

# Core and satellite species in degraded habitats: an analysis using Malagasy tree communities

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Received: 19 January 2005 / Accepted: 20 March 2006 / Published online: 9 July 2006  
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**Abstract** Core-satellite theory predicts that, via the “rescue effect”, widespread, abundant species should have reduced risk of local extinctions. We test this hypothesis in southeastern Malagasy littoral forest using data on distribution and abundance of trees and woody understory vegetation in tropical forest fragments along a disturbance gradient. We partition the mortality risk into two kinds of extinction factors, separately operating at demographic (local) and landscape (regional) scales, contrary to core-satellite predictions, for both trees and woody understory vegetation, that the relative number of core (abundant) species declined significantly with increasing disturbance. In the least-degraded forest fragments there was a strong mode of core species, while in the moderately- and severely-degraded fragments the species distributions were essentially log-normal, lacking a substantial core mode. While the rescue effect mitigates one kind of extinction risk, namely local environmental and demographic stochasticity, it may not counterbalance widespread pervasive sources of mortality. The amount of internal forest fragmentation appears to have a much greater effect on species richness and diversity than either fragment size or shape.

**Keywords** Diversity · Extinction · Fragmentation · Madagascar · Metacommunity · Metapopulation

## Core-satellite hypothesis and human-caused habitat degradation

Understanding processes that underpin patterns of species distribution and abundance has long been at the heart of modern ecology (e.g., Wallace 1892; Preston

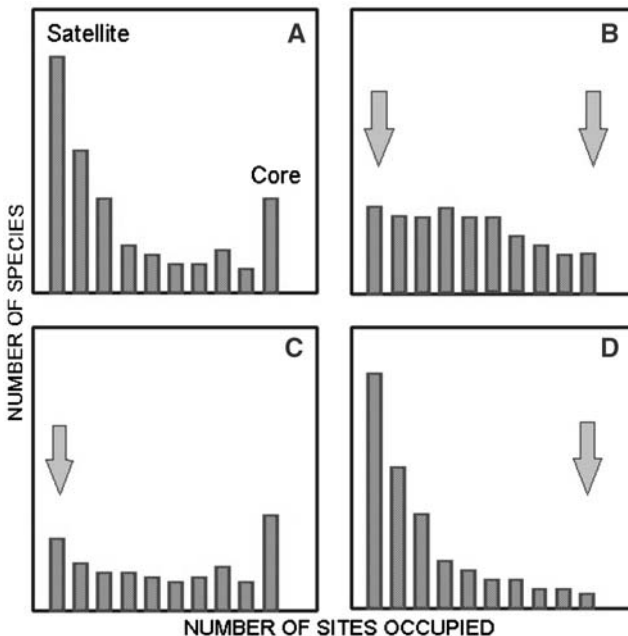
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1962; Whittaker 1965; Rabinowitz 1981; Hanski 1982; Brown 1984; 1995; Holt et al. 1997; Hubbell 2001). Most species, in one sense or another, are rare at some time, somewhere. Indeed, conceptually (Rabinowitz 1981; Gaston 1994) and empirically (Murça Pires et al. 1953; Novotný and Basset 2000; Cadotte et al. 2002), 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 (e.g., Hanski 1982; Brown 1984; Gotelli and Simberloff 1987; Collins and Glenn 1990; 1991; Murray et al. 1999; Guo et al. 2000; Murphy et al. 2006).

One way in which species abundances and distributions are examined is through histograms of the proportion of species occupying each site or sampling locale,  $n_i$ , for  $i$  sites (Fig. 1). Regionally-based studies often find a large mode of rare species (those found at few locales), while a terminal mode of widespread species is often also present (Hanski 1982; Gotelli and Simberloff 1987; Collins and Glenn 1990; 1991; cf., Gaston and Lawton 1989). This bimodal distribution has been said to represent a “core-satellite” pattern (Fig. 1A). According to Hanski’s (1982) modification of Levins’s (1969) metapopulation model, core species are those which are both regionally widespread and locally abundant, while satellite species are characterized by low abundance and restricted regional distribution. The core species are predicted to readily re-colonize open patches (and thereby “rescue” deficient populations), and to persist in a region potentially indefinitely, because the rate of extinction is negatively correlated with the number of patches occupied. In contrast,



**Fig. 1** Theoretical species range distributions showing (A) the core-satellite pattern (Hanski 1982); plus patterns predicted by three hypotheses examining how restricted and widespread species respond to habitat degradation (see text). Arrows indicate mode reduced by habitat degradation. (B) All species are adversely impacted, restricted species go extinct and abundant taxa become rarer; (C) restricted species are disproportionately adversely affected; and (D) core species are disproportionately adversely affected

satellite species are predicted to be less invasive and have lower persistence time (Hanski 1982).

In Levins's (1969) original metapopulation model:

$$dp/dt = ip(1 - p) - ep \quad (1)$$

where  $p$  is the fraction of sites (or patches) occupied, and  $i$  and  $e$  are species-specific constants for immigration and extinction, respectively, extinction rate is linearly related to the number of habitat patches occupied. The first term,  $ip(1-p)$  is the rate at which new (or empty) sites are colonized, while  $ep$  is the rate of local extinctions (Levins 1969). If immigration and extinction are varied stochastically over time, the model produces a unimodal distribution (Gotelli and Simberloff 1987; Collins and Glenn 1991). In Hanski's (1982) core-satellite model:

$$dp/dt = ip(1 - p) - ep(1 - p) \quad (2)$$

the extinction term,  $ep(1-p)$  (i.e., the rescue effect), is greatest when a moderate number of habitat patches are occupied, and least at either low or high patch occupancy (Fig. 2).

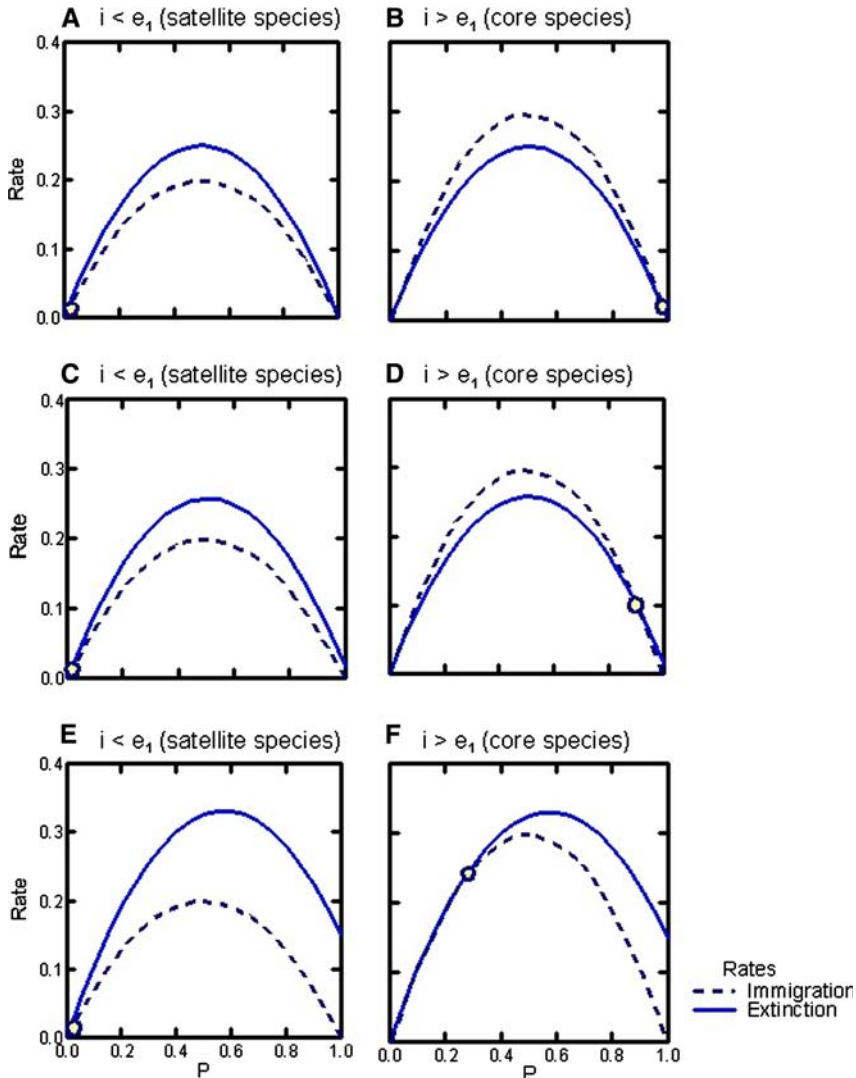
However, Hanski's model fails to account for situations in which relatively common species are more adversely affected by change than are rare species (e.g., Tilman et al. 1994; Nason and Hamrick 1997). Under certain circumstances (e.g., severe environmental changes, generalist predator outbreaks, habitat destruction, pathogen epidemics, etc.) high-abundance species may, disproportionately be adversely affected compared to rarer species in the region. Under such circumstances, we envision two independent extinction factors operating at two different scales. In this model:

$$dp/dt = ip(1 - p) - e_1p(1 - p) - e_2p \quad (3)$$

Hanski's extinction term,  $e_1p(1-p)$ , operates at local patch-level scale, and is in effect a product of local environmental and demographic stochasticity. The second extinction term,  $e_2p$ , operates at larger spatial-scales where the most abundant species have concomitantly greater patch extinction risk.

The two extinction rates,  $e_1$  and  $e_2$ , do not need to be spatially or temporally fixed, or even correlated. Under certain conditions, extinction due to local stochastic processes ( $e_1$ ) may be much more important than widespread extinction pressure ( $e_2$ ) (Fig. 2). Or at other times, such as when humans selectively remove large-boled trees,  $e_2$  overrides any potentially mitigating effect that the rescue effect may have (Fig. 2).

This pervasive extinction risk is likely an important driver in high diversity tropical forest, as they are under sustained pressure from human activities (Whitmore 1997). One of the more insidious consequences of human-caused deforestation is fragmentation of formerly contiguous communities. Fragmentation, besides representing a reduction in area of habitat (Simberloff 2000), creates access and inroads to forest resources for human populations (Laurance 2001). This increased access equates to increased pressure on the remaining communities. Nowhere is the trend towards fragmentation and degradation more of a concern than in the coastal forests of eastern Madagascar (Dumetz 1999; Cadotte et al. 2002; Watson et al. 2004).



**Fig. 2** Immigration and extinction rates related to the proportion of habitat patches occupied ( $P$ ), from Eq. 3. In panels (A) and (B) the second extinction term ( $e_2p$ ) is zero. Therefore the equilibrium proportion of habitat patches occupied by a single species (circle) is zero if the extinction rate is greater than the immigration rate (A), or 1 if immigration is greater (B). At low  $e_2$  (C and D) the curves are qualitatively similar to (A) and (B) except that when  $i > e_1$  (D) the equilibrium  $P$  is less than 1. Finally when  $e_2$  is higher, the time to extinction when  $i > e_1$  is much quicker (relative distance between the  $i$  and  $e$  curves) (E). When  $i < e_1$  the equilibrium  $P$  is much lower than 1 (F). In A, C, and E:  $i=0.8$ ,  $e_1=1$ ; for B, D, and F:  $i=1.2$ ,  $e_1=1$ ; and  $e_2=0$  (A and B), 0.015 (C and D), or 0.15 (E and F)

### Madagascar tree communities as an example

Elsewhere we have described significant differences in tree and woody understory species abundance, richness and diversity among large forest fragments of south-eastern Madagascar (Cadotte et al. 2002). Here we use Malagasy data to examine

species abundance and distribution patterns among forest fragments in different stages of degradation. Specifically, given that the extent of forest degradation has resulted in species loss, we analyze persistence and loss patterns in these fragments in the context of three metapopulation models. There are three possible effects of habitat degradation (see Fig. 1B–D). First, that the two modes (satellite and core) as well as intermediate classes are all negatively affected by habitat degradation, with rare species disappearing and common species becoming relatively less abundant (Fig. 1B); secondly, that degradation disproportionately reduces rare species (Fig. 1C); and finally, that degradation disproportionately affects common species retaining a significant proportion of satellite species (Fig. 1D). We test two hypotheses: (1) if communities really do operate under Hanski's core-satellite metapopulation dynamics then core species ought to be relatively resistant to extinction pressure (Fig. 1C); or (2) if the distribution of species is niche-based then altering niches (through degradation) can have very dramatic effects on core species (Fig. 1D).

Validation of these patterns not only comes from the distribution of the number of sites occupied, but also from the correlation between abundances and number of sites occupied (Gotelli and Simberloff 1987). Levins' (1969) model predicts no relationship between species abundance within plots and number of sites occupied, while Hanski's (1982) model predicts a strong positive relationship (Gotelli and Simberloff 1987). We expect that forest fragments undergoing Hanski-type processes (Eq. 2) will also have a significant relationship between abundance and number of sites occupied, while the opposite should be true for fragments subject to Levins-type processes (Eq. 1).

### Study area and sampling method

The littoral forest fragments used here are located along the southeastern coast of Madagascar (see Cadotte et al. [2002] for maps and descriptions of the region and forest fragments). The four forest fragments which we use in this analysis were referred to by regional acronyms in the previous publication (SL3, SL2, SL1, LOK, respectively) and are here referred to as Least degraded 1, Least degraded 2, Moderately degraded, and Degraded, respectively. Degradation of these fragments was defined as degree of change (in species composition and richness) from an assumed pre-fragmentation continuous forest, and which we will justify, below.

Within each fragment, we sampled 20 randomly placed 50 × 50 m plots. All trees with a diameter at breast height (DBH) ≥ 10 cm were recorded. In addition, sixty 10 × 10 m plots along transects from edge to interior in three fragments were sampled completely for all woody vegetation taller than 1 m. For complete sampling details see Cadotte et al. (2002).

It should be noted at the outset that the design of this study suffers from the problem of pseudo-replication (see Hurlbert 1984) with respect to degradation pressure (i.e., unreplicated degraded fragments). Yet we feel the trends we observed have validity. Inadequacy in the design of this experiment is mitigated to some extent, as we examined a gradient of effects over large spatial scales (see Wiens and Parker 1995 for a review of the inherent difficulties in analyzing environmental impacts). Sampling over large spatial scales reduces the influence of localized phenomena, and samples along a gradient enable comparisons along a continuous

gradient instead of generating results from an otherwise pseudo-replicated comparison (i.e., degraded- vs. undegraded fragments). Moreover in the present study, the same general result was detected using two separate and independent sampling methods, measuring two different groups of taxa (trees vs. woody understory vegetation). The patterns observed in this data could be a useful platform from which, deductive approaches could be derived (e.g., see Oksanen 2001).

### Justifying degradation

A large part of this study supposes that the different forest fragments are in different stages of degradation. To justify this premise, we examine species richness, density and Shannon–Weiner diversity ( $H'$ ) among fragments. Results of a one-way ANOVA (Table 1) indicate that there are significant differences among fragments, with the two least degraded fragments having greatest richness, density and diversity, and the degraded fragment the lowest values, and the moderately-degraded fragment having intermediate values.

We also looked for the cause of these differences by correlating (with Bonferroni corrected probabilities) several patch-level variables with the three measures of diversity. These variables included fragment area (ha), and three indices representing the potential effect of irregular shapes on edge effects (Wilcove et al. 1986): (1) PA, perimeter to area ratio (m/ha); (2) IPA, internal perimeter (caused by roads and canopy-breaking trails) to area ratio (m/ha); and (3) TPA, total perimeter (external and internal) to area ratio (m/ha).

We also investigated human population pressure, using as an index the number of villages per forest area (/ha) in three radii, 5, 7.5 and 10 km. These radii represent probable distances rural Malagasy people tend to travel on foot to collect resources in the form of forest products (see Shyamsundar and Kramer 1997). If better demographic data had been available, then it would have been possible to standardize the index of population pressure by actual population size, but such data were unavailable. Of the approximately 30 villages in the vicinity of the four forest fragments, many are relatively small, averaging 150–300 people per village (MWC, personal observations). Values for population pressure were log transformed for analysis as these values were highly variable, and in some cases different by an order of magnitude.

Results of these correlations (Table 2) reveal that the internal perimeter to area ratio (**IPA**) is significantly related to differences in richness, density and diversity. Internal fragmentation corresponds to the degree of human access to forest resources; the index supports the notion that human-caused degradation is driving species diversity patterns. IPA values should become increasingly important as forest habitats become increasingly exploited by humans.

### 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, enabling inferences about relative change. A null distribution was constructed using Ecosim ver. 7 (Gotelli and Entsminger 2004); we used the species-by-site matrix and allowed Ecosim to randomly resample

**Table 1** Results of one-way ANOVA for diversity and density measures among the four forest fragments

Variable	Trees ≥10 cm dbh					All woody vegetation ≥1 m ht						
	Source	d.f.	MS	F-ratio	P	LSD (D, MD, LD2, LD1) <sup>a</sup>	Source	d.f.	MS	F-ratio	P	LSD (D, MD, LD1) <sup>a</sup>
Richness	Forest	3	1466.18	26.46	<0.001	a b c c	Forest	2	8435.22	204.76	<0.001	a b c
	Error	16	55.02				Error	57	41.20			
Density	Forest	3	5530.80	3.74	0.033	a ab b b	Forest	2	20132.52	45.20	<0.001	a b c
	Error	16	1480.68				Error	57	4454.23			
Diversity	Forest	3	3.66	49.45	<0.001	a b b b	Forest	2	27.16	244.15	<0.001	a b c
	Error	16	0.07				Error	57	0.11			

LSD refers to the results of post hoc least significant differences analyses ( $P < 0.05$ )

<sup>a</sup> Acronyms in parentheses refer to order of forest fragments (D = degraded, MD = moderately degraded, LD1 = least degraded 1, and LD2 = least degraded 2), and the alphabetic code refers to significant differences (with “a” representing the smallest mean, followed by “b” and so on) between these fragments, in the specified order ( $P < 0.05$ )

**Table 2** Pearson correlations (and Bonferroni probabilities) between landscape-level variables and mean richness and density values

Landscape variables <sup>a</sup>	Trees $\geq 10$ cm dbh				All woody vegetation $\geq 1$ m ht			
	<i>N</i>	Richness	Density	<i>H'</i>	<i>N</i>	Richness	Density	<i>H'</i>
Area	4	0.29 <sup>ns</sup>	0.16 <sup>ns</sup>	0.47 <sup>ns</sup>	3	0.36 <sup>ns</sup>	0.37 <sup>ns</sup>	0.52 <sup>ns</sup>
PA	4	-0.11 <sup>ns</sup>	-0.12 <sup>ns</sup>	-0.26 <sup>ns</sup>	3	0.14 <sup>ns</sup>	0.13 <sup>ns</sup>	-0.03 <sup>ns</sup>
IPA	4	-1.0**	-0.99*	-0.98*	3	-1.0*	-0.99*	-1.0*
TPA	4	-0.70 <sup>ns</sup>	-0.70 <sup>ns</sup>	-0.79 <sup>ns</sup>	3	-0.56 <sup>ns</sup>	-0.57 <sup>ns</sup>	-0.70 <sup>ns</sup>
Vill-5	4	-0.92 <sup>ns</sup>	-0.98*	-0.85 <sup>ns</sup>	3	-0.96 <sup>ns</sup>	-0.96 <sup>ns</sup>	-0.90 <sup>ns</sup>
Vill-7.5	4	0.45 <sup>ns</sup>	0.25 <sup>ns</sup>	0.52 <sup>ns</sup>	3	0.94 <sup>ns</sup>	0.94 <sup>ns</sup>	0.98 <sup>ns</sup>
Vill-10	4	-0.36 <sup>ns</sup>	-0.22 <sup>ns</sup>	-0.53 <sup>ns</sup>	3	-0.44 <sup>ns</sup>	-0.45 <sup>ns</sup>	-0.59 <sup>ns</sup>

ns—refers to the result being “non-significant”

\* refers to  $P < 0.05$ ; \*\*  $P < 0.01$

<sup>a</sup>Landscape variables are: Area, area of fragment (ha); PA, perimeter to area ratio; IPA, internal perimeter to area ratio; TPA, PA + IPA; Vill-5, the number of villages per forest area (ha) in a 5 km radius; Vill-7.5, in a 7.5 km radius; and Vill-10, in a 10 km radius

sites within a fragment. We kept the number of species per site constant but allowed the number of sites each species occurs in to vary (i.e., each species had an equal chance at being selected). We saved the output of ten randomizations and used the mean variance (which was small in all cases) from the random sample in the T-test statistics.

We then compared each of the observed occupancy distributions to what we would expect if species were randomly distributed. This allows us to first determine whether the observed distribution deviates from random sorting, and, secondly, to compare the ways in which they differ from randomness, enabling inferences about the effects of degradation.

We compared the observed to the null distributions by using one sample T-tests with Bonferroni corrected probabilities. Since we are testing  $H_0: \mu_r \neq \mu_o$ , where  $H_0$  is the observed number of species, and hence not random, we derived our  $P$ -values from 5000 randomizations.

Finally, a regression of the log-transformed abundances versus the number of sites occupied was carried out for each distribution. This was done to determine if there was a positive relationship, as predicted by Hanski (1982). All statistics were done using NCSS (Hintze 2001).

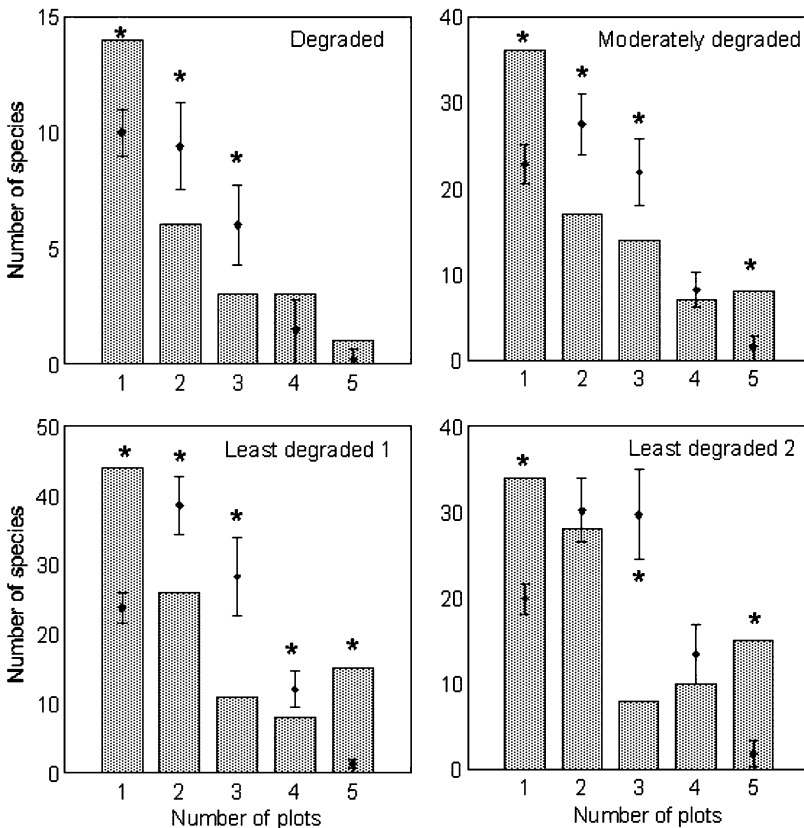
### Metapopulation assumptions

We assume that, within the continuous pre-fragmentation forest, populations exhibit metapopulation structuring, similar to what other authors have envisioned with continuous vegetation communities (e.g., Gotelli and Simberloff 1987; Collins and Glenn 1990; 1991). With fragmentation of this forest, an even more rigid metapopulation structure is placed upon the communities. The primary fragmentation events (for these forests) occurred over 50 years ago (MWC—personal communication with local elders), meaning that, since littoral trees do not survive as long as inland trees (de Gouvenian and Silander 2003), the younger generation of mature trees has grown within this fragmented metapopulation landscape in which fragment dynamics are likely driving the observed patterns.

## Results

### Distributional patterns for 50 × 50 m plots

Each distribution differed significantly from the null distribution (Fig. 3), suggesting that these distributions are likely structured by non-random processes. All these distributions indicate more rare species than expected. Most important is the difference in the terminal mode. The final two occupancy classes in the degraded fragment does not differ from the null, while those in the other three distributions do differ. The moderately-degraded fragment has a core mode significantly different from the null model. The two least-degraded fragments have significantly larger terminal modes, compared with the null, but these modes also show a greater magnitude in these differences compared with that from the moderately-degraded fragment.



**Fig. 3** The bars show the species range distributions for the four forest fragments sampled using 50 × 50 m plots. Mean randomized distributions and their variances are represented by the dots with error bars ( $\pm$ SD). \* Refer to significant departures from the null distribution using T-tests with *P*-values produced with 5000 randomizations and with Bonferroni corrections ( $<0.05$ )

## Distributional patterns for 10 × 10 m plots

The patterns observed from the 10 × 10 m understory plots were qualitatively similar to those for the 50 × 50 m plots. Each distribution differed from the null distributions (Fig. 4). Again the occupancy patterns of these fragments is evidently not structured by random processes, and each distribution contained more rare species than expected. For understory species, both the degraded and moderately-degraded fragments lack a core mode. The least-degraded fragments had a significant mode of core species.

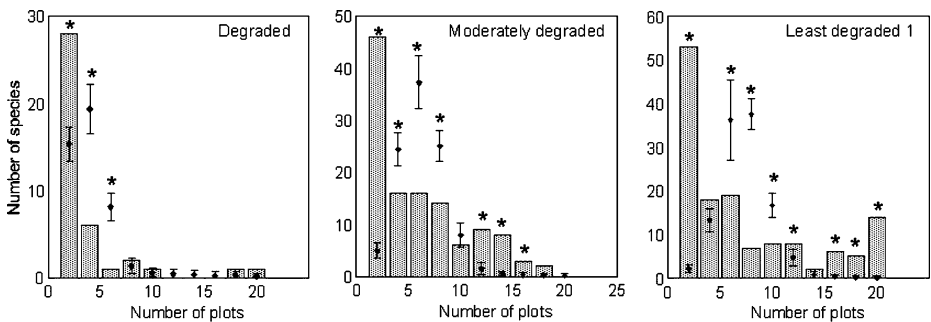
## Abundance–distribution relationships

There was a significant relationship between species abundance and the number of sites occupied ( $P < 0.01$ ). This confirms that Hanski-type processes (Eq. 2) are occurring whether or not there is a significant core mode. The relationships in the 10 × 10 m data were not so strong as those for the 50 × 50 m data ( $R^2 = 0.14$ – $0.40$  vs.  $0.61$ – $0.72$ , respectively).

## Discussion

Human-caused habitat degradation represents a broad environmental factor in which plant community responses can be examined. We used the differing levels of human influence on four forest fragments to test whether or not common (core) species are resistant, via immigration, to adverse conditions. These fragments also likely face differing levels of natural disturbance beyond human disturbance. These fragments are all within 4 km of the coast, but susceptibility to cyclone damage along the east coast can measurably decline over a few kilometres (de Gouvenain and Silander 2003). Regardless, our results point to a profound effect from human caused degradation.

How do theoretical explanations of distribution patterns account for our observed change in the core-satellite pattern (namely, the reduction in core species), following pervasive environmental change? Theories invoking spatial dynamics (e.g., Hanski 1982; Tokeshi 1992; Hanski et al. 1993) assume that, in a patchy environment,



**Fig. 4** The bars show the species range distributions for the four forest fragments sampled using 10 × 10 m plots. Mean randomized distributions and their variances are represented by the dots with error bars ( $\pm$  SD). \* Refer to significant departures from the null distribution using T-tests with  $P$ -values produced with 5000 randomizations and with Bonferroni corrections ( $<0.05$ )

immigration and extinction events for any given species are dependent on the spatial patterns of occupied habitat patches (Cottenie et al. 2003; Cadotte 2006). Assuming that communities that 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?

Our results suggest that the rescue effect may not function under pervasive environmental change. Even following a dramatically increased extinction term in Eq. 2, core species ( $P=1$ ) ought, in theory, to maintain a negligible extinction rate. Yet our results suggest core species seem to have high extinction rates in degraded forests. A likely reason for this discrepancy is shown in Fig. 2. By adding an extinction term ( $e_2p$ ) in Eq. 3, which increases in proportion to patch occupancy, we can account for the observed patterns. The second extinction term ( $e_2p$ ), depending upon environmental conditions, could range from having a negligible effect to negating any rescue effect (Fig. 2).

Although adding an extinction term ( $e_2p$ ) to a spatial model may account for the fact that common species do not appear to be more extinction resistant, it does not address directly the underlying causes of that observed pattern. Addition of a second extinction term may not represent spatially-related population dynamics per se, rather it may simply reflect an underlying organism–environment interaction. In general, the distribution and abundance patterns of species has been attributed to evolutionary history, especially relating to habitats or niches where (or when) species have positive net fitness values (Brown 1984; Holt 1987; Holt and Gaines 1992; Brown et al. 1995). Population-level dynamics (via birth and death rates) could serve as a measure of where (or when) a species is occupying such an evolutionarily-derived niche. Just as organisms exhibit habitat selection as a vehicle for increasing their fitness (Holt 1987), altered habitats (by following landscape degradation) may change the relative fitnesses of co-occurring species, especially in sessile organisms. Holt et al. (1997) recently developed a model invoking demographic variables, density dependent birth rates and density independent death rates to account for both species range size and average density. All other things held 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). Thus, as habitat is altered by fragmentation effects, the fundamental niche of most species is also affected, selecting most against these species. Habitat degradation may shift the niche or preferred habitat of a species (Holt 1987), thereby denying core species their optimal habitat.

### Conservation issues

A number of studies have shown that fragmentation has observable effects on species richness and abundances (Diamond and May 1976; Wilcove et al. 1986; Klein 1989; Scariot 1999; Ochoa-Gaona et al. 2004; Watson et al. 2004; Zhu et al. 2004; cf. Simberloff 2000). Smaller fragments cause faster population declines in susceptible species (Ferroz et al. 2004), and increases in species capable of using the inter-patch matrix (Summerville 2004). Further, fragmentation has been shown to alter mortality and recruitment dynamics in tree communities (Laurance et al. 1998a, b; 2000). What these studies do not address is the impact that continuing human-caused degradation can have on fragmented habitats, especially in places where significant

proportions of people use forest resources. Butler et al. (2004) showed how fragmentation patterns can to some extent be driven by socio-economic factors in the USA, but in tropical countries fragmentation also increases access to forest resources (Laurance 2001). Here we speculate how human demographic patterns can continue to drive change within fragments.

The dynamics of individual species and populations may reveal more about the diverse effects of fragmentation than purely community-based demographic studies. For example, 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 may suffer lower reproductive rates than rare, pollinator-specific trees, in which flying pollinators can travel long distances between conspecifics (Nason and Hamrick 1997).

The species involved seem to show different dynamics in the different fragments (Cadotte 2001). *Dracaena* spp. and *Cremocarpon lantzii* appear to have high levels of recruitment in moderately-disturbed sites, where they also have 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 attains extremely high densities. In the degraded fragment, *T. purpurea* becomes a monodominant, distinctly characterizing that fragment (Cadotte et al. 2002). Essentially, different taxa appear to respond in different ways to the altered habitats, possibly reflecting life-history features of particular species. Very few species thrive in heavily disturbed forests; rather more manage in moderately disturbed forest, and many are successful in undisturbed fragments. Cunningham (2000a, b) showed that an individual taxon's reproductive success was closely tied to fragmentation effects, with plant species either increasing or decreasing in reproductive success as a result of fragmentation.

More important to species diversity than fragment size were anthropogenic landscape variables at the meso- and macro-scale. Most studies examining biotic effects of fragmentation have not evaluated external influences on the plant community within the fragment. Janzen (1983; 1986) investigated effects of surrounding vegetation and the influence that pesticides and fire may have, and Goosem (1997) studied effects of roads, yet none have looked at human activities in the form of the proximity of communities and path access into vegetation fragments, for people whom subsistence includes direct resource extraction. Here we show that the amount of internal fragmentation (IPA) appears to have a much greater effect on species richness and diversity than either fragment size or fragment shape.

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 (see too 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 strong test of this hypothesis (see Foster 1978 for a review of the scales at which disturbances occur in tropical forests). What we have observed was a continuum of habitat degradation, from least-degraded fragments (having most diverse communities) to most-degraded fragments (and least diverse communities).

## Conclusion

Many theoretical and empirical studies of fragmentation make an assumption that patch quality is uniform and equal (Fahrig and Merriam 1994). The present study has shown that anthropogenic environmental disturbance and degradation can be far more detrimental to forest community composition than effects of 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 population dynamics and environmental responses.

**Acknowledgements** We thank Parc Botanique et Zoologique de Tsimbazaza for allowing us to undertake a research programme in Madagascar, as well as for final determinations of voucher specimens; ONG Azafady, the villages of Manafiafy and Evatra, plus Felix Rakotondraparany, Rakotonasolo Franck, Ludovic Reza, Monsieur Rigobert and Mosa Davis for field assistance and invaluable logistical support; we are grateful to J.A. Drake, S.M. McMahon, T. Fukami and R.T. M'Closkey for useful comments on the manuscript. We are especially grateful to T. Fukami for suggesting Fig. 2. This work benefited from financial support of the Ontario Public Interest Research Group, the University of Windsor, and a Research Grant to JLD from the Natural Sciences and Engineering Research Council of Canada.

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