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Tree and shrub diversity and abundance in fragmented littoral forest of southeastern Madagascar

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Abstract. In the coastal littoral forest of extreme southeastern Madagascar, we studied tree diameter at breast height (DBH) $\geq$ 10 cm in 20, 50 × 50 m plots in each of four forest fragments, and understory woody vegetation (DBH $<$ 10 cm, $\geq$1 m tall) in 60, 10 × 10 m plots in three of the fragments. One forest fragment was located in the highly degraded Lokaro region, and three in the nearby Sainte-Luce forest. A total of 3476 trees, representing 169 species in 55 families, were recorded in the 50 × 50 m plots, and 10 282 understory stems, representing 195 species in 54 families, were found in the 10 × 10 m plots. For each tree, DBH was recorded. Mean tree diameter and patterns of tree size class distribution did not differ among the four forest fragments. However, the fragments differed significantly in both tree and understory stem densities, species richness and diversity values, and family richness values, with the Lokaro fragment having the lowest values for all measures. Furthermore, floristic patterns, family importance values, and community similarity measures revealed that the species composition at the Lokaro fragment was very different from the Sainte-Luce fragments. Anthropogenic disturbance appears most pronounced in the isolated Lokaro forest, where biotic resources are limited to this single fragment.

Introduction

Recent reports have recognized the need for greater effort in studying the threatened biodiversity of tropical hotspots (Mittermeier et al. 1998; Myers et al. 2000). Researchers are actively trying to understand patterns in tropical forests in particular (e.g., Lieberman et al. 1985, 1996; Josse and Balslev 1993; Johnston and Gillman 1995; Condit et al. 1996; He et al. 1996; Ferreira and Prance 1998). For example, spatial and taxonomic patterns of the very highly diverse forest communities in Madagascar have begun to receive close scrutiny (Gentry 1988; Sussman and Rakotozafy 1994; Dumetz 1999; Rakotomalaza and Messmer 1999).

Madagascar is a large island (594 000 km^2); it has a disproportionately high number of plant taxa (10 000) and extremely high levels of endemism across all taxa (upwards of 90%) (Groombridge 1992). Consequently, Madagascar is one of the top conservation priorities in the world (Myers et al. 2000). Madagascar's natural forests have been severely impacted since the arrival of humans *ca.* 1500 years ago (Battistini and Verin 1972; Richard and O'Connor 1997). Over the past few decades, deforestation has proceeded at an alarming rate (Green and Sussman 1990), with less than 15% of forests remaining intact (Groombridge 1992). These remaining forests, whilst disappearing, still hold a plethora of undescribed species and indeed in some cases entire communities are under-described, and remain poorly known to scientists (Helme and Rakotomalaza 1999; Prance et al. 2000).

The destruction and removal of intact forests results in the creation of a patchwork of forest fragments, which result in many measurable changes (Bierregaard et al. 1992; Turner 1996). These changes may be in the form of diminished species richness (Wilcove et al. 1986; Anderssen et al. 1997; Debinski and Holt 2000), isolation of formerly continuous populations (Gascon et al. 1999), changes in relative abundances of predators or competitors (Lynam 1997), or demographic shifts within populations (Klein 1989; Matthysen et al. 1995; Somanathan and Borges 2000).

The purpose of the present investigation was to investigate diversity patterns in a fragmented Malagasy forested landscape. What is the nature of floristic diversity and species richness patterns generally, and what are the effects of habitat fragmentation? We examined understory species and trees separately, to examine the relationship between floristic diversity patterns and plant life forms. We also sought to compare these patterns from an understudied region of Madagascar with patterns elsewhere.

Study area

Four littoral forest fragments located along the southeastern coast of Madagascar were used in this study (Figure 1). The forests in this region are all highly fragmented, but continue to hold a tremendous array of habitat and species diversity (Goodman 1999). This region has also been found to be the most diverse compared to other regions along the eastern coast (Rabevohitra et al. 1998). These fragments grow on sandy substrata (Dumetz 1999), and exist within a Malagasy ecozone known as the eastern forests (Chauvet 1972; Lowry et al. 1997) – a forested band along the east coast, with a maximum elevation of 800 m (Lowry et al. 1997; Dumetz 1999).

Methods

Within each forest fragment, 20 randomly placed 50 × 50 m plots (see Figure 2) were completely censussed for all trees with a diameter at breast height (DBH) ≥10 cm. The first corner of a plot was selected to approximate a randomly preselected direction and the 50 m sides were measured accordingly, and marked at 5 m intervals with flagging tape. Numerating and measuring the diameter of all trees with DBH ≥ 10 cm was done systematically, with trees being marked to avoid re-censussing. For individual trees with multiple stems (especially *Ravenala madagascariensis*, Strelitziaceae), DBH was recorded for the largest stem; for trees that branched below breast height, the diameter was taken just below the first

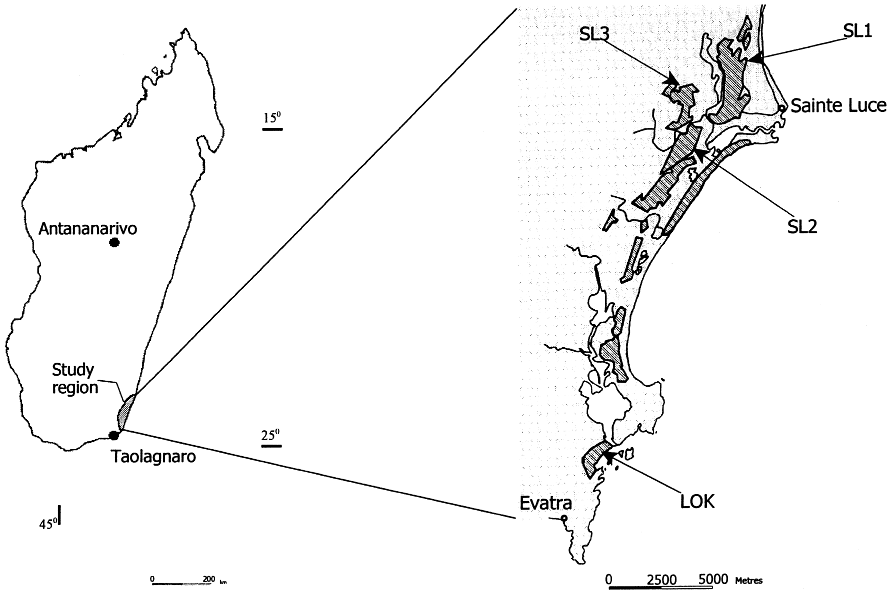

Figure 1. Location of the study region in southeastern Madagascar, and of the four forest fragments used in this study.

branch; and for buttressed trees (especially *Uapaca* spp., Euphorbiaceae), the diameter was taken just above the buttress. In each forest fragment, a sample of vegetative structures and, if available, a reproductive sample of each species was collected and tentatively identified, pressed and later deposited at Parc Botanique et Zoologique de Tsimbazaza, Madagascar for final verification.

For the second part of this study, 60 10 × 10 m plots were completely censussed for all woody vegetation (trees plus shrubs) taller than 1 m. Plots were positioned along 100 m transects running from edge to interior (see Figure 2 for the starting location of each transect). Diameter was recorded for all individuals taller than 1 m. Voucher specimens were collected for each species in each forest for identification and deposited at Parc Botanique et Zoologique de Tsimbazaza.

Analysis of variance and least significant difference *post hoc* tests were used with SYSTAT 9 to compare results among forest fragments (SPSS 1999). The Shannon–Wiener index of diversity (Barbour et al. 1999) was used to characterize species richness and abundance. It was calculated as:

$$H' = -\sum_{i=1}^{S} (\rho_i)(\ln \rho)$$

where s is the total number of species and ρ_i the proportion of all individuals in a sample that belong to the ith species.

Species–area curves were created by taking 10 randomly shuffled samples, across

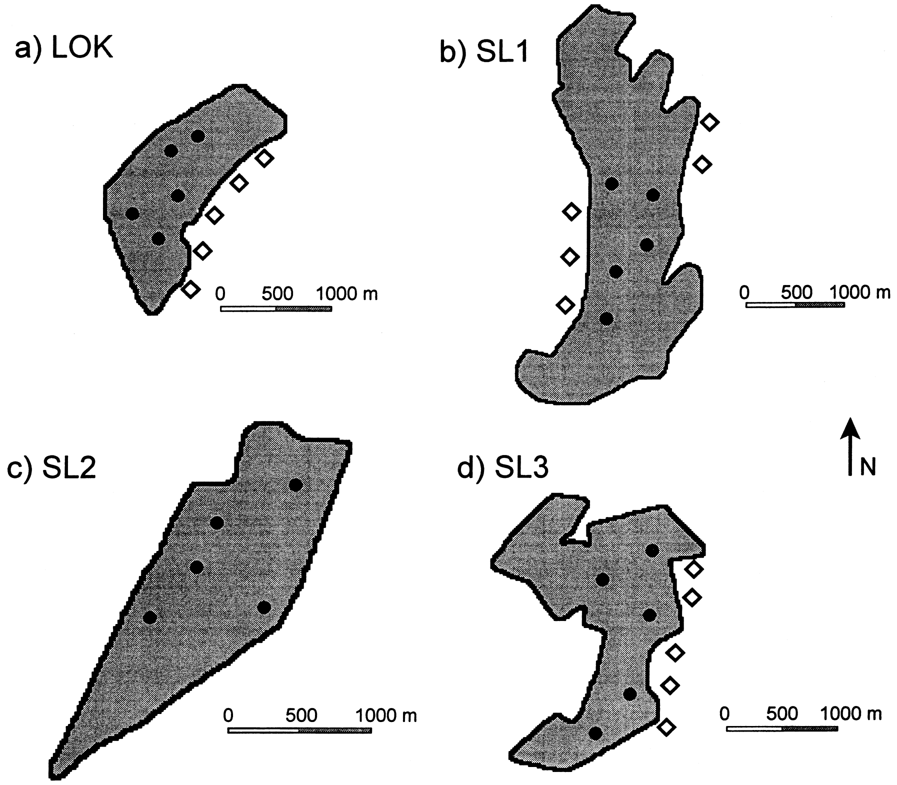

Figure 2. Location of (●) 50 × 50 m plots and the starting point (◇) of 100 m long transects in (a) Lokaro forest, (b) Sainte-Luce forest 1, (c) Sainte-Luce forest 2, and (d) Sainte-Luce forest 3.

all fragments, using the re-sampling procedure in *Species*, *Diversity*, and *Richness*, version 2 (Pisces Conservation Ltd., UK). (Random re-sampling was used to minimize effects of sample order.) An expected species–area curve was created using rarefaction analysis (Simberloff 1978), and the hypergeometric equation to calculate an expected number of species (S_m), given a particular sample size (m):

$$S_m = S - \binom{N}{m} \sum_i \binom{N-n_i}{m}$$

where S is the total number of species, N the total number of individuals, and n_i the number of individuals in the ith species (Brewer and Williamson 1994). The species accumulation curve and the curve produced by the rarefaction calculations were compared using the binomial (sign) test for paired comparisons (Underwood 1997). This test evaluates the number of times the measurements of one curve are greater than those of the other:

$$\mathrm{Prob}(r) = \frac{n!}{r!(n-r)!} P^r (1-P)^{(n-r)}$$

where n is the number of samples, r the number of expected values that are greater than observed (or less than, depending on hypotheses); and p the probability that any expected data point should be either greater or less ($P = 0.5$, when null hypothesis is no difference) (Underwood 1997).

Jaccard's coefficient of similarity was used to compare the number of species shared between plots in different forest fragments. Jaccard's coefficient, $J = A/(A + B + C)$, divides the species shared between two plots (A) by the sum of species occurring only in one plot (B), species occurring only in a second plot (C), and the number of shared species. For each comparison of fragments using 50 × 50 m plots, 25 coefficients were calculated (since each plot was compared to a plot in a second fragment [$5 \times 5 = 25$]). Similarly, for comparisons using 10 × 10 m plots, each plot in a single fragment was compared with each plot in a second fragment, giving 400 (20 × 20) similarity coefficients for each fragment comparison. Two sample *t*-tests were used to compare mean coefficients, to determine whether some fragments were more similar than others.

Finally, family importance values (FIV) (following Mori et al. 1983) were used to compare the relative contribution of each taxonomic family to forest species composition. FIV was determined for each forest fragment, and was calculated as the sum of the following three variables:

$$\text{Relative diversity} = \frac{\text{No. of species in family}}{\text{Total no. of species}} \times 100$$

$$\text{Relative density} = \frac{\text{No. of individuals in family}}{\text{Total no. of trees}} \times 100$$

$$\text{Relative dominance} = \frac{\text{Basal area of family}}{\text{Total basal area}} \times 100$$

Results

Overall across the four forest fragments, 3476 trees were identified and measured in the 50 × 50 m plots. These samples contained a total of 169 species in 55 families (Table 1). Average density (trees per 0.25 ha) differed significantly between fragments ($F = 3.74$, $P = 0.033$). Least significant difference (LSD) *post hoc* analysis revealed that fragments SL2 and SL3 had significantly greater mean densities than LOK (Figure 3a). Mean number of species per 0.25 ha differed significantly among the four fragments ($F = 26.65$, $P < 0.0001$). *Post hoc* LSD tests showed that fragments SL2 and SL3 had a significantly greater mean number of species per 0.25 ha than both SL1 and LOK, and SL1 had significantly more species than LOK (Figure 4a). Mean number of families per 0.25 ha also differed significantly between the four fragments ($F = 25.30$, $P < 0.0001$). Fragment SL3 had significantly greater mean number of families than fragments SL1 and LOK, while SL2 and SL1 had significantly more than LOK (Figure 5a). Shannon–Wiener functions (Table 1) differed significantly among forests ($F = 49.47$, $P < 0.0001$), with the Lokaro forest having significantly lower values than the others.

Table 1. Richness and abundance parameters (±SD) for five plots (50 × 50 m) in four coastal forest fragments.

	LOK	SL1	SL2	SL3	Total
No. of trees	645	845	1020	966	3476
No. of species	30	81	97	107	169
No. of families	21	35	43	45	55
Mean no. of trees per plot	129.0 (33.7)	169.1 (25.4)	204.0 (46.9)	193.2 (44.0)	–
Mean no. of species per plot	10.6 (2.9)	36.4 (5.5)	46.4 (8.5)	47.4 (10.7)	–
Mean no. of families per plot	9.8 (3.1)	23.2 (3.2)	26.4 (2.1)	28.8 (4.4)	–
Shannon–Wiener index	1.56 (0.243)	3.14 (0.216)	3.34 (0.321)	3.31 (0.296)	

LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3.

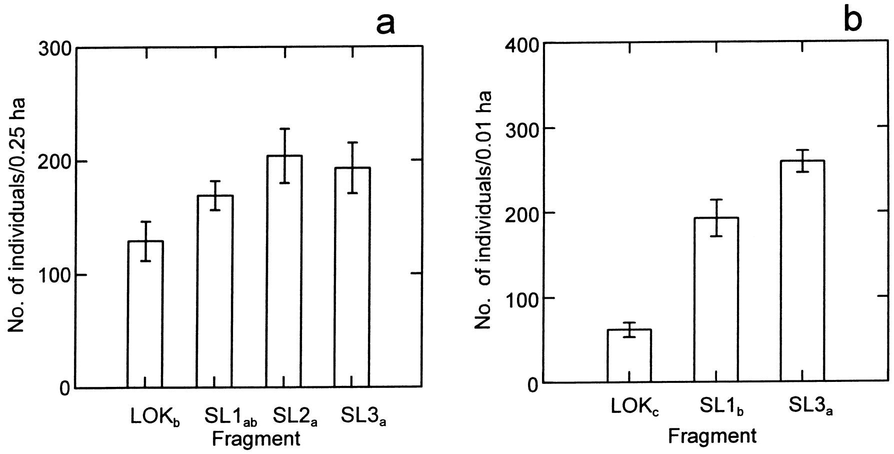

Figure 3. The mean number of individuals: (a) per 50 × 50 m plot; and (b) per 10 × 10 m plot. Subscripts show results of least significant difference *post hoc* analysis. (No significant difference between bars having the same subscript.) LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3, respectively.

In the 10 × 10 m plots, 10700 individuals (10282 of which were understory [diameter < 10 cm] woody vegetation) were identified and measured. These samples represented a total of 203 species in 55 taxonomic families. Excluding trees, there were 195 species in 54 families (Table 2). The average woody understory density (stems per 0.01 ha) differed significantly between fragments ($F = 45.20$, $P < 0.0001$). *Post hoc* analysis showed that both fragments SL1 and SL3 had significantly greater densities than LOK ($P < 0.05$), and SL3 had a greater mean density than SL1 (Figure 3b). The mean number of understory species per 0.01 ha differed significantly among the three fragments ($F = 204.76$, $P < 0.0001$). Fragments SL1 and SL3 had significantly more species than LOK, and SL3 had more than SL1 (Figure 4b). Mean number of families also differed significantly among fragments ($F = 163.67$, $P < 0.0001$); SL3 included significantly more families than SL1, which had more than LOK (Figure 5b). Shannon–Wiener values

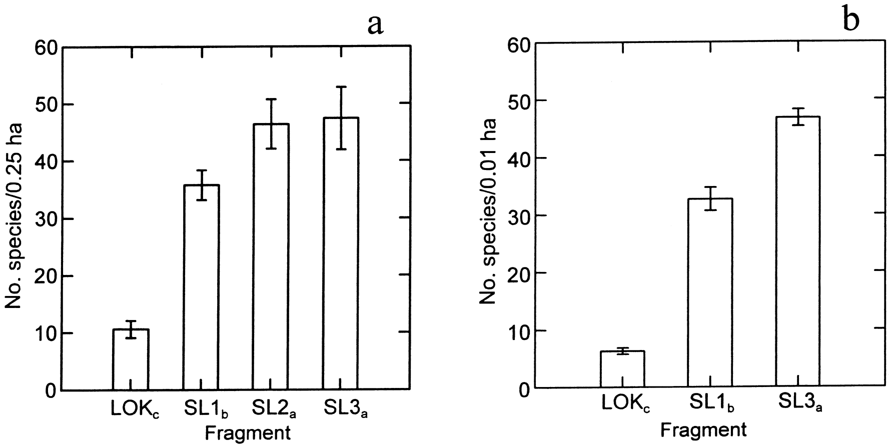

Figure 4. The mean number of species: (a) per 50 × 50 m plot; and (b) per 10 × 10 m plot. Subscripts show results of least significant difference *post hoc* analysis. (No significant difference between bars having the same subscript.) LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3, respectively.

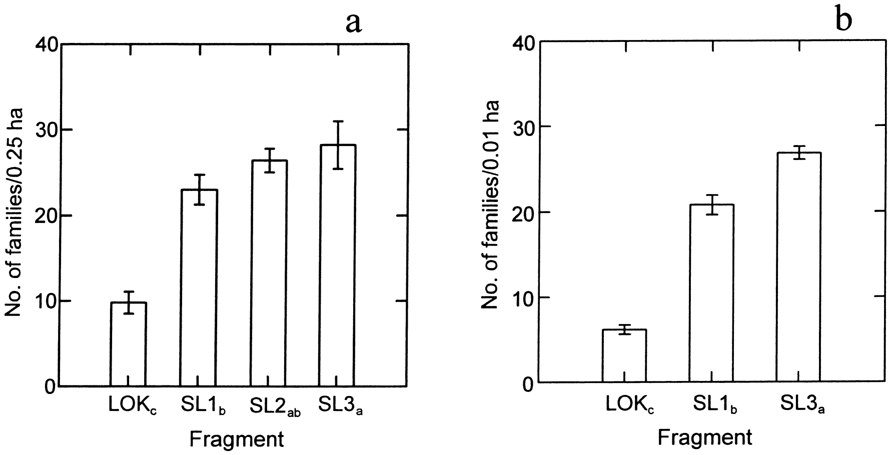

Figure 5. The mean number of families: (a) per 50 × 50 m plot; and (b) per 10 × 10 m plot. Subscripts show results of least significant difference *post hoc* analysis. (No significant difference between bars having the same subscript.) LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3, respectively.

(Table 2) differed significantly among fragments ($F = 244.15$, $P < 0.0001$), again with the LOK fragment having the lowest mean values.

Species abundance patterns in the three Sainte-Luce fragments mirror the right tail of a lognormal distribution, both for trees in the 50 × 50 m plots and understory woody vegetation in the 10 × 10 m plots (Figure 6a and b). More than two-thirds of tree species (68.0, 69.3, and 73.9% respectively) and understory species (65.6 and

Table 2. Richness and abundance parameters (±SD) in 10 × 10 m plots along 100-m long transects in three coastal forest fragments.

	LOK	SL1	SL3	Total
All woody individuals, height >1 m				
No. of individuals	1336	3997	5367	10 700
No. of species	42	131	145	203
No. of families	23	47	50	55
Mean no. of trees per plot	66.1 (36.0)	199.2 (93.93)	267.6 (55.9)	–
Mean no. of species per plot	7.1 (2.4)	34.6 (9.0)	48.8 (5.9)	–
Mean no. of families per plot	6.2 (2.1)	22.1 (4.8)	27.8 (3.5)	–
Shannon-Wiener index	1.23 (0.405)	2.96 (0.350)	3.36 (0.166)	–
Individuals < 10 cm *DBH*				
No. of trees	1242	3853	5187	10 282
No. of species	42	119	140	195
No. of families	23	45	47	54
Mean no. of trees per plot	62.1 (37.3)	192.6 (94.2)	259.4 (55.6)	–
Mean no. of species per plot	6.3 (2.4)	32.7 (8.8)	46.8 (6.4)	–
Mean no. of families per plot	5.5 (1.9)	20.6 (4.9)	27.0 (3.4)	–
Shannon–Wiener index	1.13 (0.420)	2.91 (0.351)	3.32 (0.182)	–

LOK – Lokaro forest; SL1 and SL3 – Sainte-Luce forests 1 and 3.

64.6%) in each of the Sainte-Luce forests are found in the first three abundance classes of the log-distribution (1, 2, and 3–4 individuals), while fewer than 10% were found in each of the final two abundance classes (17–32 and 33–64 individuals). Species abundance was bimodal at LOK (Figure 6a and b), with modes in the first and final abundance classes.

Mean DBH for trees was remarkably similar across the four forest fragments (16–17 cm; see Table 3). The majority of trees (50–60%) had a DBH between 10 and 15 cm, and the distribution for all forests dramatically dropped off to a long right tail (Figure 7). However, several species did attain a DBH > 40 cm in at least one forest fragment, including: *Asteropeia micraster* (Asteropiaceae), *Casuarina equisitifolia* (Casuarinaceae), *Cynometra cloiselii* and *Instia bijuga* (both Fabaceae),

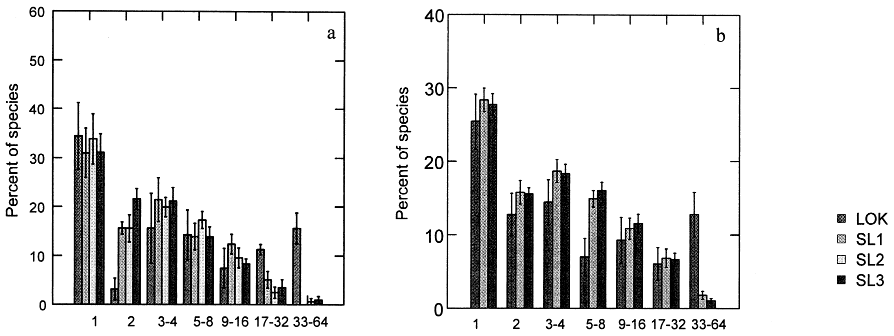

Figure 6. Log distribution of trees per species per plot in four forest fragments. LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3, respectively.

Dypsis saintelucei (Arecaceae), *Elaeodendron alluaudianum* (Celastraceae), *Faucherea aff. tampoloensis* and *Mimusops commersonii* (both Sapotaceae), *Leptolaena delphinensis* and *Sarcolaena multiflora* (both Sarcolaenaceae), *Magnistipula tamenaka* (Chrysobalanaceae), *Poupartia chapelieri* (Anacardiaceae), *Symphonia fasculata* (Clusiaceae), *Tambourissa purpurea* (Monimiaceae), *Uapaca louvelii* (Euphorbiaceae). Basal area calculated for trees (DBH $>$10 cm) in 10 × 10 m plots appears to underestimate the basal area compared to that extrapolated from the 50 × 50 m plots (Table 3).

Figures 8a and b show the species–area curves separately for the two sampling methods utilized here. It appears that even after 5 ha (i.e., 20 plots @ 0.25 ha per plot), the species–area curve for trees still has not reached an asymptote (Figure 8a). However, the rarefaction-produced expected species abundance curve did intersect with the species accumulation curve. The binomial test for paired data indicates that there is no significant difference between the species accumulation and rarefaction curves ($P_r = 0.074$). The species–area curve for understory species also fails to reach an asymptote (Figure 8b). However, the binomial test for paired data indicates no significant difference between the two curves ($P_r = 0.099$).

Mean Jaccard's coefficient of similarity between two fragments was compared by the two-sample *t*-test (Table 4). The three values giving tree species similarity in 50 × 50 m plots, in which LOK was one of the fragments being compared, were the lowest. They had significantly lower mean similarity coefficients. Even though only three fragments were used in the 10 × 10 m sampling, limiting the number of combinations, the same pattern appeared (Table 4). Similarity coefficients including LOK in the pair were significantly lower than those including only Sainte-Luce fragments.

Species patterns

The most common species in the Lokaro forest was *T. purpurea* (Monimiaceae), accounting for 45.7% of all individuals sampled in 50 × 50 m plots and 46.4% in 10

Table 3. Mean DBH and basal area (BA) from 50 × 50 m and 10 × 10 m plots in the four forest fragments.

Forest	DBH (cm)			BA (m^2/ha)	
	Maximum	Mean	SD		
50 × 50 m *plots*					
Lokaro	63	16.53	6.3	31.4	
SL1	66	16.94	7.12	44.54	
SL2	54	15.96	5.86	47.81	
SL3	51	16.23	6.23	38.25	
10 × 10 m *plots*				*BA* $\geq$ *10* cm	*BA* $<$ *10* cm
Lokaro	56	3.61	5.47	17.92	4.65
SL1	54	2.14	3.2	15.61	7.63
SL3	45	2.15	3.2	22.33	11.89

LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3.

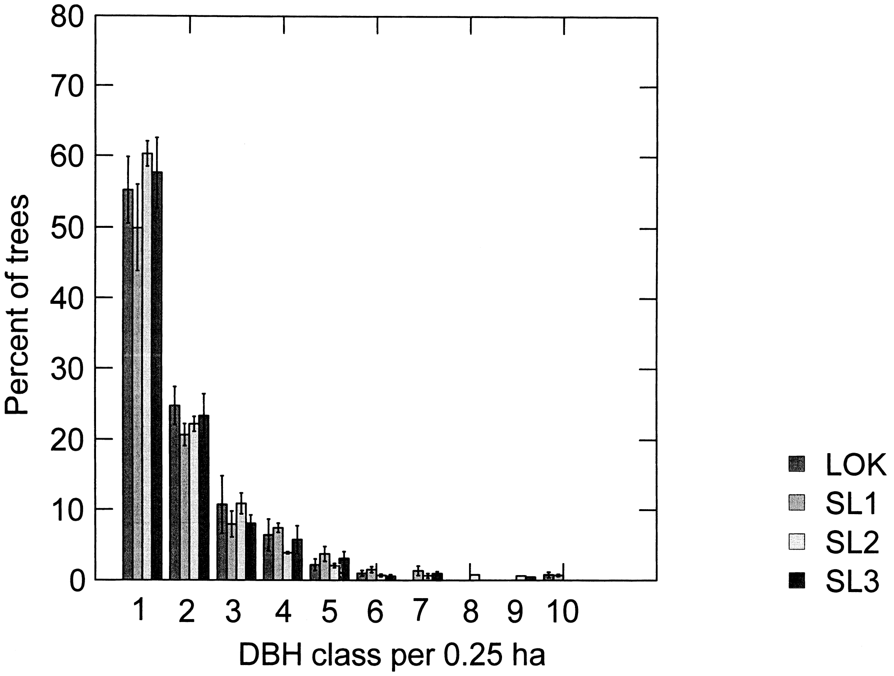

Figure 7. Distribution of tree DBH in four forest fragments. DBH classes are in increments of 5 cm, (1) 10–15 cm, (2) 15.1–20 cm, and so on, class 10 is DBH > 55 cm. LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3, respectively.

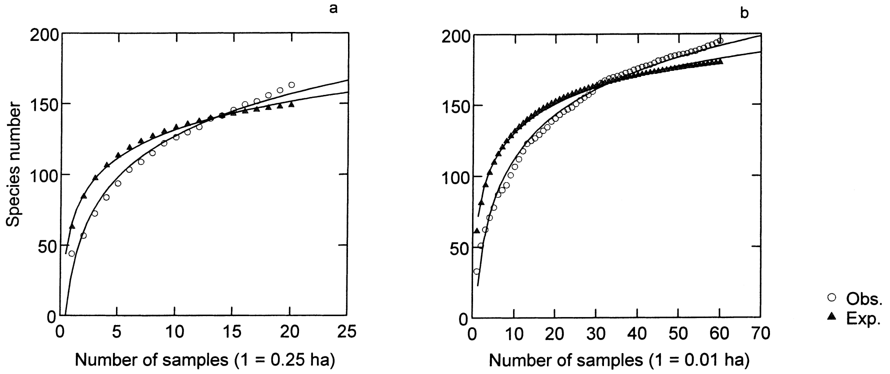

Figure 8. Rarefaction (expected) and species accumulation (observed) curves for (a) trees in 50 × 50 m plots, and (b) understory woody vegetation measured in 10 × 10 m plots. Binomial (sign) test for paired data showed no significant difference between observed and expected curves ($P > 0.05$).

× 10 m plots. In marked contrast, the most common tree species in the Sainte-Luce fragments (*Pandanus concretus*, Pandanaceae in SL1; *Asteropeia micraster*, Asteropeiaceae in SL2; and *Intsia bijuga*, Fabaceae in SL3) accounted for 8.1, 9.3, and

Table 4. Results of *t*-tests comparing mean Jaccard's coefficient of similarity between forest fragments.

50 × 50 m plots	LOK–SL1 0.037 (0.026)	LOK–SL2 0.029 (0.018)	LOK–SL3 0.032 (0.015)	SL1–SL2 0.314 (0.051)	SL1–SL3 0.327 (0.052)
LOK–SL2 0.029 (0.018)	ns				
LOK–SL3 0.032 (0.015)	ns	ns			
SL1–SL2 0.314 (0.051)	***	***	***		
SL1–SL3 0.327 (0.052)	***	***	***	ns	
SL2–SL3 0.359 (0.062)	***	***	***	**	*

10 × 10 m plots	LOK–SL1 0.042 (0.025)	LOK–SL3 0.042 (0.02)
LOK–SL3 0.042 (0.02)	ns	
SL1–SL3 0.258 (0.104)	***	***

ns – no significance; *$P < 0.05$; **$P < 0.005$; ***$P < 0.0001$. Mean coefficient (±SD) is shown (it was calculated for all combinations of plots between two fragments). There were five 50 × 50 m plots in each fragment, giving 25 (5 × 5) possible comparisons between any two fragments. There were 20 10 × 10 m plots in each of three fragments, giving 400 (20 × 20) possible comparisons between two fragments.

6.4%, respectively. Also, the most common understory species in SL1 and SL3 (*Pyrostria medea*, Rubiaceae) accounted for 10.9 and 10.3% of individuals, respectively. A total of 22 tree species occurred at an abundance of 5 trees per 0.25 ha or greater in at least one fragment, and 7 at an abundance of 10 trees per 0.25 ha or greater (Table 5). Among understory species, 29 species were found at abundances of 100 individuals per 0.25 ha or greater, and 11 at 200 individuals or more (Table 6).

Considering just the most common species (i.e., those that are represented by more than 10 stems per 0.25 ha), the community composition of the forest fragments is strikingly different. The Lokaro forest is primarily a *T. purpurea–Ravenala madagascariensis–Myrica spathulata* forest; whereas the Sainte-Luce fragments are all dominated by *A. micraster–I. bijuga–L. delphinensis–P. concretus.*

Family patterns

Species-level differences were also reflected in family-level patterns. A total of 17 families were represented by either a tree or understory species in only a single forest fragment, with LOK and SL3 having the most unshared families (Table 7).

The 10 families having greatest mean FIVs in 50 × 50 m plots from each forest fragment are shown in Table 8. The top 10 families in the Lokaro forest accounted for 56.7% of the species and 90.7% of individuals. The family with the highest FIV in Lokaro, Monimiaceae, contained just one species but was represented by 45.7%

Table 5. Species exceeding 5 (+) and 10 (++) trees per 0.25 ha in four forest fragments.

Species	LOK	SL1	SL2	SL3
Pourpartia chapelieri (Guillaumin) H. Perrier (Anacardiaceae)				+
Elaeodendron sp. (Celastraceae)		+	+	
Diospyros lanceolata Poiret (Ebenaceae)		+	+	+
Uapaca louvelii Denis var. *louvelii* (Euphorbiaceae)				+
Cynometra cloiselii Drake (Fabaceae)				+
Intsia bijuga (Colebr.) Kuntze (Fabaceae)		++	++	++
Homalium axillare Baillon (Flacourtiaceae)		+	+	
H. involucratum (DC) O. Hoffm. (Flacourtiaceae)				+
H. louvelianum H. Perr. (Flacourtiaceae)	+			
Scolopia erythrocarpa Perr. (Flacourtiaceae)		+	+	
Dicoryphe stipulacea St. Hil. (Hamamelidaceae)		+	+	+
Strychnos diplotricha Leeuwenberg (Loganiaceae)	+			
Tambourissa purpurea (Tul.) A. DC. (Monimiaceae)	++			
Ampalis mauritiana (Jacq.) Urban (Moraceae)	+			
Myrica spathulata Mirbel (Myricaceae)	++			
Brochoneura acuminata (Lamk.) Warburg (Myristicaceae)				+
Eugenia cloiselii H. Perr. (Myrtaceae)		+	+	+
Pandanus concretus Baker (Pandanaceae)		++	++	++
Leptolaena multiflora Thouars (Sarcolaenaceae)		++	++	++
Sarcolaena multiflora Thouars (Sarcolaenaceae)		+	+	+
Ravenala madagascariensis Sonn. (Strelitziaceae)	++			
Asteropeia micraster Hallier var. *micraster* (Theaceae)		++	++	+

LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3, respectively.

of individuals. Similarly, the top 10 families from the three Sainte-Luce fragments accounted for about half of all species in each forest fragment, 54.3, 44.3, and 42.1%, respectively. However, the top 10 Sainte-Luce families represented about two-thirds of individuals (71.1, 67.7, and 62.2%, respectively).

The 10 families in 10 × 10 m plots with the highest mean FIVs are shown in Table 9. The top 10 in LOK accounted for 38.1% of all understory species, 91.6% of all individuals. Again (and similar to LOK), the top 10 families in SL1 and SL3 accounted for 42.0 and 34.3% of understory species, respectively. Unlike LOK, the top 10 families in SL1 and SL3 accounted for just 69.2 and 65.1% of individuals.

Discussion

Species–area curves for neither of the two sampling procedures (trees in 50 × 50 m plots and understory woody vegetation in 10 × 10 m plots) showed an asymptotic leveling-off that would indicate most species in the community being accounted for after a limited number of samples. The spatial distribution of species in southeastern Madagascar's coastal littoral forest is very heterogeneous, reflected by most species having low densities and patchy distributions. Rarefaction analysis revealed that, at a minimum, 30% fewer samples of 50 × 50 m plots would have sufficed, and about 50% fewer 10 × 10 m samples (see Heck et al. 1975). However, it should be noted

Table 6. Species with DBH < 10 cm, exceeding 100 (+) and 200 (++) stems per 0.25 ha in three forest fragments.

Species	LOK	SL1	SL3
Dracaena elliptica Thunb. & Dallm. (Agavaceae)		+	+
D. reflexa var. *angustifolia* Baker (Agavaceae)			+
D. reflexa var. *subelliptica* H. Perr. (Agavaceae)		+	
Cabucala madagascariensis (DC.) Markgraf (Apocynaceae)			+
Plectonia densiflora Baker (Rubiaceae)	+		+
Polyscias sp1 (Araliaceae)			++
Dypsis lutescens Beentje (Arecaceae)		+	++
Colea obtusifolia DC. (Bignoniaceae)	++		
Mystroxylon aethiopicum (Thumb.) Loes. (Celastraceae)		+	++
Weinmannia louveliana Bernardi (Cunoniaceae)		+	
Diospyros lanceolata Poiret (Ebenaceae)			++
Diospyros sp1 (Ebenaceae)			+
Antidesma petiolare Tul. (Euphorbiaceae)		+	
Suregada baronii (Moore) Croizat (Euphorbiaceae)			+
Homalium axillare Baillon (Flacourtiaceae)			+
Homalium sp1 (Flacourtiaceae)		++	
Ludia mauritiana J. Gmelin (Flacourtiaceae)		+	
Scolopia erythrocarpa H. Perr. (Flacourtiaceae)			+
Buddleia indica Lam. (Loganiaceae)			+
Tambourissa purpurea (Tul.) A. DC. (Monimiaceae)	++		+
Brochoneura acuminata (Lam.) Warb. (Myristicaceae)			+
Campylospermum obtusifolium (Lam.) Tieghem (Ochnaceae)		+	++
Norhonia sp1 (Oleaceae)			++
Cremocarpum lantzii Bremek. (Rubiaceae)		++	+
Pyrostria medea (A Rich.) Cavaco (Rubiaceae)		++	++
Saldinia axillaris (Lam.) Ex. Poir. Bremek. (Rubiaceae)			+
Tarenna thouarsiana (Drake) Homolle (Rubiaceae)			+
Fauchera hexandra (Lecomte) Lecomte (Sapotaceae)		+	
Sarcolaena multiflora Thouars (Sarcolaenaceae)		+	+

LOK – Lokaro forest; SL1 and SL3 – Sainte-Luce forests 1 and 3, respectively.

Table 7. The 17 families found only in a single forest fragment.

Forest fragment	Families found
LOK	Casuarinaceae, Hernandiaceae, Malvaceae, Myricaceae, Pinaceae, Sterculiaceae, Tiliaceae
SL1	Scrophulariaceae
SL2	Annonaceae, Meliaceae
SL3	Apocynaceae, Capparaceae, Icacinaceae, Lecythidaceae, Melastomataceae, Menispermaceae, Thymelaeaceae

LOK – Lokaro forest; SL2 and SL3 – Sainte-Luce forests 2 and 3.

that at larger spatial scales information used in analyses would be missing, since species–area curves did not level off. Recent results from a rainforest community in Brazil (Ferreira and Prance 1998) showed that even a sampling area of 1 ha ($n = 4$) was inadequate to capture local species richness. Likewise, Rakotomalaza and Messmer (1999), studying the forests of Madagascar's Andohahela Reserve, located

Table 8. The 10 families with the highest mean FIV for trees with DBH ⩾ 10 cm, in four forest fragments from 50 × 50 m plots.

LOK		SL1		SL2		SL3	
Family	FIV	Family	FIV	Family	FIV	Family	FIV
Monimiaceae	87.91	Sarcolaenaceae	35.61	Theaceae	28.27	Sarcolaenaceae	32.26
Strelitziaceae	29.57	Flacourtiaceae	31.3	Sarcolaenaceae	27.99	Fabaceae	27.66
Flacourtiaceae	29.38	Fabaceae	25	Fabaceae	24.74	Myrtaceae	20.67
Myricaceae	26.49	Ebenaceae	22.78	Flacourtiaceae	21.93	Flacourtiaceae	17.71
Loganiaceae	19.85	Myrtaceae	17.7	Myrtaceae	17.35	Euphorbiaceae	16.71
Moraceae	19.59	Lauraceae	14.23	Ebenaceae	17.05	Sapotaceae	15.35
Combretaceae	11.91	Euphorbiaceae	13.95	Euphorbiaceae	16.58	Ebenaceae	15.02
Casuarinaceae	11.8	Pandanaceae	13.92	Anacardiaceae	15.31	Anacardiaceae	12.51
Sapotaceae	9.81	Celastraceae	13.47	Lauraceae	11.27	Pandanaceae	11.89
Tiliaceae	8.52	Oleaceae	11.89	Pandanaceae	11.23	Celastraceae	9.6
Total	254.83	Total	199.85	Total	191.72	Total	179.38
Remainder (11)	49.32	Remainder (25)	85.07	Remainder (33)	103.28	Remainder (35)	124.53

LOK – Lokaro forest; SL1, SL2, and SL3 – Sainte-Luce forests 1, 2, and 3.

Table 9. The 10 families with the highest mean FIV for woody plants < 10 cm DBH in three forest fragments from 10 × 10 m plots.

LOK		SL1		SL3	
Family	FIV	Family	FIV	Family	FIV
Monimiaceae	140.53	Rubiaceae	47.92	Rubiaceae	38.78
Bignoniaceae	41.28	Flacourtiaceae	32.93	Flacourtiaceae	21.18
Apocynaceae	18.39	Euphorbiaceae	26.98	Agavaceae	18.41
Agavaceae	14.73	Agavaceae	20.51	Euphorbiaceae	18.31
Rubiaceae	10.01	Cunoniaceae	11.66	Ebenaceae	16.78
Sapotaceae	8.2	Sarcolaenaceae	11.34	Arecaceae	13.8
Hernandiaceae	7.36	Celastraceae	10.21	Araliaceae	12.38
Rutaceae	6.47	Sapotaceae	9.84	Fabaceae	11.47
Myricaceae	5.41	Apocynaceae	9.76	Oleaceae	10.4
Combretaceae	4.13	Bignoniaceae	8.57	Ochnaceae	10.1
Total	256.4	Total	189.72	Total	171.61
Remainder (12)	22.04	Remainder (36)	110.09	Remainder (38)	118.73

LOK – Lokaro forest; SL1 and SL3 – Sainte-Luce forests 1, 2, and 3.

in a mountainous region approximately 25–30 km from our study sites, showed that for mid-elevation (altitude = 1150 m) montane forests, species–area curves also did not reach an asymptote for 1 ha plots.

Comparisons with other tropical forests reveal some important similarities with respect to community structure (Table 10). One hectare plots generally have between 500 and 800 trees, around 100 tree species, and a total basal area between 30 and 40 m^2 (Table 10). Results from other Malagasy studies (Rabevohitra et al. 1998; Dumetz 1999; Rakotomalaza and Messmer 1999) show that diversity, density, and size structure of forest communities there appear to be very similar to other ‘high diversity’ centres in central and South America.

It is important to note that comparing results from studies in different places can

Table 10. Comparison of tree species diversity, density, and size from different tropical forests. All values are sampled from, or calculated to, 1 ha.

	SE Madagascar[a]	Sainte-Luce Madagascar[b]	Androhahela Madagascar[c]	Guyana[d]	Costa Rica[e]	Amazon[f]
No. of species	86.3	111–116	121–146	50–71	100–149	137–168
No. of families	41.9	43–44	31–34	23–26	41–55	34–43
No. of trees	869	1037–1064	739–880	357–742	425–565	639–713
Basal area (m^2)	40.5	–	34.1–43.2	32.3–34.6	23.5–30.3	32.8–40.2

[a] These values from the present study are extrapolated to 1ha samples by randomly sampling four 0.25 ha (50 × 50 m) plots 10 times. [b] Rabevohitra et al. (1998); [c] Rakotomalaza and Messmer (1999): only samples taken below 1000 m; [d] Johnston and Gillman (1995); [e] Lieberman et al. (1996): only samples taken below 1000 m; [f] Ferreira and Prance (1998).

lead to incorrect conclusions due to inherent differences between geographic regions, but also due to differences in sampling methods and experimental design (Ferreira and Prance 1998). Permanent plots are probably the best tool available for evaluating and understanding tropical ecology, despite the required resources, time, and expertise (Sheil 1995). Permanent plots would definitely be very valuable in clarifying the effects of habitat fragmentation and community degradation in southeastern Madagascar (see also Cadotte and Lovett-Doust 2001).

The general consensus from descriptive tropical studies such as this one is that more research is desperately needed, since so many tropical forest species are new to science (see, e.g., Prance et al. 2000). For example, in the present study, from the 50 × 50 m data, 39 taxa could not be identified to species level, including one to genus level, and five to family level. The situation is even worse for the smaller woody vegetation. From the 10 × 10 m plots, 68 taxa could not be identified to species level, including six to genus level, and 32 to family level. Dumetz (1999) similarly found that four out of the 26 most common taxa in Malagasy coastal forests could not be identified to species level. Rakotomalaza and Messmer (1999) were unable to identify to species level five out of the nine most abundant taxa in a montane plot. An even more dramatic example: on a recent expedition to Madagascar, Dransfield and Beentje, experts on Palms (Arecaceae), discovered three new genera and 85 new species of palm in eastern Madagascar (Prance et al. 2000).

Community patterns between fragments

There were significant differences among the four forest fragments in this study in terms of Shannon–Wiener index of diversity, number of trees, species richness, family richness, and species composition. These differences may be the result of highly localized edaphic and micro-climatic differences, though all forest fragments grow on sand substrate and are exposed to generally similar conditions (Dumetz 1999). Likely factors influencing forest fragment differences are marine influences (where the Lokaro forest is closer to the coast than the other fragments), the degree of isolation of the forest from other large forests, and extent of anthropogenic disturbances. The Lokaro fragment is very isolated compared to the other three fragments and consequently may be a more focal resource source for people living in local villages, thereby undergoing more intense anthropogenic disturbance compared to the Sainte-Luce fragments (Cadotte 2001; Cadotte and Lovett-Doust 2002). Increased isolation may also have biotic repercussions in trees and shrubs, such as effects on pollinators (Nason and Hamrick 1997; Somanathan and Borges 2000), because of increased dependence on a pollinator's dispersal patterns. Somanathan and Borges (2000) found that dioecious tree species occurring in anthropogenically fragmented forests in India showed female-biased sex ratios compared to those in natural, undisturbed populations. Investigating whether disturbance alters community structure, rather than isolation *per se*, Shackleton et al. (1994) examined gradients of disturbance centred around rural villages in eastern Transvall Lowveld, South Africa. They found that proportional size class distributions of trees did not alter along the disturbance gradients, however, patterns of density, biomass, basal area, and diversity were significantly negatively correlated with increasing disturbance. Similarly, Chittibabu and Parthasarathy (2000), studying disturbance in tropical evergreen forest in the Eastern Ghats in India, found reduced richness, diversity, density, and basal area, as well as altered species composition in disturbed plots, relative to undisturbed plots. In our study, all fragments had very similar distributions of tree size classes, while measures of diversity, richness, and density differed significantly among fragments.

Jaccard's similarity measures, as well as patterns of floristic composition, showed the Lokaro forest to be strikingly different from the other three, Sainte-Luce fragments. The plots in the Lokaro fragment were dominated by only one or two species (especially *T. purpurea*, Monimiaceae). Monodominance, as exhibited by the extremely high densities of *T. purpurea* in the Lokaro forest fragment, can be a consequence of the removal of competing species (ecological release) or perhaps a reduction in the numbers of natural predators (e.g., see Groombridge 1992). Torti et al. (2001) showed that monodominance in tropical forests is not easily attributable to any single trait, rather it appears to be a combination of environmental conditions and particular life history attributes. Either way, *T. purpurea* appears to be benefitting from conditions present at the Lokaro fragment.

Understory richness

Studies of tropical forests have shown that non-tree species can also exhibit high levels of species richness (Gentry and Dodson 1987; Nieder et al. 2000). Gentry and Dodson (1987) found that in 0.1 ha samples in three different forests of western Ecuador, non-tree woody species richness was 2–4 times that of tree species richness. This suggests a shortcoming in characterizing tropical forests by tree species richness alone (Gentry and Dodson 1987). Our data show that, extrapolating the species–area curve to 1 ha for the understory species in 10×10 m plots, understory species richness may be as high as 195 species per hectare, surpassing the value of 86.3 species per hectare for trees. One caveat to the difference in tree and understory richness involves the spatial scale of the study. Trees and understory richness patterns appear to be measurable at separate spatial scales (see Figure 8).

Understory species richness reaches 150 at about 0.3 ha of sampled area, while that of trees reaches 150 at about 3.75 ha of sampled area. Larger sampling units would be required to determine the relationship between understory and tree species richness.

Conservation priority

The heterogeneous nature of the eastern littoral forests of Madagascar, and the high species richness, along with the degree of habitat destruction and fragmentation ought to be an obvious indicator of the need to protect the remaining forest vestiges. We found that 17 taxonomic families were represented in only a single forest fragment, again highlighting the heterogeneous nature of the forests, but also the fact that some fragments contain a disproportionate amount of phylogenetic information. Fragments over-represented by these restricted families will harbor a greater evolutionary history compared to, say, a patch with many closely related taxa (e.g., see Vane-Wright et al. 1991). Conservation priorities need to be mindful not only of diversity, but also of phylogenetic uniqueness.

Even though Malagasy forests have similar richness patterns to other tropical forests, they harbor an enormous number of endemic species (more than 80%), making Madagascar one of the highest conservation priorities in the world (Myers et al. 2000). Furthermore, Madagascar as a whole has eight endemic families comprising *ca.* 98 species (Schatz et al. 2000), which ought to be of special concern as significant parts of their genome are not shared with species anywhere else in the world.

These forests are under constant threat from traditional human activities, and now are the subject of possible development of a large-scale mining project in the region (Cadotte 2000). These forest fragments contain animal species that have very limited ranges (e.g., see Nussbaum et al. 1999), as well as undescribed and understudied taxa (e.g., see Razafimandimbison and Taylor (2000)). Even fragmented and degraded habitats can have a high conservation value (Foster 1978).

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