

EFFECTS OF WITHIN- AND BETWEEN-PATCH PROCESSES ON COMMUNITY DYNAMICS IN A FRAGMENTATION EXPERIMENT

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Abstract. The effects of the experimental fragmentation of native eucalypt forest on the beetle community were tested, in a controlled, replicated, long-term experiment. Included in our design were three fragment sizes, fragment edge and interior sites, and sites in the surrounding exotic pine plantation matrix. We followed 325 species through 28 sampling periods over seven years, including two years pre-fragmentation. We examined effects of fragmentation on four attributes of community structure: (1) species richness, (2) species composition, (3) relative abundance, and (4) the changes in occurrence of all species individually by the traits of rarity, degree of isolation (dispersal ability), and trophic group. We also considered how changes in these attributes altered community dynamics (turnover).

We used both community-level and species-level responses to determine the relative importance of processes acting at the within-patch and between-patch scales.

At the within-patch scale there were two findings. (1) There was no evidence of an increase in the extinction rate on fragments, as was hypothesized. Neither species richness nor the occurrence of rare species declined on fragments compared to continuous forest. (2) Edge effects altered species occurrences and abundances on fragments compared to continuous forest. There was evidence of two edge effects, with different penetration distances. Species richness increased at fragment edges in response to a shallowly penetrating edge effect. Species relative abundance and composition changed on fragments in response to a deeply penetrating edge effect, which also caused increases in the occurrences of detritivores and fungivores.

At the between-patch scale there were three findings. (1) There was no evidence of a reduction in the colonization rate of fragments. There was no reduction in species richness or in the occurrence of individual species with poor dispersal abilities on fragments compared to continuous forest. (2) The matrix between fragments altered between-patch processes by providing alternative habitat for some species. These species increased in occurrence on fragments compared to continuous forest, supporting the predictions of recent metacommunity theory. However, the matrix did not act as a source of invading species. (3) Turnover was reduced in fragments compared to continuous forest. Thus, the effect of fragmentation was to stabilize community dynamics.

Key words: *Australia; beetles; community dynamics; edge effects; forest fragmentation; local processes.*

INTRODUCTION

As continuous habitat continues to be fragmented, it is critical to understand which processes drive changes in the biodiversity of fragmented landscapes. To fully understand the effects of fragmentation extensive spatiotemporal data sets are needed. The beetle data set considered here includes 28 sample periods over seven years, for 188 sites, for 325 beetle species. Thus, we were able to test for the effects of fragmentation set against the natural spatial and temporal variability of the community and of individual species.

The persistence of species and the dynamics of com-

munities in fragmented landscapes are affected by processes operating at more than one spatial scale. We recognize two classes of processes: (1) those that alter population processes at the within-patch scale, particularly extinction rate, growth rate, or carrying capacity, and (2) those that alter processes at the between-patch scale, particularly dispersal and colonization. Below we consider how theory predicts that these processes will change.

Within-patch scale processes

At the within-patch scale, fragmentation can increase the risk of local extinction. The factors that contribute to extinction risk when populations are made small on fragments are (1) environmental stochasticity, particularly the effect of extreme events or disturbance (e.g., drought, fire), and (2) deterministic threats (e.g., habitat

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degradation; Harrison and Taylor 1997). Two other often-cited effects are probably of less importance, but may help to finish off a declining population. These are (3) demographic stochasticity, which affects only very small populations, and (4) loss of genetic variation, which acts relatively slowly (Harrison and Taylor 1997).

Mounting empirical evidence suggests that habitat modification (a deterministic threat, factor [2] above) may be one of the most significant influences of habitat fragmentation on biota. However, habitat modification may increase or reduce extinction risk. This is because habitat modification has the potential to reduce or increase growth rates or carrying capacities. Empirical evidence suggests that often a change that negatively affects one species benefits another (e.g., Didham et al. 1998, Davies et al. 2000). Habitat is modified as a result of changes in fluxes of wind, water, and solar radiation (Saunders et al. 1991), which can cause changes to vegetation structure (Malcolm 1994, Laurance et al. 1998), microclimate (Kapos 1989, Kapos et al. 1997), and ground cover (Didham et al. 1998). These changes are usually greatest at fragment edges (e.g., Malcolm 1994, Laurance et al. 1998).

Between-patch scale processes

Processes operating at the between-patch scale also affect the persistence of species. The core conceptual framework of both metapopulation theory (Levins 1969) and the equilibrium theory of island biogeography (MacArthur and Wilson 1967) is that within-patch dynamics are influenced not only by local extinction but also by colonization from elsewhere in the landscape. As the landscape becomes more fragmented, colonization rates are reduced. Then, within-patch species richness will decline (MacArthur and Wilson 1967) and extinction risk at the scale of the entire metapopulation will increase (Levins 1969, Hanski 1994).

A feature that distinguishes fragmented landscapes from simple island-sea models is that the matrix in which habitat fragments are embedded is often hospitable to varying degrees to many species. Then, the matrix will have a strong influence on between-patch processes. The matrix has three potential roles: (1) altering dispersal and colonization rates, which may be reduced or enhanced, depending on the characteristics of each species; (2) providing alternative habitat to existing species (for some species matrix habitat may be of lower quality than the original habitat, while for others it may be of higher quality); and (3) as a source of novel invading species for fragments, as the matrix may provide habitat for new species (Fahrig and Merriam 1994, Saurez et al. 1998).

Theoretical predictions from a recent metacommunity model formalize some of these observations about the potential effects of the matrix on communities in patchy environments (Holt 1997). Holt (1997) considered patches in a habitable matrix and allowed species

to be either specialists or generalists on the two habitat types (fragment or matrix). One prediction was that species that were abundant in the common habitat (matrix) had potential to become more common members of local communities in the sparser habitat (fragments) than species that did not inhabit the common habitat. This spillover effect had potential to be important in determining which species make up local communities.

Aim and hypotheses

We set out to determine the relative importance of the processes operating at these two spatial scales (within and between patch) in altering the structure of the beetle community as a whole, as the result of the fragmentation of the landscape. We recognized five kinds of possible changes to beetles, at both community and population levels of organization, in response to the experimental fragmentation of their forest habitat. These are described below as five hypotheses. We considered three basic attributes of community structure: the number of species (species richness), the identity of those species (species composition, i.e., presence-absence), and the abundances of those species (relative abundance). We also considered the effects of fragmentation on turnover, and we tested for changes in the occurrence of individual species by traits.

Within-patch scale.—

Hypothesis 1.—Species richness will decline on habitat fragments compared to continuous forest, more so on small than on large fragments. This is because populations can become small on fragments and the risk of extinction is greater for small populations (e.g., Diamond et al. 1987, Robinson and Quinn 1988). Clearly, the processes that lead to this hypothesis only involve species that are isolated on fragments (i.e., habitat specialists that do not also inhabit the matrix). However, a decline in the richness of habitat specialists will result in a decline in the richness of the whole community. A further prediction is that rare species will be more susceptible to extinction than common species because their populations become smaller than those of co-occurring species of higher natural abundance.

Hypothesis 2.—Deterministic habitat changes manifested as edge effects will alter the occurrence and abundance of species, and result in changes to species richness, species composition, and relative abundance compared to fragment interiors and continuous forest. Following Malcolm (1994), we recognize that the edge effect at a site within a fragment is not determined solely by the influence from the nearest point on an edge but is the integral of the influences from all points on all edges. The pattern of change in community structure will depend on how much the effect diminishes as a function of distance from the edge. Depending on the penetration distance of the edge effect, the size and shape of the fragment may be important. Any of the patterns in Fig. 1 may occur.

Between-patch scale.—

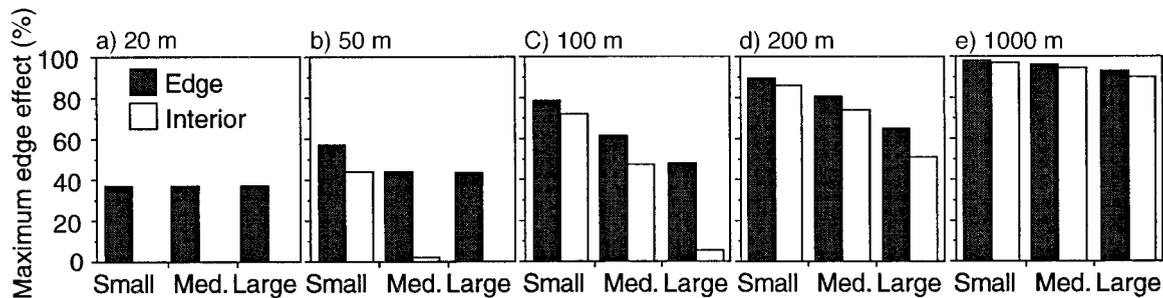


FIG. 1. Predictions from the integrated edge-effect model (Malcolm 1994) for edge and interior sites in fragments of the Wog Wog habitat fragmentation experiment in southeastern Australia. The experiment has three fragment sizes (small, 50×50 m; medium, 93.54×93.54 m; large, 175×175 m). The magnitude of the integrated edge effect has been scaled to the maximum possible integrated effect and therefore represents the relative effect. Predictions are for a point edge effect that declines linearly to zero at (a) 20 m, (b) 50 m, (c) 100 m, (d) 200 m, and (e) 1000 m from an edge. This illustrates that the pattern of population or community change that we expect to see depends both on how much the effect diminishes as a function of distance from an edge and on the size of the fragment. Depending on the penetration distance of the edge effect we can expect any of the patterns from (a) to (e). Note that pure edge effects can appear as apparent size effects [e.g., (c) and (d)].

Hypothesis 3.—As the result of a reduction in colonization rate, species richness will decline on fragments compared to continuous forest. We can distinguish between a reduction in species richness due to increased extinction rate (hypothesis 1) vs. a decreased colonization rate by examining the responses of individual species. If a reduced colonization rate is important, then we expect the poorest dispersers to be the most susceptible.

Hypothesis 4.—An alternative to hypothesis 3 is that species richness will not decline because the matrix is suitable habitat for many fragment-inhabiting species and thus that the rate of colonization into fragments will not change. Or further, the matrix will act as a source of invading species, so that colonization will increase, increasing species richness in fragments. Then, we expect the community structure of fragment edges to be more like the matrix than interiors.

Hypothesis 5.—Temporal variability in species composition (turnover) on habitat fragments will either increase or decline relative to continuous forest, because the balance between extinction and colonization rates will be altered.

Of these five hypotheses, some apply more to some species than others. For example, some hypotheses apply only to those species that are truly isolated on fragments while others apply to the whole community, including those species that inhabit the matrix. However, our intention was to discover how changes in the processes outlined in these five hypotheses manifested as changes in the whole community. Thus, our approach was to examine the effects of fragmentation on the community as a whole and then to use the responses of individual species to help to explain these responses. This approach allowed us to assess the relative importance of within- and between-patch processes at the level of the whole beetle community.

METHODS

Experimental design

The Wog Wog habitat fragmentation experiment is located in southeastern Australia ($37^{\circ}04'30''$ S, $149^{\circ}28'00''$ E; Fig. 2), in native *Eucalyptus* forest between 80 and 100 yr old. The experimental design and the rationale for it are described by Margules (1993). The experiment consists of six replicates (Fig. 2). Each replicate contains three plots (fragments): one is small (0.25 ha), one is medium (0.875 ha), and one is large (3.062 ha). This gives a total of 18 plots (fragments). Four replicates of each plot size became habitat fragments when the surrounding *Eucalyptus* forest was cleared during 1987 and planted to *Pinus radiata*, for plantation timber in winter 1988. Two replicates of each plot size remain in uncleared continuous forest, and serve as unfragmented control plots. Two years of data were collected prior to the fragmentation treatment for all plots.

Within each plot there are eight monitoring sites, which are stratified in two ways. First, sites are stratified by habitat type (topography) into slopes and drainage lines because the vegetation communities associated with these topographic features are different (Austin and Nicholls 1988). Slopes are characterized by a grassy understory and scattered shrubs below open eucalypt forest. Drainage lines are dominated by ti tree, which is a small shrubby tree that forms dense stands. Second, sites were stratified by proximity to the fragment edge (edge or interior). There are two monitoring sites in each of the four strata (slope edge, slope interior, drainage line edge, drainage line interior), totaling eight sites within each plot and a total of 144 sites over the 18 plots (fragments). Following clearing, an additional 44 monitoring sites were established in the *P. radiata* plantation between the habitat fragments, also stratified by habitat type. Two permanent pitfall

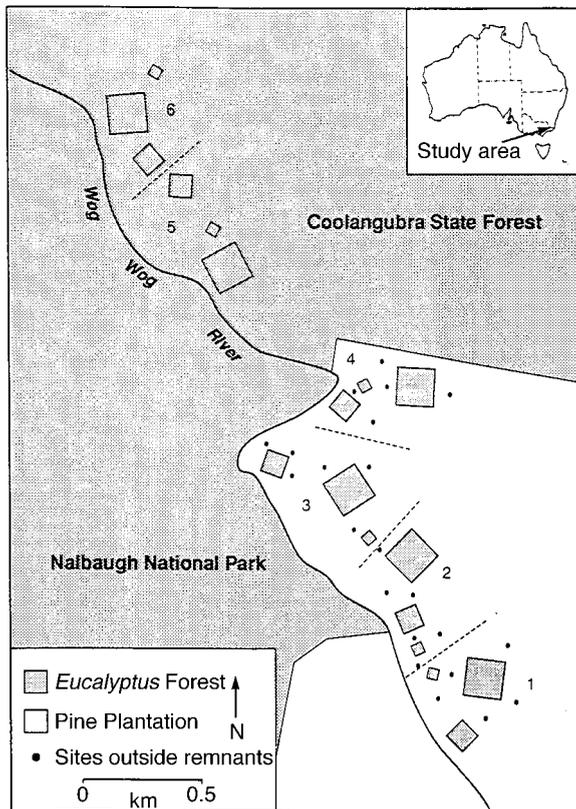


FIG. 2. Map of the Wog Wog experimental site in south-eastern Australia showing eucalypt forest fragments and control plots in continuous forest. There are eight monitoring sites within each fragment. In addition, each dot represents the approximate location of a pair of monitoring sites (a slope site and a drainage line site) established in the pine matrix between the remnants after habitat fragmentation. In total there are 44 monitoring sites in the pine matrix. Fragments are separated by a minimum of 50 m. Numbers index the replicate stratum. The plot stratum consists of three plots of different size within each replicate.

traps are located at each monitoring site. Traps are opened for seven days, four times a year, that is, once during each season. Monitoring commenced in February 1985.

Records of beetle species have so far been processed up until 1991 (five years post-fragmentation) over which time 655 beetle species were captured. About half of these are as yet unnamed but all of them can be recognized to species level and have been allocated a voucher number by J. F. Lawrence (Australian National Insect Collection, CSIRO Entomology, Canberra). More than a third of these species were trapped only one or two times, while six species were trapped over one thousand times each. The incidental captures may represent species that are either rare, are not habitually ground dwelling, are "tourists" (just passing through), or that move little and are therefore unlikely to fall into pitfall traps. In this study, we included only

those species that were caught three or more times (325 species).

Changes in community structure

Exploratory data analysis and previous studies revealed that the effects of fragmentation on arthropods were different in slope and drainage line habitat (Sisk and Margules 1993, Margules et al. 1994). Thus, we looked for effects of fragmentation on richness, composition, and relative abundance, separately for slopes and drainage lines. We used Genstat 5 release 4.1 for all analyses (Genstat 5 Committee 1997).

Species richness.—Our approach to the analysis is described in detail in Davies and Margules (1998). We give a brief description here. We used a Poisson regression analysis to test for the effects of habitat fragmentation per se, fragment size, and edge effects on the annual beetle species richness over five years post-fragmentation. The natural logarithm of the average richness in the two years before fragmentation was included as a covariate to control for spatial variability in richness across the landscape before fragmentation. The explanatory variables were defined as follows. Fragmentation was a factor with two levels, fragments and controls. Size was a factor with three levels, small, medium, and large. Edge was a factor with two levels, inner sites and outer sites. Year was a factor with five levels (1987–1991).

Model fitting took place as follows. The full model was fitted. Each variable was then dropped from the full model one at a time. For separate analyses of habitat type the experimental design is a split-split-split plot with replicate stratum as the whole plot, plot stratum as the split plot, the site stratum as the split-split plot, and the year stratum as the split-split-split plot. To deal with this nested error structure in the Poisson regression, we included three extra variables as error terms. The variables that we included to account for random variation at the whole plot, split plot, and split-split plot levels were as follows (see Table 3): Replicate (between replicate variability) at the replicate stratum, Replicate \times Size (between fragment variability) at the plot stratum, Replicate \times Size \times Site (between site variability) at the site stratum. The regression residual accounted for random variation in the year stratum (between year variability). Year was the bottom level of the sampling structure (Table 3) because the sampling had a repeated-measures design, with samples taken at the same sites through time. *P* values were calculated by comparing the change in deviance associated with dropping a term to a chi-square distribution. A variable was considered significant when $P < 0.05$. Only the significant variables were included in the final model. Departures of the data from the model assumptions were determined by viewing histograms of the data, plots of residuals vs. fitted values, and plotting residuals as a normal order probability plot.

Species composition and relative abundance.—To

TABLE 1. Matrices constructed for the partial Mantel tests for a fragmentation effect.

| A: dissimilarity after | | | | | | B: design matrix | | | | | | C: dissimilarity before | | | | | | |
|------------------------|----------------|----------------|----------------|----------------|----------------|------------------|----------------|----------------|----------------|----------------|----------------|-------------------------|----------------|----------------|----------------|----------------|----------------|---|
| C ₆ | C ₅ | F ₄ | F ₃ | F ₂ | F ₁ | C ₆ | C ₅ | F ₄ | F ₃ | F ₂ | F ₁ | C ₆ | C ₅ | F ₄ | F ₃ | F ₂ | F ₁ | |
| C ₆ | 0 | . | . | . | . | C ₆ | 0 | 0 | 1 | 1 | 1 | C ₆ | 0 | . | . | . | . | |
| C ₅ | | 0 | . | . | . | C ₅ | | 0 | 1 | 1 | 1 | C ₅ | | 0 | . | . | . | |
| F ₄ | | | 0 | . | . | F ₄ | | | 0 | 0 | 0 | F ₄ | | | 0 | . | . | |
| F ₃ | | | | 0 | . | F ₃ | | | | 0 | 0 | F ₃ | | | | 0 | . | |
| F ₂ | | | | | 0 | F ₂ | | | | | 0 | F ₂ | | | | | 0 | |
| F ₁ | | | | | | F ₁ | | | | | | F ₁ | | | | | | 0 |

Notes: C_i designates a control, while F_i designates a fragment, where *i* indexes the replicates indicated in Fig. 2. Dots indicate dissimilarity values calculated from the data.

examine the effects of fragmentation on species composition and relative abundance, we used an approach based on dissimilarity measures. We asked whether communities in the fragments became more dissimilar from the controls after fragmentation, or became more similar to communities in the pine matrix after fragmentation. Two dissimilarity measures were used. We used the Bray-Curtis measure (Bray and Curtis 1957) to measure the dissimilarity in relative abundance. The Bray-Curtis measure is widely used in community studies and has been shown to provide a robust estimate of the difference in structure between communities (Faith et al. 1987). It is most sensitive to differences in the relative abundance of species between communities, although it is also affected by species richness and species composition. We used the Sorensen-Czekanowski measure (Czekanowski 1913, Digby and Kempton 1987) to measure the dissimilarity in species composition (i.e., the presence-absence pattern). The Sorensen-Czekanowski measure is closely related to the Bray-Curtis measure but it is based only on presence-absence data. It is most sensitive to species composition but is also affected by species richness.

We used Mantel tests to determine whether communities in the fragments became more dissimilar from the controls after fragmentation, for each of species composition and relative abundance. To do this, we first constructed a 6 × 6 symmetric matrix of the dissimilarity between pairs of control and fragment sites (matrix **A**, Table 1). In other words, the dissimilarity was between replicates (Table 1, Fig. 2) but calculated at the site level. Since more than one site was contrasted between two replicates, we computed all pairwise dissimilarities and took the average to construct the dissimilarity matrix. Although the diagonal elements of **A** are positive when averaged at the site level, they are not informative and we set them to zero (Table 1). We constructed one matrix for each combination of size, edge, and year after fragmentation (30 combinations for each of slope and drainage line habitats). Thus, taking one combination as an example, we computed the F₄-C₆ dissimilarity (Table 1) as the average dissimilarity between (1) sites in C₆ classed as medium, outer, drainage lines, for 1990, and (2) sites in F₄ of the same class. We constructed a second 6 × 6 symmetric matrix

specifying the experimental design (Fortin and Gurevitch 1993, Legendre and Legendre 1998), which we coded 0 for each within-treatment dissimilarity, and 1 for each between-treatment dissimilarity (matrix **B**, Table 1). The experiment has six replicates (two controls, four fragments), which gives eight possible fragment-to-control (i.e., between treatment) contrasts and seven possible (nondiagonal) within-treatment contrasts (Table 1). We constructed a third 6 × 6 dissimilarity matrix for the pre-fragmentation data, for each combination of habitat type, size, and edge, taking the site-level dissimilarity averaged over the two years (matrix **C**, Table 1).

To test for an effect of fragmentation on species composition and relative abundance we computed the partial Mantel statistic $r_{AB.C}$ (the correlation between matrix **A** and **B**, given **C**). This statistic describes the effect of the fragmentation treatment on community structure when spatial variation in community structure across the site before fragmentation is removed. A positive value for $r_{AB.C}$ indicates an effect of fragmentation (i.e., the between-treatment dissimilarity is greater than the within-treatment dissimilarity), whereas $r_{AB.C}$ equal to or less than zero indicates no effect. We conducted partial Mantel tests for positive $r_{AB.C}$ by the first method of Smouse et al. (1986), using the algorithm given in Legendre and Legendre (1998:558). For each test, we used 9999 permutations and calculated the one-tail permutation probabilities. We conducted separate tests for each combination of size, edge, and year, as well as tests for an overall effect of fragmentation (i.e., averaged over site and edge).

We used the same approach to determine whether beetle communities in the fragments became more similar to beetle communities in the pine matrix (i.e., the vegetation type in which the fragments are embedded) than the controls were to the pine matrix. Since the term matrix here has both an ecological meaning and a mathematical meaning, in this paragraph we refer to the pine matrix as “pines” and reserve “matrix” to refer to the mathematical matrices constructed to conduct the Mantel tests. We first constructed a dissimilarity matrix consisting of pine-control, pine-fragment and pine-pine contrasts (matrix **D**, Table 2). As above, the dissimilarity was between replicates but calculated

TABLE 2. Matrices constructed for the partial Mantel tests of whether fragments were more similar to pines than controls were to pines.

| D: dissimilarity | | | | E: design matrix | | | | F: distance | | | | |
|------------------|----------------|----------------|----------------|------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|---|
| P ₄ | P ₃ | P ₂ | P ₁ | P ₄ | P ₃ | P ₂ | P ₁ | P ₄ | P ₃ | P ₂ | P ₁ | |
| C ₆ | . | . | . | C ₆ | 1 | 1 | 1 | C ₆ | 2 | 3 | 4 | 5 |
| C ₅ | . | . | . | C ₅ | 1 | 1 | 1 | C ₅ | 1 | 2 | 3 | 4 |
| F ₄ | X | . | . | F ₄ | X | 0 | 0 | F ₄ | 0 | 1 | 2 | 3 |
| F ₃ | . | X | . | F ₃ | 0 | X | 0 | F ₃ | 1 | 0 | 1 | 2 |
| F ₂ | . | . | X | F ₂ | 0 | 0 | X | F ₂ | 2 | 1 | 0 | 1 |
| F ₁ | . | . | . | F ₁ | 0 | 0 | 0 | F ₁ | 3 | 2 | 1 | 0 |
| P ₄ | 0 | . | . | P ₄ | — | — | — | P ₄ | 0 | 1 | 2 | 3 |
| P ₃ | . | 0 | . | P ₃ | — | — | — | P ₃ | . | 0 | 1 | 2 |
| P ₂ | . | . | 0 | P ₂ | — | — | — | P ₂ | . | . | 0 | 1 |
| P ₁ | . | . | . | P ₁ | — | — | — | P ₁ | . | . | . | 0 |

Notes: C_{*i*} designates a control, F_{*i*} a fragment, and P_{*i*} pines, where *i* indexes the replicates indicated in Fig. 2. Dots indicate dissimilarity values calculated from the data. X indicates excluded values. Dashes indicate that coding was not applicable for the Mantel tests.

as a site-level average. Matrix **D** is an extension of **A** to include contrasts involving pines. The question of whether communities in the fragments were more similar to the pines than the controls were to the pines involves only the upper part of matrix **D** (the pine-fragment and pine-control contrasts). We computed also the pine-pine contrasts, although these were not involved in any Mantel tests. As above, we constructed one matrix for each combination of size, edge, and year after fragmentation (24 combinations in each habitat type). We omitted 1987 because trapping did not begin in the pines until half way through the sampling year. We constructed a second matrix specifying the experimental design, which we coded 0 for each pine-fragment dissimilarity and 1 for each pine-control dissimilarity (matrix **E**, Table 2). We excluded within-replicate pine-fragment contrasts because these were not possible for pine-control contrasts. We constructed a third matrix that coded for the physical distance be-

tween replicates (matrix **F**, Table 2) to account for spatial structure (Fortin and Gurevitch 1993). To test whether fragments were more similar to the pines than controls to the pines, we computed the partial Mantel statistic r_{DEF} . As mentioned, this was done only for the upper part of **D**, **E**, and **F**. This statistic describes the degree to which the fragments were more like the pines after accounting for spatial structure. A positive value for r_{DEF} indicates that the fragments were more like the pines than the controls were like the pines, whereas r_{DEF} equal to or less than zero indicates no effect. We conducted partial Mantel tests as described previously.

Using this approach, the experiment-wise Type I error rate is inflated because multiple tests were made. We applied a Bonferroni correction to the significance level (nominally $P < 0.05$) to obtain a corrected significance level. For the tests involving size and edge combinations, the corrected significance level was $P < 0.05/30 = 0.0017$ (pine analysis $P < 0.05/24 = 0.0021$)

TABLE 3. Summary of Poisson regression analysis of the effect of experiment forest fragmentation on species richness.

| Source | df | Slopes | | Drainage lines | |
|------------------------------------|-----|----------|----------|----------------|----------|
| | | Deviance | <i>P</i> | Deviance | <i>P</i> |
| Replicate stratum | | | | | |
| Fragmentation | 1 | 12.20 | <0.001 | 28.72 | <0.001 |
| Replicate (residual) | 4 | 7.72 | 0.10 | 8.51 | 0.07 |
| Plot stratum | | | | | |
| Fragmentation × Size | 4 | 3.59 | 0.46 | 8.01 | 0.09 |
| Replicate × Size (residual) | 8 | 11.12 | 0.19 | 10.55 | 0.23 |
| Site stratum | | | | | |
| Fragmentation × Edge | 2 | 11.23 | 0.004 | 2.12 | 0.35 |
| Log richness before fragmentation | 1 | 15.62 | <0.001 | 14.23 | <0.001 |
| Replicate × Size × Site (residual) | 51 | 53.93 | 0.36 | 65.25 | 0.09 |
| Year stratum | | | | | |
| Year | 4 | 65.02 | <0.001 | 37.58 | <0.001 |
| Year × Fragmentation | 4 | 3.91 | 0.42 | 5.45 | 0.25 |
| Year × Fragmentation × Edge | 8 | 10.91 | 0.21 | 5.30 | 0.73 |
| Residual | 272 | 177.59 | | 195.11 | |
| Total | 359 | 372.85 | | 412.32 | |

and for fragmentation overall, the significance level was $P < 0.05/5 = 0.01$ (pine analysis $P < 0.05/4 = 0.0125$). However, the Bonferroni correction is too conservative for a large number of tests, so we interpreted Mantel tests with uncorrected permutation probability < 0.05 as providing cautious support for the effect of fragmentation and those less than the Bonferroni corrected level as providing strong support.

Turnover

We calculated percentage turnover from year to year as

$$\frac{C_{\text{obs}} + E_{\text{obs}}}{S_i + S_{i+1}} \times 100 \quad (1)$$

where S_i is the number of species at a site in year i , C_{obs} is the number of species present in year $i + 1$ but not in year i (i.e., the number of species observed to colonize) and E_{obs} is the number of species absent in year $i + 1$ but present in year i (i.e., the number of species observed to become extinct). Eq. 1 is equivalent to the Sorensen-Czekanowski dissimilarity measure, where i indexes sites instead of years. We tested for the effects of fragmentation, size, edges, and year on turnover using ANOVA, separately for each habitat type. We specified the error structure as a split-split-split plot as for the species richness analysis. We used a Greenhouse-Geisser adjustment to adjust probabilities in the year stratum for repeated measures (Greenhouse and Geisser 1959, von Ende 1993). Turnover between the two years before fragmentation was used as a covariate to control for spatial variation in turnover across the landscape before fragmentation.

Individual species change in occurrence by traits

We conducted an analysis of the responses of the 325 species to determine the effect of three traits: natural abundance, isolation, and trophic group. For each species, the effect size was calculated as

$$\pi_{\text{fragments}} - \pi_{\text{controls}} \quad (2)$$

where $\pi_{\text{fragments}}$ is the probability of occurrence in the fragments and π_{controls} is the probability of occurrence in the controls. The effect size was calculated for each of six treatment types (small-fragment edge, small-fragment interior, medium edge, medium interior, large edge, large interior). To calculate $\pi_{\text{fragments}}$ we first calculated the mean probability of occurrence in each of these treatment types for each post-fragmentation year (five years) and then calculated the mean of the annual values. We calculated π_{controls} in the same way but did not calculate the probability of occurrence separately for each treatment type in order to give a larger sample size. The effect size was either positive or negative depending on whether a species had become more, or less, likely to occur in a given treatment type (e.g., small interior sites) than in the controls.

Regressing effect size against traits of species.—

Three traits of species were considered. A fourth, body size, was tested in a previous analysis of traits by change in abundance and was not significant (Davies et al. 2000) so it was not considered here.

1. *Natural abundance.*—For each species, we summed catches for the two years of sampling that took place before the fragmentation treatment was applied.

2. *Isolation.*—In the absence of dispersal information, we calculated instead an isolation index for each species by dividing the number of individuals caught in the pine matrix (44 sites) by the number caught in the fragments (96 sites), post-fragmentation, after first equalizing the data for trapping effort. Beetles fell into two categories. (1) Never trapped in the pine matrix (isolated). For a species to be isolated two conditions were necessary: (a) the species did not occur in the matrix. That is, the species was a habitat specialist of eucalypt habitat, and (b) the species did not disperse between fragments. Given that roughly one-quarter of the trapping effort was in the matrix, we are confident that if a species was not caught in the matrix in five years of trapping, it did not occur there. Similarly, we are confident that these species did not disperse along the ground through the matrix, or rarely did so. Unfortunately, we can say little about other modes of dispersal. Thus, it is possible that some species categorized as isolated met the first condition but were able to disperse, undetected, between fragments. (2) Trapped in the pine matrix (not isolated). These species either had populations established in the pine matrix (were habitat generalists), or dispersed through the matrix between fragments. Given these caveats, we believe that these isolation categories are useful as a first approximation, particularly given that the contrasts that we make are relative rather than absolute.

3. *Trophic group.*—Beetles were assigned to one of four trophic groups: (a) species feeding on detritus and deadwood (hereafter referred to as detritivores), (b) fungivores, (c) herbivores, and (d) predators. Depending on the knowledge of the species, the assignments were made at the species or genus or, in some cases, subfamily level by J. F. Lawrence (Australian National Insect Collection, CSIRO Entomology, Canberra).

We used multiple regression to test for the effects of these three traits on the responses of beetles to fragmentation in different parts of the experiment (small edges, small interiors, medium edges, medium interiors, large edges, large interiors). The effect size was weighted by total occurrence before fragmentation so that less weight was placed on the responses of those species that occurred only a few times. Model fitting took place as follows. First, the full model was fitted including the three traits as variables. Each variable was dropped from the full model one at a time and then replaced. P values were calculated from variance ratios and a variable was considered significant when $P < 0.05$. Only the significant variables were included in the final model. Departures of the data from the

model assumptions were determined by viewing histograms of the data, plots of residuals vs. fitted values, and plotting residuals as a normal order probability plot.

RESULTS

The structure of the beetle community was significantly different in slope compared to drainage line habitat for all measures (richness, Poisson regression, $P = 0.001$; species composition, Mantel test, $P < 0.001$; relative abundance, Mantel test, $P < 0.001$, turnover, ANOVA, $P < 0.001$). In all subsequent analyses, we considered slopes and drainage lines separately.

Species richness

There was a significant effect of habitat fragmentation on species richness (Table 3). In slope habitat, species richness increased by one to two species per site at fragment edges compared to fragment interiors and continuous forest (Fig. 3, Table 3), but there was no effect of fragment size (Table 3, Fragment \times Size). The pattern in species richness on slopes corresponds with the model for an edge effect that penetrates 20 m or less (contrast Fig. 1a and Fig. 3). That is, only edges were affected in all fragment sizes, not interiors. In the drainage line habitat, species richness increased slightly in fragments compared to controls but there was no effect of fragment size or of edges (Table 3). For both slopes and drainage lines, removing new colonizers (species not present in the landscape before fragmentation) from the analyses had no effect on these results. Thus, the increase in richness at fragment slope edges and in fragment drainage lines was not explained by new species colonizing from the matrix.

Species composition

Species composition changed significantly in fragments compared to continuous forest (Fig. 3, Table 4). However, in drainage line habitat a significant effect was observed only for small edges in 1988 (Table 4). In slope habitat, the change in composition was greatest in years 1989 and 1990 (3–4 yr post-fragmentation). For these years, there was a tendency for small fragments to be most different from controls and for large interior sites to be most similar to controls (Fig. 3). Thus, in years 1989 and 1990, the pattern was consistent with a 50–100 m edge effect (contrast Fig. 1c and Fig. 3 slope habitat).

Relative abundance

Changes in the relative abundance of species due to habitat fragmentation were more pronounced than changes in species composition (Fig. 3). The biggest effects of fragmentation were observed in slope habitat. In slope habitat, a significant effect of fragmentation was observed for years 1988–1991 (Table 4) and was greatest in 1989 and 1990 (Fig. 3). Significant changes in relative abundance were also detected in drainage

line habitat, where small and medium fragments were significantly different from controls in years 1989 to 1991 (Fig. 3, Table 4). Differences due to fragment size and edge effects in both habitats did not become apparent until three years post-fragmentation (1989), when small and medium fragments were most different from controls and large fragments were most similar to controls (Fig. 3). For slopes, the pattern in relative abundance corresponded to model predictions for an edge effect that penetrated 100 m (contrast Fig. 1c and Fig. 3 slope habitat).

Turnover

Fragmentation significantly reduced species turnover in slope habitat but not in drainage line habitat (Table 5, Fig. 4). This was set against a decline in turnover over the period of the experiment, in both fragments and controls (Fig. 4). Turnover was significantly different from year to year (Table 5). There were no size or edge effects on species turnover (Table 5).

The matrix

There were three results. First, in many later years, the species composition and relative abundance of sites in the pine matrix were more like the fragments than the controls were like the pine matrix (Fig. 5) although the difference was significant only in some years and more often in drainage lines (Table 6). Second, in drainage line habitat in the later years, the species composition and relative abundance of small-fragment edges were most like the matrix and large-fragment interiors were least like the matrix (Fig. 5). This pattern corresponded to model predictions for an edge effect that penetrated 50–100 m (contrast Fig. 1c and Fig. 5 drainage line habitat). In slope habitat, while the species composition and relative abundance of fragments were most like the matrix in some years, averaged over all size and edge classes (Table 6), there did not appear to be a consistent pattern related to size or edge (Table 6, Fig. 5). Third, species richness was significantly lower at matrix sites than at fragment and continuous forest sites, by one to two species (Poisson regression, $P = 0.002$, Fig. 3).

Individual species responses and traits

Rarity.—Natural abundance affected the responses of species to fragmentation (Fig. 6, Table 7). Species with high natural abundances increased in occurrence in fragments compared to continuous forest, while rare species were not affected. The relationship between rarity and response to fragmentation was not different in different parts of the fragmented landscape (e.g., small-fragment edges vs. large-fragment interiors).

Isolation.—Species that were not isolated increased in occurrence in fragments (Fig. 6, Table 7). They increased most at small edges and least at large interiors (Fig. 6). Species that were isolated on fragments were only slightly affected by fragmentation. There were

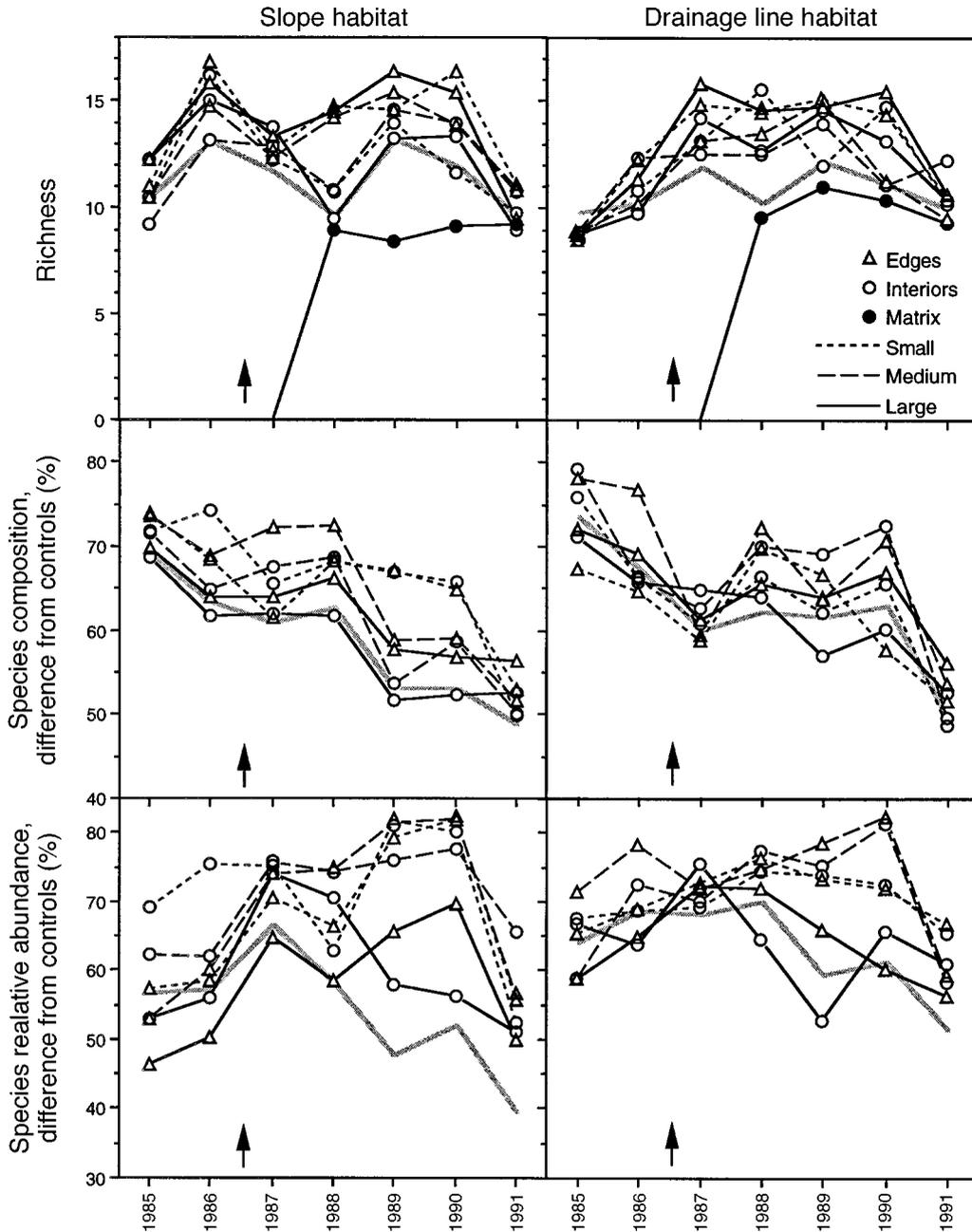


FIG. 3. Effects of experimental fragmentation, fragment size, and edges on species richness, species composition, and species relative abundance, over seven years. For species composition (presence-absence) and relative abundance, the dark lines are the average fragment-control dissimilarity (from A, Table 1), for each combination of habitat type (slopes, drainage lines), fragment size, and edge. The gray lines are the average within-treatment dissimilarity (from A, Table 1), further averaged across sizes and edges. The gray lines thus represent the expected pattern for the null hypothesis of no fragmentation effect. Dissimilarities after fragmentation shown here are not adjusted for dissimilarity before fragmentation. Arrows indicate when fragmentation occurred. Significance levels appear in Table 4.

small declines in the occurrence of species in small fragments and at medium-fragment edges (Fig. 6).

Trophic group.—There was a significant effect of trophic group on species' responses to fragmentation (Table 7). Detritivores and fungivores occurred at more sites post-fragmentation but occurrences of herbivores

were variable, while predators occurred at fewer sites post-fragmentation (Fig. 6).

Evidence of a deeply penetrating edge effect.—For both isolation and trophic group, the pattern of change in occurrence corresponded with a deeply penetrating edge effect (compare Fig. 6 and Fig. 1c, e.g., ~100

TABLE 4. Randomization significance levels for the effects of forest fragmentation on species composition and relative abundance, for slope and drainage line habitat.

| Effect | Permutation probability | | | | |
|------------------------------------|-------------------------|---------------|-----------------|-----------------|-----------------|
| | 1987 | 1988 | 1989 | 1990 | 1991 |
| Composition, slopes | | | | | |
| Fragmentation | 0.2008 | 0.0036 | 0.0006 | 0.0066 | 0.0094 |
| Small edge | 0.1236 | 0.0992 | 0.0026 | 0.0118 | 0.0953 |
| Small interior | 0.2467 | 0.0149 | 0.0628 | 0.0080 | 0.3565 |
| Medium edge | 0.0768 | 0.3665 | 0.2154 | 0.0862 | 0.1374 |
| Medium interior | 0.2242 | 0.2757 | 0.3110 | 0.1278 | 0.7854 |
| Large edge | 0.1532 | 0.1563 | 0.0670 | 0.0261 | 0.0445 |
| Large interior | 0.3986 | 0.1423 | 0.4113 | 0.7465 | 0.0439 |
| Composition, drainage lines | | | | | |
| Fragmentation | 0.3398 | 0.0065 | 0.1629 | 0.0809 | 0.0706 |
| Small edge | 0.5689 | 0.0001 | 0.1233 | 0.5569 | 0.1082 |
| Small interior | 0.8942 | 0.1273 | 0.6934 | 0.1043 | 0.3663 |
| Medium edge | 0.1837 | 0.1094 | 0.1027 | 0.5633 | 0.3318 |
| Medium interior | 0.7255 | 0.1597 | 0.0109 | 0.0991 | 0.4587 |
| Large edge | 0.2310 | 0.3399 | 0.6953 | 0.4077 | 0.1734 |
| Large interior | 0.0952 | 0.0836 | 0.8349 | 0.5489 | 0.3397 |
| Relative abundance, slopes | | | | | |
| Fragmentation | 0.0547 | 0.0024 | 0.0001 | < 0.0001 | < 0.0001 |
| Small edge | 0.3129 | 0.0041 | 0.0001 | < 0.0001 | 0.0001 |
| Small interior | 0.0445 | 0.0220 | < 0.0001 | 0.0003 | 0.1259 |
| Medium edge | 0.0434 | 0.1077 | < 0.0001 | < 0.0001 | 0.0045 |
| Medium interior | 0.0347 | 0.0085 | 0.0004 | 0.0025 | 0.0003 |
| Large edge | 0.6246 | 0.2983 | < 0.0001 | < 0.0001 | 0.1052 |
| Large interior | 0.1186 | 0.2889 | 0.0082 | 0.0408 | 0.1954 |
| Relative abundance, drainage lines | | | | | |
| Fragmentation | 0.0510 | 0.1229 | 0.0003 | < 0.0001 | 0.0027 |
| Small edge | 0.1622 | 0.0094 | 0.0052 | < 0.0001 | 0.0004 |
| Small interior | 0.7002 | 0.4668 | 0.0608 | 0.0197 | 0.0015 |
| Medium edge | 0.0279 | 0.4297 | 0.0028 | 0.0421 | 0.4237 |
| Medium interior | 0.5879 | 0.0910 | < 0.0001 | 0.0002 | 0.0315 |
| Large edge | 0.0581 | 0.5395 | 0.3146 | 0.1920 | 0.0519 |
| Large interior | 0.0325 | 0.7799 | 0.8130 | 0.7485 | 0.1714 |

Notes: Permutation probabilities are the proportions of times that the partial Mantel statistic obtained by random permutation exceeded the observed partial Mantel statistic. Bold values indicate permutation probability <0.05. Underlined values indicate permutation probability less than the Bonferroni-corrected Type I error rate.

m). This gradient corresponded with the changes seen in the community-level measures, in relative abundance and to a smaller extent in species composition, which were greatest at small-fragment edges and smallest in large-fragment interiors (Figs. 3 and 5).

DISCUSSION

There were four main findings. First, experimental forest fragmentation affected species composition, relative abundance, and richness via two edge effects with different penetration distances. The pattern of change in species composition and species relative abundance corresponded with a deeply penetrating edge effect (to 100 m). That is, changes were generally greatest at small-fragment edges and negligible at large-fragment interiors. Species richness increased slightly at slope edges but there was no fragment-size effect, corresponding with model predictions for a shallowly penetrating edge effect (to 20 m). Second, fragmentation reduced species turnover. Further, changes in turnover and the other measures of community structure (rich-

ness, composition, relative abundance) were set against large background spatial and temporal variation in community structure that declined over the period of the experiment reported here. Third, matrix sites were more like fragments than continuous forest sites, in species composition and relative abundance, and they were less species rich than fragment and continuous-forest sites. In drainage line habitat, small-edge sites were most like the matrix and large interior sites were least like the matrix. This pattern of change also corresponds with a deeply penetrating edge effect. Fourth, changes in the occurrences of individual species were linked to rarity, degree of isolation, and trophic group, and these changes in occurrence also tended to be greatest at small-fragment edges and smallest at large-fragment interiors.

Thus, habitat fragmentation significantly changed beetle community structure via processes operating at the within-patch scale, as edge effects. Processes operating at the between-patch scale were less important over the time scale of the experiment. Following we

TABLE 5. Repeated-measures ANOVA of the effect of experimental forest fragmentation on species turnover.

| Source | df | Slopes | | | | Drainage lines | | | |
|-----------------------------------|-----|--------|-------|--------|--------|----------------|------|--------|--------|
| | | MS | F | P | Adj P | MS | F | P | Adj P |
| Replicate stratum | | | | | | | | | |
| Fragmentation | 1 | 0.21 | 9.50 | 0.05 | | 0.02 | 0.15 | 0.72 | |
| Log turnover before fragmentation | 1 | 0.03 | 1.29 | 0.33 | | 0.01 | 0.06 | 0.82 | |
| Residual | 3 | 0.02 | | | | 0.10 | | | |
| Plot stratum | | | | | | | | | |
| Fragmentation × Size | 4 | 0.02 | 0.44 | 0.78 | | 0.02 | 0.95 | 0.49 | |
| Log turnover before fragmentation | 1 | 0.00 | 0.03 | 0.87 | | 0.14 | 8.86 | 0.02 | |
| Residual | 7 | 0.05 | | | | 0.02 | | | |
| Site stratum | | | | | | | | | |
| Fragmentation × Edge | 2 | 0.03 | 1.60 | 0.21 | | 0.04 | 3.02 | 0.06 | |
| Log turnover before fragmentation | 1 | 0.00 | 0.00 | 1.00 | | 0.01 | 0.79 | 0.38 | |
| Residual | 51 | 0.02 | | | | 0.02 | | | |
| Year stratum | | | | | | | | | |
| Year | 4 | 0.15 | 17.80 | <0.001 | <0.001 | 0.12 | 9.32 | <0.001 | <0.001 |
| Year × Fragmentation | 4 | 0.02 | 2.24 | 0.07 | 0.11 | 0.02 | 2.16 | 0.07 | 0.12 |
| Year × Fragmentation × Edge | 8 | 0.01 | 1.34 | 0.22 | 0.34 | 0.01 | 0.98 | 0.45 | 0.59 |
| Year × Fragmentation × Size | 16 | 0.01 | 1.08 | 0.38 | 0.55 | 0.01 | 0.85 | 0.63 | 0.78 |
| Residual | 256 | 0.01 | | | | 0.01 | | | |
| Total | 359 | | | | | | | | |

Note: Greenhouse-Geisser adjusted probabilities ("Adj P") are given for the year stratum.

discuss within-patch processes and between-patch processes in more detail.

Within-patch processes

Hypothesis 1 predicted that species richness would be reduced as a result of an increased extinction risk in small populations on fragments. Contrary to this prediction, species richness increased (Fig. 3, discussed further in relation to hypothesis 2). Further, at the species level there was little evidence of an increase in extinction rate since the occurrence of rare species was not affected by fragmentation (Fig. 6). Previously we found that rare species declined in abundance in fragments compared to continuous forest (Davies et al. 2000), suggesting that fragmentation affected the abundance but not the occurrence of rare species. Nevertheless, those declines in abundance may in time become changes in species occurrences.

In support of hypothesis 2, edge effects altered the occurrences and abundances of species on fragments compared to continuous forest. Two edge effects, with different penetration distances, changed the structure of the beetle community. One penetrated a short distance and altered species richness in slope habitat while the other penetrated deeply and affected species relative abundance in both slope and drainage line habitats and, to a lesser extent, species composition in slope habitat.

A shallow edge effect in richness.—In slope habitat, species richness increased by 1–2 species, at fragment edges, in all fragment sizes, consistent with model predictions for an edge effect that penetrated 20 m (compare Fig. 3 and Fig. 1a). This was probably not the result of the colonization of fragment edges by species

from the matrix because the species composition of slope fragment edges was no more like the matrix than fragment interiors (Fig. 5). Neither was the increase due to species that were new to the landscape. Thus, the extra species at slope edges came from within the fragments themselves. The change in richness at edges may have resulted from habitat modification at edges. Slope habitat is characterized by open eucalypt forest so, for example, productivity may have increased at edges as the result of an increase in solar radiation.

In contrast, in drainage line habitat, species richness increased by 1–2 species in fragments compared to continuous forest but there was no difference in effect between edge and interior sites. The vegetation in drainage lines is different from the slope habitat, so it is not surprising that there is a different result between the two habitats. However, in addition to the vegetation being different, drainage lines also have a hydrological function in the landscape. There is anecdotal evidence that the hydrology of fragment drainage lines was altered when the land surrounding the fragments was cleared and that they now experience greater fluxes of water than the continuous forest controls. Since these changes result from landscape-wide alterations, they might be expected not to exhibit edge effects. However, it is not clear that such hydrological changes are linked to the increase in species richness.

Few other studies have reported increases in species richness as the result of fragmentation. In the large-scale fragmentation experiment at Manaus in Brazil, small-mammal and frog diversity increased in fragments because of colonization by generalist species that were able to inhabit the matrix surrounding fragments (Gascon et al. 1999). In Californian grassland the spe-

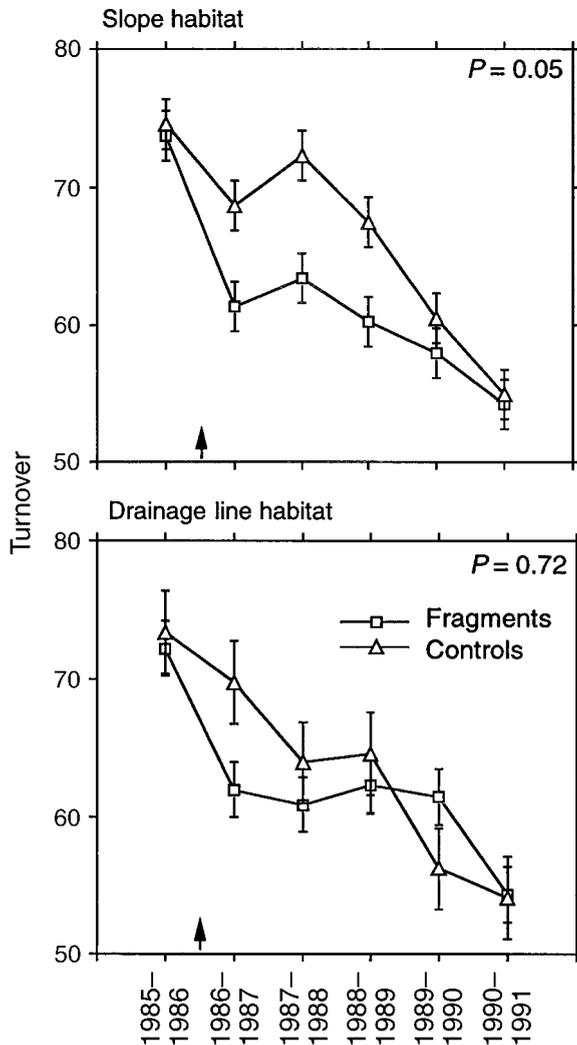


FIG. 4. Mean turnover (percentage change in species composition) from one year to the next for sites in fragments and continuous forest. Means and standard errors are from ANOVA. The arrows indicate when fragmentation occurred. P values are for the significance of the difference between fragments and controls after fragmentation. There was not a significant effect of fragment size or edges.

cies richness of flowering plants and insects increased with increasing habitat subdivision (Quinn and Robinson 1987).

However, many studies have reported declines in richness as the result of fragmentation. In the Brazilian experiment, the richness of insectivorous birds (Stouffer and Bierregaard 1995) and of dung and carrion beetles (Klein 1989) declined with isolation. In scrub habitat fragments in southern California, ant species richness was lower in smaller fragments (Saurez et al. 1998). In subtropical dry forest in northwest Argentina, the richness of native flower visitors was lower in smaller fragments (Aizen and Feinsiger 1994). In a Kansas oldfield, larger patches were more species rich than small patches (Holt et al. 1995).

A deeply penetrating edge effect in relative abundance and composition.—A pattern consistent with model predictions for a deeply penetrating edge effect occurred in (1) changes in species' relative abundance and composition (Fig. 3), and (2) as increases and declines in individual species' occurrences by trophic group and degree of isolation (Fig. 6). The degree of change for each combination of fragment size and edge was close to the pattern predicted by the model for an edge effect that penetrated ~ 100 m (Fig. 1c). That is, changes were largest at small-fragment edges and negligible at large-fragment interiors. This pattern was strongest for changes in the relative abundance of species in the beetle community. The pattern was also present for species composition. The edge effect had a greater impact on species' abundance than on their occurrence.

We hypothesize that habitat modification is the main cause of this edge effect, although the exact form of modification is not clear. For example, the edge effect was evident as increases in the occurrence of detritivores and fungivores (Fig. 6). This may have been in response to an increase on the forest floor of litter and dead wood, and thus also fungal spores. Although there was visual evidence of increased windthrow at fragment edges, we have not yet documented this empirically. Nonetheless, in another forest fragmentation experiment at Manaus in Brazil, edge effects that altered microclimate and increased wind turbulence near edges were considered the most important cause of increased tree mortality and damage in rain forest fragments (Laurance et al. 1998).

The effects of altered forest structure and microclimate have also been documented in the Brazilian experiment as greater changes in community structure of small than large fragments. Like our findings, beetle community structure (relative abundance) was affected by fragment size and edges and was most different from continuous forest in the smallest fragments (Didham et al. 1998). For insectivorous bird communities, the relative abundance of 1-ha fragments diverged more from pre-fragmentation communities than did 10-ha fragments (Stouffer and Bierregaard 1995). In the dung and carrion beetle community, the relative abundance of species in small and large fragments was different and both sizes were different from continuous forest (Klein 1989).

Between-patch scales

Hypothesis 3 predicted that dispersal between fragments would decrease as a result of fragmentation, leading to a reduction in species richness on fragments. As already discussed, species richness was not reduced. In addition, there was little evidence of a reduction in colonization to fragments. Although isolated species declined in abundance on fragments compared to continuous forest (Davies et al. 2000), their occurrences declined only slightly on small fragments and at the edges of medium fragments.

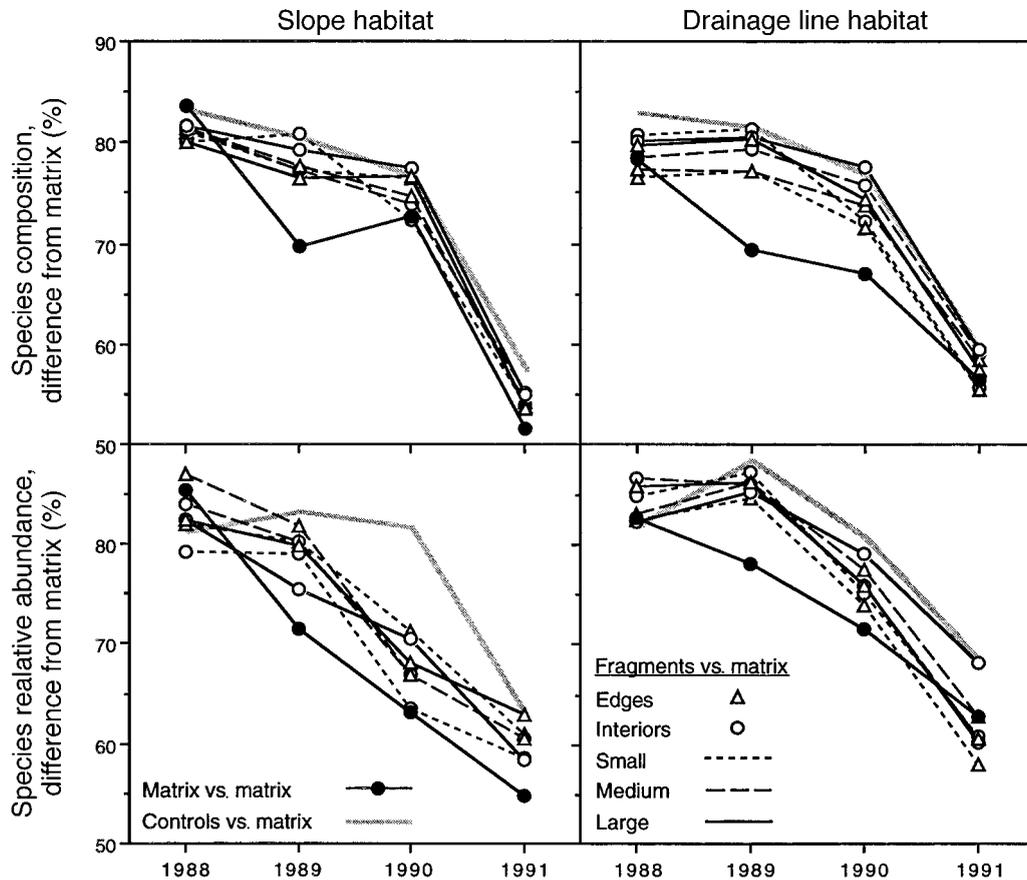


FIG. 5. Mean difference in species composition (presence-absence) and relative abundance of sites in the pine matrix compared to other sites. Three dissimilarities were computed: pine matrix vs. control, pine matrix vs. fragment, and pine matrix vs. pine matrix. For species composition and relative abundance, the dark lines are the average fragment-matrix dissimilarity (from **D**, Table 2), for each combination of habitat type (slopes, drainage lines), fragment size, and edge. The gray lines are the average control-matrix dissimilarity (from **D**, Table 2), further averaged across sizes and edges. The gray lines thus represent the expected pattern for the null hypothesis of no fragmentation effect. Departures in the downward direction from the gray line indicate that fragment sites were more similar to matrix sites than control sites were to matrix sites. The matrix-matrix comparison represents the spatial variability in community structure among sites in the matrix (average from **D**, Table 2). Significance levels appear in Table 6.

There are two possible reasons for these findings. First, dispersal between fragments was reduced, affecting abundance (e.g., Hanski et al. 1994), but not enough time had elapsed for extinctions to occur. This explanation highlights a problem common to fragmentation experiments conducted at landscape scales, that processes contributing to extinction within fragments operate over time scales longer than most fragmentation experiments have been running. Extinction events that result from environmental stochasticity, demographic stochasticity, or loss of genetic variation are more likely to be observed over decades than years.

Second, dispersal between fragments was not reduced because the matrix was not inhospitable to fragment-inhabiting species (hypothesis 4). Many fragment-inhabiting species occurred in the matrix, in some cases in high abundances (Davies et al. 2000). Further, species that were captured in the matrix were captured at more sites in fragments than in continuous forest;

that is, they increased their occurrence within fragments. Species that were abundant in the matrix also increased in abundance on fragments compared to continuous forest (Davies et al. 2000). Thus, for many species, the effect of modifying the landscape may have been to reduce the probability of extinction within fragments by increasing the net flow of individuals in to fragments. Our findings support predictions from a metacommunity model that species that are abundant in the common habitat (matrix) have potential to become more common members of local communities in the sparser habitat (fragments) than species that do not inhabit the common habitat (Holt 1997).

The effect of fragmentation on community dynamics was also detected as a change in turnover. Turnover was reduced in habitat fragments. Thus, paradoxically, the effect of habitat fragmentation was to stabilize community dynamics at the within-fragment scale. It is difficult to determine whether this was due to a change

TABLE 6. Randomization significance levels for whether the species composition and relative abundance of fragments were more similar to the pine matrix than controls were to the pine matrix, for slope and drainage line habitat.

| Effect | Permutation probability | | | |
|---|-------------------------|---------------|---------------|-------------------|
| | 1988 | 1989 | 1990 | 1991 |
| Composition, slopes | | | | |
| Fragmentation | 0.4086 | 0.1238 | 0.2507 | 0.0244 |
| Small edge | 0.5975 | 0.0443 | 0.2066 | 0.1181 |
| Small interior | 0.5620 | 0.0631 | 0.2642 | 0.0293 |
| Medium edge | 0.3986 | 0.2213 | 0.0964 | 0.4993 |
| Medium interior | 0.1925 | 0.3755 | 0.1977 | 0.3510 |
| Large edge | 0.3003 | 0.1327 | 0.9549 | 0.0362 |
| Large interior | 0.5218 | 0.2984 | 0.2113 | 0.2284 |
| Composition, drainage lines | | | | |
| Fragmentation | <0.0001 | 0.2731 | 0.0021 | 0.0930 |
| Small edge | 0.0042 | 0.0193 | 0.3478 | 0.8043 |
| Small interior | 0.0523 | 0.7135 | 0.0020 | 0.2359 |
| Medium edge | 0.0004 | 0.5610 | 0.0133 | 0.1779 |
| Medium interior | 0.0637 | 0.0035 | 0.0007 | 0.6219 |
| Large edge | 0.0010 | 0.4415 | 0.1404 | 0.0201 |
| Large interior | 0.0048 | 0.9752 | 0.2172 | 0.0603 |
| Relative abundance, slopes | | | | |
| Fragmentation | 0.7471 | 0.0797 | 0.0002 | 0.1356 |
| Small edge | 0.6563 | 0.0254 | 0.0183 | 0.3925 |
| Small interior | 0.7385 | 0.0013 | 0.0005 | 0.0833 |
| Medium edge | 0.8837 | 0.0435 | 0.0001 | 0.6055 |
| Medium interior | 0.7732 | 0.6417 | 0.0020 | 0.4240 |
| Large edge | 0.6307 | 0.6673 | 0.0064 | 0.1433 |
| Large interior | 0.6235 | 0.0708 | 0.0090 | 0.0133 |
| Relative abundance, drainage lines | | | | |
| Fragmentation | 0.8345 | 0.0335 | 0.0275 | <0.0001 |
| Small edge | 0.9489 | 0.0931 | 0.1727 | 0.0013 |
| Small interior | 0.6962 | 0.1090 | 0.0427 | 0.0035 |
| Medium edge | 0.6519 | 0.0724 | 0.0424 | 0.0703 |
| Medium interior | 0.9237 | 0.0112 | 0.0028 | 0.0036 |
| Large edge | 0.7381 | 0.0185 | 0.0549 | 0.0002 |
| Large interior | 0.5806 | 0.5674 | 0.2452 | 0.0184 |

Notes: Permutation probabilities are the proportions of times that the partial Mantel statistic obtained by random permutation exceeded the observed partial Mantel statistic. Bold values indicate permutation probability <0.05. Underlined values indicate permutation probability less than the Bonferroni-corrected Type I error rate.

in extinction rate or to a change in colonization rate because these rates are not the same as E_{obs} and C_{obs} in Eq. 1. For example, the number of species observed to go extinct in one period (E_{obs}) depends on both the true extinction rate and the colonization rate. However, since turnover results from the net effect of extinction and colonization, the fact that turnover changed means that one or both of these rates was altered by fragmentation. Paradoxically, our other results suggest that either the extinction rate was reduced or the colonization rate increased, since the occurrences of species within fragments increased.

Turnover appeared to be independent of habitat modification because there were no edge or size effects in turnover, which is in contrast to Bengtsson et al. (1997) who found that habitat stability contributed to community stability in British woodland birds. Three studies have recorded increased community variability as

the result of habitat fragmentation. Holt et al. (1995) found that spatial heterogeneity in vegetation composition increased in grassland patches, less so in large patches. Boulmier et al. (1998) found that temporal variability in the richness of forest breeding birds increased as the result of higher local extinction rates. Finally, Laurance et al. (1998) found that tree turnover was significantly higher at the edges of 18-yr-old tropical rain forest fragments, as the result of increased mortality.

IMPORTANT CONSIDERATIONS

Two final points deserve consideration. First, the effects of fragmentation on community structure were set against high natural spatial and temporal variability in community structure. Spatial and temporal variability in community structure declined over the period of the experiment (1985–1991). That is, the species composition and relative abundance of species in the fragments, continuous forest, and the matrix became more similar from site to site (reduced spatial variation, Fig. 3) and more similar from year to year (reduced temporal variability, Fig. 4). This inherent temporal and spatial variability in community structure highlights the necessity of long-term, controlled and replicated field experiments. For example, had our experimental design included only before and after data, with no controls, we would have reached very different conclusions.

Second, while this is one of the larger habitat fragmentation experiments, the spatial scale of the experiment is still quite small. The largest forest fragment is 175 × 175 m in area and fragments are separated by 50 m. However, the scale of the experiment is probably well matched to the scale at which the study organisms move around in the landscape. Half of the 325 species considered were never trapped in the matrix between fragments. Given that roughly one-quarter of the trapping effort was in the matrix, we are confident that if a species was not caught in the matrix in five years of trapping, it did not occur there. Similarly, we are confident that these species did not disperse along the ground through the matrix, or rarely did so. Unfortunately, we can say little about other modes of dispersal. Thus, it is possible that some of these species were able to disperse, undetected, between fragments. The other half of the 325 species considered, were trapped in the pine matrix. These species either had populations established in the matrix or were able to disperse through the matrix between fragments. Thus, the scale at which beetle species use the fragmented landscape at Wog Wog might be comparable to the way bird species use a much larger fragmented landscape, where some species are able to disperse easily between fragments while other species never venture beyond a given fragment. We are currently documenting dispersal distances for several beetle species. Preliminary evidence for four large wingless carabids suggests that,

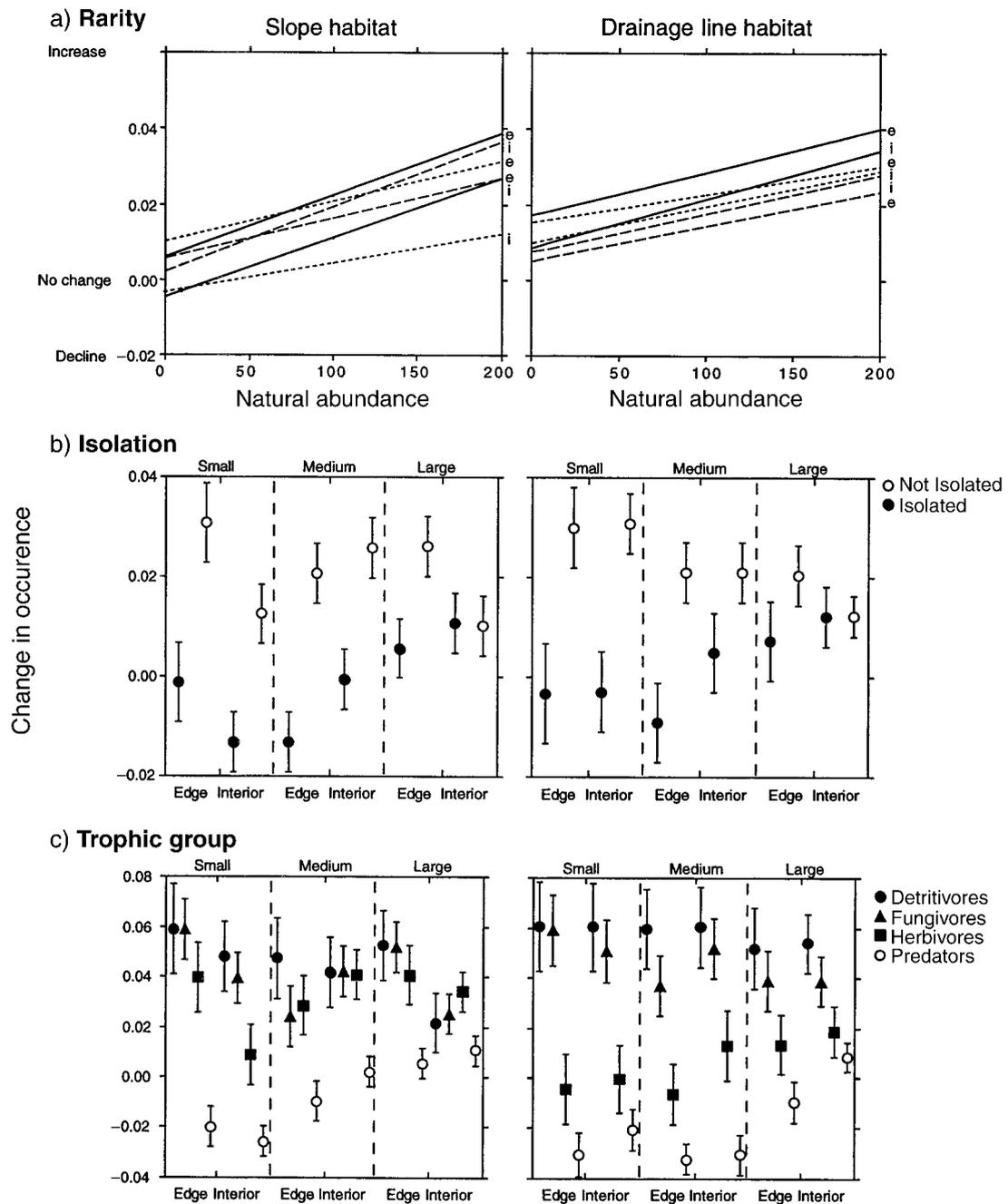


FIG. 6. Change in occurrence of individual species in fragments compared to continuous forest, regressed against traits of species ($n = 325$): (a) rarity, (b) degree of isolation, and (c) trophic group. A change in occurrence of 0.02, for example, means that species occurred at 2% more sites in the fragments than in the controls. Change in occurrence was calculated for three fragment sizes (small, medium, and large), at fragment edges and interiors. For (a), small dashes are small fragments, large dashes are medium fragments, and hard lines are large fragments; e = edge, and i = interior. Error bars represent standard errors. Significance levels appear in Table 7.

on a timescale of months, individuals rarely move further than 10 m.

CONCLUSIONS

We set out to determine which population-level processes were altered and thus changed the structure of

the beetle community as a whole, as the result of forest fragmentation. Processes operating at the within-patch scale were responsible for most of the changes that we observed. We did not detect an increase in extinction rate or reduction in colonization rate as the result of fragmentation. It is possible that these rates had altered

TABLE 7. Summary of multiple regression analyses of individual species changes in occurrence and their traits for three fragment sizes at fragment edges and interiors.

| Source | df | Small edge | | Small interior | | Medium edge | | Medium interior | | Large edge | | Large interior | |
|---------------|-----|------------|--------|----------------|--------|-------------|--------|-----------------|--------|------------|--------|----------------|--------|
| | | F | P | F | P | F | P | F | P | F | P | F | P |
| Slope habitat | | | | | | | | | | | | | |
| Rarity | 1 | 1.60 | 0.21 | 0.15 | 0.70 | 2.34 | 0.13 | 12.55 | <0.001 | 20.88 | <0.001 | 75.51 | <0.001 |
| Isolation | 1 | 12.23 | <0.001 | 6.97 | 0.009 | 9.77 | 0.002 | 27.56 | <0.001 | 17.96 | <0.001 | 2.31 | 0.12 |
| Trophic | 3 | 28.02 | <0.001 | 20.86 | <0.001 | 12.57 | <0.001 | 22.73 | <0.001 | 23.16 | <0.001 | 19.88 | <0.001 |
| Error | 288 | | | | | | | | | | | | |
| Drain habitat | | | | | | | | | | | | | |
| Rarity | 1 | 2.13 | 0.15 | 1.41 | 0.23 | 0.04 | 0.84 | 1.48 | 0.23 | 4.35 | 0.04 | 11.88 | <0.001 |
| Isolation | 1 | 3.22 | 0.07 | 6.84 | 0.009 | 8.07 | 0.005 | 1.54 | 0.22 | 7.17 | 0.008 | 2.35 | 0.13 |
| Trophic | 3 | 20.58 | <0.001 | 28.48 | <0.001 | 33.77 | <0.001 | 31.02 | <0.001 | 25.90 | <0.001 | 20.21 | <0.001 |
| Error | 288 | | | | | | | | | | | | |

but it was too early to detect their consequences. Instead, edge effects had an overwhelming influence on community structure at the within-fragment scale. Processes operating at the between-fragment scale were less important, supporting the suggestion that the role of local processes in regional persistence may have been underemphasized (Harrison and Taylor 1997, Harrison and Bruna 1999). Unexpectedly, turnover declined on fragments compared to continuous forest, either as the result of a reduction in extinction rate or an increase in the colonization rate, or both. Further, the matrix had a stabilizing role on the fragment community by allowing species that could persist in the matrix to increase their occurrences within fragments.

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