TREE DIVERSITY ON SMALL PLOTS IN MADAGASCAR :
A PRELIMINARY REVIEW

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INTRODUCTION

Madagascar is an island larger than France (590 000 km^2) stretching from 11° 57' to 25° 32' south latitude (Koechlin, 1972). While still part of East Gondwanaland (which was composed primarily of India, Australia and Antarctica), Madagascar split off from Africa between 160 and 130 million years ago (Storey, 1995), before toads (Bufonidae) reached the shores of the Indian Ocean 130 million years ago (Blommers-Schlösser & Blanc, 1993). By 110 million years ago, Australia and Antarctica were quite separate from Madagascar and India (Lawver *et al.,* 1992). India finally split off from Madagascar and began its voyage to Asia about 85 million years ago (Storey *et al.,* 1995). Madagascar has a continental diversity of habitats : « spiny forest » resembling the vegetation of southern Arizona's Sonoran desert in the southwest, rain forest on the eastern slopes, which extends to a strip of the northwest coast, deciduous dry forest along much of the west coast, and the endless rolling grasslands and savannas in the center of the island (Humbert & Cours-Darne, 1965 ; Koechlin, 1972 ; Koechlin *et al.,* 1974). As some genera have done in Hawaii (Carlquist, 1980), genera such as *Diospyros* and *Terminalia* have radiated into all the major types of natural forest and bush in Madagascar, suggesting that Madagascar was a quasi-independent experiment in plant evolution. This view is supported by the high proportion of endemics — 94 % among Madagascar's trees and shrubs (Koechlin, 1972, p. 156).

Is Madagascar small enough to limit the diversification and evolution of its plants ? On small, isolated islands such as Mauritius or Réunion, which, to be sure, are much younger (Réunion was formed by volcanic activity only three million

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years ago, while Mauritius is 7.8 million years old : Strasberg, 1995 ; Lorence & Sussman, 1988) forest diversity is much lower than in continental settings with similar climates (Vaughan & Wiehe, 1941). Moreover, on these small islands, mature forest is very susceptible to invasion by alien plants such as Chinese guava, *Psidium cattleyanum* and lantana, *Lantana camara* (Lorence & Sussman, 1988 ; Macdonald *et al.,* 1991). On the other hand, New Guinea, whose area of 808 000 km^2 is a third larger than Madagascar's, has evolved rain forest far more diverse than Africa's (Paijmans, 1970). Where does Madagascar fit on this scale ? To answer, we compare small forest plots in Madagascar with those elsewhere in the tropics.

At this point, custom would have us urge that much of Madagascar's forest has been destroyed, and that an expanding, and very impoverished, population is pressing hard on Madagascar's remaining forests. Thus it is important to describe what is left of Malagasy nature, in the hope that greater knowledge will create greater interest in conservation and provide some of the data needed to plan it. If this hope proves vain, it is all the more urgent to document for future generations, while we still can, the outcome of the magnificent natural experiment in evolution which occurred in Madagascar. All this is true (Humbert, 1927 ; Phillipson, 1994). Nonetheless, these sentiments have been so widely communicated that it appears necessary to assure our readers that Madagascar still has magnificent natural forests, and that natural forests with abundant and diverse populations of primates and other mammals are far easier to reach in Madagascar than in many Latin American countries, where populations of forest mammals are hunted out long before the woodcutters arrive (Smythe, 1978).

To compare diversity on plots of different sizes, we shall use the rule, discovered by Condit *et al.* (1996), that $S(N)$, the number of species on a nearly square plot containing N stems, is nearly independent of the minimum diameter of the stems sampled, provided that stems of this minimum diameter are *understorey,* not canopy trees. This assumption has been verified for 50-hectare plots in three very different types of forest (Condit *et al.,* 1996). On a 50-hectare plot of lowland monsoon forest on Barro Colorado Island, Panamá, a sample of about 170 stems yields 50 to 55 species, while a sample of about 4 000 stems yields 160 to 180 species, whether the stems sampled are stems ⩾ 1 cm dbh (diameter at breast height, 1.3 m above the ground) or stems ⩾ 20 cm dbh (Table I). In lowland dipterocarp forest of the Pasoh Reserve, Malaysia, and in deciduous dry forest at Mudumalai, in south India, the number of species in a plot also depends far more on the number of stems sampled than on their minimum diameter (Table I). A rule which applies to trees in such different forests may be trustworthy : we shall check it, and use it to compare a variety of studies.

The new data reported in this paper include :

1) a census of stems ⩾ 30 cm gbh (girth, or circumference, at breast height, ≈ 9.5 cm dbh) in a hectare of dry forest at Kirindy (CFPF), 50 km N of Morondava in western Madagascar (Fig. 1),

2) a census of stems ⩾ 5 cm dbh on a 70 × 100 m plot of plateau forest at 1 550 m. This plot is in the Réserve Spéciale Botanique d'Ambohitantely, 8 km east of the highway leading north from Antananarivo to Mahajanga, on the Tampoketsa (high plateau) of Ankazobe, near the Station Forestière de Manankazo (Fig. 1).

TABLE I

Number of species (S) in a sample of a given number of trees (N) for different lower size limits.

Stems included	Plot Size	N	S	Plot Size	N	S
Barro Colorado Island, Panamá						
≥ 1 cm dbh	100 × 100 m	4 881	172	20 × 20 m	195	54
≥ 5 cm dbh	200 × 200 m	4 089	184	40 × 40 m	164	58
≥ 10 cm dbh	250 × 250 m	2 670	163			
≥ 20 cm dbh	500 × 500 m	3 878	163	100 × 100 m	155	54
≥ 30 cm dbh	1 000 × 500 m	4 120	146	150 × 150 m	185	54
Pasoh Reserve, Malaysia						
≥ 1 cm dbh	100 × 100 m	6 702	495	20 × 20 m	268	127
≥ 5 cm dbh	200 × 200 m	5 270	498	40 × 40 m	211	123
≥ 10 cm dbh	250 × 250 m	3 306	441			
≥ 20 cm dbh	500 × 500 m	4 203	442	150 × 150 m	378	151
≥ 30 cm dbh	1 000 × 500 m	3 770	377	200 × 200 m	302	113
Mudumalai, south India						
≥ 1 cm dbh	200 × 200 m	2 056	44	100 × 100 m	514	22
≥ 5 cm dbh	250 × 250 m	2 577	46			
≥ 10 cm dbh	250 × 250 m	1 880	44	150 × 150 m	677	32
≥ 20 cm dbh	500 × 500 m	2 440	47	250 × 250 m	610	31
≥ 30 cm dbh	1 000 × 500 m	2 685	45			

Note : Data from Condit *et al.* (1996).

3) a census of stems ≥ 5 cm dbh on an 0.51 ha plot of montane forest at 1 000 m in the Réserve de Faune de Périnet-Analamazaotra, east of the road leading north to Andasibé (Périnet) from km 137 of the highway from Antananarivo to Madagascar's east coast (Fig. 1).

STUDY AREAS

KIRINDY (CFPF)

The forest of Kirindy (CFPF) (20° 3' S, 44° 39' E) is 50 km N of Morondava along the highway to Belo-sur-Tsiribihina, on its east side. This 10 000 ha tract is an experimental forest, managed by the Centre de Formation Professionnelle Forestière de Morondava as a model for sustainable forest exploitation (Covi, 1988 ; Ganzhorn & Sorg 1996).

Morondava receives 700-800 mm of rain a year. Rainy season begins in November or December, and ends in March or April. The dry season lasts 6 to 8 months, and during this period, the total rainfall is 20-30 mm (Covi, 1988). The wettest month is January, which averages 221 mm (Table II). Average annual temperature is 21 °C, and the average diurnal temperature range is 10 °C. In January, the warmest month, the average temperature is 27.7 °C, and the average
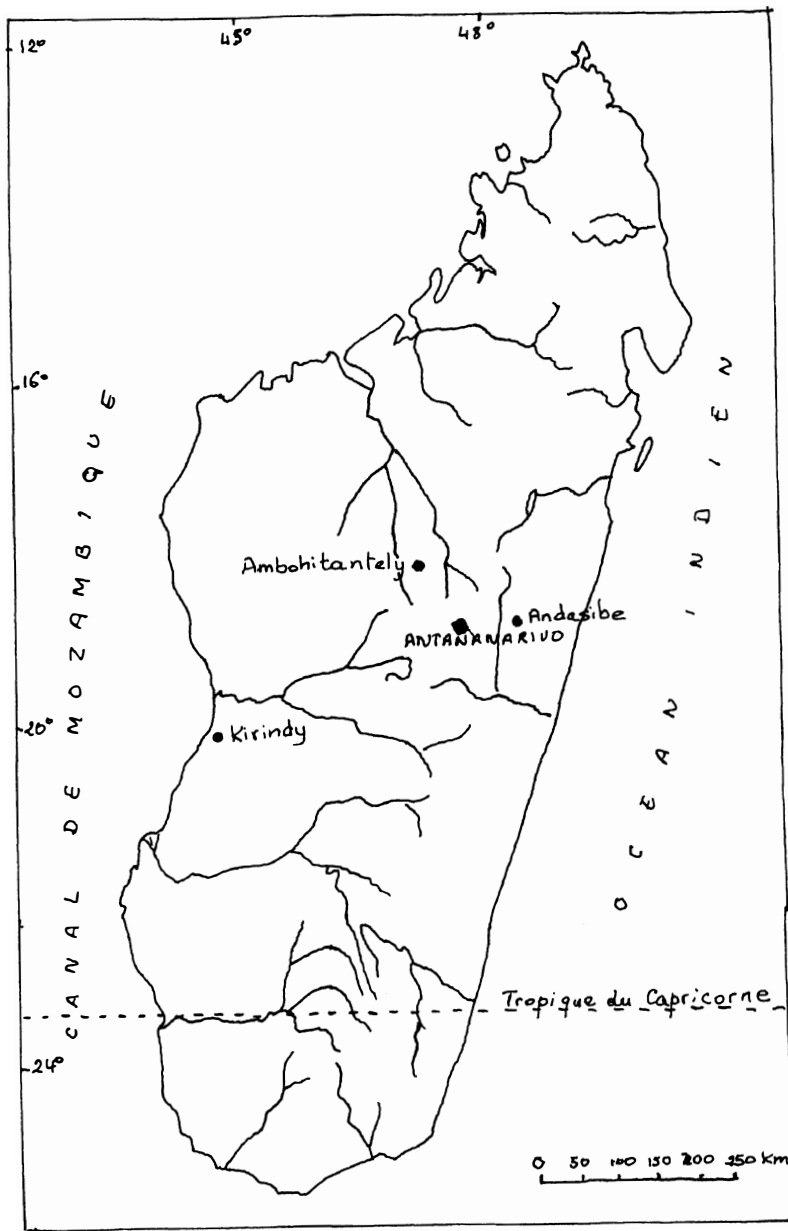
Figure 1. — Location in Madagascar of the three sample plots.

diurnal temperature range is 8.1 °C, while in July, the coolest month, the average temperature is 21 °C and the average diurnal temperature range is 13 °C.

TABLE II

Climate at selected study sites.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total/Av.
						Morondava							
Rain (mm)	221	198	86	13	8	8	3	3	8	10	18	135	711
Ave T	28	28	28	27	24	22	21	22	24	26	27	28	25.3
Ave ΔT	9	9	9	11	12	13	13	13	12	10	10	9	10.6
					Tsaramandroso (Ankarafantsika)								
Rain (mm)	407	333	277	63	8	4	3	2	5	25	131	250	1 507
Ave T	27	28	28	28	27	25	25	25	27	28	29	28	27.0
Ave ΔT	11	11	11	12	13	14	14	15	15	16	14	12	13.1
					Ambohitantely (Manankazo)								
Rain (mm)	391	299	323	70	10	8	14	10	11	48	220	409	1 820
Ave T	20	20	19	18	16	14	13	14	16	18	19	20	17.3
Ave ΔT	10	10	10	11	11	11	11	12	14	15	13	10	11.6
# days fog	4	7	5	8	2	10	7	9	7	11	2	1	73
						Analamazaotra							
Rain (mm)	306	320	262	92	61	77	78	67	51	44	112	238	1 708
Ave T	22	22	21	20	18	16	15	16	17	18	21	22	19.0
Ave ΔT	10	11	9	10	10	10	10	10	11	12	12	11	10.4

Note : Average monthly rainfall, mm, average temperature, and average diurnal temperature range ΔT, °C, for each month and (for Manankazo, near Ambohitantely) average number of days of fog each month. Data for Morondava from Lebedev (1970), for Tsaramandroso from Andriatsarafara (1988), for Manakazo from Rakotondrainibe (1985) ; for Analamazaotra from Bailly *et al.* (1974).

The 8 × 12 km forestry concession is divided into six rows of 12 compartments each : the rows are oriented roughly WNW-ESE. The sample plot, which was intended to be 100 × 100 m, was in an unlogged portion of compartment N5 (shown in Fig. 2 of Covi, 1988) : this plot is 5 km from the highway along the concession's northern edge.

Compartment N5 of Kirindy forest has three nectarivorous bird species, four species of frugivorous bird (Langrand, 1990), and eight species of lemurs (Ganzhorn, 1992, 1995) : this forest appears to have an adequate array of vertebrate pollinators and seed dispersers (Baum, 1995).

AMBOHITANTELY

The forest of Ambohitantely (18° 10' S, 47° 17' E) is on the eastern flank of the Tampoketsa d'Ankazobe. This 1 600 ha tract is one of the largest fragments left of a forest which once covered over a quarter of Madagascar. Most of this forest has been replaced by a sterile grassland which burns every year (Bastian, 1964) : this grassland is an empty country of rolling hills and ridges. Near Ambohitantely, small fragments of forest are scattered through this grassland, in valley bottoms and on some slopes.
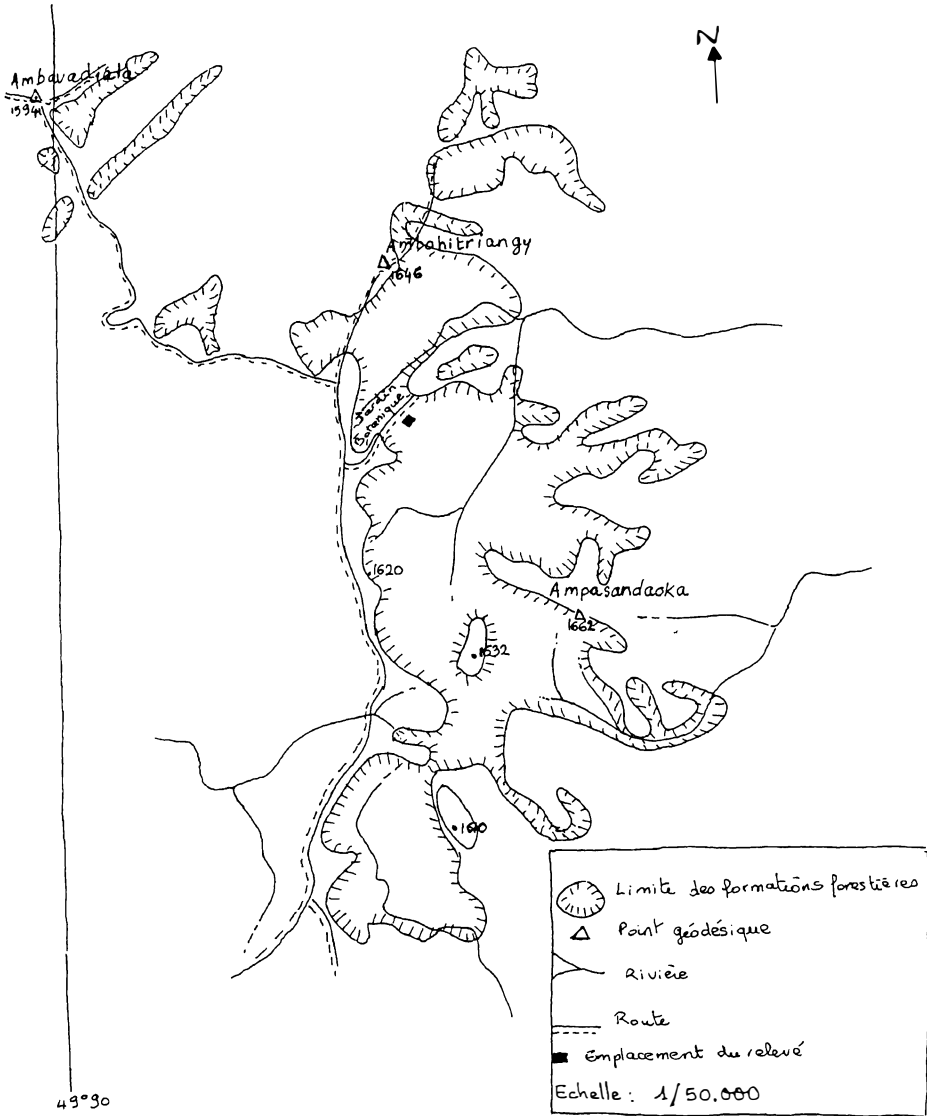
Figure 2. — Location within the Forêt d'Ambohitantely of our sample plot.

On this plateau, bedrock is a thick layer of « migmatite granitoïde ». Soils are deeply weathered : « les horizons inférieurs sont constitués de sols ferralitiques de couleur rouge, plus ou moins jaunes dans leurs parties supérieures, surmontés d'un horizon humifère noirâtre de 2 à 40 cm, relativement riche » (Rakotondrainibé, 1985).

The nearby Station Forestière de Manankazo averages 1 820 mm of rain per year, of which 1 644 mm falls from November through March, and 53 mm from May through September (Table II). Fog is rather frequent from June through October. Forests extract water from fog which rain gauges never register (Cavelier & Goldstein, 1989). Even at the height of the dry season, the soil and litter on our forest plot were often damp.

A small road, which crosses the forest at its narrowest point, separates our plot from the Swiss-run Jardin Botanique (Fig. 2). The Jardin Botanique slopes down from the road to a deeply incised stream and extends some way up the other side. Our 70 × 100 m plot (Fig. 3) is a few hundred paces beyond the other side of the road, on a surface at about 1 550 m, which begins to slope downhill, very gently but progressively, away from that road. The forest has a fairly even canopy of small-crowned trees roughly 12 m tall, many of which have coriaceous leaves held inclined or upright in dense tufts on orthotropic twigs, a leaf arrangement characteristic of tropical montane cloud forests the world around (Leigh, 1990).

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70   69   68   67   66   65   64   63   62   61

51   52   53   54   55   56   57   58   59   60
          ↘
            ↘
50   49   48↘  47   46   45   44   43   42   41
              ↘
              ↓
31   32   33 ↓ 34   35   36   37   38   39   40
              ↓
               ↘
30   29   28  ↘27   26   25   24   23   22   21
                ↘
                  ↘
11   12   13   14↘  15   16   17   18   19   20
                   ↘
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10    9    8    7    6 ↘  5    4    3    2    1
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Path to the road and the Jardin Botanique
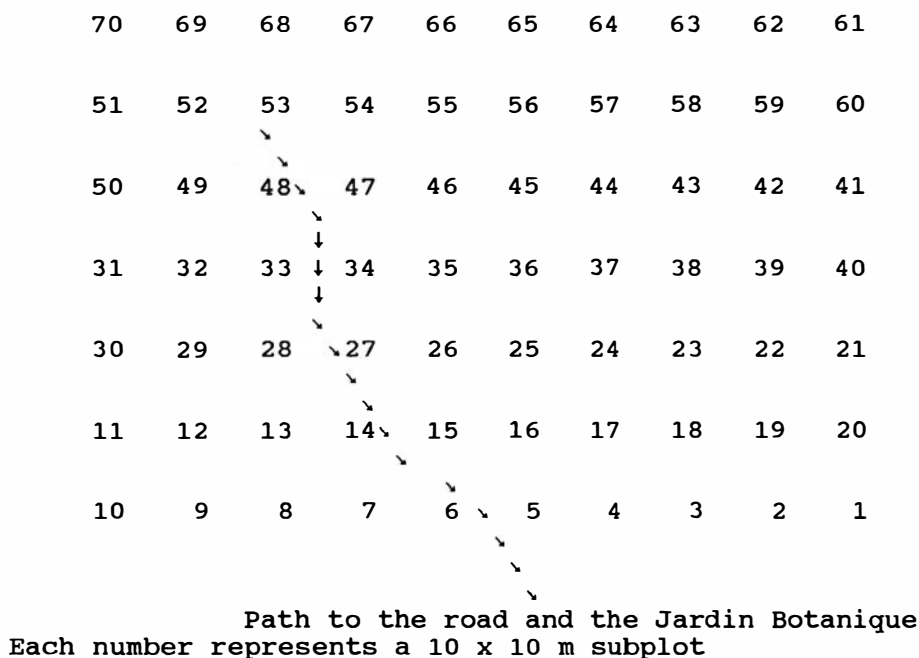**Each number represents a 10 x 10 m subplot**

Figure 3. — Shape of plot and arrangement of 10 × 10 m subplots at Ambohitantely.

Where this road emerges from the forest, one sees a rolling grassland with some massive pink « lavakas » (erosion gullies) in the distance. A path drops downhill, and winds away out of sight among these grassy hills. Very rarely, one can see a small group of people walking along this path, bringing zebus or other produce to market from who knows how far away.

At Ambohitantely, two species of lemur (Nicoll & Langrand, 1989), two species of nectarivorous bird, and four species of primarily frugivorous birds (Langrand, 1990), could presumably serve as pollinators and seed dispersers.

ANALAMAZAOTRA

The réserve de faune d'Analamazaotra (18° 28' S, 48° 28' E) is an 810 hectare tract whose entrance is 25 minutes walk from the railway station at Andasibé along the road to km 137 of the main highway from Antananarivo to the east coast. Analamazaotra is not far west of the brow of the scarp or « falaise de Betsimisaraka » (Bailly *et al.,* 1974), the lower of the two scarps one must descend to reach the east coast from Antananarivo.

More of the natural vegetation has survived in the mountain country between Madagascar's central plateau and the foothills and coastal plain behind its eastern shore, than in most other areas of Madagascar. Analamazaotra is one of a series of parks and reserves, such as the Montagne d'Ambre, Marojejy, Mantadia, Ranoma-fana and Andohahela, instituted to protect this forest.

Analamazaotra receives 1 708 mm of rain a year. This rainfall is more evenly distributed than Ambohitantely's : from November through March, Analamazaotra averages 1 238 mm, while from May through October it averages 378 mm. The driest month is October, which averages 44 mm (Bailly *et al.,* 1974). Despite the seasonal rhythm in rainfall, this forest is essentially everwet, thanks to the cool weather that prevails during its dry season.

Near our study area, bedrock is a gneiss with muscovite, biotite, amphibolite and pyroxene patchily and inhomogeneously distributed through it, so that analyses of soil at nearby sites yield clearly different results (Bailly *et al.,* 1974). Under natural forest near our plot, a litter layer, 5 to 7 cm thick, lies atop a dense root mat 1-2 cm thick. The soil is acid, and poor in phosphate. Mineralization of organic matter is slow, so that the C/N ratio in the upper 20 cm of the soil is high (17 to 18), and the soil's organic matter content is also high — 10 % in the top 5 cm of soil, and 6.5 % at 10-20 cm (Bailly *et al.,* 1974).

Our plot is atop a ridge which is 10 minutes' walk along the drive leading from the reserve's main entrance toward Lac Vert, nestled between the main tourist path and a pisciculture at the base of the ridge (Fig. 4). The ridge bearing our plot separates the pisciculture and its valley from the « bassin versant d'Ampangalatsary », where Bailly *et al.* (1974) measured rainfall and runoff for eight years. A good path leads from the entrance drive up the ridge, which borders the drive on the right, and continues along its level, flat crest. Our plot includes a 40 × 40 m block adjoining a 60 × 60 m block (Fig. 4) : one side of the 60 × 60 m block runs parallel to the ridgetop trail, 3 m into the forest, and another runs roughly parallel to the cross trail, about 10 m from it. The portion of the 60 × 60 m block furthest from the ridgecrest trail sloped gently downhill toward the pisciculture valley. The 10 × 10 m corner square of the 40 × 40 m block facing the entrance drive and the pisciculture, where the grown dropped off sharply toward the valley, was omitted.

The forest here is 20 to 30 m tall, and its canopy is irregular. It was selectively logged in the 1920's (Bailly *et al.,* 1974), and a few trees may have been poached since. The reserve was declared to protect the babakoto, *Indri indri,* Madagascar's largest living lemur, which is quite abundant in the forest of Analamazaotra. The

ridgecrest trail is used by many tourist and Malagasy student groups : indeed, this reserve is the most accessible site in all Madagascar for seeing lemurs in the rain forest. Analamazaotra has three species of nectarivorous birds, seven species of primarily frugivorous birds (Langrand, 1990), and eleven species of lemur, seven of which are reasonably common (Ganzhorn 1988) : this forest, like Kirindy, probably has an adequate array of vertebrate pollinators and seed dispersers.

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  Path to
Pisciculture

    ↑    45  46  47  48  49  50
    ↑
    ↑    40  41  42  43  44  51
    ↑                                      ⤴ Cliff
    ↑    39  35  31  27  23  22  21  20  19  ⤴
    ↑                                          ⤴
    ↑    38  34  30  26  18  13  12  11  10   9
    ↑
    ↑    37  33  29  25  17  14   7   6   1   2
    ↑
    ↑    36  32  28  24  16  15   8   5   4   3
→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→  →→ Path to Entrance
                                                                Drive
        Each number represents a 10 x 10 m plot
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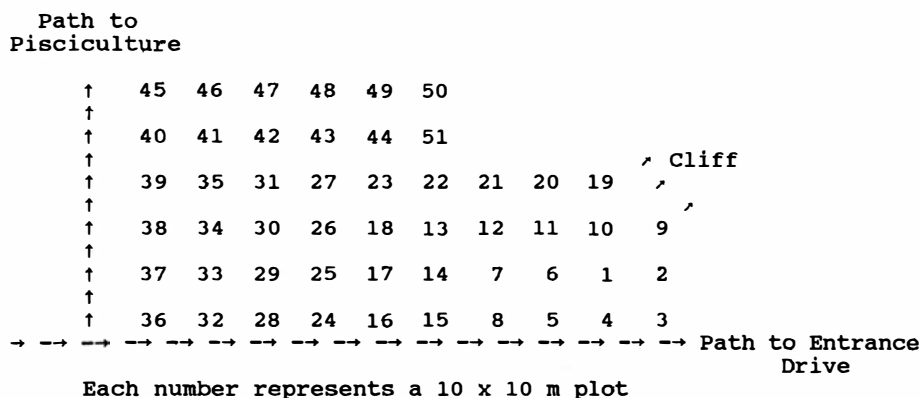
Figure 4. — Site and shape of plot and arrangement of 10 × 10 m subplots at Analamazaotra.

METHODS

COLLECTING THE DATA

We measured off successive 10 × 10 m plots using a steel tape measure, and judging right angles by eye. We demarcated their boundaries with string tied to stakes or to the bases of conveniently located saplings : this string was removed for reuse when the comptage was completed. These plots were not surveyed, for lack of time or the appropriate equipment, and their areas are only approximate. A more exact remeasurement of the Kirindy « hectare » showed that its area was 0.93 ha.

In each 10 × 10 m plot, all stems ≥ 5 cm in diameter at breast height (dbh, diameter 1.3 m above ground), including iianas, were marked by numbered aluminum tags (ALTAG, Forestry Supply Co.) tied to their trunks with string. Marked stems were identified, and their diameters measured, either with diameter calipers (averaging two diameters taken at right angles if the stem was not circular) or by dividing the measured circumference by π. Trees at Kirindy and Analamazaotra were identified on the spot by Jean-Prosper Abraham : in a few cases, he removed a sprig of foliage to verify his identification at leisure. Trees at Ambohitantely were identified by Mady Randrianasolo and Rakotonirina Benja.

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Measuring diversity

Our primary measure of diversity is the number of species S as a function of the number N of stems sampled.

We also measure diversity by Fisher's α (Fisher *et al.*, 1943), whose value is usually relatively independent of sample size. This index was originally designed to measure the diversity of insects caught at light traps. The distribution of abundance of insect species sampled at a light trap, like that of tree species on small plots, often follows the log series distribution whereby there is a positive constant α and another constant x, $0 < x < 1$, such that the number $p(m)$ of species represented by m individuals apiece is $p(m) = \alpha x^m / m$ (Fisher *et al.*, 1943 ; Williams, 1964 ; Foster & Hubbell, 1990) : α is assumed to be a measure of diversity independent of sample size, while x increases toward 1 as sample size increases.

This distribution applies for a « null model » where all species are alike to natural selection, that is to say, a tree's fate is not influenced by what species it belongs to (Watterson, 1974 ; Hubbell, 1979). More specifically, the log series distribution applies both to the trees on a large isolated plot, and to any sufficiently large subsample of these trees, if

i. each tree alive at the beginning of year t has the same probability, independent of the fate of its fellows, of dying before year $t + 1$,

ii. each dead tree is immediately replaced, and

iii. a dead tree's replacement has probability v of being a truly new species, and probability $(1 - v) p_j$ of belonging to species j, where p_j is the proportion of the trees on the plot just before the death of the tree to be replaced, which belong to species j (Watterson, 1974).

When the log series distribution applies, the number N of stems on a plot and the number S of species included among them are related to α and x as follows :

$$N = \sum_{m=1} mp(m) = \frac{\alpha x}{1 - x} \tag{1}$$

$$S = \sum_{m=1} p(m) = \alpha \ln \frac{1}{1 - x} = \alpha \ln \left(1 + \frac{N}{\alpha} \right) \tag{2}$$

By solving the equation $S = \alpha \ln(1 + N/\alpha)$ numerically, one can calculate α for given N and S. Even when the log series does not apply, however, Fisher's α is a useful measure of diversity.

It is well known that there is no « minimal area » that guarantees representation of all species in a habitat type : the number S of species found generally increases at least as rapidly as log N, where N is the number of stems in the sample plot. Still, we shall use our data to ask whether small areas suffice for comparing stem diversities among different sites. A different minimal area applies to the study of biological processes affecting the distribution of species abundance. Where the

log series applies, the sample is so small that the distribution of species abundances is ruled purely by chance. If the number of species represented by a single individual apiece is not significantly below that predicted by the log series, one has not sampled enough stems to make inferences about biological processes affecting the relative abundance of species.

Comparing diversity

We tabulate N, S and α for stems of different lower diameter limit on subplots of different sizes, to assess the applicability of the log series, to learn how α depends on the number, and the minimum size, of stems sampled, and to learn how sensitive the number of species S found among a fixed number N of stems depends on the minimum size of these stems and the shape of the sample plot containing them. N, S and α will be tabulated with and without lianas.

RESULTS

INVENTORIES

The Kirindy « hectare » (Tab. III) contained 778 stems $\geqslant$ 30 cm gbh, among which were 45 species representing at least 23 families : here, Fisher's $\alpha = 10.4$. The 70×100 m plot at Ambohitantely contained 948 stems $\geqslant$ 10 cm dbh, among which were 73 species from 42 families : here, Fisher's $\alpha = 18.4$. The 0.51 ha plot at Analamazaotra contained 540 stems $\geqslant$ 10 cm dbh, among which were 126 species from 39 families : here, Fisher's $\alpha = 51.7$. If we exclude the one liana $\geqslant$ 10 cm dbh, $\alpha = 51.1$.

TABLE III

Number of species (S) and number (N) of trees in different plots, by family.

	Kirindy		Ahitantely		Périnet	
	S	N	S	N	S	N
Lauraceae	0	0	5	32	13	94
Guttiferae	0	0	5	56	10	45
Rubiaceae	5	65	3	14	10	31
Myrtaceae (*Eugenia*)	0	0	4	34	8	27
Euphorbiaceae	3	376	2	210	8	71
Flacourtiaceae	2	9	2	10	6	11
Anacardiaceae	2	14	5	154	5	23
Sapindaceae	1	2	2	4	5	29
Sapotaceae	1	1	0	0	5	14
Leguminosae	7	31	1	1	4	23
Papilionoideae	2	3	1	1	2	12
Mimosoideae	0	0	0	0	2	11

	Kirindy		Ahitantely		Périnet	
	S	N	S	N	S	N
Caesalpinoideae	5	28	0	0	0	0
Melastomaceae	1	1	1	3	4	4
Annonaceae	0	0	2	6	3	24
Moraceae	1	1	1	1	3	23
Erythroxylaceae (*Erythroxylum*)	1	1	1	4	3	22
Monimiaceae (*Tambourissa*)	0	0	2	5	3	14
Sterculiaceae	1	1	1	12	3	4
Oleaceae	0	0	2	14	2	9
Araliaceae	0	0	3	36	2	6
Burseraceae	1	12	1	6	2	6
Compositae	1	4	1	1	2	6
Hypericaceae	0	0	0	0	2	4
Meliaceae	4	107	2	2	2	2
Cunoniaceae	0	0	1	36	2	2
Icacinaceae	0	0	1	2	2	2
Apocynaceae	0	0	1	2	2	2
Pittosporaceae (*Pittosporum*)	0	0	1	6	1	8
Verbenaceae	0	0	3	12	1	4
Proteaceae	0	0	2	2	1	4
Loganiaceae	2	70	1	8	1	4
Olacaceae (*Olax*)	0	0	1	3	1	4
Tiliaceae (*Grewia*)	3	26	1	4	1	3
Rutaceae	1	2	1	32	1	2
Ebenaceae (*Diospyros*)	1	3	1	5	1	1
Ochnaceae (*Campylospermum*)	0	0	0	0	1	1
Lecithidaceae (*Foetidia*)	0	0	0	0	1	1
Elaeocarpaceae (*Elaeocarpus*)	0	0	0	0	1	1
Aquifoliaceae (*Ilex*)	0	0	0	0	1	1
Sarcolaenaceae	0	0	2	90	0	0
Ericaceae	0	0	2	32	0	0
Canellaceae (*Cinnamosma*)	0	0	1	16	0	0
Rhizophoraceae (*Cassipourea*)	0	0	1	8	0	0
Celastraceae	1	3	1	7	0	0
Bignoniaceae	2	37	1	1	0	0
Myrsinaceae (*Monoporus*)	0	0	1	1	0	0
Bombacaceae (*Adansonia*)	1	5	0	0	0	0
Linaceae (*Hugonia*)	1	4	0	0	0	0
Combretaceae (*Terminalia*)	1	1	0	0	0	0
Unidentified (Trontsifaka)	1	2	—	—	—	—
Podocarpaceae (*Podocarpus*)	0	0	1	26	0	0
Strelitziaceae (*Ravenala*)	0	0	0	0	1	1
Palmae (*Chrysalidocarpus*)	0	0	0	1	0	0
Liliaceae (*Dracaena*)	0	0	1	4	1	4
Pandanaceae (*Pandanus*)	0	0	1	34	0	0
Totals	45	778	73	948	125	539

Note : Number of species, and number of individuals, ⩾ 10 cm dbh, family by family, in an 0.93 ha plot at Kirindy (CFPF), Ambohitantely (Ahitantely) and Analamazaotra (Périnet).

The Ambohitantely plot contained 2 808 stems ⩾ 5 cm dbh, including 102 species from 44 families : none of these were lianas. Here, Fisher's α = 20.75. The Analamazaotra plot contained 1 423 stems ⩾ 5 cm dbh,

representing 189 species of 50 families : here, Fisher's α = 58.5. Thirty-nine of these stems, including 12 species, were lianas : if we exclude these, this plot had 1 384 free-standing stems including 177 species, and Fisher's α = 53.9.

In all these plots, the most common tree $\geqslant$ 10 cm dbh was of the family Euphorbiaceae. At Kirindy, 365 of the 778 trees $\geqslant$ 30 cm gbh were *Securinega seyrigii* ; at Ambohitantely, 207 of the 948 trees $\geqslant$ 10 cm dbh were *Uapaca densifolia,* and at Analamazaotra, 39 of the 539 trees $\geqslant$ 10 cm dbh were *Blotia madagascariensis.* At Ambohitantely and Analamazaotra, moreover, the commonest species $\geqslant$ 5 cm dbh were Euphorbiaceae. At Ambohitantely, 360 of the 2 808 stems $\geqslant$ 5 cm dbh were *Uapaca densifolia,* while at Analamazaotra, the two commonest species $\geqslant$ 5 cm dbh were *Suregada laurina,* with 112 stems, and *Blotia madagascariensis,* with 85 stems.

In other respects, the species composition of the three plots differed markedly. Lauraceae, Guttiferae and Myrtaceae (*Eugenia*), three of the most speciose families at Ambohitantely and Analamazaotra, are entirely absent from the Kirindy hectare, while caesalpinoid legumes, which are diverse and conspicuous at Kirindy, are not represented on our plots at Ambohitantely and Analamazaotra (Table III).

ASSESSING DIVERSITY

If lianas are excluded, a sample of about 100 stems at Analamazaotra yields roughly the same value of Fisher's α whether the sample be of stems $\geqslant$ 5 cm dbh on 20 × 20 m subplots, stems $\geqslant$ 10 cm dbh on 30 × 30 m subplots, or trees $\geqslant$ 20 cm dbh on the whole plot (Table IV). Similarly, a sample of 400 to 500 stems at Analamazaotra yields roughly the same value of Fisher's α whether the sample be of stems $\geqslant$ 5 cm dbh on 40 × 40 m subplots, or of all stems $\geqslant$ 10 cm dbh on the Analamazaotra plot (Table V). Including lianas causes Fisher's α to decrease with increase in the minimum diameter of stems sampled.

TABLE IV

Diversity among samples of ca 100 stems at Analamazaotra.

Dbh & Plot Size	$\geqslant$ 5 cm, 20 × 20 m					$\geqslant$ 10 cm, 30 × 30 m					$\geqslant$ 20 cm
Nuclear Plot #	50	45	36	15	4	50	45	36	15	4	Average
					Including lianas						
N	103	83	96	116	115	103	94	80	95	93	110
S	59	49	55	54	55	52	48	48	51	48	55
α	57	50	54	39	41	39	42	51	45	40	43.8
Average α			48.4					43.3			43.8
					Excluding lianas						
N	102	80	94	113	111	103	94	80	94	93	110
S	58	46	53	52	53	52	48	48	50	48	55
α	56	45	50	37	40	39	42	51	43	40	43.8
Average α			45.7					43.0			43.8

Similarly, at Kirindy, a sample of 180 stems yields about the same value of Fisher's α whether they be the stems over 50 cm gbh on the whole hectare, or stems ⩾ 30 cm gbh on 50 × 50 m subplots (Table VI). At Ambohitantely, however, 44 of the 134 trees ⩾ 20 cm dbh are *Uapaca densifolia,* and 34 are *Sarcolaena multiflora :* there are only 25 species among the 134 trees ⩾ 20 cm dbh, giving a Fisher's α of 9.1.

TABLE V

Diversity of stems of various sizes at Analamazaotra.

	Totals		Stems ⩾ 5 cm, 40 × 40 m subplots	
	⩾ 5 cm	⩾ 10 cm,	Nuclear plot # 45	15
	Including Lianas			
N	1 423	540	477	431
S	189	126	116	126
α	58.5	51.7	48.8	59.9
	Excluding Lianas			
N	1 384	539	460	420
S	177	125	109	119
α	53.9	51.1	45.1	55.3

TABLE VI

Diversity among samples of ca 180 stems at Kirindy.

Gbh & Plot Size	⩾ 30 cm, 50 × 50 quadrats				Total ⩾ 50 cm
N	178	202	198	200	174
S	25	30	29	20	25
α	7.92	9.74	9.36	5.50 (Av. = 8.14)	8.00

It makes little difference whether one samples stems from 10 × 100 m strips or 30 × 30 m plots (Table VII). At Ambohitantely, Fisher's α for stems ⩾ 5 cm dbh for six 30 × 30 m plots was 22.3 ± 1.9 (mean ± standard deviation), while for stems ⩾ 5 cm dbh on seven 10 × 100 m plots, α = 22.9 ± 2.3.

In small samples from all three plots, species abundances follow the log series (Table VIII), whereby the number $p(m)$ of species with m individuals apiece is

$$p(m) = \alpha x^m / m, \; x = \frac{N}{N + \alpha} \tag{3}$$

TABLE VII

Diversity of stems on plots of different shape.

	Analamazaotra, stems ≥ 10 cm dbh					
	10 × 100 m			30 × 30 m		
End/Corner Plot #	3	2	9	36	15	4
N	112	102	96	80	90	93
S	57	52	54	48	54	48
α	46.5	42.5	51.0	50.7	43.4	39.9

	Ambohitantely, stems ≥ 5 cm dbh, 10 × 100 m plots						
Plot Numbers	1-10	11-20	21-30	31-40	41-50	51-60	61-70
N	383	363	382	431	435	380	434
S	69	59	67	63	72	71	66
α	24.6	20.0	23.5	20.3	24.6	25.8	21.7

	Ambohitantely, stems ≥ 5 cm dbh, 30 × 30 m plots					
Corner Plot Nos.	1	4-6	10	61	62-65	70
N	331	323	343	369	356	397
S	58	58	63	63	64	72
α	20.4	20.6	22.6	21.8	22.8	25.7

TABLE VIII

Distributions of tree abundances in small samples : predicted and observed number p(m) of species with m stems apiece.

	Analamazaotra		Ambohitantely		Kirindy	
Sample	≥ 30 cm dbh, all		≥ 5 cm dbh, 10 × 10 m		≥ 60 cm gbh, all	
N, α	43,	34.81018	50,	19.89779	85,	9.62609
S, x	28,	0.552629	25,	0.715329	22,	0.898282
	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.
p(1)	19	19.24	14	14.23	9	8.65
p(2)	7	5.32	6	5.09	3	3.88
p(3)	1	1.96	1	2.43	2	2.33
p(4)	0	0.81	1	1.30	1	1.57
p(5)	0	0.36	1	0.75	2	1.13
p(6)	0	0.17	2	0.44	0	0.84
p(7)	1	0.08	0	0.27	1	0.65
p(8)	0	0.04	0	0.17	0	0.51
p(9)	0	0.02	0	0.11	1	0.41
p(10)	0	0.01	0	0.07	0	0.33
p(> 10)	0	0.01	0	0.13	3	1.71

Note : Predictions are based on the log series : $p(m) = \alpha x^m / m$.

In large samples (stems ≥ 5 cm dbh on 60 × 60 m squares) at Ambohitantely and Analamazaotra, species abundances deviate more markedly from the log series.

The Ambohitantely square has too few species with only one stem apiece (Table IX). If, on a plot of 158 species distributed among 956 stems, like the 60×60 m plot at Analamazaotra (Table IX), species abundances are distributed according to the log series, the probability that there is a species represented by over 70 stems is about 1/4, yet the 60×60 m plot at Ambohitantely has 73 *Suregada laurina* and 82 *Blotia madagascariensis*.

<div align="center">TABLE IX</div>

Distribution of abundances among species of non-liana stems ≥ 5 cm dbh on 60×60 m plots.

	Analamazaotra		Ambohitantely	
N	956		1 479	
S	158		89	
α	53.92386		20.80450	
x	0.946606		0.98613	
p(m) :	obs.	predicted	obs.	predicted
1	53	51.04	11	20.52
2	27	24.16	11	10.12
3	14	15.25	5	6.65
4	10	10.82	3	4.92
5	4	8.20	4	3.88
6	5	6.47	5	3.19
7	4	5.25	5	2.70
8	8	4.35	3	2.33
9	5	3.66	5	2.04
10	5	3.12	2	1.81
11-15	7	10.40	8	6.77
16-20	4	5.66	2	4.53
21-30	7	5.45	11	5.82
31-50	1	3.24	6	6.05
> 50	2	0.94	8	7.70

Note : Predictions are based on the log series : $p(m) = \alpha x^m / m$.

DISCUSSION

PATTERNS OF DIVERSITY WITHIN MADAGASCAR

No plot from lowland rain forest of Madagascar's east coast was included among the data so far presented in this paper. In the Biosphere Reserve of Mananara Nord, however, Mme Fidèle Raharimalala found 129 species among 364 stems $\geq$ 15 cm gbh on a 16×20 m plot : here, Fisher's $\alpha = 71.31$. However, a 50×50 m plot with one 20×20 m corner missing contained only 72 species among 249 trees $\geq$ 30 cm gbh : for this sample, Fisher's $\alpha = 34.0$. These data suggest that the rainforest of Madagascar's east coast and the montane rainforest at Analamazaotra are decidedly more diverse than the plateau forest at Ambohitantely, which is in turn decidedly more diverse than the deciduous dry

forest along Madagascar's west coast. At Mananara Nord, however, there is a striking discrepancy between the diversity of stems ≥ 15 cm gbh and the diversity of stems ≥ 30 cm gbh. Diversity among stems ≥ 5 cm dbh is a third higher at Mananara Nord than at Analamazaotra, whereas diversity among trees ≥ 10 cm dbh is a third *lower* at Mananara than at Analamazaotra.

How does this conclusion square with earlier work ? Gentry (1993) censused one 2 × 500 m transect in lowland rain forest at Nosy Mangabé, near Maroantsetra on Madagascar's east coast ; another 2 × 500 m transect at Analamazaotra, and a third in deciduous dry forest at Ankarafantsika, roughly 100 km SE of Mahajanga. In general, diversity in a 2 × 500 m transect is 10 % higher than in a square plot of the same area, 0.1 ha (Condit *et al.,* 1995), but Gentry's transects were also unusually flexible, in order to include amusing or unusual plants. Nonetheless, they can be compared among themselves. Even though the average annual rainfall at Analamazaotra, at 1 700 mm, is far closer to Ankarafantsika's 1 600 mm than to Maroantsetra's 3 000 + mm, diversity at Analamazaotra is roughly comparable to that at Nosy Mangabé, while diversity at Ankarafantsika is much lower (Table X). The cause of the low diversity at Ankarafantsika is probably the fact that the dry season there is much more prolonged and severe than Analamazaotra's. Thus Gentry's thesis that, given adequate annual rainfall (1 700 mm or more), tree diversity is higher the shorter and/or less severe the dry season, appears to hold true in Madagascar.

TABLE X

Diversity in selected transects of Gentry (1993) in Madagascar (excluding lianas).

	Nosy Mangabé		Analamazaotra		Ankarafantsika	
dbh :	≥ 2.5 cm	≥ 10 cm	≥ 2.5 cm	≥ 10 cm	≥ 2.5 cm	≥ 10 cm
N	580	160	634	122	337	61
S	171	80	159	76	64	28
α	81.7	63.7	68.2	86.2	23.4	20.4

How do our data compare with the results of other work in similar habitats ? Data are most abundant from the dry forest near Morondava (Hladik, 1980 ; Ganzhorn, 1995 ; Table XI). In general, their results are in reasonable accord with our own, but a transect at CS7 close to the river of Kirindy (Ganzhorn, 1995, Appendix) recorded incongruously high diversity.

On behalf of the Missouri Botanical Garden, Schatz & Malcomber (1995) established a 20 × 500 m plot at 1 000-1 100 m at Ranomafana National Park (21° 16' S, 47° 28' E). They found between 105 and 112 species among the 658 trees and two lianas ≥ 10 cm dbh on this plot, for a Fisher's α of about 36.7. As at Analamazaotra, Lauraceae have the most species and highest basal area of any family on the plot. A striking contrast with Analamazaotra is that the Ranomafana plot has 5 species of *Dombeya* (Sterculiaceae). This is probably a sign of recent disturbance. The Ranomafana plot is distinctly less diverse than our

TABLE XI

Tree diversity in dry forest plots near Morondava in western Madagascar.

| | Kirindy CFPF (240 m transects) | | | Marosalaza (440 × 5 m plot) |
	N5	CN5	CS7	
N	300	300	300	149
N'	166	163	34	80
S	30+	28+	63+	25
α	8.3+	7.6+	24.3+	8.6

Note : Each 240 m transect consists of 75 points. The surroundings of each point were divided into four quadants or quarters, and the tree nearest the point in each quadant was sampled (Ganzhorn, 1995). N is the number of trees ≥ 10 cm dbh (Kirindy) or ≥ 30 cm gbh (Marosalaza) ; N' is the number of these trees belonging to the species *Securinega seyrigii* ; S is the number of species among these N trees, and α is Fisher's alpha. Marosalaza is roughly 20 km N. of Kirindy, on the other side of the road to Beroboka. Data for Kirindy (CFPF) are from Ganzhorn (1995), data for Marosalaza are from Hladik (1980).

plateau at Analamazaotra. Does the reduced diversity reflect recent disturbance, greater seasonality owing to a more southerly latitude, or some other, more accidental, factor ? We lack the information to decide.

COMPARISON OF MADAGASCAR WITH OTHER REGIONS

The eastern rainforests of Madagascar, lowland and midmontane, are distinctly less diverse than most of their counterparts in Malaysia or the Neotropics (Table XII). Madagascar's limited area may have limited speciation, or it may have provided insufficient refuge during the climatic revolutions of the Pleistocene. Plots in the eastern rainforests of Madagascar are more diverse than nearly all the plots reported from tropical Africa, probably because the African forests all have a more pronounced dry season (Gentry, 1993).

The plateau forest at Ambohitantely is about as diverse as montane forest at 1 550 m on the slopes of Java's Mt. Gedeh (Table XII). It is somewhat less diverse than forest at 1 600 m on Sabah's Mt. Kinabalu. There, Kitayama (1992) found 58 species among 212 trees ≥ 10 cm dbh in an extended point-quarter transect, giving an α of 26.4, while at Ambohitantely the average 10 × 100 m transect contained 67 species among 401 stems ≥ 5 cm dbh, for an α of 22.9, and the average 0.15 ha transect (a 10 × 100 m strip, parallelled by a 10 × 50 m strip along half its length) contained 46 species among 203 stems ≥ 10 cm dbh, for an α of 18.6. The plateau forest at Ambohitantely is also somewhat less diverse than cloud forest at similar altitude in Costa Rica (Table XII).

The forests of Madagascar, both wet and dry, are decidedly more diverse than their counterparts in India and Sri Lanka, perhaps because the latter areas suffered extraordinary vicissitudes of climate during their voyage to Asia. The forest at Kirindy is more diverse than the dry forest at Mudumalai in south India, even though the latter has an annual rainfall of 1 100 mm, and a 5-6 month dry season,

TABLE XII

Tree diversity in selected forest plots.

Site	Altitude	A	N	S	α
Madagascar					
Analamazaotra	1 000 m	0.51	539	125	51.1
Ranomafana	1 000 m	1.00	660	108	36.7
Ambohitantely	1 550 m	0.70	948	74	18.8
Kirindy (CFPF)	20-100 m	0.93	778	45	10.4
Mascarenes (everwet forest)					
La Réunion	270 m	1.00	1 079	40	8.2
Mauritius	550 m	0.10	126	30	12.5
Neotropics (everwet forest)					
Volcan Barva, Costa Rica	1 000 m	1.00	546/528	109	41.7
Volcan Barva, Costa Rica	1 500 m	1.00	553/499	65	19.9
Monteverde, Costa Rica	1 480 m	1.00	559	76	23.7
Bajo Calima, Colombia	50 m	1.00	664	252	148.1
Jatun Sacha, Ecuador	450 m	1.00	724	246	131.2
Añangu, Ecuador	370 m	1.00	734	153	58.8
Yanamono, Peru	140 m	1.00	574	283	221.1
Africa					
Korup, Cameroun	lowland	0.64	301	75	32.0
Oveng, Gabon	lowland	1.00	485	123	53.1
Doussala, Gabon	lowland	1.00	413	100	42.0
India/Sri Lanka					
Mudumalai, India, dry forest	900 m	2.25	677	32	7.0
Kottawa, Sri Lanka, everwet	lowland	4.00	2 100	101	22.1
Southeast Asia (everwet forests)					
Pasoh, Malaysia	100 m	1.00	530	210	123.8
Danum Valley, Sabah, 30 cm gbh	220 m	4.00	1 936	247	75.1
Danum Valley, Sabah, 10 cm gbh	220 m	4.00	8 975	388	82.6
New Guinea	700 m	1.00	426	145	77.5
New Guinea	900 m	1.00	528	122	49.8
Tjibodas, Java	1 550 m	1.00	427	57	17.7

Note : Area, A, of sample plot, number N of trees $\geqslant$ 10 cm dbh, number S of species among them, and Fisher's α in selected forests. Data for Réunion from Strasberg (1995), data for Mauritius from Vaughan & Wiehe (1941). Data for Volcan Barva from Heaney & Proctor (1990) (the 546 stems at 1 000 m include 12 missing specimens and 6 unidentified plants which were not counted in the total number of species ; the 553 stems at 1 500 m include 15 missing specimens and 39 unidentified plants which were omitted from species count), data for Bajo Calima from Faber-Langendoen & Gentry (1991), data for Jatun Sacha, Añangu and Yanamono from Phillips *et al.* (1994), data for Korup from Gartlan *et al.* (1986), data for Oveng and Doussala from Reitsma (1988), data for Mudumalai from Condit *et al.* (1996), data for Kottawa from Gunatilleke & Ashton (1977), data for Pasoh from Kochummen *et al.* (1990), data for Danum Valley from Newbery *et al.* (1992), data for New Guinea from Paijmans (1970), data for Tjibodas, Java from Yamada (1975).

shorter than Kirindy's (Murali & Sukumar, 1993). Similarly, the forest at Analamazaotra is decidedly more diverse than everwet rainforest in Sri Lanka (Table XII).

OTHER OBSERVATIONS

The vegetation of Madagascar before human settlement has been a subject of some controversy (Koechlin *et al.,* 1974 ; MacPhee *et al.,* 1985 ; Burney, 1987a,

1987b). Was it entirely forested, or were parts of Madagascar covered by grassland or savanna ? On the one hand, modern grasslands in Madagascar are depauperate, and dominated by pantropical species characteristic of disturbed settings (Humbert, 1927). On the other hand, at least one species of giant subfossil lemur, *Hadropithecus,* was a grazer (Tattersall, 1982, p. 220), which presupposes grasslands where it could graze. Pollen spectra from central Madagascar seem inconsistent with the view that Madagascar was completely forested before human settlement (MacPhee *et al.,* 1985 ; Burney, 1987a, 1987b). Perhaps the greatest puzzle of all is that on the one hand, most types of natural forest in Madagascar are quite sensitive to fire (Humbert, 1927), while Madagascar lacks an aggressive secondary vegetation that could readily make up the ground thus lost ; on the other hand, fires occurred frequently in Madagascar long before humans appeared on the scene (Burney, 1987b). This contradiction is rather puzzling.

CONCLUDING REMARKS

Although the forests of Madagascar are quite diverse, we believe that the diversity of its eastern rainforests is lower than their climates would lead one to expect. Other features also suggest that plant evolution in Madagascar has somehow been less effective than in mainland settings. Madagascar's lack of an aggressive secondary vegetation comparable to Africa's (Koechlin *et al.,* 1974) has played a major rôle in Madagascar's deforestation.

There are three other ways to assess the competitiveness of Madagascar's forest. First, how effectively does the forest use the available light ? The remarkably thick ground-herbage in many Malagasy forests, including our sample plot at Analamazaotra, some treefall gaps which were thickly grassed, suggests that in Madagascar, the forest overstory is perhaps less efficient at taking up available light than the overstory in mainland rain forests. Second, how well defended against herbivores is the forest ? Hawaii, for example, has few poisonous plants, and, in general, Hawaiian plants are less well defended by either chemicals or spines than their mainland relatives (Carlquist, 1980, pp. 173-177). Madagascar's forest foliage appears, however, to have a more normal array of defenses (Ganzhorn, 1988, 1989, 1992 : Jeannoda, 1986). Third, how susceptible is the vegetation, especially mature forest, to invasion by exotics ? Madagascar's mature forests are not particularly susceptible to invasion by exotics (Phillipson, 1994), in striking contast to the depauperate forests of Réunion or Hawaii (Lorence & Sussman, 1988 ; MacDonald *et al.,* 1991). Are they still vulnerable compared, say, to the forests of Africa ? That question needs more attention.

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SUMMARY

Trees $\geq$ 30 cm girth on a 0.93 ha plot of deciduous dry forest at Kirindy (CFPF), 50 km N. of Morondava, at 20-100 m in western Madagascar, stems $\geq$ 5 cm diameter on 0.7 ha of evergreen plateau forest at 1 550 m at Ambohitantely, 130 km N of Antananarivo, and stems $\geq$ 5 cm diameter on 0.51 ha of montane rain forest at 1 000 m near Périnet, 140 km E of Antananarivo, were marked, identified, and their diameters measured. The 778 marked stems at Kirindy included 45 species, the 2 808 marked stems at Ambohitantely included 102 species, and the 1 384 marked non-liana stems near Perinet included 177 species.

We use Fisher's α to compare diversity among sites. A site's α is related to its number N of sampled stems and the number S of species among them by the equation $S = \alpha \ln (1 + N/\alpha)$. For $N > 500$, α usually depends little on the number N of stems sampled or their lower size limit. Tree diversity (measured by α) is lower on Malagasy sample plots than in Amazonian or Malaysian forest plots of comparable climate, but decidedly higher than on forest plots of comparable climate in India or Sri Lanka.

Has Madagascar's limited size limited plant diversification ? We propose other ways to assess whether, and to what degree, Madagascar's limited size has restricted the evolution of truly competitive vegetation, such as the variety and effectiveness of chemical and morphological defenses against herbivores among the plants of Madagascar, and the susceptibility of Madagascar's vegetation, especially mature forests, to invasion by exotics.

RÉSUMÉ

La diversification des espèces végétales de Madagascar a-t-elle été limitée par la surface relativement réduite de cette île, comparée aux blocs continentaux ? Nous proposons une approche des aspects de la diversification des espèces à Madagascar — et de l'intensité de cette diversification — basée sur une série de relevés dans différents types de forêts.

Ces relevés portent sur :

• l'ouest de Madagascar où tous les arbres de plus de 30 cm de circonférence ont été identifiés sur 0,93 ha dans la forêt sèche caducifoliée de Kirindy (CFPF, à 50 km au nord de Morondava ; altitude 20 à 100 m) ;

• la forêt sempervirente du plateau à Ambohitantely (à 130 km au nord de Tananarive ; altitude 1 550 m) où les tiges de plus de 5 cm de diamètre ont été répertoriées sur 0,7 ha ;

• la forêt sempervirente de montagne, à Anamalazaotra (près de Périnet, à 140 km à l'est de Tananarive ; altitude 1 000 m) où les tiges de plus de 5 cm de diamètre ont été répertoriées sur 0,51 ha.

Chaque tige ayant été marquée, mesurée et identifiée, nous obtenons, à Kirindy un total de 778 tiges de 45 espèces ; à Ambohitantely, 2 808 tiges appartenant à 102 espèces ; à Périnet, sans prendre en compte les lianes, les 1 384 tiges correspondent à 177 espèces.

Nous avons utilisé l'indice α de Fisher pour comparer la diversité spécifique de ces sites. Cet indice est fonction du nombre N de tiges répertoriées et du nombre d'espèces S, selon la formule $S = \ln (1 + N/\alpha)$. Pour $N > 500$, α ne varie relativement en général que très peu en fonction du nombre N de tiges répertoriées et de la limite inférieure du diamètre considéré. La diversité spécifique des arbres — mesurée par l'indice α — est plus faible à Madagascar que dans les forêts d'Amazonie ou de Malaisie, si l'on considère des régions où le climat est sensiblement identique. Elle est cependant supérieure à celle de forêts à climat comparable de l'Inde ou du Sri Lanka.

Dans la discussion, nous montrons également que l'intensité de la compétition entre les végétaux peut être mesurée par l'efficacité de leurs systèmes de défense contre les consommateurs de feuillage — basés sur des adaptations chimiques et morphologiques — ainsi que par la susceptibilité de la flore de Madagascar — en particulier celle des forêts matures — aux invasions par des espèces exotiques.

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