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Plant Diversity and Structural Analysis of a Tropical Dry Forest in Southwestern Madagascar[1]

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ABSTRACT

For this paper, we sampled a fenced and an unprotected portion of a dry gallery forest (the Beza Mahafaly Reserve) in southwestern Madagascar for structure and floristic composition. Seedling plots were also sampled to assess invasion and regeneration. A total of 923 plants ≥2.5 cm diameter at breast height (DBH) were censused in 25 transects. Sixty-nine species and 43 genera were represented. In plant density, diversity, and size classes of individuals, the forest is similar to many continental tropical dry forests in Africa and the Neotropics. Over 80 percent of those species identified were native, as were 26 percent of the genera. Unlike many insular forests, Beza Mahafaly is not being invaded by fast-growing exotic species. There were no noticable differences in density, diversity, size classes, or proportion of native species between transects within and outside of the protected reserve.

Two distinct microhabitats were noticed. Individual plants were more dense on "drier" soils; whereas, large trees ≥25 cm DBH were over twice as frequent on "wetter" soils. The floristic composition also differed, with only two species of tree, *Tamarindus indica* and *Azima tetracantha,* being common to both habitats. The distribution and density of lemur populations within the forest appear to be directly related to microhabitat differences.

Key words: dry tropical forest; floral composition; forest structure; Madagascar.

Many conservation biologists believe that Madagascar should be considered among the highest conservation priorities on earth (Raven & Axelrod 1974, National Research Council 1980, Myers 1988, Mittermeier *et al.* 1992). Although the rapid destruction of the rain forests of Madagascar (and elsewhere) is receiving a great deal of notice, deforestation in the semiarid regions of southern Madagascar is proceeding at an even faster pace. This reflects the general world situation, with tropical dry forest on the whole in far worse shape conservationally than moist and wet forest (Lerdau *et al.* 1991; Gentry, in press).

Although general floristics, morphology, taxonomy, and plant geography of the Malagasy vegetation have been investigated (*e.g.,* Perrier de la Bâthie 1921, Humbert 1927, Cabanis *et al.* 1969, Koechlin *et al.* 1974, Leroy 1978, Gentry 1988), knowledge of the floristic composition, diversity patterns, and structure of plant communities is scant. Even fewer data exist on the dynamics of regeneration and the invasion rates of exotic plant species. In the arid regions of southern Madagascar, no detailed quantitative study of floristic composition exists. In fact, most studies of forest composition worldwide have been conducted on rain forest vegetation, and there are relatively few data available on tropical dry forest communities (but see Bullock *et al.,* in press).

Successful conservation of these forests will ultimately depend upon an understanding of forest ecosystem dynamics (Leigh *et al.* 1985, Gentry 1990, Hartshorn 1990). Given the alarming rates at which indigenous Malagasy floras are disappearing, it is imperative that baseline data on forest composition and regeneration be acquired as soon as possible.

The objectives of this study were to sample and describe the density, diversity, and floristic composition of two distinct habitat areas of gallery forest in the Beza Mahafaly Reserve, southwestern Madagascar; to survey a number of seedling plots to assess the dynamics of regeneration within this forest; and, to compare these patterns both within and outside of the protected portion of the reserve.

STUDY SITES

The Beza Mahafaly Reserve is a Special Government Reserve established in 1986 to promote conservation, education, research, and development in southern Madagascar (Richard *et al.* 1987). It is located

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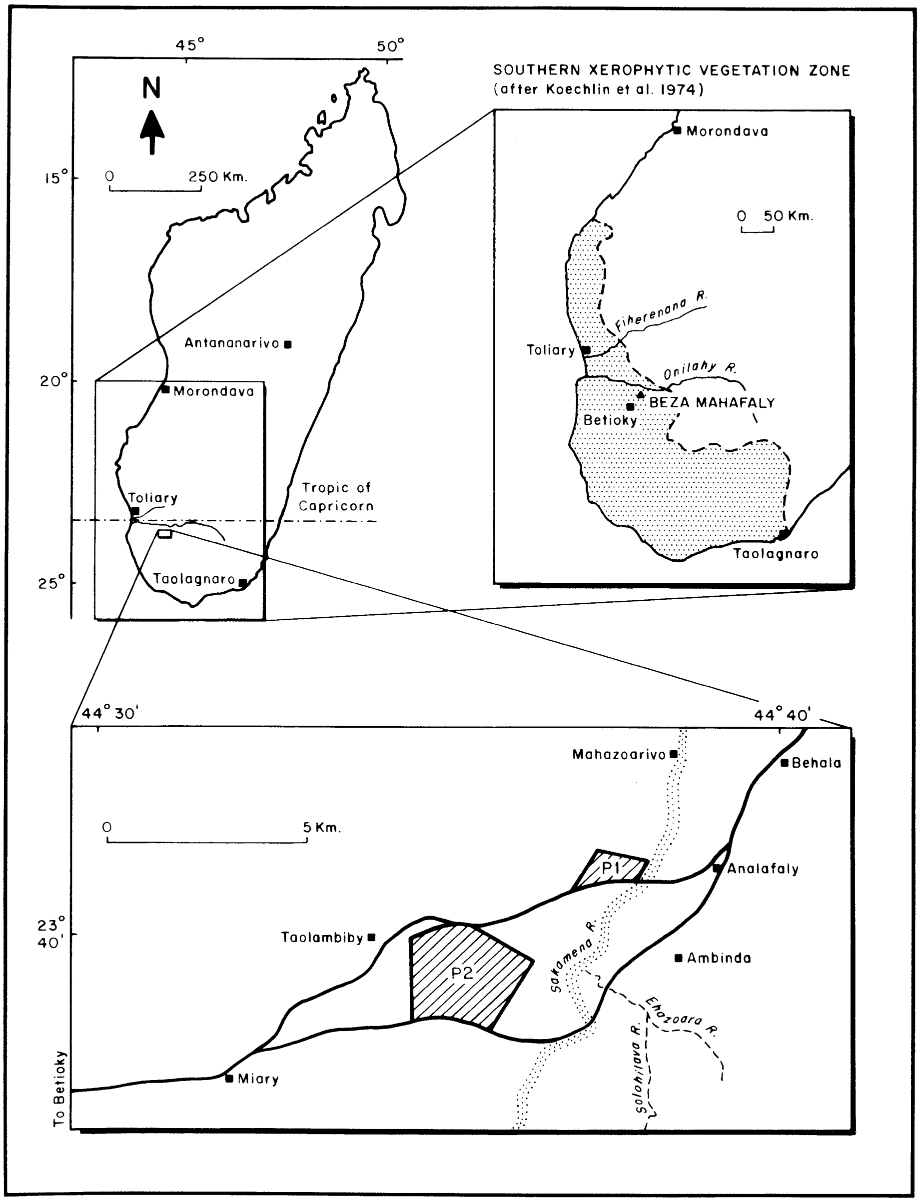

FIGURE 1. Map of the location of the Beza Mahafaly Reserve.

ca 23° 30′ S, 44° 40′ E, just west of the Sakamena River about 35 km northeast of Betioky (Fig. 1). The reserve is divided into two parcels, one containing 100 ha of gallery forest dominated by *Tamarindus indica* (Parcel #1) and the other approximately 500 ha of thorn-scrub *Didierea* forest (Parcel #2). Parcel #1 was completely enclosed by a barbed wire fence in 1979. Before this, it was exposed to cattle and goats, and was exploited for various resources by the local people. The reserve boundaries are fairly arbitrary and the forest is contiguous with unprotected forests of the same type throughout the region. This study was conducted in Parcel #1 and in unfenced, unprotected forest adjacent to it.

The gallery forest study site lies on flat terrain at an altitude of 100–200 m. Southern Madagascar is characterized by a long dry season (<40 mm/mo of rain) and a short wet season (>50 mm/mo), although the amount of rain can vary tre-

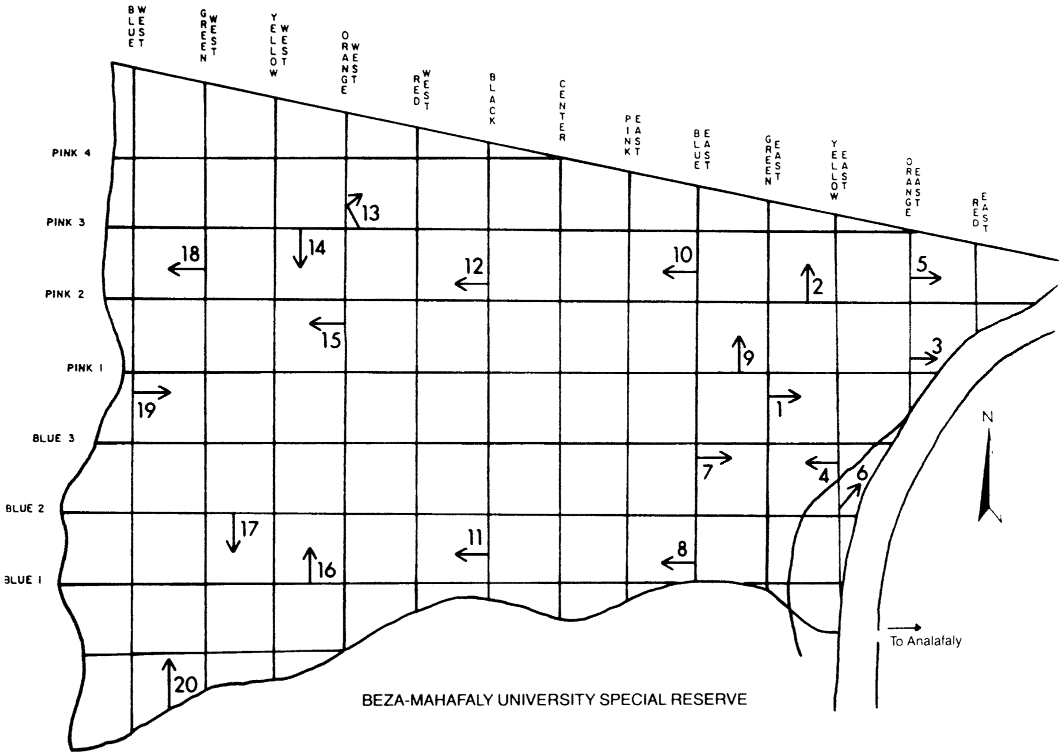

FIGURE 2. Map of the twenty vegetation transects within the fenced portion of the Beza Mahafaly Reserve.

mendously from year to year. Annual rainfall in the region of the reserve is about 750 mm, of which 600 mm falls during the austral summer, November–March. The wet season is also characterized by high ambient temperatures, averaging around 34°C and reaching highs of 48°C. Temperatures during the driest and coolest months (June–August) usually range between 23°C and 30°C, but can fall to 3°C at night. Annual temperatures average 25°C (data from meteorological station at Betioky, 1951–1980).

The gallery forests of the southwest grow on sandy soils derived from Triassic, Jurassic, and Cretaceous sandstones. Vegetation varies according to the depth and moisture content of the soil. On drier soils there are fewer tall trees but vegetation becomes more dense, distinctions between canopy strata are obscured, and forest gradually passes into thicket. On more moist soils large *Tamarindus indica* trees are dominant. In this paper, we further describe the distinctions between flora found bordering the Sakamena River and on transects further from the river. Gallery forests of this type are found throughout the south and southwest where conditions are favorable. However, this type of forest is being cut at a very rapid pace and is one of the most endangered in Madagascar. In fact in the driest region of the island, south of Toliara and the Fiherenana River, there are only around 5000 ha of gallery forest remaining (see Fig. 1).

METHODS

Measurement of trees.—Twenty-five transects of 50 × 2 m were laid out giving a total of 2500 m^2 (0.25 ha), and all individuals ≥2.5 cm DBH and rooted within the plot were recorded (Gentry 1982). Each plant was assigned to a size class (2.5–5 cm, 5–10 cm, 10–15 cm, . . . , 25+ cm) and size classes were combined for analysis. Ten transects were located near the river, ten further away from the river bank (Fig. 2), and five were located in similar forest adjacent to but outside of the fenced reserve. The location of these transects was selected because we recognized two physiognomically different plant communities and were attempting to measure the differences between them. Within these areas, tran-

TABLE 1. *Total number of trees (density) of different size classes in the three habitats (percentage in parentheses).*

	<10 cm	10–25	>25	Total
Transects 1–10 (wet soil)				
1000 m^2	245 (86)	18 (6)	23 (8)	286 (100)
Transects 11–20 (dry soil)				
1000 m^2	384 (87)	47 (11)	9 (2)	440 (100)
Transects 21–25 (nonfenced)				
500 m^2	174 (88)	8 (4)	15 (8)	197 (100)
Total	803 (87)	73 (8)	47 (5)	923 (100)

sects were positioned perpendicular to paths and randomly with respect to each other.

Given a number of factors, we believe that the forests closer to the river are more mesic and generally on more moist soils, and those further from the river are more xeric and on dryer soils. For example, near the river there are darker near surface soils, and the soils are more clay-rich and have a deeper litter depth then those further from the river. Soils further from the river are lighter, dryer to the touch, and more sandy (G. Green, pers. comm.). We, therefore will refer to transects 1–10 as those on "wet" soils and transects 11–20 as those on "dry" soils.

Identifications were made in the field except for problematic individuals which were vouchered for later identification at the Tsimbazaza Herbarium in Antananarivo (TAN). Voucher specimens of most species were deposited there and also in the Missouri Botanical Garden Herbarium (MO).

ESTIMATION OF SEEDLING REGENERATION.—Twenty-five seedling plots of 2 × 2 m each were selected, one per transect, for a total of 90 m^2. The location of the seedling plot within each transect was chosen at random. All seedlings and young plants of angiosperms less than 2.5 cm diameter were sampled, noting species and number of individuals. A general description of the seedling plot was also noted, indicating whether it was open or covered, larger

TABLE 2. *Density (number of individuals) and proportion of native and exotic plants ≥2.5 cm DBH (%) in three microhabitats at Beza Mahafaly. Percentage in parentheses.*

	Identified		Not identified	Total
	Native	Exotic		
Wet soils				
Individuals	195 (68)	46 (16)	45 (16)	286 (100)
Lianas	6 (2)	0	2 (0.7)	8 (3)
All trees	189 (66)	46 (16)	43 (15)	278 (97)
Large trees (>10 cm)	28 (10)	13 (5)	0	41 (14)
Dry soils				
Individuals	215 (49)	87 (20)	138 (31)	440 (100)
Lianas	16 (4)	0	10 (2)	26 (6)
All trees	199 (45)	87 (20)	128 (29)	414 (94)
Large trees (>10 cm)	32 (7)	18 (4)	6 (1)	56 (13)
Out of reserve				
Individuals	164 (83)	12 (6)	21 (11)	197 (100)
Lianas	6 (3)	0	0	6 (3)
All tress	159 (80)	12 (6)	21 (11)	191 (97)
Large trees (>10 cm)	19 (10)	4 (2)	0	23 (12)
Totals				
Individuals	574 (62)[a]	145 (16)	204 (22)	923 (100)
Lianas	28 (3)	0	12 (1)	40 (4)
All trees	546 (59)	145 (16)	192 (21)	883 (96)
Large trees (>10 cm)	79 (9)	35 (4)	6 (1)	120 (13)

[a] 62% of all individuals were native; 80% of all those identified (574 of 719) were native.

TABLE 3. *Number of individuals of most common tree species in different habitats and size classes.*

	Wet soils			Dry soils			Unfenced		
	Diam (cm)			Diam (cm)			Diam (cm)		
Species	2.5–10	10–25	>25	2.5–10	10–25	>25	2.5–10	10–25	>25
Acacia rovumae	16	4	4	1	0	0	3	3	1
Azima tetracantha	34	0	0	38	0	0	47	1	0
Crateva excelsa	18	0	0	1	0	0	14	0	0
Euphorbia tirucalli	8	3	2	35	11	1	1	0	0
Gardenia sp.	20	0	0				3	0	0
Gelonium adenophorum				28	2	0			
Grewia sp. 2	2	0	0	48	2	0			
Grewia sp. 8	1	0	0	25	0	0			
Grewia sp. 9				13	0	0			
Rhigozum madagascariensis				20	0	0	3	0	0
Rhopalocarpus lucidus	2	0	0	23	2	0	2	0	0
Salvadora angustifolia	1	0	0	23	4	2	3	0	0
Stereospermum variable	20	0	0						
Tamarindus indica	7	7	17	7	8	5	1	3	13
Tarenna pruinosum	51	0	0	5	0	0	28	0	0

plants present, the type of soil, and general physiographic features.

RESULTS

PHYSIOGNOMY.—The forest represented in Parcel #1 of the Beza Mahafaly Reserve may be classified as western Malagasy dry deciduous forest (White 1983). It is a riverine forest dominated by *Tamarindus indica,* as is typical of the gallery forests of southwestern and southern Madagascar.

A total of 923 plants ≥2.5 cm DBH were censused in the 25 transects (Table 1). This is a density of 369 individuals per 1000 m^2. Comparison of the ten transects (#1–10) closest to the Sakamena River with those (#11–20) further to the west shows that the forest further from the river is 50 percent more dense than that near the river (440 vs 286 individuals ≥2.5 cm DBH/1000 m^2). However, large trees ≥25 cm DBH were over 2.5 times more frequent on wet than on dry soils (the equivalent of 230/ha vs 90/ha). Transects outside of the fenced reserve (#21–25) were intermediate in density.

In Table 2 we examine the density of life forms and the proportion of native individual woody plants in the two microhabitats. The proportion of trees over 10 cm DBH is similar, 13–14 percent, in both microhabitats. It is only in large trees over 25 cm DBH that a distinction is seen between wet and dry soils. Of those individuals in which identifications are complete, 80 percent are native, and there is little difference in the proportion of native individuals between microhabitats. There are more lianas ≥2.5 cm DBH on the dry soils (6% of the individual plants) than on wet (3%); overall, lianas make up 4 percent of the individual plants.

Physiognomically, the upper stratum on wet soils forms a closed canopy, mostly uniform in height (15–20 m). Members of the upper stratum are species whose trunks generally exceed 25 cm DBH and may attain 50 cm DBH or more, especially on wet soils. The most common canopy species are *Tamarindus indica, Acacia rovumae, Euphorbia tirucalli,* and *Salvadora angustifolia.* It is interesting to note that the above species are considered by many botanists to be exotic and recently introduced, although their origin and biogeography is still questionable (Perrier de la Bâthie 1936, Cabanis *et al.* 1969, Leroy 1978). Other species of large trees such as *Commiphora* spp., *Gyrocarpus americanus, Terminalia* spp., and *Acacia bellula* are present in our transects, but were few in number or only occurred as smaller individuals in the lower strata. One species, *Quivianthe papinae,* commonly reached the upper stratum in height but did not normally exceed 25 cm DBH. The common canopy species occur in different size classes (Table 3) suggesting ongoing regeneration. (Also, see the seedling data.)

Most trees in the forest were small, constituting a middle stratum from about 2 to 15 m tall. Many species are restricted to this layer, generally not exceeding 25 cm or even 10 cm DBH (Table 3, Appendix 1). The most common of these are *Azima tetracantha, Crateva excelsa, Gardenia* sp., *Gelonium adenophorum, Grewia* spp., *Rhigozum mada-*

TABLE 4. *Diversity and proportion of native and exotic species >2.5 cm DBH. Percentage in parentheses.*

	Identified		Not identified	Total
	Native	Exotic		
Wet soils				
Species	23 (55)	5 (12)	14 (33)	42 (100)
Lianas	2 (0.5)	0	2 (0.5)	4 (10)
All trees	21 (50)	5 (12)	12 (28)	38 (90)
Large trees (>10 cm)	4 (10)	2 (5)	0	6 (14)
Dry soils				
Species	24 (52)	6 (13)	16 (35)	46 (100)
Lianas	4 (9)	0	1 (2)	5 (11)
All trees	20 (43)	6 (13)	15 (33)	41 (89)
Large trees (>10 cm)	7 (15)	2 (4)	4 (9)	13 (28)
Out of Reserve				
Species	17 (53)	6 (19)	9 (28)	32 (100)
Lianas	2 (6)	0	0	2 (6)
All trees	15 (47)	6 (19)	9 (28)	30 (94)
Large trees (>10 cm)	3 (9)	2 (6)	0	5 (16)
Totals (all 25 transects)				
Species	31 (45)[a]	9 (13)	29 (42)	69 (100)
Lianas	4 (6)	0	3 (4)	7 (10)
All trees	27 (39)	9 (13)	26 (38)	62 (90)
Large trees (>10 cm)	9 (13)	3 (4)	4 (6)	16 (23)

[a] 45% of all species were native, 78% of those identified (31 of 40) were native. It should also be noted that many of the species not identified are in genera in need of revision in Madagascar (*e.g., Grewia* and *Commiphora*) or are rarely occurring lianas.

gascariensis, Rhopalocarpus lucidus, Stereospermum variabile, and *Tarenna pruinosum.* Lianas are few in our plots, both in terms of individuals and species, and include only *Marsdenia cordifolia, M. verrucosa, Pentopetia androsaemifolia, Roupellina boivini, Secamone* sp., and one unidentified species of Passifloraceae. Palms are absent in this forest.

DIVERSITY.—Twenty-five families are represented with plants ≥2.5 cm DBH in all 25 transects, with Tiliaceae having the most species (15), followed by Burseraceae (7), Leguminosae (7), and Euphorbiaceae (6) (see Appendix 1). One family, Sphaeprosepalaceae is endemic. A second endemic family, Didieriaceae, is present in the forest but was not found in our transects. The number of woody species in the transects with individuals ≥2.5 cm DBH was 69 of which 78 percent (of those identified) are native (Table 4). Twenty-six percent of the 43 genera also are native. Ten percent of the woody species are lianas.

Species composition close to the river differs to a great degree from that further from the river. Although the total number of species on wet and dry soils was similar (42 and 46, respectively), only 26 species were found in both microhabitats. Seventeen species were found only on wet soils and 20 species only on dry soils (see Appendix 1). In Table 3, we list the 15 most common tree species in Parcel #1 of the Beza Mahafaly Reserve. Only two species are common throughout the forest, *Tamarindus indica* and *Azima tetracantha.* In general, those species found in both microhabitats are not equally distributed (Appendix 1). Five of the most common species are found mainly on wet soils and eight mainly on dry soils.

SEEDLING PLOTS.—The seedling plots enabled us to examine the floristic composition, density and diversity of lower stratum and ground layer species, and to evaluate regeneration of the middle and upper stratum tree species. These plots also allowed us to compare the regeneration of tree species both inside and out of the fenced portion of the reserve. The lower stratum and ground level consisted of herbs, small lianas, and some grasses (all of these are native taxa), and of seedlings and saplings of middle and upper stratum species. Unlike the insular forests we studied in Mauritius (Lorence & Sussman 1988), the deciduous gallery forest in this region of Madagascar is not being invaded by recently introduced, fast growing exotic plants. In

TABLE 5. *Diversity and density of plants (<2.5 cm DBH) in the 25 transects. Percentages in parentheses.*

	Grass	Herbs	Liana	Small tree	Large tree	Total
Seedling plots 1–10						
Individuals	47 (7)	170 (26)	205 (31)	180 (27)	56 (9)	658 (100)
Species	4	8	17	20	5	54
Endemic genera 5 (11%) of 45 identified, ? = 4						
Species 20 (65%) of 31 identified, ? = 23						
Seedling plots 11–20						
Individuals	36 (4)	358 (42)	207 (25)	182 (22)	60 (7)	843 (100)
Species	3	7	9	19	7	45
Endemic genera 6 (16%) of 42 identified, ? = 5						
Species 19 (76%) of 25 identified, ? = 20						
Seedling plots 21–25						
Individuals	79 (25)	51 (16)	77 (24)	94 (29)	20 (6)	321 (100)
Species	3	3	7	15	4	32
Endemic genera 4 (15%) of 26 identified, ? = 2						
Species 16 (76%) of 21 identified, ? = 11						
Totals						
Individuals	162 (9)	579 (32)	489 (27)	465 (25)	136 (7)	1822 (100)
Species	6	11	21	35	7	80
Endemic genera 10 (13%) of 61 identified, ? = 6						
Species 33 (68%) of 44 identified, ? = 36						

continental tropical forests, invasion of individual exotics is virtually nonexistent (A. Gentry, pers. comm.). Thus, the major conservational concern in these forests is whether the flora of the gallery forest, especially the upper stratum species that form the closed canopy, are regenerating.

A definite patchiness was noted in the distribution and density of various life forms, especially of grasses and herbs. This was related to subtle topographical features of the land, differences in heavily shaded and more open areas, natural troughs where flooding periodically occurred, and amount of sand in the soil in certain areas (probably related to periodic flooding).

There were a total of 1822 plants counted in the seedling plots (Appendix 2). Just as in the transects, plants were more densely distributed on the dry soils (plots 11–20), especially with herb species, than on the wet soils (plots 1–10) (Table 5). Seedling plots outside of the fenced reserve (plots

TABLE 6. *Comparison of species diversity and density between some Neotropical continental sites and Beza Mahafaly.*

Site	Plot size (ha)	Number of species, Lower limit 2.5 cm	Number of species, Lower limit >10 cm	Number of individuals, Lower limit 2.5 cm	Number of individuals, Lower limit >10 cm	Precipitation (mm)	Altitude (m)	Source
Neotropical continental moist forest average (4 sites)	0.1	109	28	314	41	1830–2433	<300	Gentry 1982
Neotropical continental wet forest average (4 sites)	0.1	143	30	349	51	2650–3000	<300	Gentry 1982
Upper Amazonian forest average (10 sites)	0.1	180	44	398	67	2000–4000	<400	Gentry 1987
Beza Mahafaly	0.25	69	10	369	48	750	<200	This study

21–25) also appeared to be similar to those within the fence, except that grasses were relatively more common and other herbs less common. The proportion of saplings and juveniles of middle and upper stratum trees was similar in the three sets of transects. Seedlings of all but one (*Stereospermum variabile*) of the most common middle and upper stratum species were recorded, making up 26 percent and 7 percent, respectively, of the individuals overall (Table 5). We could discern no appreciable differences between the plots in the fenced and unfenced portion of the forest.

DISCUSSION

The diversity and floristic composition of Beza Mahafaly, a lowland, dry forest in Madagascar, is similar in many ways to that of dry forests in continental Africa and the Neotropics (Table 6). We found an average of 369 individuals $\geq$2.5 cm DBH/1000 m^2 in the forest at Beza Mahafaly. Using similar methods, Gentry (1993, in press) found an average of 370 individuals $\geq$2.5 cm DBH/1000 m^2 in a series of Neotropical lowland dry forests, and 361 individuals in dry forests in Africa. The average number of species with representative plants $\geq$2.5 cm DBH per 0.1-ha samples at Beza Mahafaly (48) is within the range of typical dry forests in Africa and the Neotropics. In general, Beza Mahafaly appears to be a structurally normal continental tropical dry forest, except that there are fewer individuals and species of lianas represented, and the number of species of large trees is relatively low (Table 6).

Although some of the characteristic canopy species at Beza Mahafaly have been suggested to be exotic, it seems unlikely that most of the larger and most common tree species are recently introduced. For example, *Tamarindus indica* is the dominant species of the riverine forests in southwest Madagascar and also of the dry forests further north. As noted by Cabanis *et al.* (1969), many botanists believe this species is introduced. However, Perrier de la Bâthie (1936) considered it to be native. This also is likely to be true of *Euphorbia tirucalli* and *Acacia rovumae,* both of which belong to widespread tropical genera well represented in Madagascar. In fact, our data suggest that these species, although sometimes listed as exotic, are all functioning as stable components of the Beza Mahafaly forest and may indeed all be native.

Many island forests are threatened by invasion of exotic, weedy species (see, for example, Lorence & Sussman 1986, 1988). As in most continental forests, this does not seem to be the case in southwestern Madagascar. The main threat to the dry forests of Madagascar is slash-and-burn agriculture which totally destroys the forest and widens the areas of grassland and scrub species. Another problem is overgrazing by goats and cattle which destroys the seedlings and saplings of the larger tree species. We could find no evidence of this in the Beza Mahafaly Reserve, except perhaps in the low frequency of lianas represented.

In areas of Madagascar with high human population density, cutting for charcoal is a major cause of deforestation. Although the protected area of gallery forest at Beza Mahafaly did not show the effects of human cutting, many forest areas in the vicinity of the reserve are being cut or degraded. The gallery forests of southwestern Madagascar may be among the most endangered vegetation types on the island, with only around 5000 ha still remaining.

Although Parcel #1 of the Beza Mahafaly Reserve is not being invaded by recently introduced, fast-growing exotic plants, the local reserve guards report that some parts of it may be threatened by a native species of vine, *Sarcostemma viminale* (locally called "try") of the Asclepiadaceae. Evidently cattle and goats fed on this plant in the past, and currently the guards are keeping it under control within the reserve (A. Richard, pers. comm.). Although we did not encounter *S. viminale* in our transects, it is obvious that both the protected and unprotected portions of the forest are undergoing dynamic changes and that there is a need for further study of these changes. Only seasonal and long-term monitoring of the transects at Beza Mahafaly and future comparative studies will allow us to understand the dynamics of these forests and the effects that reduced grazing might have upon them.

In most studies of this sort, large areas of forest are surveyed. These surveys might miss microhabitat distinctions within the study area. We found large differences within the 100 ha forest at the Beza Mahafaly Reserve. Individual plants were more dense in the transects located further from the river; whereas, large trees $\geq$25 cm DBH were over twice as frequent in transects closer to the river. Furthermore, floristic composition differed in the two microhabitats, with only two of the most frequently occurring tree species being common in both.

From our studies of lemur population demography, it appears that the density and distribution of the vegetation in the gallery forest is very critical to that of the lemur populations (Sussman 1991). The population density of the ringtailed lemur (*Le-*

mur catta), for example, is much higher near the river than away from it (175/km² vs 115/km² for the whole reserve), and those groups living near the river have home ranges averaging 17 ha; whereas, those further from the river have average home ranges of 32 ha. The sizes of ranges of the ringtailed lemur groups were found to correlate with the average number of large trees ≥25 cm DBH found within the group's home range. It is also possible that certain tree species (such as *Tamarindus indica* or *Salvadora augustifolia*) are keystone species to these lemurs, and that the density and ranging patterns of the animals is closely tied to the density, distribution, and phenology of these plant species.

Preliminary study of another species of lemur, *Propithecus verreauxi,* indicates that it may use the forest in a very different fashion from *Lemur catta* (A. Richard, pers. comm.). *Propithecus verreauxi* is highly folivorous and has very different dietary preferences from *Lemur catta* (A. Richard 1978, Sussman 1988). In contrast to the ringtailed lemur, *Propithecus verreauxi* appears to have larger groups, smaller home ranges, and a higher density of individuals in the drier portions of the Beza Mahafaly forest further from the river than in portions closer to the river. Thus, microhabitat differences within the Beza Mahafaly forest, which include the distribution of large trees, plant density, and floristic composition, appear to correlate with differences in habitat use by these two lemur species. These differences will be the subject of future study.

CONCLUSION

A high proportion of the plant species and genera in the Beza Mahafaly Reserve are endemic, as are two plant families. There also have been 60 species of birds, 11 species of mammals, and 18 species of reptiles recorded in this reserve (Jenkins 1987, Richard *et al.* 1987), many of which are endemic. The conservation status of many of these species is directly tied to that of the gallery forests. For example, although the ringtailed lemur is considered to be one of the less endangered species of Malagasy lemur, the rapid destruction of these forests is surely affecting its population density in this region.

Our data indicate that the gallery forests of southwestern Madagascar are structurally much like continental dry tropical forests of Africa and the Neotropics. Unlike insular forests, they are not being invaded by fast-growing exotic plant species. Instead, the main threats of deforestation are overgrazing, slash-and-burn agriculture, and other human-caused disturbances. The disappearance of the gallery forests in southwestern Madagascar is proceeding at a rapid pace, and if it continues, will lead to the extinction of a unique community of plants and animals.

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Appendix 1. *Numbers of individuals encountered in twenty-five 50 × 2 m transects. * = Exotic species.*

	Transects					
	1–10 (wet)		11–20 (dry)		21–25 (unfenced)	
Family and species	<10 cm	>10 cm	<10 cm	>10 cm	<10 cm	>10 cm
Apocynaceae						
Roupellina boivinii M. Pichon	—	—	1	0	—	—
Asclepiadaceae						
Marsdenia cordifolia P. Choux	—	—	2	0	3	0
Marsdenia verrucosa Decne.	2	0	7	0	3	0
Pentopetia androsaemifolia Decne.	4	0	6	0	—	—
Secamone sp.	—	—	10	0	—	—
Bignoniaceae						
Fernandoa madagascariensis Baker	2	0	2	0	—	—
Rhigozum madagascariensis Drake	—	—	20	0	3	0
Stereospermum variabile H. Perr.	14	0	—	—	—	—

Appendix 1. *Continued.*

Family and species	Transects 1–10 (wet) <10 cm	1–10 (wet) >10 cm	11–20 (dry) <10 cm	11–20 (dry) >10 cm	21–25 (unfenced) <10 cm	21–25 (unfenced) >10 cm
Boraginaceae						
Ehretia sp.	—	—	—	—	4	—
Burseraceae						
Commiphora sp. A	1	0	—	—	—	—
Commiphora sp. B	1	0	1	2	—	—
Commiphora sp. C	—	—	6	1	—	—
Commiphora aprevalii H. Baillon	1	0	—	—	—	—
Commiphora brevicalyz H. Perr.	1	0	—	—	0	1
Commiphora grandifolia Engl.	4	0	1	0	7	0
Commiphora simplicifolia H. Perr.	—	—	—	—	1	0
Capparidaceae						
Cadaba virgata Boj.	—	—	2	0	2	0
Creteva excelsa Boj.	18	0	1	0	14	0
Physena sessiflora Pul.	3	0	—	—	4	0
Combretaceae						
Terminalia fatraea DC.	—	—	5	0	—	—
Terminalia tricristata H. Perr.	—	—	1	2	—	—
Terminalia sp.	—	—	1	0	—	—
Celastraceae						
Hippocratea sp.	1	0	—	—	—	—
Ebenaceae						
Diospyros sp.	1	0	—	—	—	—
Euphorbiaceae						
Antidesma petiolare Tril.	4	0	—	—	—	—
Bridelia pervilleana H. Baillon	1	—	1	0	—	—
**Euphorbia tirucalli* L.	8	5	35	12	1	0
**Fluggea obovata* Wall.	2	0	—	—	11	0
Gelonium adenophorum Mull.-Arg.	2	0	28	2	—	—
Sapium madagascariensis Mull.-Arg.	—	—	2	0	—	—
Hernandiaceae						
**Gyrocarpus americanus* Jacq.	—	—	—	—	—	1
Leguminosae						
Albizia sp.	—	—	2	0	—	—
Acacia bellula Drake	0	2	6	5	—	—
**Acacia rovumae* Oliv.	16	8	1	0	3	4
Acacia sp.	0	0	1	0	—	—
**Dichrostachys cinerea* R. Vig.	—	—	1	0	—	—
Dichrostachys tenuifolia Benth.	—	—	3	0	4	0
Tamarindus indica L.	7	24	7	13	1	16
Loganiaceae						
Strychnos madagascariensis Poir.	—	—	8	0	—	—
Meliaceae						
Quivisianthe papinae H. Baillon	4	1	3	5	1	0
Oleaceae						
Noronhia sp.	6	0	—	—	6	0
**Olax andronensis* Baker	2	0	—	—	—	—
Passifloraceae						
Indet.	1	0	—	—	—	—
Portulacaceae						
Talinella dauphinensis Scott-Elliot	2	0	—	—	3	0

Appendix 1. *Continued.*

Family and species	Transects					
	1–10 (wet)		11–20 (dry)		21–25 (unfenced)	
	<10 cm	>10 cm	<10 cm	>10 cm	<10 cm	>10 cm
Ptaeroxylaceae						
Cedrolopsis grevei Pt. H. Baillon	1	0	3	3	—	—
Rhamnaceae						
Scutia myrtina Kurz	—	—	—	—	1	0
Rubiaceae						
Gardenia sp.	20	0	8	0	3	0
Hymenodictyon sp.	—	—	—	—	1	0
Tarenna pruinosum H. Baillon	51	0	5	0	28	0
Salvadoraceae						
Azima tetracantha Lam.	34	0	38	0	47	1
**Salvadora angustifolia* Turril	1	0	23	6	3	0
Sapindaceae						
**Allophylus decaryi* Choux	—	—	3	0	—	—
Sphaerosepalaceae						
Rhopalocarpus lucidus Boj.	2	0	23	2	2	0
Tiliaceae						
Grewia grevei H. Baillon	2	1	8	0	7	0
**Grewia triflora* W.	6	0	6	0	—	—
Grewia sp. 1	2	0	1	0	4	0
Grewia sp. 2	2	0	48	2	—	—
Grewia sp. 3	1	0	2	0	3	0
Grewia sp. 4	1	0	—	—	—	—
Grewia sp. 5	2	0	—	—	—	—
Grewia sp. 6	2	0	1	0	—	—
Grewia sp. 7	3	0	—	—	—	—
Grewia sp. 8	—	—	25	0	—	—
Grewia sp. 9	—	—	13	0	—	—
Grewia sp. 10	—	—	3	0	—	—
Grewia sp. 11	—	—	2	0	—	—
Grewia sp. 12	0	0	0	1	—	0
Grewia sp. indet.	0	0	—	—	2	0
[*Grewia* totals]	[21]	[1]	[109]	[3]	[16]	[0]
Verbenaceae						
Clerodondron sp.	7	0	8	0	2	0

Appendix 2. *Floristic data from twenty-five 2 × 2 m seedling plots. * = Exotic species.*

Family and species	Transects 1–10	Transects 11–20	Transects 21–25	Form
Acanthaceae				
Blepharis glomerans R. Ben	10	301	13	Herb
Dicliptera sp.	3			Herb
Ruellia anatocollis R. Ben	127	27	34	Herb
Amaranthaceae				
**Achyranthes aspera* L.	9	1	4	Herb
Aristolochiaceae				
Aristolochia sp.	3			Liana

Appendix 2. *Continued.*

Family and species	Transects 1–10	Transects 11–20	Transects 21–25	Form
Asclepiadaceae				
Cynanchum sp.	2	1		Liana
Gonocrypta grevei H. Baillon	5			Liana
Indet.	37	1		Liana
Marsdenia cordifolia P. Choux	2			Liana
Marsdenia sp.	1			Liana
Secamone sp.	13	8	9	Liana
Bignoniaceae				
Rhigozum madagascariensis Drake		5		Small tree
Burseraceae				
Commiphora sp.	1	1		Small tree
Commiphora simplicifolia H. Perr.		1		Large tree
Capparidaceae				
Cadaba virgata Boj.		2		Small tree
Capparis chysomeria Boj.		1	1	Liana
**Cleome tenella* L.	1			Herb
Creteva excelsa Boj.	1		2	Small tree
Maerua filiformis Drake	1			Small tree
Celastraceae				
Maytenus sp.	1			Small tree
Hippocratea angustipetela H. Perr	1			Liana
Hippocratea sp.	1		1	Liana
Combretaceae				
Terminalia fatraea DC.		9		Large tree
Commelinaceae				
**Commelina scandens* Willd.	1			Herb
Convolvulaceae				
Indet.		177	55	Liana
Metaporana parviflora Verdc.		4	1	Liana
Cucurbitaceae				
Cucumis sp.	1			Liana
Euphorbiaceae				
Acalypha reticulata Mull.	4			Small tree
Antidesma petiolare Tril.	8			Small tree
Croton sp.		18		Small tree
Euphorbia tirucalli L.	1	23	2	Large tree
Gelonium adenophorum Mull. Arg.		1		Small tree
Phyllanthus sp.			1	Small tree
Cyperaceae				
Cyperus sp.		3		Herb
Flacourtiaceae				
Flacourtia ludiaefolia H. Perr.			1	Small tree
Gramineae				
Digitaria sp.		15		Herb
Eragrostis sp.		3		Herb
Indet.	28	5	34	Grass
**Oplismenus burmanii* P. Beauv.	5	1		Grass
**Panicum maximum* L.	4			Grass
Perrierbambus sp.			44	Grass
Setaria cf. *scottii* A. Camus	10		1	Grass

Appendix 2. *Continued.*

Family and species	Transects 1–10	Transects 11–20	Transects 21–25	Form
Leguminosae				
**Abrus precatorius* L.	2			Liana
**Acacia minutifolia* Drake	3			Small tree
Acacia sp.	1	10		Large tree
Albizia sp.		1	1	Small tree
Indet.	109			Liana
Mimosa sp.		11		Small tree
Tamarindus indica L.	16	2	7	Large tree
Tephrosia sp.	3			Liana
**Teramnus labialis* Spreng.	1	3		Liana
Rhynchosia sp.	19			Liana
Malvaceae				
Abutilon pseudocleistogamum Hochr.	11	10	11	Small tree
Hibiscus sp.	10		1	Small tree
**Sida acuta* Burm.	7			Herb
Meliaceae				
Cedrelopsis grevei H. Baillon	1			Small tree
Quisivianthe papinae H. Baillon	17	5	8	Large tree
Nyctaginaceae				
**Boerhavia diffusa* L.	2			Herb
Oleaceae				
Noronhia sp.	27			Small tree
Passifloraceae				
Adenia olabuensis Clav.	3	1		Small tree
Pedaliaceae				
Uncarina grandidieri Stapf.		1		Small tree
Plumbaginaceae				
**Plumbago aphylla* Boj.		8		Herb
Portulaceae				
Talinella dauphinensis Scott-Elliot		2		Small tree
Rubiaceae				
Gardenia sp.	28	5	1	Small tree
Paederia grevei Drake	1			Liana
Salvadoraceae				
Azima tetracantha Lam.	2	44	7	Small tree
**Salvadora angustifolia* Turril	21	10	3	Large tree
Sphaerosepalaceae				
Rhopalocarpus lucidus Boj.		5	4	Small tree
Sterculiaceae				
Byttneria voulily H. Baillon	4	3	9	Liana
Sapindaceae				
**Allophylus decaryi* P. Choux			1	Liana
Tiliaceae				
Grewia grevei H. Baillon	2	1	5	Small tree
Grewia sp.		34	7	Small tree
Grewia (1)	1			Small tree
Grewia (2)			1	Small tree
Grewia (3)	7		10	Small tree
Grewia (4)		2	3	Small tree
Grewia (5)	2			Small tree
Indet. liana		9		Liana
Indet. tree	1	1		Small tree