plots were sampled, which determined their order in the species-area curves, affected the outcome. To eliminate this cause of variation, species-area curves were determined for four area steps – 25 m² (12 subplots), 50 m² (6 subplots), 100 m² (5 subplots), and 500 m² (1 subplot). For each area, the average number of species by life form was calculated. Figure 21.8 shows highly significant linear correlations between the species richness of each life form and increasing plot size within the limits of our plots. The slopes ranged from 0.1 for trees to 0.02 for vines, which may indicate different patterns of species-richness distribution for each life form in the sampled areas. The greater slope of the tree line and the fact that it crosses the line for shrubs and lianas may indicate a wider dispersion of arboreal species. At the largest plot size, tree species dominated species representing each of the other life forms. This is also true for data on the same types of forest throughout the Sinamary River basin. Nevertheless, at all scales, species richness was lower for trees than for an aggregate of all other life forms combined, showing the weight of small-size species in estimating plant species richness and their importance in measuring forest biodiversity.

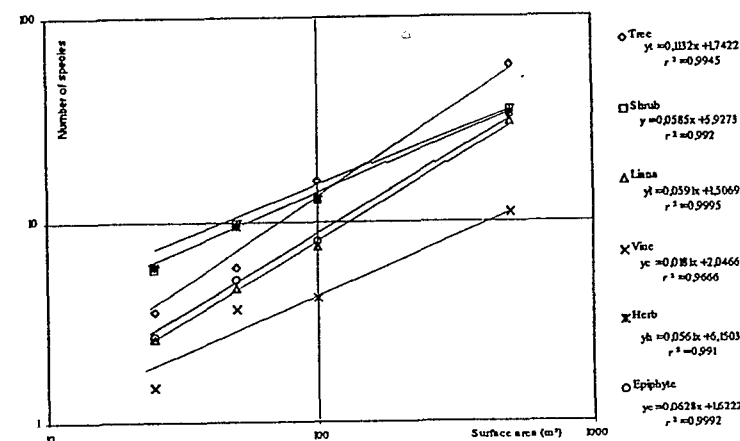


Figure 21.8 Number of species by life form and sampling-area size (25 m², 50 m², 100 m², and 500 m²)

Number of species by surface area

Figure 21.9 presents the number of species for differently sized areas (25 m², 50 m², 100 m², 200 m², and 500 m²). The number progresses in a highly significant linear fashion expressed by:

$$y = 0.3715x + 20.256 \text{ with } r^2 = 0.9943$$

where x = number of species, y = sampled surface, and r^2 = determination coefficient. Within the sampling limits, the number of species increased in proportion to the area of forest sampled. The slope of this line was an indicator of the distribution of species richness. Extended to larger areas, the data points would be expected to reach an asymptote corresponding to the total number of species present in the vegetation type – terra firme forest – present in the study area.

Species richness by diameter class

Species richness was analyzed for each of four diameter classes – < 2.5 cm dbh, ≥ 2.5 cm dbh but < 10 cm dbh, ≥ 10 cm dbh but < 25 cm dbh and ≥ 25 cm dbh. Among the 203 vascular plant species, 82 were ≥ 2.5 cm dbh, 43 were ≥ 10 cm dbh, and 16 were ≥ 25 cm dbh. In other words, only 8% of vascular plant diversity in the study plots was represented when sampling was limited to individuals ≥ 25 cm dbh. This proportion rose to 21% when stems at least 10 cm dbh were included. Cumulative species-area curves for these diameter classes are shown in Figure 21.10. For the smallest diameter class (< 2.5 cm dbh), more than 70% of the species richness found in the five study plots was present in the first two plots sampled. For herbaceous species (herbs, epiphytes,

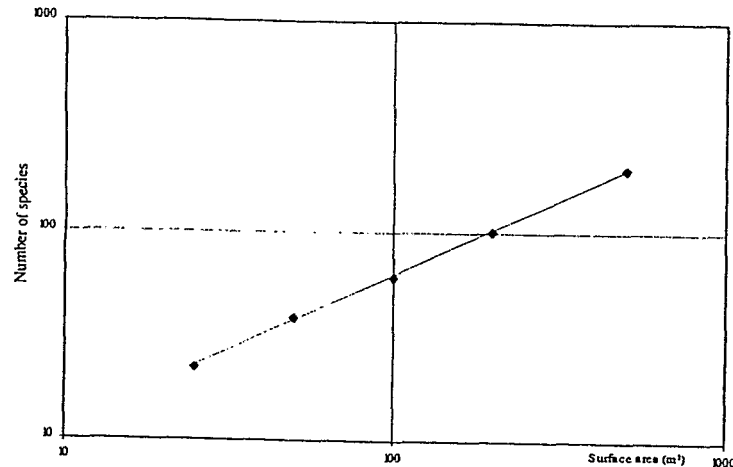


Figure 21.9 Species richness for different sample areas (25 m², 50 m², 100 m², and 200 m² and 500 m²); $r^2 = 0.9943$

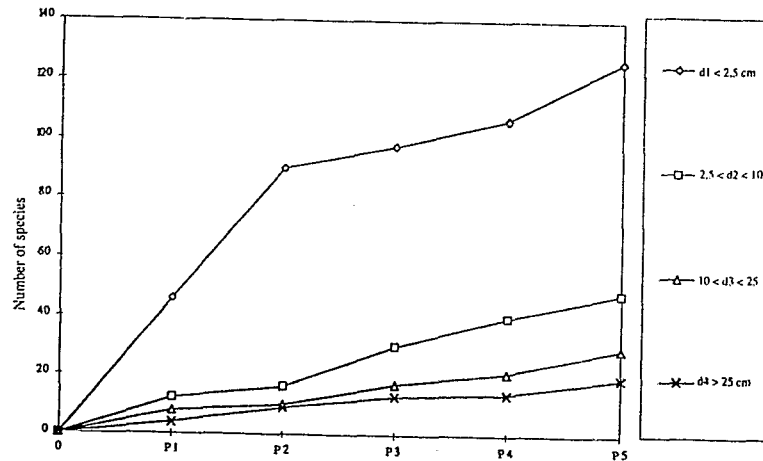


Figure 21.10 Cumulative species-area curve for dbh classes in five plots (each 100 m² in size)

and vines), 78% of those found in the entire 500-m² were sampled in the first 200 m². In contrast, the ratio of species in the first 200 m² to species in the entire 500 m² was only 30% for woody species (trees, shrubs, and lianas). Based on the shape of the cumulated species-area curves by diameter classes as well as those by life forms, it seems that the minimum representative sampling area in an homogenous terra firme vegetation type is only a few hundred m² for herbaceous life forms, whereas a much greater area is necessary for woody taxa.

CONCLUSION

Comparison of species distribution by life form at a regional scale (the Sinamary River basin) and at a single station shows that the relative proportions of herbs and shrubs are equivalent in both cases. Epiphytes, lianas, and vines are better represented at the smaller scale and in flooded forest than they are in well-drained *terra firme* forest. This difference is probably an artifact reflecting a more complete botanical exploration of flooded and riparian forest.

As noted by Prance (1994), vascular plant species richness in tropical rain forest appears to be very high at a local level. The results presented here on local-scale species richness point toward a high alpha diversity. Other plot studies of vascular plant species richness in neotropical rain forests (Gentry and Dodson, 1987; Duivenvoorden, 1994) suggest that the hypothetical minimum sampling area required for accurate assessment of local species richness is extremely large because of species-distribution heterogeneity patterns in different biotops. The size of plots used reveals patterns of heterogeneity at different scales. Small plots provide valuable information for small-size vascular plant species, especially vines and epiphytes. As noted by Korning *et al.*, (1991), quadrat-plot sampling methods fit better for identifying specific units of the forest, whereas transects with centered point-quarter methods seem preferable for a broad introduction to vegetation in an area. It would be interesting to adapt the point-quarter system for a comprehensive sampling of all vascular plant species and compare the results obtained with those from plots. In all cases, results from intermediary sampling steps should be maintained to determine the smallest floristic units and assess the heterogeneity scale. It also seems advisable to seek agreement on a system of simple, distinctive life-form definitions for tropical forest vascular plants in order to facilitate comparison of data sets.

The results obtained from the exhaustive sampling used in this work provide precise information on a very small area of a lowland tropical rain forest in French Guiana. They reveal a surprising diversity of species found at a remarkably small scale – hundreds of various species living together in an area the size of a back yard, a wealthy and wild natural botanical garden bearing witness to great speciation and rich with potential uses. Even greater levels of diversity are found when observations are extended to larger areas, leading to more than 1000 different taxa at the scale of a single river basin. This quantification of vascular plant species richness, analyzed through life forms, families, and diameter classes, makes it possible to characterize the structure of vascular-plant populations at the scale of delimited plots. Such an inventory may, however, only be achieved in regions where repeated botanical explorations at different times of the year have allowed the compilation of a precise reference flora, which is an essential precursor to any subsequent ecological studies.

At every scale – whether at a single site, within a given locality, or throughout a region – species-richness data covering all vascular plants are important to characterize and quantify forest biodiversity. Levels of endemism and scarceness

of each species, as indicated by botanical collections, are also essential information for conservation efforts.

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PREFACE

UNESCO's Man and the Biosphere Programme

Improving scientific understanding of natural and social processes relating to human interactions with the environment; providing information useful to decision-making on resource use; promoting the conservation of genetic diversity as an integral part of land management; enjoining the efforts of scientists, policy-makers, and local people in problem-solving ventures; mobilizing resources for field activities; strengthening of regional cooperative frameworks – these are some of the generic characteristics of UNESCO's Man and the Biosphere (MAB) Programme.

The MAB Programme was launched in the early 1970s. It is a nationally based, international programme of research, training, demonstration, and information diffusion. The overall aim is to contribute to efforts for providing the scientific basis and trained personnel needed to deal with problems of rational utilization and conservation of resources and resource systems and problems of human settlements. MAB emphasizes research for solving problems. It thus involves research by interdisciplinary teams on the interactions among ecological and social systems, field training, and application of a systems approach to understanding the relationships among the natural and human components of development and environmental management.

MAB is a decentralized programme with field projects and training activities in all regions of the world. These are carried out by scientists and technicians from universities, academies of sciences, national research laboratories, and other research and development institutions under the auspices of more than one hundred MAB National Committees. Activities are undertaken in co-operation with a range of international governmental and non-governmental organizations.

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The Man and the Biosphere Book Series was launched to communicate some