Inventory of a 1-ha lowland rainforest plot in Manongarivo, (NW Madagascar)

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ABSTRACT

D'AMICO, C. & L. GAUTIER (2000). Inventory of a 1-ha lowland rainforest plot in Manongarivo, (NW Madagascar). *Candollea* 55: 319-340. In English, English and French abstracts.

A forest inventory was conducted in lowland rainforest on the southwestern border of Manongarivo Special Reserve, nothwestern Madagascar. At 220 m elevation, a one hectare area (20 × 500 m) was sampled for all trees with a dbh of 10 cm or more. 90 species represented by 728 individuals, with a total basal area of 22.4 m^2/ha, were recorded in the plot. Most of the trees are 15-25 m high, with a dbh of 10-20 cm, but an appreciable number reach higher values, up to 40 m high and 60 cm diameter. The five most important families in terms of density, diversity and dominance are *Clusiaceae, Euphorbiaceae, Myrtaceae, Rubiaceae* and *Myristicaceae.* Together they account for 46% of the total family importance values (FIV). In this forest, few common species dominate: 19% of all species account for 60% of the total importance value index (IVI). Only 21% of species are represented by one individual. The species with higher IVI are *Mauloutchia chapelieri, Syzygium* sp., *Uapaca ferruginea, Canarium madagascariense, Symphonia eugenioides, Anthostema madagascariensis* and *Ochrocarpos decipiens*. Forest structure and composition appear typical of Malagasy lowland rainforest in general and of Sambirano rainforests in particular. The great majority of species are Malagasy endemics, and 14% are Sambirano local endemics. Apart from species that occur widely in Malagasy forests, the remainder are mainly shared with the Eastern and Western Domains, a finding that supports the classical phytogeographic classification of Perrier de la Bâthie and Humbert.

RÉSUMÉ

D'AMICO, C. & L. GAUTIER (2000). Inventaire d'une parcelle de 1 ha en forêt dense humide de basse altitude à Manongarivo (NW Madagascar). *Candollea* 55: 319-340. En anglais, résumés anglais et français.

Un inventaire forestier a été réalisé à la limite sud-ouest de la Réserve Spéciale de Manongarivo, au nord-oest de Madagascar. A une altitude de 220 m, une surface d'un hectare (20 × 500 m) a été inventoriée et tous les arbres d'un diamètre à hauteur de poitrine égal ou supérieur à 10 cm ont été recensés. On y a trouvé 728 individus, appartenant à 90 espèces et représentant une aire basale de 22.4 m^2/ha. La plupart des arbres ont entre 15 et 25 m de haut et des diamètres ente 10 et 20 cm, mais un nombre important d'individus atteignes des valeurs supérieures, jusqu'à 40 m de haut et 60 cm de diamètre. Les 5 familles les plus importantes en termes de densité, diversité et dominance sont les *Clusiaceae, Euphorbiaceae, Myrtaceae, Rubiaceae* et *Myristicaceae.* Ensemble, elles représentent 46% de la valeur d'importance familiale (FIV). La composition spécifique révèle qu'un petit nombre d'espèces communes dominent la forêt: 19% des espèces représentent 60% de l'index de valeur d'importance (IVI). Seulement 21% des espèces ne sont représentées que par un seul individu. Les espèces principales sont *Mauloutchia chapelieri, Syzygium* sp., *Uapaca ferruginea, Canarium madagascariense, Symphonia eugenioides, Anthostema madagascariensis* et *Ochrocarpos decipiens*. La structure et la composition de la forêt est typique des forêts denses sempervirentes de basse altitude de Madagascar en général, et de celles du Sambirano en particulier. La grande majorité des espèces sont des endémiques malgaches et 14% d'entre elles sont des endémiques locales du Sambirano. En dehors d'espèces largement répandues dans les forêts malgaches, le reste des espèces est commune aux domaines de l'Est et de l'Ouest. Ces résultats confirment la classification phytogéographique classique de Perrier de la Bâthie et de Humbert.

KEY-WORDS: Tropical forest – Madagascar – 1-ha plot – Floristic composition – Sambirano.

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Introduction

Madagascar is characterized by an extraordinary variety of vegetation types, related to the diversity of climatic and geological features of the island. In an attempt to classify the different bioclimatic and phytogeographic regions, PERRIER DE LA BATHIE (1921, 1936) and HUMBERT (1955, 1965) divided Madagascar into five main domains. The Eastern and the Central Domains are under the influence of the south-eastern trade winds, which lead to cloud formation and heavy rainfall throughout the year due to the orographic ascent of humid air masses along the eastern escarpment. The climax vegetation is dense humid evergreen rainforest. The Western Domain, being in the orographic rain shadow of the trade winds, receives rainfall only during the monsoon. It has a contrasted tropical climate with a dry season of 5 to 10 months, culminating in August. The main vegetation type is dry deciduous forest. The dry season has an increasing importance as one moves to the southwest of the island. In the extreme south-west (Southern Domain) the climate is semi-desert and the typical vegetation is spiny desert.

Due to topographical features in the north, especially the Tsaratanana massif, the humid trade winds are deflected and reach ca. 100 km across a small portion of the western side of the island (HUMBERT, 1965; DONQUE, 1972). As a consequence, this region also receives appreciable rainfall during the dryer months. The dry season is only 3-4 months long and the amount of rainfall exceeds 2000 mm (LEGRIS & BLASCO, 1965; DONQUE, 1972). This region includes the Sambirano valley up to an elevation of 800 m, a portion of the northwestern coast between Ambaro Bay and Sahamalaza Bay, and the island of Nosy Be (HUMBERT, 1965). The climate is warm and humid enough for a climax of dense humid evergreen lowland rainforest similar to that on the eastern side of the island, and the Sambirano region has thus been incorporated into the "Région du Vent" of PERRIER DE LA BATHIE (1921) or the "Région orientale" of HUMBERT (1955). However, the Sambirano is separated from the Eastern Domain by the middle and high elevation rainforests of the Central Domain. As a consequence, a local endemic element is present in the flora which has never been accurately measured, despite an attempt by PERRIER DE LA BATHIE (1936) at a time when knowledge of plant species and distribution in Madagascar was still very incomplete. This endemic element has drove him to consider the area as a phytogeographically distinct entity, the Sambirano Domain (PERRIER DE LA BATHIE, 1936; HUMBERT; 1955). In the classical description of HUMBERT (1965), the lowland rainforest of the Sambirano Domain was described as the "Série à Chlaenacées (= Sarcolaenaceae) – Myristicacées – *Anthostema*", the abundance of *Sarcolaenaceae* being the distinctive character separating the Sambirano rainforests from those of the Eastern Domain.

This classical approach to classify the Madagascar vegetation received the support of KOECHLIN & al. (1974), with some restrictions however, especially regarding the higher elevations, the western slopes and the extreme south. They did not question the validity of the Sambirano Domain, and state that its flora is made up of three components: a) a basic element shared with Eastern forests, b) a Western component, which penetrates into the domain due to proximity and climatic similarities, especially in degraded formations, and c) a specific component of endemic taxa with affinities in the Eastern as well as the Western Domains. In their recent work using GIS to compare natural vegetation with geological information, DU PUY & MOAT (1996) considered the Sambirano region as physionomically belonging to the evergreen humid rainforest of the East, but also as a local center of endemicity. Humbert's system of classification has recently been criticized by LOWRY & al. (1997), who consider that much more field work, including the establishment of 1-ha permanent plots inventories and accurate species distribution maps, is necessary to develop a sound understanding of Madagascar phytogeography. It would then be possible to apply a more objective approach such as the one WHITE (1983) applied to continental Africa. They propose that phytogeographic divisions should rather be based on the bioclimatic map of CORNET (1974), which puts much emphasis on the rainfall regime and less on the temperature, resulting in the inclusion of most of the Sambirano Domain of HUMBERT (1965) in the bioclimatic zone of the central part of the island, with its margins belonging to the dry tropical bioclimate of the West.

The lowland rainforests on the southwestern foothills of the Manongarivo massif are located on the Western edge of the Sambirano Domain as classically defined, close to the boundaries of the Western and Central Domain. This location renders them an interesting spot to study structure and floristic composition in relation to the phytogeographic issues exposed above.

Deforestation around the Manongarivo massif has been increasing in the last decades due to heavy human pressure for local agriculture (shifting rice cultivation). In some places it penetrates into the Manongarivo Special Reserve along the main rivers (GAUTIER & al., 1999). It was therefore urgent to make an assessment of this type of forest, and the opportunity came within the framework of the botanical investigations conducted by the Botanical Garden of Geneva as part of the research project entitled "Ecologie Politique et Biodiversité" funded by Swiss National Fund. Although other vegetation analysis was conducted in the project using the linear sampling method (GAUTIER & al., 1994), the methodology that was implemented here was the classical 1-ha permanent plot sampling, which allows comparison with similar work conducted in many tropical forests. In Madagascar, this method has been widely implemented by various researchers (SCHATZ, 1994; RABEVOHITRA & al., 1996).

The vegetation of Manongarivo Special Reserve has already been studied at sites between 750 and 1200 m elevation by RAZAFIMANDIMBISON (1993) and between 150 and 700 m elevation by RAHARIMALALA (1991). The latter study included 6 plots, four of which were

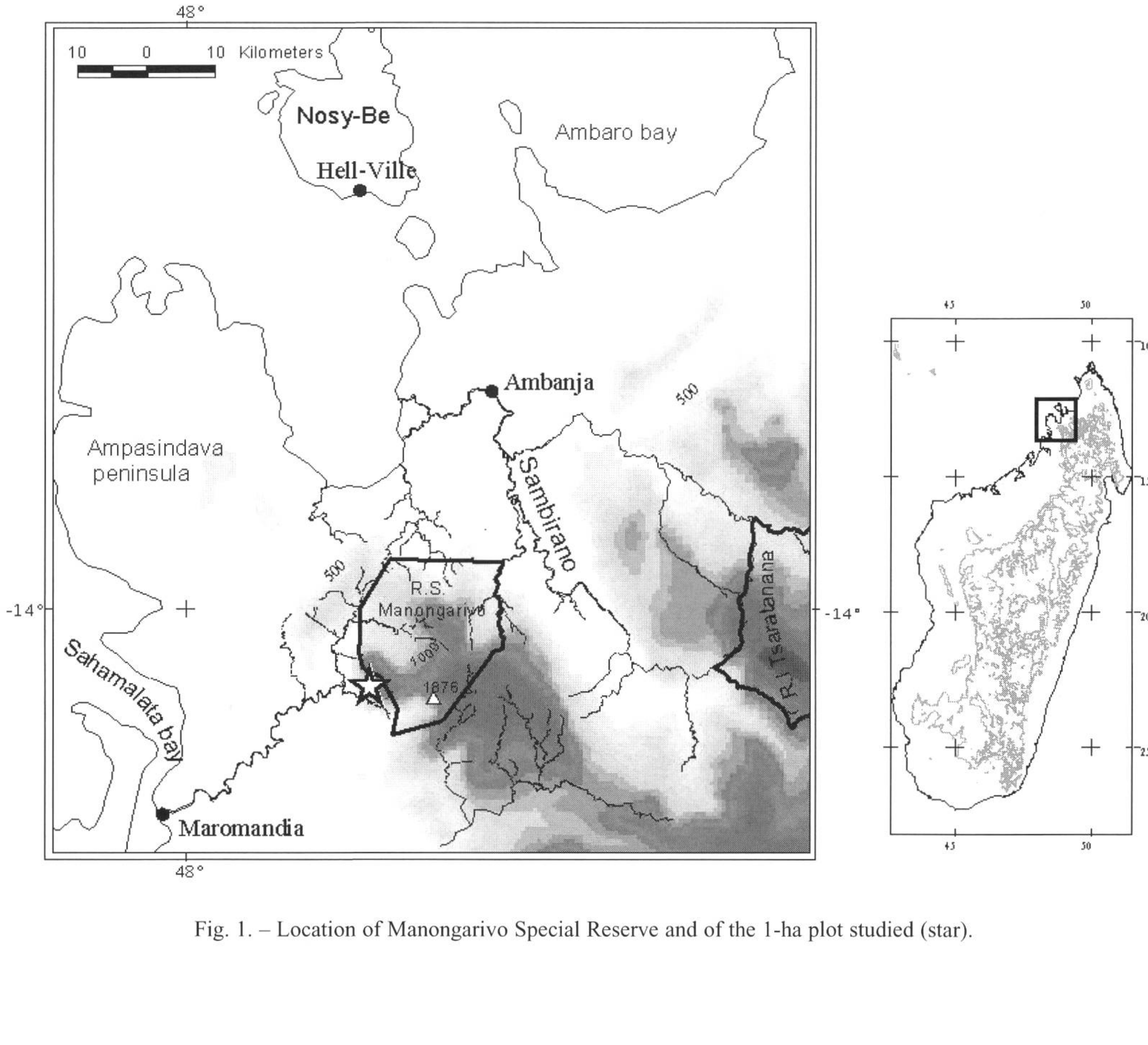

Fig. 1. – Location of Manongarivo Special Reserve and of the 1-ha plot studied (star).

located in the same forest block as the 1-ha plot used for this study, the remaining two being at higher elevation, on the slopes of the Bekolosy chain. According to her study, forest in the lower plots has a smaller stature than in the upper plots, with trees of the upper stratum reaching only 15-25 m in height. Main species in the lower plots included *Brochoneura rarabe* (= *Mauloutchia chapelieri*), *Leptolaena* sp., *Uapaca ambanjensis* and *Uapaca littoralis*.

Study site

The study was conducted in the southwestern foothills of the Manongarivo massif (Fig. 1), a western extension of the main orographic axis that extends in a N-N-E to S-S-W direction, along the east coastline of Madagascar. This massif reaches an altitude of 1876 m and includes the Manongarivo Special Reserve, a protected area of 35'000 ha of forest. According to HUMBERT's phytogeographical system (1965), the reserve belongs to the Sambirano Domain below 800 m elevation, and to the Central Domain above, but the southwestern foothills are not far from the limit of the Western Domain.

The plot studied was selected in a lowland rainforest southwest of the Manongarivo massif, below the Bekolosy chain, on the Besinkara plateau (14°04'S; 48°17'E). This plateau, which was originally included in the Manongarivo Special Reserve, was excluded from it when the boundaries were redefined in 1977. Although most of the plateau has since been clear-felled for upland rice cultivation, a forest covering ca. 1 × 2 km has been preserved (GAUTIER & al. 1999) with no major human disturbance except for the occasional harvest of non-timber forest products.

The geology of the Sambirano region is made up of cristalline rocks (gneiss and migmatites) and basaltic volcanic rocks. The Bekolosy chain consists principally of alcaline granites, depleted of quartz and feldspath but containing much silica (RAZAFIMANDIBISON, 1993). Soils below 700 m elevation are mainly ferruginous on sandy substrate and young brown soils on volcanic material (RAHARIMALALA, 1991).

The climate of the the Sambirano Domain is subequatorial, with annual rainfall exceeding 2000 mm and a mean annual temperature of 26°C. Temperature and rainfall are affected by the monsoon air currents (running N-W) and the south-east trade wind (which predominates all seasons) produced by the Indian Ocean high. Seasonal temperature variations are not noticable, and the dry season is moderated by the high humidity, which never drops below 70%. Eighty percent of total precipitation falls during the warmest season, from November to April. Between May and August temperature and rainfall tend to decrease, and the minimum rainfall occurs during September and October. Over 800 m of elevation there is a cold-humid tropical climate, with temperatures averaging between 15° and 20°C (RAHARIMALALA, 1991).

The nearest meteorological stations (Ambanja and Nosy-Be) report the following climatic datas, based on 50 years of records (Table 1).

Table 1. – Meteorological data from Ambanja (13°40'S, 48°27'E; 40 m) and Nosy-Be (13°19'S, 48°19'E; 9 m).

	Ambanja	***Nosy-Be***
Annual precipitation	2094.7 mm	2254.5 mm
Days with recorded precipitation	120.6	172.7
Mean annual humidity	77%	74%
Mean annual temperature	26.0°C	25.9°C

Methods

Field work was conducted in September 1996 and September 1997. The inventory was done using the permanent 1-ha plot method. A 1-hectare surface was established in the shape of a

20 × 500 m transect, located ca. 1.5 km South of the settlement of Ambalafary. Extreme coordinates of the plot are 599520; 1332800 and 599808; 1332464 (Laborde projection). Mean elevation was 220 m. The transect was divided in 25 quadrats (20 × 20 m), which were considered as sampling units. All trees with a diameter at breast height of at least 10 cm were marked with a numbered copper tag. For each tree ≥10 cm dbh, diameter was measured, tree height was estimated and vernacular names were recorded. Specimens of most of the individuals were collected (2 sheets for sterile plants, 7 for fertile material). Following a first field identification, further identification was performed at 'Parc Botanique et Zoologique de Tsimbazaza' (TAN), at the 'Département des recherches forestières et piscicoles du FOFIFA' (TEF), and at the 'Conservatoire et Jardin botaniques de Genève' (G). Fertile specimen were also sent to specialists at various institutions. Individuals were then regrouped by species following identifications, and by morphospecies for unidentified material. Fertile specimens were deposited at G, TAN, TEF, P, MO, K and WAG, and sterile specimens at G.

From the original data, we calculated the density of trees and the basal area. To assess forest structure, trees were grouped in diameter and height classes, which were plotted on a histogram.

Using standard methodology (CURTIS & McINTOSH, 1951; MORI & al., 1983), the following parameters were calculated. At specific and family level: relative density and relative dominance; at specific level only: relative frequency; at the family level only: relative diversity. From these data, Importance Value Index (IVI) and Family Importance Value (FIV) were calculated for species and families, respectively. In order to construct a species-area curve, the number of additional species occurring in each consecutive sub-samples unit (20 × 20 m) was plotted against surface increment.

The phytogeographic affinities of the species encountered in the plot were assessed based on their known distribution according to the Flore de Madagascar et des Comores (HUMBERT, 1935-) as well as on other botanical revisions for families not yet published in this flora or for which a more recent treatment was available. Additional information on distribution was extracted from the Tropicos database of the Missouri Botanical Garden (http://mobot.mobot.org/Pick/Search/pick.html), which includes the botanical information of the Conspectus of the Vascular Plants of Madagascar projet (SCHATZ & al., 1996). This geographic information was converted when necessary to the phytogeographical system of HUMBERT (1955).

Results

Forest structure

In the one hectare sampled, a density of 728 trees dbh ≥10 cm was recorded, representing a basal area of 22.4 m^2.

Considering tree diameter, 51.0% of individuals occur in the 10-15 cm dbh size-class, 22.7% in the 15-20 cm range. The lowest percentages occur in the 45-50 cm range (0.55%), 50-55 cm range (0.96%) and 55-60 cm range (0.27%). Altogether, 96.8% of trees are less than 40 cm dbh (Table 2). The biggest trees, represented by *Mauloutchia chapelieri*, have a dbh of 57.9 and 59.8 cm. Distribution in dbh classes shows an inversed J-shaped curve (Fig. 2).

Distribution of trees by height classes shows a bell-shaped curve, but the values do not include trees smaller than 10 cm dbh, which have a great influence on classes shorter than 15 m (Fig. 3). Most of the trees fall within the 15-20 m height class (29.8%) and the 20-25 m height class (29%), which correspond to the average height of the canopy. There is no clearcut stratification of trees. Only a few trees are emergent, but they do not exceed 40 m in height (Table 3).

Table 2. – Distribution of trees in 5 cm dbh interval size classes.

DBH [cm]	***N° of trees***	***% of trees***
[10-15]	371	51.0
[15-20[	165	22.7
[20-25]	71	9.8
[25-30]	48	6.6
[30-35]	32	4.4
[35-40]	18	2.5
[40-45]	10	1.4
[45-50]	4	0.6
[50-55]	7	1.0
[55-60]	2	0.3

Table 3. – Distribution of trees in 5 m height interval size classes.

Height [m] (DBH≥10cm)	***N° of trees (DBH≥10cm)***	***% of trees***
< 5	0	0.0
[5-10]	6	0.8
[10-15]	86	11.9
[15-20]	216	29.8
[20-25]	195	26.9
[25-30]	113	15.6
[30-35]	78	10.7
[35-40]	32	4.4

Table 4. – Families with highest values of relative density, relative dominance, relative diversity, and FIV, in descending order. Families that do not rank among the ten most important in FIV value appear in italics.

Relative density		**Relative dominance**		**Relative diversity**		**FIV**	
Clusiaceae	17.7	Clusiaceae	15.3	Rubiaceae	12.2	Clusiaceae	40.8
Myrtaceae	12.2	Myristicaceae	13.0	Lauraceae	8.9	Euphorbiaceae	29.1
Euphorbiaceae	11.7	Euphorbiaceae	13.0	Clusiaceae	7.8	Myrtaceae	27.2
Rubiaceae	5.9	Myrtaceae	10.5	Euphorbiaceae	4.4	Rubiaceae	21.2
Myristicaceae	5.0	Burseraceae	8.0	Myrtaceae	4.4	Myristicaceae	19.0
Burseraceae	4.7	*Sarcolaenaceae*	4.8	Sapotaceae	4.4	Lauraceae	16.3
Erythroxylaceae	4.4	*Asteraceae*	4.6	Erythroxylaceae	3.3	Burseraceae	13.8
Lauraceae	4.1	*Combretaceae*	3.4	Annonaceae	3.3	Sapotaceae	10.5
Sapotaceae	3.9	Lauraceae	3.3	*Ebenaceae*	3.3	Erythroxylaceae	9.5
Arecaceae	3.7	Rubiaceae	3.1	*Anacardiaceae*	3.3	Annonaceae	9.4

Floristic composition

Family Level – Thirty-eight families were recorded in the plot, treating *Papilionoideae, Mimosoideae* and *Caesalpinioideae* as a single family *(Leguminosae).* In Table 4, the ten most important families for each relative parameter and FIV are listed. The value of each relative parameter for the ten families with the highest FIV are represented in Figure 4. The complete results for each family are given in Appendix 1.

Regarding relative density, the 10 most abundant families are *Clusiaceae, Myrtaceae, Euphorbiaceae, Rubiaceae, Myristicaceae, Burseraceae, Erythroxylaceae, Lauraceae, Sapotaceae* and *Arecaceae. Clusiaceae* account for 17.7 % of all individuals. The densities of *Myrtaceae* and *Euphorbiaceae* exceed 10%, while those of all the other families do not reach 6 %. *Clusiaceae, Myrtaceae, Euphorbiaceae* are clearly the most abundant families: together they contribute 41.6% of all trees censed in the plot.

Families with highest dominance are *Clusiaceae, Myristicaceae, Euphorbiaceae, Myrtaceae, Burseraceae, Sarcolaenaceae, Asteraceae, Combretaceae, Lauraceae* and *Rubiaceae.* Together they account for 78.9% of the total basal area. It is striking that the basal area of *Myristicaceae* (13%) is due to a single species, *Mauloutchia chapelieri.*

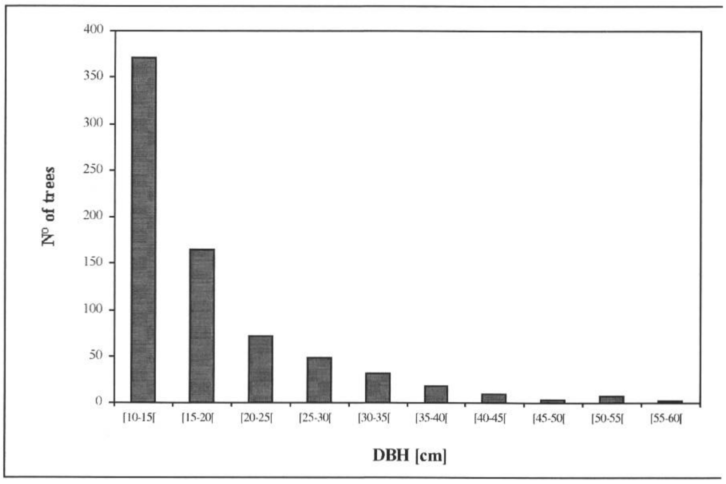

Fig. 2. – Distribution of trees in 5 cm dbh interval size classes.

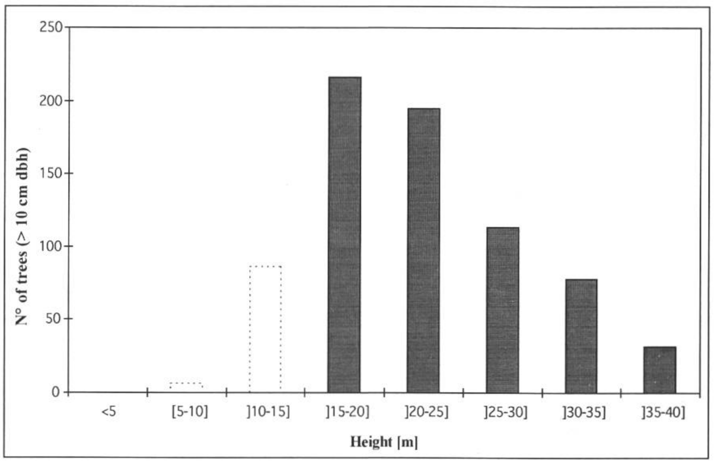

Fig. 3. – Distribution of trees in 5 m height interval size classes.

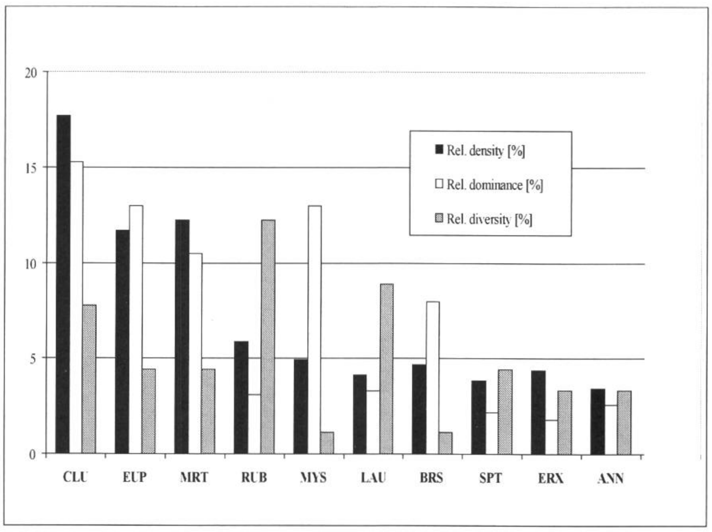

Fig. 4. – Relative density, relative dominance, and relative diversity of the ten most important families in FIV (CLU: Clusiaceae; EUP: Euphorbiaceae; MRT: Myrtaceae; RUB: Rubiaceae; MYS: Myristicaceae; LAU: Lauraceae; BRS: Burseraceae; SPT: Sapotaceae; ERX: Erythroxylaceae; ANN: Annonaceae).

The 10 most species-rich families are *Rubiaceae, Lauraceae, Clusiaceae, Euphorbiaceae, Myrtaceae, Sapotaceae, Erythroxylaceae, Annonaceae, Ebenaceae* and *Anacardiaceae.* The relative diversity value of *Rubiaceae* (11 species) represents 12.2% of the total species diversity of the plot. Nineteen families are represented by a single species, 6 by 2 species, 7 by 3 species and 3 by 4 species.

Regarding Family Importance Value (FIV), *Clusiaceae* are the most important family in the plot, with an FIV of 40.8. They also have the highest relative density and relative dominance values. When comparing FIV and the 3 relative values of the ten most important families, only *Clusiaceae, Euphorbiaceae, Myrtaceae, Rubiaceae* and *Lauraceae* appear among the first ten families for all parameters. *Myristicaceae* and *Burseraceae* have high density and dominance values, but they are both represented by a single species (*Mauloutchia chapelieri* and *Canarium madagascariense*, respectively). *Annonaceae* are at tenth in FIV due to their relative diversity. *Arecaceae* are tenth in relative density, but they drop to position 15 in FIV, because of their low relative dominance and relative diversity: they are represented only by two species (*Ravenea sambiranensis* and *Arecaceae* indet.1) and the trees have small dbh values. Considering relative dominance, three families, *Sarcolaenaceae, Asteraceae* and *Combretaceae,* have rather high values and account for 12.8% of total basal area, but they are represented by only a few individuals, and by one or two species. Thus, they are not among the 10 families with the highest FIV.

Specific level – Ninety species were recorded in the plot. Table 5 lists the ten most important species in each relative parameter. The value of each parameter for the ten species with the higher IVI are represented in Figure 5. Appendix 2 gives the results for all species.

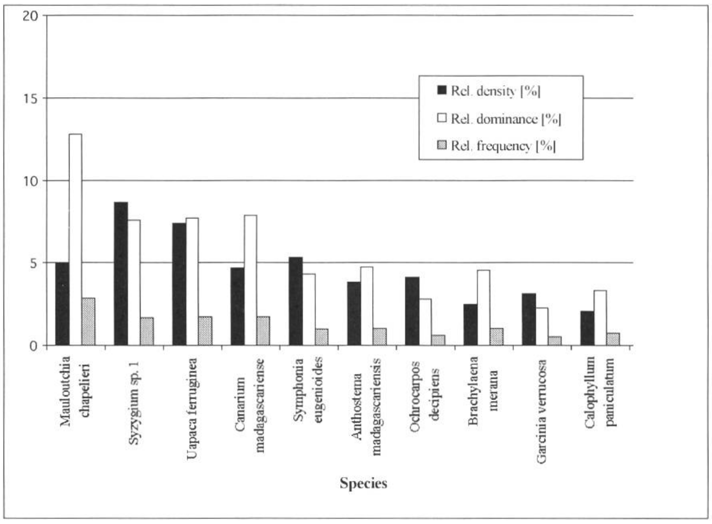

Fig. 5. – Relative density, relative dominance, and relative frequency of the ten most important species in IVI.

A small group of species dominates the plot: 11 common species (12.2% of the total number of species) account for 50.5 % of all trees. The majority of species (55.5%) are represented by less than 5 individuals: 16 species are represented by 2 individuals, but only 19 species (21.11%) are represented by a single individual. Regarding relative dominance, less than 8% of the species contribute 50% of total basal area. High dominance may be achieved by a great number of small trees or by few large trees. *Ravenea sambiranensis* is eighth in relative density (26 individuals), but it drops to 26th position in relative dominance. On the contrary, *Leptolaena cuspidata* and *Terminalia perrieri* are represented only by 7 individuals, but they are sixth and nineth in relative dominance, respectively.

Figure 6 shows the species/area accumulation curve for the plot. It follows a classical accumulation curve. In four consecutive quadrats (n° 20-23) no new species occur. Nevertheless in quadrat n° 24 two additional species were encountered making it difficult to determine if one hectare is satisfactory for a fully representative sample for this forest.

Table. 5. – Species with highest values of relative density, relative dominance, relative frequency, and IVI, in descending order. Underlined: species that do not occur among the ten most important in IVI.

Relative density	%	**Relative dominance**	%	**Relative frequency**	%	**IVI**	%
Syzygium sp.1	8.65	*Mauloutchia chapelieri*	12.99	*Syzygium* sp.1	4.89	*Mauloutchia chapelieri*	21.93
Uapaca ferruginea	7.42	*Canarium madagascariense*	7.84	*Mauloutchia chapelieri*	4.00	*Syzygium* sp.1	21.24
Symphonia eugenioides	5.36	*Uapaca ferruginea*	7.84	*Canarium madagascariense*	4.00	*Uapaca ferruginea*	19.26
Mauloutchia chapelieri	4.95	*Syzygium* sp.1	7.70	*Uapaca ferruginea*	4.00	*Canarium madagascariense*	16.66
Canarium madagascariense	4.67	*Anthostema madagascariensis*	4.82	*Symphonia eugenioides*	3.56	*Symphonia eugenioides*	13.32
Ochrocarpos decipiens	4.12	*Leptolaena cuspidata*	4.65	*Ochrocarpos decipiens*	3.33	*Anthostema madagascariensis*	10.66
Anthostema madagascariensis	3.85	*Brachylaena merana*	4.64	*Garcinia verrucosa*	3.11	*Ochrocarpos decipiens*	10.33
Ravenea sambiranensis	3.57	*Symphonia eugenioides*	4.40	*Calophyllum paniculatum*	2.67	*Brachylaena merana*	8.89
Garcinia verrucosa	3.16	*Calophyllum paniculatum*	3.69	*Canthium* sp. 1	2.67	*Garcinia verrucosa*	8.57
Brachylaena merana	2.47	*Terminalia perrieri*	3.40	*Polyalthia richardiana*	2.44	*Calophyllum paniculatum*	8.42

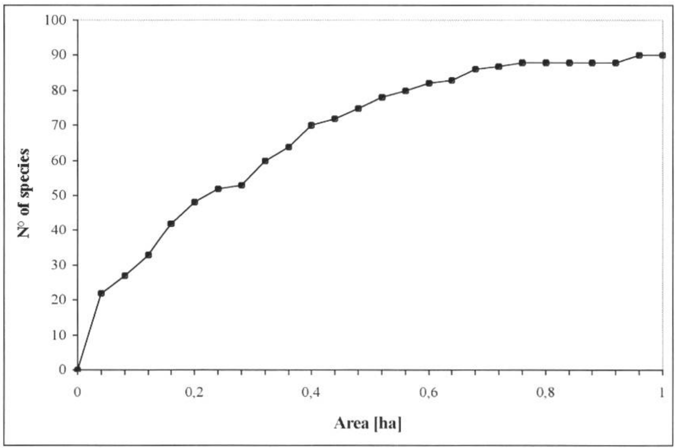

Fig. 6. – Species-area accumulation curve of the 1-ha plot in Manongarivo. Each sub-unit is represented by a 20 × 20 m quadrat.

Phytogeographic affinities

Of the 90 species recorded in the plot, 58 were identified to specific level (64% of the species, representing 75% of the number of individuals and 79% of basal area). The known distribution of these species is given in Appendix 2, and reveals that 54 (93%) are endemic to Madagascar. Within Madagascar, the occurrence of these 58 species in the main phytogeographic domains is given in Table 6. The contribution of Sambirano local endemics is 14%. The majority of the species (33 species; 57%) are shared with the Eastern Domain. Twenty-eight species (48%) have also been recorded from the Central Domain, and 26 (45%) from the Western Domain. Only 2 species (3%) are shared with the Southern Domain. Figure 7 shows the proportion of species according to major distribution pattern.

Table 6. – Phytogeographic affinities of the identified species of the Manongarivo plot.

Phytogeographic affinities	***Sambirano endemics***	***Species in common with the:***			
		Eastern Domain	***Central Domain***	***Western Domain***	***Southern Domain***
number of species	8	33	28	26	2
percentage	13.8%	56.9%	48.3%	44.8%	3.4%

Discussion

Forest structure

The density of 728 trees ≥10 cm dbh is within the range of 167 to 1947 trees per hectare reported by GENTRY (1982) for neotropical forests sampled by different methods. ROLLET (1983) estimates that the relative density in tropical forests around the world averages 552 trees/ha (dbh ≥10cm). A series of 1-ha plots set in low elevation rainforests of eastern Madagascar (RABEVOHITRA & al., 1996; RAKOTOMALAZA & MESSMER, 1999) record a number of trees (dbh ≥10cm) between 542 and 1223 trees per hectare (Table 7). The comparison with woody plant inventories of tropical rainforests sampled in various continents shows that tree density seems to have a similar range of variation throughout the world (Table 8).

Table 7. – Number of trees per hectare (dbh ≥10 cm) in Manongarivo Special Reserve and in low elevation rainforests sites along the east coast of Madagascar.

Site	*Reference*	*N° of trees/ha (dbh ≥10cm)*
Manongarivo		**728**
Andranomintina (plot 1)	RABEVOHITRA & al., 1996	1223
Andranomintina (plot 2)	RABEVOHITRA & al., 1996	1105
Tampolo (plot 1)	RABEVOHITRA & al., 1996	869
Tampolo (plot 2)	RABEVOHITRA & al., 1996	679
Tanambao (plot 1)	RABEVOHITRA & al., 1996	542
Tanambao (plot 2)	RABEVOHITRA & al., 1996	690
Manombo (plot 1)	RABEVOHITRA & al., 1996	789
Manombo (plot 2)	RABEVOHITRA & al., 1996	603
Ste-Luce (plot 1)	RABEVOHITRA & al., 1996	1064
Ste-Luce (plot 2)	RABEVOHITRA & al., 1996	1037
Andohahela	RAKOTOMALAZA & MESSMER, 1999	739

Table 8. – Number of trees per hectare (dbh ≥10cm) in various tropical rainforest sites.

Site	*Reference*	*N° of trees/ha (dbh ≥10cm)*
Yapo (floodplain forest), Ivory Coast	CORTHAY, 1996	605
Yapo (unflooded forest), Ivory Coast	CORTHAY, 1996	649
Jenaro Herrera, Peru	SPICHIGER & al., 1996	482
Alto Parana	SPICHIGER & al., 1992	442
Alto Ivon, Bolivia	BOOM, 1986	649
Yasunì (floodplain forest), Ecuador	BALSLEV & al., 1987	417
Yasunì (unflooded forest), Ecuador	BALSLEV & al., 1987	728

The basal area (22.4 m²/ha) is close to the lowest value, reported by MORI & al. (1983) for five moist lowland neotropical forests (ranging from 21.5-53.0 m²/ha) sampled by the point-centered quarter method (COTTAM & CURTIS, 1956). Low basal area have also been found in other lowland rainforests of Madagascar sampled using the permanent 1-ha plot method: 34.1 m²/ha at Andohahela (RAKOTOMALAZA & MESSMER, 1999), and a range of 19.0 to 38.9 m²/ha in ten different eastern lowland forests (RABEVOHITRA & al., 1996). Other African and neotropical samples record higher basal areas (Table 9).

The sampling method used here is not adequate to address properly the question of vertical structure of the vegetation and stature of the forest, because a small number of very large trees can have a strong contribution to the canopy if their crown is large. Nevertheless, the conclusion of RHARIMALALA (1991), who worked in the same forest and found it was rather low in stature, is not supported by our data. In fact, the forest of the Besinkara Plateau lies in some places on very shallow soil near rocky outcrops, in which some plots were set in her study, whereas our 1-ha plot was located in a stand where forest was fully developped on a deeper soil.

Floristic composition

Family Level – In the plot sampled, more than 50% of all trees are represented by 5 families. Similar results were recorded at Andohahela (Madagascar), where 50% of trees were represented by 9 families (RAKOTOMALAZA & MESSMER, 1999). According to

Table 9. – Basal area/ha in Manonagarivo and in other lowland tropical rainforests sites.

	Site	Reference	Basal area [m²]
Madagascar	**Manongarivo**		**22.4**
	Andohahela	RAKOTOMALAZA & MESSMER, 1999	34.1
	Tampolo (plot 1)	RABEVOHITRA & al., 1996	33.3
	Tampolo (plot 2)	RABEVOHITRA & al., 1996	38.9
	Tanambao (plot 1)	RABEVOHITRA & al., 1996	29.2
	Tanambao (plot 2)	RABEVOHITRA & al., 1996	23.6
	Manombo (plot 1)	RABEVOHITRA & al., 1996	24.0
	Manombo (plot 2)	RABEVOHITRA & al., 1996	19.0
	Ste. Luce (plot 1)	RABEVOHITRA & al., 1996	29.0
	Ste. Luce (plot 2)	RABEVOHITRA & al., 1996	25.9
	Andranomintina (plot 1)	RABEVOHITRA & al., 1996	27.9
	Andranomintina (plot 2)	RABEVOHITRA & al., 1996	25.3
Yasunì, Ecuador		BALSLEV & al., 1987	33.7
Bahía, Brazil		MORI & al., 1983	51.9
Alto Parana		SPICHIGER & al., 1992	18.5
Jenaro Herrera, Peru		SPICHIGER & al., 1996	22.6
Yapo, Ivory Coast		CORTHAY, 1996	40.0

RABEVOHITRA & al. (1996) 4, 5 or 6 families always represent more than 50% of total trees in littoral forests along Madagascar's east coast. Table 10 shows that in Manonagrivo and in plots in eastern Madagascar, *Myrtaceae, Euphorbiaceae, Flacourtiaceae, Clusiaceae* and *Lauraceae* are frequently among the ten most abundant families. *Erythroxylaceae* and *Arecaceae* seem to be the only numerically important families of the Manongarivo plot that do not occur in the first ten positions in other plots in Madagascar.

According to GENTRY (1988), family composition of lowland rainforests of the tropics tend to be similar. He lists 11 families *(Leguminosae, Lauraceae, Annonaceae, Rubiaceae, Moraceae, Myristicaceae, Sapotaceae, Meliaceae, Arecaceae, Euphorbiaceae* and *Bignoniaceae)* that contribute half of the species richness to 0.1-ha samples in lowland neotropical forests. At least eight of these families are always among the ten most species-rich families. The same families, except for *Bignoniaceae* and *Arecaceae,* are the most species-rich in Africa and Asia as well. GENTRY (1988) also remarks that the dominance of *Leguminosae* in the Neotropics and Africa is equal when only trees ≥10cm dbh are considered.

Among the above-mentioned families, *Rubiaceae, Lauraceae, Euphorbiaceae, Sapotaceae* and *Annonaceae* are among the ten most important families for relative diversity and FIV in the plot sampled here (Table 11). It is remarkable that in Madagascar, *Leguminosae* seem to be much less important than in neotropical and African lowland forests. In Manongarivo they are 13th in FIV (FIV value: 7.71), while at Andohahela (RAKOTOMALAZA & MESSMER, 1999) they are 19th out of 31 families, with an FIV value of 5.37. The same scarcity of *Leguminosae* in Madagascar was recorded by SCHATZ (1994) during the inventory of three 1-ha plots in lowland forests of Ranomafana National Park. On the other hand, in Madagascar *Clusiaceae* and *Myrtaceae* are much more abundant and more species-rich.

HUMBERT (1965), in his description of Malagasy lowland rainforests composition, indicated *Rubiaceae, Euphorbiaceae, Araliaceae, Ebenaceae, Sapindaceae, Anacardiaceae, Elaeocarpaceae, Lauraceae, Clusiaceae, Myrtaceae, Malpighiaceae, Monimiaceae, Flacourtiaceae, Loganiaceae* and *Leguminosae* as the most representative families. Among these, only *Elaeo-*

carpaceae and *Malpighiaceae* did not appear in Manongarivo, while *Loganiaceae* and *Monimiaceae* were represented by only two and one individual, respectively.

Specific level – In this inventory 90 species were encountered. The number of species per hectare seems to be fluctuating in Madagascar as in other tropical countries: a series of 1-ha plots sampled by the same method display a range of 38 to 146 species (RAKOTOMALAZA & MESSMER, 1999; RABEVOHITRA & al., 1996). In one hectare of unflooded forest in Amazonian Ecuador, BALSLEV & al. (1987) recorded 228 species. In French Guiana, MORI & BOOM (1987) found 241 species in a 619-tree sample (approximately 1-hectare), and in Alto Ivon (Bolivia) the number of species/ha was 94 (BOOM, 1986). Lower diversity values were recorded in Côte d'Ivoire, where CORTHAY (1996) found 76 and 77 species/ha in two plots in the Yapo forest, and in the Alto Parana, where SPICHIGER & al. (1992) found 60 species.

According to ROLLET (1983), 50% of individuals on average are represented by 20 species in undisturbed lowland Amazonian forests of Venezuela. In Manonagrivo, half of the trees are represented by only 11 species. A similar value (12 species) was found at Andohahela, Madagascar (RAKOTOMALAZA & MESSMER, 1999).

Table 10.- The ten most abundant families in Manongarivo and in 7 other Malagasy lowland forests. Families among the ten most abundant in at least five plots appear in bold type.

Manongarivo	**Andohahela**	**Andranomintina (plot 1-2)**	**Tampolo (plot 1-2)**
	RAKOTOMALAZA & MESSMER, 1999	RABEVOHITRA & al., 1996	RABEVOHITRA & al., 1996
Clusiaceae	Rubiaceae	Fabaceae	**Euphorbiaceae**
Myrtaceae	**Clusiaceae**	**Euphorbiaceae**	Lecytidaceae
Euphorbiaceae	**Lauraceae**	Sapotaceae	Apocynaceae
Rubiaceae	Myrsinaceae	**Myrtaceae**	Myristicaceae
Myristicaceae	Monimiaceae	Sarcolaenaceae	**Fabaceae**
Burseraceae	Anacardiaceae	**Clusiaceae**	Burseraceae
Erythroxylaceae	Aquifoliaceae	**Lauraceae**	Simaroubaceae
Lauraceae	Liliaceae	Oleaceae	**Myrtaceae**
Sapotaceae	Sapotaceae	Annonaceae	**Clusiaceae**
Arecaceae	**Myrtaceae**	Anacardiaceae	**Flacourtiaceae**

Tanambao (plot 1-2)	**Manombo (plot 1)**	**Manombo (plot 2)**	**Ste. Luce (plot 1-2)**
RABEVOHITRA & al., 1996	RABEVOHITRA & al., 1996	RABEVOHITRA & al., 1996	RABEVOHITRA & al., 1996
Euphorbiaceae	**Myrtaceae**	Fabaceae	**Flacourtiaceae**
Apocynaceae	Annonaceae	Compositae	Fabaceae
Clusiaceae	Tiliaceae	Ebenaceae	**Euphorbiaceae**
Annonaceae	Moraceae	**Euphorbiaceae**	Pandanaceae
Araliaceae	**Lauraceae**	Anacardiaceae	**Myrtaceae**
Myrtaceae	**Flacourtiaceae**	**Flacourtiaceae**	Ebenaceae
Flacourtiaceae	**Euphorbiaceae**	Asteraceae	Canellaceae
Sarcolaenaceae	Sapotaceae	Verbenaceae	Anacardiaceae
Lauraceae	Myristicaceae	Oleaceae	Oleaceae
Monimiaceae	Monimiaceae	Icacinaceae	Agavaceae

Table 11. – Family Importance Value of the 15 most important plant families in Manongarivo and in other lowland tropical forests (for MORI & al., 1983 only the first 10 FIV were reported).

Manongarivo (Madagascar)		***Andohahela (Madagascar)***		***Yapo (Ivory Coast)***	
		RAKOTOMALAZA & MESSMER, 1999		CORTHAY, 1996	
Family	***FIV***	***Family***	***FIV***	***Family***	***FIV***
Clusiaceae	40.78	Rubiaceae	31.10	Sapotaceae	34.15
Euphorbiaceae	29.09	Clusiaceae	28.40	Leguminosae	32.27
Myrtaceae	27.17	Lauraceae	19.41	Burseraceae	24.83
Rubiaceae	21.23	Elaeocarpaceae	16.51	Euphorbiaceae	18.88
Myristicaceae	19.04	Sapotaceae	14.30	Meliaceae	18.70
Lauraceae	16.32	Myrsinaceae	13.81	Sterculiaceae	18.57
Burseraceae	13.77	Myrtaceae	12.33	Ebenaceae	15.49
Sapotaceae	10.48	Moraceae	11.42	Clusiaceae	14.85
Erythroxylaceae	9.51	Euphorbiaceae	11.21	Olacaceae	13.51
Annonaceae	9.37	Monimiaceae	10.48	Chrysobalanaceae	12.08
Sarcolaenaceae	8.27	Aquifoliaceae	9.61	Flacourtiaceae	11.91
Asteraceae	8.22	Annonaceae	9.32	Combretaceae	8.75
Leguminosae	7.71	Liliaceae	7.74	Lecythidaceae	6.64
Ebenaceae	7.57	Anacardiaceae	7.67	Irvingiaceae	6.37
Arecaceae	7.17	Sterculiaceae	7.58	Scytopetalaceae	6.35

Yasunì (Ecuador)		***Jenaro Herrera (Peru)***		***Alto Parana (Paraguay)***	
BALSLEV & al., 1987		SPICHIGER & al., 1996		SPICHIGER & al., 1992	
Family	***FIV***	***Family***	***FIV***	***Family***	***FIV***
Arecaceae	55.66	Leguminosae	29.07	Meliaceae	44.4
Moraceae	36.48	Sapotaceae	28.22	Lauraceae	42.4
Leguminosae	23.73	Moraceae	23.50	Sapotaceae	39.4
Bombacaceae	19.66	Myristicaceae	18.84	Leguminosae	31.9
Myristicaceae	19.59	Lauraceae	18.28	Rutaceae	25.4
Rubiaceae	14.73	Chrysobalanaceae	18.05	Moraceae	20.4
Meliaceae	11.62	Lecythidaceae	17.38	Boraginaceae	14.7
Euphorbiaceae	8.15	Burseraceae	11.84	Arecaceae	11.1
Cecropiaceae	7.86	Annonaceae	10.67	Annonaceae	10.1
Lecythidaceae	7.54	Arecaceae	9.47	Bignoniaceae	8.2
Lauraceae	7.37	Vochysiaceae	9.43	Solanaceae	4.6
Sterculiaceae	6.72	Humiriaceae	8.52	Myrtaceae	3.5
Flacourtiaceae	6.18	Cecropiaceae	7.89	Sapindaceae	3.2
Polygonaceae	6.07	Rubiaceae	7.79	Flacourtiaceae	2.7
Sapotaceae	5.59	Combretaceae	7.50	Euphorbiaceae	2.5

Alto Ivon (Bolivia)		***Bahia (Brazil)***	
BOOM, 1986		MORI & al., 1983	
Family	***FIV***	***Family***	***FIV***
Moraceae	53.3	Myrtaceae	52.2
Myristicaceae	41.1	Sapotaceae	39.4
Palmae	35.7	Caesalpiniaceae	28.5
Leguminosae	30.1	Lauraceae	20.8
Melastomataceae	20.1	Chrysobalanaceae	15.4
Cecropiaceae	15.3	Euphorbiaceae	12.1
Vochysiaceae	13.9	Bombacaceae	11.9
Annonaceae	8.7	Lecythidaceae	9.5
Chrysobalanaceae	8.3	Melastomataceae	9.4
Rubiaceae	8.3	Moraceae	9.4
Lauraceae	7.2		
Burseraceae	6.8		
Euphorbiaceae	5.7		
Flacourtiaceae	5.2		
Myrtaceae	4.5		

MORI & al. (1983) consider as rare species those who are found only once in the sample. In a lowland forest of eastern Brazil 41% species were rare, according to this definition. In the study by BALSLEV & al. (1987) the percentages of species represented by only one individual were 55% in unflooded forest and 62% in a floodplain forest of Ecuador. Similar values were found in Peru – 55% – (SPICHIGER & al., 1996) and in French Guiana – 60.1% – (MORI & BOOM, 1987). A forest inventory in Andohahela, Madagascar (RAKOTOMALAZA & MESSMER, 1999) recorded a value of 38.8 %. In our study, the percentage of species represented by only one individual (21.1%) is much lower than reported in all the above-mentioned studies and is close to the value reported in Alto Parana – 22% – (SPICHIGER & al., 1992) . The individual/species ratio in the Manongarivo plot is 8.1. In other 1-ha plots in Madagascar recorded values were 6.1 (RAKOTOMALAZA & MESSMER, 1999) and 9.17 to 22.1 (RABEVOHITRA & al., 1996). In Yapo, Côte d'Ivoire, CORTHAY (1996) found 7.96 and 8.42 individual/species ratios in two different plots. A series of 1-hectare forest inventories sampled in the Neotropics recorded the following values: 8.42 in Southern Bahia, Brasil (MORI & al., 1983), 7.37 in Alto Parana, Paraguay (SPICHIGER & al., 1992), 6.90 in Alto Ivon, Bolivia (BOOM, 1986), 2.79 in a floodplain forest of Ecuador (BALSLEV & al., 1987), and 2.05 in Jenaro Herrera (SPICHIGER & al., 1996).

The IVI of *Mauloutchia chapelieri* (21.72), the species with the highest value in the plot, falls within the 12.5-28.7 range of highest IVI recorded by MORI & BOOM in lowland moist forests (BALSLEV & al., 1987). Similar values were recorded at Andohahela, Madagascar – 19.7 – (RAKOTOMALAZA & MESSMER, 1999), in Yapo, Côte d'Ivoire – 26.95 – (CORTHAY, 1996) and in Yasunì National Park, Ecuador – 27.1 – (BALSLEV & al., 1987). Higher values were recorded in a terra firmae forest of Alto Ivon, Bolivia (BOOM, 1986), where the most important species had an IVI of 29.58, in a well-drained plateau forest of Alto Parana, Paraguay (SPICHIGER & al., 1992) with an IVI of 33.4, and in a gallery forest of Mogi-Guaçu, Brazil (GIBBS & al., 1980), where the highest IVIs were 43.5 and 37.7. In all the inventories cited above, a species with an IVI value higher than 10 always belong to one of the ten highest IVIs of the sample.

The floristic composition of the forest sampled at Manongarivo matches to some extent that reported by RAHARIMALALA (1991) for the same forest. However, there are some discrepancies for certain species, which can certainly be explained by identification problems of sterile material. Unfortunately, it was not possible for us to access her voucher material.

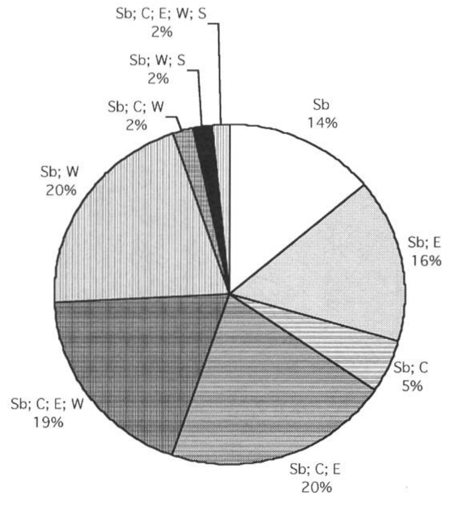

Fig. 7. – Distribution of the identified species of the Manongarivo 1-ha plot according to main geographic patterns within Madagascar. Sb: Sambirano Domain; E: Eastern Domain; C: Central Domain; W: Western Domain; S: Southern Domain.

As indicated above, the main families recorded are in agreement with HUMBERT's (1965) description of Malagasy rainforests. Furthermore, the presence of *Myristicaceae, Sarcolaenaceae* and of *Anthostema* clearly corresponds to his description of typical forests of the Sambirano Domain.

Phytogeographical affinities – Comparing floristic composition of the Manongarivo forest and eleven Eastern Malagasy lowland rainforests sampled by the same method, 13 species are shared with at least one eastern plot. They are *Anthostema madagascariensis, Crysophyllum boivinianum, Dracaena reflexa, Aphloia theiformis, Uapaca ferruginea, Diospyros haplostylis, Ocotea laevis, Protorhus ditimena, Campnosperma micrantheia, Anisophyllea fallax, Homalium involucratum, Burasaia madagascariensis, Ochna ciliata, Mascarenhasia arborescens* and *Tambourissa purpurea. Anthostema madagascariensis*, which is sixth in IVI in the Manongarivo forest, occurs with a comparable density in five other plots. It is worth mentioning that among *Clusiaceae,* widely abundant in all Malagasy rainforests, no species were shared between Manongarivo and eastern forests.

The phytogeographic affinities of the species recorded here falls within 6 major distribution patterns (Fig. 7). 19% of the species are widely distributed in Malagasy forests in both major regions (W and E). 21% are distributed throughout the "région orientale", in the Eastern, Sambirano and Central Domains. 16% of the species are shared only with the Eastern Domain, and their populations are thus geographically discontinuous. 21% are shared only with the Western Domain, and 5% with the Central Domain only. As indicated above, the percentage of Sambirano endemics reaches 14%. These figures clearly corroborate the opinion of KOECHLIN & al. (1974), who state that, apart from a local endemic element, the Sambirano flora is mainly linked with both the Eastern and Western Domains. Most species shared with the Central Domain are also present in either the Eastern Domain or both the Eastern and Western Domains.

Does the Sambirano region deserve the rank of "Domain" or should it be included in the Eastern Domain only as a specific "Sector"? This question deserves further study based on the level of endemism in the Sambirano flora as a whole. Before any final conclusion can be drawn, taxonomic problems must also be solved, as exemplified by one of the dominant species in our plot which was first identified as *Uapaca amplifolia*, a taxon endemic to the Sambirano but which was ultimately considered as conspecific with *U. ferruginea* (Gordon McPherson, pers. comm.), a species that also occurs in the Central and Eastern Domains.

Conclusion

Based on its structure and composition at the family level, the forest sampled in this study is clearly best classified as dense humid lowland rainforest. In comparison with other tropical rainforests in the world, it displays a relatively low value for basal area, a relatively low diversity together with a low number of rare species, a low FIV for *Leguminosae,* and a high FIV for *Clusiaceae* and *Myrtaceae.* All these features are generally reported for other Malagasy lowland rainforests. The family composition of the plot studied fits well within HUMBERT's (1965) description of Malagasy lowland rainforests as a whole, and of those of the Sambirano Domain in particular. Floristic affinities of the species show that almost all are Malagasy endemics. Some are widely distributed on the island, whereas others are shared mainly with the Eastern and Western Domains. There is also a clear component of Sambirano local endemic species. Although these results give clear support to HUMBERT's (1955) classical phytogeographic classification of Madagascar, it is not yet possible to evaluate whether the Sambirano area should be included in the Eastern Domain as a separate sector or remain as a domain on its own. Merging the Sambirano area with a Central phytogeographic unit, as suggested by LOWRY & al. (1997) following Cornet's bioclimatic map, does not find support in our data.

Like elsewhere in Madagascar, much more quantitative as well as qualitative data on the vegetation of the Sambirano area are needed to develop a clearer picture of the phytogeography of the island. However, 1-ha permanent plot studies are very time-consuming. In our case, field work conducted by a team of three persons took more than 3 weeks (> 63 person-days). Other sampling techniques have been proposed such as the linear 100 point sampling method (GAUTIER & al., 1994), which only takes ca. 3 days (9 person-days) to generate comparable results. This method has already been implemented at various other sites in Madagascar (MESSMER & al., 2000) and Côte d'Ivoire (CHATELAIN, 1996) for the study of forest vegetation, and gives much more accurate results on forest structure.

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Appendix 1. – Density, basal area, diversity, and FIV of the plant families encountered in the 1-ha Manongarivo plot, presented by decreasing FIV.

Family	***N° of trees***	***Relative density [%]***	***Basal area [m²/ha]***	***Relative dominance [%]***	***N° of species***	***Relative diversity [%]***	***FIV [%]***
Clusiaceae	129	17.72	3.4281	15.28	7	7.78	40.78
Euphorbiaceae	85	11.68	2.9104	12.97	4	4.44	29.09
Myrtaceae	89	12.23	2.3558	10.50	4	4.44	27.17
Rubiaceae	43	5.91	0.6960	3.10	11	12.22	21.23
Myristicaceae	36	4.95	2.9137	12.99	1	1.11	19.04
Lauraceae	30	4.12	0.7429	3.31	8	8.89	16.32
Burseraceae	34	4.67	1.7926	7.99	1	1.11	13.77
Sapotaceae	28	3.85	0.4911	2.19	4	4.44	10.48
Erythroxylaceae	32	4.40	0.3986	1.78	3	3.33	9.51
Annonaceae	25	3.43	0.5841	2.60	3	3.33	9.37
Sarcolaenaceae	9	1.24	1.0802	4.81	2	2.22	8.27
Asteraceae	18	2.47	1.0400	4.64	1	1.11	8.22
Leguminosae	14	1.92	0.5508	2.45	3	3.33	7.71
Ebenaceae	19	2.61	0.3661	1.63	3	3.33	7.57
Arecaceae	27	3.71	0.2791	1.24	2	2.22	7.17
Anacardiaceae	14	1.92	0.2402	1.07	3	3.33	6.33
Combretaceae	7	0.96	0.7639	3.40	1	1.11	5.48
Ochnaceae	10	1.37	0.1525	0.68	3	3.33	5.39
Flacourtiaceae	8	1.10	0.0974	0.43	3	3.33	4.87
Meliaceae	4	0.55	0.2555	1.14	2	2.22	3.91
Melastomataceae	8	1.10	0.1267	0.56	2	2.22	3.89
Connaraceae	10	1.37	0.1967	0.88	1	1.11	3.36
Myrsinaceae	5	0.69	0.0537	0.24	2	2.22	3.15
Pandanaceae	4	0.55	0.0499	0.22	2	2.22	2.99
Araliaceae	7	0.96	0.0793	0.35	1	1.11	2.43
Sapindaceae	6	0.82	0.1068	0.48	1	1.11	2.41
Chrysobalanaceae	7	0.96	0.0728	0.32	1	1.11	2.40
Anisophylleaceae	3	0.41	0.1263	0.56	1	1.11	2.09
Loganiaceae	2	0.27	0.1284	0.57	1	1.11	1.96
Olacaceae	4	0.55	0.0449	0.20	1	1.11	1.86
Indet.	1	0.14	0.1284	0.57	1	1.11	1.82
Moraceae	2	0.27	0.0443	0.20	1	1.11	1.58
Dracaenaceae	2	0.27	0.0391	0.17	1	1.11	1.56
Verbenaceae	2	0.27	0.0264	0.12	1	1.11	1.50
Sterculiaceae	1	0.14	0.0357	0.16	1	1.11	1.41
Menispermaceae	1	0.14	0.0183	0.08	1	1.11	1.33
Apocynaceae	1	0.14	0.0109	0.05	1	1.11	1.30
Monimiaceae	1	0.14	0.0092	0.04	1	1.11	1.29
TOTAL	**728**	**100.00**	**22.4368**	**100.00**	**90**	**100.00**	**300.00**

Appendix 2. – Density, basal area, frequency, and IVI of the species of the Manongarivo 1-ha plot and their geographic distribution (Com: Comores; EAfr: Eastern Africa; Sey: Seychelles, Sb: Sambirano Domain; E: Eastern Domain; C: Central Domain; W: Western Domain; S: Southern Domain), presented by decreasing IVI. (***Rel den*** = Relative density; ***Rel dom*** = Relative dominance; ***Abs freq*** = Absolute frequency; ***Rel freq*** = Relative frequency).

Species	*Family*	*Distribution of identified species*						*N° of trees*	*Rel dens [%]*	*Basal area [m²/ha]*	*Rel dom [%]*	*Abs freq*	*Rel freq [%]*	*IVI [%]*
		Outside Madagascar	*Within Madagascar*											
			Sb	*E*	*C*	*W*	*S*							
Mauloutchia chapelieri Warb.	Myristicaceae		+	+				36	4.95	2.914	12.99	18	4.00	21.93
Syzygium sp. 1	Myrtaceae							63	8.65	1.727	7.70	22	4.89	21.24
Uapaca ferruginea Baill.	Euphorbiaceae		+	+	+			54	7.42	1.759	7.84	18	4.00	19.26
Canarium madagascariense Engl.	Burseraceae		+	+	+	+		34	4.67	1.793	7.99	18	4.00	16.66
Symphonia eugenioides Baker	Clusiaceae		+					39	5.36	0.988	4.40	16	3.56	13.32
Anthostema madagascariensis Baill.	Euphobiaceae		+	+				28	3.85	1.080	4.82	9	2.00	10.66
Ochrocarpos decipiens Baill.	Clusiaceae		+			+		30	4.12	0.645	2.87	15	3.33	10.33
Brachylaena merana (Baker) Humbert	Asteraceae		+	+	+	+		18	2.47	1.040	4.64	8	1.78	8.89
Garcinia verrucosa Jum. & H. Perrier	Clusiaceae		+		+	+		23	3.16	0.517	2.30	14	3.11	8.57
Calophyllum paniculatum P. F. Stevens	Clusiaceae		+	+	+			15	2.06	0.828	3.69	12	2.67	8.42
Leptolaena cuspidata Baker	Sarcolaenaceae		+			+		7	0.96	1.044	4.65	6	1.33	6.95
Polyalthia richardiana Baill.	Annonaceae		+					16	2.20	0.452	2.01	11	2.44	6.66
Myrtaceae indet. 1	Myrtaceae							17	2.34	0.454	2.02	9	2.00	6.36
Ravenea sambiranensis Jum. & H. Perrier	Arecaceae		+	+	+	+		26	3.57	0.265	1.18	7	1.56	6.31
Ochrocarpos punctatus H. Perrier	Clusiaceae		+			+		13	1.79	0.328	1.46	11	2.44	5.69
Terminalia perrieri Capuron	Combretaceae		+					7	0.96	0.764	3.40	5	1.11	5.48
Dalbergia sp. 1	Leguminosae							12	1.65	0.494	2.20	7	1.56	5.40
Diospyros haplostilis Hiern	Ebenaceae		+			+		16	2.20	0.242	1.08	9	2.00	5.28
Erythroxylum excelsum O. E. Schulz	Erythroxylaceae		+	+				13	1.79	0.158	0.70	10	2.22	4.71
Chrysophyllum perrieri (Lecomte) G. E. Schatz & L. Gaut.	Sapotaceae		+	+	+			10	1.37	0.248	1.11	7	1.56	4.04
Erythroxylum lanceum Bojer	Erythroxylaceae		+	+				13	1.79	0.154	0.69	7	1.56	4.03
Faucherea manongarivensis Aubrév.	Sapotaceae		+	+				10	1.37	0.163	0.73	8	1.78	3.88
Rubiaceae indet. 1	Rubiaceae							9	1.24	0.112	0.50	9	2.00	3.73
Ocotea cf. *laevis* Kosterm.	Lauraceae		+	+				8	1.10	0.210	0.94	6	1.33	3.37
Ellipanthus madagascariensis (G. Schellenb.) Keraudren	Connaraceae		+					10	1.37	0.197	0.88	5	1.11	3.36
Myrtaceae indet. 2	Myrtaceae							8	1.10	0.152	0.68	7	1.56	3.33
Protorhus sp. 1	Anacardiaceae							8	1.10	0.150	0.67	7	1.56	3.33
Diporidium greveanum Tiegh.	Ochnaceae		+			+		7	0.96	0.104	0.46	7	1.56	2.98
Canthium sp. 1	Rubiaceae							1	0.14	0.010	0.04	12	2.67	2.85

Appendix 2 (*cont.*). – Density, basal area, frequency, and IVI of the species of the Manongarivo 1-ha plot and their geographic distribution (Com: Comores; EAfr: Eastern Africa; Sey: Seychelles, Sb: Sambirano Domain; E: Eastern Domain; C: Central Domain; W: Western Domain; S: Southern Domain), presented by decreasing IVI. (***Rel den*** = Relative density; ***Rel dom*** = Relative dominance; ***Abs freq*** = Absolute frequency; ***Rel freq*** = Relative frequency).

Species	Family	Distribution of identified species						N°	Rel	Basal	Rel	Abs	Rel	IVI
		Outside Madagascar	Within Madagascar					of	dens	area	dom	freq	freq	
			Sb	E	C	W	S	trees	[%]	[m²/ha]	[%]		[%]	[%]
Peponidium pervilleanum (Baill.) Arènes	Rubiaceae		+			+		6	0.82	0.125	0.56	6	1.33	2.71
Tarenna sp. 1	Rubiaceae							8	1.10	0.151	0.67	4	0.89	2.66
Polyscias nossibensis (Baker) Harms	Araliaceae		+			+		7	0.96	0.079	0.35	5	1.11	2.43
Tinopsis sp. 1	Sapindaceae							6	0.82	0.107	0.48	5	1.11	2.41
Lauraceae indet. 2	Lauraceae							4	0.55	0.212	0.95	4	0.89	2.39
Xylopia ambanjensis Cavaco & Keraudren	Annonaceae		+			+		6	0.82	0.090	0.40	5	1.11	2.34
Warneckea sansibarica (Taub.) Jacq. Fél.	Melastomataceae	E Afr.	+			+		6	0.82	0.077	0.34	5	1.11	2.28
Alberta sambiranensis Cavaco	Rubiaceae		+	+	+			5	0.69	0.073	0.33	5	1.11	2.12
Erythroxylum sphaeranthum H. Perrier	Erythroxylaceae		+		+			6	0.82	0.087	0.39	4	0.89	2.10
Campnosperma micranteium Marchand	Anacardiaceae		+	+				5	0.69	0.065	0.29	5	1.11	2.09
Garcinia sp. 1	Clusiaceae							5	0.69	0.086	0.38	4	0.89	1.96
Grangeria porosa Baill.	Chrysobalanaceae		+			+		7	0.96	0.073	0.32	3	0.67	1.95
Chrysophyllum boivinianum (Pierre) Baehni	Sapotaceae		+	+	+			6	0.82	0.072	0.32	3	0.67	1.81
Anisophyllea fallax Scott-Elliot	Anisophylleaceae		+	+	+			3	0.41	0.126	0.56	3	0.67	1.64
Olax thouarsii (DC.) Baill.	Olacaceae		+	+				4	0.55	0.045	0.20	4	0.89	1.64
Oncostemum elephantipes H. Perrier	Myrsinsceae		+	+	+			4	0.55	0.043	0.19	4	0.89	1.63
Symphonia sp. 1	Clusiaceae							4	0.55	0.037	0.17	4	0.89	1.60
Diospyros sp. 1	Ebenaceae							3	0.41	0.107	0.48	3	0.67	1.56
Canthium sp. 2	Rubiaceae							4	0.55	0.068	0.30	3	0.67	1.52
Cryptocarya sp. 1	Lauraceae							4	0.55	0.057	0.26	3	0.67	1.47
Potameia antevaratra Kosterm.	Lauraceae		+	+	+			4	0.55	0.050	0.22	3	0.67	1.44
Cedrelopsis sp. 1	Meliaceae							2	0.27	0.156	0.70	2	0.44	1.41
Aphloia theaeformis (Vahl) Benn. & R. Br.	Flacourtiaceae	Masc, Com, Sey, E Afr	+	+	+	+		4	0.55	0.044	0.20	3	0.67	1.41
Anthocleista madagascariensis Baker	Loganiaceae		+	+	+			2	0.27	0.128	0.57	2	0.44	1.29
Cryptocarya sp. 2	Lauraceae							4	0.55	0.062	0.28	2	0.44	1.27
Gaertnera macrostipulata Baker	Rubiaceae		+	+	+			3	0.41	0.043	0.19	3	0.67	1.27
Polyalthia sambiranensis Le Thomas & G. E. Schatz	Annonaceae		+					3	0.41	0.042	0.19	3	0.67	1.27
Pandanus sp. 2	Pandanaceae							3	0.41	0.036	0.16	3	0.67	1.24
Psychotria sp. 1	Rubiaceae							3	0.41	0.035	0.16	3	0.67	1.24
Cedrelopsis grevei Baill.	Meliaceae		+			+	+	2	0.27	0.100	0.44	2	0.44	1.16

Appendix 2 *(cont.)*. – Density, basal area, frequency, and IVI of the species of the Manongarivo 1-ha plot and their geographic distribution (Com: Comores; EAfr: Eastern Africa; Sey: Seychelles, Sb: Sambirano Domain; E: Eastern Domain; C: Central Domain; W: Western Domain; S: Southern Domain), presented by decreasing IVI. (***Rel den*** = Relative density; ***Rel dom*** = Relative dominance; ***Abs freq*** = Absolute frequency; ***Rel freq*** = Relative frequency).

Species	***Family***	***Distribution of identified species***						***N° of trees***	***Rel dens [%]***	***Basal area [m²/ha]***	***Rel dom [%]***	***Abs freq***	***Rel freq [%]***	***IVI [%]***
		Outside Madagascar	***Within Madagascar***											
			Sb	***E***	***C***	***W***	***S***							
Lauraceae indet. 1	Lauraceae							2	0.27	0.096	0.43	2	0.44	1.15
Indet.	Indet.							1	0.14	0.128	0.57	1	0.22	0.93
Trilepisium madagascariense DC.	Moraceae		+	+	+	+		2	0.27	0.044	0.20	2	0.44	0.92
Dracaena reflexa Lam.	Dracaenaceae		+	+	+	+		2	0.27	0.039	0.17	2	0.44	0.89
Xyloolaena richardii (Baill.) Baill.	Sarcolaenaceae		+	+	+			2	0.27	0.036	0.16	2	0.44	0.88
Cryptocarya sp. 3	Lauraceae							2	0.27	0.036	0.16	2	0.44	0.88
Ochna pervilleana Baill.	Ochnaceae		+			+		2	0.27	0.029	0.13	2	0.44	0.85
Drypetes perrieri Leandri	Euphorbiaceae		+	+	+	+		2	0.27	0.028	0.12	2	0.44	0.84
Vitex cauliflora Moldenke	Verbenaceae		+	+	+	+		2	0.27	0.026	0.12	2	0.44	0.84
Homalium sp. 1	Flacourtiaceae							2	0.27	0.023	0.10	2	0.44	0.82
Potameia chartacea Kosterm.	Lauraceae		+	+	+			2	0.27	0.019	0.08	2	0.44	0.80
Rubiaceae indet. 3	Rubiaceae							2	0.27	0.018	0.08	2	0.44	0.80
Dionycha triangularis Jum. & H. Perrier	Melastomataceae		+		+			2	0.27	0.050	0.22	1	0.22	0.72
Homalium involucratum (DC.) O. Hoffm.	Flacourtiaceae		+	+				2	0.27	0.030	0.13	1	0.22	0.63
Rubiaceae indet. 2	Rubiaceae							1	0.14	0.052	0.23	1	0.22	0.59
Cassia sp. 1	Leguminosae							1	0.14	0.048	0.22	1	0.22	0.58
Uapaca ambanjensis Leandri	Euphorbiaceae		+					1	0.14	0.044	0.19	1	0.22	0.55
Nesogordonia fertilis H. Perrier	Sterculiaceae		+					1	0.14	0.036	0.16	1	0.22	0.52
Protorhus sp. 2	Anacardiaceae							1	0.14	0.025	0.11	1	0.22	0.47
Myrtaceae indet. 3	Myrtaceae							1	0.14	0.023	0.10	1	0.22	0.46
Ochna ciliata Lam.	Ochnaceae	Com	+	+	+	+	+	1	0.14	0.019	0.09	1	0.22	0.44
Burasaia madagascariensis DC.	Menispermaceae		+	+	+	+		1	0.14	0.018	0.08	1	0.22	0.44
Diospyros sp. 2	Ebenaceae							1	0.14	0.017	0.08	1	0.22	0.43
Arecaceae indet. 1	Arecaceae							1	0.14	0.014	0.06	1	0.22	0.42
Pandanus manongarivensis Huynh	Pandanaceae		+					1	0.14	0.014	0.06	1	0.22	0.42
Mascarenhasia arborescens A. DC.	Apocynaceae	Com, Sey, E Afr	+	+	+	+		1	0.14	0.011	0.05	1	0.22	0.41
Monoporus sp. 1	Myrsinsceae							1	0.14	0.010	0.05	1	0.22	0.41
Mapouria sp. 1	Rubiaceae							1	0.14	0.010	0.05	1	0.22	0.41
Tambourissa purpurea (Tul.) A. DC.	Monimiaceae		+	+	+	+		1	0.14	0.009	0.04	1	0.22	0.40
Albizia mainaea Villiers	Leguminosae		+			+		1	0.14	0.009	0.04	1	0.22	0.40
Mimusops ankaibeensis Aubrév.	Sapotaceae		+		+			1	0.14	0.008	0.04	1	0.22	0.40
	TOTAL							**728**	**100.00**	**22.437**	**100.00**	**450**	**100.00**	**300.00**