Research Article

Characterization of community composition and forest structure in a Madagascar lowland rainforest

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Abstract

This study documents the community composition and forest structure of lowland rainforest in eastern Madagascar, with a first quantitative description of the primary lowland rainforest of Reserve Naturelle Intégrale de (RNI) Betampona. An intensive field survey of vegetation and environmental factors was conducted over two consecutive field campaigns in RNI Betampona, an isolated primary forest reserve located *ca.* 40 km northwest of the city of Toamasina. One hundred 10 m-diameter vegetation survey plots were inventoried and re-measured in 2004 and 2005. Two hundred forty-four tree species belonging to 49 families comprised the 2,487 stems greater than or equal to 5cm diameter at breast height (DBH) measured in 2004, with an average of 19.27 species per plot (2,227 and 15.71 respectively in 2005). Stem density per plot ranged from 12 to 52 for trees ≥5cm-DBH in 2004 (12 to 38 in 2005), while regeneration stems less than 5cm-DBH had a per-plot average of 57.28 in 2005 (range 19 to 140) and 94.19 (range 22 to 224) per hectare in 2004. The substantial decrease in ≥5cm-DBH trees and in stems <5cm-DBH from 2004 to 2005 suggests a forest undergoing thinning, perhaps following recovery from gap formation. Importance Value Indices (IVI) calculated for tree species indicated that an unidentified *Uapaca* species, *Ravenala madagascariensis*, *Anthostema madagascariensis*, *Canarium spp* and *Cassipourea lanceolata* were the most important species according to their overall frequency, dominance and abundance values, and accounted for 10% of the overall IVI.

Keywords: importance value index, Madagascar, rainforest, tree species diversity

Résumé

Cette étude présente la composition de la communauté et la structure de la foret tropicale humide de l'Est de Madagascar avec une première description quantitative de la foret tropical humide primaire de la Reserve Naturelle Intégrale de (RNI) Betampona. Une enquête de terrain intensive des variables environnementales fut menée sur deux campagnes de terrain consécutives dans la RNI Betampona, une réserve forestière primaire isolée, située ca. 40 km au nord-ouest de la ville de Toamasina. Cent parcelles d'étude de la végétation de 10 m de diamètre furent inventoriés et réévalués en 2004 et 2005. Deux cent quarante-quatre espèces d'arbres appartenant à 49 familles comprenaient les 2487 tiges supérieures ou égales à 5 cm de diamètre à hauteur de poitrine (DHP), mesuré en 2004 avec une moyenne de 19,27 espèces par parcelle (2227 et 15,71 en 2005). La densité des tiges à l'hectare variait de 12 à 52 pour les arbres ≥ à 5cm-DHP en 2004 (12 à 38 en 2005), tandis que la régénération des tiges de moins de 5cm-DHP eut une moyenne à l'hectare de 57.28 en 2005 (intervalle de 19 à 140) et 94.19 (intervalle de 22 à 224) par hectare en 2004. La baisse considérable du nombre d'arbres ≥ 5 cm DHP et de tiges <5cm-DHP de 2004 à 2005 suggère une forêt éclaircissante, peut-être après la récupération de la formation de trouées. Les indices de la valeur d'Importance (IVI), calculés pour les espèces d'arbres indiquaient qu'une espèce non identifiée d'Uapaca, Ravenala madagascariensis, Anthostema madagascariensis, Canarium spp et Cassipourea lanceolata étaient les espèces les plus importantes en fonction de leur valeurs de fréquence, de domination et d'abondance et représentaient 10% de la IVI globale.

Mots Clés: Index de valeur d'Importance, Madagascar, Foret Humide, diversité d'espèces forestières

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Introduction

Removal and conversion of tropical forest ecosystems have occurred at an alarming rate globally [1-4]. Tropical deforestation causes grave consequences on local and global scales, such as crashing biodiversity numbers, increased carbon emissions to the atmosphere and permanent changes to local hydrology. The omnipresence of tropical forest clearing inspires research on these ecosystems, as well as a need for increased conservation measures. Most studies have found low forest-recovery rates and a lack or delay of recovery following land clearing or agriculture abandonment [5-7], resulting in large areas of severely degraded landscapes. The African island nation of Madagascar represents an extreme example of these trends. Scientific study of many of Madagascar's highly threatened habitats is still in initial biological descriptive stages, highlighting the fundamental need for understanding the structure and function of these habitats on an ecosystem level lest they disappear.

As one of the world's most threatened hotspots for terrestrial biodiversity, Madagascar is an island with a high conservation priority [2, 8, 9]. It has an exceptional degree of endemism and biodiversity, with estimates of vascular plant diversity ranging between 10,000-12,000 species [13-15]. The rates of endemism for both flora and fauna are estimated around 80% to 90% [1,16, 17], and tree and large shrub species have endemism as high as 96% [14]. These species face extinction due to habitat loss and fragmentation caused by land conversion practices [1, 10-12]. Indeed, deforestation in Madagascar is estimated at 1,100km^2 per year, resulting in the loss and degradation of over 90% of the original forest cover, especially in low topographic and highly populated areas. [17-19]. In the face of this extreme deforestation, the survival of numerous plant and animal species currently is severely threatened.

Lowland rain forests in Madagascar are characterized by the presence of dense closed-canopy stands of evergreen trees with canopies rarely exceeding and usually less than 30 meters in height. There is relatively low diversity of large-leaved plants, particularly monocots — a feature that has been attributed to acclimation or adaptation to poor soils and low water supply [23]. The eastern lowland rainforests of Madagascar have also been noted for their unique richness of palm (Arecaceae), pandan (Pandanaceae), bamboo (Graminaceae) and tree-fern species (Cyatheaceae). For example, the pandan (Pananaceae) family is represented by 70 species found mostly in the eastern forests of Madagascar [16]. This contrasts with large areas of tropical East Africa, where there are few species of palms and pandans, which are confined to topographically-determined wet sites [23]. Canopy emergents such as *Canarium* sp. (Burseraceae), *Albizia* sp. (Fabaceae), and *Brochoneura acuminata* (Myristaceae) are abundant. Other common tree species include the following genera (and families): *Uapaca*

(Euphorbiaceae), *Diospyros* (Ebenaceae), *Ocotea* (Lauraceae), *Symphonia* (Clusiaceae), *Tambourissa* (Monimiaceae), and *Dalbergia* (Fabaceae) [24].

There have been numerous inventories of the floral composition of Malagasy rainforests [20-24], and other studies have classified the spatial extent of the remaining forests using remote sensing [18, 25-27]. In addition, physiologically descriptive botanical classification investigations are ongoing in many of Madagascar's unique ecosystems. However, few, if any publications document the patterns of tree species composition, diversity and forest structure within Malagasy lowland rainforest ecosystems. Clearly, such characterization, in conjunction with ongoing botanical descriptions, is needed for the successful conservation of the biodiversity of Madagascar's lowland rainforests.

At the current study site, a few unpublished forest inventories have been recorded. However, these studies were confined to small geographic areas within the Reserve or concentrate on proximity to habitat and food sources for faunal species of interest, *eg*. the black-and-white-ruffed lemur, *Varecia variegata, (*unpublished*)*. The objectives of the present study are to: (i) identify and inventory tree species in RNI Betampona primary forest, (ii) detail forest structure and composition patterns in this forest (in terms of tree height, density and basal area), (iii) describe the patterns of diversity and evenness of tree species' rarity and commonness, and (iv) compare the diversity and species composition to other rainforests worldwide.

Methods

Study site

For this study, field measurements were carried out in Reserve Naturelle Integrale de (RNI) Betampona (translated: Betampona Special Reserve), a protected rainforest site in eastern Madagascar (Fig. 1). This forest is one of very few remaining tracts of primary lowland rainforest in Madagascar [18]. RNI Betampona is highly protected and only accessible for scientific research through governmental approval. The 2228-hectare reserve is situated to the northwest of the port town of Tamatave (17^{o}15' - 17^{o}55' S; 49^{o}12' - 49^{o}15' E), about 45km west from the Indian Ocean coast. The forests have been under some form of government protection since 1927, but enforcement of protection laws was mostly absent until the late 1980s. According to the Reserve officials, *ca* 50% of RNI Betampona is undisturbed primary rainforest, with an additional *ca* 35% characterized as recovering primary rainforest and the remainder as secondary forest.

Vegetation inventory plots 2004-2005

To inventory tree species in RNI Betampona, field surveys were completed in 2004 and 2005. Between July and September in 2004, one hundred 10m-diameter circular plots were established in primary or recovering primary forest (Fig. 1). Locations for these plots were chosen at random intervals along the trail route followed on a given day. Once located, plot centers were flagged and specific locations were described in detail for repeat plot measurements in 2005. Qualitative boundary descriptions to indicate location on slope, canopy gap effects, proximity to water and other notable descriptive features were recorded in the four compass directions. Percent canopy cover was taken from plot center using a densiometer. The plots were relocated and all measurements were re-recorded using the same methodology from August to October of 2005. In addition, the geographical coordinates of the plots were recorded in June 2006 with a GPS to add spatial context to the study.

Tree species were identified by a local guide who was the resident expert on plant and tree species and taxonomic comparison to previous studies. Species were recorded by Malagasy name. Scientific names were then determined for the vernacular names by (i) referencing Schatz (2001); (ii) using previously documented (incomplete) species lists (*unpublished*) from the Madagascar Fauna Group (MFG), the international organization that oversees research and conservation efforts in RNI Betampona; (iii) consulting with botanists at the Missouri Botanical Garden (MBG) office in Antananarivo, Madagascar; and (iv) consulting with the local MFG director. When the scientific name for a Malagasy vernacular name could not be determined, name, leaf and twig samples were collected, wiped with alcohol and pressed. These specimens were divided into two subsets and given to botanists at the MBG office and Parc Tsimbazaza Zoologique for identification. If species could not be identified to the species level, then genus only (and in one case, family only) was recorded. In order to keep these unknown species separate when compiling the dataset, names were given in the format of *genus sp1*, *genus sp2*, and so forth.

For all trees greater than 5cm in diameter at breast height (DBH), the following information was recorded: species identification, DBH, height and presence of qualitative health characteristics such as bole wounding, disease, rot evidence or strangling vines. All regeneration less than 5cm DBH was enumerated during both surveys, though the species were only listed during the 2005 plot survey. Finally, to obtain a sample of ground cover in the plot, a 1m x 1m square mini-plot was randomly located within the plot and all species of groundcover and regeneration shorter than breast height were identified and recorded.

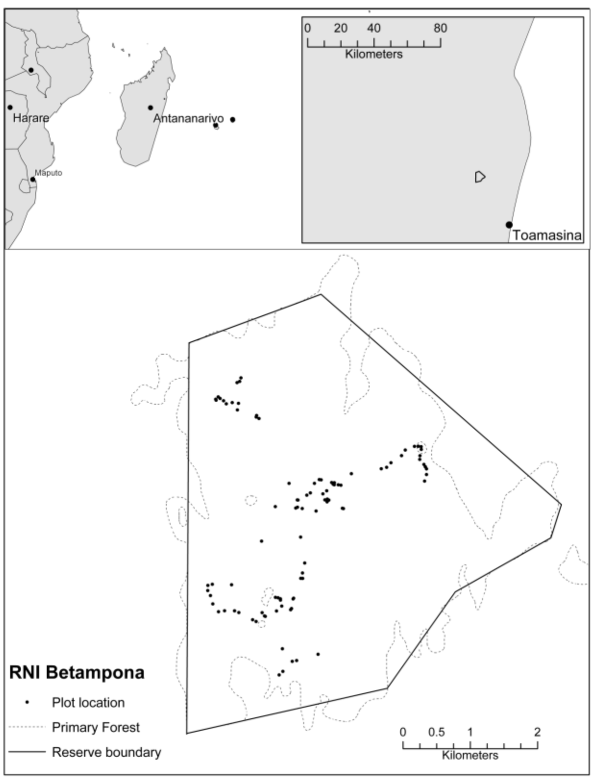

Fig. 1. Location of Reserve Naturelle Integrale de (RNI) Betampona, the study site in Eastern Madagascar. Approximately 45km from the small port city of Toamasina midway up the East Coast of the island, RNI Betampona is one of the last vestiges of primary lowland rainforest in the region. Plot locations are indicated by black dots on the Reserve Map.

Data treatment

Following the field study and compilation of the tree species list for RNI Betampona, plot data were analyzed and compared over the two respective field seasons. Tree species stem count and stem area were compared both among plots within the Reserve and among other rainforest sites worldwide. Species and family dominance curves were drawn to delineate composition characteristics for RNI Betampona. Further, trees and regeneration counts were compiled and compared along <10cm, 10-30cm, ≥30cm diameter size classes to detect size differences in species composition. Changes in tree height with DBH were compared over the two study years to reveal forest structure characteristics and also to detect large-scale changes within the reserve. Plot-wide stem area (m^2 ha^{-1}), canopy cover (%) and groundcover (%) were evaluated for differences over the study years using ANOVA (Sokal & Rohlf 1981).

Species richness and abundance within the equation:

$$IVI_i = (A_i \times 100) + (F_i \times 100) + (D_i \times 100)$$

where:

$$A_i = Abundance_i = \frac{stem\ count\ of\ species\ i}{stem\ count\ of\ all\ species}$$

$$F_i = Frequency_i = \frac{occurrence\ of\ species\ i\ in\ plots}{occurrence\ of\ all\ species\ in\ plots}$$

$$D_i = Dominance_i = \frac{basal\ area\ of\ species\ i\ in\ (m^2/\hbar a)}{total\ basal\ area\ in\ (m^2/\hbar a)}$$

Eq 1

Importance Value Index (IVI) was calculated because it combines and quantifies the three commonly used vegetation-descriptors of abundance, frequency and dominance as an index. The Index values are unitless and total 300 for all RNI Betampona species.

To understand species diversity and evenness both among plots and throughout RNI Betampona as a whole, we used the Shannon-Weiner Indices. Calculated using the equation:

$$H' = -\sum(p_i)(\log p_i) \qquad Eq\ 2$$

where p_i is the proportion cover of the *i*th species in a plot and logarithm is calculated with a base of *e*. The Shannon-Weiner Index makes the two assumptions that: (1) individuals are randomly sampled from an infinitely large population and (2) that all the species from the community are included in the sample [29]. Evenness (J), which was defined as the diversity divided by the maximum possible diversity, was also calculated for each survey plot with the equation:

$$J = \frac{H'}{H'_{max}} = \frac{\sum_{i=1}^{s} p_i \log p_i}{\log s} \qquad Eq\ 3$$

where s is the number of species and where *e* is the base of the logarithm. Tree species diversity and evenness were first calculated for each plot to test the variability among plots captured by the randomness of the plots sampled. In addition, tree species were divided into height classes to test species diversity and evenness among sub-canopy, canopy and super-canopy strata within RNI Betampona. Finally, trees were also divided into diameter classes following that of Newberry *et al.* [30] by adjusting size classes based on smaller overall diameter size ranges.

Significant differences in species diversity and evenness within plots and between years were revealed using Student's *t* tests and ANOVA [31] where appropriate. Diversity and evenness analyses were performed using Multivariate Statistical Package 3.1 (MVSP, Kovach Computing Services, 2000), and ANOVA was performed in Excel (Microsoft Office 2008).

Results

Species composition and importance

Within the 100 survey plots, a total of 244 tree species belonging to 49 families comprised the 2,847 stems ≥5cm measured and the 9,419 stems <5cm counted during the 2004 plot survey. However, in total 288 tree species were noted within the limits of RNI Betampona. This species number discrepancy occurred for two reasons. First, a number of species are known to exist in RNI Betampona but were not identified within the 100 vegetation survey plots. Secondly, some trees could only be identified to the genus level and though it was known that there was more than one species with the same Malagasy vernacular name, species could not be distinguished due to field limitation such as inability to collect leaves from tall trees. For instance, the tree known in Malagasy as 'Famelona' (*Chrysophyllum spp*., Family: *Sapotaceae*) taxonomically is two distinct species that can be differentiated by their smooth or hairy leaves, but due to the height of the specimens measured in the survey plots it was impossible to tell which tree belonged to the smooth-leaved or rough-leaved species. Because these species were indistinguishable except by their leaves, *Famelon*a was treated as a single tree species for this analysis.

In 2005, 2,227 trees ≥5cm at DBH were measured and 5,728 stems were noted in the <5cm regeneration stem count. Stems per plot ranged from 12 to 52 for trees ≥5cm-DBH (mean = 28.47 per 78.54m^2 plot or 3603.8 stems per hectare) and 22 to 224 for trees <5cm (mean = 94.19 per plot or 11,922.8 stems per hectare). These numbers decreased in 2005 when ≥5cm-DBH trees ranged from 12 to 38 stems per plot (mean 22.27 per plot or 2,818.99 per hectare) and 19 to 140 stems per plot (mean 57.28 stems per plot or 7250.63 stems per hectare) were recorded for stems <5cm-DBH per hectare. In addition, species per plot averages fell from 19.27 per plot in 2004 to 15.71 per plot in 2005. The overall trend in tree numbers follows dynamics seen in other rainforests worldwide [32, 33] where local thinning occurs following recovery from the formation of canopy gaps by disturbance. This inference is supported by an increase in the average DBH from 12.77cm to 13.50cm in the trees measured in 2004 to 2005. Also supporting the hypothesis that the forest is undergoing thinning and forest development, the average per plot stem area (m^2/ha) decreased from 75.85m^2/ha to 65.34m^2/ha and average plot canopy cover (%) increased from 79% to 83% from 2004 to 2005, respectively.

Out of a total of 191 floral families found in Madagascar, 50 were measured in varying abundances within RNI Betampona survey plots (Fig. 2a). Species dominance across RNI Betampona, shown in Figure 2b above, follows the "broken-stick model" characteristic of dominance-diversity curve relationships found in other rainforests worldwide [34, 35]. However, the high stem abundances of the three most dominant species: *Anthostema madagascariensis* (2005: 118; 2004: 151), *Uapaca* spp (2005: 110; 2004: 123), and *Cassipourea lanceolata* (2005: 62; 2004: 102), relative to the abundances of the rest of the species, is a slight departure from trends exhibited in other rainforests, where stem numbers are more uniformly distributed among species and thus dominance diversity curves have a smaller initial slope (*for examples see*: (Hubbell [35], Whitmore [36], Condit et al. [37], and Duivenvoorden [38]).

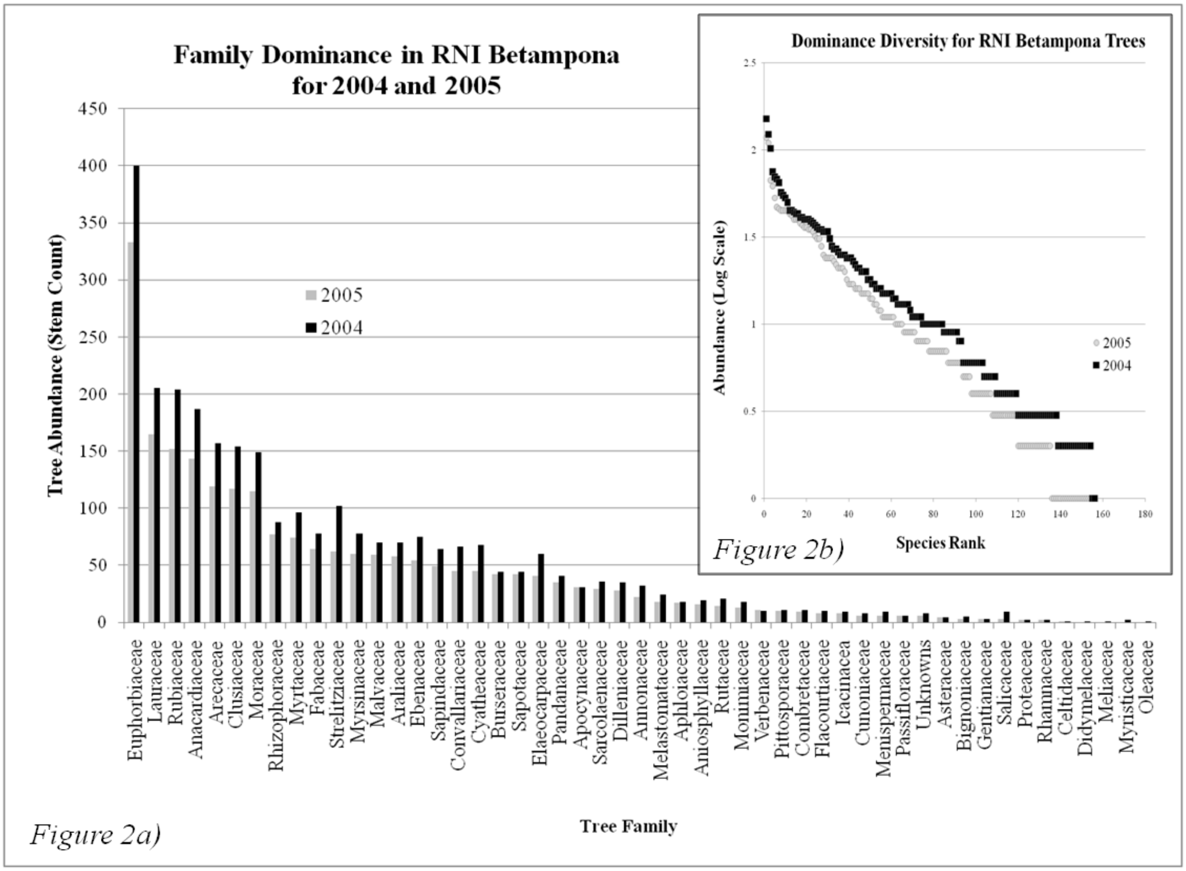

Fig. 2a shows the dominance of the tree families present in RNI Betampona listed as stem counts. Figure 2b is the inset showing the dominance diversity curves for both 2004 and 2005 trees measured in RNI Betampona. Tree abundance is shown on a logarithmic scale.

Results of the Importance Value Index values were calculated individually for 2004 and 2005 (Fig. 3). There was no significant difference among the most important species in RNI Betampona. Of the 192 tree species included in the IVI calculation, 118 species were among the top 95% of Importance Values. The most important species included: *Uapaca spp* (family: *Euphorbiaceae*) with an IVI of 16.80; *Ravenala madagascariensis* (family: Strelitziaceae) with an IVI of 16.33, *Anthostema madagascariensis* (family: *Euphorbiaceae*; IVI: 11.98), *Canarium spp*[*] (family: *Burseraceae*; IVI: 7.99); *Cassipourea lanceolata* (family: *Rhizophoraceae*; IVI: 6.35), *Faucherea sp1* (family: *Sapotaceae*; IVI: 6.17) and *Dalbergia bathiei* (family: *Fabaceae*; IVI: 6.06) (Fig. 3).

[*] The genus *Canarium* in Madagascar is currently being revised at the time of this publication and research is on-going.

The Euphorbiaceae Family was found to be the most important family, with a combined Importance Value of 39.58 among its 11 species, accounting for 13.19% of the overall IVI. Both the first (*Uapaca sp1*) and third (*Anthostema madagascariensis*) are members of the Euphorbiaceae family. *Uapaca sp1*, with an IVI of 16.80, had the highest dominance with a stem area of 7.022m^2/ha in 2005 and was found in 40 plots (2005). *Anthostema madagascariensis*, though third in the IVI calculation with 11.98, was highest in overall abundance with 118 stems measured in the RNI Betampona survey plots in 2005 compared to 110 for *Uapaca sp1* and 69 for *Ravenala madagascariensis*, the second most important species.

The total stem area for *Anthostema madagascariensis* was found to be 3.167m^{2}ha^{-1}, which was less than half of that of *Uapaca sp1* or *R. madagascariensis*. Indeed, though there were more stems of *Anthostema madagascariensis*, the size of the stems present was on average significantly smaller than that of *Uapaca sp1* or *R. madagascariensis*. This is further confirmed by comparison of average diameter at breast height (DBH) for the three species. *R. madagascariensis* had an average DBH of 30.46cm (range 5.00 to 46.10) and *Uapaca sp1* was 21.10cm (range: 5.10 to 67.10) compared to 14.22cm-DBH for *Anthostema madagascariensis* (range: 5.20 to 45.10).

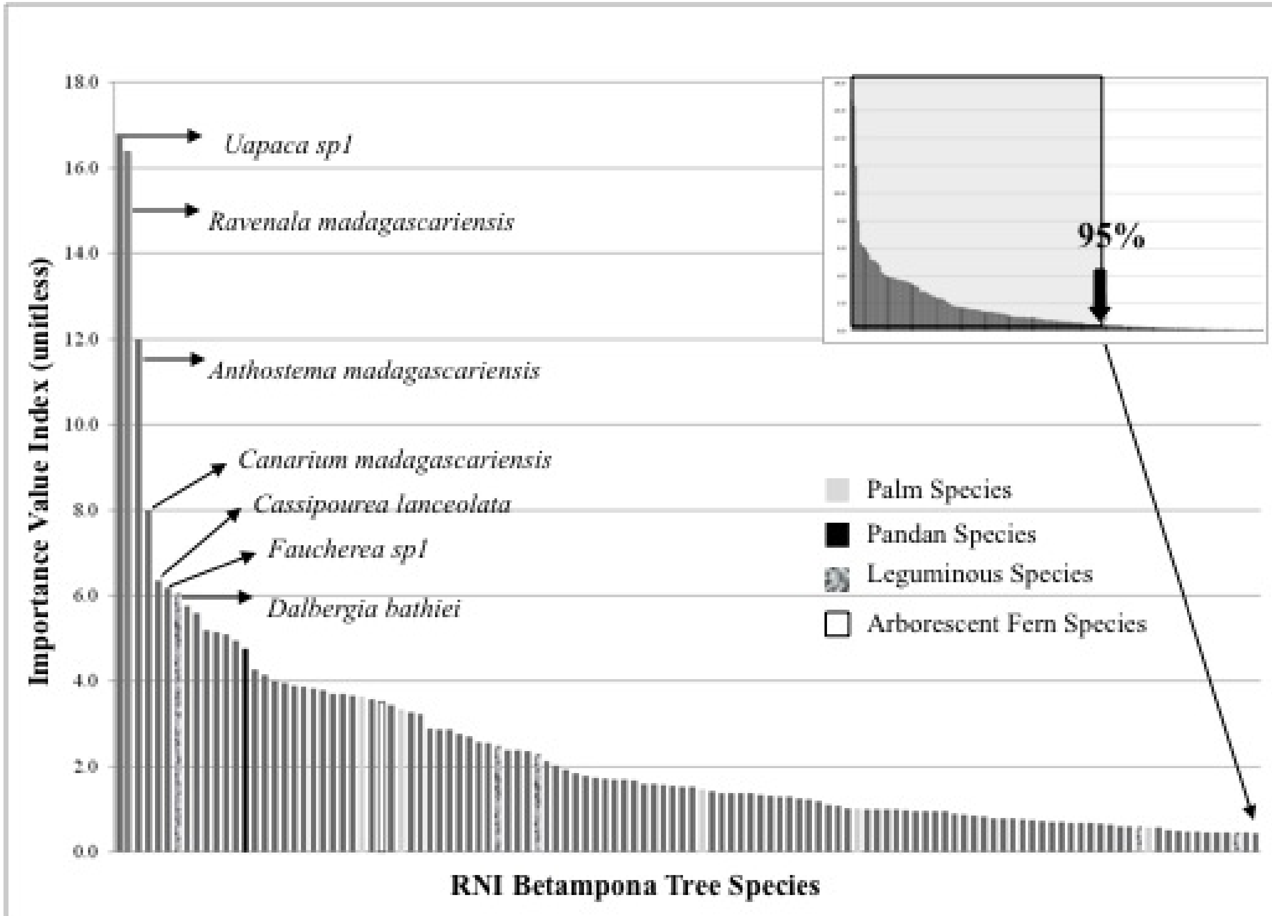

Fig. 3 Graph depicting results of the Importance Value Index (IVI) analysis showing 95% Importance of RNI Betampona Species. Top six species are labeled. Notable tree species types (palms, pandans, leguminous species and arborescent ferns are shown in light grey, black, textured and white, respectively.

The nine true palm and one palm-like species identified in RNI Betampona accounted for 9.84% of the IVI, with a combined value of 29.51 (true palms accounted for 4.39% and 13.18 respectively). The palm-like *Ravenala madagascariensis* (family: *Strelitziaceae*) was the second most important species overall in RNI Betampona. The significant importance of palms and palm relatives in RNI Betampona is an uncommon feature for rainforests worldwide. Another notable feature of RNI Betampona is the overall importance of leguminous tree species (family: *Fabaceae*), with 7 species together accounting for 4.10% of the importance (IVI: 12.31). Of these, *Dalbergia bathiei* was the most prevalent (31 stems in 23 plots) and was ranked seventh by the IVI calculation. A large deciduous tree, *Dalbergia bathiei,* had an average DBH of 22.57cm but ranged from 6.90 to 94.60cm in the RNI Betampona survey plots.

As noted by Goodman [16], Madagascar lowland rainforests are known for their high abundance and diversity of palms, pandans and tree fern species. In the RNI Betampona survey plots, tree ferns (*Cyathea spp*) had an overall IV of 4.76 and accounted for 1.59% of the index value. Though it was known that there were 12 species or sub-species of tree fern in RNI Betampona, they could not all be visually distinguished from one another in situ. They were therefore treated as one species group for IVI and diversity analyses. Similarly, pandan species, *Pandanus spp.* were also found among the top 95% of species importance, with an IV of 3.51 (1.17% IVI overall). It is unknown whether there is more than one species of Pandanus in RNI Betampona. Though they were relatively small in stature, with average DBHs of 7.03cm and 10.32cm and average heights of 6.49m and 5.30m for *Pandanus spp* and *Cyathea spp* respectively, both species were abundant in RNI Betampona plot, with 45 stems in 24 plots for *Cyathea spp* and 35 stems in 30 plots for *Pandanus spp*. Descriptive data for all Betampona species can be found in Appendix A and B of this article.

Plot level diversity

To quantify the diversity of species occurring in RNI Betampona plots, Shannon-Weiner (S-W) Indices were calculated for each survey plot for the 2005 dataset. As stated by Kent and Coker [29], values of the index usually lie between 1.5 and 3.5, with some exceptional cases exceeding 4.5. When tree species abundances were amassed into one RNI Betampona-wide dataset, the resultant S-W Index value of 4.466 indicated RNI Betampona species diversity overall is extremely high, with an associated evenness of 0.884. Results comparing diversity between plots indicated that within plot diversity varied from 1.609 in plot 100 (P100) to 3.226 in P013, with a plot-wide mean of 2.581 and evenness of 0.947 (Table 1). Diversity and evenness were further compared by height class and diameter class in order to investigate patterns occurring at different canopy strata and girth sizes. Results by height class indicate a strong decrease in diversity and increase in evenness from sub-canopy to super-canopy trees.

To further compare patterns of diversity in RNI Betampona, tree species abundances were divided into diameter-size classes, and S-W Index and Evenness values were calculated. As with the height class comparison, results indicated decreasing diversity index values with increasing tree diameter, with a smaller range of 3.051 to 4.255 as compared to that of the height class investigation, which ranged from 2.452 to 4.385 (Table 1). These findings are similar to that of Newberry and others [30] who showed a similar trend of decreasing diversity with increasing girth size in their 1992 study of a Dipterocarp forest in Sabah, Malaysia. However, in their study, evenness increased slightly along the small to large diameter gradient (0.75 - 0.86). Our calculations however, showed a patternless fluctuation of evenness along the size gradient with small range (0.828 to 0.895) and an average 0.871. This fluctuation was despite a large decrease in both stem count and species number along the size gradient from small to large trees.

Table 1. Results of the Shannon-Weiner diversity Index calculations for: a) RNI Betampona survey plots, including all plots calculated together, the least and most diverse plots and a plot-wide average b) tree species divided into height class and c) tree species divided into diameter classes. Evenness, number of species and stem counts are included.

	S-W Index *H'*	Evenness J	Number of Species	Stem Count
a) *Survey Plots 2005*				
All Plots	4.466	0.884	156	2227
Minimum Plot (P100)	1.609	0.774	8	18
Maximum Plot (P013)	3.226	0.979	27	34
Plot Average	**2.581**	**0.947**	**16**	**22**
b) *by Height Class*				
x <10m	4.385	0.89	138	1009
10m ≤ x < 16m	4.278	0.892	121	444
16m ≤ x < 24m	3.762	0.851	83	371
24m ≤ x < 33m	3.266	0.905	37	69
x ≥ 33m	2.452	0.956	13	19
Average	**3.629**	**0.899**	**78**	**382**
c) *by Diameter Class*				
x > 5cm	4.255	0.873	131	5619
5cm ≤ x < 10cm	4.383	0.888	139	1202
10cm ≤ x < 20cm	4.206	0.895	110	641
20 ≤ x < 40cm	3.528	0.828	71	303
x ≥ 40cm	3.051	0.873	33	74
Average	**3.885**	**0.871**	**97**	**1568**

The smaller depth in variability of S-W diversity index values over the diameter class gradient along with the fluctuation in evenness suggests that height plays a greater role in constraining species than the diameter classes assigned by this study. This inference was upheld by both quantitative and qualitative observations made during the field survey. Tree diameters in RNI Betampona were found to be smaller overall than those described in other lowland rainforests worldwide, a feature also noted by Grubb [23]. Qualitatively, it was quite common for a tall canopy dominant tree to have the same diameter as a sub-canopy tree that was half as tall.

Forest structure and density

Analyses of variance (1-way ANOVA) of canopy coverage (%), basal area (m^2/ha), and groundcover (%) between plots for each year showed significant among-plot variation for these variables for 2004 and 2005 (p<0.0001). Further, Student's *t* tests of each variable comparing sampling years lead to rejection of the null hypotheses at p<0.0001 that there were no differences in canopy cover, basal area or groundcover between 2004 and 2005. The average plot-wide canopy cover (%) increased from 79.23% in 2004 to 82.59% in 2005 (Table 2). In addition, per plot averaged stem area (m^2/ha) decreased from 75.85m^2/ha to 65.34m^2/ha, and groundcover (%) increased over the study years from 41.45% to 58.83%, respectively.

Table 2. Summary of results per plot comparison of stem count, species count, regeneration stem count, basal area (m^2/ha), canopy cover (%) ground cover (%), diameter at breast height (cm) and height (m) values for 2004 and 2005 survey years. Average, minimum and maximum diameter growth increment (cm/year) and height growth increment (m/year) are also reported plot-wide.

		Stems Count	Species Count	Regen Stem Count	Basal Area (m^2/ha)	Canopy Cover (%)	Ground Cover (%)	DBH (cm)	Height (m)	Diameter Growth Increment (cm/year)	Height Growth Increment (m/year)
	AVERAGE	28.47	19.27	94.19	61.64	79.23%	41.45%	12.96	10.86		
	Minimum	12	10	22	22.94	50%	10%	5	0.77		
	Maximum	52	30	224	126.16	95%	85%	97.5	45.59		
2004	**Total**	2847		9419							
	AVERAGE	22.27	15.71	57.28	81.11	82.59%	58.83%	13.45	12.1	**0.3**	**0.82**
	Minimum	12	8	19	36.7	55%	10%	5	1.09	**0**	**0**
	Maximum	38	28	140	153.69	95%	95%	97.5	46.88	**10.03**	**3.88**
2005	**Total**	2227		5728							

The average DBH (cm) of trees >5cm within the survey plots also increased from 12.96cm in 2004 to 13.45cm in 2005, though the range stayed the same (5.00cm to 97.50cm). A two-tailed paired *t*test indicated the DBH growth to be statistically significant from 2004 to 2005 (95% confidence interval, p<0.0001). Height had a similarly statistically (95% CI, p<0.0001) significant increase over the study years from 10.86 to 12.10. Further evidence of thinning occurring in the plots, this indicates that there were fewer small trees in 2005 than in 2004 in the survey plots. Diameter growth increment averaged 0.3cm/year among the 2227 trees measured in 2004 and 2005, with annual growth ranging from no growth to 10.03cm/year. Height growth increment was 0.82m/year on average, with a range of no height gain to 3.88m/year for trees >5cm-DB measured in the survey plots. These growth values are the first to be recorded for Malagasy rainforest.

Comparison to other rainforests worldwide

Comparing the 244 tree species sampled in this study in RNI Betampona to those sampled in other rainforests worldwide with study areas of similar size (Table 3) further highlights the significant levels of species diversity found in Madagascar's lowland rainforest. The number of species is closest to that of Yanomamo, Peru, where 292 species were found in a one-hectare forest plot, as reported by Whitmore [36]. Species numbers were also similar to rainforests in Pasoh, Malaysia [38] and Kalimantan, Indonesia [36], though the latter study area was twice that of the *ca.* 0.79ha study area in RNI Betampona. Species numbers for RNI Betampona were more than twice that of Korup National Park in Cameroon [36], despite the similar study area size. Our comparison included more South American and Asian forests, partly because African rainforests are comparatively poor in floral diversity as compared to other rainforests worldwide [33].

Species endemism and diversity of Madagascar's biota have been explained by 165 million years of separation from mainland Africa, resulting in an independent evolutionary history on the island [1, 12, 16, 39]. The more recent separation from the Indian continent (*c.* 88 million years) has resulted in clear relationships with the flora of Asia, particular that of India, Sri Lanka and the Malesian region [12-14, 40]. Dufils [12] also notes a small but significant South American relationship to Madagascar tree species in addition to the African and Asian species affinities. Indeed, inventories have shown around 26 genera that are present in Madagascar and South America, but not necessarily found in Africa. An example of this is the 'Travelers palm' or Ravenala tree (*Strelitziacae*), which is represented by a single widespread endemic species (*R. madagascariensis*) in Madagascar, and the only other species in the genus found in Brazil and Guyana [12, 40].

Table 3. Results comparing species number for RNI Betampona, Madagascar as compared to other rainforest study sites of similar size worldwide.

Rainforest Location	Species Number	Sample Area (ha)
Yanamomo, Peru[†]	292	1
RNI Betampona, Madagascar	**244**	**0.79**
Pasoh, W. Malaysia[σ]	210	1
Bukit Lagong, Malaysia[†]	180	1
Wanariset, Kalimantan, Indonesia[§]	239	1.6
Northwest Amazonia, Columbia*	178	1
Sungei Menyala, Malaysia[†]	170	1
Korup National Park, Cameroon[†]	140	0.63
Jaro, Kalimantan, Indonesia [†]	135	1
Papua New Guinea[†]	115	0.8
Papua New Guinea[†]	75	0.8

[†]Whitmore (1990); *Duivenvoorden (1996);
σKochummen et al. (1990); §Kartawinata et al. (1981)

Discussion

The findings of this study are the first undertaking of a comprehensive tree species inventory recorded for lowland rainforest in this region of Madagascar. A total of 244 tree species belonging to 49 families comprised the 2,847 stems ≥5cm measured and the 9,419 stems <5cm counted during the 2004 plot survey. In 2005, 2,227 trees ≥5cm were measured and 5,728 stems (of 135 species) were noted in the <5cm regeneration stem count. This trend follows dynamics seen in other rainforests worldwide [32, 33] where local thinning occurs following recovery from the formation of canopy gaps by disturbance. This inference is supported by an increase in the average DBH in the trees measured as well as total plot basal area and average canopy cover (%) from 2004 to 2005. Family dominance across RNI Betampona follows expected dominance diversity curve behavior for rainforests worldwide (Figure 2).

Whereas in many Asian lowland rainforests dominant tree species belong to the *Dipterocarpaceae* family, in RNI Betampona the dominant tree species are of the *Euphorbiaceae* family. The Euphorbs had the highest representation in both survey years, with a total of 333 trees ≥5cm measured in 71 plots in 2005 (400 stems in 76 plots in 2004). Other well represented families included *Lauraceae, Rubiaceae, Anacardiaceae, Arecaceae, Clusiaceae, Moraceae and Rhizophoraceae*, which together with *Euphorbiaceae* accounted for more than 50% of the individual trees measured during both survey years. Two other notable families found in RNI Betampona, *Sarcolanaceae* (containing 10 genera 35 species) and *Didymelaceae* (one genus, two species total), are among the total of 8 entirely endemic families in Madagascar [16].

Results of the Importance Value Index were calculated for 2004 and 2005 (Figure 3) and showed no significant difference among the most important species in RNI Betampona. Of the 192 tree species included in the IVI calculation, 118 species were among the top 95% of importance values. The seven most important species included two *Euphorbiaceae* species, a palm-like [14] tree species, and a nitrogen-fixing member of the *Fabaceae* family. Together the top 10 species account for *c.* 30% of the IVI overall (Figure 3). The significant importance of palms and the palm-like *R. madagascariensis* in RNI Betampona is an uncommon feature for rainforests worldwide.

The significant variability of the tree species diversity and evenness among Betampona plots suggests a mosaic patterning of species distribution in RNI Betampona. An examination of diversity by height class indicated a strong decrease in diversity and increase in evenness from sub-canopy to super-canopy trees. This finding supports Whitmore's [32] assertion that species diversity decreases with increasing elevation within in the forest canopy and is highest among the regeneration as this canopy layer is a combination of larger tree species competing for canopy dominance and small sub-canopy trees already at their maximum height. The fact that species number and stem count both decrease with increasing height class confirms successful competitive strategies for a few canopy dominant species in RNI Betampona, rather than a random occurrence of the achievement of canopy dominance by many species.

Tree species abundances were also divided into diameter size classes and S-W Index and Evenness values were calculated. Results also indicated decreasing diversity index values with increasing tree diameter but with a smaller range compared to that of the height class investigation (Table 1). These findings are similar to those of Newberry and others [30], who showed a similar trend of decreasing diversity with increasing girth size in their 1992 study of a Dipterocarp forest in Sabah, Malaysia. The smaller depth in variability of S-W diversity index values over the diameter class gradient, along with the fluctuation in evenness, suggests that height plays a greater role in constraining species than the diameter classes assigned by this study. This inference was upheld by both quantitative and qualitative observations made in during the field survey. Tree diameters in RNI Betampona were found to be smaller overall than those described in other lowland rainforests worldwide, a feature also noted by Grubb [23]. Qualitatively, it was quite common for a tall canopy dominant tree to have the same diameter as a sub-canopy tree that was half as tall.

Statistical testing of each measured variable within the survey plots comparing sampling years indicated that there were no differences in canopy cover, basal area or groundcover between 2004 and 2005. The increasing trend of these three variables taken with the decrease of >5cm tree stem count and regeneration stem counts from 2004 to 2005 is further evidence of a forest undergoing thinning. The average size of trees (DBH (cm) and height (m)) within the survey plots also increased over the study years, providing evidence of thinning occurring within the forest.

Fig. 4. Clockwise from left right: A typical first order stream in primary forest with moss covered rocks and epiphytes, a forest clearing made by an old landslide off the western ridge of the main crest trail, the main crest trail in RNI Betampona and a canopy emergent species in the genus *Faucherea* (family: Sapotaceae) with abundant epiphytes and lianas.

Implications for conservation

A significant challenge for the scientific community over the past few decades has been how to quantify the biomass that exists in remote forested regions and measure the effect of change where there is a lack of baseline data. With the development and testing of new conservation measures such as carbon (C) finance mechanisms to reduce greenhouse gas (GHG) emissions and conserve biodiversity in the forested areas across the planet, the need for monitoring and understanding these remote forested regions will only increase. Madagascar is one such place. With levels of biodiversity that are among the highest worldwide, the island is in many ways on the verge of ecological collapse [1, 2, 8, 16, 19 *see also* Jernvall and Wright 1998). This research sought to describe diversity, structure and function in one of these understudied ecosystems, and has culminated in the only multi-year survey dataset that exists for lowland rainforest in the Toamasina region of Madagascar.

Conserving biological diversity in Madagascar has become an issue of increasing priority and urgency within the international scientific and policy communities in recent years. Expanding human population combined with the continuing practice of slash and burn clearing as an agricultural technique are two associated factors in the destruction and fragmentation of the remaining forest habitats on the island. Madagascar has lost over 90% of its original rainforest, damage that is in many cases irreversible [12] and has resulted in Madagascar being considered one of the world's most threatened hotspots for terrestrial biodiversity [18]. Given the rapid rate at which the lowland rainforests in particular are being fragmented and consumed, it is projected that there will be no primary forest left outside of protected reserves by the year 2020 [16]. However, this may become a reality sooner as the anthropogenic pressure on the flora and fauna as well as on the resources that sustain them has been been on the rise due to lack of conservation enforcement since the government coup in early 2009 [41-44].

Efforts to conserve Madagascar rainforest were initiated in the 1990s but became more large-scale in the early 2000s at both local and international levels in an attempt to save what is left of these unique ecosystems. A key element in development of an appropriate management system to protect and maintain Malagasy rainforests is a comprehensive knowledge base of information about structure and function of the forest ecosystem. This has thus far been a challenge for conservation planners and the scientific community due to both the lack of infrastructure and the difficulty of accessing primary lowland rainforest. Additionally, this lack of accessibility has resulted in much of the reported research being in less comprehensive, descriptive phases.

Equally important in our understanding of how best to manage and conserve Madagascar's remaining rainforests is an understanding of the dynamic relationships among endemic flora and fauna at the ecosystem level. Comprehensive ecosystem studies that include species inventories, structure, growth, diversity information, and comparisons to other rainforests worldwide provide a foundation for future research. In addition, the publication of this research provides a basis for comparison to future studies using wider-scope, cutting-edge techniques such as remote sensing of forest extent, 3D structure imaging, and ground-truthing of forest-wide biomass estimates essential to economic incentive-driven conservation approaches, such as that of the UNFCCC's Agreement on Reduced Emissions from Deforestation and Degradation (REDD+) [45] and the UN-REDD[†] programs.

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