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Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments

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A first analysis of the stability of trophic structure following tropical forest fragmentation was performed in an experimentally fragmented tropical forest landscape in Central Amazonia. A taxonomically and trophically diverse assemblage of 993 species of beetles was sampled from 920 m^2 of leaf litter at 46 sites, varying in distance from forest edge and fragment area. Beetle density increased significantly towards the forest edge and showed non-linear changes with fragment area, due to the influx of numerous disturbed-area species into 10 ha and 1 ha fragments. There was a marked change in species composition with both decreasing distance from forest edge and decreasing fragment area, but surprisingly this change in composition was not accompanied by a change in species richness. Rarefied species richness did not vary significantly across any of the sites, indicating that local extinctions of deep forest species were balanced by equivalent colonization rates of disturbed-area species.

The change in species composition with fragmentation was non-random across trophic groups. Proportions of predator species and xylophage species changed significantly with distance from forest edge, but no area-dependent changes in proportions of species in trophic groups were observed. Trophic structure was also analysed with respect to proportions of abundance in six trophic groups. Proportions of abundance of all trophic groups except xylomycetophages changed markedly with respect to both distance from forest edge and fragment area.

Local extinction probabilities calculated for individual beetle species supported theoretical predictions of the differential susceptibility of higher trophic levels to extinction, and of changes in trophic structure following forest fragmentation. To reduce random effects due to sampling error, only abundant species ($n \geqslant 46$) were analysed for extinction probabilities, as defined by absence from samples. Of these common species, 27% had significantly higher probabilities of local extinction following fragmentation. The majority of these species were predators; 42% of all abundant predator species were significantly more likely to be absent from samples in forest fragments than in undisturbed forest. These figures are regarded as minimum estimates for the entire beetle assemblage because rarer species will inevitably have higher extinction probabilities. Absolute loss of biodiversity will affect ecosystem process rates, but the differential loss of species from trophic groups will have an even greater destabilizing effect on food web structure and ecosystem function.

Keywords: tropical forest fragmentation; trophic structure stability; biodiversity loss; extinction rates; edge effects; Central Amazonia

1. INTRODUCTION

Species are not affected equally by habitat fragmentation. Though intuitive, this tenet is fundamental to the way we approach biodiversity studies. Spatial models of population dynamics make it clear that habitat subdivision can alter the stability of populations and species interactions, but in contrasting ways (Kareiva 1990). The most extreme expression of such changes is local or regional population extinction. Most empirical studies of habitat fragmentation have focused on single-species dynamics, on pair-wise interactions, or on many species within one trophic level (reviews in Kareiva 1990; Saunders *et al*. 1991; Andrén 1994, 1996; Didham *et al*. 1996; Turner 1996), and have attempted to define species traits that affect vulnerability to local or regional extinction (review in Gaston 1994). Such traits include: life-history strategy, body size, habitat or diet specificity, longevity, dispersal ability, population variability, rarity and trophic level (Pimm 1982, 1991; Soulé 1983, 1987; Diamond 1984; Simberloff 1986; Pimm *et al*. 1988; Laurance 1991; Cracraft 1992; Nee & May 1992; Caughley 1994; Gaston 1994; Tilman *et al*. 1994). Of these, little attention has been paid to the influence of trophic level on extinction probability (Lawton 1995), or to the stability of trophic structure in fragmented habitats (Mikkelson 1993). Without such data it may be impossible

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to extrapolate from individual species responses to the effects of fragmentation on food webs or entire communities (Kareiva 1990).

Theory predicts that trophic position confers a differential probability of extinction on species following perturbation. Specifically, species at higher trophic levels are more vulnerable to extinction (Pimm & Lawton 1977, 1978, 1995; Polis *et al*. 1989; Schoener 1989; Pimm 1991; but, see Lawler 1993) as a result of lower absolute population sizes (Holt 1996), higher population variability (den Boer 1993; Kruess & Tscharntke 1994) and the dependence of higher trophic levels on their prey populations (Schoener 1989; Holt 1996). Consequently, food chain length appears shorter in unpredictable systems (Pimm & Kitching 1987; Pimm *et al*. 1991) and in small habitat fragments (Schoener 1989).

Some successional communities show shifts in trophic structure following disturbance. Dynamic models predict that early successional webs should depart significantly from the norm, for example in having unusual predator to prey ratios (Mithen & Lawton 1986; Pimm *et al*. 1991). Empirical support includes studies of successional insect communities in Britain (Brown & Southwood 1983), and island recolonization experiments in Florida, USA (Heatwole & Levins 1972).

Application of these predictions to communities in fragmented habitats has recently been formalized by Holt (1996). His island biogeographic perspective on spatial variation in food web structure explicitly predicts that the slope of the species-area curve increases with trophic level. This implies that: (i) predator species will go extinct more rapidly than prey species with declining area; and (ii) proportions of species in different trophic groups will change with declining area. To the extent that these predictions can be extrapolated to habitat islands, habitat specialists on isolated habitat patches might be expected to show similar extinction dynamics to real island species, and the community in general to exhibit a significant shift in trophic structure following fragmentation. But an important, additional complication in fragmented habitats may be added changes in trophic structure driven by species influxes from adjacent, disturbed habitats (Laurance 1991; Pimm 1991).

Holt (1996) cites support for his model from Schoener *et al*. (1995), who showed significant effects of island area and isolation on the proportions of parasitoids on Bahamian islands. Similarly, Patterson (1984) found that species in higher trophic levels went extinct faster within mammal assemblages of the Southern Rocky Mountains, USA. J. Zabel and T. Tscharntke (unpublished results) found significant changes in the trophic structure of insect communities on nettle (*Urtica dioica*) patches of differing area and isolation, with predators being more affected by habitat isolation and herbivores more affected by habitat area. Finally, Kareiva (1987) and Kruess & Tscharntke (1994) found that predators were more sensitive to habitat fragmentation than their phytophagous prey.

In contrast, a number of studies have shown no significant effect of fragment area on trophic structure: Brown (1978) found no change in the trophic structure of boreal mammals and birds on different-sized habitat fragments in the Great Basin, USA; Hamilton & Stathakis (1987) found equivalent trophic group proportions in soil arthropod communities on remnant prairie patches of 2–25 ha in Illinois, USA; Heatwole & Levins (1972) showed that trophic group proportions were constant across islands of varying size, both before defaunation and after a sufficiently long period of colonization; and, in the most detailed study to date, Mikkelson (1993) found invariant proportions of species in different trophic groups among vertebrates and plants on habitat islands that varied widely in area and degree of isolation, in both North America and Australia.

It should be noted that the scales at which these studies were conducted have some bearing on the interpretation of trophic structural stability. Recent analyses suggest that many important attributes of food webs, including the proportions of species in different trophic groups, are scale-dependent (Martinez 1994; Deb 1995; Martinez & Lawton 1995).

Trophic structural stability is of more than just academic interest. Although there are well-formulated arguments for the conservation of all species (Kunin & Lawton 1996; Leemans 1996), we are most concerned with the maintenance of ecosystem function. There is a recognized relationship between food web structure and ecosystem function (Pimm 1982) that is supported by recent empirical findings (Naeem *et al*. 1994, 1995, 1996; Tilman & Downing 1994; Mooney *et al*. 1995; Didham *et al*. 1996; Johnson *et al*. 1996). Thus, if, as appears to be the case, species at different trophic levels are differentially affected by habitat fragmentation, then there will be an inevitable alteration to ecosystem functioning.

A specific test of the effects of fragmentation on the stability of trophic structure in a diverse beetle (Coleoptera) assemblage was performed in an experimentally fragmented tropical forest landscape in Central Amazonia. Tropical forest fragmentation is of particular concern to conservationists because of the rapid rate of deforestation in tropical countries (Skole & Tucker 1993; Vitousek 1994), and the high levels of biodiversity and endemicity of tropical forests. Insects represent the major portion of this diversity (Hammond 1995), and beetles in particular are taxonomically and trophically among the most diverse of all animal groups. Experiments were designed to resolve differences in trophic structure due to: (i) fragment area; and (ii) edge effects. This is the first study of trophic structural stability in tropical forest fragments, and the first to describe community-level changes in trophic group proportions supported by local extinction probabilities for individual species.

2. METHODS

(a) *Study sites*

The study was carried out from January through May 1994 at the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, Central Amazonia, Brazil (2°25′ S 59°50′ W) (figure 1). The BDFFP is administered by the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Smithsonian Institution, and is the only experimental forest fragmentation project of its kind in the world, offering unique opportunities to study the impact of fragmentation on biotic and abiotic processes in tropical forest fragments of known age and history.

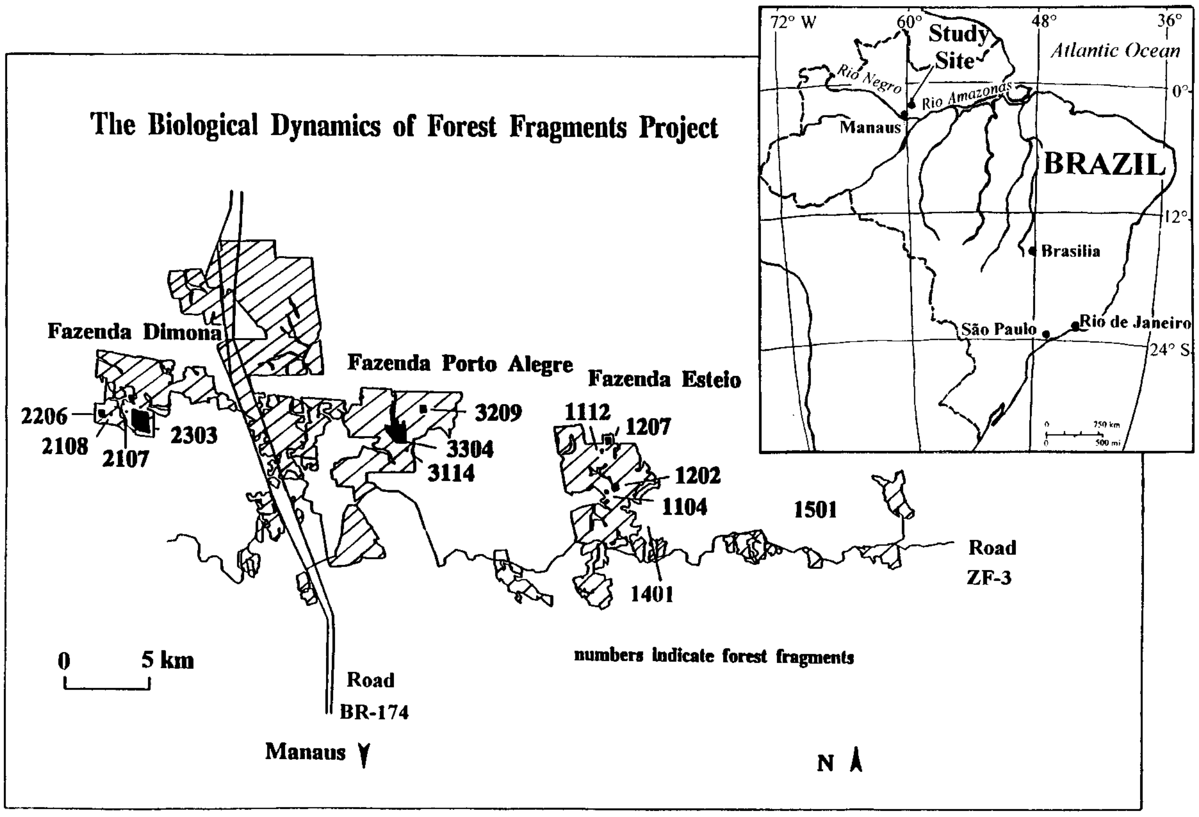

Figure 1. Location and layout of forest fragments at the BDFFP, 80 km north of Manaus, Central Amazonia, Brazil. Forest fragments (numbered) are located in extensive clearcut areas (shaded) on three fazendas (farms).

The forest is a uniform upland dry (*terra firma*) forest on yellow alic latosol soils of high clay content (Chauvel 1983; Lovejoy & Bierregaard 1990; Chauvel *et al*. 1991; Camargo 1992; Camargo & Kapos 1995). Vegetation of the region is described by Prance (1990), and of the BDFFP fragments by Rankin-de-Merona *et al*. (1992). Forest disturbance in the area is principally due to cattle ranching, with pastures created and maintained by fire (Jordan 1986; Fearnside 1989, 1990; Nepstad *et al*. 1993, 1996). For further description of the study area see Lovejoy *et al*. (1986) and Bierregaard *et al*. (1992).

The leaf-litter beetle fauna was sampled with respect to fragment area and distance from forest edge. Forest fragments and continuous forest edges were selected to minimize unexplained variation in community composition. Hence, all sites were upland (*terra firma*) forests on similar soil types (Lovejoy *et al*. 1986; Rankin-de-Merona *et al*. 1992), forest edges were adjacent to well-maintained pasture without secondary regrowth, all but one of the edges were west-facing (see below), the shape of all fragments was similar and the year and distance of isolation from continuous forest were fairly constant across sites (fragments isolated in 1980–84, except BDFFP fragment number 2303, designated 100 ha 1, where isolation of north and west edges was completed in 1990, by distances of 100–500 m; Lovejoy *et al*. 1986; Bierregaard *et al*. 1992).

The sampling design was based on a comparison of two independent transects sampled at each of three locations (figure 2): (*a*) deep within undisturbed continuous forest (>10 km from the nearest edge); (*b*) from the edge to the interior of continuous forest; and (*c*) from the edge to the interior of two 100 ha isolated forest fragments. The two 100 ha fragments (BDFFP numbers 2303 and 3304 (see figure 1), designated 100 ha 1 and 2, respectively) were *ca*. 20 km apart; the two continuous forest edges, edge 1 and edge 2, were separated by a distance of 2 km (both on the western edge of continuous forest 1401, figure 1); and the deep-forest control plots, interior 1 and interior 2, were 2 km apart (both in control site 1501, figure 1). The edges were west-facing with the exception of 100 ha 2, where the only edge abutting well-maintained pasture was north-facing.

Beetles were collected at seven distances along each of the six transects: 0, 13, 26, 52, 105, 210 and 420 m (figure 2). This sampling protocol reflected the *a priori* expectation that changes in beetle community structure would be greatest near the forest edge. In addition, to assess beetle communities in small forest fragments, two 10 ha fragments (numbers 3209 and 1202, designated 10 ha 1 and 2, respectively) were sampled at 105 m from the edge, and two 1 ha fragments (numbers 2107 and 2108, designated 1 ha 1 and 2, respectively) were sampled at 52 m from the edge.

(b) *Beetle collection*

Twenty random, 1 m^2 leaf-litter samples were collected at each of the 46 sites over a 5-month period. Daily sampling was randomly allocated between different transects and sites to prevent bias arising from daily and seasonal variation in activity patterns of beetles; typically, only 4–6 m^2 were collected from any one site on each of four visits spread approximately evenly throughout the 5-month sampling period. All friable leaf litter was scraped rapidly from the quadrat and placed in a large bag-sieve to minimize beetle escape. The material was immediately sieved over a 9 mm mesh by vigorously shaking the bag-

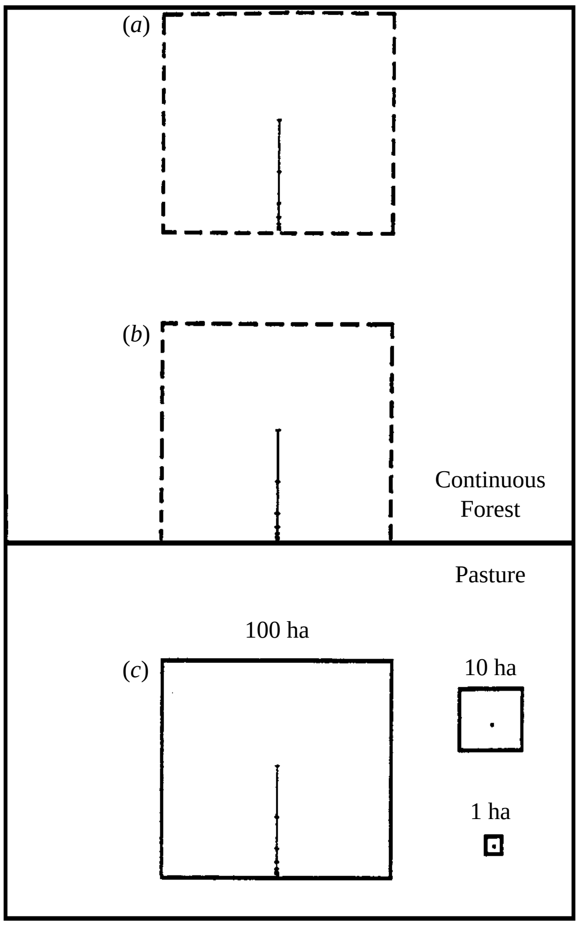

Figure 2. Sampling protocol. Transects sampled at seven distances (0, 13, 26, 52, 105, 210 and 420 m) in: (*a*) continuous forest ('interior'); (*b*) edge of continuous forest ('edge'); (*c*) 100 ha fragments. Additional samples were taken at 105 m into 10 ha fragments and at 52 m into 1 ha fragments. The entire design was replicated once. Distances between sites were 2–50 km, not the stylized arrangement illustrated here.

sieve for approximately 5 min. The fine, sieved litter containing beetles was then transported to the laboratory in individual cotton bags. Beetles were extracted using the Winkler method, whereby sieved leaf litter was carefully placed into coarse mesh bags, which were then suspended gently inside a large sealed cloth bag and hung for 3 d. As the leaf litter dried out, beetles sensitive to desiccation moved downwards through the mesh bag and fell into a jar of alcohol below. We operated 40 Winkler bags continuously for 5 months.

The Winkler method proved to be sensitive to climate and collection methods and hence required a strict, standardized methodology. We only collected samples from plateau forest areas (i.e. transects were not located in gullies or seasonally flooded areas) and only on dry mornings when there had been no rain the previous late-afternoon or night. Leaf-litter sampling was discontinued if it rained. All samples were dried for 3 d and no extra hand-sorting of litter was performed. Despite these restrictions, the Winkler method is still inherently a 'relative' trapping method and, as with most invertebrate sampling methods, does not sample all taxa with equal efficiency, although it is particularly useful for the rapid and efficient extraction of beetles from large numbers of samples (Besuchet *et al.* 1987; Nadkarni & Longino 1990). The changes in trophic groups reported here are therefore relative, not absolute effects.

(c) *Species sorting*

Beetles were sorted to morphospecies (Hammond 1994), hereafter referred to as species. All taxa were sorted by the authors with the aid of the Natural History Museum, London, collections. In problematic cases, specimens were dissected for genitalial characters or checked by specialists (see acknowledgements at end). Nomenclature follows Lawrence & Newton (1995). Specimens have been deposited at the Department of Entomology, INPA, Manaus, Brazil, and a reference collection at the Natural History Museum, London, UK. Species represented by a single individual and designated holotypes remain the property of INPA.

The error rate in species sorting was estimated by a comparison of species sorting of Pselaphinae (Staphylinidae) by the authors with a check by a specialist in this group. Of 109 species of Pselaphinae recognized, one species was considered by the specialist to be incorrectly assigned; an error rate of less than 1%. The Pselaphinae are among the most diverse and poorly known groups of beetles in tropical leaf litter, here represented by 109 species in 42 genera, of which at least seven genera were undescribed. The proportion of undescribed species in the total assemblage is estimated to be approximately 90%.

(d) *Trophic group assignment*

Beetle species were assigned to six trophic groups according to Hammond (1990) (see Appendix 1): fungivores, herbivores, predators, saprophages, xylophages and xylomycetophages (specialists on 'ambrosia' fungi inside wood). There were no positive identifications of parasitoids in the assemblage, so this trophic group was not included. Where only one feeding biology was known for a family, all species were assigned to that trophic group. In other cases, where multiple feeding biologies were known to occur, species were assigned on an individual basis using mouthpart and general morphological characters, as well as published details of the feeding biology of the genus, or of related genera. For six species of Elateridae (out of the total assemblage of 993 beetle species), however, it was impossible to accurately determine trophic groups, so species were assigned proportionally (and at random) to trophic groups based on worldwide average proportions of species with different feeding biologies (i.e. approximately one-third herbivores, one-third xylophages and one-third predators; Appendix 1).

(e) *Analyses*

(i) *Species richness*

Raw species richness values were corrected for sample abundance using the rarefaction method of Simberloff (1978). Rarefied species richness values were calculated using a BASIC computer program modified from Krebs (1989).

(ii) *Trophic structure*

Changes in the proportional representation of species and abundance in each of the six trophic groups were analysed using multiple logistic regression (Sokal & Rohlf

1995), with distance from forest edge and fragment area as independent variables. For the purposes of analysis, continuous forest was enumerated as 10 000 m from the forest edge and 10 000 ha in area. In the two analyses, logistic regressions were applied to each of the six trophic groups and the null hypothesis of no overall change in proportions rejected at a Bonferroni-corrected α' of 0.0083. Proportional changes across many trophic groups do not necessarily indicate which group or groups are particularly sensitive to fragmentation. To determine whether the overall pattern for each trophic group was derived from similar, or varying, individual family responses, further analysis of changes in the proportional representation of species in different beetle families was performed for each of the trophic groups, again with a Bonferroni correction for multiple tests.

(iii) *Extinction probability*

Local extirpation probabilities (referred to here simply as extinction probabilities) for abundant beetle species were estimated in two separate analyses, one for changes in extinction probability with distance from forest edge, and the other with respect to fragment area. The two variables are highly interdependent, but too few replicates were available to factor both of the variables into the analysis. Where both variables significantly affected extinction probabilities, no conclusion was drawn as to the determining variable. For the analyses, only the 32 most abundant species ($n \geqslant 46$ individuals, representing 3.2% of total species richness and 47% of total beetle abundance across all sites; Appendix 2) were included, so as to reduce spurious effects due to low sample size. Theoretically, if each common species were distributed at random there would be an equal probability of detecting species presence at all 46 sites.

In these analyses, 'probability of extinction' actually consists of two variables: (i) genuine local extinction (species absent); and (ii) sampling errors (species present, but undetected). As species become rarer, the probability of sampling errors (false zeros) increases. We cannot distinguish between genuine local extinction and false zeros. For brevity, we refer to all absences as 'probabilities of extinction'.

In the first analysis, the probability of extinction of each of the 32 species was calculated as the probability of species absence in samples at each of eight distances from the forest edge. For example, if a species were absent from three of four sites sampled at 0 m from the forest edge, then a crude estimate of local extinction probability would be 0.75. The trend in extinction probabilities with distance from edge was then tested with logistic regression with binomial errors. Numbers of sites at each distance were: 0–26 m, $n=4$; 52–105 m, $n=6$; 210–420 m, $n=4$; and 10 000 m, $n=14$.

In the second analysis, the probability of extinction for each of the 32 common species was calculated for four fragment sizes: 1 ha and 10 ha, $n=2$; 100 ha, $n=14$; and 10 000 ha, $n=28$.

For each analysis, a Bonferroni correction for multiple tests was applied and the null hypothesis of no change in extinction probability rejected at $\alpha'=0.00156$. The low sample sizes for 1 ha and 10 ha fragments are a limitation on the analysis of area effects, but the tests applied are extremely conservative.

Note that the analyses performed here are the inverse of incidence function analyses used by Diamond (1975), Gilpin & Diamond (1976, 1981), Diamond & May (1981) and Hanski (1992). The results give a snapshot of changes in species' local extinction probabilities following fragmentation.

3. RESULTS

(a) *Beetle density, species richness and species composition*

A total of 8454 beetles comprising 993 species were sampled from 920 m^2 of leaf litter. The average beetle density in undisturbed continuous forest was low for moist tropical forests, at just 7.83 m^{-2} (total area sampled 280 m^2). Beetle density increased significantly towards the forest edge, and changed non-linearly with decreasing fragment area (polynomial regression, parameter *t*-tests, all d.f. 42, $p<0.001$, $r^2=0.50$; figure 3*a*); density decreased markedly from undisturbed continuous forest to 100 ha forest fragments, then increased sharply again in 10 ha and 1 ha fragments. A simpler, linear model of changes in density with fragment area was significant ($F_{2,43}=6.87$, $p<0.005$, $r^2=0.21$), but explained less variation in the data.

Species richness patterns were identical to density patterns due to a strong correlation between richness and sample abundance ($r=0.91$, $p<0.0001$). Following rarefaction (at $n=77$) there was no detectable difference in species richness across sites ($F_{2,43}=3.16$, n.s.; figure 3*b*). Despite this, the similarity of species composition between fragment sites and undisturbed continuous forest decreased significantly with proximity to forest edge and with decreasing fragment area (logistic regression, $G=8.38$, d.f. 2, $p<0.02$; figure 3*c*). Species similarity among the 14 undisturbed forest sites averaged just 16% as a result of sampling pseudoturnover; that is, differences in species composition due to drawing small samples from a very large species pool.

(b) *Trophic structure*

(i) *Species richness*

To maintain constant rarefied species richness values across sites, the local extinction of continuous forest species (figure 3*c*) must have been balanced by colonization of new species at forest edges and in small fragments. The most notable consequence of this shift in species composition was that mean proportions of species in the six trophic groups (see figure 4*a* for undisturbed continuous forest values) changed significantly following forest fragmentation (figure 5). Distance from forest edge had a significant effect on the proportions of predator species (logistic regression, $G=12.67$, d.f. 1, $p<0.001$) and on the proportions of xylophage species ($G=8.58$, d.f. 1, $p<0.005$; figure 5). However, proportions of species in different trophic groups did not vary significantly with fragment area (all $p>0.0083$).

Edge responses for individual beetle families or subfamilies were not consistent within a given trophic group (table 1). The edge response for all predators was dominated by increased proportions of Pselaphinae (Staphylinidae) ($G=16.41$, d.f. 1, $p<0.0001$) and Scydmaenidae ($G=8.18$, d.f. 1, $p<0.005$) at the forest edge (table 1), and the trend for all xylophages was dominated by the edge response of Curculioninae (Curculionidae)

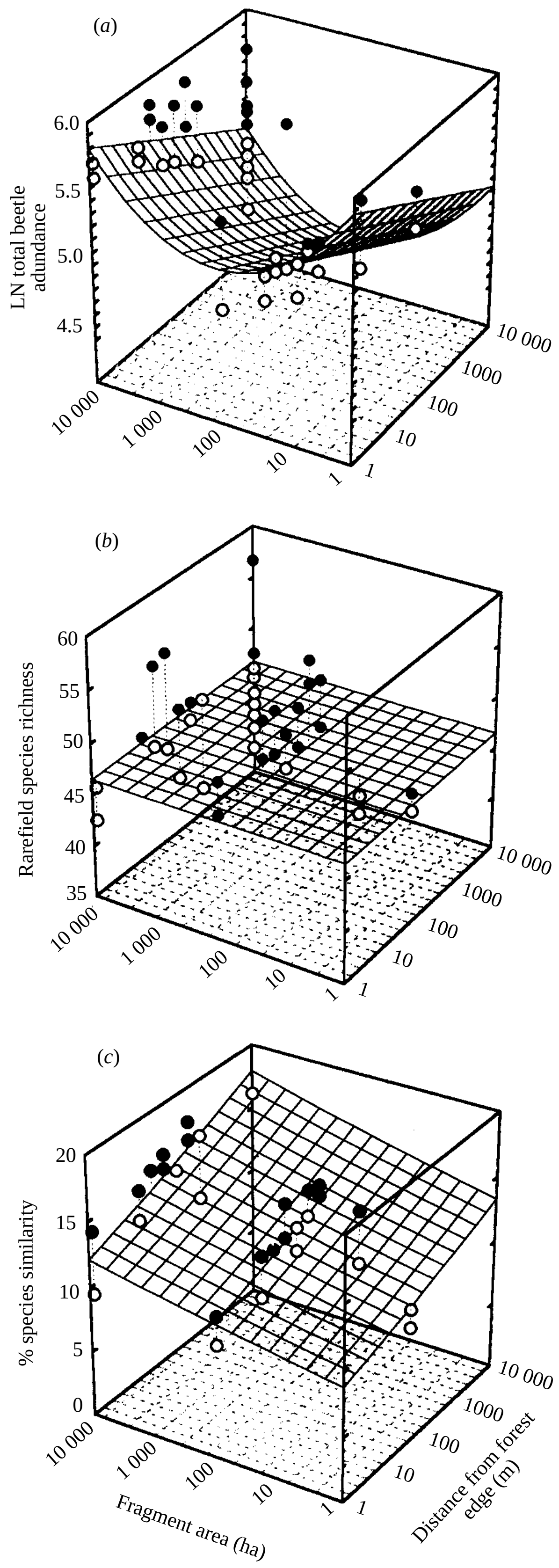

Figure 3. Changes in the beetle assemblage sampled from 20 m^2 of leaf-litter at each of 46 sites varying in distance from forest edge (LNDIST) and fragment area (LNAREA) in Central Amazonia: (*a*) fitted polynomial regression of (log) total abundance of beetles. Equation of the fitted surface: log abundance$=5.84-0.08$(LNDIST) -0.29(LNAREA) $+0.03$(LNAREA)^2, $r^2=0.50$. All parameters entered the regression at $p<0.001$. (*b*) Rarefied species richness (at $n=77$). Equation of model with intercept only fitted: rarefied species richness$=46.53$. There were no significant edge or area effects. (*c*) Multiple logistic regression of mean Jaccard's similarity coefficients (% beetle species shared) between each fragment site and the 14 continuous forest sites. Within-continuous forest similarity was calculated as the mean of all pairwise comparisons among the 14 continuous forest sites ($n=91$). Equation of the fitted surface: % similarity$=$ $e^{(-2.32+0.05x+0.04y)}/(1+e^{(-2.32+0.05x+0.04y)})$, where $x=$LNDIST and $y=$LNAREA. Lines project points to their mean values on the fitted surfaces; filled circles indicate points above the fitted surfaces.

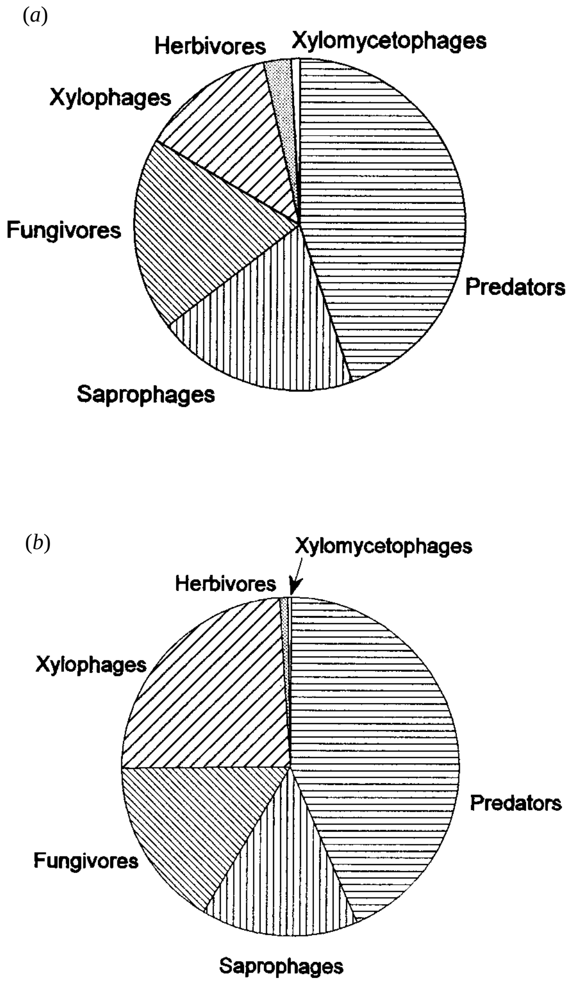

Figure 4. Proportions of (*a*) species richness (total $S=445$) and (*b*) abundance (total $n=2192$) of leaf-litter beetles in six trophic groups sampled from undisturbed continuous forest in Central Amazonia (total area sampled 280 m^2).

($G=8.16$, d.f. 1, $p<0.005$; table 1). The proportions of species in other families were not significantly affected by fragmentation, although the Aleocharinae (Staphylinidae) showed a weak inverse trend compared with Pselaphinae or Scydmaenidae (the edge response for Aleocharinae was not significantly different from zero at a Bonferroni-corrected α' of 0.0063, but a multiple comparison of slopes test using the *T*-method and Gabriel's approximate test showed that the slope for Aleocharinae was significantly different ($p<0.05$) from the slopes for Pselaphinae, Scydmaenidae and all predators combined; table 1).

(ii) *Abundance*

An alternative way to analyse these data is to look at the total number of individuals in each trophic group,

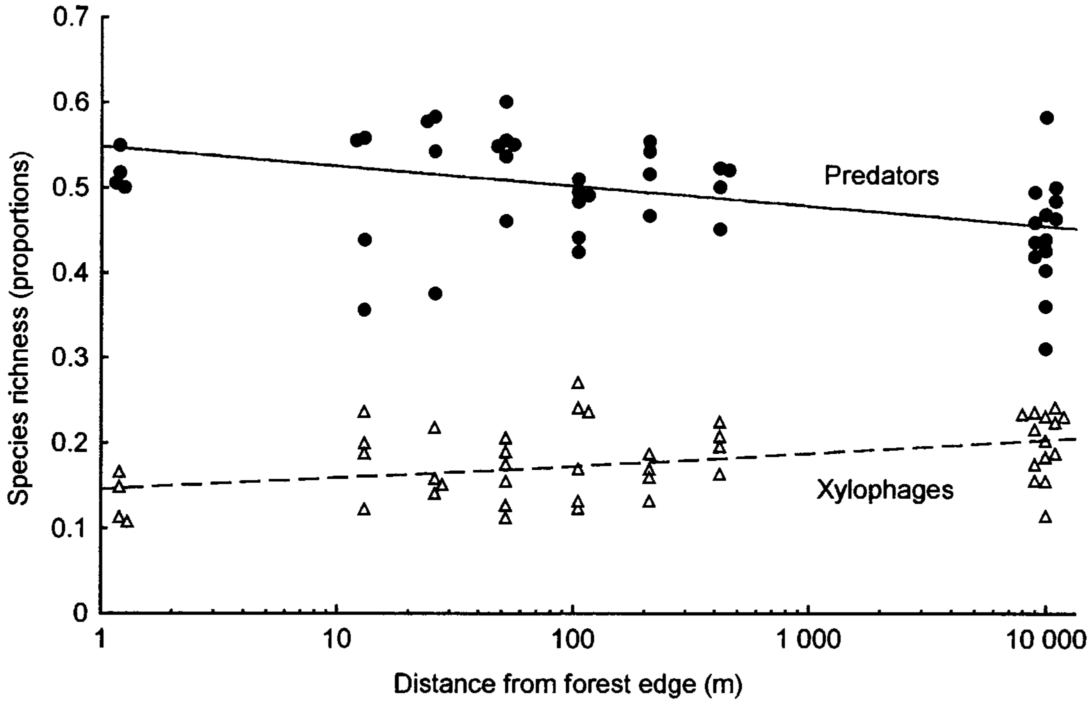

Figure 5. Changes in proportions of predator species and xylophage species with distance from forest edge. Predators: $y = e^{(-0.19-0.04x)}/(1+e^{(-0.19-0.04x)})$; Xylophages: $y = e^{(-1.77+0.04x)}/(1+e^{(-1.77+0.04x)})$. Overlapping points are offset. See text for statistical significance.

Table 1. *Comparison of logistic regression slope parameters, standard errors (s.e.) and G-statistics for significant effects of distance from forest edge on the proportions of species in dominant beetle families within four trophic groups*

(Other families tested, but not significant: (1) fungivores: Acanthoceridae, Ciidae, Corylophidae, Endomychidae, Leiodinae, Ptiliidae, and Scaphidiinae; (2) predators: Carabidae, Hydrophilidae, Aleocharinae, Paederinae, Staphylininae, and Tachyporinae; (3) saprophages: Lagriinae, Catopinae, Nitidulidae, Ptiliidae, Scarabaeinae, Osoriinae, Oxytelinae, Piestinae; and (4) xylophages: Scolytinae.)

	slope	s.e.	G	p
all fungivores	0.0137	0.0164	n.s.	—
all predators	−0.0406	0.0114	12.671	0.0004
Staphylinidae: Pselaphinae	−0.0694	0.0173	16.405	<0.0001
Scydmaenidae	−0.0454	0.0159	8.181	0.0043
all saprophages	0.0333	0.0156	n.s.	
all xylophages	0.0437	0.0149	8.580	0.0030
Curculionidae: Curculioninae	0.0164	0.0215	8.156	0.0043

irrespective of species. We refer to these data as proportions of abundance (see figure 4*b* for undisturbed continuous forest values). These proportions were also significantly affected by fragmentation, except those for xylomycetophages (table 2). The differences were more pronounced than for species proportions, with significant changes caused by both edge and area effects in different trophic groups: (i) proportions of fungivore abundance decreased significantly towards the forest edge; (ii) herbivore proportions increased towards the forest edge; (iii) predator proportions increased with decreasing fragment area; (iv) saprophage proportions decreased towards the forest edge and increased with decreasing fragment area; and (v) xylophage proportions decreased with decreasing fragment area (table 2).

(c) *Extinction probability*

The extinction probabilities of common ($n \geqslant 46$) predator species were significantly greater than for species in other trophic groups (table 3). Of the 32 common species, none of the four fungivores had significantly altered extinction probabilities in fragmented forest, 1 of 5 saprophages showed a significant change in extinction probability (figure 6*a*), 3 of 10 xylophages showed significant changes (figures 6*b* and 7*a*), and 6 of 13 predator species showed altered extinction probabilities (figures 6*c* and 7*b* and table 3). Thus, 31% of all common species were significantly affected by fragmentation, the majority (eight species) having significantly higher probabilities of extinction in forest fragments of 1–100 ha than in undisturbed continuous forest. In general, extinction probabilities varied most significantly with changes in fragment area, but some species were markedly affected by edge effects (e.g. *Phaenostoma* sp. 0307, Hydrophilidae), or by a combination of area and edge effects (e.g. *Tachys* sp. 0268, Carabidae). The remaining two species (*Phaenostoma* sp. 0306 and *Araptus* sp. 0887, Scolytinae) were edge specialists, with lower extinction probabilities near forest edges and in small forest fragments (figures 6 and 7).

4. DISCUSSION

(a) *Beetle density, species richness and species composition*

Forest fragmentation had a significant effect on the density, richness and composition of the leaf-litter beetle

Table 2. *Summary results of multiple logistic regression analyses of proportions of abundance in six trophic groups*

(Significant edge (LNDIST) and area (LNAREA) effects were accepted at a Bonferroni-corrected α′ of 0.0083.)

				parameter estimates (s.e.)		
source	*G*	d.f.	*p*	intercept	LNDIST	LNAREA
fungivores						
LNDIST (adjusted for LNAREA)	14.081	1	0.0002	—	—	—
LNAREA (adjusted for LNDIST)	2.384	1	n.s	—	—	—
final model: constant+LNDIST	19.863	1	<0.0001	−2.256 (0.071)	0.051 (0.012)	—
herbivores						
LNDIST (adjusted for LNAREA)	21.305	1	<0.0001	—	—	—
LNAREA (adjusted for LNDIST)	1.695	1	n.s.	—	—	—
final model: constant+LNDIST	21.399	1	<0.0001	−3.696 (0.171)	−0.157 (0.036)	—
predators						
LNDIST (adjusted for LNAREA)	6.681	1	n.s.	—	—	—
LNAREA (adjusted for LNDIST)	10.953	1	<0.0010	—	—	—
final model: constant+LNAREA	18.134	1	<0.0001	0.120 (0.061)	—	−0.033 (0.008)
saprophages						
LNDIST (adjusted for LNAREA)	17.935	1	<0.0001	—	—	—
LNAREA (adjusted for LNDIST)	10.751	1	0.0010	—	—	—
final model: constant+LNDIST+LNAREA	22.170	2	<0.0001	−1.831 (0.091)	0.050 (0.012)	−0.038 (0.012)
xylophages						
LNDIST (adjusted for LNAREA)	1.905	1	n.s.	—	—	—
LNAREA (adjusted for LNDIST)	24.630	1	<0.0001	—	—	—
final model: constant+LNAREA	22.731	1	<0.0001	−1.402 (0.074)	—	0.043 (0.009)
xylomycetophages						
LNDIST (adjusted for LNAREA)	4.123	1	n.s.	—	—	—
LNAREA (adjusted for LNDIST)	0.284	1	n.s.	—	—	—

fauna in Central Amazonia. Beetle density increased significantly towards the forest edge, as is typical of the majority of invertebrate fragmentation studies (review in Didham 1997). This is generally the result of an increase in productivity at the forest edge and the influx of disturbed-area species. Area-dependent changes in invertebrate density have also been noted in previous studies (e.g. Jaenike 1978; Bach 1988; Martins 1989; Sowig 1989), but our study is unusual in showing clear, non-linear trends in beetle density with fragment area. Beetle density initially declined from continuous forest to 100 ha forest fragments, and then increased again in 10 ha and 1 ha fragments. The increase in density in the smallest fragments may be explained by the mass influx of disturbed-area species. Indeed, data show that there is a rapid loss of deep-forest species with decreasing distance from forest edge and decreasing fragment area. Despite this marked change in species composition, however, rarefied species richness was remarkably constant across all sites, indicating that local species extinctions were balanced almost exactly by the colonization of new (disturbed-area) species. Why this should be so is unclear.

(b) *Trophic structural stability*

(i) *Edge effects*

Trophic structure varied with forest fragmentation, although, interestingly, proportions of species in trophic groups only varied significantly with distance from forest edge and not with fragment area. Predators were particularly strongly affected by edge effects. Contrary to theoretical expectations (Pimm 1991; Pimm *et al*. 1991; Lawton 1995), however, proportions of predator species were higher in the most disturbed sites, rather than lower. Other empirical evidence is equivocal on the significance of this finding: two studies support increased proportions of predators at forest edges (Ozanne *et al*. 1997) or in highly disturbed successional sites (Heatwole & Levins 1972), and two studies showed reduced proportions of predators (Brown & Southwood 1983; P. Eggleton, P. M. Hammond, J. G. Davies and N. A. Mawdsley, unpublished results). This inconsistency may be due to the differential opportunities available for predators in different systems under disturbance (Power *et al*. 1996). When broken down, the patterns observed for predators were found to derive largely from increased proportions of two groups of mite predators, Pselaphinae (Staphylinidae) and Scydmaenidae, inferring a possible increase in mite density at the forest edge (see Heck *et al*. 1989; Clopton & Gold 1993). In one other trophic group, xylophages, reduced proportions of wood-feeding Curculioninae (Curculionidae) at the forest edge may again be a response to changes in resource availability.

(ii) *Area effects*

Contrary to the predictions of Holt (1996), proportions of species in trophic groups did not vary significantly with fragment area. Once again, empirical support for stability

Table 3. *Logistic regression analyses of changes in the local extinction probabilities of* 32 *common* ($n \geqslant 46$) *leaf-litter beetle species in fragmented forests in Central Amazonia*

(Each species was tested separately for the effects of fragment area (LNAREA) and distance from forest edge (LNDIST) on local extinction probabilities. Significant changes in extinction probabilities were accepted at a Bonferroni-corrected α' of 0.00156. See § 2 for further details. Other species tested, but not significantly affected by fragmentation, are listed in Appendix 2.)

taxon	species	abundance		*G*	*p*
saprophages					
Leiodidae: Catopinae	*Adelopsis* sp.	88	LNAREA:	34.586	<0.0001
	(0313)		LNDIST:	2.457	n.s.
predators					
Carabidae: Trechinae	*Tachys* sp.	170	LNAREA:	23.082	<0.0001
	(0268)		LNDIST:	12.799	0.0004
Carabidae: Trechinae	*Tachys* sp.	79	LNAREA:	16.104	<0.0001
	(0269)		LNDIST:	6.912	n.s.
Hydrophilidae: Sphaeridiinae	*Phaenostoma* sp.	59	LNAREA:	10.161	0.0015
	(0306)		LNDIST:	11.455	0.0008
Hydrophilidae: Sphaeridiinae	*Phaenostoma* sp.	165	LNAREA:	9.210	n.s
	(0307)		LNDIST	10.716	0.0011
Staphylinidae: Pselaphinae	*Jubus* sp.	125	LNAREA;	27.206	<0.0001
	(0793)		LNDIST:	0.103	n.s.
Staphylinidae: Tachyporinae	*Coproporus* sp.	283	LNAREA;	10.372	0.0013
	(0002)		LNDIST:	5.010	n.s.
xylophages					
Curculionidae: Curculioninae	?genus	84	LNAREA:	19.441	<0.0001
	(0980)		LNDIST:	2.388	n.s.
Curculionidae: Scolytinae	*Araptus* sp.	214	LNAREA:	1.219	n.s.
	(0887)		LNDIST:	23.246	<0.0001
Curculionidae: Scolytinae	*Araptus* sp.	399	LNAREA:	15.092	<0.0002
	(0919)		LNDIST:	2.910	n.s.

in trophic structure with decreasing habitat area is equivocal, with three studies showing altered trophic structure in small fragments (Patterson 1984; Schoener *et al*. 1995; J. Zabel and T. Tscharntke, unpublished results) and four showing no change (Heatwole & Levins 1972; Brown 1978; Hamilton & Stathakis 1987; Mikkelson 1993; see § 1).

The conflict between theory and empirical data may be due to the confounding interaction of disturbed-area species with habitat specialists inside fragments (see Janzen 1983, 1986; Doak *et al*. 1992; Didham 1997). While Holt's (1996) predictions hold for real islands (Schoener *et al*. 1995), our study showed no change in trophic structure with fragment area under the strong influence of edge effects and a shift in species composition due to disturbance. Thus, disturbance effects may readily enhance, nullify or even reverse area-dependent changes in trophic structure. Community-level data are inadequate to distinguish the influences of area and disturbance, or to validate theoretical predictions of the differential susceptibility of higher trophic levels to extinction. These questions require knowledge of the extinction probabilities for individual species.

(c) *Extinction dynamics*

As noted earlier, 'extinctions' here refer to both local disappearance of species (genuine local extinction) and sampling zeros, and can more broadly be thought of as a measure of species' decline under fragmentation. Ten of 32 abundant species of beetles (representing 47% of total beetle abundance at all sites) had significantly altered extinction probabilities in fragmented forest. Two of these species were clearly edge specialists and were not found commonly in deep continuous forest. However, the remaining 8 of 30 species (27%) were significantly more likely to become extinct (or at least to decline to the point where sampling failed to detect them) in small fragments or near forest edges than in undisturbed continuous forest. Only one of these species (the saprophagous *Adelopsis* sp. 0313, Leiodidae, Catopinae) belonged to any of the fungivore, saprophage, herbivore or xylomycetophage groups, even though these four trophic groups contained more than 40% of all species. These data on the commonest species are therefore consistent with the constant proportions of all the species in the data set in these four trophic groups following fragmentation. In contrast, marked changes in trophic structure were observed in predators and xylophages, and species in these groups also showed big changes in extinction dynamics. The majority of species affected were predators, confirming the differential susceptibility of higher trophic levels to extinction (Lawton 1995; Holt 1996). Five of 12 predator species (42%) were prone to extinction (as defined here) following fragmentation.

The loss of, or major decline in, a large number of abundant species in the predator and xylophage groups might be expected to lower the proportions of these trophic groups in terms of their total abundances following fragmentation. While this was true for xylophages, the reverse was true for predators. In general, the relationships between changes in species extinction probabilities, changes in species proportions, and changes in proportions of abundance of different trophic groups were not always obvious. The majority of the abundant beetle species were deep-forest species, indicating that few of the species that

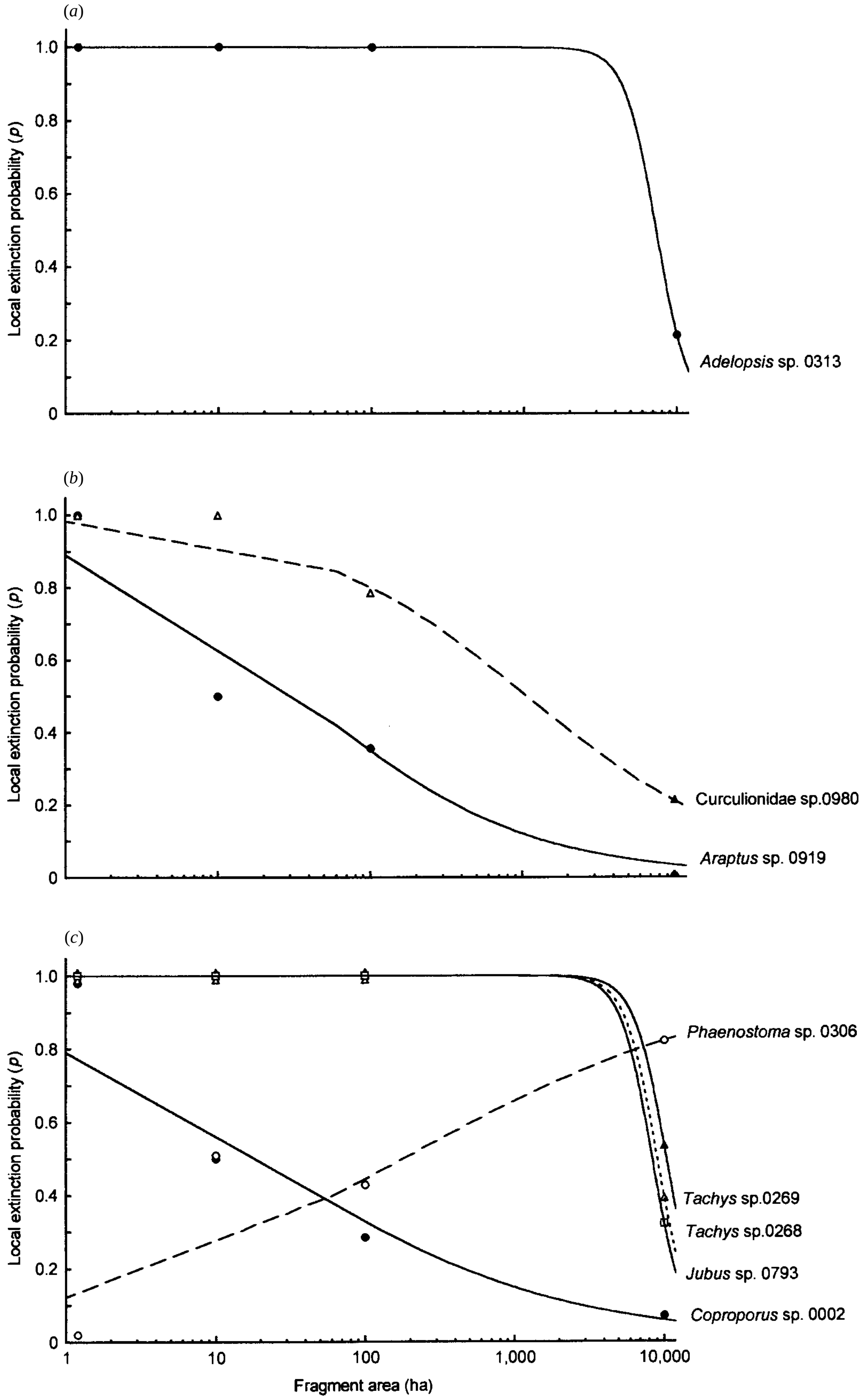

Figure 6. Fitted logistic regressions estimating local 'extinction probabilities' of beetle species from the proportion of sites where species were absent in forest fragments of four sizes (see § 2 for details): (*a*) a saprophagous species, *Adelopsis* sp. 0313 (Leiodidae, Catopinae), $y=e^{(37.43-4.21x)}/(1+e^{(37.43-4.21x)})$. (*b*) Two xylophagous species, *Araptus* sp. 0919 (Curculionidae, Scolytinae), $y=e^{(2.10-0.59x)}/(1+e^{(2.10-0.59x)})$, and sp. 0980 (Curculionidae, Curculioninae), $y=e^{(4.13-0.59x)}/(1+e^{(4.13-0.59x)})$. (c) Five predacious species, *Tachys* sp. 0268 (Carabidae, Trechinae), $y=e^{(37.43-4.11x)}/(1+e^{(37.43-4.11x)})$, Tachys sp. 0269, $y=e^{(37.43-4.05x)}/(1+e^{(37.43-4.05x)})$, *Jubus* sp. 0793 (Staphylinidae, Pselaphinae), $y=e^{(37.43-4.15x)}/(1+e^{(37.43-4.15x)})$, *Coproporus* sp. 0002 (Staphylinidae, Tachyporinae), $y=e^{(1.34-0.45x)}/(1+e^{(1.34-0.45x)})$, and *Phaenostoma* sp. 0306 (Hydrophilidae, Sphaeridiinae), $y=e^{(-1.96+0.38x)}/(1+e^{(-1.96+0.38x)})$. See table 3 for statistical significance.

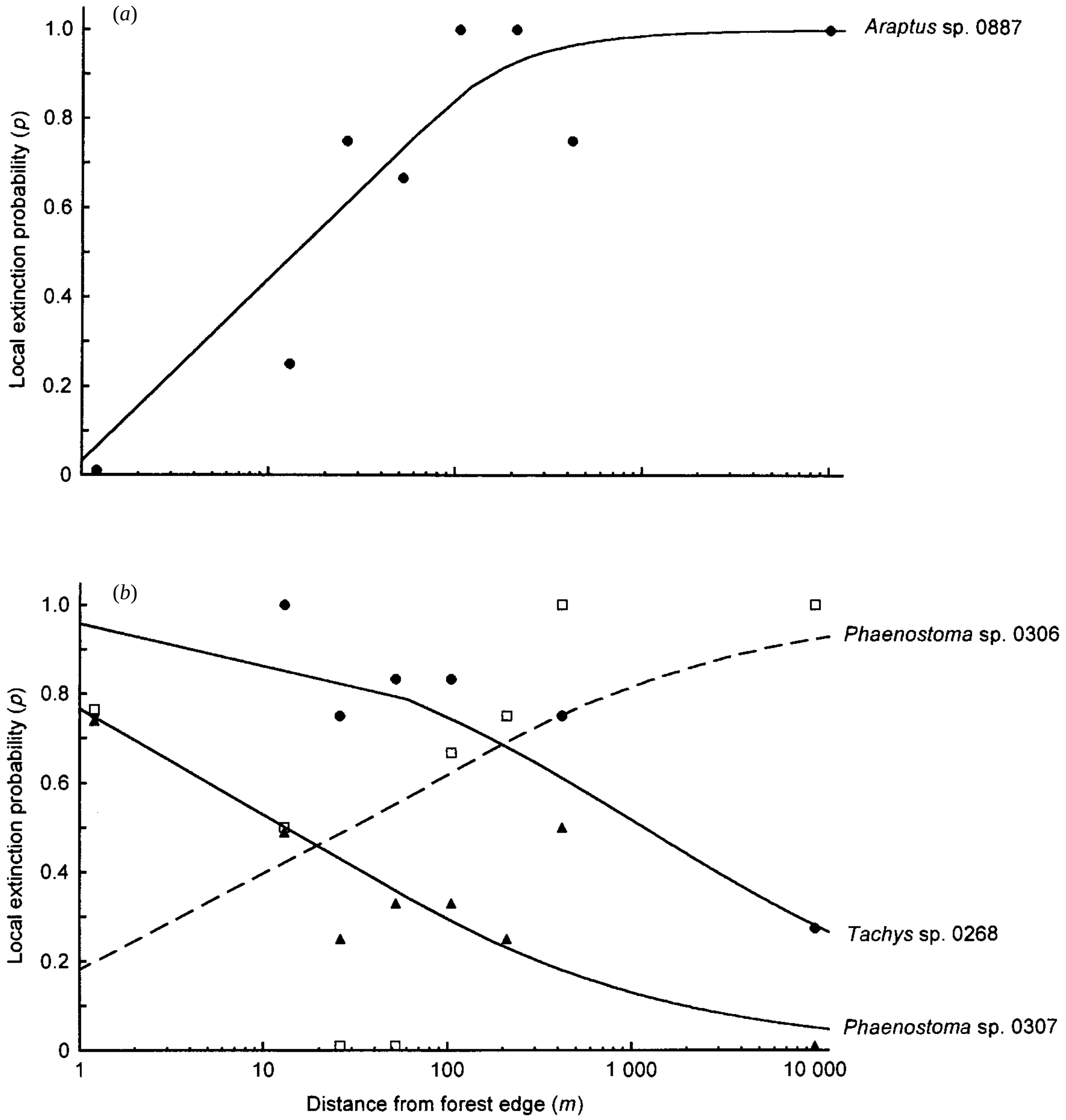

Figure 7. Fitted logistic regressions estimating local 'extinction probabilities' of beetle species from the proportion of sites where species were absent at eight distances from the forest edge (see § 2 for details): (*a*) a xylophagous species, *Araptus* sp. 0887 (Curculionidae, Scolytinae), $y=e^{(-3.42+1.12x)}/(1+e^{(-3.42+1.12x)})$. (*b*) Three predacious species, *Tachys* sp. 0268 (Carabidae, Trechinae), $y=e^{(3.11-0.44x)}/(1+e^{(3.11-0.44x)})$, *Phaenostoma* sp. 0306 (Hydrophilidae, Sphaeridiinae), $y=e^{(-1.56+0.43x)}/(1+e^{(-1.56+0.43x)})$, and *Phaenostoma* sp. 0307, $y=e^{(1.19-0.45x)}/(1+e^{(1.19-0.45x)})$. See table 3 for statistical significance.

invaded the leaf-litter community in disturbed areas established large populations. Thus, the increased proportion of predator species and changes in the proportional abundance of trophic groups near the forest edge, both seem to be due to the influx of numerous rare species (transients) from disturbed areas.

The probability of a species being absent from a fragment by chance is clearly inversely proportional to its density (Gaston 1994). Purely at random, rare species will be excluded from fragments more often than common species (see Gaston 1994; Andrén 1996). Lower absolute population sizes of rare species in small fragments confer a further susceptibility to extinction (Gaston 1994), making the likelihood of population survival in small fragments extremely poor. Intuitively, then, we would expect rare species to have significantly higher local extinction probabilities than those recorded for common species in the present study. If, on the other hand, there is a strong interspecific trade-off between dispersal and competitive abilities, inferior competitors may benefit from the susceptibility of common species (superior competitors) to forest fragmentation (Nee & May 1992; Tilman *et al.* 1994).

5. CONCLUSIONS

Beetle density and species composition were significantly affected by forest fragmentation. Surprisingly, however, rarefied species richness was roughly constant across all sites. The shift in species composition was non-random across trophic groups, indicating that forest fragmentation significantly affected trophic structure.

However, changes in proportions of species in trophic groups did not accord with spatial models of food web structure (Holt 1996), probably because of a confounding of disturbance-induced and area-induced changes in trophic structure. Overall, 27% of all abundant beetle species examined were significantly less likely to appear in samples (which we interpret as significantly more prone to extinction) following forest fragmentation. The figure for abundant predator species was even higher at 42% of all species. These figures are probably minimum estimates for the total beetle assemblage, because rarer species will inevitably have higher local extinction probabilities (Gaston 1994; Andrén 1996). Finally, we note that these findings have implications for the maintenance of ecosystem function. Loss of biodiversity from particular trophic levels, or uniformly across all trophic levels, has been shown to influence ecosystem process rates (Naeem *et al.* 1994, 1995, 1996; Tilman & Downing 1994; Mooney *et al.* 1995; Didham *et al.* 1996; Johnson *et al.* 1996; Tilman *et al.* 1996); differential loss of species from different trophic groups may have an even bigger impact on food web structure and ecosystem function (Pimm 1982; Ulanowicz 1996). The consequences of such effects for the long-term dynamics and persistence of invertebrate communities in forest fragments remain unexplored.

APPENDIX 1.

Trophic group assignments for beetles sampled from 920 m^2 *of leaf litter in Central Amazonia*

(Note that some families occur in more than one trophic group. Nomenclature follows Lawrence & Newton (1995).)

	total number of species collected	total number of individuals collected
fungivores		
Acanthoceridae	15	55
Aderidae	1	1
Biphyllidae	1	1
Cerylonidae	9	21
Ciidae	22	107
Colydiidae	1	5
Corylophidae	12	34
Endomychidae: Merophysiinae	2	4
Endomychidae (other)	16	97
Erotylidae	6	6
Laemophloeidae	3	5
Languriidae	3	6
Latridiidae	1	2
Leiodidae: Leiodinae	8	336
Melandryidae	1	1
Nitidulidae	4	4
Phalacridae	1	1
Ptiliidae	32	141
Rhysodidae	1	9
Salpingidae: Prostominiinae	1	1
Silvanidae	4	10
Staphylinidae: Aleocharinae	8	16
Staphylinidae: Scaphidiinae	23	133
Tenebrionidae (other)	7	24
herbivores		
Buprestidae	2	2
Chrysomelidae	16	52
Curculionidae: Brachycerinae	2	2
Curculionidae: Curculioninae	6	15
Curculionidae: Dryophthorinae	2	2
Elateridae	2	2
Hydraenidae	1	6
Nitidulidae	1	2
Phalacridae	2	2
Scarabaeidae: Melolonthinae	4	9
Tenebrionidae: Lagriinae	1	1
predators		
Carabidae	33	377
Coccinellidae	2	2
Dytiscidae	1	56
Elateridae	2	2
Histeridae	19	26
Hydrophilidae	14	254
Scydmaenidae	133	939
Staphylinidae: Aleocharinae	97	400
Staphylinidae: Euaesthetinae	7	15
Staphylinidae: Megalopininae	2	9
Staphylinidae: Paederinae	45	246
Staphylinidae: Pselaphinae	109	1172
Staphylinidae: Staphylininae:	18	101
Staphylinidae: Steninae	4	14
Staphylinidae: Tachyporinae	11	359
saprophages		
Anthicidae	1	3
Dermestidae	3	3
Leiodidae: Catopinae	7	148
Limnichidae	2	5
Nitidulidae	19	99
Ptiliidae	29	61
Ptilodactylidae	4	10
Scarabaeidae: Aphodiinae	2	29
Scarabaeidae: Scarabaeinae	15	86
Staphylinidae: Osoriinae	43	249
Staphylinidae: Oxytelinae	8	210
Staphylinidae: Piestinae	4	112
Tenebrionidae: Lagriinae	26	122
Tenebrionidae (other)	5	12
xylophages		
Anobiidae	2	3
Curculionidae: Cossoninae	4	8
Curculionidae: Curculioninae	41	573
Curculionidae: Dryophthorinae	3	10
Curculionidae: Scolytinae	44	1549
Elateridae	2	2
xylomycetophages		
Curculionidae: Platypodinae	1	4
Curculionidae: Scolytinae	10	69
total	993	8454

(*continued*)

APPENDIX 2.

Total abundances, trophic groups and body sizes of the 32 most abundant beetle species sampled from 920 m^2 *of leaf-litter in Central Amazonia*

(Trophic group assignments (Hammond 1990): F, fungivore, Pr, predator, S, saprophage, X, xylophage. Body size is mean (±s.e.) of all individuals.)

species code	family: subfamily	genus	trophic group	abundance	body size (mm (±s.e.)
0002	Staphylinidae: Tachyporinae	*Coproporus* sp.	Pr	283	2.62 (0.013)
0018	Staphylinidae: Oxytelinae	*Carpelimus* sp.	S	114	1.85 (0.015)
0179	Staphylinidae: Aleocharinae	?genus	Pr	46	2.15 (0.024)
0268	Carabidae: Trechinae	*Tachys* sp.	Pr	170	1.97 (0.006)
0269	Carabidae: Trechinae	*Tachys* sp.	Pr	79	1.16 (0.009)
0306	Hydrophilidae: Sphaeridiinae	*Phaenostoma* sp.	Pr	59	2.25 (0.013)
0307	Hydrophilidae: Sphaeridiinae	*Phaenostoma* sp.	Pr	165	3.53 (0.016)
0312	Leiodidae: Catopinae	*Adelopsis* sp.	S	47	1.45 (0.012)
0313	Leiodidae: Catopinae	*Adelopsis* sp.	S	88	1.64 (0.008)
0356	Dytiscidae	*Copelatus* sp.	Pr	56	3.87 (0.028)
0422	Leiodidae: Leiodinae:	?*Agathidium* sp.	F	196	1.09 (0.007)
0541	Staphylinidae: Scaphidiinae	*Baeocera* sp.	F	59	1.09 (0.008)
0569	Nitidulidae	*Stelidota* sp.	S	48	1.89 (0.018)
0575	Staphylinidae: Piestinae	*Piestus* sp.	S	66	3.99 (0.031)
0584	Leiodidae: Leiodinae	*Aglyptinus* sp.	F	76	1.17 (0.013)
0606	Ptiliidae	?*Ptenidium* sp.	F	82	0.82 (0.006)
0714	Scydmaenidae	*Euconnus* sp.	Pr	205	1.20 (0.003)
0720	Staphylinidae: Pselaphinae	*Globa* sp.	Pr	142	1.05 (0.004)
0724	Staphylinidae: Pselaphinae	*Goniacerus* sp.	Pr	48	1.45 (0.013)
0770	Staphylinidae: Pselaphinae	*Phalepsoides* sp.	Pr	53	1.03 (0.006)
0785	Staphylinidae: Pselaphinae	*Tuberoplectus* sp.	Pr	195	1.20 (0.005)
0793	Staphylinidae: Pselaphinae	*Jubus* sp.	Pr	125	1.46 (0.007)
0887	Curculionidae: Scolytinae	*Araptus* sp.	X	214	1.17 (0.003)
0888	Curculionidae: Scolytinae	*Araptus* sp.	X	123	1.16 (0.006)
0905	Curculionidae: Scolytinae	?*Hypothenemus*	X	87	1.12 (0.008)
0918	Curculionidae: Scolytinae	*Araptus* sp.	X	183	1.30(0.010)
0919	Curculionidae: Scolytinae	*Araptus* sp.	X	399	1.27 (0.003)
0924	Curculionidae: Scolytinae	*Araptus* sp.	X	75	2.08 (0.022)
0929	Curculionidae: Scolytinae	*Araptus* sp.	X	205	1.43(0.009)
0980	Curculionidae: Curculioninae	?genus	X	84	1.85 (0.018)
0985	Curculionidae: Curculioninae	?genus	X	145	2.96 (0.018)
0986	Curculionidae: Curculioninae	?genus	X	59	4.80 (0.049)

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