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Tree Structure and Diversity in Human-Impacted Littoral Forests, Madagascar

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ABSTRACT / This research surveyed human-impacted littoral forests in southeastern Madagascar to determine (i) how forest structural features, indicative of human impact, are related to total, utilitarian, and endemic tree diversity; (ii) the distribution, abundance, and demographics of tree species groups (i.e., total, useful, endemic) across the landscape; and (iii) the amount of basal area available per human use category. We also use these data to consider issues of sustainable use and how human impact may influence littoral forest tree community composition across the landscape. Within 22 transects of 400 m^2 each, we recorded a total of 135 tree species and 2155 individuals. Seventy-nine species (58%) were utilitarian and 56 (42%) were nonutilitarian species. Of the 2155 individuals, 1827 (84%) trees were utilitarian species. We recorded 23 endemic species (17% of the total species) and 17 (74%) of these were utilitarian species. Basal area was significantly correlated with Shannon Weiner Index values for total ($r = 0.64$, $P < 0.01$), utilitarian ($r = 0.58$, $P < 0.01$), and endemic tree diversity ($r = 0.85$, $P < 0.01$). Basal area was significantly correlated with the Simpson's index values for the endemic species ($r = 0.74$, $P < 0.01$). These correlations suggest that endemic tree species, of high global conservation value, may be the species group most influenced by changes in forest structure. Utilitarian species constituted 84% of the total basal area. The use category contributing the highest amount of basal area to the landscape was firewood. The results presented herein demonstrate that the landscape of southeastern Madagascar, commonly perceived as degraded, retains high value for both global conservation purposes and for local livelihoods. Thus, valuable opportunities may exist for developing conservation incentives that leverage both global and local conservation needs.

Researchers have claimed that the conservation of biodiversity and human use of tropical forest resources in developing countries are in conflict with one another (Kramer and others 1997, Singh 1998, Bruner and others 2001) because of the strong dependency of people on natural resources for daily subsistence in many tropical countries (Dasmann 1976, Olindo 1989). Such issues are of paramount importance in Madagascar, one of the world's foremost biodiversity hotspots (Myers and others 2000) and one of the world's least developed countries (UN 2003). The stark contrast between the rich natural environment and extreme human poverty have resulted in challenges between conservation, development, and livelihood security (Ferraro 2002, Cadotte and Lovette-Doust, in press). Approximately 80% of Madagascar's 16 million inhabitants live in rural areas and exploit natural resources for their daily needs. Concern over the island's rapidly diminishing rain forest and consequential losses of biodiversity have resulted in large sums of money, research, and extensive conservation efforts (Kull 1996). Currently, only 3% of the country's land area has protected status, although President Marc Ravalomanana recently pledged at the World's Park Congress in September 2003 to increase that amount to 10% (UNESCO 2003).

A significant proportion of Madagascan and global biodiversity remains outside of protected areas (Hannah and others 1998, Heywood and Iriondo 2003). Although many forests outside of parks or reserves may be anthropogenically altered, human impacted forests often have high conservation value (Shwartzmann and others 2000a). Because of their dependency on forest resources, traditional peoples often have high incentives for protecting the forest (Col-

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chester 2000), and thus can be the conservationist's greatest and most dependable allies when compared to ineffective, beleaguered state bureaucracies (Colchester 1998). Thus, supporting the management of unprotected forests by local people can be a very effective and cost-efficient way of using the limited resources and money available for conservation. The protection of the vast majority of tropical biodiversity in unprotected areas in developing countries requires the adoption of ''win-win'' scenarios that optimize both livelihood security and biodiversity protection. For these reasons, understanding human use of forest resources and the impacts of humans on forest biodiversity may provide crucial information necessary for developing sustainable resource management schemes in unprotected areas.

Assessing Human Impact on Biodiversity

The structure of a forest stand can provide a useful indicator of human impact, because measures such as forest basal area and stem density have documented responses to disturbances. For example, mean basal area in a stand may decrease as a consequence of increasing disturbance pressure, whereas stem density of smaller trees may increase after disturbance (Macedo and Anderson 1993, Bhat and others 2000, Chittibabu and Parthasarathy 2000, Bhuyan and others 2003). Other structural indicators, such as the number of cut trees or coppiced individuals can also indicate degree of disturbance (McLaren and McDonald 2003). However, disturbances associated with certain human uses of the forest such as selective extraction of leaves, flowers, or berries for medicine or food may not be easily observed through structural changes.

The identification of structural features that represent both degree of human impact and biodiversity would be useful for aiding natural resource management. Researchers have observed significant relationships between species diversity and forest structural features that respond to disturbance, such as stand density, stem diameter, and stem size class distributions (Huang and others 2003) and have reported declines in both species diversity and equitability (equitability, also referred to as evenness, is a measure of the extent to which species are evenly represented within a community) of tropical forests with increasing degrees of disturbance (Rao and others 1990). However, the impacts of disturbances on species richness and equitability are often complex and inconsistent across tree size classes (Guariguata and others 1997, Okuda and others 2003). For these reasons, no general, robust theory exists for predicting the impact of environmental change on tropical forest species diversity at local-landscape scales (Sheil 1999, Huang and others 2003). Every site possesses unique environmental and anthropogenic factors, and, thus, predictive theory requires a strong foundation in specific site conditions and the range of factors that operate in those conditions (Sheil 1999).

Conservation Across the Landscape: The Importance of Species Richness and Abundance Data

Species richness and abundance data are crucial for assessing the impacts of disturbance on biodiversity, conservation priority setting, and long-term monitoring. Plant biodiversity conservation planning often uses criteria of high botanical richness, centers of endemism, and rarity for priority setting (van Jaarsveld and others 1998, Myers and others 2000, Heywood and Iriondo 2003). Globally, these priority systems can work well in delivering specified conservation objectives (but see Jepson and Canney 2001). However, at a landscape level, the relationship between endemism and diversity in a highly fragmented landscape (in a single phytogeographic unit) may be less predictable because diversity tends to increase with area while ecological endemics tend to aggregate in small and distinct habitats (ter Steege and others 2000).

In countries where humans are an integral part of the natural environment, the inclusion of utilitarian species conservation in land-use planning and priority setting schemes could provide multiple benefits. Useful native plants can be indicators for monitoring the progress of conservation and development projects because they simultaneously provide information on both ecological and socioeconomic change (Kremen and others 1998). Furthermore, information on utilitarian species used with data on species richness and endemic and rare species may assist conservationists and natural resources managers in determining how local and global conservation priorities overlap across a landscape. Such information could support land use planning that seeks to maximize environmental protection and human livelihoods.

This study aims to investigate human impact and tree community composition in the littoral forests of southeastern Madagascar. Our specific objectives are to (i) identify the relationship between structural features of the forest (indicative of human impact) and measures of total, utilitarian, and endemic tree diversity; (ii) assess the distribution, abundance, and basal area of total, utilitarian, and endemic tree species in the littoral forests; (iii) assess the amount of basal area available for different human uses of forest resources; and (iv) use these data to consider issues of sustainable use and how humans may be influencing tree community composition across the landscape. Although some botanical work has been undertaken in the littoral forests (Dumetz 1999, Gadotte and Lovette Doust in press), we are unaware of previous research into these issues.

Materials and Methods

Site Description

The study area comprises approximately 2,800 ha (Vincelette and others 2003) of tropical lowland rain forest in south-eastern Madagascar, distributed across three areas: Ste. Luce, Mandena, and Petriky (Figure 1). The forests of St. Luce and Mandena comprise a mosaic of forest fragments of different sizes and shapes, whereas Petriky exists predominantly as one large forest parcel. The three sites constitute a subtype of rainforest known as ''littoral forest on sand'' because of the distinct soils underlying the forests (Dumetz 1999). Collectively, Mandena, Ste. Luce, and Petriky are the only patches of this forest type in Madagascar and are floristically and structurally similar to one other, while being structurally distinct from other forests in the region, in their low canopy height and low diameter at breast height (dbh) values (Dumetz 1999). A distinct climatic gradient exists across the study area, with conditions becoming drier and hotter to the south (Goodman and others 1997). The wet season occurs from November to May, with annual mean rainfall amounts averaging 2400 mm in Mandena and Ste. Luce and 1200 mm in Petriky (QMM 2001). The forests are located at elevations less than 50 m and comprise a relatively narrow band of coastal plain and adjacent foothills averaging approximately 7 km in width and extending from 24°35′S to 25°08′S latitude (Lewis Environmental Consultants 1992).

The forests are the proposed site for a large-scale ilmenite mine that will be established by QIT-Madagascar Minerals (QMM), a subsidiary of the multinational corporation Rio Tinto. The mining is proposed to begin first in Mandena as early as 2006 and, following this, to progressively mine the other sites of Petriky and Ste. Luce (QMM 2001). The mining project would remove approximately two thirds of the current total littoral forest cover (QMM 2001). However, the mining company maintains throughout their Social and Environmental Impact Assessment that if the mining activity were not to take place, most of this forest will be degraded or deforested because of local use over the next 40 years (QMM 2001). In fact, much of the littoral forest is currently considered to be degraded or secondary because of long-term human pressure (Dumetz 1999).

The mining company has classified the forest stands across the landscape as belonging to one of five classes of forest condition based on assessments of forest structure, namely, measures of canopy openness (MIR Télédétection Inc.1998, QMM 2001, Figure 1). They determined these classifications using a semiquantitative visual assessment technique combined with a qualitative classification system (see Lowry and others 1999 and QMM 2001 for full descriptions), which cannot be replicated easily because of biases associated with the observer's judgments. Because each fragment is treated as a unit, this survey failed to capture the full range of structural heterogeneity and variability in human impact across each fragment (see Ingram and others, 2005). Ingram and others (2005) have produced a quantitative method for assessing littoral forest basal area at the study site using a combination of ground collected data and spectral information available from satellite imagery, which may permit more refined future monitoring of human impact on forest stands. These two studies, although varying in approach and findings, are among the only studies on landscape scale patterns in littoral forest structure.

Disturbances in the littoral forest include both human and natural disturbances, although, we have little historical, quantitative information on the extent and impacts of these agencies. Local people are known to use the forests for a variety of subsistence purposes such as firewood, construction materials, food and medicine. Itinerant people, who recently have migrated from the more southerly regions of the country into Mandena because of its close proximity to the township of Fort Dauphin, utilize the forests for charcoal production (QMM 2001). Natural disturbances include frequent cyclones between the months of January and March when winds along the East Coast reach speeds up to 300 km/hr (Donque 1972). Such events may result in the uprooting of trees across hundreds of hectares (Chauvet 1972). The combination of shallow root systems, sandy soils, and extreme winds make the littoral forests exceptionally vulnerable to uprooting because of cyclonic activity (Day 1950, de Gouvenain and Silander 2003). Leigh (1988) hypothesizes that the frequent cyclone disturbances are responsible for the relatively short canopy of Madagascar's eastern lowland rainforests.

Researchers have recommended that the littoral forests be a national conservation priority (Ganzhorn and others 2001). The sites of Petriky, Mandena, and Ste. Luce possess high degrees of faunal biodiversity and unique assemblages of faunal species (Ganzhorn

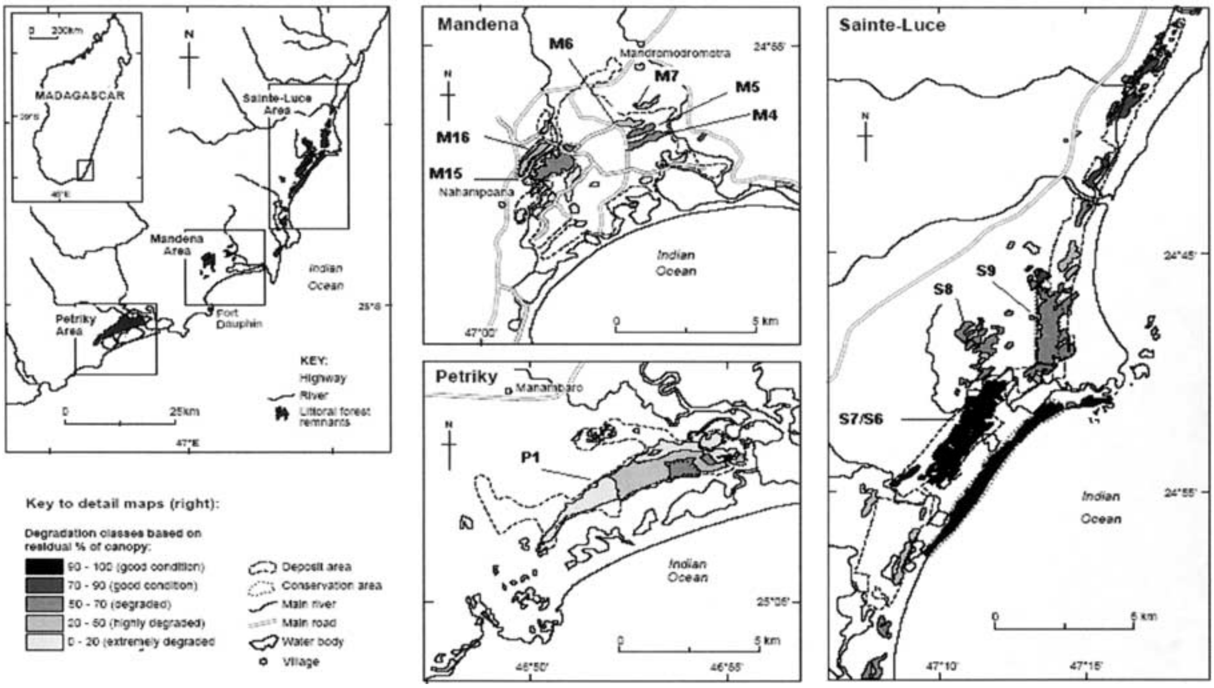

Figure 1. Map of southeastern Madagascar and the condition of the littoral forest stands in the Petriky, Ste. Luce, and Mandena study sites. Adapted from an original map provided by Rio Tinto Iron and Titanium, London (personal communication, Martin Theberge, 2003).

1998, Watson and others 2004, in press). Collectively, the forests in the region constitute one of the world's most biodiverse concentrations of plants because of high tree species richness and the high proportion of species endemic to Madagascar (Dumetz 1999).

Field Surveys

In November 2001, we surveyed 22 belt transects in the three study sites. We sited transects randomly in six forest stands representative of four of the five classes of forest condition as designated by QMM (2001): the largest forest stand in Petriky (denoted P1); two stands in Mandena (M16 and M4); and three stands in Ste. Luce (S8, S7 and S9) (Figure 1). Each transect was 100 m by 4 m and at least 100 m from the forest edge. The cardinal direction of each transect was randomly selected unless the selected direction would extend the transect into a land-cover type other than forest (i.e., swamp) or would involve traversing a localized elevational gradient (i.e., down a slope). Site locations (Appendix 1) were recorded with a Geographical Positioning System, apart from two sites where we could not obtain satellite readings. In each transect, all trees with a dbh (diameter at breast height, 1.3 m) ≥5 cm were measured and identified and identified by local expert botanist, Ramesy Edmonds, using the vernacular name. For multiple-stemmed individuals, we recorded the dbh of all stems ≥5 cm dbh. We also identified (where possible) all trees that had been cut. We defined cut trees as live or dead stumps that appeared to have been cut by humans rather than natural causes. Because of the small size of the trees in the littoral forests, stems were divided into 5–9.9 cm, 10–14.9 cm, and ≥15 cm dbh size classes.

Scientific Taxonomic Classification of Vascular Plant Names

Botanists from Kew Gardens and local Malagasy taxonomists collected voucher specimens to match the vernacular names of tree species with the formal Latin nomenclature (Appendix 2). Missouri Botanical Gardens (MBG) has followed a similar methodology for identifying plants in the region. For this study, we have used the Latin names provided by Kew and, if necessary, consulted the MBG database for Latin names not included within the Kew database. The researchers at Kew found an approximately 95% agreement between identification of species using the vernacular and Latin naming system. This is the highest level of agreement between a vernacular and Latin classification system observed by our colleagues at Kew Gardens (P. Smith 2003, personal communication, A. Davis, 2003, personal communication). Because several of the species collected could not be provided with a Latin name, we use the vernacular names in this study, following the practice of similar studies in Madagascar (e.g., Kremen and others 1998). The fact that these species have not yet been described using the Latin system should not delay studying them, especially, because of the threats facing these forests in the immediate future. From the total species list, we categorized species into utilitarian and/or endemic species groups using the following classifications.

Utilitarian Species Classification

Dr. Clement Sambo, social anthropologist at the University of Tulear, conducted extensive research in the study area to determine the forest species used by local people (C. Sambo 2001, unpublished data). He identified the following primary uses of tree species: energy, three different timber uses, medicine/spiritual uses, animal food, human food, fibers, and oil (Appendix 3). Herein, we have reorganized these classifications into the human use categories of timber, firewood, charcoal, medicine, human food, and other uses. The latter represents a combination of oil and fibrous material sources, both of which were rare in our data. We have also divided the energy sector into charcoal and firewood categories because separate social groups practice the two harvesting techniques, and these techniques have very different impacts on forest structure (QMM 2001, JCI, author's personal observations).

Endemic Species Classification

Missouri Botanical Gardens (MBG) scientists and other taxonomists used voucher specimens, desk studies, and field inventories to determine endemic species classifications for plants in the study sites (Lowry 2001). They identified four different conservation priority groups (Appendix 4). *Priority 1*: species endemic to the mining sector; *Priority 2:* species endemic to the littoral forest zone (some forest occurs outside of the mining path); *Priority 3*: species endemic to the southeastern region of Madagascar; *Priority 4*: species endemic to the island of Madagascar.

Analytical Methods

We constructed a mean species accumulation curve using the Species Diversity and Richness software to assess the ability of the sampling regimen to capture the diversity of species across the landscape (Henderson and Seaby 2000). Because the order in which samples are taken alters the shape of the curve (Henderson 2003), we randomized the order of the transects 22 times.

In addition to species richness, we calculated diversity indices for all species and for each group, utilitarian and endemic species, per transect. We selected three indices that provide, between them, metrics of varying sensitivity to species richness, evenness, and dominance: the Shannon Weiner (SW) Index, the Simpson's index, and the Berger Parker index (Henderson 2003). The SW Index of diversity is the most widely used index that combines species richness with abundance (Kent and Coker 1992). Both the number of species and their equitability affect the values of this index, which should, theoretically, reach a maximum value when a high number of species are present at relatively equal abundances. The value of the index typically ranges between 1.5 and 3.5. The Simpson's index (Simpson 1949) is a measure of the probability that two randomly sampled individuals belong to different species. It provides a measure of dominance because it weights towards the most common species in the system. Simpson's index is useful because of its ability to produce unbiased estimations from a sample of reasonable size, its predictable dependence on sample size/sampling effort (which permits accurate extrapolations), and its ability to measure similarity between communities (Lande and others 2000). The larger the value of the index, the more equal is the distribution of species throughout the sample. Thus, as the index value decreases, species dominance increases. The Berger Parker index is also a dominance index, recommended by Henderson (2003). The index value increases with increasing dominance of one species.

We calculated Pearson's correlation coefficients using SPSS (version 11.5). We calculated basal area and created rank abundance plots for utilitarian, nonutilitarian, and endemic species sets. Also, we analyzed the demographics of species using the following size classes: 5–9.9 cm, 10–14.9 cm, and ≥15 cm dbh.

We divided the utilitarian species into the different use categories and for each use category, total basal area was calculated. Although density is a useful comparative measure, the basal area of stems above some marketable diameter is a better measure of site occupancy by timber species (Chazdon and Coe 1999) and of energy available for human use across the landscape. Frequency, rather than basal area, is likely to be the more important measure for medicinal species because species substitutability is likely to be lower for medicinal purposes when compared to other forest uses (Gordon and others 2003). For this reason, we also calculated the number of individuals of medicinal species per transect.

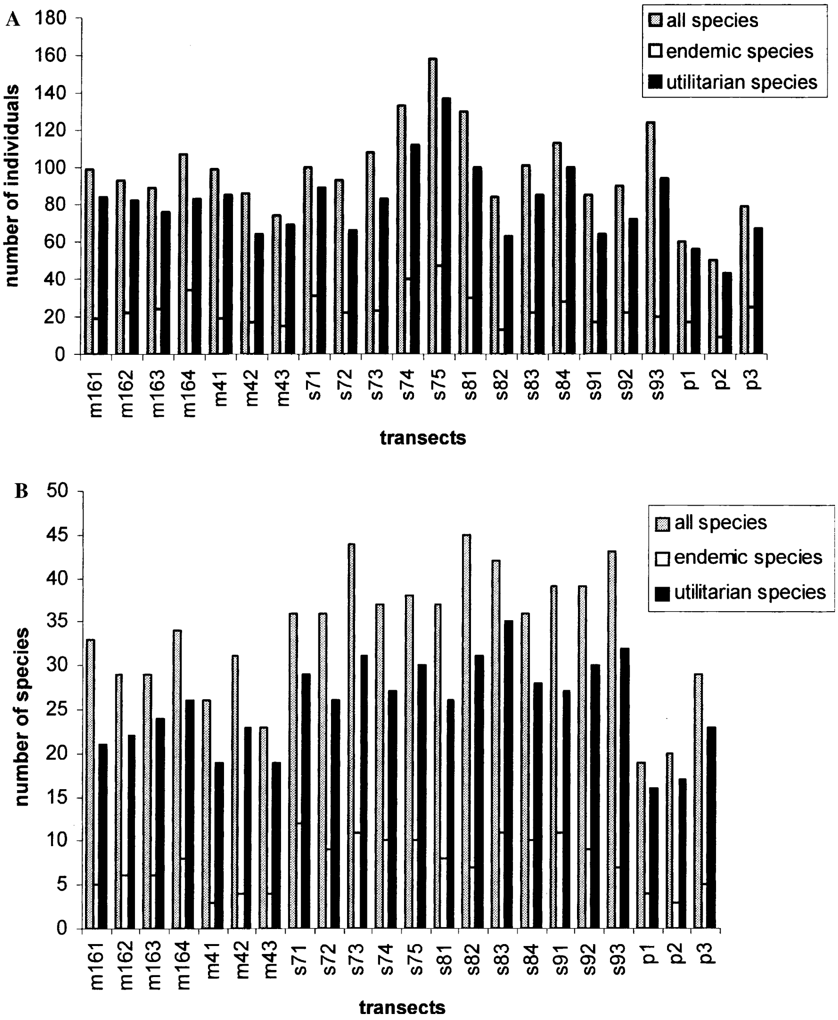

Figure 2. The number of individuals and tree species recorded during ground surveys divided into three categories: "all" species, endemic and utilitarian species. (a) Number of individuals recorded within each category. (b) Number of species recorded within each category.

Results

In total, we recorded 2155 individuals of 135 tree species (Appendix 2), with maximum values in a single transect of 158 individuals and 45 species (Figure 2). Thirty-two (24%) species were singletons, represented by only one individual tree. Seventy-nine of the recorded species (58%) were utilitarian and 56 (42%) were nonutilitarian species. We recorded 23 endemic species (17% of total species) and 17 (74%) of these were also utilitarian species. Of the 2155 individuals recorded, 1827 were utilitarian species (84%).

Relationship Between Structure and Diversity

One transect, S93, was omitted from the structure and diversity correlation analyses only, because of its anomalously high basal area, which was a result of one very large, dominant species (all of the other analyses in this study utilize data from the complete set of 22 transects). Inclusion of this transect weakened the relationships considerably. The correlations between basal area and measures of diversity were stronger than with stem density (Table 1). The relationships between basal area and diversity were highest for the endemic subset, and weakest for the utilitarian species. However, there were fewer endemic species than utilitarian species and, thus, less spread in the data, which may have contributed to the observed, stronger relationship between basal area and endemic species. For "all" species and utilitarian species, only the SW index and species richness measures showed significant relationships with stand basal area. The correlations with stem density and diversity measures show similar but weaker relationships than observed with basal area. For all species and utilitarian species, the only significant correlations with stem density were in relation to species richness.

Table 1. Relationship between structure and diversity[a]

	Basal area		
	Utilitarian	All	Endemic
Shannon Weiner Index	0.58**	0.64**	0.85**
Simpson's Index	0.30	0.35	0.74**
Berger Parker Index	−0.25	−0.29	−0.79**
Species Richness	0.71**	0.74**	0.74**
	Stem density		
	Utilitarian	All	Endemic
Shannon Weiner Index	0.37	0.41	0.57**
Simpson's Index	0.02	0.02	0.28
Berger Parker Index	−0.05	−0.08	−0.57**
Species Richness	0.58**	0.57**	0.57**

[a] Pearson's correlation coefficients based on untransformed data for 21 transects.

Denotes significance at $P < 0.05$. The correlation between basal area and stem density: 0.60.

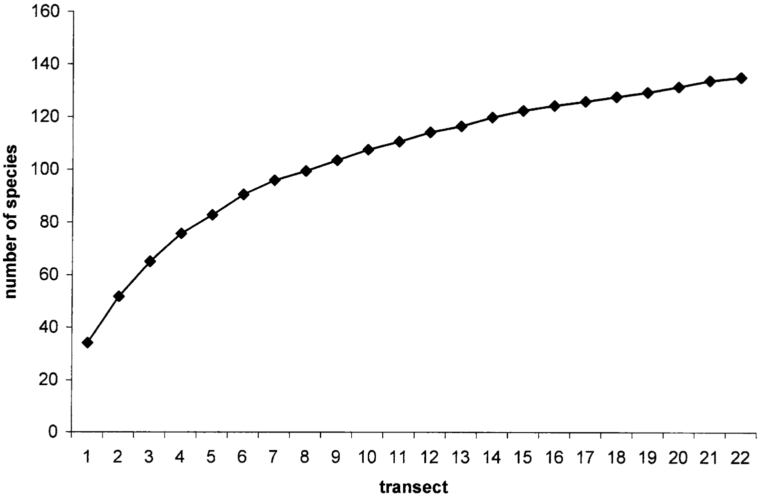

Figure 3. The mean species accumulation curve for all stems ≥5 cm dbh within 22 transects and randomized 22 times using Species Diversity and Richness software (Henderson and Seaby 2000).

Species Abundance Across the Landscape

The species accumulation curve gradually flattened, although it does not quite plateau (Figure 3). The final data point represents an incremental increase of only 0.9%, and thus we can assume that, at a landscape scale, we have captured the majority of the common species in the area. The rank abundance plots (Figure 4a,b) show the abundance patterns of the different groups of species. The proportion of singletons in the utilitarian species group (13% singletons) was much lower than in the nonutilitarian species group (40% singletons). The most abundant nonutilitarian species, Zoralahy (*Dicoryphe stipulacea*), was represented by 51 individuals. In comparison, 11 utilitarian species were represented by >60 individuals, the most abundant of which were Kalavelo (*Suregada baronii*) (115 indviduals), Harandrato (*Intsia bijuga*) (108 individuals), and Rotry (*Syzygium emirnesis*) (94 individuals). Although we recorded far fewer endemic species than nonendemics, several species were quite abundant and only 13% of all endemic species occurred as singleton records (Figure 4b). The two most abundant endemics were also utilitarian species: Rotry (a priority 4 species) and Fanolamena (*Asteropeia micraster*) (79 individuals, a priority 2 species). The third most abundant endemic species was Zoralahy (a priority 2 species), which was not identified as a utilitarian species.

Size Distributions and Basal Area Across the Landscape

A comparison of the basal area of utilitarian versus nonutilitarian species per transect revealed that the basal area of utilitarian species as a group comprised the majority of the basal area across the landscape (84%) and per transect (Figure 5). The species that contributed the highest amount of basal area to the

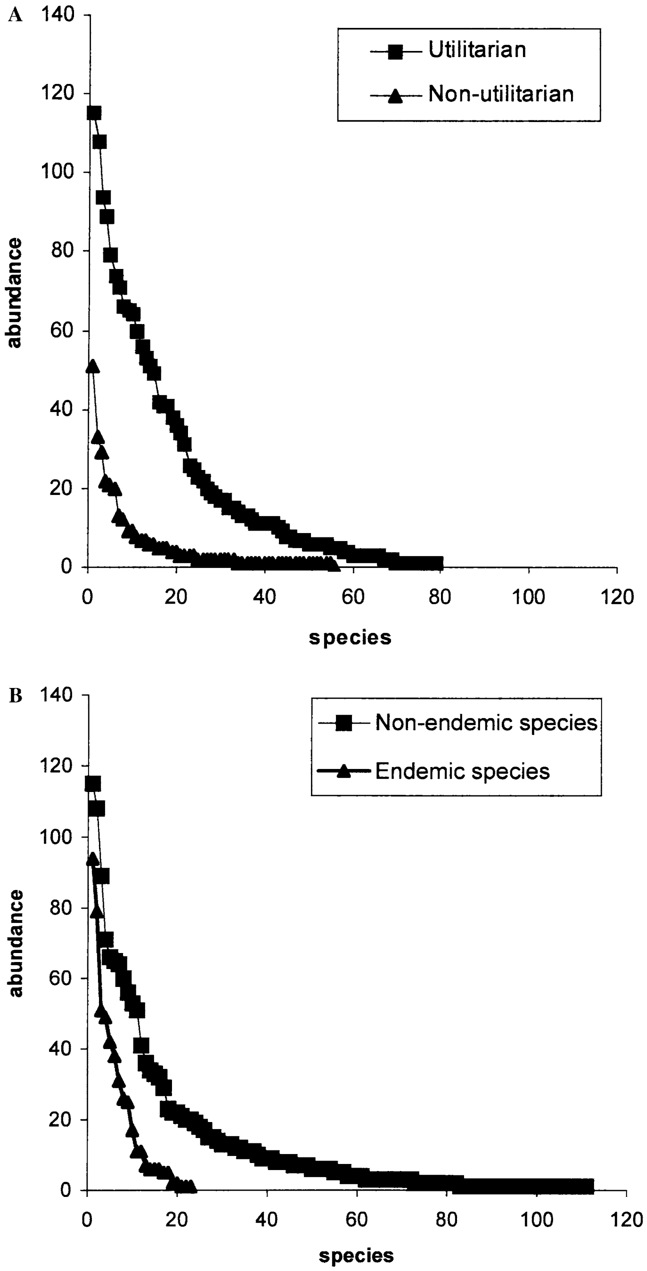

Figure 4. Rank abundance plots for all transects. (a) The number of individuals of utilitarian and nonutilitarian species. (b) The number of individuals of endemic species and nonendemic species.

landscape were utilitarian species: Harandrato (7.54% of total basal area), Rotry, (6.68%), Hazomainty (*Diospyros mampingo*) (4.77%), Fanolamena (4.44%) and Meramaintso (*Sarcolaena multiflora*) (3.77%).

An assessment of the abundance of utilitarian versus nonutilitarian species in different tree size classes (Figure 6a–c) reveals that, in every transect, utilitarian species contribute the highest proportion of individuals within each of the three size classes. In the ≥15-cm dbh class, 8 of the 22 transects contained only utilitarian species and, in the 10–14.9-cm dbh class, three transects possessed only utilitarian species. Rank abundance plots of species in the largest size class and their representation in the smallest class (Figure 7) provide insight into the regeneration potential of the most abundant large species. Rotry (25 individuals), Hazomainty (22), Harandrato (21), Fanolamena, (16) and Vahabatra (*Cinnamosma madagascariensis*) (15) were the most frequently recorded species across the landscape in the ≥15-cm dbh size class. The most abundant species in the smallest size class of 5–9.9 cm dbh, which were also highly abundant in the largest size class, were Harandrato (69 individuals), Rotry (61), Hazomainty (57) and Fanolamena (42).

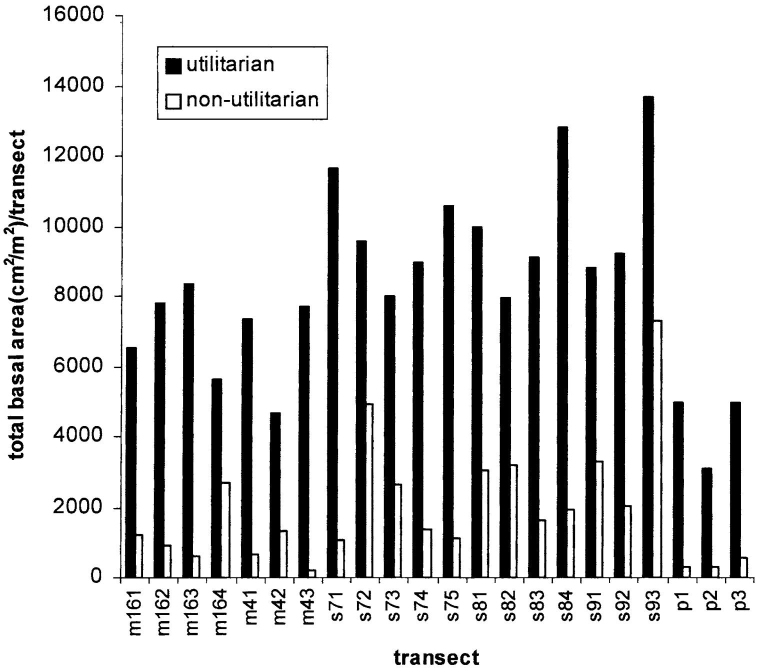

Figure 5. The total basal area (cm^2/m^2) for all stems ≥5 cm dbh in each 400 m^2 transect for utilitarian and nonutilitarian species.

Basal Area and Abundance of Trees in Different Use Categories

A breakdown of the utilitarian species into use categories revealed variable amounts of basal area available at a landscape scale for different utilitarian purposes (Figure 8a–f). The field inventories recorded 8 species used for charcoal (QMM 2001), 63 used for firewood, 26 used for construction, 20 used for medicine, 2 used for human food, and 8 used for fibrous material or oil. It is possible that not all of the tree species in each use category will be used or preferred equally by local people. Thus, some species may be cut more often than others.

Basal area across the landscape was highest in the firewood category, followed by construction, medicine, charcoal, food, and other nontimber uses. Values for oil/fibrous material, human food, and charcoal were lowest in the stand M4. The basal area available for fibrous material usage and human food was also very low in other transects outside of M4, whereas the basal area available for charcoal was comparatively higher in all transects located in forest stands other than M4. The number of species available for medicine (Figure 8g) was between 5 and 14 for all of the transects, with the lowest number of medicinal species occurring in Petriky.

Indicators of Human Impact on Landscape

We recorded a total of 323 trees as cut; however, only 232 were identifiable to a species level, which resulted in a list of 59 cut species. Fifteen of the identified cut species were not previously identified as utilitarian species, and 13 of these 15 were recorded as cut only once. The other two species were Zoralahy (which was observed cut twice) and Fanola (*Asteropeia* sp.) (cut four times). We recorded 34 of the 44 utilitarian species as cut more than once. The most commonly cut species was Harandrato (57 cuts), which people use for timber and medicine. We recorded Forofky (also known as korofky) (*Diospyros littoralis*), used for firewood, timber, and medicine, as cut 12 times. The surveys recorded Rotry as cut 11 times. Local people use Rotry for firewood, timber, medicine, and human food.

The species with the highest number of coppicing individuals (which may have coppiced from natural or anthropenic disturbance) were the utilitarian trees Ambora (10), Meramaintso (10), Harandrato (9), and Rotry (9). Four coppiced nonutilitarian species were recorded once (Beronono, *Trilepisium madagascariense*; Disaky, *Garcinia aphanophlebia*; Hazofotsy, *Homalium planiflorum*; Tombobitsy, *Psorospermun* sp.), one coppiced nonutilitarian species, Katrafay (*Terminalia fatrae*) was encountered twice, and six coppiced individuals were recorded for the nonutilitarian tree, Zoralahy.

The fragment with the highest amount of cutting per m^2 was M4, with 0.06 cuts/m^2 (Table 2). Altogether, we recorded 12 species as cut, 11 of which have known utilitarian purposes that include medicine, human food, firewood, timber, and charcoal. The most frequently cut species was Harandrato. Of the uncut trees

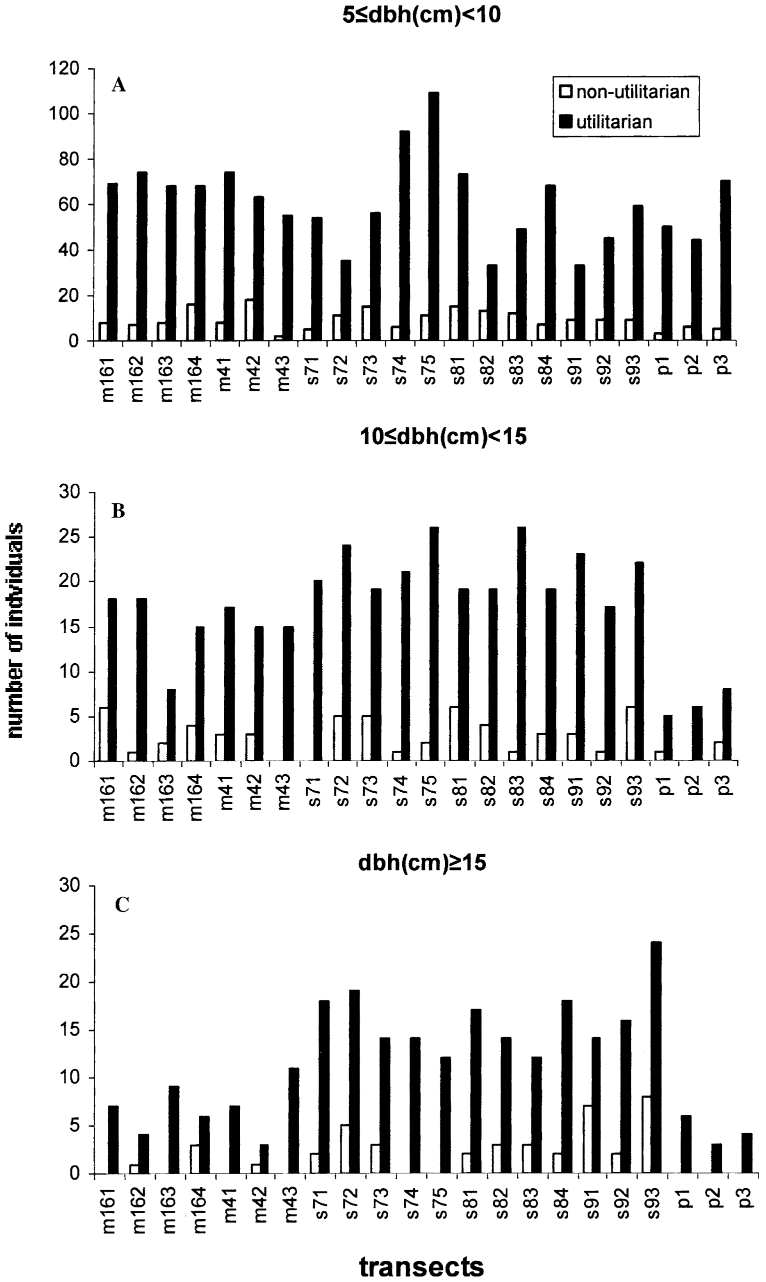

Figure 6. Abundance of utilitarian and nonutilitarian species divided into three size classes. (a) Number of individuals with a dbh greater than or equal to 5 cm and less than 10 cm. (b) Number of individuals with a dbh greater than or equal to 10 cm and less than 15 cm. (c) Number of individuals with a dbh greater than or equal to 15 cm. Nonutilitarian species are colored white and utilitarian species are black on the graphs.

in the transects in the stand, the utilitarian species Meramaintso (used for firewood and construction) possessed the highest number of individuals (34) and the highest amount of basal area. Harandrato contributed the second highest number of individuals (27) and the second highest amount of basal area to the stand.

Discussion

Relationship Between Structure and Biodiversity

In this study, basal area appears to be the most useful of the two structural measures assessed for indicating species richness and species diversity for all of the groups considered. However, species richness data are not sufficient for informing management strategies (Balmer 2002). In the present study, basal area appears to be a useful indicator of species abundances patterns, or evenness measures, only for endemic species. Thus, in this region, landscape scale maps of forest basal area (see Ingram and others 2005) may be useful for identifying sites of high basal area and, consequently, potential sites of endemic species conservation that are high in species richness and equitability. However, it may not be possible to use

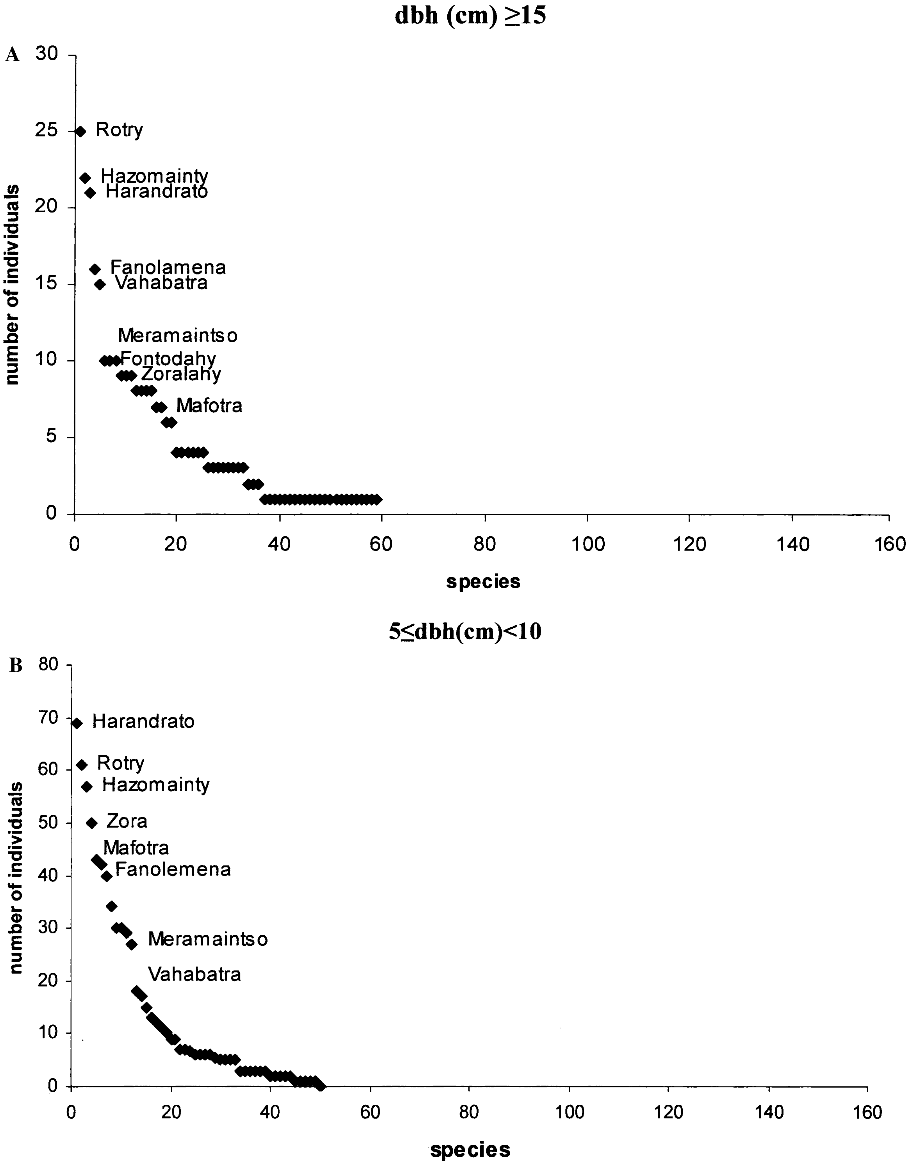

Figure 7. Rank abundance plots of trees in the largest and smallest size classes. (a) Rank abundance plot of trees with a dbh greater than or equal to 15 cm (the largest size class). (b) Rank abundance plot of trees with a dbh greater than or equal to 5 cm and less than 10 cm (the smallest size class) that were also recorded within the ≥15 cm dbh class.

structure to indicate patterns of total or utilitarian tree abundances because of the weaker, insignificant relationships between measures of equitability of these groups to basal area.

Although researchers have classified these three forest sites as a unique subtype of forest relative to other rainforests in the region (Dumetz 1999), differences do exist between the three sites. Our findings support previously observed trends of higher floristic diversity in Ste. Luce and Mandena compared to Petriky and higher dbh values of trees in Ste. Luce (Dumetz 1999), at the northern extreme of the climatic gradient, when compared to the other two sites. Thus, both human impact and climate appear to influence forest structure across the sites and should be considered in concert when assessing landscape patterns in forest structure. To distinguish these effects from one another, it would be useful for future research to test the relationship between structure and diversity *within* each forest site, which would require more replicates than were possible to obtain in this study.

Species Abundance, Basal Area, and Human Impact Across the Landscape

Our results indicate that these forests have high conservation value not only for biodiversity but also for human subsistence. This finding resonates with Kremen and others (1999), who found that 90% of all of the individual plants recorded during forest inventories in Madagascar's Masaola peninsula were utilitarian

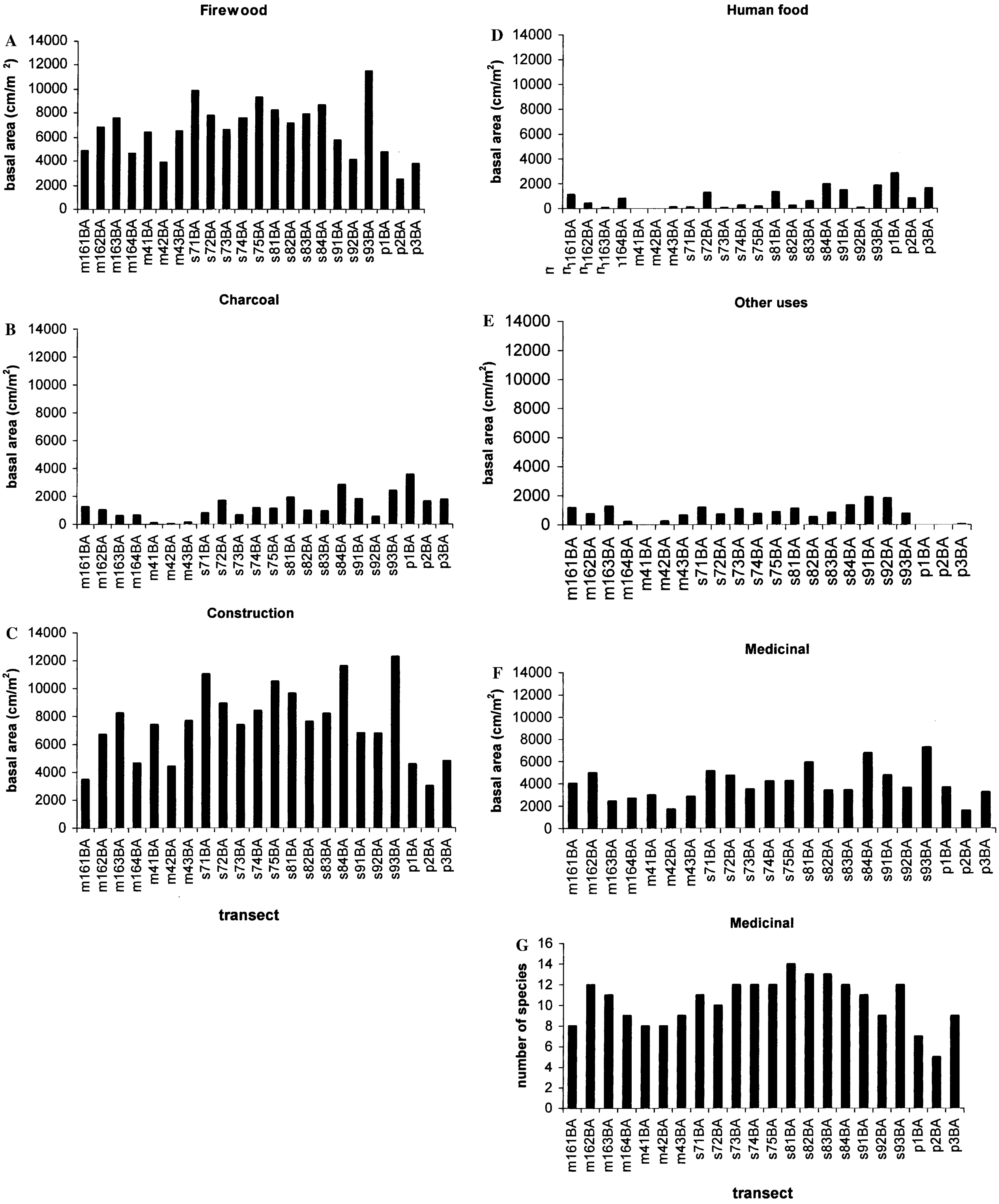

Figure 8. (a–f) Total basal area present within each transect for the different use categories. (g) Total number of medicinal species within each transect.

species. In the present study, 84% of all individual trees and 58% of species were utilitarian species. This broad, landscape pattern of utilitarian species and abundance was evident in all transects. The comparatively high

Table 2. Number of cut stumps per transect and per fragment[a]

Cuts per transect		Cuts per fragment (cuts/m^2)	
Transect	Number of cuts	Fragment	Cuts/m^2
M16.1	6	M16	0.014
M16.2	7	M4	0.062
M16.3	10	S7	0.043
M16.4	0	S8	0.026
M4.1	8	S9	0.038
M4.2	34	Petriky	0.045
M4.3	33		
S7.1	26		
S7.2	14		
S7.3	15		
S7.4	19		
S7.5	11		
S8.1	7		
S8.2	12		
S8.3	8		
S8.4	14		
S9.1	21		
S9.2	16		
S9.3	8		
P.1	21		
P.2	12		
P.3	21		

[a] The fragment number is given followed by the transect number.

number of singletons in the nonutilitarian category indicates that this group consists of a high number of relatively rare species and, thus, people generally appear to be using the species that are most common across the landscape. These results suggest that the exploitation of a species for human use does not necessarily equate to low abundance (in comparison to other species present), regeneration potential, or basal area across a landscape. However, degradation could be ongoing and root stocks could eventually deteriorate if coppicing occurs too frequently. Thus, because this study represents only a snapshot in time, it is possible that on a longer time scale 1) site degradation could be occurring and/or 2) utilitarian or endemic species could be in a state of decline if current disturbances are increasing beyond a sustainable threshold. However, if degradation by local people had already reached an unsustainable endpoint, we would expect to see low abundances and low basal area values for utilitarian species and higher abundances and values of basal area for nonutilitarian species as the landscape becomes increasingly less useful to humans. Our results did not support this expectation.

The two most frequently cut species, Harandrato and Rotry, provide useful examples for assessing human impact on species abundance and basal area. Harandrato was the second most abundant species across the landscape and constituted the highest basal area overall. It represented just 7.54% of the total basal area, however, indicative of the relatively high overall alpha and beta diversity of the three forest systems. Harandrato was also cut and coppiced frequently across the landscape. However, the very high abundance of this species in both the smallest and largest size class demonstrates that the species is well represented demographically and is recruiting. Rotry is also a utilitarian species and is endemic at the national scale. This species was abundant in the largest size classes, constituted the second highest amount of basal area, was widely used across the landscape, as the second most frequently cut tree, and also possessed a comparatively high number of coppiced individuals.

The ability of these species to coppice may provide them with a strong advantage for recovery from disturbance (McLaren and McDonald 2003), which may partially explain why they are so abundant despite frequent cutting. Another factor is the cultural belief that spirits live in very large trees, such as Rotry (QMM 2001), which, we speculate, may inhibit local people from cutting it at large stem sizes. Our study has focused on extractive uses of the forest and, for this reason, the abundance and diversity of tree species with spiritual value were not considered categorically. However, these uses may have a considerable influence on tree community composition and conservation. For example, several forest patches across the landscape in Mandena, known as ''fady forests,'' are not cut by local people because they are revered as sacred (McConnell and others 2004). This observation highlights the importance of understanding human resource use and cultural traditions within conservation programs.

Abundance and Basal Area Available for Different Uses

An analysis of the different use categories showed that the amount of basal area available for certain purposes varied between transects and between use categories. The firewood sector possessed the highest amount of basal area of any use category. This was somewhat surprising because the energy crisis has been considered a major threat to forest cover in Africa (Mearns 1995). However, this crisis has been exaggerated largely because of a failure to account for the substantial amount of fuel available from dead wood (Abbot and Homewood 1999). Many people living proximate to the littoral forests collect dead wood for energy fuel (QMM 2001). For this reason, deforestation in the littoral forests because of firewood extraction may be minimal in comparison to other forest use practices. The ability of many trees to regenerate through coppicing can also diminish the degrading effects of local harvesting practices (Nyerges 1989, Medley 1993). The high frequency of coppicing firewood species suggests that these trees recover from a certain degree of disturbance.

Firewood and charcoal are the primary sources of energy in the region. In the rural areas, firewood provides 90% of the energy needs, while charcoal is the primary energy source for the township of Fort Dauphin (QMM 2001). Charcoal production has increased recently in the Mandena region because of the influx of outside groups, such as the Antandroy from the south, who have come into the Mandena area specifically to harvest trees for charcoal to sell in Fort Dauphin (QMM 2001). This activity has been a primary source of recent, extensive deforestation in Mandena and is observable from satellite imagery and aerial photographs. The impact of this practice on species diversity was apparent in the transects located in the unprotected stand, M4, in Mandena; these were the only transects completely depauperate of species used for charcoal. Species in the fiber/oil and human food categories were also absent from these transects, but species in these categories were also absent from transects located in other forest stands. The paucity of charcoal species in M4 could be due to the fact that these species do not naturally occur in the fragment or, alternatively, because charcoal species have been overharvested from the Mandena region. The former scenario is unlikely because a species used for charcoal, Fanola, was recorded as cut in one of the M4 transects, although we recorded no intact individuals of this species in the stand. Additionally, the stand, M16, also in Mandena, did possess tree species used for charcoal. This may be due to the fact that destructive charcoal making is prohibited in M16 because it is part of a conservation zone recently established and managed by the mining company under an agreement, Gestation d'Eau et Forêt, made with local communities.

A high abundance of timber species occurred in all of the transects, despite the fact that cutting for timber is also a destructive activity. Firewood and timber use of the forest trees are practiced primarily by the indigenous local communities, whereas charcoal making is practiced primarily by itinerant Antandroy people who have migrated into the Mandena sector from more southerly regions (QMM 2001). The higher amount of total basal area available for timber and firewood in contrast to the low abundance and basal area of species used for charcoal making suggests that local practices seem to have a lesser impact on tree communities than the practices of itinerant people. In rural Madagascar, migrants are often responsible for deforestation and, thereby, may disrupt the local social structure and cohesion that is based on a respect for traditional values and production systems (Durbin and others 2003). The incursion of outside pressures, changing values, livelihoods, and markets are common factors known to alter the relationships between local people and their natural environment, causing intensified resource use (Colchester 1981, Adams and McShane 1992). Deforestation associated with external pressures, such as a growing migrant population, is often more accentuated at the limits of territories, between communities, or on land where ownership by government, clans, lineages, or communities is relatively uncertain (Durbin and others 2003). This scenario is likely to be the case in Mandena. Previously, the land rights in the area were designated by custom and practice (Lewis Environmental Consultants 1992). However, more recently, the very conspicuous presence of the mining company, staff, and associated infrastructure necessary for the premining exploratory phase may have caused confusion over traditional land-ownership rights and boundaries. Although these ideas are plausible, to date we do not have the baseline data to examine this hypothesis further.

Medicinal plants are also very important across the landscape. Villagers consider the forest to be their pharmacy and, thus, rarely use western medicine because of the expense and doubt concerning its effectiveness (QMM 2001). Compared to the other use categories, there was not a high amount of basal area available for medicinal purposes; very few of the medicinal species actually occurred within the ≥15-cm dbh class. This could be because these species naturally do not reach large girths in these forests or, alternatively, because they have been overharvested. Further research on the growth patterns of these species would be useful. Individual medicinal species may often have very specific purposes when compared to other use categories, in which one species may be substituted for another. Thus, there may be more of a concern in losing specific medicinal species when compared to species within other use categories. Sites with a low medicinal species richness, such as Petriky, may require special consideration with respect to human needs if land-use planning and development projects proceed in the area. More research is necessary to determine whether medicinal species have decreased throughout time here, which could be determined through interviews with local people on their perception of current versus past medicinal plant availability. Of special concern was the medicinal plant Vahabatra, which was among the most abundant tree species in the largest size class but present at comparatively low abundances in the smallest size classes. Potentially, this species may not be regenerating well and may require focused conservation measures as well as monitoring of the medical needs of local people for which this plant is useful.

Human Use of the Forests and Impacts Across the Landscape

Much of the research recently published about this region has discussed how degraded the littoral forest landscape has become over the past few decades because of continual human use and disturbance (Dumetz 1999, QMM 2001, Cadotte and Lovette-Doust, in press). However, the results of this research indicate that, despite long-term human pressure and regular disturbance, the littoral forest landscape of southeastern Madagascar retains a high abundance and high basal area of both useful and endemic species. Thus, it is not too late to conserve these forests. Because of the presence of local people living in and around these forests, surrounding communities could play an active role in future management plans. People who have a knowledge of natural resource potential and who regularly use forest resources are often the most effective managers and stewards of the natural environment (Posey 1983, McNeely 1989, Medley 1993, Shwartzmann and others 2000b), especially when they have multiple incentives to do so (Colchester 2000). For example, in parts of continental Africa, local people have been known to enhance the abundance and distribution of certain species (Fairhead and Leach 1998). Formalized community management of certain littoral forest sites has already begun, and this study supports continued development of such programs.

Conservation is especially challenging in situations in which multiple stakeholders possess divergent interests as to how a forest should be managed. However, it is often possible to find commonalities of interest between stakeholders and, thereby, to identify conservation strategies that minimize conflicts (Barrance 1997). One such approach is to identify species that are of both conservation concern (e.g., endemics) and of utilitarian value (Gordon and others 2003). This approach may be possible at this study site where there is a high degree of congruence between utilitarian and endemic species lists. For this reason, the littoral forests of southeastern Madagascar could provide valuable opportunities for conservationists to work alongside local people to find ways to simultaneously maximize biodiversity conservation and the needs of local people.

This study represents only a snapshot in time and, although there seems to be a high degree of regeneration occurring, this study would ideally be supplemented by ongoing ecological monitoring in the likely case that resource pressures increase throughout the region. Long-term ecological monitoring of endemic species or rare species abundance is often included as a crucial part of many conservation programs. However, an important yet frequently overlooked component of conservation programs in tropical, developing countries is the monitoring of species indicative of human well-being. In many parts of Madagascar and other countries where humans are highly dependent on forest resources for daily needs, livelihood monitoring can occur synchronously with ecological monitoring because the abundance and distribution of utilitarian species can provide important indications of human security (Kremen and others 1999). The potential for the development of such a regional socioecological monitoring program is promising for the littoral forests, as supported by the results presented here, and could be used together with recently developed remote sensing methods for monitoring littoral forest basal area at a landscape scale (Ingram and others, in press).

Conclusions

After a recent workshop to assess conservation and scientific priorities in Madagascar, Hannah and others (1998) stated that the compatibility between the multiple uses of forests and biodiversity must be demonstrated in ways that have failed in temperate areas. The littoral forests of southeastern Madagascar could provide such an example because of the global and local conservation value resulting from high species richness, endemism, and abundance of species useful to local people. This study has demonstrated that forest structural features, such as basal area and stem density, known to indicate human impact or disturbance, can be related to species richness for total, utilitarian, and endemic species and equitability for endemic species. The high abundance, high basal area, and promising regeneration potential of highly exploited utilitarian species across the landscape indicates that these forests have significant value for human well-being, which has not been irreversibly lost despite long-term human pressure on these systems. The high percentage of endemic species that were also utilitarian species demonstrates a high congruence between western and local conservation values and, thereby, presents an opportunity to protect simultaneously both biodiversity and human security. Sites of high endemic tree richness and useful species richness did not always overlap, suggesting that the selection of a few forest stands for conservation may not result in adequate protection of all species of interest. Other researchers have demonstrated a strong case for conserving these forests for various taxonomic groups, including lemurs, birds, and amphibians (Ganzhorn 1998, Ranamananjato 2000, Watson and others, in press). The present study adds to this body of knowledge by demonstrating the extremely high value of these forests to another important group: humans.

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Appendix 1:

Geographical positions for transects

Transect	Longitude	Latitude
M16.1	46.99	−24.95
M16.2	46.99	−24.95
M16.3	46.99	−24.96
M16.4	46.99	−24.95
M4.1	47.03	−24.95
M4.2	47.03	−24.95
M4.3	47.03	−24.95
S7.1	47.15	−24.79
S7.3	47.15	−24.79
S7.4	47.15	−24.80
S7.5	47.15	−24.80
S8.1	47.15	−24.77
S8.2	47.15	−24.77
S8.3	47.15	−24.77
S8.4	47.15	−24.77
S9.1	47.17	−24.76
S9.2	47.17	−24.76
P.1	46.89	−25.06
P.2	46.88	−25.06
P.3	46.87	−25.06

GPS positions could not be obtained for two of the transects (S9.3 and S7.2).

Appendix 2:

Latin and common names for the tree species recorded during ground surveys, 2001

Latin name	Common name
Ophiocolea delphinense	Akondronola
Plagiosciphus	Ambiropiso
Tambourissa sp.	Ambora
Dypsis scotiana	Amboza
Vepris eliottii	Ampoly
—	Arotsy
Noronhia sp.	Belavenoke
Crataeva obavta	Belataka
Bembicia uniflora	Bemalemy
—	Benalessy
—	Beondue
Dombeya mandenensis	Berehoka
Trilepisium madagascariense	Beronono
Betarepokala	Betarepokala
Dypsis stlucei	Boaka
Dypsis sp.	Boakabe
Garcinia sp.	Disaky
—	Dona
Dracaena reflexa	Falinandro
Dracaena fontanesiana	Falinandrobe
Euphorbia laro	Famanta
Vernonia pectoralis	Famoty
Polycardia phyllanthoides	Fandrianakanga
Asteropeia sp.	Fanola
Asteropeia multiflora	Fanolafotsy
—	Fanolalohy
Asteropeia micraster	Fanolamena
Physena madagascariensis	Farisaty
Canthium sp.	Fantsikahitra
Clerodendrum sp.	Fantiskoho
Vepris fitoravina	Fitoravy
Leptolaena pauciflora	Fonto
Diospyros littoralis	Forofoka
Leptolaena delphinensis	Fotombavy
Schizolaena elongata	Fotondahy
Ambavia gerrardii	Fotsivavo
Grewia delphinense	Hafipotsy
—	Hainiha
Podocarpus madagascariensis	Harambilo
Elaeodendron pauciflorum	Haramboanzo
Intsia bijuga	Harandrato
—	Harompanitsy
Dais glaucescens	Havohoa
—	Hazimina
Homalium planiflorum	Hazofotsy
—	Hazohiha
Diospyros mampingo	Hazomainty
Anisophyllea fallax	Hazomamy
Homalium sp.	Hazombato
Mammea parviflora	Hazomiteraka
Tricalysia cryptocalyx	Hazongalala
Oncostemum sp.	Iona
Mammea sessiliflora	Jambo
Cerbera manghas	Kabokala
Suregada baronii	Kalavelo
Drypetes madagascariensis	Kambatsikambatsy
Rhus thouarsii	Kangy

Latin name	Common name
Terminalia fatrae	Katrafay
Tricalysia cryptocalyx	Kotofotsy
Noronhia sp.	Lahinampoly
Scolopia erythrocarpa	Lapivahatra
—	Lengohazo
Monoporus bipinnatus	Lona
Brochoneura acuminata	Mafotra
Macaranga obovata	Makarangana
Cynometra cloiselii	Mampay
—	Manary
—	Mangaroa
Enterospermum	Mangavoa
—	Manobary
Enterospermum aff. berieranium	Maranitratoraka
Homalium nudiflorum	Marankoditra
Blotia hildebrantii	Maroando
Aspidostemon elliotii	Menahihy
Sarcolaena multiflora	Meramaintso
—	Merana
Zanthoxyllum tsihanihimposa	Mohongo
Faucherea hexandra	Nato
Mimusops coriacea	Natobonaka
—	Natohetike
Faucherea hexandra	Natotendrokazo
Vitex bracteata	Nofotrakoho
Ficus reflexa	Noroka
Pandanus concretus	Pandanus
Rakotofotsy	Rakotofotsy
Homalium albiflorum	Ramirisa
Canarium madgascariensis	Ramy
Beilschmiedia madagascariensis	Resonjo
Eugenia cloiselii	Ropasy
Syzygium emirnesis	Rotry
Astrotrichilia elliotii	Sagnira
—	Sagnirana
Macphersonia radlkoferi	Sagnirambaza
—	Sahinipotsira
Turraea lanceolata	Sakaimboalavo
Elaeocarpus alnifolius	Sana
—	Sanikalal
Astrotrichilia elliotii	Sanirana
Malleastrum mandanese	Sarigoavy
Rhus taratana	Sarinato
Sinoronoro	Sinoronoro
Poupartia chapelieri	Sisikandrongo
—	Sivory
—	Soazanahary
Rhodocolea racemosa	Somotsoy
Phylloxylon xylophylloides	Sotro
Gaertenera arenaria	Tagnatagnanala
Tahambasiky	Tahambasiky
Hyperacanthus mandenensis	Taholanga
Erythrina sp.	Talanosy
Petchia madagascariensis	Tandrokosy
Taolonana	Taolonana
Rothmania mandenensis	Tavlana
Cryptocarya oblonga	Tavolohazo
Ocotea laevis	Tefimoa
Psorospermun sp.	Tombobitsy
Erythroxylum corymbosum	Tomizo
Homalium involucratum	Tsanihiposa
Rhopalocarpus coriaceus	Tsilavimbinato
Cinnamosma madagascariensis	Vahabahatra
Agelaea pentagyna	Vahimainty
Clematis sp	Vahivoraka
Pandanus concretus	Vakoa
—	Vaksa
—	Vantrilana
Protorhus ditimena	Varongy
Brexia madagascariensis	Voakarepokala
Homalium albiflorum	Voankazoala
Uapaca louvelii	Voapaky
—	Voavoa
Schefflera vantsilana	Voatsilana
Phyllarthron ilicifolium	Zahambe
Mammea perrieri	Zambo
Homalium viguirei	Zora
Dicoryphe stipulacea	Zoralahy

Latin names were determined using voucher specimens from Kew gardens and during QMM's botanical studies conducted by Missouri Botanical Gardens. Latin names were not available for some species.

Appendix 3:

Utilitarian tree species listed by common name and their uses to humans[a]

Common name	Use
Ambora	Firewood, construction, medicine
Ampoly	Firewood, construction, medicine
Belataka	Firewood, medicine
Bemalemy	Firewood, construction
Berehoka	Firewood, construction, fibers
Falinandrobe	Firewood, construction, medicine
Famoty	Firewood, construction, medicine
Fandrianakanga	Firewood, construction
Fanola	Charcoal
Fanolafotsy	Firewood, construction
Fanolamena	Firewood, construction, medicine
Fantiskoho	Firewood, construction
Fantsikahitra	Firewood, construction, charcoal
Fonto	Firewood, construction, food
Forofoka	Firewood, construction, medicine
Fotombavy	Firewood, construction, food
Fotondahy	Firewood, construction, food
Fotsivavo	Construction
Harambilo	Firewood, construction
Haramboanzo	Firewood, construction
Harandrato	Construction, medicine
Hazomainty	Firewood, construction
Hazomamy	Firewood, construction
Hazombato	Firewood, construction
Hazomiteraka	Firewood, construction, medicine
Hazongalala	Firewood, construction, food
Kabokala	Firewood, construction
Kalavelo	Firewood, construction, medicine
Kambatsikambatsy	Firewood, construction
Kangy	Firewood, construction

Common name	Use
Kotofotsy	Firewood, construction
Lapivahatra	Firewood, construction
Lona	Firewood, construction
Mafotra	Charcoal, construction, medicine, oil
Makarangana	Firewood, construction
Mampay	Firewood, construction, medicine
Marankoditra	Firewood, construction
Menahihy	Firewood, construction, charcoal
Meramaintso	Firewood, construction
Nato	Charcoal, construction
Natobonaka	Firewood, construction
Natotendrokazo	Firewood, construction
Nofotrakoho	Firewood, construction
Ramirisa	Firewood, construction
Ramy	Firewood, construction, medicine
Resonjo	Firewood, construction, medicine
Ropasy	Firewood, construction, medicine, food
Rotry	Firewood, construction, medicine, food charcoal
Sagnirambaza	Firewood, construction, medicine
Sarigoavy	Firewood, construction, charcoal
Sarinato	Firewood, construction
Sisikandrongo	Firewood, construction
Sivory	Firewood, construction
Sotro	Firewood, construction, medicine
Tagnatagnanala	Firewood, construction, medicine
Talanosy	Firewood, construction
Tandrokosy	Firewood, constructionz
Tavolohazo	Firewood, construction
Tefimoa	Firewood, construction
Tombobitsy	Construction
Tomizo	Firewood, construction
Tsanihiposa	Firewood, construction
Tsilavimbinato	Firewood, construction, charcoal
Varongy	Firewood, construction, construction
Voakarepokala	Firewood, construction
Voankazoala	Firewood, construction
Voapaky	Firewood, construction, medicine, fibers
Zambo	Firewood, construction, medicine
Zora	Firewood, construction, medicine

Appendix 4:

Endemic species listed by vernacular name and priority status of each species

Species	Priority status[a]
Akondronola	3
Amboza	4
Berehoka	2
Falinandro	2
Fanola	2
Fanolamena	2
Fonto	2
Fotondahy	2
Harambilo	3
Havohoa	3
Hazomamy	3
Lona	4
Mampay	3
Manobary	2
Nofotrakoho	2
Ropasy	4
Rotry	4
Sanirana	2
Sarigoavy	2
Taolonana	4
Voatsilana	3
Zahambe	2
Zoralahy	2

[a] The priority status of the species has been defined by Lowry (2001). *Priority 1* species are presumed to be endemic to the mining sector; *Priority 2* species are presumed to be endemic to the littoral zone; *Priority 3* species are presumed to be endemic to the southeastern region of Madagascar; *Priority 4* species are presumed to be endemic to the island of Madagascar.

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