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PLANT COMMUNITY RESPONSES TO HABITAT FRAGMENTATION AND ANTHROPOGENIC DEGRADATION IN THE LITTORAL FORESTS OF SOUTHEASTERN MADAGASCAR

by

Marc W. Cadotte

A thesis submitted to the Faculty of Graduate Studies and Research through the Department of Biological Sciences in partial fulfillment of the requirements for the Degree of Master of Science at the University of Windsor

Windsor, Ontario, Canada

2001

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ABSTRACT

Conversion of intact forest into smaller, isolated fragments results in a number of profound and quantifiable changes. The purpose of this research was to examine the effects of fragmentation and to understand better how Malagasy forest structure and composition is affected by landscape-level factors. A total of 3476 trees representing 169 species in 55 families were recorded in 50x50 m plots, and 10,282 understory stems representing 195 species in 54 families were found in 10x10 m plots. Fragments differed significantly in both tree and understory stem density, species richness and diversity values, and family richness values. Patch- and landscape-level features were used to examine the patterns of density and diversity, and included: fragment size, fragment perimeter-area index, internal perimeter created by roads and trails in each fragment, and the number of villages (as an indicator of human population pressure) per hectare of forest in three expanding radii of 5, 7.5, and 10 km. Estimates of internal fragmentation and population pressure were significantly linearly associated with density and richness ($P<0.05$) for both trees and understory vegetation. It appears as though there is a continuum of habitat degradation in these forest fragments, which is a product of human population pressure and resource utilization.

Undegraded communities exhibited 'core-satellite' patterns wherein species' distributions exhibited two modes — species either found only at a single site or species found across all sites. Both for trees in 50x50 m plots and

for understory woody vegetation in 10x10 m plots, the degraded fragments had lost their mode of core species. Habitat degradation may have a greater adverse effect on common species than on rare species.

I also examined the extent of edge-to-interior differentiation within forest fragments, as affected by habitat degradation. In both the intact forest fragment and the moderately-degraded fragment, heights of trees and other woody taxa, stem/bole elongation patterns, and the height-to-first branching, all increased significantly with increasing distance from the edge. The edge effect extended 25-50 m into the intact and moderately-degraded fragments. In the intact forest, distance-from-edge was the only significant factor, while in the moderately-degraded forest fragment, the number of trails along the transect was also a highly significant factor. In the highly-degraded fragment, the interaction between these two factors was the most significant factor.

SYNOPSIS

Madagascar embodies the present-day concern about the global biodiversity crisis. Doubtless, the greatest threat to Madagascar's biodiversity is the burgeoning human population pressure placed upon its unique and highly diverse ecosystems. The impetus for research focusing on the effects of deforestation and fragmentation of the forests of Madagascar is self-evident. Degradation and ongoing fragmentation of intact forests usually results in the creation of a patchwork of forest fragments. Conversion of intact forest into smaller, isolated fragments results in a number of profound and quantifiable changes. The purpose of this research was to examine the effects of fragmentation and to understand better how Malagasy forest structure and composition is affected by landscape-level factors. Specifically, I compare floristic, diversity, and abundance patterns in isolated forest patches and in relatively less-fragmented forest patches. I also analyze the landscape-level patterns of the forest fragments, namely, the size, isolation, internal fragmentation, and proximity to villages.

In Chapter II, I describe the coastal littoral forest of extreme southeastern Madagascar, where I studied trees (Diameter at Breast Height ≥10 cm) in twenty, 50x50 m plots in four forest fragments, and understory woody vegetation (DBH <10 cm, ≥1 m tall) in 60, 10x10 m plots in three of the fragments. A total of 3476 trees representing 169 species in 55 families were recorded in the 50x50 m plots, and 10,282 understory stems representing 195 species in 54 families were

found in the 10x10 m plots. Fragments differed significantly in both tree and understory stem density, species richness and diversity values, and family richness values, with the Lokaro fragment having the lowest values for all measures. Furthermore, floristic, family importance values, and community similarity measures revealed that species composition remaining at the Lokaro fragment is very different from the Sainte-Luce fragments.

In Chapter III, I describe the effects of fragmentation and landscape-level features on trees and understory woody vegetation. Patch- and landscape-level features included: fragment size, fragment perimeter-area index, internal perimeter created by roads and trails in each fragment, and the number of villages (as an indicator of human population pressure) per hectare of forest in three expanding radii of 5, 7.5, and 10 km. Estimates of internal fragmentation and population pressure were significantly linearly associated with density and richness ($P<0.05$) for both trees and understory vegetation. Species evenness was also lowest in the most degraded forest fragment, resulting from the competitive release of *Tambourissa purpurea* in degraded plots. Demographic responses to the effects of fragment degradation differed among taxa. Finally, degraded tropical forest fragments may have important benefits to the conservation of biodiversity, especially where local human populations rely on a subsistence lifestyle, and these fragments should be included in management planning.

Most communities exhibit 'core-satellite' patterns where in species' distributions exhibit two modes, one of species found only at a single site and another of species found across all sites. In Chapter IV, I show that, both for trees in 50x50 m plots and for understory woody vegetation in 10x10 m plots, the intact fragments showed two modes, while degraded fragments had lost their mode of core species. Habitat degradation may have a greater adverse effect on common species than on rare species.

In Chapter V, I examine the extent of edge-to-interior differentiation within forest fragments, as affected by habitat degradation. In both the intact forest fragment and the moderately-degraded fragment, heights of trees and other woody taxa, stem/bole elongation patterns, and the height-to-first branching, all increased significantly with increasing distance from the edge. The edge effect extended 25-50 m into the intact and moderately-degraded fragments. In the intact forest, distance-from-edge was the only significant factor, while in the moderately-degraded forest fragment, the number of trails along the transect was also a highly significant factor. In the highly-degraded fragment, the interaction between these two factors was the most significant factor.

In the intact forest fragment, common ("core") species increased in number with increasing distance from the edge; there was a significant core species mode beyond 25-50 m from the edge. In the moderately-degraded fragment there was also an increase in number of core species with distance from the edge, but there was no mode of core species. In the highly-degraded fragment, there was no change with respect to species distributions and no mode of core species.

Chapters II-V in this thesis represent results that have been submitted to scientific journals, and so there is a certain amount of repetition or redundancy associated with presentation here of the methodology. Chapter I lays out the generality of my methodology and site locality designations.

ACKNOWLEDGMENTS

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CHAPTER I:

INTRODUCTION

A major obstacle to the long-term persistence of global biodiversity is the progressive accumulation of many degraded and destroyed local habitats. The cumulative contribution of many injurious human interactions with intact natural habitats has brought us to the present global crisis. Nowhere is this more relevant than in the biologically rich and diverse tropical ecosystems. More than half of all tropical forests have vanished and a further 1-2% is cleared or degraded each year (Ehrlich and Wilson 1991; Whitmore 1997; Laurance 1999). As species go extinct and become forever lost, the unfortunate reality is that we cannot fully articulate what we are losing, because so many of the species that constitute tropical forests remain grossly under-described (Prance et al. 2000). In fact, scientists can only roughly guess at the numbers of species presently inhabiting Earth. Current estimates place the number of species somewhere between 3 and 30 million species, mainly concentrated in the tropics (May 1994). As these species vanish, they carry with them potential important food and medicinal sources. But more important, however, is the loss of vital local and global ecosystem functions, such as carbon sink, climate moderation, water filtration, soil generation, and reduction of albedo (Laurance 1999; Tilman 2000).

Forest Fragmentation

The degradation and haphazard removal of intact forests usually results in the creation of a patchwork of forest fragments. The conversion of intact forest into smaller, isolated fragments results in a number of profound and quantifiable changes (Bierregaard et al. 1992;Turner 1996). Undoubtedly, reduction in the extent of natural cover will result in the loss of species (Wilcove et al. 1986; Anderssen et al. 1997; Debinksi and Holt 2000), especially in regions in which there is a high level of habitat heterogeneity coupled with patchy species distributions. Of course, the outright loss of natural cover is more detrimental to taxa than fragmentation *per se*, even for highly mobile species such as the avifauna of the temperate zone (Trzcinski et al. 1999). However, there are insidious long-term consequences associated with fragmentation. Many species find the resulting inter-patch matrix inhospitable (especially less-mobile species such as tropical birds, mammals, amphibians and plants), and so may be more susceptible to extinction in fragmented landscapes (Gascon et al. 1999). Fragmentation changes community dynamics for interacting species in the patches. Reduction in competition or local extirpation of predators and parasites affects relative abundances of any number of species; rare taxa may become relatively common, or *vice versa* (Lynam 1997). Terborgh et al. (1997) showed that the phenomenon of ecological release (i.e., the increase in density of a species following removal of a competitor or predator) in forest fragments appears most commonly with generalist herbivores. Furthermore, fragmentation may facilitate the competitive replacement of native species by exotics, with smaller fragments especially vulnerable (Lynam 1997; Kemper et al. 1999). For example, Lynam (1997) showed that *Rattus rattus* quickly became the most abundant mammal on habitat islands, five years after flooding the Chiew Larn reservoir in Thailand.

There are also less apparent, population-level effects on dynamics with in forest fragments. From plants to insects to vertebrates, taxa exhibit an array of physical and demographic responses to fragmentation, ranging from diminished population density to smaller body size (Klein 1989; Matthysen et al. 1995; Restrepo et al. 1997; Sumner et al. 1999). Dioecious trees have been found to exhibit lower fecundity with increasing isolation (Somanathan and Borges 2000), and abundant generalist pollinator species may show lower fruit production, because of pollen limitation and inbreeding depression as pollinators become less able to travel among fragments to search out a specific species (Nason and Hamrick 1997). The long-term well-being of many species existing in fragmented landscapes may be in jeopardy as fragmented populations are increasingly susceptible to erosion of genetic resources (Hall et al. 1996).

Fragmenting a formerly continuous forest increases the relative amount of perimeter per unit area, inflating the amount of forest exposed to altered habitat. Such an 'edge effect' (as physical and biological responses to the increased perimeter are called) can be manifested in many ways (Bierregaard et al. 1992). For trees, the annual mortality rate significantly increases up to 100 m from the forest edge (Ferreira and Laurance 1997; Laurance et al. 1998a; Mesquita et al. 1999). This reveals that the physical habitat associated with the edge is altered likely because of changing environmental conditions, including decreased humidity, and increased temperature, desiccation, and light. Life on the edge also means that external abiotic threats (fire, storms, pesticides, etc.), as well as increased competition from pioneer, invasive, and successional species (Janzen 1983, 1986; Sizer and Tanner 1999) are greater.

Madagascar

Since naturalists first began to explore the globe, Madagascar has been a source of wonder and fascination. In his 2nd edition of 'Island Life' (1892), Alfred Russell Wallace wrote:

> Madagascar possesses an exceedingly rich and beautiful fauna and flora, rivaling in some groups most tropical countries of equal extent, and even when poor in species, of surpassing interest from the singularity, the isolation, or the beauty of its forms of life.

This fourth largest (594,180 km^2) of island nations is located 450 km off the east coast of Mozambique in the Indian Ocean, and it remains a place for scientific discovery. With 15-20% of its flora undescribed (Groombridge 1992), Madagascar is in dire need of an organized and systematic floral survey. In a single brief expedition recently, two palm experts (Arecaceae) discovered three new genera and 85 new species of Arecaceae in Madagascar (Prance et al. 2000).

Madagascar embodies the present-day concern for the biodiversity crisis. Traveling in Madagascar, one quickly appreciates how it acts out the global tragedy. Visitors bear witness to the truly phenomenal biodiversity, much of it endemic, as well as massive deforestation and crippling poverty. Because of this duality, Madagascar is considered one of the top, if not the premier conservation priority on earth (Myers et al. 2000).

Doubtless, the greatest general threat to Madagascar's biodiversity is the burgeoning human population pressure placed upon its unique and highly diverse ecosystems. The population of Madagascar is presently 15 million, but it is undergoing a massive explosion in numbers, one of the highest growth rates in the world, increasing at 2.75-3.30% per year (compared with the overall global rate of 1.20) (Myers 1995; Cincotta et al. 2000). Phenomenology of this population pressure includes slash and burn agriculture, cutting and gathering forest wood for fuel; and direct resource extraction (importantly, food items and building materials). Deforestation data reveal that, excluding steep mountainsides, Madagascar will have no intact forest cover by 2025 (Green and Sussman 1990). Presently the extent of general habitat loss is estimated to exceed 90% (Mittermeier et al. 1998; Myers et al. 2000). In a recent study of deforestation and fragmentation of forests in western Madagascar, Smith (1997) reported that forest patches there were shrinking and disappearing at an excessive rate, 62,500 ha/year, with only 2.8% of original cover remaining in the western forests (Fig. 1-1).

A couple of examples may highlight the effect of this habitat loss on endemic species in Madagascar –which there are more than 9,700 endemic plants and 770 endemic vertebrates (Myers et al. 2000). Many species of lemur are expected to be lost; even lemurs with highly generalized habitat use are expected to become extinct in the near future, as they appear to be undergoing population collapses (Jernvall and Wright 1998). Anthropogenically originated grasslands, which presently cover much of Madagascar, are disproportionately poor in herpetofauna, compared to primary and secondary forest (Raxworthy and Nussbaum 1996). Similarly, shrinking forests and increased fragmentation in Madagascar are causing forests to lose significant numbers of their avifauna (Langrand and Wilmé 1997).

The impetus for research focusing on the effects of deforestation and fragmentation in Malagasy forests is (I hope) self-evident. The purpose of this research was to examine the ecological effects of fragmentation and to better understand how landscape dynamics are affecting forest structure and composition in Madagascar. Specifically, I compare floristic, diversity, and abundance patterns in isolated patches and in relatively un-isolated forest patches. I analyze the landscape-level patterns of forest fragments, namely, the size, isolation, internal fragmentation, and proximity to villages.

FIELD METHODS

Site

Field work was carried out in the extreme southeast region of Madagascar (Fig. 1-2), from August 15, 1999 until February 15, 2000. This region is known for its striking habitat diversity (Goodman 1999), where a number of different ecoregions meet, including lowland rainforest, montane moist forests, seasonal forests, and dry scrub-land. Field research included two separate sampling episodes. The first (from August-October) examined five 50x50 m plots in each of four forests, the Lokaro forest (122 ha) and Sainte Luce forests 1, 2, and 3 (457, 206, and 191 ha, respectively) (Fig. 1-2). These four forests were selected on the basis of accessibility, and because the villages near these forests were receiving health and sanitation assistance from a non-governmental organization (NGO), Azafady which provided accommodation and some logistic support in this locality. Plot locations were selected randomly by placing a numbered grid over a map of each forest and using a random number table to indicate sites to be censussed (Fig. 1-3). Plot locations were moved if a recent tree-clearing or site burning had occurred within or near the site of the proposed plot.

The second study methodology was comprised of five 100 m long transects penetrating into each of three of the forests (Fig. 1-3). Along each transect, 10x10 m plots were centred at 5, 25, 50, and 100 m from the edge. Transects were evenly spaced along the seaward side, except in SL1, where three transects had to be moved because of recent deforestation events along the seaward edge.

Sampling

For the first study episode, the twenty randomly placed 50x50 m plots (Fig. 1-3) were completely censussed for all trees with a diameter at breast height (DBH) greater than 10 cm. First corner of a plot was selected by trying to approximate the location which was randomly selected beforehand. 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 trees with multiple stems (especially *Ravenala madagascariensis*, Strelitziaceae), DBH of the largest stem was recorded; for trees that branched lower than breast height, the diameter was taken below the first branch, and for buttressed trees (e.g., *Uapaca* spp., Euphorbiaceae), the diameter was recorded above the buttress. In each forest, a live branch sample and if available a sample of flowering or fruiting structures of each species encountered was identified by its Malagasy name, pressed and later sent to Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar for identification and verification. Subsequent confirmations were provided by Dr. G. Schatz at the Missouri Botanical Garden, St. Louis, Missouri.

In the second part of the study, the sixty 10x10 m plots were completely censussed for all woody vegetation taller than 1 m. Plots were centred around points 5, 25, 50, or 100 m from the forest edge, with one side parallel to the edge. Diameter and height were recorded for all individuals taller than 1 m;

additionally, for individuals with a DBH >10 cm, the canopy width and height-to-first branching were recorded. To estimate height for trees >2.5 m, a reference pole 5 m tall, with markings at 2.5 and 5 m was used. Height was estimated simultaneously by two researchers to increase precision. Again voucher specimens were collected for each species in each forest for identification and deposited at Parc Botanique et Zoologique de Tsimbazaza.

Habitat and geographic variables

Since the four forest fragments were all relatively small in size (122-457 ha), those with an irregularly-shaped perimeter might be more susceptible to adverse edge effects (Wilcove et al. 1986). A simple index, **PA** = perimeter (m)/patch area (ha), was used as a relative measure of shape irregularity for each of the four forest fragments (Fig. 1-3).

The forest fragments were not "islands" of continuous forest. Rather they had been subjected to varying degrees of internal fragmentation due to roads and large trails. The lengths and widths of all roads and canopy-breaking trails penetrating the four forest fragments were measured. Lengths were added to the total perimeter of each site, and the area occupied by these roads and trails was subtracted from the total patch area. An index of internal fragmentation:

$$\mathrm{IPA} = \frac{\text{internal perimeter (m)}}{\text{patch area (ha)}}$$

was used to compare relative values between forests. Similarly, an index of total perimeter-to-area:

$$\text{TPA} = \frac{\text{internal + external perimeter (m)}}{\text{patch area (ha)}}$$

was used to compare cumulative effects of internal fragmentation and shape irregularity.

To measure effects of human population pressure exerted on the forest fragments, the following landscape-level index was used:

$$\text{Population pressure} = \frac{\text{the number of villages}}{\text{forested area (ha)}}$$

which was measured in three expanding contour gradients, of radii 5, 7.5, and 10 km from centre of forest fragment of interest. These radii represent probable distances rural Malagasy people would travel on foot to collect resources in the form of forest products (see Shyamsundar and Kramer 1997). If more precise human demographic data were available, then we could have standardized the index of population pressure by actual population size, but such data were not available. However, of the approximately 30 villages in the vicinity of the four forest fragments, many are quite small, averaging a few hundred people per village (personal observations). Values for population pressure were log transformed for analysis, as individual values for forest fragments were highly variable, and in some cases different by an order of magnitude.

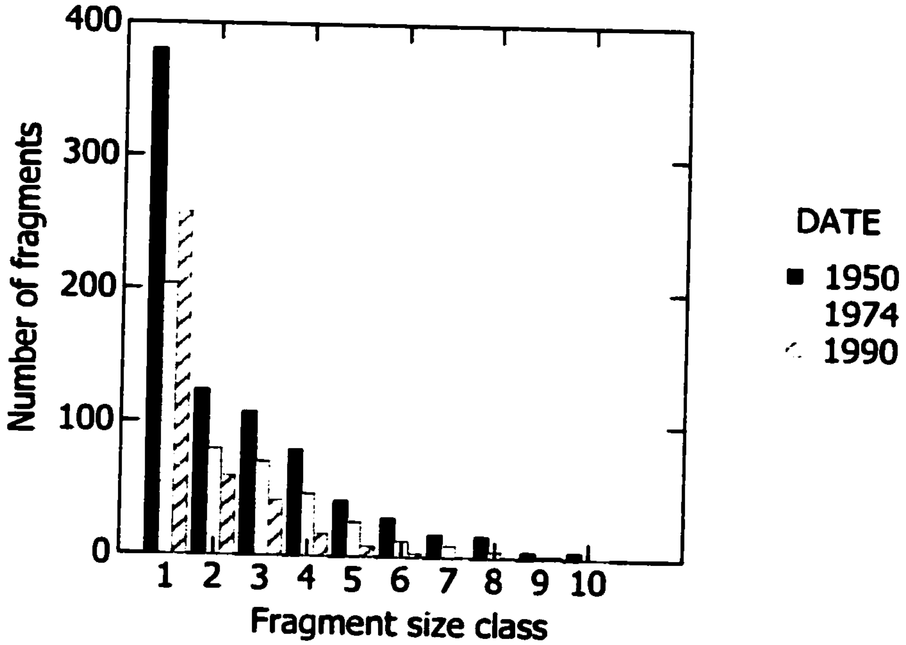

Figure 1-1: Change over time in the number of different size classes in western Malagasy forest patches. Size classes are octaves of 4 km^2 units: 1 = 1; 2 = 2; 3 = 3-4; 4 = 5-8; 6 = 17-32; 7 = 33-64; 8 = 65-128; 9 = 129-256; 10 > 256 (data from Smith 1997).

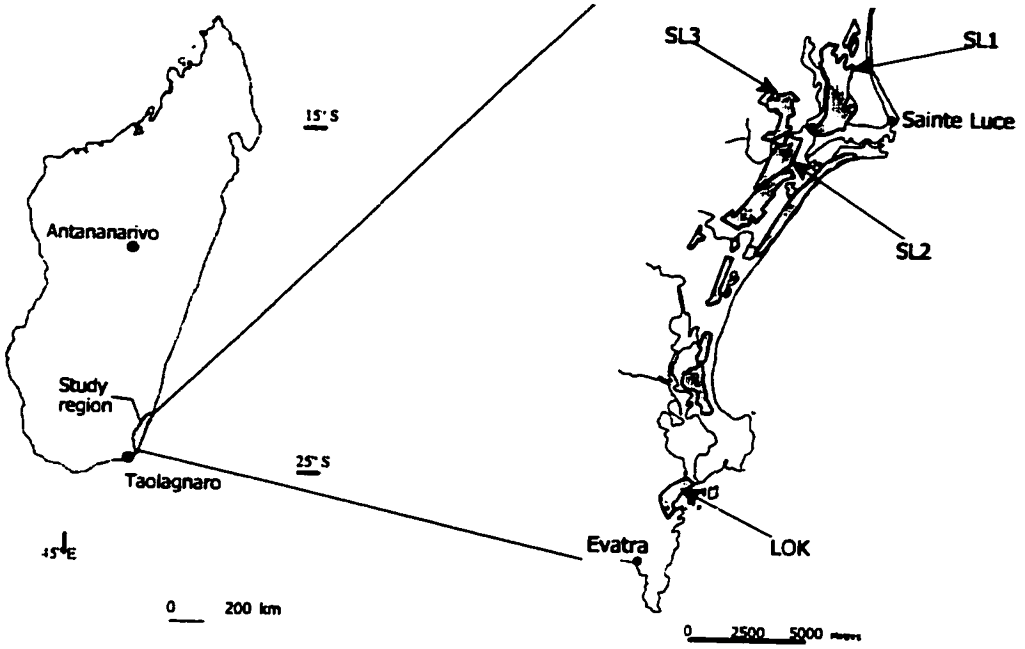

Figure 1-2: Location of the general study region in southeastern Madagascar, and of the four forest fragments used in this study.

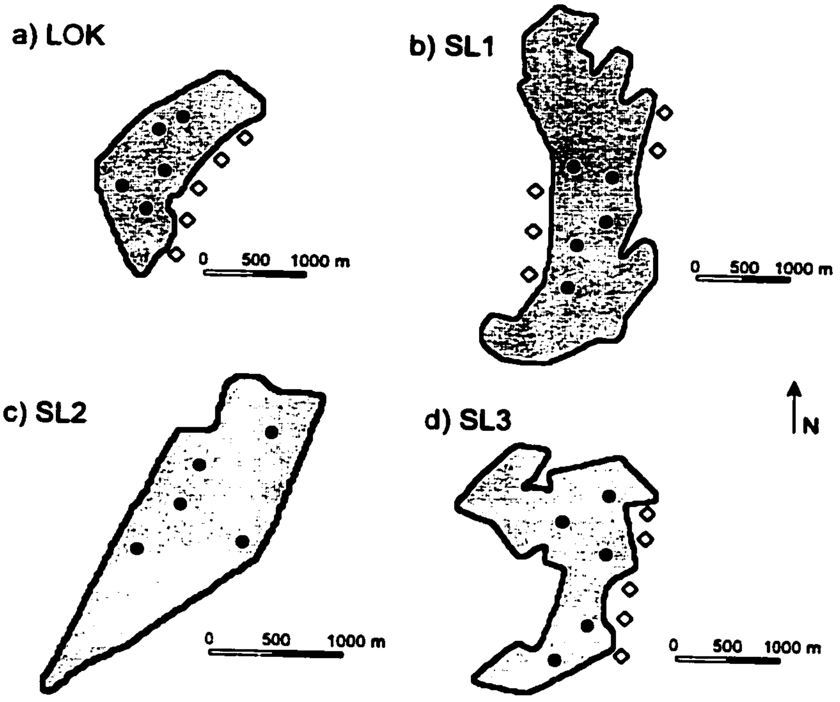

Figure 1-3: Location of (●) 50x50 m plots and the starting point (◇) of 100 m long transects in: a) Lokaro forest; b) Sainte Luce forest 1; c) Sainte Luce forest 2; and d) Sainte Luce forest 3.

CHAPTER II:

TREE AND SHRUB ABUNDANCE AND DIVERSITY IN FRAGMENTED COASTAL TROPICAL FOREST OF SOUTHEASTERN MADAGASCAR

ABSTRACT

In the coastal littoral forest of extreme southeastern Madagascar, I studied trees (DBH ≥10 cm) in twenty, 50x50 m plots in four forest fragments, and understory woody vegetation (DBH <10 cm, ≥1 m tall) in 60, 10x10 m plots in three of the fragments. One of the forest fragments was located in the extremely fragmented and more isolated Lokaro region. A total of 3476 trees representing 169 species in 55 families were recorded in the 50x50 m plots, and 10,282 understory stems representing 195 species in 54 families were found in the 10x10 m plots. For each tree, diameter at breast height 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 density, species richness and diversity values, and family richness values, with the Lokaro fragment having the lowest values for all measures. Furthermore, floristic, family importance values, and community similarity measures revealed that the species composition remaining at the Lokaro fragment is very different from the Sainte-Luce fragments. Anthropogenic disturbance appears to be most pronounced in the isolated Lokaro forest, where forest 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 1994; 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 the close scrutiny they deserve (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 assaulted since the arrival of humans c. 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, disappearing as they may be, still hold a plethora of undescribed species and indeed in some cases entire communities are underdescribed, 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 may result in any number of measurable changes (Bierregaard et al. 1992; Turner 1996). These changes may be in the form of lower species richness (Wilcove et al. 1986; Anderssen et al. 1997; Debinksi 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 relation 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 (Fig. 1-2). 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 sand substrata (Dumetz 1999), and exist within a Malagasy ecozone called the eastern forests which are tropical moist 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, twenty randomly placed 50x50 m plots (see Fig. 1-3) were completely censussed for all trees with a diameter at breast height (DBH) >10 cm. First corner of a plot was selected to approximate a randomly pre-selected 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 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, sixty 10x10 m plots were completely censussed for all woody vegetation (trees plus shrubs) taller than one m. Plots were positioned along 100 m transects running from edge to interior (see Fig. 1-3 for starting location of each transect). Diameter was recorded for all individuals taller than one 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 the 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 is the proportion of all individuals in a sample that belong to the ith species.

Species-area curves were created by taking ten randomly shuffled samples, across all fragments, using the re-sampling, with replacement, 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):

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

where S is total number of species, N is total number of individuals, and n_i is the number of individuals in the i^{th} 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 the other:

$$\text{Prob}(r) = \frac{n!}{r!(n-r)!} \; p^r (1-p)^{(n-r)}$$

where n =number of samples, r =number of expected values that are greater than observed (or less than, depending on hypotheses), and p=probability that any expected data point should be either greater or less (p=0.5, when null hypothesis is no difference) (Underwood1997).

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

50x50 m plots, 25 coefficients were calculated (since each plot was compared to a plot in a second fragment [5x5=25]). Similarly, for comparisons using 10x10 m plots, each plot in a single fragment was compared with each plot in a second fragment, giving 400 (20x20) 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 compared 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:

- Relative diversity = $\frac{\text{no. of species in family}}{\text{total no. of species}} \times 100$
- Relative density = $\frac{\text{no. of individuals in family}}{\text{total no. of trees}} \times 100$
- 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 50x50 m plots. These samples contained a total of 169 species in 55 families (Table 2-1). Average density (trees per 0.25 ha) differed significantly among 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 (Fig. 2-1). 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 significantly greater mean numbers of species per 0.25 ha than both SL1 and LOK, and SL1 had significantly more species than LOK (Fig. 2-2a). Mean number of families per 0.25 ha also differed significantly between the four forest fragments (F=25.30, P<0.0001). Fragment SL3 had significantly greater mean numbers of families than fragments SL1 and LOK, while SL2 and SL1 had significantly more than LOK (Fig. 2-3a). Shannon-Wiener functions (Table 2-1) differed significantly between forests (F=49.47, P<0.0001), with the Lokaro forest having significantly lower values than the others.

In the 10x10 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 2-2). 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 (Fig. 2-1b). 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 (Fig. 2-2b). 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 (Fig. 2-3b). Shannon-Wiener values (Table 2-2) differed significantly among fragments (F=244.15, P<0.0001), again with the LOK fragment having 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 50x50m plots and understory woody vegetation in the 10x10 m plots (Fig. 2-4a & b). More than two-thirds of tree species (68.0%, 69.3%, and 73.9% respectively) and understory species (65.6% and 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 (Fig. 2-4a-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 2-3). The majority of trees (50-60%) had a DBH between 10-15 cm, and the distribution for all forests dramatically dropped off to a long right-tail (Fig. 2-5). 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), *Dypsis saintelucei* (Arecaceae), *Elaeodendron alluaudianum* (Celastraceae), *Faucherea aff. tampoloensis* and *Mimusops commersonii* (both

Sapotaceae), *Leptolaena delphinensis* and *Sarcolaena multiflora* (both Sarcolaenaceae), *Magnistipula tamenaka* (Chrysobalanaceae), *Pourpartia chapelieri* (Anacardiaceae), *Symphonia fasculata* (Clusiaceae), *Tambourissa purpurea* (Monimiaceae), *Uapaca louvelii* (Euphorbiaceae). Basal area calculated for trees (DBH>10 cm) in 10x10 m plots appears to underestimate the basal area compared to that extrapolated from the 50x50 m plots (Table 2-3).

Figure 2-6a and b, shows the species-area curve separately for the two sampling methods utilized here. It appears that even after five ha (i.e., 20 plots @ 0.25 ha a plot), the species-area curve for trees still has not reached an asymptote (Fig. 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 (Fig. 2-6b). 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 2-4). The three values giving tree species similarity in 50x50 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 10x10 m sampling, limiting the number of combinations, the same pattern appeared

(Table 2-4). 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 *Tambourissa purpurea* (Monimiaceae), accounting for 45.7% of all individuals sampled in 50x50 m plots and 46.4% in 10x10 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 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 five trees per 0.25 ha or greater in at least one fragment, and seven at an abundance of ten trees per 0.25 ha or greater (Table 2-5). 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 2-6).

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 *Tambourissa purpurea* - *Ravenala madagascariensis* - *Myrica spathulata* forest; whereas the Sainte Luce fragments are all dominated by *Asteropeia micraster* -

Intsia bijuga - Leptolaena delphinensis - Pandanus concretus.

Family patterns

Species-level differences were also reflected in family-level patterns. A total of 17 families was represented by either a tree or understory species in only a single forest fragment, with LOK and SL3 having the most unshared families (Table 2-7).

The ten families having greatest mean Family Importance Values (FIVs) in 50x50 m plots from each forest fragment are shown in Table 2-8. The top ten 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% of individuals. Similarly, the top ten 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 ten Sainte Luce families represented about two-thirds of individuals (71.1%, 67.7%, and 62.2%, respectively).

The ten families in 10x10 m plots with the highest mean FIVs are shown in Table 2-9. The top ten in LOK accounted for 38.1% of all understory species 91.6% of all individuals. Again (and similar to LOK), the top ten families in SL1 and SL3 accounted for 42.0 and 34.3% of understory species, respectively. Unlike LOK, the top ten 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 50x50 m plots and understory woody vegetation in 10x10 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 50x50 m plots would have sufficed, and about 50% fewer 10x10 m samples (see Heck et al. 1975). However it should be noted that at larger spatial scales information used in analyses would be missing, since species-area curves didn't level-off. Recent results from a rainforest community in Brazil (Ferreira and Prance 1998) showed that even a sampling area of one hectare (n=4) was inadequate to capture local species richness. Likewise, Rakotomalaza and Messmer (1999) studying the forests of Madagascar's Andohahela Reserve, located 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 one hectare plots.

Comparisons with other tropical forests reveal some important similarities with respect to community structure (Table 10). One hectare plots generally have between 500-800 trees, around a hundred tree species, and a total basal area between 30-40 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 appears 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 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 Cadotte 2000).

The general consensus from descriptive tropical studies such as this 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 50x50 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 10x10 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 five out of the nine most abundant taxa, to species level, in a montane plot. An even more dramatic example: on a recent expedition to Madagascar, J. Dransfield and H. Beentje, experts on Palms (Arecaceae) discovered three new genera and 85 new species of palm in eastern Madagascar (Prance et al. 2000).

Community patterns among fragments

There were significant differences among the four forest fragments in this study in terms of Shannon-Weiner index of diversity, numbers 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 and Lovett-Doust 2001a). 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 *Tambourissa 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 Gross et al. 2000). Torti et al. (2001) showed that monodominance in tropical forests, is not easily attributable to any one 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; Neider 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 two-to-four 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 one hectare for the understory species in 10X10 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 Fig. 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 seventeen 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 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 c. 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).

Table 2-1: Richness and abundance parameters (±SD) for five plots (50x50 m) in four coastal forest fragments. LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3.

	LOK	SL1	SL2	SL3	Total
All trees and shrubs					
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 trees per plot	129.0 (33.7)	169.1 (25.4)	204.0 (46.9)	193.2 (44.0)	----
Mean species per plot	10.6 (2.9)	36.4 (5.5)	46.4 (8.5)	47.4 (10.7)	----
Mean 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)	

Table 2-2: Richness and abundance parameters (±SD) in 10x10 m plots along 100 m long transects in three coastal forest fragments. LOK=Lokaro forest; SL1, and SL3=Sainte Luce forests 1, and 3.

	LOK	SL1	SL3	Total
No. of individuals	1336	3997	5367	10700
No. of species	42	131	145	203
No. of families	23	47	50	55
Mean trees per plot	66.1 (36.0)	199.2 (93.93)	267.6 (55.9)	—
Mean species per plot	7.1 (2.4)	34.6 (9.0)	48.8 (5.9)	—
Mean 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	10282
No. of species	42	119	140	195
No. of families	23	45	47	54
Mean trees per plot	62.1 (37.3)	192.6 (94.2)	259.4 (55.6)	—
Mean species per plot	6.3 (2.4)	32.7 (8.8)	46.8 (6.4)	—
Mean 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)	—

Table 2-3: Mean diameter at breast height (DBH) and basal area (BA) from 50x50 m and 10x10 m plots in the four forest fragments. LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3.

	Forest	DBH (cm)				
		Maximum	Mean	SD	BA m^2/ha	
50x50 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	
10x10 m plots					BA >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

Table 2-4: Results of t-tests comparing mean Jaccard's coefficient of similarity between forest fragments. Mean coefficient (±SD) is shown (it was calculated for all combinations of plots between two fragments). There were five 50x50 m plots in each fragment, giving 25 (5 x 5) possible comparisons between any two fragments. There were 20 10x10 m plots in each of three fragments, giving 400 (20 x 20) possible comparisons between two fragments.

50x50 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)	***	***	***	**	*

10x10 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

Table 2-5: Species exceeding 5 (+) and 10 (++) trees per 0.25 ha in four forest fragments. LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3, respectively.

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)		+	+	
Homalium involucratum (DC) O. Hoffm. (Flacourtiaceae)				+
Homalium 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)		++	++	+

Table 2-6: Species with DBH < 10 cm, exceeding 100 (+) and 200 (++) stems per 0.25 ha in three forest fragments. LOK=Lokaro forest; SL1 and SL3 = Sainte Luce forests 1 and 3, respectively.

Species	LOK	SL1	SL3
Dracaena elliptica Thunb. & Dallm. (Agavaceae)		+	+
Dracaena reflexa var. *angustifolia* Baker (Agavaceae)			+
Dracaena reflexa var. *subelliptica* H. Perrier (Agavaceae)		+	
Cabucala madagascariensis (DC.) Markgraf (Apocynaceae)			+
Plectonia densiflora Baker (Rubiaceae)	+		+
Polscias 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)	+	+

Table 2-7: The 17 families found only in a single forest fragment. LOK=Lokaro forest; SL2 and SL3=Sainte Luce forests 2 and 3.

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

Table 2-8: The ten families with the highest mean Family Importance Value (FIV) for trees with DBH > 10 cm, in four forest fragments from 50x50 m plots. LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3.

LOK		**SL1**	
Family	FIV	Family	FIV
Monimiaceae	87.91	Sarcolaenaceae	35.61
Strelitziaceae	29.57	Flacourtiaceae	31.3
Flacourtiaceae	29.38	Fabaceae	25
Myricaceae	26.49	Ebenaceae	22.78
Loganiaceae	19.85	Myrtaceae	17.7
Moraceae	19.59	Lauraceae	14.23
Combretaceae	11.91	Euphorbiaceae	13.95
Casuarinaceae	11.8	Pandanaceae	13.92
Sapotaceae	9.81	Celastraceae	13.47
Tiliaceae	8.52	Oleaceae	11.89
Total	254.83	Total	199.85
Remainder (11)	49.32	Remainder (25)	85.07

SL2		**SL3**	
Family	FIV	Family	FIV
Theaceae	28.27	Sarcolaenaceae	32.26
Sarcolaenaceae	27.99	Fabaceae	27.66
Fabaceae	24.74	Myrtaceae	20.67
Flacourtiaceae	21.93	Flacourtiaceae	17.71
Myrtaceae	17.35	Euphorbiaceae	16.71

Ebenaceae	17.05	Sapotaceae	15.35
Euphorbiaceae	16.58	Ebenaceae	15.02
Anacardiaceae	15.31	Anacardiaceae	12.51
Lauraceae	11.27	Pandanaceae	11.89
Pandanaceae	11.23	Celastraceae	9.6
Total	191.72	Total	179.38
Remainder (33)	103.28	Remainder (35)	124.53

Table 2-9: The ten families with the highest mean Family Importance Value (FIV) for woody plants < 10 cm DBH in three forest fragments from 10x10 m plots. LOK=Lokaro forest; SL1, and SL3=Sainte Luce forests 1, 2, and 3.

LOK		**SL1**	
Family	FIV	Family	FIV
Monimiaceae	140.53	Rubiaceae	47.92
Bignoniaceae	41.28	Flacourtiaceae	32.93
Apocynaceae	18.39	Euphorbiaceae	26.98
Agavaceae	14.73	Agavaceae	20.51
Rubiaceae	10.01	Cunoniaceae	11.66
Sapotaceae	8.2	Sarcolaenaceae	11.34
Hernandiaceae	7.36	Celastraceae	10.21
Rutaceae	6.47	Sapotaceae	9.84
Myricaceae	5.41	Apocynaceae	9.76
Combretaceae	4.13	Bignoniaceae	8.57
Total	256.4	Total	189.72
Remainder (12)	22.04	Remainder (36)	110.09

SL3

Family	FIV
Rubiaceae	38.78
Flacourtiaceae	21.18
Agavaceae	18.41
Euphorbiaceae	18.31
Ebenaceae	16.78

Arecaceae	13.8
Araliaceae	12.38
Fabaceae	11.47
Oleaceae	10.4
Ochnaceae	10.1
Total	171.61
Remainder (38)	118.73

Table 2-10: Comparison of tree species diversity, density, and size from different tropical forests. All values are sampled from or calculated to 1 ha.

	SE Madagascar[¶]	Sainte-Luce Madagascar[a]	Androhahela Madagascar[b]	Guyana[c]	Costa Rica[d]	Amazon[e]
No. species	86.3	111-116	121-146	50-71	100-149	137-168
No. families	41.9	43-44	31-34	23-26	41-55	34-43
No. 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

[¶] These values from the present study are extrapolated to 1 ha samples by randomly sampling four 0.25 ha (50x50 m) plots 10 times.

[a] Rabevohitra et al. (1998); [b] Rakotomalaza and Messmer (1999): only samples taken below 1000 m; [c] Johnston and Gillman (1995); [d] Lieberman et al. (1996): only samples taken below 1000 m; [e] Ferreira and Prance (1998)

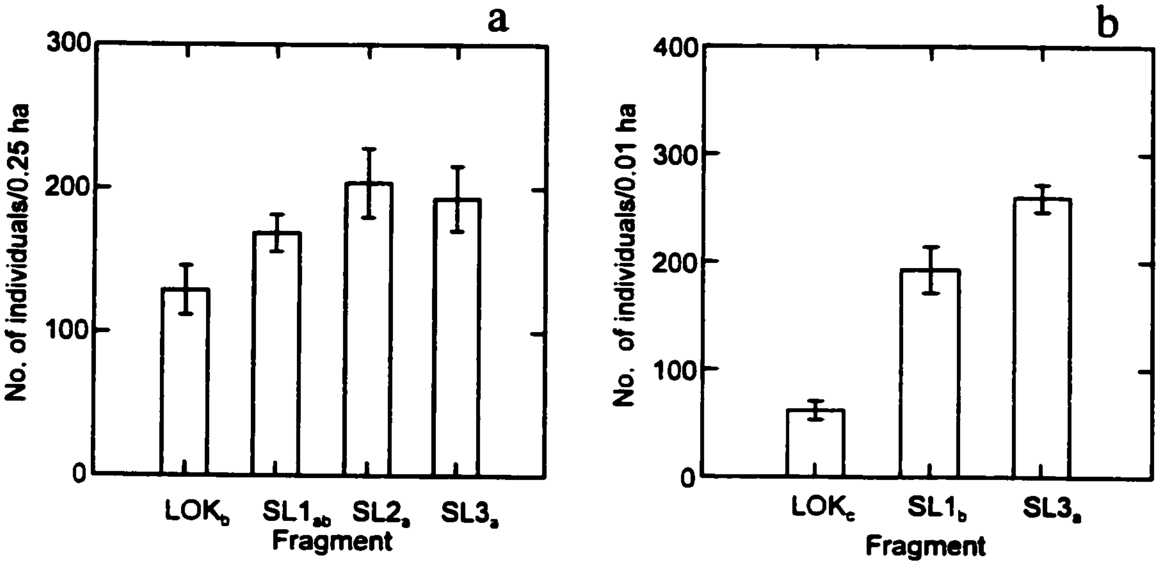

Figure 2-1: The mean number of individuals: a) per 50x50 m plot; and b) per 10x10m plot. Subscripts show results of least significant difference post hoc analysis. (No significant difference between bars having the same subscript.) LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3, respectively.

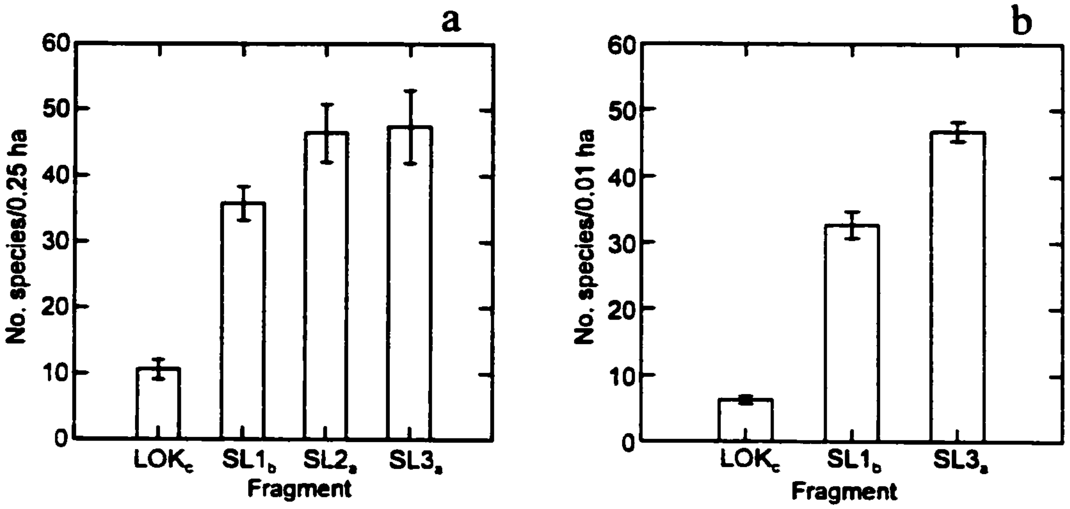

Figure 2-2: The mean number of species: a) per 50x50 m plot; and b) per 10x10m plot. Subscripts show results of least significant difference post hoc analysis. (No significant difference between bars having the same subscript.) LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3, respectively.

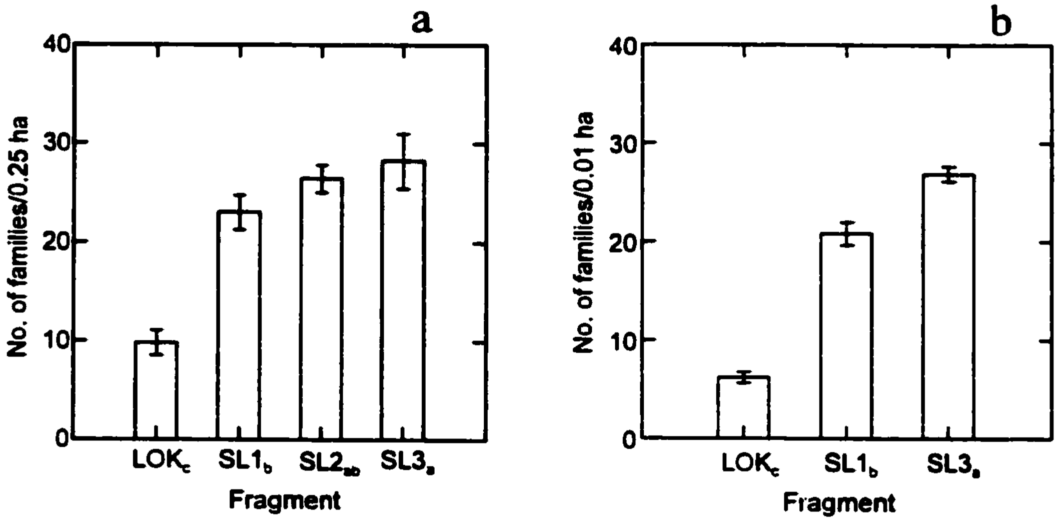

Figure 2-3: The mean number of families: a) per 50x50 m plot; and b) per 10x10m plot. Subscripts show results of least significant difference post hoc analysis. (No significant difference between bars having the same subscript.) LOK=Lokaro forest; SL1, SL2, and SL3=Sainte Luce forests 1, 2, and 3, respectively.

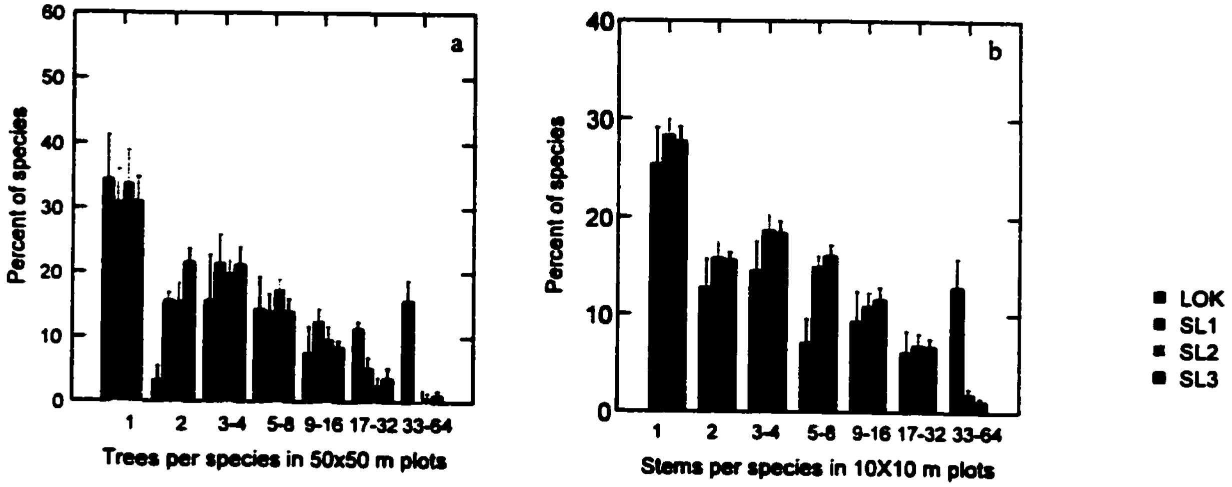

Figure 2-4: Log distribution of trees per species per plot in four forest fragments. LOK=Lokaro forest; SL1, SL2, and 3=Sainte Luce forests 1, 2, and 3, respectively.

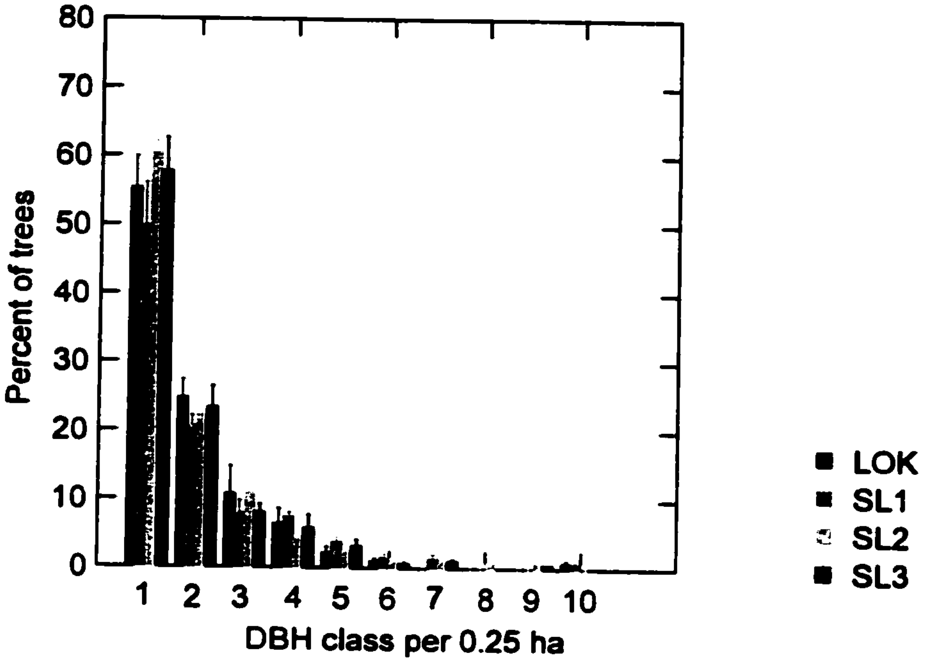

Figure 2-5: Distribution of tree DBH in four forest fragments. DBH classes are in increments of 5 cm, 1= 10-15 cm, 2= 15.1-20 cm, and so on, class 10 is DBH>55cm. LOK=Lokaro forest; SL1, SL2, and 3=Sainte Luce forests 1, 2, and 3, respectively.

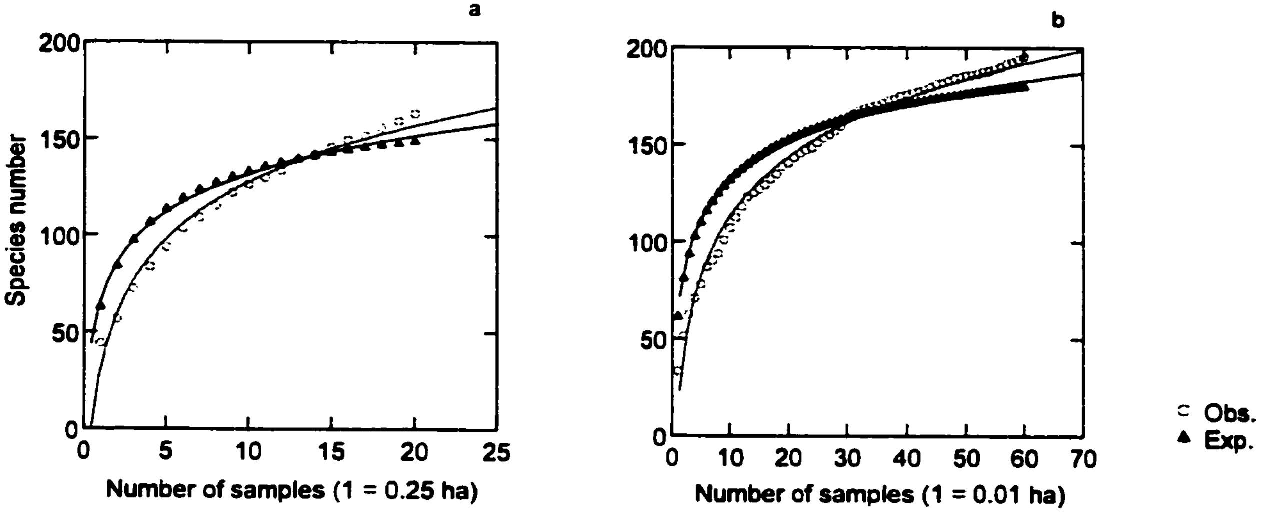

Figure 2-6: Rarefaction (expected) and species accumulation (observed) curves for a) trees in 50x50 m plots, and b) understory woody vegetation measured in 10x10 m plots. Binomial (sign) test for paired data showed no significant difference between observed and expected curves (P>0.05).

CHAPTER III:

HABITAT FRAGMENTATION AND ANTHROPOGENIC PRESSURE ALTERS DIVERSITY, ABUNDANCE, AND DEMOGRAPHICS OF A TROPICAL FOREST COMMUNITY

ABSTRACT

In the coastal forest of extreme southeastern Madagascar, we examined the effects of fragmentation and landscape-level features on trees ($DBH \geq 10$ cm) in twenty 50x50 m plots in four forest fragments, and on understory woody vegetation ($DBH < 10$ cm, ≥ 1 m ht) in sixty 10x10 m plots in three of the fragments. Patch- and landscape-level features included in the study were: fragment size, fragment perimeter-area index, internal perimeter created by roads and trails in each fragment, and the number of villages (or population pressure) per hectare of forest in three expanding radii of 5, 7.5, and 10 km.

Fragment area and the perimeter-area index had no significant effect on tree density or richness ($P>0.05$). Conversely, internal fragmentation and population pressure indices were significantly linearly associated with density and richness ($P<0.05$) for both trees and understory vegetation. Species evenness was also lowest in the most degraded forest fragment, probably resulting from competitive release of *Tambourissa purpurea* in degraded plots. Demographic responses to the effects of fragment degradation differed among taxa. Understanding the response of individual taxa to anthropogenically-altered

habitats requires detailed study of population-level responses, and the relationship between life-history features and environmental changes. Finally, degraded tropical forest fragments may have important benefits to the conservation of biodiversity, especially where local human populations rely on a subsistence lifestyle, and these fragments should be included in management planning.

INTRODUCTION

One of the more insidious effects of deforestation has been the fragmentation of formerly contiguous forests. Fragmentation truncates species' ranges and population sizes, increasing the threat of localized extinction (Laurance et al. 1997a), altering allelic diversity and heterozygosity (Ellstrand and Elam 1993, Shapcott 2000), population demography (Somanathan and Borges 2000), and body size of individuals (Klein 1989).

Most studies of fragmentation traditionally have focussed on the size of the forest fragment as the major factor for explaining species diversity patterns (Diamond and May 1976, Wilcove et al. 1986, Klein 1989, Scariot 1999). Area alone may not be able to account adequately for patterns in particular taxa inhabiting a fragmented landscape (Debinski and Holt 2000). In fact, both landscape-level and smaller scale, population-level processes may negate fragment area effects (Robinson et al. 1992, Holt et al. 1995). For example, to date few studies have considered variables external to the fragments themselves, though some attention has been given to effects of surrounding vegetation

(Janzen 1983, 1986, Mesquita et al. 1999), pesticides and fire (Janzen 1986), roads (Goosem 1997), and also the ability of taxa to utilize the inter-patch matrix, where the absolute amount of habitat in a region may be more important than fragmentation *per se* (Gascon et al. 1999, Trzcinski et al. 1999).

More than half of all tropical forests have already been lost and a further 1-2% get cleared or degraded each year (Ehrlich and Wilson 1991, Whitmore 1997, Laurance 1999). The fact is that the forces that create fragmented landscapes, namely human activity, seldom cease after the initial fragmenting events. In tropical nations where many people rely on direct resource utilization, activities such as slash and burn agriculture, fuel wood collecting, and hunting are major forces of habitat destruction and degradation (Gadgil 1995, Myers 1995, Terborgh and van Schaik 1997). These activities are of an even greater consequence as the amount of natural area decreases and the remaining areas of intact forests become more valuable to people who depend on them. Nowhere is the dichotomy of human need vs biological diversity more prevalent than in Madagascar. That ancient large island not only houses extensive unique biodiversity, especially the large number of endemics (*c.* 80% of all taxa in Madagascar [Myers et al. 2000]), but Madagascar is undergoing a massive population explosion (Cincotta et al. 2000).

In a previous study, Cadotte et al. (2001) characterized the high level of diversity and community heterogeneity in forest fragments along the southeastern coast of Madagascar. Significant differences were observed in the numbers of individuals, species, and families of trees and shrubs among these fragments. The purpose of the present study was 1) to determine how landscape-level features relate to the species abundance and diversity patterns among forest fragments; and 2) to determine if these landscape-level effects change the demographic patterns of regionally common taxa.

METHODS

Study area

The four littoral forest fragments used in this study were located along the southeastern coast of Madagascar (Fig. 3-1). These forests grow in the humid sublevel of the Eastern Domain, on sand substrata (Dumetz 1999). The forests in this region are highly fragmented, but also hold a tremendous array of habitat diversity (Goodman 1999).

Within each forest fragment, twenty randomly placed 50x50 m plots (see Fig. 3-2) were completely censussed for all trees with a diameter at breast height (DBH) >10 cm. First corner of a plot was selected to approximate a randomly pre-selected direction and the 50 m sides were measured accordingly, and marked at 5 m intervals with flagging tape. Enumeration and marking of all trees with DBH >10 cm was done systematically. In each forest fragment, samples of vegetative structures and, if available, reproductive structures fo each species were collected and tentatively identified, pressed and later deposited at Parc Botanique et Zoologique de Tsimbazaza, Madagascar for final identification and verification.

In a second sampling procedure, sixty 10x10 m plots in three of the forest fragments were completely censussed for all woody vegetation taller than 1 m. The plots were positioned along 100 m transects (see Fig. 3-2 for 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.

Indices - Species richness

The Shannon-Wiener index of diversity (Barbour et al. 1999) was used to characterize species richness and abundances. This was calculated as:

$$H' = -\sum (\rho_i)(\log \rho)$$

where s is the total number of species and ρ_i is the proportion of all individuals in a sample belonging to the i^{th} species. Species evenness index (Pielou 1966) was used to determine whether equitability, or relative dominance differences were present between the forests. Evenness was determined by:

$$J = H'/H'_{max}$$

where H'_{max} is the total number of species in a plot, log transformed.

Geographical variables

Since the forest fragments being investigated here were relatively small in size (122-457 ha), any with an irregularly-shaped perimeter might be more susceptible to adverse edge effects (Wilcove et al. 1986). A simple index, **PA** = perimeter (m)/patch area (ha), was used to get a relative measure of shape irregularity for the four forest fragments (Fig. 3-2).

The forest fragments were not islands of continuous forest, rather they had been subjected to varying degrees of internal fragmentation due to roads and large trails. The lengths and widths of all roads and canopy-breaking trails penetrating the four forest fragments were measured (Table 3-1, Fig. 3-2). Lengths were added to the total perimeter of each site, and the area occupied by these roads and trails was subtracted from the total patch area (see Table 3-1). An index of internal fragmentation:

$$\text{IPA} = \frac{\text{internal perimeter (m)}}{\text{patch area (ha)}}$$

was used to compare relative values between forests. Similarly, an index of total perimeter-to-area:

$$\text{TPA} = \frac{\text{internal + external perimeter (m)}}{\text{patch area (ha)}}$$

was used to compare cumulative effects of internal fragmentation and shape irregularity.

To measure effects of human population pressure exerted on the forest fragments, the following landscape-level index was used:

$$\text{Population pressure} = \frac{\text{the number of villages}}{\text{forested area (ha)}}$$

which was measured in three expanding contour gradients, of radii 5, 7.5, and 10 km from centre of forest fragment of interest. These radii represent probable distances rural Malagasy people would travel on foot to collect resources in the form of forest products (see Shyamsundar and Kramer 1997). If more precise human demographic data were available, then we could have standardized the index of population pressure by actual population size, but such data were not available. However, of the approximately 30 villages in the vicinity of the four forest fragments, many are quite small, averaging a few hundred people per village (MWC, personal observations). Values for population pressure were log transformed for analysis, as individual values for forest fragments were highly variable, and in some cases different by an order of magnitude.

Data analysis

The effects within the 50x50 m plots of the categorical factor (fragment size class) on species and individual numbers were analysed using one-way ANOVA. Since fewer fragments were censussed using 10x10 m samples, we used a two sample t-test when testing area effects on number of species and individuals per plot. The two distributions of species number per 10x10 m plot had unequal variances ($F = 5.53$, $P<0.05$), therefore t'_{crit} incorporating a correction factor was used (see Sokal and Rohlf 1981).

The other variables were analysed using linear regression. Multiple regressions were problematic because of non-independence of several of the habitat variables, especially those that are divided by area of fragment. A multiple regression was used *ex post facto* when the fragment- and landscape-level variables that appeared to account for most of the variation in species, individuals, and diversity were identified. ANOVA's, t-tests and regressions were performed using SYSTAT 9 (SPSS 1999).

Ordination of species occupancy in the twenty 50x50 m, and sixty 10x10 m plots was done using detrended correspondence analysis (DECORANA) (Hill 1979), which gives readily interpretable results, and produces species and sample ordinations simultaneously (Hill and Gauch 1980). The program we used was *Community Analysis Package* (CAP) version 1.2 (Pisces Conservation LTD, Lymington, UK) which uses the original version of DECORANA developed by Hill (1979), and includes corrections (Oksanen and Minchin 1997).

Plant demography

Five taxa, *Dracaena* spp., *Tambourissa purpurea*, *Plectronia densiflora*, *Pyrostria media*, *Cremocarpon lantzii*, were relatively abundant enough in at least two fragments, to test hypotheses concerning demography. *Dracaena* spp. actually includes four taxa (*D. cernua*, *D. elliptica*, *D. reflexa* var. *angustifolia*, and *D. reflexa* var. *subelliptica*), which were morphologically very similar (MWC, personal observations). Understory vegetation in 10x10 m plots was used because these species reached greater densities and had less heterogeneous distributions than canopy trees in 50x50 m plots (Cadotte et al. 2001). For each of the five taxa, all individuals were pooled together and placed into size classes, depending on their overall size distributions. The proportion of individuals in each size class of the overall distribution for each taxon was used to produce an expected value for each size class in each of the forest fragments. The expected value and observed number of individuals in each size class were compared using a Chi-square test. We tested the following hypothesis: the distribution among size-classes in each fragment for a taxon was not different compared to its size-class distribution across all fragments.

RESULTS

The Lokaro forest fragment (LOK) had the most roads and canopy-breaking trails (n = 5) compared to the other forests (Table 3-1), and these trails were concentrated toward the south and east of the fragment (Fig. 3-2), mainly due to the presence of an impassible *Ravenala*-dominated swamp along the western edge. Sainte Luce Forest 1 (SL1) had the largest area occupied by roads and trails, 1.21 ha (Table 3-1). SL3 had the highest number of species, 47.4 species/0.25 ha and 46.8 understory species/0.01 ha, while SL2 had the highest density of trees (204.0 trees/0.25 ha), and SL3 had the highest density of understory vegetation (259.4 stems/0.01 ha) (Table 3-2).

Not taking roads and canopy breaking trails into account, SL3 had the highest perimeter-area ratio (PA), 54.41 (Table 3-2), mainly due to its highly irregular edge (Fig. 3-2). Once roads and trails were taken into account, LOK had the highest index of internal fragmentation, IPA, and total perimeter-area ratio, TPA (Table 3-3).

At all three spatial scales (5, 7.5, and 10 km radii), LOK had highest values for Index of Population Pressure (Table 3-4).

Analysis of landscape variables

One-way ANOVA results show that patch area had no significant effect ($P>0.05$) on the number of trees/ 0.25 ha (Fig. 3-3a), or the number of species/0.25 ha (Fig. 3-3c). In fact, even if the results were significant in a statistical sense, it is obvious that the results would be counter-intuitive, as the 50x50 m plots from the mid-sized fragment (SL2 - 206 ha) would be the most diverse. Similarly, results from two-sample t-tests show that patch area had no significant effect on the number of understory stems/0.01 ha (Fig. 3-3b), or the number of understory species/0.01 ha (Fig. 3-3c).

Linear regressions were used to analyse the rest of the spatial variables. Perimeter-area ratio had a non-significant effect ($P>0.05$) on the number of trees/ 0.25 ha, species/0.25 ha, and Shannon-Weiner index of diversity (H') (Table 3-5). However, the index of internal fragmentation (IPA) and the number of villages per hectare of forest at a radius of 5 and 7.5 km were highly significant ($P<0.01$) (Table 3-5). The total perimeter-area ratio had a significant effect ($P<0.05$) on all values, and the number of villages per hectare of forest at a radius of 10 km had a significant effect ($P<0.05$) on all values except the number of trees/0.25 ha (Table 3-5).

Since R, PA, IPA, and TPA were not independent of one another, and because the number of villages per hectare of forest at the three radii were also obviously not independent, multiple regression analysis could not be used on all variables. Instead, the geographic variable that appears to explain the most variation from each of these two classes of parameter (i.e., patch-level and landscape-level factors) was used in a multiple regression analysis (Table 3-5). IPA and the number of villages per hectare of forest in a radius of 7.5 km had a highly significant effect ($P<0.001$) on the number of species/0.25 ha, and on H', the index if diversity, and had a significant effect ($P<0.05$) on the number of trees/0.25 ha (Table 3-5). In a multiple regression, these two variables combined explained most of the variation for number of species/0.25 ha and H' (80.7 and 88.5%, respectively) in 50x50 m plots. Similarly, for understory vegetation, IPA had a highly significant effect ($P<0.001$) on stems/0.01 ha, species/0.01 ha, and H' (Table 3-5). The number of villages per hectare of forest in a radius of 5 km appeared to explain most of the variation, compared to the other two landscape variables.

Mean species evenness index from 50x50 m plots (Fig. 3-4a) was significantly different ($F = 49.45$, $P<0.001$) between the fragments, with LOK being significantly lower ($P<0.05$) than the other three forest fragments, based upon LSD post hoc test. Evenness for understory taxa in 10x10 m plots (Fig. 3-4b) was also significantly different ($F = 244.15$, $P<0.001$), with LOK again having the lowest evenness ($P<0.05$).

Ordination

The ordination of 169 different taxa in 20 plots illustrates the grouping of plots by forest (Fig. 3-5). LOK, SL1, and SL2 form discrete clusters, while SL3 ranges widely along axis 2 and very little along axis 1. All plots that belong to LOK, the forest with the greatest index of internal fragmentation and most number of villages per hectare of forest are grouped distinctly along axis 1. Species ordination also produced discrete groups (see Fig. 3-6). Species that are only found in LOK, *Ampalis mauritiana*, *Dracaena xiphophylla*, *Casuarina equisitifolia*, *Ficus lutea*, *Grewia humblotii*, *Hernandia nymphaeifolia*, *Mimusops commersonii*, *Myrica spathulata*, *Phyllanthus erythroxyloides*, *Rapanea erythroxyloides*, *Scolopia* sp. 1, *Strychnos diplotricha*, and *Terminalia cattapa*; plus species that are rare elsewhere, but relatively more common in LOK, *Brexia madagascariensis*, *Homalium aff. nudiflorum*, *H. louvelianum*, *Ravenala madagascariensis*, *Syzygium* sp. 2, *Tambourissa purpurea*, and *Vernonia* sp. 1, are all concentrated in two groups along the 2nd axis (Fig. 3-6).

The ordination of 60 plots is shown in Figure 3-7. LOK forms a discrete group along axis 1. SL1 and SL3 almost completely overlap, with little variation along axis 2. However, there appears to be a right-tail of SL1 and SL3 plots along axis 1. Of these eight plots, all but one occurred within 25 m of the edge of the fragment.

Plant demography

We examined the size-class distributions of five relatively common taxa among the different forest fragments (Figs 3-8 and 3-9). *Dracaena* spp. in SL3 were significantly under-represented ($P<0.05$) by stems in the smallest diameter-class (0-9 mm), while being significantly over-represented ($P<0.05$) by medium-sized stems (20-39 mm) (Fig. 3-8). Small diameter-class *Dracaena* stems appeared to be over-represented in LOK and SL1. *Tanbourissa purpurea* in SL1 and SL3 appeared relatively over-represented by small size-class stems (0-9 mm), while being under-represented by large stems (>100 mm) (Fig. 3-8). *Plectronia densiflora* and *Pyrostria media* in SL3 appeared to be over-represented by those in the smallest size-class, while *P. densiflora* in LOK was significantly under-represented ($P<0.05$) by small stems and *P. media* tended towards being under-represented by small stems (Fig. 3-9). The difference in size-class distribution for *Cremocarpon lantzii* was in medium-sized stems (16-20 mm), where they were significantly under-represented ($P<0.05$) in SL3 (Fig. 3-9).

DISCUSSION

Species abundance and diversity has a convoluted relationship with fragment size, to say the least. In a recent review paper (Debinski and Holt 2000), 10 out of 19 taxonomic groups from eight different study regions of the world did not show change in diversity with fragment size, and only eight out of 18 studies showed abundance or density increases with increasing fragment area. In the present study, differences in density and diversity in 50x50 m and 10x10 m plots could not be explained by fragment size. The lack of a significant relationship between fragment area and community composition has been revealed in a number of studies from different ecosystems: plants in Renosterveld shrublands, South Africa (Kemper et al. 1999); plants in an old field, Kansas (Robinson et al. 1992); butterflies in Amazonian forest fragments (Brown and Hutchings 1997); and understory birds in Amazonian fragments (Bierregaard and Stouffer 1997).

In a recent paper, Cadotte et al. (2001) reported significant differences in abundance and diversity among the fragments used in the present study. The forest fragments Sainte-Luce 2 and 3 were significantly over-represented by stems per unit area, species per unit area, and by greater taxonomic diversity (at the family level). These differences now appear to be the result of patch-level and landscape-level features.

Community-level responses, or the apparent lack thereof, may be better understood in terms of constituent population-level processes (Holt et al. 1995). The dynamics of individual species or populations may reveal more about the diverse effects of fragmentation, than purely community demographic studies. For example, and probably counter-intuitively, abundant and widespread species may be more adversely affected by fragmentation than rare and restricted species (Tilman et al. 1994). Common and widespread trees pollinated by generalist species vectors may suffer lower reproductive rates compared to rare, pollinator-specific trees in which flying pollinators may travel long distances between conspecifics (Nason and Hamrick 1997).

In the present study we found that there are significant demographic differences in just a small sample of species. Results from Cadotte et al. (2001), specifically involving richness and density values, show that the Lokaro forest fragment is the most degraded fragment, followed by Sainte-Luce 1, and then SL2 and SL3 as co-equals. In light of this, demographic differences appear discernable. *Dracaena* spp. and *Cremocarpon lantzii* appear to have high levels of recruitment in moderately-disturbed sites, where they also have the highest densities. *Tambourissa purpurea,* which is primarily a small-sized understory species in relatively undisturbed sites, becomes more abundant at large size-classes in very disturbed forests, where it obtains extremely high densities. In the Lokaro forest fragment *T. purpurea* becomes a monodominant, distinctly characterizing that fragment (Cadotte et al. 2001). Essentially, different taxa respond in different ways to the altered habitats, which makes a lot of intuitive sense. Very few species thrive in heavily disturbed forests, some do in moderately disturbed forest, and many do in undisturbed fragments. The lack of a heavy disturbance does not appear to exclude many taxa, though some are obviously absent (Cadotte et al. 2001), while disturbed fragments are conspicuously missing a large number of taxa. In a pair of papers, Cunningham (2000a, b) showed that an individual taxon's reproductive success responded uniquely to fragmentation, with plant species either increasing or decreasing in reproductive success as a result of fragmentation.

Studying the detailed life-history characteristics of individual taxa could help managers plan a regional conservation strategy, where resource-based, multi-use fragments can be utilized at a level where disturbance-resistant species could thrive. Degraded tropical forest fragments have important benefits to the conservation of biodiversity (Turner and Corlett 1996), and should be included in management planning.

Human impact

More important to species diversity than fragment size, appear to be meso- and macro-scale landscape variables, namely the amount of internal fragmentation (roads and canopy-breaking trails) proportional to the area of a fragment, and the number of villages per hectare of forest (within radii of <10 km, centred on a forest fragment). These two measures together explained >80% of the variation in the number of species per 0.25 ha, and >88% for the index of diversity per 0.25 ha. These two measures also accounted for >87% of the variation in the number of understory species per 0.01 ha and >89% for the index of diversity per 0.01 ha. Disturbance in tropical forests generally causes a decline in species diversity (e.g., Rao et al. 1990), by increasing the probability of extinction for individual populations (Foster 1978). The "intermediate disturbance" hypothesis (Grime 1973, Connell 1978), which contends that some disturbance may increase species diversity in some communities, does not appear to be the case in tropical forests (Rao et al. 1990), though a limited number of individual taxa may exhibit a positive response to disturbance (see previous section). However the present study may not be considering large enough spatial and temporal scales for a valid test of this hypothesis (see Foster 1978 for a review of the scales at which disturbances occur in tropical forests).

For trees sampled in 50x50 m plots, with a bias towards the interior of the fragments, there appears to be no continuity between the highly degraded Lokaro forest fragment, and the three Sainte-Luce fragments (Fig. 3-5). Is there no continuity in community structure between these two extremes? Results of the ordination plot for understory vegetation in 10x10 m plots (Fig. 3-7), suggest there is clearly continuity between fragments along axis 1. It appears as though the plots in the Lokaro fragment are relatively more similar to the near-edge plots of the Sainte-Luce forests than to the interior plots. If degraded fragments resemble the edges of relatively undegraded fragments, then there may be some predictable changes in community composition as the processes of degradation ensue. There is a burgeoning literature on the effects of 'life on the edge' (e.g., Laurance et al. 1998a, b, Sizer and Tanner 1999, Sumner et al. 1999). Some of the detrimental consequences of edge formation include altered environmental suitabilities, lower population recruitment, higher mortality, and other demographic changes.

As with the other biological measures in this study, species evenness was lowest in the Lokaro forest fragment, and highest in SL3. The loss of biodiversity in this case reduced community evenness, and produced very skewed abundance distributions. The Lokaro forest fragment is essentially a monodominant community (Cadotte et al. 2001). Similar to other hypotheses dealing with ecosystem functioning (see Fukami et al. 2001), a reduced evenness may diminish ecosystem "reliability", or the ability of a system to provide a consistent level of performance over time (Fukami et al. 2001). In another recent study, Wilsey and Potvin (2000) found that total and belowground biomass in experimental plant communities increased with increasing evenness.

The two landscape variables (internal fragmentation and villages per hectare of forest) measure both human activity in fragments and general population pressure. The internal fragmentation corresponds to the degree of human access to forest resources, and number of villages per hectare of forest represents local human population pressure relative to the amount of forest resources. This is an important variable, because as natural areas become increasingly used by humans, their biodiversity value increasingly declines, until there is little biodiversity and resource value remaining (i.e., there is a 'land-use cascade' effect on biodiversity; see Terborgh and van Schaik 1997).

A useful description of the dynamics of localized human resource use and habitat degradation is a negative feedback loop (Fig. 3-10). As the amount of local high-quality natural area is reduced (through agriculture and resource consumption), the value per unit area increases, which is akin to the unit area population pressure also increasing. This increase in human population pressure increasingly degrades habitat size and quality, increasing the value per unit area, and so on. Many rural Malagasy villages rely on subsistence economics. Fifty-four percent of annual household income in a similar Malagasy area is directly derived from subsistence agriculture, and 31% from forest products (Shyamsundar and Kramer 1997). This further highlights the need to include resource-based, as well as pristine protected fragments in national conservation planning strategies.

Other conservation options must be determined and implemented. At present, the only plausible options for conservation in this region involve allowing the continued localized degradation of forests; strict protection, which would exclude local people and their livelihoods; or wholesale deforestation for short-term economic development (see Cadotte 2000). None of these three options would be beneficial for the conservation of biodiversity nor the well-being of the local subsistence human populations. Other conservation and economic incentives must be offered to promote the protection of Madagascar's unique biodiversity — especially those that would see stewardship remain in the hands of local residents (e.g., Janzen 2000). Any use of protective parks must be accompanied by thorough management and enforcement, as well as direct compensation for local communities (Bruner et al. 2001).

CONCLUSION

Many theoretical and empirical studies of fragmentation make the erroneous assumption that patch quality is uniform and equal (Fahrig and Merriam 1994). The present study has shown that human-caused environmental disturbance and degradation can be far more detrimental to forest community composition than is forest fragment size. Conservation strategies need to view altered landscapes in terms of both habitat destruction (fragmentation) and habitat modification (degradation) (McIntyre and Hobbs 1999). Finally, though community patterns can be correlated with habitat degradation, the response of individual taxa to anthropogenically-altered habitats may not be as predictable without detailed study of the relationship between life-history features and environmental responses.

Table 3-1: Length, width, and area of the canopy breaking roads and trails that penetrate the four forest fragments. Numbers in parentheses correspond to locations in Fig. 2. LOK = the Lokaro forest fragment. SL1, 2, 3 = Sainte-Luce forest fragments 1, 2, and 3, respectively.

Forest	Road or trail	Length (m)	Average width (m)	Area of road or trail (m^2)	Total area of roads & trails (ha)
LOK	Main road (1)	394.1	2.12	835.47	
	South trail (2)	216.3	7.08	1531.4	
	Small road (3)	227.5	4.26	969.15	
	North veranda (4)	519	5.33	2466.27	
	South veranda (5)	976.4	5.66	5526.42	1.16
SL1	Main road (1)	550	8.76	4818	
	Trail (2)	2100	3.46	7266	1.21
SL2	None	---	---	---	0
SL3	Road (1)	269	8.1	2178.9	0.22

Table 3-2: Geographic, density, and diversity characteristics of the four forest fragments. For density and diversity indices, values in parentheses represent the standard deviation. PA is the outside perimeter divided by patch area for each fragment; H' is the Shannon-Wiener index of diversity; J is an index of evenness (see methods).

Forest	Area (ha)	Perimeter (m)	PA-ratio m/ha	Stems	Species	H'	J
50x50 m plots							
LOK	122	5784	47.41	129.0 (33.7)	10.6 (2.9)	1.56 (0.24)	0.30 (0.05)
SL1	457	14510	31.75	169.1 (25.4)	36.4 (5.5)	3.14 (0.22)	0.61 (0.04)
SL2	206	7451	36.17	204.0 (46.9)	46.4 (8.5)	3.34 (0.32)	0.65 (0.06)
SL3	191	10392	54.41	193.2 (44.0)	47.4 (10.7)	3.31 (0.30)	0.64 (0.06)
10x10 m plots							
LOK	122	5784	47.41	62.1 (37.3)	6.3 (2.4)	1.13 (0.42)	0.21 (0.08)
SL1	457	14510	31.75	192.6 (94.2)	32.7 (8.8)	2.91 (0.35)	0.55 (0.07)
SL3	191	10392	54.41	259.4 (55.6)	46.8 (6.4)	3.32 (0.18)	0.62 (0.03)

Table 3-3: Geographic characteristics including canopy-breaking roads and trails. IPA = internal perimeter/area; TPA = total perimeter/area.

Forest	Area* (ha)	Internal perimeter (m)	Total perimeter (m)	IPA* (m/ha)	TPA* (m/ha)
LOK	120.8	2333	8118	19.32	67.2
SL1	455.8	2650	17160	5.81	37.65
SL2	206	0	7451	0	36.17
SL3	190.8	269	10661	1.41	55.88

* In each case, area minus the area represented by roads and canopy-breaking trails is used.

Table 3-4: Landscape-level features within 5, 7.5, and 10 km radii from the center of each forest fragment.

	5 km			7.5 km			10 km		
	No. of villages	Forest cover (ha)	Population pressure	No. of villages	Forest cover (ha)	Population pressure	No. of villages	Forest cover (ha)	Population pressure
LOK	7	186	3.76×10^{-2}	8	401	2.00×10^{-2}	16	718	2.23×10^{-2}
SL1	5	933	5.36×10^{-3}	9	1361	6.61×10^{-3}	9	1619	5.56×10^{-3}
SL2	1	1199	8.34×10^{-4}	8	1490	5.37×10^{-3}	14	1576	8.88×10^{-3}
SL3	2	1219	1.64×10^{-3}	9	1458	6.18×10^{-3}	14	1610	8.70×10^{-3}

Table 3-5: Results of linear regressions (for perimeter-area index, PA; internal [roads and canopy-breaking trails] perimeter-area index, IPA; total perimeter (external edge and internal)-area index, TPA; log number of villages per ha of forest, V/ha, in a 5, 7.5, and 10 km radius) for number of trees, species and Shannon Weiner index of diversity (H'). Significant values ($P<0.05$) are in bold. Asterisks represent results of Bonferroni corrections; * $P < 0.05$, ** $P < 0.01$.

	Number of individuals			Species number			H'		
Factor	R^2	F	P	R^2	F	P	R^2	F	P
50x50 m plots (n = 20)									
PA	0.000	0.115	0.738	0.000	0.149	0.704	0.012	1.229	0.282
IPA	**0.366**	**11.986**	**0.003***	**0.816**	**85.263**	**<0.001****	**0.873**	**123.698**	**<0.001****
TPA	**0.145**	**4.230**	**0.054**	**0.338**	**10.695**	**0.004**	**0.520**	**21.597**	**<0.001****
Log V/ha 5	**0.375**	**12.579**	**0.002***	**0.776**	**66.782**	**<0.001****	**0.767**	**63.473**	**<0.001****
Log V/ha 7.5	**0.334**	**10.517**	**0.005**	**0.776**	**66.948**	**<0.001****	**0.891**	**156.361**	**<0.001****
Log V/ha 10	0.144	4.186	0.056	**0.468**	**17.704**	**0.001***	**0.692**	**43.778**	**<0.001****
10x10 m plots (n = 60)									
PA	0.000	0.529	0.470	0.000	0.895	0.348	0.000	0.071	0.791
IPA	**0.600**	**89.612**	**<0.001****	**0.865**	**378.145**	**<0.001****	**0.891**	**481.493**	**<0.001****
TPA	**0.167**	**12.811**	**0.001***	**0.238**	**19.412**	**<0.001****	**0.390**	**38.773**	**<0.001****
Log V/ha 5	**0.605**	**91.509**	**<0.001****	**0.875**	**412.653**	**<0.001****	**0.856**	**353.069**	**<0.001****
Log V/ha 7.5	**0.556**	**74.991**	**<0.001****	**0.799**	**253.074**	**<0.001****	**0.879**	**427.735**	**<0.001****
Log V/ha 10	**0.372**	**35.956**	**<0.001****	**0.531**	**67.810**	**<0.001****	**0.683**	**128.192**	**<0.001****

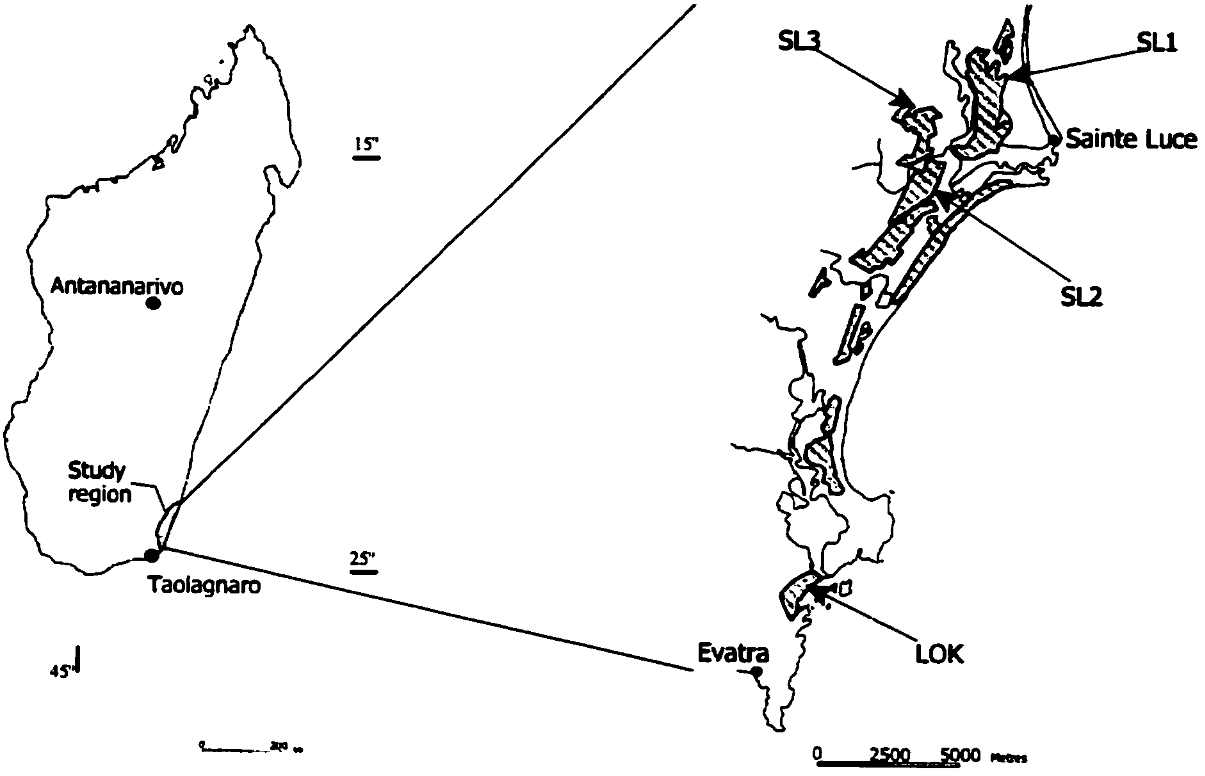

Figure 3-1: Location of the study region in southeastern Madagascar, and of the four forest fragments used in this study.

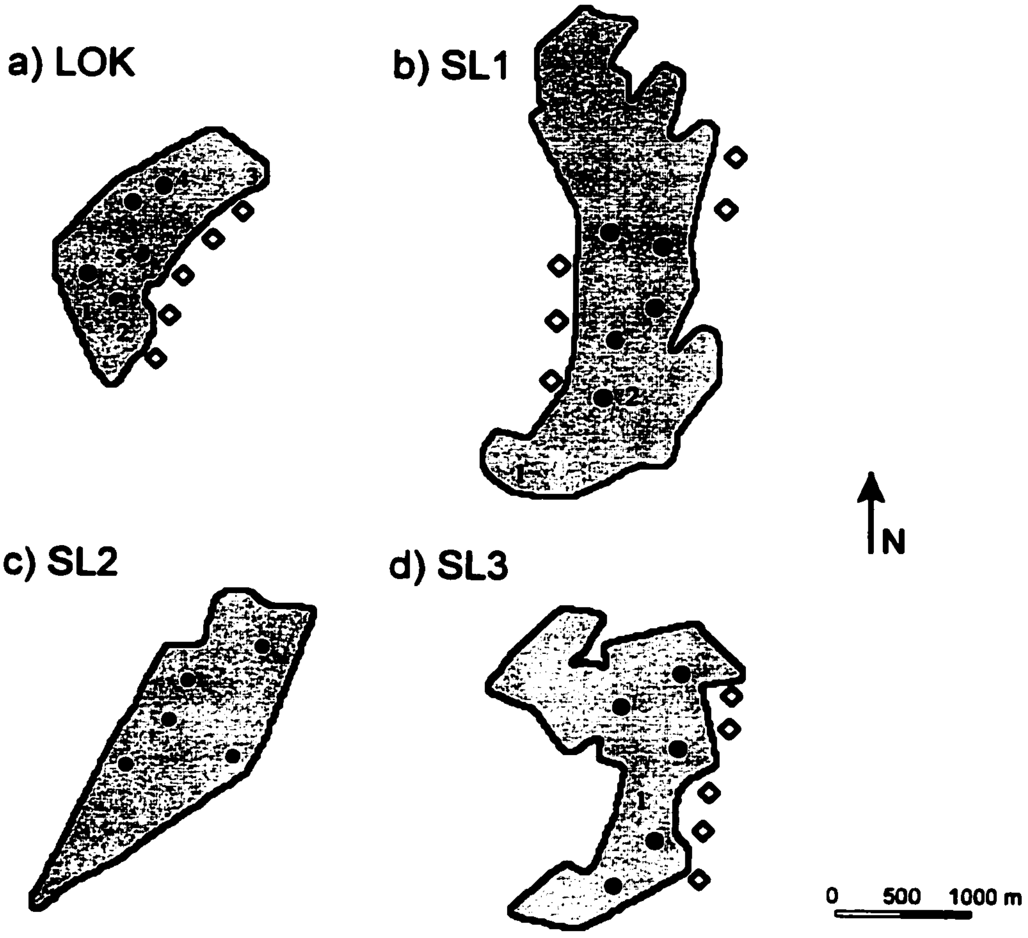

Figure 3-2: Location of 50x50 m plots (●) and the starting point (◇) of 100 m long transects in a) Lokaro forest, b) Sainte Luce forest 1, c) Sainte Luce forest 2, and d) Sainte Luce forest 3. Also shown (white broken lines) are the locations of the canopy-breaking roads and trails in the four forest fragments.

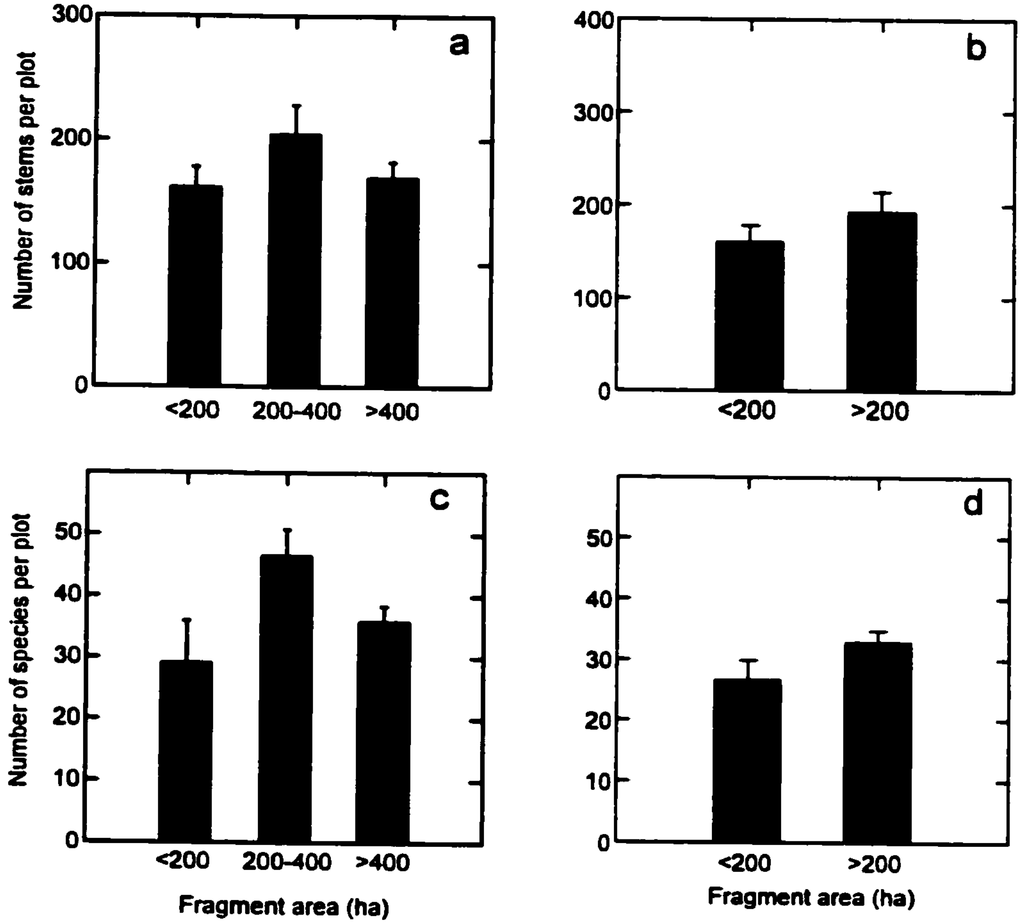

Figure 3-3: Effect of fragment size on the number of trees and species. Shown are (a) the number of trees/0.25 ha; (b) understory stems/0.01 ha; (c) species/0.25 ha; and (d) understory species/0.01 ha . All within-parameter comparisons are nonsignificant (P>0.05).

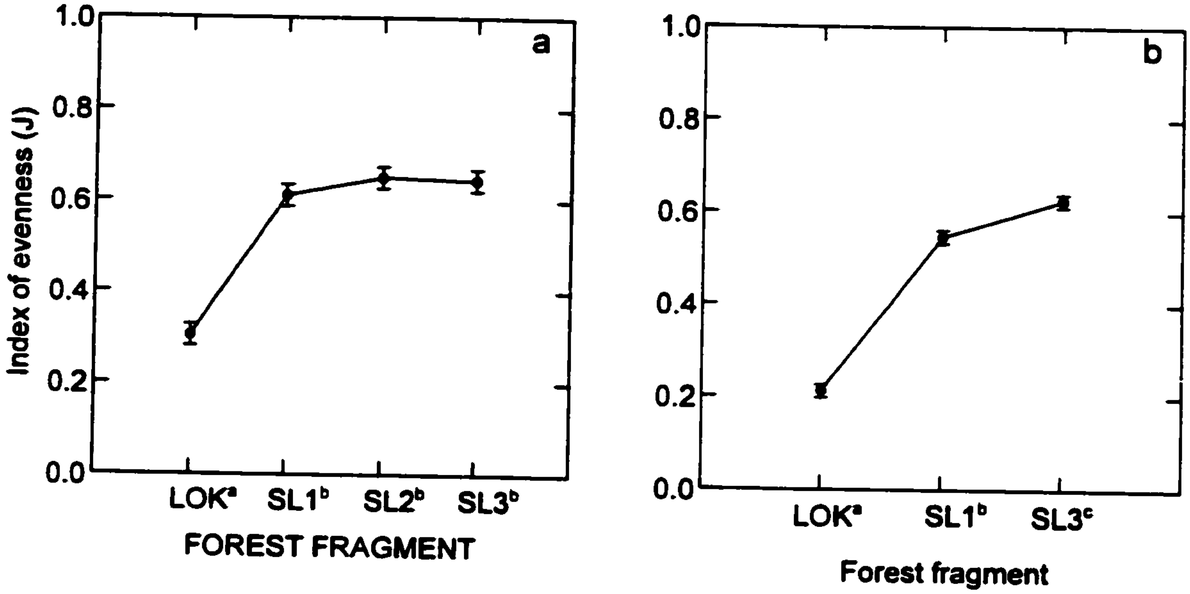

Figure 3-4: Mean index of species evenness for the four forest fragments from 50x50 m plots (a) and 10x10 m plots (b). Different superscripts denote significant differences ($P<0.05$) in evenness, determined by a least significant difference test (as a post hoc analysis to a one-way ANOVA).

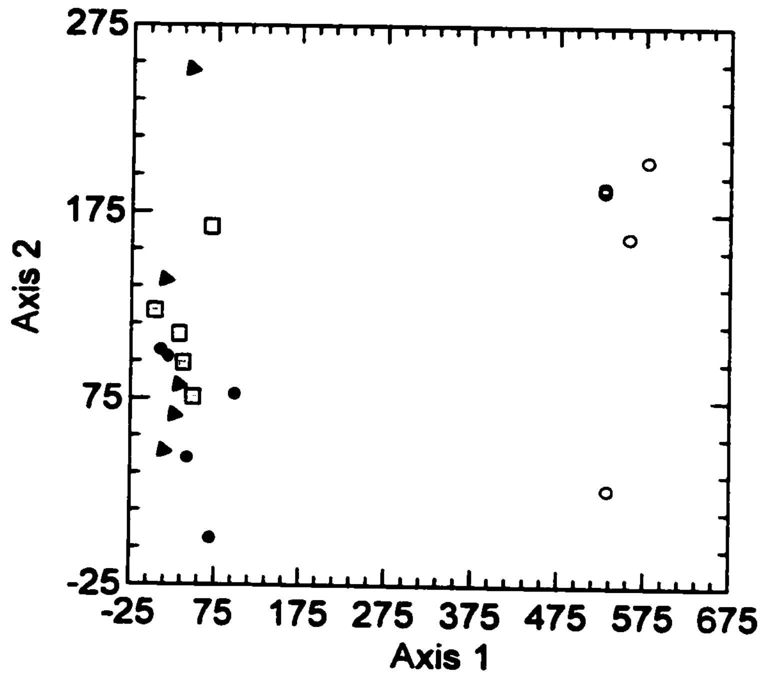

Figure 3-5: Detrended correspondence analysis ordination of plot composition from four forest fragments. 50x50 m plots are separated by forest fragment, LOK (open circles), SL1 (filled circles), SL2 (squares), and SL3 (triangles). Axis 1 is highly correlated (Pearson correlation > 0.85) with internal perimeter/area ratio, and the number of villages per ha of forest in a 5, 7.5, and 10 km radius. Axis 1 = 0.857, Axis 2 = 0.346.

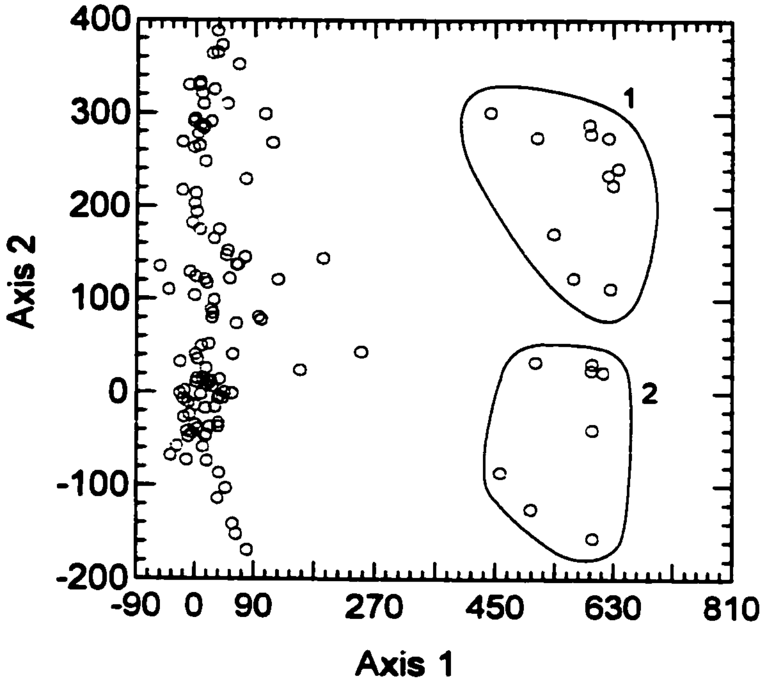

Figure 3-6: Detrended correspondence analysis ordination of species composition from four forest fragments. Groups 1 and 2 are species that either only occur, or are relatively over-represented in the degraded (Lokaro) forest.

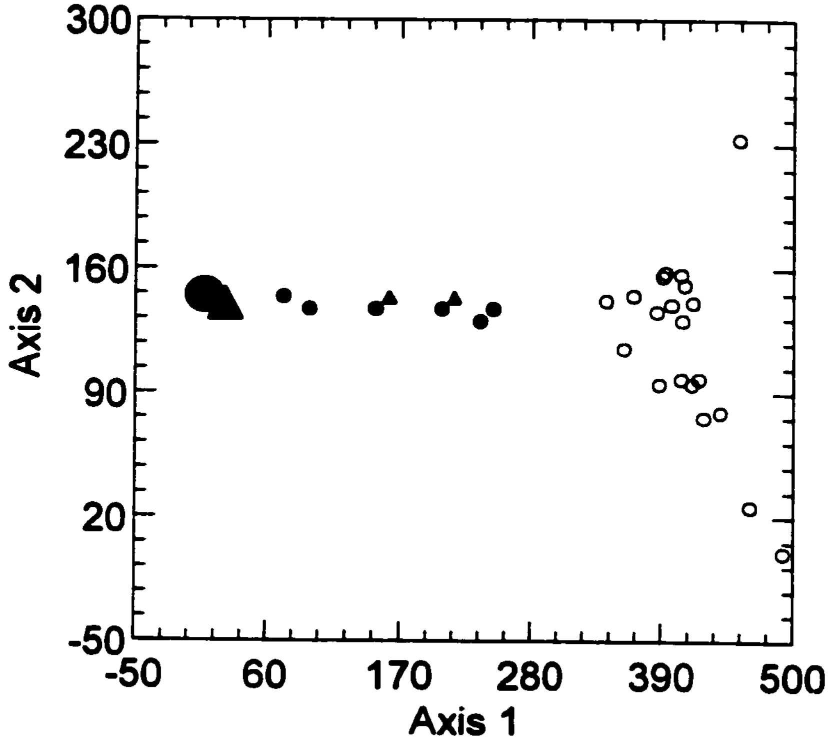

Figure 3-7: Detrended correspondence analysis ordination of plot composition from three forest fragments. 10x10 m plots are separated by forest fragment, LOK (open circles), SL1 (filled circles), and SL3 (triangles). Large circle and triangle represent clumping of 12 SL1 and 18 SL3 plots. Axis 1 is highly correlated (Pearson correlation > 0.85) with internal perimeter/area ratio, and the number of villages per ha of forest in a 5, 7.5, and 10 km radius. Axis 1 = 0.804, Axis 2 = 0.406 (plots stretching from clump are all within 25 m of edge, with one exception, see text).

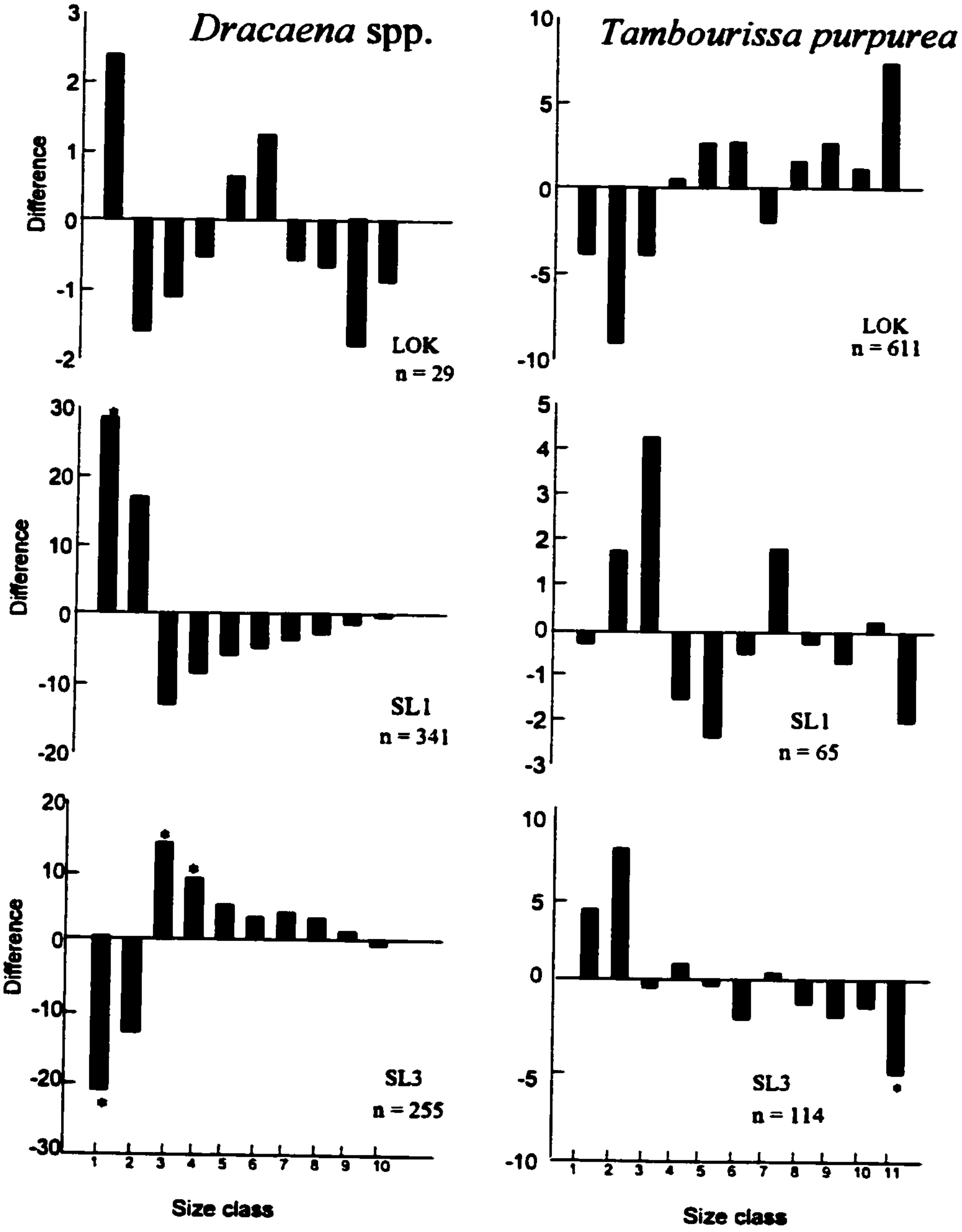

Figure: 3-8: Relative differences between observed and expected numbers of individuals per size-class in three forest fragments (LOK = the Lokaro forest fragment, SL1 and 3 = Sainte-Luce fragments 1 and 3, respectively). * denotes that difference between expected and observed is significant (P<0.05).

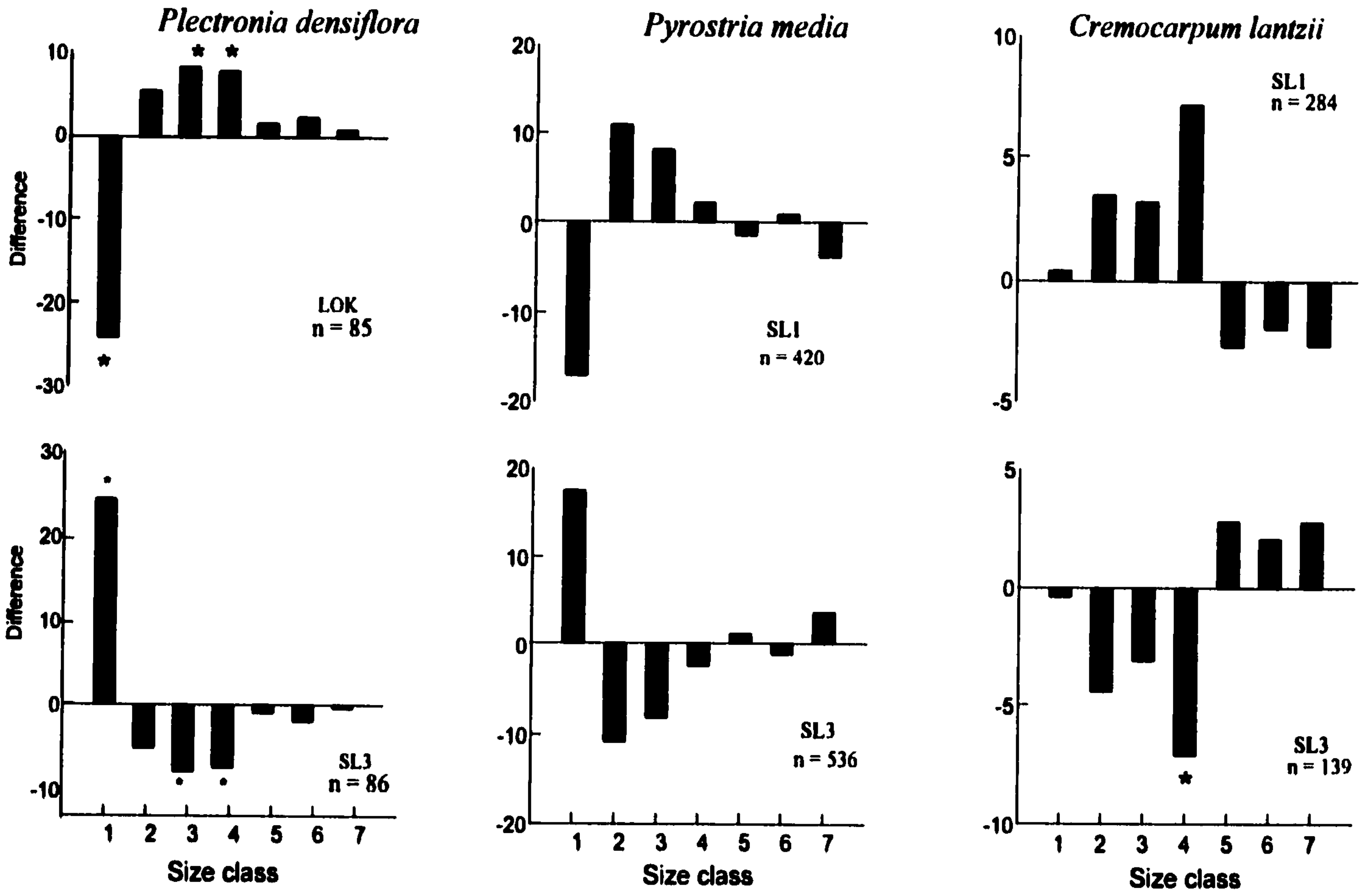

Figure 3-9: Relative differences between observed and expected numbers of individuals per size-class in three forest fragments (LOK = the Lokaro forest fragment, SL1 and 3 = Sainte-Luce fragments 1 and 3, respectively). * denotes that difference between expected and observed is significant (P<0.05).

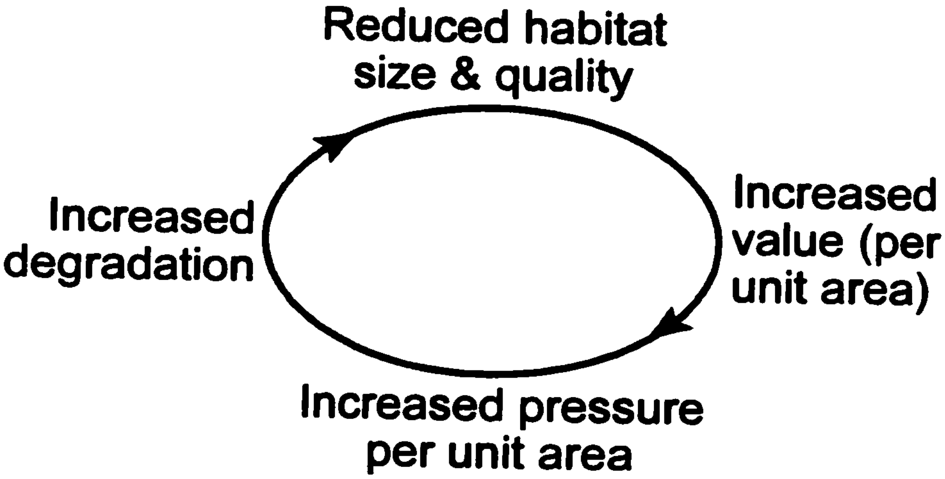

Figure 3-10: Negative feedback loop characterizing the relationship between habitat (resource) degradation and increasing human population pressure.

CHAPTER IV:

CORE AND SATELLITE SPECIES IN A DEGRADED HABITAT: CORE SPECIES ARE NOT MORE PERSISTENT

ABSTRACT

Most communities exhibit 'core-satellite' patterns wherein species' distributions exhibit two modes, one of species found only at a single site and another of species found across all sites. Here I examined species distributional patterns in degraded and relatively undegraded forest fragments by sampling trees in 50x50 m plots and understory woody vegetation in 10x10 m plots. Both for trees and for understory woody vegetation the intact fragments showed two modes, while degraded fragments had lost their mode of core species. Habitat degradation may have a greater adverse effect on common species than on rare species. Here I briefly explore theoretical explanations of the lack of a core-satellite pattern in degraded habitats.

INTRODUCTION

Understanding the processes that underpin patterns of species distribution and abundance has long been at the heart of modern ecology (e.g., Wallace 1892; Preston 1962; Whittaker 1965; Rabinowitz 1981; Hanski 1982; Brown 1984, 1995; Holt et al. 1997). Most species, in one sense or another are rare at some time, somewhere. Indeed, conceptually (Rabinowitz 1981; Gaston 1994) and empirically (Murça Pires et al. 1953; Novotný and Basset 2000), most species in any given community ought to be rare. Studies concerning commonness and rarity of species have focussed on the interaction between two quintessential attributes, abundance and distribution, and in particular the positive relationship between the two (Hanski 1982; Brown 1984; Gotelli and Simberloff 1987; Collins and Glenn 1990, 1991; Murray et al. 1999; Guo et al. 2000).

Similarly, classic biogeographic thinking contends that the distributions of species abundance in space are essentially Gaussian, that is normally distributed (Preston 1948; Whittaker 1960), especially at very large scales (Brown 1984; Collins and Glenn 1991). However, regional studies have often found that species abundances are bimodal (Hanski 1982; Gotelli and Simberloff 1987; Collins and Glenn 1990, 1991; c.f., Gaston and Lawton 1989). This bimodal distribution has been said to exhibit a 'core-satellite' pattern (Fig. 4-1a). According to Hanski (1982), core species are those that are both regionally widespread and locally abundant, while satellite species are characterized by low abundance and restricted regional distribution. The former are predicted to re-colonize open patches (and "rescue" deficient populations), and to persist in a region indefinitely, because the rate of extinction is negatively correlated with the number of patches occupied. Satellite species are predicted to be less invasive and persistent (Hanski 1982).

The core-satellite hypothesis offers a testable framework to explain the relationship between local abundance and distribution, but there are others.

Brown's (1984) niche-based model contends that the abundance and distribution of species is contingent on biotic and abiotic constraints, where species with generalized habitat requirements will be more abundant and widespread (Brown 1995). A third explanation (Holt et al. 1997) uses properties of demographic parameters (birth and death rates) to account for differences in range size among species. According to that model, species with lower death rates and/or higher birth rates will theoretically have a greater geographical distribution.

An important exercise in ecology is to try to link theories and hypotheses to real-world scenarios, in particular in human-dominated landscapes. Forest fragmentation via habitat destruction and alteration is a major source of concern regarding the maintenance of biodiversity and ecosystem function (Laurance 1999). A crucial avenue of research concerning species and community responses to fragmentation (Bierregaard et al. 1992; Laurance and Bierregaard 1997) must now consider how abundance and distributional patterns appear in these altered landscapes.

Elsewhere we have described significant differences in species abundance, richness and taxonomy among forest fragments of southeastern Madagascar (Cadotte et al. 2001; Cadotte and Lovett-Doust 2001a). These differences were all significantly negatively related to local anthropogenic pressures (measured as human population per hectare of forest cover within radii of 5, 7.5, and 10 km, and the degree to which forests were internally fragmented by canopy-breaking trails and roads). In the present paper we consider tree and woody understory species abundance and distribution patterns among forest fragments in different stages of degradation. More specifically, given that the forest degradation of these fragments has resulted in species loss, we interpret persistence and loss patterns in the context of Hanski's core-satellite model.

We test three hypotheses (see Fig. 4-1b-d). First, that the two species distribution modes are both negatively affected by habitat degradation, with rare species disappearing, and common species becoming less abundant (Fig. 4-1b); secondly, that habitat community degradation disproportionately reduces rare species (Fig. 4-1c); and finally, that degradation disproportionately affects common species (Fig. 4-1d).

METHODS

Study area and sampling method

The four littoral forest fragments used here (LOK, SL1, SL2, SL3) are located along the southeastern coast of Madagascar (see Cadotte et al. 2001). These forests occur on sand substrata and are part of the humid sublevel, Eastern Domain ecotype, characterized as low-altitude moist forest (Dumetz 1999). They are highly fragmented, but continue to contain a tremendous array of habitat diversity (Goodman 1999). The four forest fragments we studied range from least- to most-degraded as SL3 = SL2 > SL1 > LOK (Cadotte and Lovett-Doust 2001a).

Within each forest fragment, twenty randomly placed 50x50 m plots were completely censussed for all trees with a diameter at breast height (DBH) >10 cm. In addition, sixty 10x10 m plots along transects from edge to interior in three of the forest fragments were completely censussed for all woody vegetation taller than 1 m. For complete sampling details see Cadotte et al. (2001).

Null distributions

In order to examine differences in distributional patterns among fragments in different stages of degradation, it was necessary to compare each of the within-fragment distributions to a null distribution, which would enable inferences about relative change. To accomplish this, we used the regional distribution pattern (i.e., among all fragments) as the basis for comparison (separately, for each of the two sampling procedures). Distributions of species abundances have been shown to be unimodal at larger spatial scales (Collins and Glenn 1997), and our data agree with this observation (Fig. 4-2). Having a unimodal null distribution allowed us to test for relative differences in core and satellite frequency classes for each null and observed distribution. We constructed a null model derived from average, regional frequencies, based on the methods of Collins and Glenn (1990),

$$F_a = \frac{(\sum_{i=1}^{n} = f_i/n)}{N}$$

where F_a is the average frequency of species *a* among forest fragments. f_i is the species frequency in sampling plot *i*, in each of n plots across all N fragments.

These values were then used to produce a null frequency distribution having n frequency classes. The proportion of values in each frequency class was used to calculate the expected value for each observed distribution. One sampled Kolmogorov-Smirnov test, using the calculated null distribution as the expected value, to compare observed and expected frequency distributions (Sokal and Rohlf 1981). We used Chi-squared tests to determine if there were significant differences between the expected and observed number of species in each frequency class.

Finally, we determined if the frequently-observed pattern of a species average abundance being positively correlated with its distribution (Hanski 1982, Brown 1984, Gotelli and Simberloff 1987, Collins and Glenn 1990, 1991) was maintained through forest degradation. Regression analysis was used to examine the relationship between a species average abundance and its distribution.

RESULTS

Regionally (i.e, across all forest fragments), local abundance was highly significantly positively correlated with the number of sites occupied, for both 50x50 m plots (R^2=0.264, F=60.26, P<0.001) and 10x10 m plots (R^2=0.317, F=91.01, P<0.001) (Fig. 4-2). Also there were many species with highly restricted regional distributions, very few common species, and no species found at all sampling sites (Fig. 4-2).

Distributional patterns for 50x50 m plots

The overall distributions for SL1, SL2 and SL 3 were significantly different ($P<0.05$, 0.001, and 0.01, respectively) from the null distributions (Fig. 4-3a). The two relatively undegraded forest fragments (SL2 and SL3) had significantly more core species ($P<0.001$ and $P<0.01$, respectively) compared to the null distribution (Fig. 4-3a). These two fragments also had significantly fewer satellite species ($P<0.001$ and $P<0.05$, respectively) than the null distribution (Fig. 4-3a). Neither the highly-, nor the moderately-degraded forest fragments (LOK and SL1, respectively), differed in the number of core species from those predicted by the unimodal null model, while SL1 did have significantly fewer satellite species ($P<0.05$) (Fig. 4-3a).

Results from linear regressions showed that all forest fragments exhibited a highly significant positive relationship ($P<0.001$) between a species local abundance and the number of sites it inhabited (Fig. 4-3b).

Distributional patterns for 10x10 m plots

Fig. 4-4a shows results of the distribution analyses for the three fragments sampled using 10x10 m plots. These results support those for the 50x50 m plots. The overall distributions for all three, LOK, SL1 and SL3 were significantly different ($P<0.05$, 0.01, and 0.01, respectively) from the null distributions. The least-degraded fragment, SL3, was significantly over-represented by species in the two most common frequency classes ($P<0.001$ and $P<0.05$, respectively), while being significantly under-represented by the two frequency classes representing rare species (P<0.05). Similarly, the severely- and moderately-degraded fragments (LOK and SL1, respectively) did not have an excess of core species, compared to the null distribution. LOK was significantly over-represented by satellite species (P<0.05). For both sampling methods, SL1 appears transitory between the most degraded (LOK) and least degraded (SL2 and SL3).

Again, similar to the results for the 50x50 m plots, linear regressions indicate the fragments had a highly significant relationship (P<0.01) between a species local abundance and the number of sites inhabited (Fig. 4-4b).

DISCUSSION

Though this study suffers from lack of true replication (of fragment degradation status), we are confident about the patterns described here. The presence of a mode of core species in both of the two relatively undegraded fragments, plus the same patterns occurring in two different groups of taxa (trees and woody understory vegetation), attests to these patterns being legitimate.

Core-satellite patterns in a degraded landscape

Human-caused habitat degradation represents a broad environmental change in which to examine community responses. The human influence is pervasive, not a series of localized catastrophes. Figs 4-3b and 4-4b show that both local abundance and distribution decline simultaneously. If either local abundance or distribution declined, independently of the other, then the strong positive relationships observed for less degraded fragments would not persist in degraded fragments. Specifically, if local catastrophes eliminated some populations of widespread species, while not affecting the other populations, then R^2 values would have been lower in degraded habitats.

How do theoretical explanations of distribution patterns account for our observed change in the core-satellite pattern following pervasive environmental change? Theories that invoke spatial dynamics (e.g., Hanski 1982, Tokeshi 1992, Hanski et al. 1993) assume that immigration and extinction events for any given species are dependent on the spatial patterns of occupied habitat patches in a patchy environment. Assuming that the communities which make up the forest fragments are in fact comprised of any number of discrete patches, can spatial models explain why core species should be disproportionately adversely affected? In his development of Levins' (1969) distribution model, Hanski (1982) added an extinction term, dependent upon regional occurrence. In the Levins model, the rate of patch extinction increased in proportion to the number of habitat patches occupied, while in Hanski's model the extinction rate was parabolic. In Hanski's (1982) model:

$$dp/dt = ip(1-p) - ep(1-p) \qquad \text{Eq(1)}$$

where p is the fraction of sites (or patches) occupied, and i and e are constants for immigration and extinction respectively. Neither immigration nor extinction is independent of patch occupancy. This extinction parameter, termed the "rescue effect" by Hanski and others, describes species whose regional abundance is very high and that have concomitantly lower extinction rates than species inhabiting a moderate number of patches. Our results suggest that the rescue effect does not function under pervasive environmental change. Even by dramatically increasing the extinction term, core species ($p=1$) ought to maintain a negligible extinction rate. Yet, from our results core species appear to have high extinction rates in degraded forests. This discrepancy could be alleviated by adding an extinction term (e_2p) that increases in proportion to patch occupancy, similar to Levins' (1969) extinction term, so that:

$$dp/dt = ip(1-p) - e_1p(1-p) - e_2p \qquad \text{Eq(2)}$$

The second extinction term (e_2p), depending upon environmental conditions, could range from negligible effect to negating any rescue effect.

However, while adding an extinction term (e_2p) to a spatial model may incorporate an observed pattern, it does not address the underlying causes of the observed pattern. The addition of a second extinction term may not represent spatially-related population dynamics *per se*, rather it may reflect an underlying biology-environment interaction. Generally, causality underpinning the distribution and abundance patterns of species may be attributed to evolutionary history, especially relating to habitats or niches where (or when) species have positive net fitness (Brown 1984, Holt 1987, Holt and Gaines 1992, Brown et al. 1995). Population-level dynamics (i.e., birth and death rates) can be a measure of where (or when) a species is occupying its evolutionarily derived niche, or optimal habitat. Just as organisms exhibit habitat selection as a mode of increasing their fitness (Holt 1987), changing habitats (by landscape degradation) may change the relative fitness of co-occurring species through selection. Recently, Holt et al. (1997) developed a model invoking demographic variables, density dependent birth rates and density independent death rates, to account for both range size and average density. All other things constant, an increasing death rate in their model will cause a restriction in range size, as measured across an environmental gradient, and will reduce the average abundance across the species range (Holt et al. 1997).

If the number of sites occupied decreased independently of density, then we could readily evoke spatial dynamics. But since both distribution and abundance decline simultaneously, disproportionately affecting core species, we should view pervasive environmental change as causing intrinsic biological changes (e.g., birth and death rates, competitive ability). Thus habitat alters, the fundamental niche of the majority of species is also affected, selecting against (in most cases) most species, by reducing their fitness. Habitat degradation shifts the niche or preferred habitat of a species (Holt 1987), thereby denying core species their optimal habitat. These species are less likely to remain core species, thereby producing the patterns we observed.

Response of rare and common species

Do rare and common species have ecologically different responses to environmental changes? Tilman et al. (1994), using multi-species coexistence models, have shown that competitively superior, widespread species may be more prone to extinction following habitat destruction, than rare, competitively inferior species. This is due to a trade-off between competitive and dispersal ability.

It appears as though many rare species may have different life-history strategies, allowing them to persist at low densities (Kunin and Gaston 1997; Cadotte and Lovett-Doust 2001b). Rabinowitz and colleagues have shown a number of ecological differences between rare and common species. They found rare species to have superior seed-dispersal abilities (Rabinowitz and Rapp 1981); rare species maximize growth and competitive abilities at low conspecific densities (Rabinowitz et al. 1984); and that reproduction in rare species was less dependent on environmental variation than in common species, and therefore showed less variability in seed set (Rabinowitz et al. 1989).

Conclusion

Our results support the hypothesis that core species are disproportionately adversely affected by forest degradation (Fig. 4-1d). Ecological studies and conservation planning ought to recognize the counter-intuitive possibility that common widespread taxa may be highly susceptible to habitat destruction and degradation.

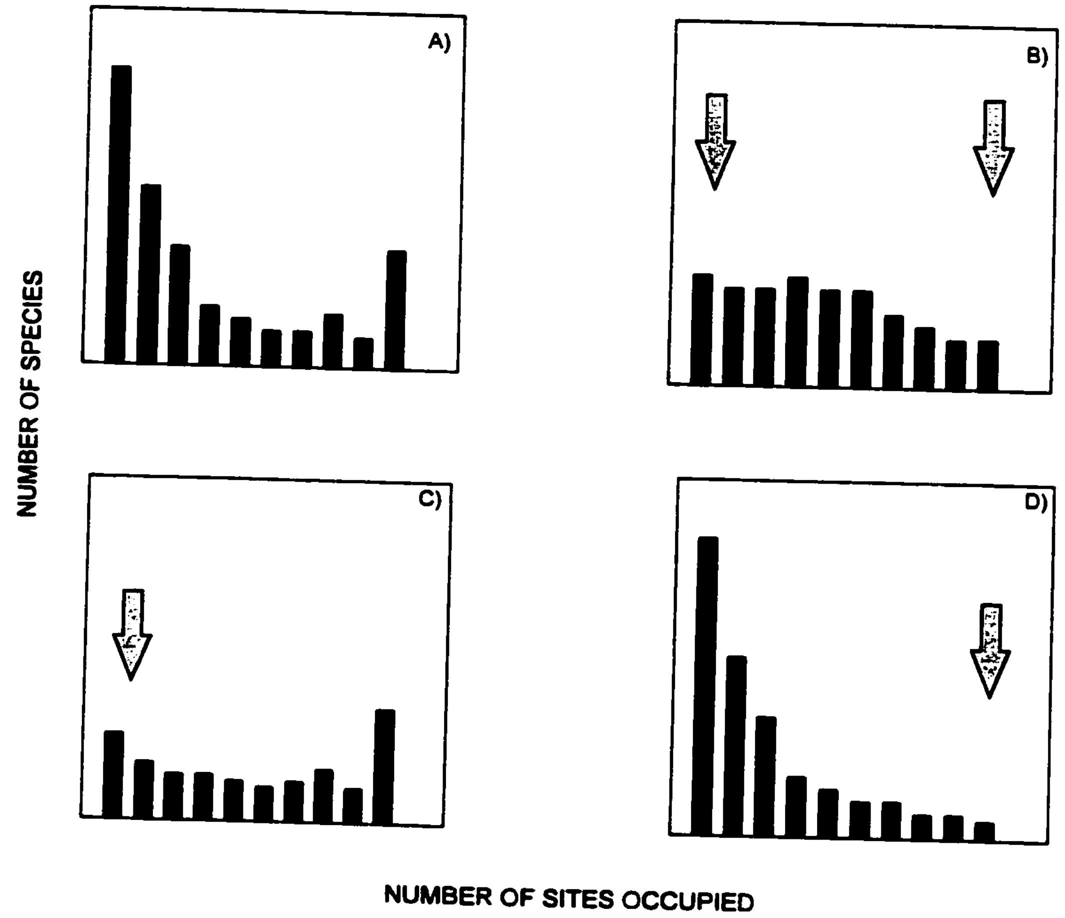

Fig. 4-1: Species range distributions showing (A) the theoretical core-satellite pattern; plus patterns predicted by three hypotheses examining how restricted and widespread species respond to habitat degradation. Arrows indicate mode reduced by habitat degradation. B) Restricted species go extinct and abundant taxa become rarer; C) restricted species are disproportionately adversely affected; and D) core species are disproportionately adversely affected.

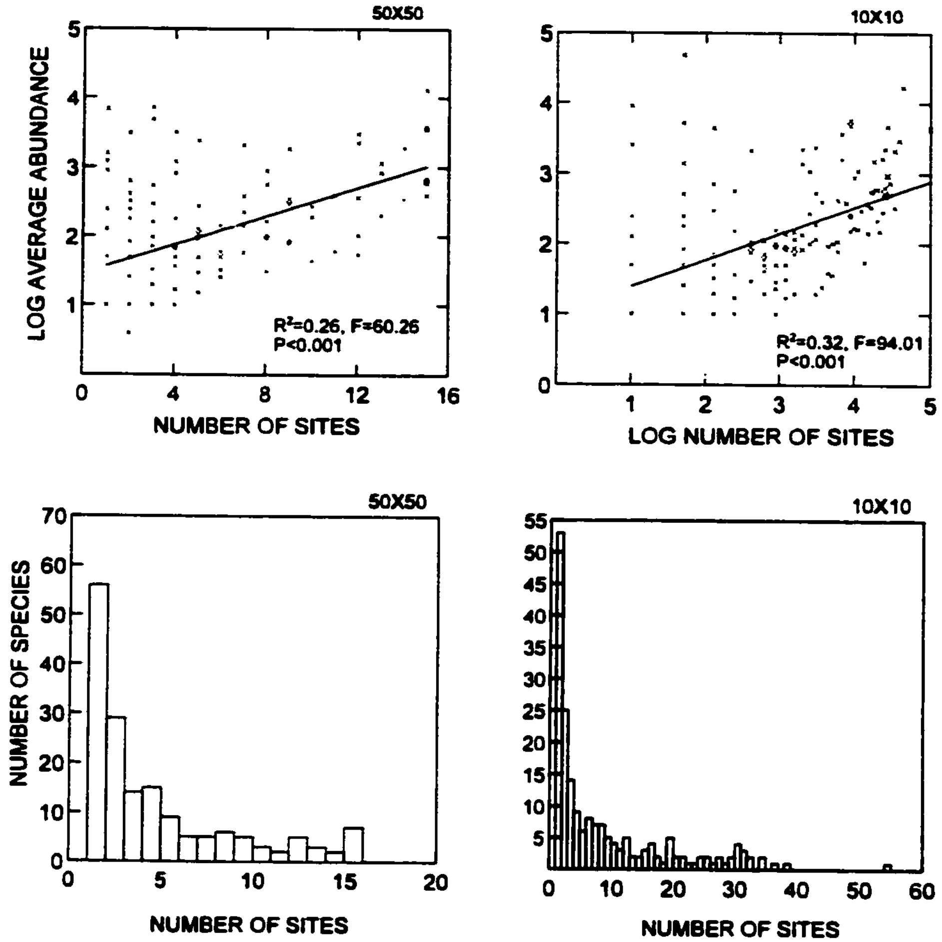

Fig. 4-2: Results of regional distribution and abundance regressions and species range distributions, for both sampling methods.

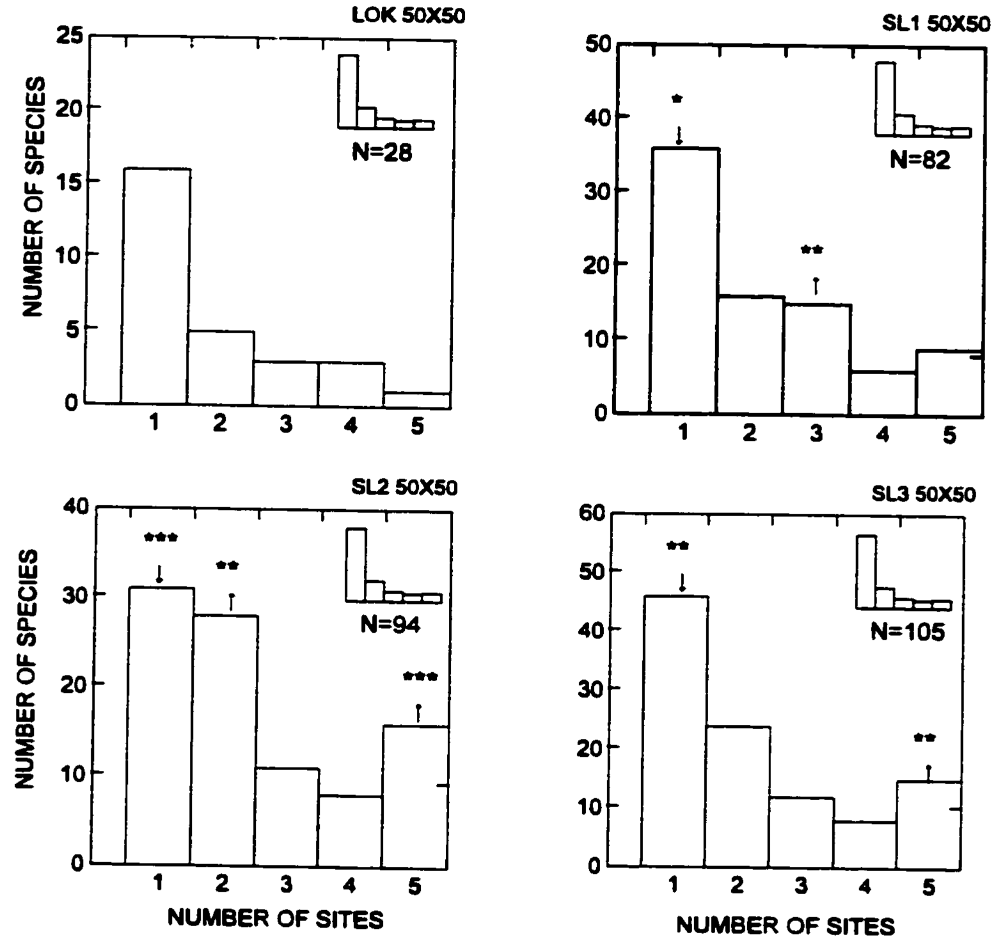

Fig. 4-3a: Species range distributions for the four forest fragments sampled using 50x50 m plots. ↑ indicates frequency bars which are significantly greater than expected according to the null model, and ↓ indicates those that are significantly less than expected. Significance shown as * = <0.05, ** = <0.01, and *** = <0.001. Histogram in upper right corner of each distribution shows distribution of the null model.

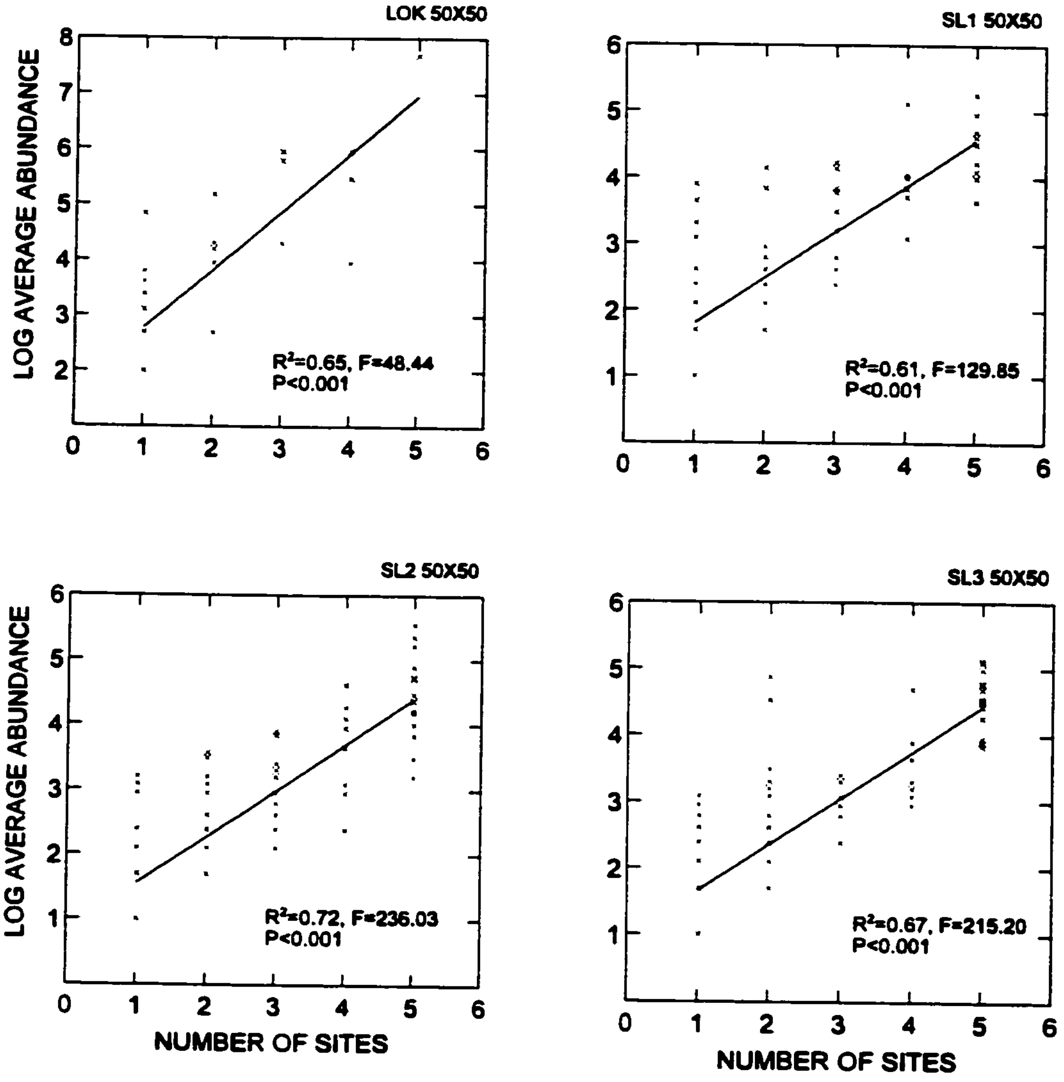

Fig. 4-3b: Abundance-distribution regressions for the four forest fragments sampled using 50x50 m plots.

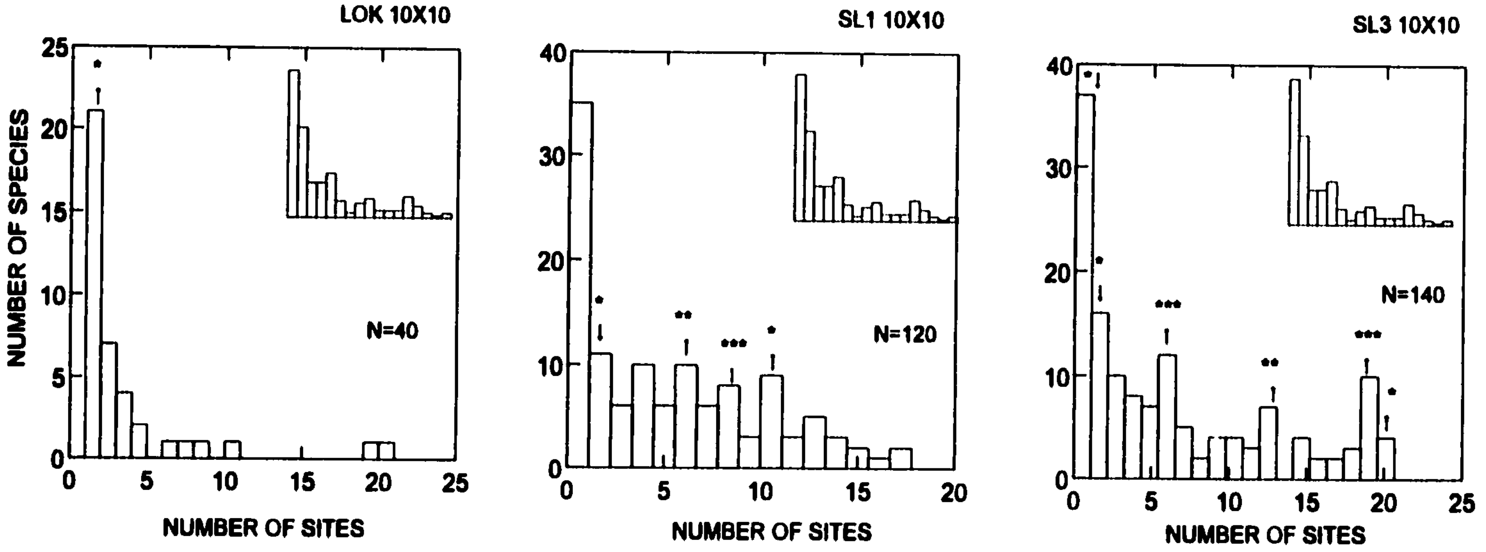

Fig. 4-4a: Species range distributions for the three forest fragments sampled using 10x10 m plots. ↑ indicates frequency bars which are significantly greater than expected according to the null model, and ↓ indicates those that are significantly less than expected. Significance shown as * = <0.05, ** = <0.01, and *** = <0.001. Histogram in upper right corner of each distribution shows distribution of the null model.

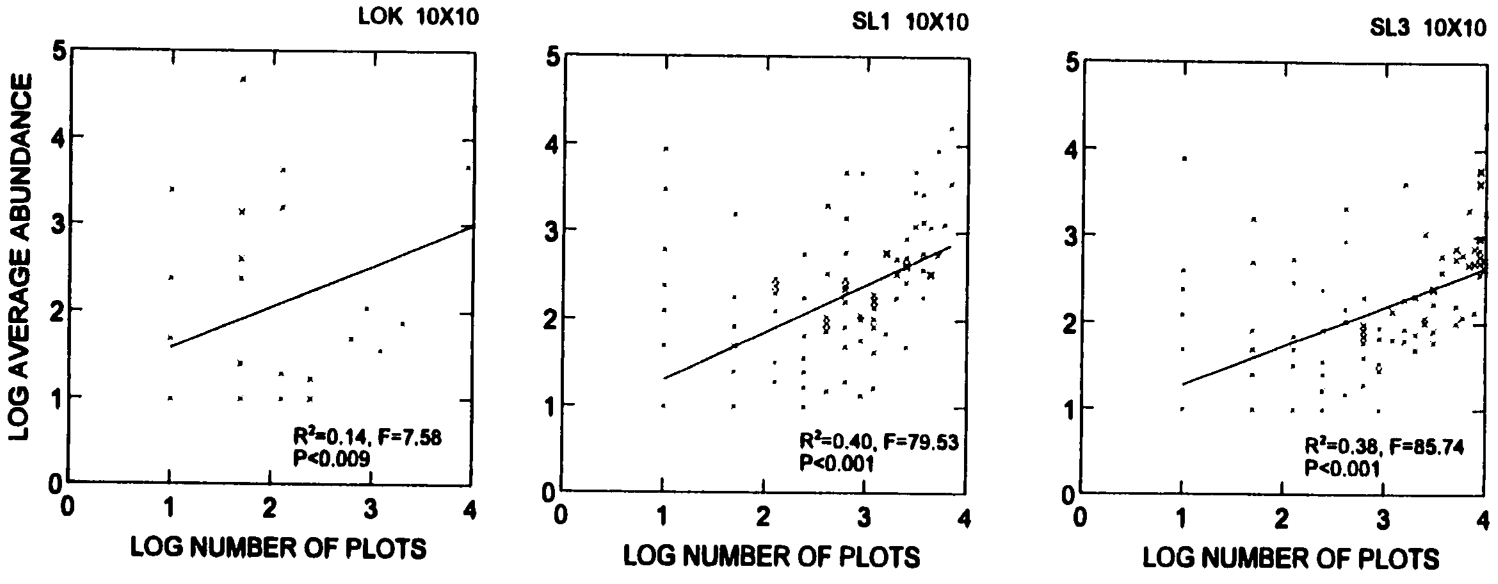

Fig. 4-4b: Abundance-distribution regressions for the three forest fragments sampled using 10x10 m plots.

CHAPTER V:

HABITAT DEGRADATION AND EDGE-INTERIOR DIFFERENTIATION IN A TROPICAL FOREST

ABSTRACT

Habitat fragmentation and degradation are large-scale habitat alterations whose anthropogenic causes can carry on past initial events and influence community structure. Here we examine the extent of edge-to-interior differentiation as effected by habitat degradation. We investigated the structure and diversity of community composition using plots 5, 25, 50, and 100 m from the edge, in three tropical forest fragments of southeastern Madagascar. Fragments differed in the degree of habitat degradation, from relatively intact, to moderately degraded, and very degraded. Two-way ANOVA was used to examine effects of distance-from-edge and the number of trails that crossed the transect on species structure and composition. Frequency distributions of species number found at plots at each sampling scale were compared to determined the extent of edge-interior differentiation, including the hypothesis that "core-satellite" distributions were maintained. In both for the intact forest fragment and the moderately-degraded fragment, the height of trees (DBH ≥ 10 cm) and other woody taxa, stem/bole elongation pattern, and the height-to-first branching, all increased significantly with increasing distance from the edge. The edge effect extended 25-50 m into the intact and moderately-degraded fragments. In the intact forest,

distance-from-edge was the only significant factor, while in the moderately-degraded forest fragment, the number of trails along the transect was also a highly significant factor. In the highly-degraded fragment, the interaction between the two factors was the most significant factor. In the intact forest fragment, common ("core") species increased in number with increasing distance from the edge; there was a significant core species mode beyond 25-50 m from the edge. In the moderately-degraded fragment there was also an increase in number of core species with distance from the edge, but there was no mode of core species. In the highly-degraded fragment, there was no change with respect to species distributions and no mode of core species. These results suggest a certain dynamism to edge effects in anthropogenically-created forest fragments. In the intact forest, the distance from the edge was the most important factor accounting for differences in a variety of demographic and diversity measures. In fragmented forests, paths cut the habitat and diminished the importance of distance from edge. In the most degraded forest, distance from the edge was no longer a factor in explaining patterns for most variables.

INTRODUCTION

The importance of edge effects in biodiversity conservation and management of fragmented forests has been studied extensively (see e.g., Bierregaard et al. 1992; Harper and Macdonald 2001). Habitat edges produced through fragmentation represent discontinuities in community spatial pattern (as opposed to pre-fragmentation continuity of habitats), and may alter species composition, densities, and population dynamics compared to interior forest (Laurance and Bierregaard 1997). Edge effects are often correlated with changes in physical parameters, such as degree of wind and light penetration, and temperature and humidity gradients (Kapos 1989; Bierregaard et al. 1992). Biologically, forest edges (compared with forest interior) may also exhibit changes in structural heterogeneity (Bierregaard et al. 1992; Baldi 1999; Harper and Macdonald 2001), species richness and composition (Sizer and Tanner 1999; Dale et al. 2000; Laurance et al. 2001), mortality and recruitment patterns (Ferreira and Laurance 1997; Laurance et al. 1998a, b; Sizer and Tanner 1999), and plant-animal interactions (Aizen and Feinsinger 1994). However, the phenomena described as 'edge effects' may not depend solely on the distance from the edge. Rather, landscape-level influences may be affecting whether or not one observes edge effects, and how strongly they appear (Hartley and Hunter 1998).

Edge effects are not necessarily separate and distinct from forces that generate the edges in the first place. For example, the destruction and degradation of continuous habitats often produces a mosaic of fragments, which may impact biological communities in any number of ways (e.g., Turner 1996). These changes may result in altered species richness, abundance, and demographic processes (see for example Wilcove et al. 1986; Klein 1989; Lynam 1997; Debinski and Holt 2000; Cadotte and Lovett-Doust 2001a). Such anthropogenic influences may also affect community-level patterns. Cadotte and Lovett-Doust (2001c) showed that in relatively undegraded forest fragments, communities had bimodal species distributions (i.e., a "core-satellite" pattern *sensu* Hanski [1982]), while semi- and highly-degraded communities appeared to have lost the mode of core (or common) species. In the degraded communities a greater proportion of species were rare, compared to intact communities (Cadotte and Lovett-Doust 2001c).

In previous assessments of fragmentation effects in southeastern littoral forest of Madagascar, we have shown that persistent anthropogenic pressure severely reduced species richness and density, and altered community structure (Cadotte et al. 2001; Cadotte and Lovett-Doust 2001a). These differences were all significantly negatively related to local anthropogenic pressures (measured as human population density per hectare of forest cover within expanding radii of 5, 7.5, and 10 km, and the degree to which forests were internally fragmented by canopy-breaking trails and roads) (Cadotte and Lovett-Doust 2001a, c). In the present paper, we examine the edge effect upon tree and shrub diversity, composition, and physical parameters, in forest fragments with differing degrees of habitat degradation. We test the hypothesis that habitat degradation reduces differentiation between edge and core habitat structure. We also examine the interior-to-edge core-satellite pattern among the forest fragments.

METHODS

Study area and sampling method

The three littoral forest fragments used here (LOK, SL1, SL3) are located along the southeastern coast of Madagascar (see Cadotte et al. 2001). They ranged in total extent from 122, to 191, to 457 ha. These forests occur on sandy substrata and are part of the humid sublevel, Eastern Domain ecotype, characterized as low-altitude moist forest (Dumetz 1999). They are highly fragmented, but continue to contain a tremendous array of habitat diversity (Goodman 1997). The three forest fragments we studied range from least- to most-degraded as SL3 > SL1 > LOK (Cadotte and Lovett-Doust 2001a).

Within each forest fragment, five 100 m transects were evenly distributed along the seaward edge, except for SL1, in which three transects were relocated to the non-seaward side, due to recent edge-habitat destruction (see Fig. 5-1 for starting location of each transect). To account for localized effects of human disturbance, the number of footpaths and trails crossing the transects were recorded. Four plots were positioned along each transect, centred around points 5, 25, 50, and 100 m from the forest edge, with one side parallel to the edge (total of 60 10x10 m plots). Diameter and height were recorded for all individuals of woody species taller than 1 m; additionally, for trees with a DBH greater than 10 cm, the canopy width and height-to-first branching were recorded. To estimate the height for trees taller than 2.5 m, a reference pole 5 m tall, with markings at 2.5

and 5 m was used, and heights were simultaneously estimated by two researchers. Voucher specimens were collected for identification of each species in each forest and deposited at Parc Botanique et Zoologique de Tsimbazaza, in Antananarivo. Nomenclature follows the Missouri Botanical Gardens W^{3}TROPICOS database (Missouri Botanical Garden 2001).

Data analyses

The variables of interest were plant height, height-to-diameter ratio (as an estimate of elongation), height-to-first branching, canopy diameter, total number of species, number of individuals with tree life-form (determined as any species having at least one individual with DBH ≥ 10 cm and height of 10 m, number of individuals with shrubby life-form (those not included in the previous group), number of saplings (tree species with DBH ≤ 25 mm and height ≤ 2.5 m), Shannon-Wiener diversity index (H), and evenness (J) (see Legendre and Legendre 1998).

We used two-way mixed factors ANOVA, with SYSTAT 9 (SPSS 1999), where a plot distance from the edge of the fragment was treated as a fixed factor and the number of trails as a random factor. The number of trails per transect were grouped into one of five categories: 1-5, 6-10, 11-15, 16-20, and >20 trails. These mixed-factors ANOVAs were done separately for the three forest fragments, in order to draw comparisons about edge-to-interior structure in relation to habitat degradation. We tested for equality of variances, for each variable across both factors using Hartley's F_{max} test (Sokal and Rohlf 1981). All variables except tree (DBH $\geq$ 10 cm) height, canopy diameter, and height-to-diameter ratio for trees (DBH $\geq$ 10 cm), were transformed because of unequal variances ($P < 0.05$). All variables were log-transformed, except height-to-diameter ratio for all individuals and evenness (J), which were square-root transformed $(x+1)^{-1/2}$ because of their low mean values (Underwood 1997).

Ordination of species occupancy in the sixty 10x10 m plots was done using detrended correspondence analysis (DECORANA) (Hill 1979), which produces species and sample ordinations simultaneously (Hill and Gauch 1980). The program version used was *Community Analysis Package* (CAP) version 1.2 (Pisces Conservation LTD, Lymington, UK) which adapts the original version of DECORANA developed by Hill (1979), to include corrections (Oksanen and Minchin 1997).

Species-specific edge-to-interior patterns were examined in detail for each fragment, using all taxa with more than 75 individuals recorded. SL3 had ten such species, SL1 had 14, and LOK had four. One-way ANOVAs, with the distance from edge as the factor, were used to evaluate changes in species density and height-to-diameter ratio. Least significant differences test (LSD) was used as a post hoc analysis, testing for significant differences ($P < 0.05$) between means. Statistics were again run using SYSTAT 9 (SPSS 1999).

Community analysis consisted of an examination of core-satellite patterns. For each forest fragment, the distribution of number of sites occupied by species, was examined for each distance-from-edge sampling unit. In order to determine if these species distributions changed from the edge-to-interior, and among forests, we constructed a null unimodal log-normal distribution, where the null modal frequency (Y_o) was:

$$Y_o = S/\ (\prod/a)^{-1/2}$$

where S is the number of species and *a* is a constant (≈0.2) (Krebs 1978). The other four null frequency classes were produced using the following equation:

$$Y = Y_0 e^{-(a\ R)^2}$$

where Y is the number of expected species in the Rth frequency class to the right of the mode, and *e* is a constant (2.71828) (Krebs 1978). Frequency classes were transformed into proportions and multiplied by the total number of species in observed distributions. A one-sample Kolmogorov-Smirnov test (Sokal and Rohlf 1981) was used to determine if observed distributions differed from the expected, log-normal distributions. Individual frequency classes were compared to expected frequency classes using X^2 tests.

RESULTS

Forest community structure

Two-way mixed ANOVAs showed significant effects of distance-from-edge on plant height (Table 5-1). Results of one-way ANOVAs show that mean plant height increased with increasing distance from edge ($P<0.001$) (Fig. 5-2a). The number of trails along a transect also had a significant effect ($P<0.001$) on mean height only in SL1, while the interaction between distance-from-edge and number of trails had a significant effect (*P*<0.001) on mean plant height in both SL1 and LOK (Table 5-1). A one-way ANOVA showed that the eight plots having most trails per transect in SL1 had the lowest mean plant height (*P*<0.001).

Distance-from-edge and number of trails also had significant effects on the extent of elongation of individuals (height-to-diameter ratio) (Table 5-1). Distance-from-edge highly significantly (*P*<0.001) affected the height-to-diameter ratio in SL3 and SL1 forest fragments (Table 5-1). One-way ANOVAs showed that the height-to-diameter ratio increased with increasing distance from the edge in these two forest fragments (Fig. 5-2b). Both SL1 and LOK showed significant effects of number of trails and the interaction between distance-from-edge and number of trails upon height-to-diameter index (Table 5-1).

Resuts of two-way ANOVAs showed no significant effect of either distance-from-edge or number of trails on the number of saplings per 10x10 m plot, for any fragment (Table 5-1). However, the interaction of distance-from-edge and number of trails was significant in LOK (*P* = 0.039).

Both distance-from-edge and its interaction with the number of trails had significant effects (*P*<0.05) on the number of individuals belonging to tree species in LOK (Table 5-2). The number of shrubby individuals per plot was significantly affected by the number of trails in SL3 (Table 5-2). One-way ANOVA showed that the eight plots associated with transects having the highest number of trails had significantly more shrubby species than plots with fewer trails (LSD test *P*<0.05).

Large trees (DBH $\geq$ 10 cm) and edge structure

Two-way ANOVAs showed no significant effect of distance-from-edge on the mean number of trees per 10x10 m plot (Table 5-3). The number of trails per transect did have a significant effect ($P<0.05$) on the mean number of trees in both SL1 and LOK (Table 5-3). Furthermore, whereas the mean number of trees decreased with increasing trails in SL1, it increased in LOK.

Tree height was very significantly affected ($P<0.001$) by distance-from-edge in fragments SL3 and SL1, and by the number of trails per transect in SL1 (Table 5-3). Fig. 5-2c shows results of one-way ANOVAs.

Height-to-first branching was highly significantly affected ($P<0.001$) by distance from the edge in both SL3 and SL1, and by the number of trails in SL1 (Table 5-3). One-way ANOVA's showed that height-to-first branching greatly increased between the first and second plots (Fig. 5-2d).

The only significant effect on canopy diameter was in SL1, where distance-from-edge was the only significant factor (P=0.025) (Table 5-3). Here, the third plot, 50 m from edge, had a significantly larger (LSD test $P<0.05$) mean canopy diameter than plots at 5, 25 and 100 m.

Distance-from-edge had a highly significant effect ($P<0.001$) on the mean height-to-diameter ratio in SL3 (Table 5-3). The mean height-to-diameter ratio increased with increasing distance from edge (Fig. 5-2e). Both distance-from-edge and number of trails per transect had highly significant effects ($P<0.001$) on the mean height-to-diameter index in SL1 (Table 5-3). The interaction of these two factors had a significant effect (P=0.002) on mean height-to-diameter index in LOK.

Number of trails

The number of trails in SL1 appeared to be the most significant factor in a number of variables (Tables 5-1, 5-2, and 5-3). Results of one-way ANOVAs showed six variables in SL1, which were significantly affected by the number of trails (Fig. 5-3a-f). Woody plant height, number of trees, tree height, height to first branching, and the height-to-diameter ratio for trees all appeared to decrease with increasing number of trails. The number of shrubs appeared to increase with increasing number of trails.

Species differences

The height-to-diameter ratios of three taxa in SL3 (*Dypsis lutescens*, *Noronhia emarginata*, and *Tambourissa purpurea*) were significantly affected by the distance from the edge (Table 5-4). All three showed increases in mean height-to-diameter ratio, with increasing distance inward from the edge of the fragment (LSD test, $P<0.05$). In SL1 the densities of four taxa (*Antidesma petiolare*, *Homalium axillare*, *Pyrostria medea*, and *Weinmannia loubeliana*) were significantly affected by distance-from-edge (Table 5-4). LSD *post hoc* analysis showed that two of these (*A. petiolare* and *W. loubeliana*) had lower densities 25-100 m into the forest fragment, while two species (*H. axillare*, and *P. medea*) increased in density with increasing distance from the edge (Table 5-4). Also in SL1, for five taxa (*Cremocarpum lantzii, Dracaena elliptica*, *Faucheria hexandra*, *P. medea*, and *Sarcolaena multiflora*) the mean height-to-diameter ratios were significantly affected by distance-from-edge. Two taxa increased in mean height-to-diameter index, one decreased, and the other three had mixed responses at 25 or 50 m from the edge (see Table 5-4). In LOK, one species (*Plectronia densiflora*) had a significantly greater mean density 100 m from the edge and one species (*T. purpurea*) had a significantly lower mean height-to-diameter index further into the forest (Table 5-4).

Community composition

Two-way ANOVAs examining effects of distance-from-edge and number of trails on species richness, diversity (H) and evenness (J) showed no significant effects (Table 5-5). However, detrended correspondence analysis (DCA) revealed that community composition of edge plots in both SL3 and SL1 were more similar to all of the LOK plots than were SL3 and SL1 interior plots (Fig. 5-4). Also, there was no significant differentiation between edge and interior plots within the LOK fragment.

Core-satellite distributions

Species distributions across the five plots at each of the four distance-from-edge units, for each forest fragment are presented in Fig. 5-5. Kolmogorov-

Smirnov one-sample tests revealed that none of the SL3 distributions differed significantly from the null distribution (Table 5-6). Sampling plots further from the edge had increased numbers of core species (Fig. 5-5). In contrast, the first two SL1 distributions differed significantly from the null distribution ($P<0.05$) (Table 5-6), seemingly due to the lack of a core species frequency class. Likewise at LOK, all four species distributions were significantly different ($P<0.01$) from the null distribution (Table 5-6). In all four distributions, the mode of satellite species was extremely high, with very low magnitudes for all other frequency classes (Fig. 5-5).

DISCUSSION

The most significant drawback of this study is pseudoreplication of the sampling unit (see Hurlbert 1984). Our inability to replicate treatments (i.e., intact, semi-degraded, and degraded forests) reflects 'on the ground' difficulties of doing research in intensively-degraded regions of Madagascar. The extent of background scientific knowledge for particular regions is sometimes so limited that sampling units can often only be discerned *in situ* and *post facto*. A second concern is the power of the statistical analyses used in this study. Harper and Macdonald (2001) recommend a randomization technique to obtain critical values from interior plots for variables of interest, in testing edge effects. Of course, in our data set the variation among transects and forest fragments is important. Furthermore, with fragments as small as those used here, obtaining independent 'interior' plots would be difficult, especially without an *a priori* understanding of the role that the number of trails along a transect may play (i.e., localized effects of degradation) which could be viewed as a confounding factor to interior plots.

Edge effects and habitat degradation

Studies of edge effects have been concerned primarily with the differences between edge and interior habitats and the extent to which these differences extend into a habitat patch (see e.g., Bierregaard et al. 1992; Ferreira and Laurance 1997; Laurance et al. 1998a, b; Sizer and Tanner 1999; Harper and Macdonald 2001). However, we were interested in relative differences in edge structure among habitat fragments having different disturbance regimes. In previous papers, we have shown that the fragments used in this study have been degraded to differing degrees. SL3 is the relatively intact, SL1 semi-degraded, and LOK, which is severely degraded (Cadotte et al. 2001; Cadotte and Lovett-Doust 2001a).

Results of the two-way ANOVAs indicate that at SL3 five variables were significantly affected by distance from the edge. In SL3 (which had consistently fewer trails), the number of trails was not a significant factor. However at SL1, which is a moderately-degraded forest, and has the greatest range in the number of trails (4-33), there were seven variables where the number of trails proved to be a significant factor (and six variables where distance-from-edge was a significant factor). At the LOK forest fragment, five variables were significantly affected by the interaction between distance-from-edge and number of trails.

These results suggest a certain dynamism to edge effects in anthropogenically-created forest fragments. Results from the intact (SL3) and semi-degraded (SL1) fragments suggest that plant and tree height, elongation extent of woody species, and height-to-first branching may be efficacious measures of edge effects. Woody stem/bole elongation patterns are unlikely to be limited to specific taxa, since light may be a general limiting resource, impacting inter-specific competitive dynamics (Tilman 1997). Sizer and Tanner (1999) found that seedlings within 10 m of the Amazonian lowland rainforest fragment edge showed increased vertical growth, and that this effect declined with increasing distance from the edge.

Our results, for all taxa and for trees only, in the intact forest fragment (SL3) showed that edge effects may occur up to 25-50 m into the fragment. This is in agreement with other results from tropical forests (40 m: Bierregaard et al. 1992; 60 m: Laurance et al. 1998a; 100 m: Laurance et al. 1997b, 1998b). Interestingly, we did not find differences in the number of saplings, individuals with different life-forms, or in species richness and diversity along edge-to-interior gradients. Cadenasso and Pickett (2000) found that herbivory rates differed between edge and interior habitats, and this might alter seedling recruitment patterns. Indeed, Harper and MacDonald (2001), studying edge effects in a boreal forest, found increased densities of saplings at the edge.

Another general result is the interactive and cumulative effects of habitat degradation on edge structure. In the moderately-degraded forest fragment (SL1), localized effects of anthropogenic degradation occurred more often due to trails than due even to distance from the edge of the habitat. In the heavily-degraded forest (LOK), the frequent occurrence of a significant interaction term in the two-way ANOVAs indicates that the two factors are no longer independent. Habitats within LOK may not be structured like the other fragments (i.e., edge to interior); instead, the more pervasive anthropogenic disturbance there may be altering habitats in other ways (e.g., small clearings, see Cadotte et al. [2001]). The DCA plot (Fig. 5-4) further shows this. Whereas fragments SL3 and SL1 have obvious species compositional differences between edge and interior habitats, LOK no longer has this discernable difference. Furthermore, LOK appears (in both edge and interior plots) more similar to the edge habitats of SL3 and SL1 than to their interior habitats.

We reported previously that two variables, internal fragmentation of a forest, and the number of villages per hectare of forest within a radius of 7.5 km, were significantly negatively correlated with density and richness measures here (Cadotte and Lovett-Doust 2001a). Essentially, it seems that as resources are consumed by local human populations, the area or quality of forest resources decline, increasing the value of remaining resources to those local human populations and producing further exploitation and degradation (see Cadotte and Lovett-Doust 2001a). This is very reminiscent of the 'land-use cascade' of Terborgh and van Schaik (1997) and seemingly directed movement from intact forests to forest fragments in various stages of degradation.

Core-satellite distribution

The undegraded fragment (SL3) shows an increase in the magnitude of the mode of core species frequencies with increasing distance from the edge, with no change after 25-50 m. This pattern is in accord with another result linking disturbance and reduction in number of common (core) species (Cadotte and Lovett-Doust 2001c). Edge habitats have little protection from environmental perturbation and disturbances (e.g., wind, storms, floods, fires, etc.); thus we should expect reduced representation in the core species frequency class, in edge habitats. The moderately-degraded fragment (SL1) does show an increase in the number of core species with increasing distance from the edge, but at the same time does not actually show a strong core mode at 50 or 100 m inside the forest. A caveat concerning this particular result is that the low numbers of core species could be partially mitigated by the fact that we had to switch sides of the fragment (from the east side to the west) when sampling (see methods). Different sides of coastal fragments may have different disturbance regimes (e.g., localized wind, storms, etc.)— though the distance across the fragment was too small at c. 1 km, to have completely different macro-climate parameters. Furthermore the two sides may have different immigration sources, possibly in part because of prevailing winds, which could lead to fewer shared species. However, it does conform to the pattern of reduced core species found by Cadotte and Lovett-Doust (2001b). Finally, the highly degraded forest (LOK) does not show any differentiation with distance from edge. The uniform pattern suggests that human disturbance is pervasive, even if not otherwise immediately evident than as pathways cutting the habitat.

Conclusions

In the intact forest fragment, an edge effect was found to extend 25-50 m. Of greater consequence, habitat degradation appears to reduce differentiation between edge and interior habitats, in terms of both species structural and compositional features. In the intact forest fragment, the distance from the edge was the most important factor accounting for differences in a number of important measures of demography and diversity. Community structure there was different from edge to interior, with the number of core species increasing with increasing distance from the edge. In the semi-degraded fragment the number of trails became the most important variable explaining differences in variables. Community structure showed little differentiation, compared to the intact forest. In the most degraded fragment the distance from the edge was no longer a factor in explaining patterns of biological variables, and there was no differentiation in community structure.

Consequences for conservation include the likelihood that, as tropical forests continue to become further fragmented and degraded, we can expect not only the absolute amount of edge to increase, but the quality of interior habitats compared to edge, to decrease. When accounting for human activity, managers may be able to predict which species would be most adversely affected by reducing interior habitat quality with reducing area.

Table 5-1: Results of two-way mixed factors ANOVA for effects of distance-from-edge and number of trails crossing transect, on plant height, height-to-diameter ratio, and number of saplings per 100 m^2. Forest fragments, Sainte-Luce 3 (SL3), Sainte-Luce 1 (SL1), and Lokaro (LOK), are listed from least to most degraded. Asterisks represent results of Bonferroni corrections; * $P < 0.05$, ** $P < 0.01$.

Dependent variable	Forest fragment	Source	ss	d.f.	ms	*F*	*P*
Plant height	SL3	Distance	14.03	3	4.68	22.69	< 0.001**
		Trails	0.01	1	0.01	0.04	0.836
		D x T	0.44	3	0.15	0.72	0.543
		Error	497.36	2413	0.21		
	SL1	Distance	9.47	3	3.16	11.67	< 0.001**
		Trails	72.99	2	36.50	134.94	< 0.001**
		D x T	22.86	6	3.81	14.08	< 0.001**
		Error	1077.50	3984	0.27		
	LOK	Distance	4.34	3	1.45	4.88	0.002*
		Trails	0.30	2	0.15	0.50	0.607
		D x T	20.08	6	3.35	11.29	< 0.001**
		Error	393.26	1326	0.30		

Height-diameter ratio	SL3	Distance	0.03	3	0.01	5.38	< 0.001**
		Trails	0.00	1	0.00	0.00	0.994
		D x T	0.01	3	0.00	0.89	0.445
		Error	4.32	2415	0.00		
	SL1	Distance	0.21	3	0.07	30.10	< 0.001**
		Trails	0.11	2	0.06	24.04	< 0.001**
		D x T	0.07	6	0.01	4.86	< 0.001**
		Error	9.04	3985	0.00		
	LOK	Distance	0.03	3	0.01	2.09	0.1
		Trails	0.06	2	0.03	5.78	0.003*
		D x T	0.10	6	0.02	3.35	0.003*
		Error	6.67	1326	0.01		
No. of saplings per plot	SL3	Distance	0.41	3	0.14	0.40	0.755
		Trails	0.16	1	0.16	0.46	0.511
		D x T	0.24	3	0.08	0.23	0.873
		Error	4.13	12	0.34		

SL1	Distance	1.49	3	0.50	1.28	0.345
	Trails	3.21	2	1.60	4.13	0.059
	D x T	0.68	6	0.11	0.29	0.954
	Error	3.11	8	0.39		
LOK	Distance	1.37	3	0.46	1.51	0.284
	Trails	0.30	2	0.15	0.51	0.617
	D x T	7.13	6	1.19	3.95	0.039
	Error	2.41	8	0.30		

Table 5-2: Results of two-way mixed factors ANOVA for effects of distance-from-edge and number of trails crossing transect, on the number of individuals for tree species and number of shrubby individuals per 100 m^2. Forest fragments, Sainte-Luce 3 (SL3), Sainte-Luce 1 (SL1), and Lokaro (LOK), are listed from least to most degraded. Asterisks represent results of Bonferroni corrections; * $P < 0.05$, ** $P < 0.01$.

Dependent variable	Forest fragment	Source	ss	d.f.	ms	*F*	*P*
Number of individuals: tree species	SL3	Distance	0.05	3	0.02	0.14	0.935
		Trails	0.08	1	0.08	0.69	0.421
		D x T	0.03	3	0.01	0.10	0.961
		Error	1.43	12	0.12		
	SL1	Distance	1.17	3	0.39	1.18	0.377
		Trails	0.73	2	0.36	1.10	0.379
		D x T	0.70	6	0.12	0.35	0.89
		Error	2.65	8	0.33		
	LOK	Distance	1.53	3	0.51	4.70	0.036
		Trails	0.66	2	0.33	3.02	0.106
		D x T	2.57	6	0.43	3.94	0.039
		Error	0.87	8	0.11		

Number of individuals: shrub species	SL3	Distance	1.07	3	0.36	0.89	0.478
		Trails	0.15	1	0.15	0.37	0.557
		D x T	0.21	3	0.07	0.17	0.915
		Error	4.83	12	0.40		
	SL1	Distance	0.18	3	0.06	0.26	0.85
		Trails	3.56	2	1.78	7.76	0.013
		D x T	0.54	6	0.09	0.39	0.867
		Error	1.84	8	0.23		
	LOK	Distance	2.63	3	0.88	0.98	0.448
		Trails	0.44	2	0.22	0.24	0.789
		D x T	3.39	6	0.56	0.63	0.703
		Error	7.14	8	0.89		

Table 5-3: Results of two-way mixed factors ANOVA for effects of distance-from-edge and number of trails crossing transect, on tree-related variables: number of trees per 100 m^2, height, height-to-first branching, canopy diameter, and height-to-diameter index. Forest fragments, Sainte-Luce 3 (SL3), Sainte-Luce 1 (SL1), and Lokaro (LOK), are listed from least to most degraded. Asterisks represent results of Bonferroni corrections; * $P < 0.05$, ** $P < 0.01$.

Dependent variable	Forest fragment	Source	ss	d.f.	ms	*F*	*P*
Number of trees per plot	SL3	Distance	0.10	3	0.03	0.22	0.88
		Trails	0.15	1	0.15	1.03	0.33
		D x T	0.11	3	0.26	0.26	0.856
		Error	1.72	12	0.14		
	SL1	Distance	0.60	3	0.20	1.13	0.393
		Trails	1.80	2	0.90	5.11	0.037
		D x T	0.63	6	0.11	0.59	0.73
		Error	1.41	8	0.18		
	LOK	Distance	2.18	3	0.73	3.69	0.062
		Trails	1.97	2	0.98	5.00	0.039
		D x T	1.95	6	0.32	1.65	0.25
		Error	1.57	8	0.20		

Tree height	SL3	Distance	161.97	3	53.99	8.71	< 0.001**
		Trails	2.39	1	2.39	0.39	0.535
		D x T	12.49	3	4.16	0.67	0.571
		Error	1085.24	175	6.20		
	SL1	Distance	366.65	3	122.22	23.41	< 0.001**
		Trails	190.65	2	95.33	18.26	< 0.001**
		D x T	43.26	6	7.21	1.38	0.227
		Error	699.48	134	5.22		
	LOK	Distance	19.80	3	6.60	0.60	0.62
		Trails	1.38	2	0.69	0.06	0.94
		D x T	152.79	6	25.47	2.30	0.042
		Error	930.91	84	11.08		
Height to first branching	SL3	Distance	17.81	3	5.94	9.20	< 0.001**
		Trails	0.25	1	0.25	0.39	0.533
		D x T	3.32	3	1.11	1.73	0.163
		Error	99.16	155	0.64		

	SL1	Distance	16.69	3	5.56	15.43	< 0.001**
		Trails	6.93	2	3.46	9.60	< 0.001**
		D x T	1.44	6	0.24	0.67	0.677
		Error	41.46	115	0.36		
	LOK	Distance	0.19	3	0.06	0.12	0.947
		Trails	0.38	2	0.19	0.37	0.689
		D x T	1.98	6	0.33	0.64	0.694
		Error	36.85	72	0.51		
Canopy diameter	SL3	Distance	16.78	3	5.59	1.43	0.236
		Trails	1.34	1	1.34	0.34	0.559
		D x T	15.95	3	5.32	1.36	0.257
		Error	637.25	163	3.91		
	SL1	Distance	26.02	3	8.67	3.21	0.025
		Trails	4.41	2	2.20	0.82	0.445
		D x T	10.79	6	1.80	0.67	0.677
		Error	332.17	123	2.70		

	LOK	Distance	28.60	3	9.53	2.20	0.094
		Trails	11.12	2	5.56	1.29	0.282
		D x T	33.96	6	5.66	1.31	0.263
		Error	350.31	81	4.33		
Height-diameter ratio	SL3	Distance	0.01	3	0.00	8.78	< 0.001**
		Trails	0.00	1	0.00	1.33	0.251
		D x T	0.00	3	0.00	0.23	0.876
		Error	0.08	175	0.00		
	SL1	Distance	0.02	3	0.01	14.59	< 0.001**
		Trails	0.01	2	0.00	9.62	< 0.001**
		D x T	0.00	6	0.00	0.98	0.444
		Error	0.06	134	0.00		
	LOK	Distance	0.00	3	0.00	1.67	0.179
		Trails	0.00	2	0.00	0.76	0.471
		D x T	0.01	6	0.00	3.83	0.002*
		Error	0.04	84	0.00		

Table 5-4: Results of one-way ANOVAs for effects of distance-from-edge on the number of individuals and the height-to-diameter index for common species ($n \geq 75$ per fragment). Least significant difference (LSD) post hoc tests compare differences among means. Significant differences ($P < 0.05$) in means (for each distance-from-edge plot, at 5, 25, 50, and 100 m, respectively) are represented by lower case letters, where *a* is the lowest mean, through to *c*.

			Number of individuals		Height-diameter index	
	Taxa	N	*F*	LSD	*F*	LSD
SL3	*Ouratea obtusifolia* (Lam.) Gilg	99	0.95	—	2.41	—
	Diospyros myriophylla (H. Perrier) ined.	170	1.69	—	0.02	—
	Dracaena reflexa Lam.	77	0.44	—	0.75	—
	Dypsis lutescens (H. Wendl.) Beentje & J. Dransf.	184	0.99	—	2.23*	a ab b b
	Noronhia emarginata (Lam.) Stadman ex A. Thouars	123	0.24	—	3.59**	a ab b b
	Polyscias aff. ornifolia (Baker) Harms	125	1.68	—	0.78	—
	Pyrostria medea (A. Rich. ex DC.) Cavaco	81	0.19	—	0.18	—
	Sarcolaena multiflora Thouars	80	0.43	—	2.14	—
	Scolopia erythrocarpa H. Perrier	90	0.13	—	2.28	—
	Tambourissa purpurea (Tul.) A. DC.	75	0.41	—	8.20***	a b b b
SL1	*Antidesma madagascariense* Lam.	102	2.98*	b ba a a	na	na

	Ouratea obtusifolia (Lam.) Gilg	139	1.00	—	1.86	—
	Cremocarpum lantzii Bremek.	168	0.14	—	3.52*	b a a b
	Dracaena elliptica Thunb.	110	0.73	—	3.92**	b a b b
	Dracaena reflexa Lam.	226	0.17	—	0.77	—
	Dypsis lutescens (H. Wendl.) Beentje & J. Dransf.	86	0.36	—	0.94	—
	Faucherea hexandra (Lecomte) Lecomte)	131	1.15	—	3.52*	a a a b
	Homalium axillare (Lam.) Benth.	86	7.63**	a ab b c	0.58	—
	Ludia mauritiana J. F. Gmel.	149	0.34	—	0.92	—
	Mystroxylon aethiopicum (Thunb.) Loes.	95	0.34	—	na	na
	Pyrostria medea (A. Rich. ex DC.) Cavaco	420	4.00*	a ab c bc	2.98*	a ab a b
	Sarcolaena multiflora Thouars	137	0.68	—	2.78*	a b a a
	Uapaca littoralis M. Denis	90	0.30	—	0.36	—
	Weinmannia madagascariensis DC.	88	5.22**	b a a a	na	na
LOK	*Colea obtusifolia* A.. DC.	279	0.55	—	0.85	—
	Myrica spathulata Mirb.	79	0.94	—	na	na
	Plectaneia thouarsii Roem. & Schult.	85	2.83*	a a a b	na	na
	Tambourissa purpurea (Tul.) A. DC.	611	2.22	—	3.77**	ab b a a

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. na represents species for which no statistic was run because too few individuals were recorded at some sampling intervals.

Table 5-5: Results of two-way mixed factors ANOVA for effects of distance-from-edge and number of trails crossing transect on species richness, Shannon-Weiner index of diversity (H) and evenness (J). Forest fragments, Sainte-Luce 3 (SL3), Sainte-Luce 1 (SL1), and Lokaro (LOK), are listed from least to most degraded.

Dependent variable	Forest fragment	Source	ss	d.f.	ms	*F*	*P*
Number of species	SL3	Distance	0.01	3	0.00	0.12	0.948
		Trails	0.04	1	0.04	2.39	0.148
		D x T	0.03	3	0.01	0.64	0.604
		Error	0.21	12	0.02		
	SL1	Distance	0.43	3	0.14	1.32	0.335
		Trails	0.03	2	0.01	0.13	0.879
		D x T	0.57	6	0.10	0.88	0.55
		Error	0.87	8	0.11		
	LOK	Distance	0.12	3	0.04	0.14	0.932
		Trails	0.01	2	0.00	0.01	0.986
		D x T	0.75	6	0.13	0.46	0.82
		Error	2.17	8	0.27		

Species richness (H)	SL3	Distance	0.00	3	0.00	0.49	0.693
		Trails	0.00	1	0.00	0.00	0.964
		D x T	0.01	3	0.00	1.87	0.189
		Error	0.02	12	0.00		
	SL1	Distance	0.07	3	0.02	2.63	0.122
		Trails	0.00	2	0.00	0.02	0.982
		D x T	0.06	6	0.01	1.20	0.396
		Error	0.07	8	0.01		
	LOK	Distance	0.06	3	0.02	0.41	0.749
		Trails	0.02	2	0.01	0.15	0.86
		D x T	0.23	6	0.04	0.74	0.634
		Error	0.42	8	0.05		
Species evenness (J)	SL3	Distance	0.00	3	0.00	2.30	0.128
		Trails	0.00	1	0.00	4.60	0.053
		D x T	0.00	3	0.00	3.11	0.064
		Error	0.00	12	0.00		

SL1						
	Distance	0.00	3	0.00	2.67	0.119
	Trails	0.00	2	0.00	0.50	0.626
	D x T	0.00	6	0.00	0.93	0.523
	Error	0.00	8	0.00		
LOK						
	Distance	0.01	3	0.00	0.53	0.677
	Trails	0.00	2	0.00	0.23	0.797
	D x T	0.03	6	0.01	0.96	0.508
	Error	0.04	8	0.01		

Table 5-6: Results of one sample Kolmogorov-Smirnov tests, examining the difference between null and observed species distributions (see Fig. 5-5). D is the observed Kolmogorov-Smirnov statistic, and D_α is the critical value at α.

Forest fragment	Distance from edge	D	D_α	α
SL3	5	0.09	0.13	0.05^{ns}
	25	0.09	0.14	0.05^{ns}
	50	0.11	0.14	0.05^{ns}
	100	0.09	0.14	0.05^{ns}
SL1	5	0.2	0.19	0.01^{*}
	25	0.16	0.15	0.05^{*}
	50	0.14	0.15	0.05^{ns}
	100	0.01	0.15	0.05^{ns}
LOK	5	0.35	0.35	$0.01^{=}$
	25	0.35	0.35	$0.01^{=}$
	50	0.46	0.44	0.001^{*}
	100	0.48	0.42	0.001^{*}

ns means that $D < D_\alpha$, not significant at α.

* means $D > D_\alpha$, significant at α.

= means $D = D_\alpha$.

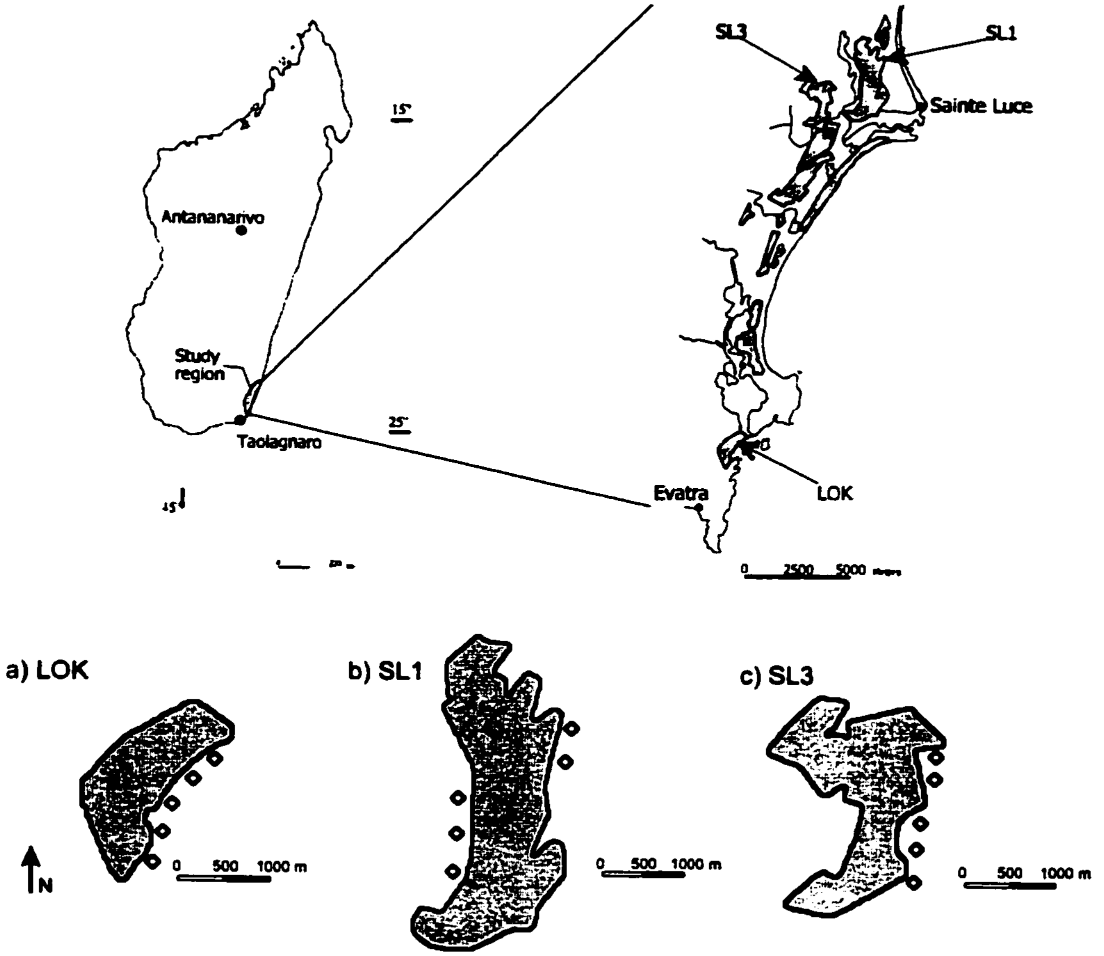

Figure 5-1: Location of the study region in southeastern Madagascar, and of the three forest fragments used in this study, and the starting points (◇) of 100 m transects in a) Lokaro forest, b) Sainte Luce forest 1, c) Sainte Luce forest 3.

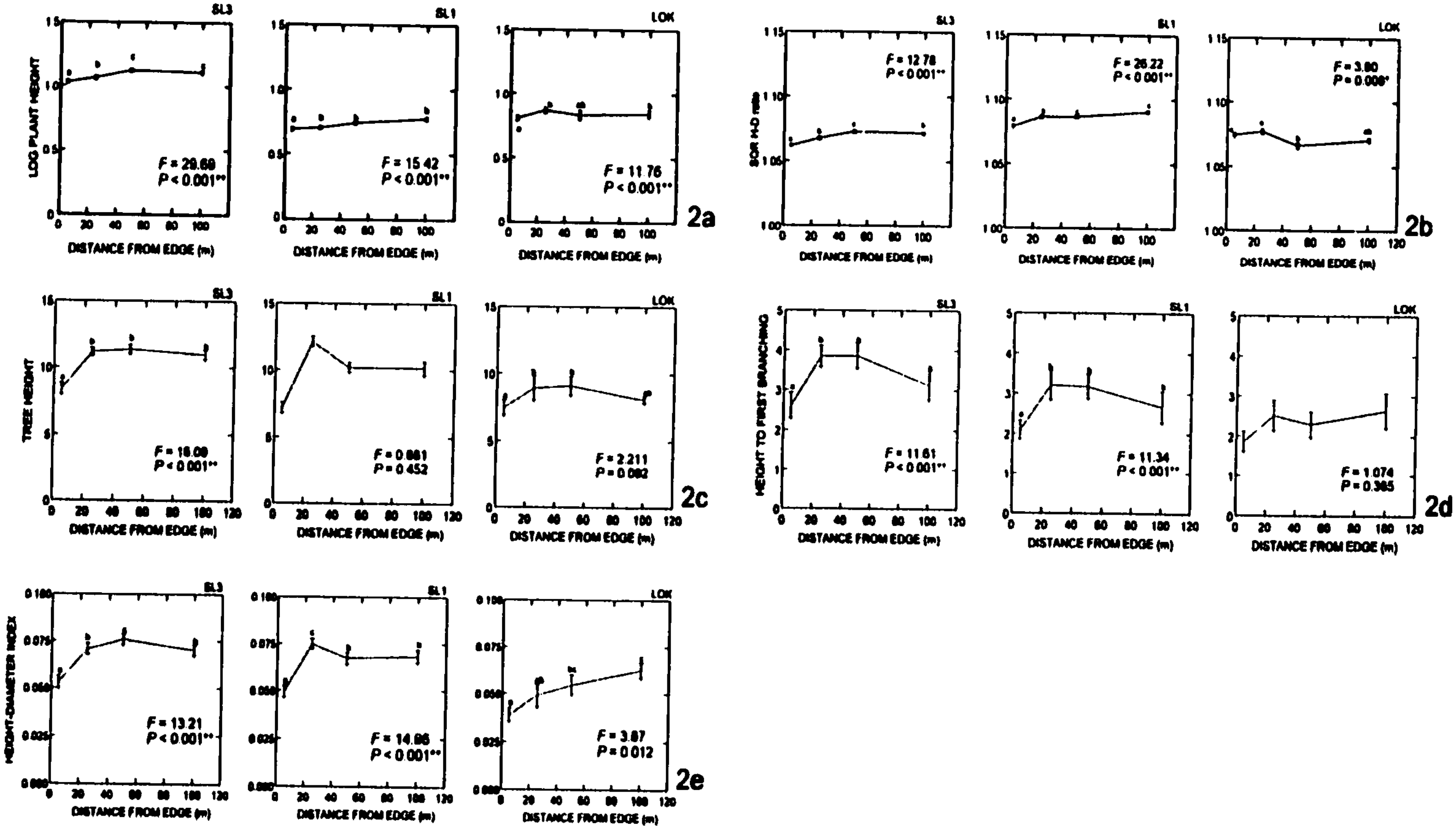

Figure 5-2: Results of one-way ANOVAs examining effects of distance-from-edge on: (a) woody plant height; (b) the square-root of plant height-to-diameter ratio; (c) tree height; (d) height-to-first branching for trees; (e) tree height-to-diameter ratio. Results of LSD post hoc analyses shown with lower case letters; different letters = significant difference between values ($P < 0.05$). Asterisks represent results of Bonferroni corrections; * $P < 0.05$, ** $P < 0.01$.

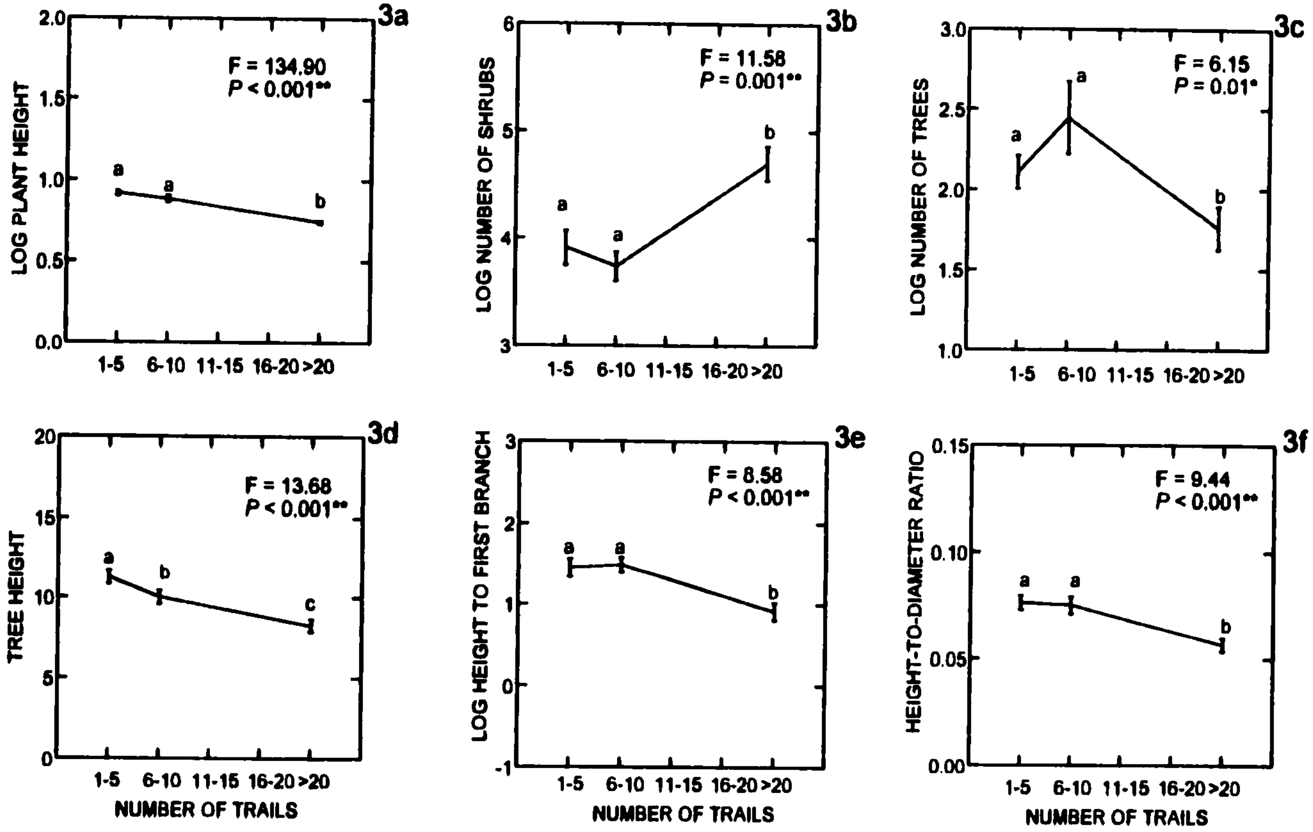

Figure 5-3: Results of one-way ANOVAs examining effects of the number of trails in SL1 on: (a) woody plant height; (b) number of shrubs; (c) number of trees (d) tree height; (e) height-to-first branching for trees; (f) tree height-to-diameter ratio. Results of LSD post hoc analyses shown with lower case letters; different letters = significant difference between values ($P < 0.05$). Asterisks represent results of Bonferroni corrections; * $P < 0.05$, ** $P < 0.01$.

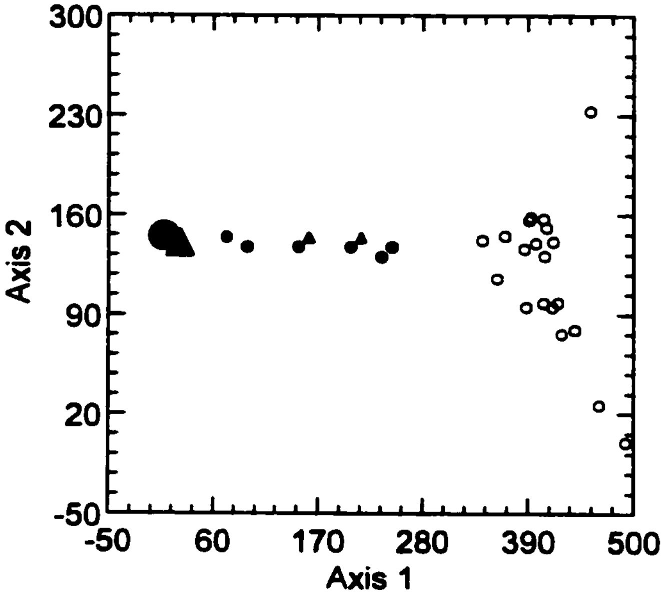

Figure 5-4: Detrended correspondence analysis ordination of plot composition from three forest fragments: LOK (open circles), SL1 (filled circles), and SL3 (triangles). Large circle and triangle represent clumping of 12 SL1, and 18 SL3 plots, respectively. Eigenvalues for Axis 1 = 0.804, for Axis 2 = 0.406.

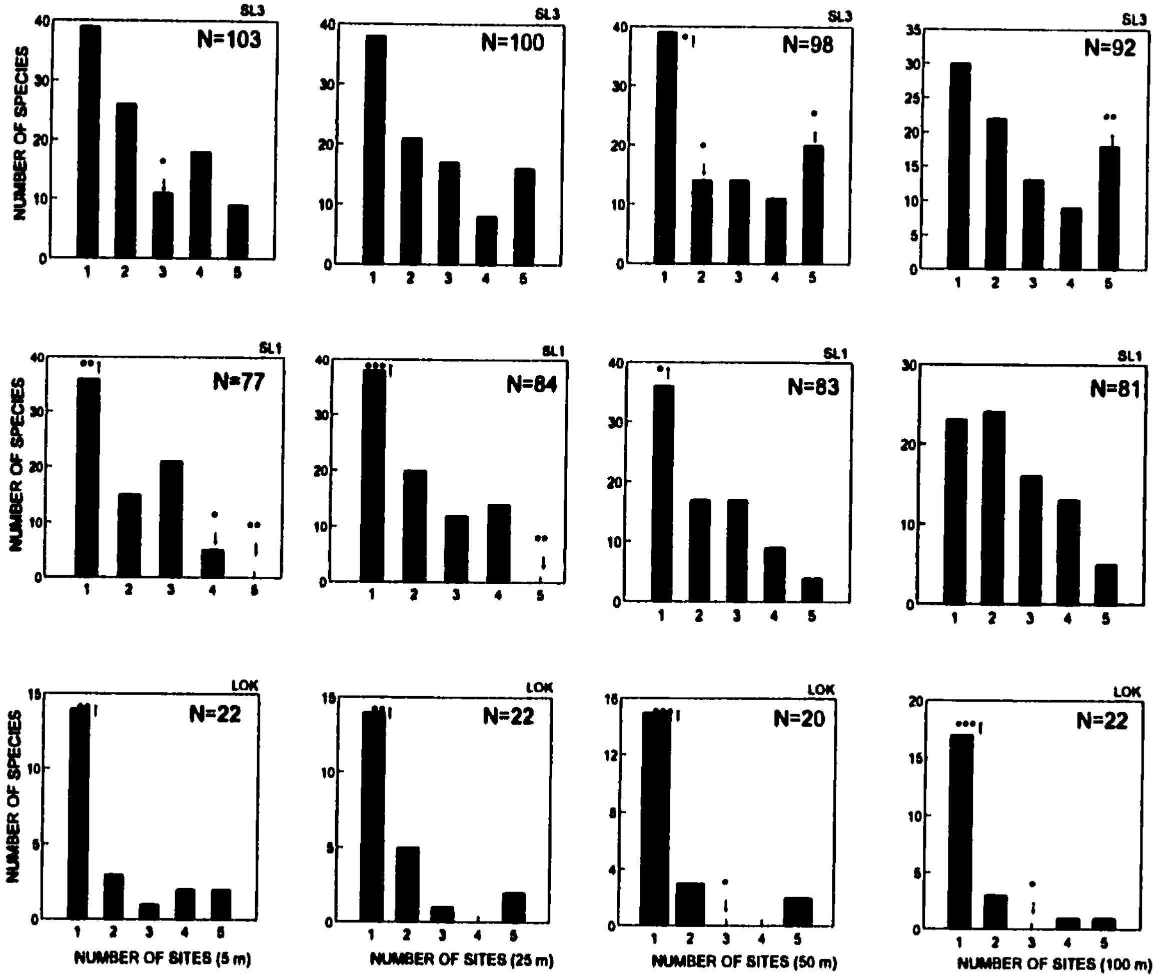

Figure 5-5: Species range distributions for the three forest fragments sampled using 10x10 m plots. N = number of species. ↑ indicates frequency bars that are significantly greater than expected according to the null model, and ↓ indicates those that are significantly less than expected. Significance shown as * = <0.05, ** = <0.01, *** = <0.001.

CHAPTER VI:

GENERAL DISCUSSION AND CONCLUSIONS

The degradation and haphazard removal of intact forests usually results in the creation of a patchwork of forest fragments. The conversion of intact forest into smaller, more isolated fragments results in a number of profound and quantifiable biological changes (Bierregaard et al. 1992;Turner 1996). The priority for thorough studies into the effects of tropical forest fragmentation cannot be overstated. Nowhere is this more true than in Madagascar. Madagascar is considered by some as one of the world's top conservation priorities (Myers et al. 2000), and furthermore Madagascar is severely understudied (Prance et al. 2000); the need for studies such as this is great.

The highly diverse and heterogeneous nature of these forests was evident in the present study. Species-area curves for neither of the two sampling procedures (trees in 50x50 m plots and understory woody vegetation in 10x10 m plots) showed an asymptotic leveling-off, which would indicate most species in the community had been 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. Likewise, Rakotomalaza and Messmer (1999), studying the forests of Madagascar's Andohahela Reserve, located 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 one hectare plots.

As with the other biological measures in this study, species evenness was lowest in the Lokaro forest fragment, and highest in SL3. The loss of biodiversity in this case reduced community evenness, and produced very skewed abundance distributions. The Lokaro forest fragment is essentially a monodominant community (Cadotte et al. 2001). Similar to other hypotheses dealing with ecosystem functioning (see Fukami et al. 2001), a reduced evenness may diminish ecosystem "reliability," or the ability of a system to provide a consistent level of performance over time (Fukami et al. 2001). In another recent study, Wilsey and Potvin (2000) found that total and below-ground biomass in experimental plant communities increased with increasing levels of community evenness. Evenness may be a mesure of relative ecosystem function, more so than diversity per se. If so, then degraded forests will offer fewer, and diminished levels of ecosystem services, especially during periods of stochastic environmental change.

There were significant differences among the four forest fragments in this study in terms of Shannon-Weiner index of diversity, numbers 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). In this 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 *Tambourissa 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 Gross et al. 2000).

Results from Chapter II, specifically involving richness and density values, show that the Lokaro forest fragment is the most degraded fragment, followed by Sainte-Luce 1, and then SL2 and SL3 as co-equals. This hierarchy of 'intactness' was the focus of Chapters III, IV, and V.

In Chapter III, differences in species density and diversity in 50x50 m and 10x10 m plots could not be explained by fragment size. The lack of a significant relationship between fragment area and community composition has been revealed in a number of studies from different ecosystems: plants in Renosterveld shrublands, South Africa (Kemper et al. 1999); plants in an old field, Kansas (Robinson et al. 1992); butterflies in Amazonian forest fragments (Brown and Hutchings 1997); and understory birds in Amazonian fragments (Bierregaard and Stouffer 1997). More important to species diversity than fragment size, appear to be meso- and macro-scale landscape variables, especially anthropogenic influences. These variables, the amount of internal fragmentation (including extent of roads and canopy-breaking trails) proportional to the area of a fragment, and the number of villages per hectare of forest (within radii of <10 km, centred on a forest fragment), together explained >80% of the variation in the number of species per 0.25 ha, and >88% for the index of diversity per 0.25 ha. These two measures also accounted for >87% of the variation in the number of understory species per 0.01 ha and >89% for the index of diversity per 0.01 ha. Disturbance in tropical forests generally causes a decline in species diversity (e.g., Rao et al. 1990), by increasing the probability of extinction for individual populations (Foster 1978). The "intermediate disturbance" hypothesis (see e.g., Grime 1973, Connell 1978), which contends that some disturbance may increase species diversity in some communities, does not appear to be the case in tropical forests (Rao et al. 1990), though a limited number of individual taxa may exhibit a positive response to disturbance (see Chapter II). However the present study may not be considering large enough spatial and temporal scales for a valid test of this hypothesis (see Foster 1978, for a general review of the scales at which disturbances occur in tropical forests).

The two landscape variables (internal fragmentation and villages per hectare of forest) measure both human activity in fragments and general population pressure. The internal fragmentation corresponds to the degree of human access to forest resources, and number of villages per hectare of forest represents local human population pressure relative to the amount of forest resources. This is an important variable, because as natural areas become increasingly used by humans, their biodiversity value increasingly declines, until there is little biodiversity and resource value remaining (i.e., there is a 'land-use cascade' effect on biodiversity; see Terborgh and van Schaik 1997).

Many theoretical and empirical studies of fragmentation make the erroneous assumption that patch quality is uniform and equal (Fahrig and Merriam 1994). The present study has shown that human-caused environmental disturbance and degradation can be far more detrimental to forest community composition than is forest fragment size. Conservation strategies need to view altered landscapes in terms of both habitat destruction (fragmentation) and habitat modification (degradation) (McIntyre and Hobbs 1999).

In Chapter IV, I showed that human-caused habitat degradation represents a broad environmental change, in which one could examine community responses. The human influence is pervasive, not a series of localized catastrophes. We know this because, if local catastrophes eliminated some populations of widespread species, while not affecting the other populations, then R^2 values (in Figs. 4-3b and 4-4b) would have been lower in degraded habitats.

How do theoretical explanations of distribution patterns account for our observed change in the core-satellite pattern following pervasive environmental change? Theories that invoke spatial dynamics (e.g., Hanski 1982, Tokeshi 1992, Hanski et al. 1993) assume that immigration and extinction events for any given species are dependent on the spatial patterns of occupied habitat patches in a patchy environment. In his development of Levins' (1969) distribution model, Hanski (1982) added an extinction term, dependent upon regional occurrence. In the Levins model, the rate of patch extinction increased in proportion to the number of habitat patches occupied, while in Hanski's model the extinction rate was parabolic. Neither immigration nor extinction is independent of patch occupancy. This extinction parameter, termed the "rescue effect" by Hanski and others, describes species whose regional abundance is very high and that have concomitantly lower extinction rates than species inhabiting a moderate number of patches. Our results suggest that the rescue effect does not function under pervasive environmental change. Even by dramatically increasing the extinction term, core species ($p=1$) ought to maintain a negligible extinction rate. Yet, from our results core species appear to have high extinction rates in degraded forests. Generally, causality underpinning the distribution and abundance patterns of species may be attributed to evolutionary history, especially relating to habitats or niches where (or when) species have positive net fitness (Brown 1984, Holt 1987, Holt and Gaines 1992, Brown et al. 1995). Population-level dynamics (i.e., birth and death rates) can be a measure of where (or when) a species is occupying its evolutionarily derived niche, or optimal habitat. Just as organisms exhibit habitat selection as a mode of increasing their fitness (Holt 1987), changing habitats (by landscape degradation) may change the relative fitness of co-occurring species through selection.

Studies of edge effects have been concerned primarily with the differences between edge and interior habitats and the extent to which these differences extend into a habitat patch (see e.g., Bierregaard et al. 1992; Ferreira and Laurance 1997; Laurance et al. 1998a, b; Sizer and Tanner 1999; Harper and Macdonald 2001). However, in Chapter V I was interested in relative differences in edge structure among habitat fragments having different disturbance regimes. Results of the two-way ANOVAs indicate that at SL3 five variables were significantly affected by distance from the edge. In SL3 (which had consistently fewer trails), the number of trails was not a significant factor. However at SL1, which is a moderately-degraded forest, and has the greatest range in the number of trails (4-33), there were seven variables where the number of trails proved to be a significant factor (and six variables where distance-from-edge was a significant factor). At the LOK forest fragment, five variables were significantly affected by the interaction between distance-from-edge and number of trails. These results suggest a certain dynamism to edge effects in anthropogenically-created forest fragments. Results from the intact (SL3) and semi-degraded (SL1) fragments suggest that plant and tree height, elongation extent of woody species, and height-to-first branching may be efficacious measures of edge effects. Our results, for all taxa and for trees only, in the intact forest fragment (SL3) showed that edge effects may occur up to 25-50 m into the fragment. This is in agreement with other results from tropical forests (40 m: Bierregaard et al. 1992; 60 m: Laurance et al. 1998a; 100 m: Laurance et al. 1997b, 1998b).

The undegraded fragment (SL3) shows an increase in the magnitude of the mode of core species frequencies with increasing distance from the edge, with no change after 25-50 m. This pattern is in accord with another result linking disturbance and reduction in number of common (core) species (Cadotte and Lovett-Doust 2001c). Edge habitats have little protection from environmental perturbation and disturbances (e.g., wind, storms, floods, fires, etc.); thus in edge habitats we should expect reduced representation in the core species frequency class. The moderately-degraded fragment (SL1) does show an increase in the number of core species with increasing distance from the edge, but at the same time does not actually show a strong core mode at 50 or 100 m inside the forest. Finally, the highly degraded forest (LOK) does not show any differentiation with distance from edge. The uniform pattern suggests that human disturbance is pervasive, even if not otherwise immediately evident than as pathways cutting the habitat.

Consequences for conservation include the likelihood that, as tropical forests continue to become further fragmented and degraded, we can expect not only the absolute amount of edge habitat to increase, but the quality of interior habitats compared to edge, to decrease. When accounting for human activity, managers may be able to predict which species would be most adversely affected by reductions in interior habitat quality with reducing area.

The general consensus from descriptive tropical studies such as this 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 50x50 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 10x10 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 five out of the nine most abundant taxa, to species level, in a montane plot. An even more dramatic example: on a recent expedition to Madagascar, J. Dransfield and H. Beentje, experts on Palms (Arecaceae) discovered three new genera and 85 new species of palm in eastern Madagascar (Prance et al. 2000). 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 seventeen 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 phylogenetic uniqueness (Cadotte and Lovett-Doust 2001d).

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 c. 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 high conservation value (Foster 1978). Madagascar as a country, and in particular this region, needs proactive, aggressive conservation efforts if Madagascar's valuable and unique treasure trove of biodiversity are to survive well into the future.

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