

WHICH TRAITS OF SPECIES PREDICT POPULATION DECLINES IN EXPERIMENTAL FOREST FRAGMENTS?

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Abstract. Theory suggests that species with particular traits are at greater risk of extinction than others. We assumed that a decline in abundance in forest fragments, compared to continuous forest, equated to an increase in extinction risk. We then tested the relationships between five traits of species and decline in abundance for 69 beetle species in an experimentally fragmented forest landscape at Mt. Wog Wog in southeastern Australia. The experiment was controlled and replicated. Monitoring ran for two years before forest fragmentation; in this paper, we examine data for five years postfragmentation. We tested five hypotheses: (1) Species that occur naturally at low abundance are more likely to decline as a result of fragmentation than are abundant species. (2) Isolated species are more likely to decline than species that are not isolated. (3) Large species are more likely to decline than small species. (4) Species in trophic groups at the top end of food chains are more likely to decline than species in trophic groups lower in the food chain. (5) Because traits are often shared by related species, populations of more closely related species will respond in the same way.

We found that: (1) rare species were more likely to decline than abundant species; (2) isolated species were more likely to decline than species that were not isolated; (3) body size was not correlated with response to fragmentation; (4) among species that declined, predators declined most; and (5) taxonomically related species did not respond in the same way to fragmentation. Thus, our results confirm theories predicting that isolated, rare, or predaceous species will be lost first from fragmented landscapes.

Key words: *beetles; body size; dispersal; experimental fragmentation; extinction risk; forest fragments; isolation; rarity; traits; trophic group.*

INTRODUCTION

Habitat fragmentation is considered to be one of the greatest threats to biological diversity. However, mounting empirical evidence suggests that not all species decline toward extinction as a result of the fragmentation of their habitat (e.g., Margules et al. 1994, 1995, Davies and Margules 1998, Didham et al. 1998, Dooley and Bowers 1998). This suggests that some species are at greater risk in fragmented landscapes than are others. Identifying these species would be useful.

Theory predicts that species with particular traits may be at greater risk of extinction when populations are made small and isolated, the most serious consequences of habitat fragmentation. We set out to test the relationships between population declines and traits that are predicted to increase extinction risk for species in an experimentally fragmented forest landscape. We considered four traits of species that have been linked, in theory, to extinction risk.

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Natural abundance

Both theory and empirical evidence predict that small populations are at greater risk of extinction than large populations because small populations are vulnerable to the proximate causes of extinction: demographic and environmental stochasticity, genetic deterioration, and social dysfunction (Simberloff 1986, Pimm et al. 1988, Pimm 1991, Caughley 1994, Lawton 1994). Similarly, species that occur naturally at low abundance are likely to be more extinction-prone than are those that occur at high abundance (e.g., Diamond et al. 1987, Robinson and Quinn 1988) because, when isolated on fragments, their populations become smaller than those of co-occurring species with higher abundance. Here, we test the prediction that species that occur naturally at low abundance decline more following fragmentation than do more abundant species, and therefore have a greater risk of extinction.

Isolation and dispersal

When there is migration between small populations, then the collection of subpopulations on habitat fragments in a landscape comprises a metapopulation (Hanski 1994). In classic metapopulation theory, subpopulations living on isolated patches periodically go extinct

and are recolonized by individuals migrating from other patches (Levins 1969). Metapopulations go extinct when the rate of extinction of individual patches is greater than the rate of dispersal among patches (Hanski 1991). More recent formulations of metapopulation theory show that dispersal can also affect the abundance of populations in patches (Hanski et al. 1994). Here, we test the prediction that isolated species are at greater risk of extinction than species that are not isolated, in fragmented forest compared to continuous forest.

Body size

It has often been claimed that large-bodied species are at a greater risk of extinction than small-bodied species (Gaston and Blackburn 1996a). Body size is correlated with at least three variables, population abundance, population fluctuations, and speed of recovery from low population numbers, which are in turn correlated with extinction risk (Lawton 1994). However, there is contention over the form of these relationships (Chesson 1991, Pimm 1991, McArdle and Gaston 1993, Gaston and Blackburn 1996c, Blackburn and Gaston 1997, Navarrete and Menge 1997), and they offer contradictory predictions about whether it is small or large species that are at greater risk of extinction (Lawton 1994, Gaston and Blackburn 1995). We test the prediction that body size affects extinction risk and determine the form of the relationship in an experimental setting.

Trophic group

Theory predicts that species at the top end of food chains are more prone to extinction than species at lower levels because the former tend to have more unstable population dynamics and are less likely to persist in a fluctuating environment (Pimm and Lawton 1977, Lawton 1995, Holt 1996). We test the prediction that species in trophic groups at the top end of food chains are at the greatest risk of extinction in experimentally fragmented forest.

Taxonomic relationships

We also test whether response to fragmentation was correlated with the taxonomic group (family) of beetles, as traits are often shared by related species.

Extinction and decline

We note that whether declining species are headed toward extinction is uncertain, and that this does not necessarily follow as a prediction of theory. However, large populations typically become small populations before going extinct (Hanski et al. 1994). In what follows, we assume that a greater decline in abundance in fragments than in controls equates with increased extinction risk.

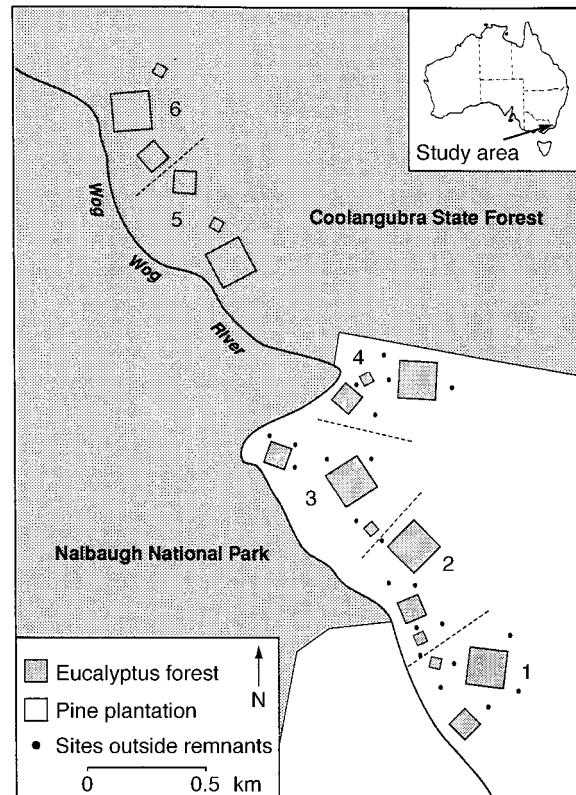


FIG. 1. Map of the experimental site at Mt. Wog Wog, southeastern Australia, showing eucalypt forest fragments and control plots in continuous forest. Each dot represents the approximate location of a pair of monitoring sites (a slope site and a drainage-line site) established in the pine matrix between the remnants after habitat fragmentation. A eucalypt forest corridor, 50–100 m wide, was retained along the river (not shown).

METHODS

Experimental design

The Wog Wog habitat fragmentation experiment was located in southeastern New South Wales, Australia (37°04'30" S, 149°28'00" E; Fig. 1), in regrowth *Eucalyptus* forest 80–100 yr old. The experimental design was described in detail elsewhere (Margules 1993). Briefly, the experiment consisted of three plot sizes: 0.25 ha, 0.875 ha, and 3.062 ha; the larger plots were 3.5 times the area of the smaller ones. Four replicates of each size (12 plots) became habitat fragments when the surrounding *Eucalyptus* forest was cleared in 1987 and planted to *Pinus radiata* for plantation timber. Two replicates of each size (six plots) remained in uncleared continuous forest, and served as the unfragmented control plots. Fragments within replicates were grouped more closely together but were located ≥ 50 m apart. This was considered sufficient to isolate fragments. Fragment distance from continuous forest was not part of the design, although fragments were roughly the same distance from continuous forest. A eucalypt forest

corridor, 50–100 m wide, was retained along the river. For all plots, two years of data were collected prior to the fragmentation treatment.

Within each plot, monitoring sites were stratified by topography (into slopes and drainage lines) and proximity to the remnant edge (into inner and outer zones). Thus, each of the 18 plots was divided into four strata (inner slope, outer slope, inner drain, and outer drain). There were two monitoring sites in each of the four strata, totaling eight sites within each plot, for a total of 144 sites over the 18 plots. Following clearing, an additional 44 monitoring sites were established in the *Pinus radiata* plantation between the habitat remnants. Two permanent pitfall traps were located at each monitoring site. Traps were opened for seven days, four times a year; that is, once during each season.

Monitoring commenced in February 1985. The experimental treatment, forest habitat fragmentation, took place over nine months in 1987. The pine plantation was established in winter 1988. By 1992, the pines had grown to a height of ~4 m.

In total, 655 beetle species were captured within the experiment, half of which are as yet unnamed; more than one-third (263) of these species were trapped only a few times. At the other end of the scale, six species were trapped >1000 times each, and one of these species was trapped 15 421 times. The incidental captures may represent species that are either rare, are not habitually ground-dwelling, or that move little and are therefore unlikely to fall into pitfall traps. Although it would be interesting to know the effect of habitat fragmentation on these species, there is little that we can infer from so few captures. We chose to study species that had been trapped ≥ 40 times since the fragmentation treatment was applied, because this was a minimum for which inferential statistics could be used with confidence. From a total of 655 species trapped, this gave us a total of 69 study species.

Data analysis: Traits and responses of beetle species to fragmentation

The dependent variable.—We analyzed the response of each of these 69 species to habitat fragmentation using nested analysis of covariance or Poisson regression, depending on whether the data were normally distributed or dominated by zeroes and ones, respectively (Day and Quinn 1989, McCullagh and Nelder 1989). The analysis is described in detail in Davies and Margules (1998). Here, we give a brief description.

To determine the response of each species to habitat fragmentation, we analyzed the total number caught at each of the 144 sites for years 3–5, postfragmentation. For nearly all species, there were not enough data to treat years or seasons separately. For the very abundant species, for which we could have considered years separately, visual inspections of the data suggested that the summed responses were representative. Data from the two years immediately after fragmentation were not

included because the disturbances that occurred during that period (clearing, burning, and planting of *Pinus radiata*) may have been confounding. We tested for the effect of fragmentation by contrasting captures in the fragments and in the controls. Captures from the two years before fragmentation were included in the model as a covariate, the \log_e of abundance before fragmentation. This covariable acted to remove any effect of uneven distribution in abundance before fragmentation.

We used these analyses to estimate the mean abundance in fragments vs. continuous forest controls for each of the 69 species. We estimated the response to fragmentation as the ratio of beetles in the fragments and continuous forest:

$$y = \log_e \left(\frac{\text{mean no. beetles in fragments}}{\text{mean no. beetles in controls}} \right).$$

Subsequently, we used this ratio to indicate the change in abundance due to fragmentation.

The independent variables: species traits.

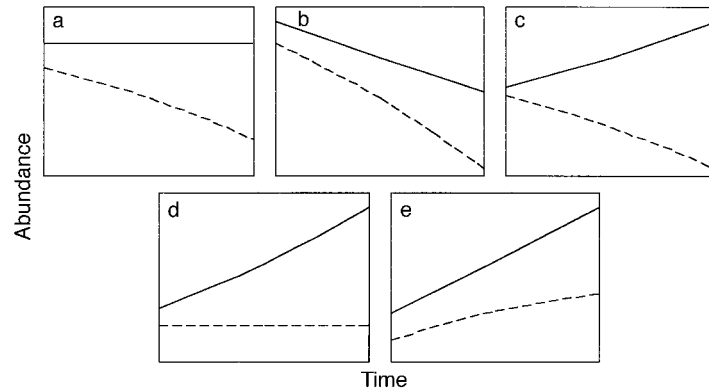
1. *Natural abundance.*—For each species, we summed catches for the two years of sampling that took place before the fragmentation treatment was applied.

2. *Isolation.*—In the absence of dispersal information for each species, we instead calculated an isolation index and divided species into three categories (see Fig. 3). We divided the number of individuals caught in the pine matrix (44 sites) by the number caught in the fragments (96 sites) in years 3–5 postfragmentation, after first equalizing the data for trapping effort. Beetles fell into three categories: never trapped in the pine matrix (completely isolated); trapped less often in the pine matrix than in the fragments (semi-isolated); and trapped more often in the pines than in the fragments (not isolated). We assumed that if a species was not caught in the matrix in five years of trapping, it did not occur there; neither did it disperse along the ground through the matrix, or rarely did so. It is possible that some species in this category were able to move between fragments by modes of dispersal not detected by our ground-based trapping method and were thus misclassified. For the semi-isolated and not isolated categories, we assumed that the number of beetles trapped in the matrix compared to the fragments reflected the degree of mixing at the between-fragment scale. That is, species trapped less often in the matrix (semi-isolated) either had smaller populations there or dispersed through the matrix less than did those species trapped at higher numbers (not isolated). Given these caveats, we believe that our isolation categories are useful as a first approximation, particularly given that the contrasts that we make are relative.

3. *Body size.*—With microcallipers, we measured total beetle body length and breadth across the widest part of the body, in millimeters, to the nearest 50 microns. We then multiplied these measures.

4. *Trophic group.*—Beetles were assigned to one of

FIG. 2. Five different ways in which 16 beetle species could decline in experimental forest fragments (dashed lines) compared to continuous forest controls (solid lines): (a) control populations do not change, fragment populations decline; (b) both control and fragment populations decline, but fragment populations decline significantly more; (c) control populations increase, fragment populations decline; (d) control populations increase, fragment populations do not change; and (e) both control and fragment populations increase, but control populations increase significantly more. All of these declines can be attributed to the effects of forest fragmentation. Species had responses similar to $a = 3$, $b = 2$, $c = 0$, $d = 3$, $e = 8$ [e.g., three species responded as modeled in panel (a), two as in panel (b), etc.].



three trophic groups: species feeding on dead wood and detritus, herbivores, and predators.

Correlating traits and the responses of beetles to fragmentation.—We used multiple regression to test for effects of four traits on beetle responses to fragmentation: natural abundance, degree of isolation on fragments, body size, and trophic group. The responses of beetle species to fragmentation were weighted by their standard errors ($1/SE^2$) in the trait analysis. This was so that the beetle species' responses in which we had greatest confidence (small standard errors) had more influence, whereas the responses in which we had less confidence (large standard errors) had less influence.

Model fitting took place as follows. The full model was fitted, including the four traits as variables and first-order interactions. Each variable was dropped from the full model, one at a time, and then replaced. The P values were calculated from variance ratios; a variable was considered significant when $P < 0.05$. The final model was fitted including only the significant variables.

Departures of data from the model assumptions were determined by viewing histograms of the data and plots of residuals vs. fitted values, and by plotting residuals as a normal order probability plot. The body size data required log transformation, which successfully stabilized the variance. We checked and were satisfied that the variables were not correlated. The strongest correlation was between natural abundance and isolation at 0.18.

Definition of decline.—A species that “declined” was one for which the mean abundance in fragments was significantly lower than the mean abundance in continuous forest, standardized for abundance before fragmentation across fragment and control sites. Species declined in five different ways (Fig. 2): (a) control populations did not change, but fragment populations declined; (b) both control and fragment populations declined, but fragment populations declined significantly more; (c) control populations increased and fragment populations declined (no species responded in this

way, but this option is included for completeness); (d) control populations increased, but fragment populations did not change; and (e) both control and fragment populations increased, but control populations increased significantly more. All of these declines can be attributed to negative effects of forest fragmentation. For example, for case (e) in which both control and fragment populations increased (but fragments less so), the treatment had a negative effect on populations in the fragments. This response has been documented for amphipods in this experiment (Margules et al. 1994).

Taxonomic relationships and response to fragmentation.—We also tested for a correlation between taxonomic relationship and the response of beetles to fragmentation. We used multiple regression, as before, grouping beetle responses by a single factor, family, with 16 categories, one for each family: (1) Anobiidae, (2) Bostrichidae, (3) Carabidae, (4) Corylophidae, (5) Cryptophagidae, (6) Curculionidae, (7) Elateridae, (8) Lathridiidae, (9) Leiodidae, (10) Oedemeridae, (11) Pselaphidae, (12) Ptiliidae, (13) Scarabaeidae, (14) Scydmaenidae, (15) Staphylinidae, and (16) Tenebrionidae. We first tried including family as a fifth variable in the trait analysis; however, there was confounding of family with other traits. Thus, examining family separately was the only way to investigate whether related beetles responded in similar ways to fragmentation.

Data analysis: Traits of species' response groups

To further investigate species' responses and their correlations with traits, we repeated the multiple regression analyses for four subgroups of species (Fig. 3): species that were completely isolated ($n = 21$), species that declined by $>20\%$ ($n = 16$), species that increased by $>20\%$ ($n = 20$), and species that were not affected by fragmentation ($n = 33$) compared to continuous forest controls.

RESULTS

Which traits make species decline?

Natural abundance.—Beetle species that naturally occurred at low abundances declined following frag-

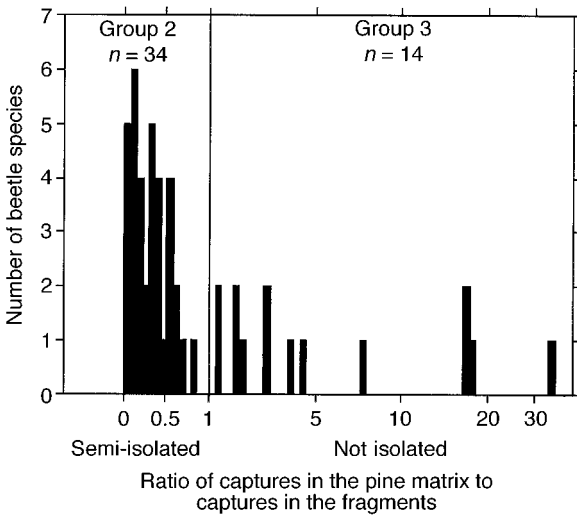


FIG. 3. The 69 study species were divided into three groups based on their level of isolation in the eucalypt fragments. Two groups are shown, not three. We divided the number of times that a species was caught in the pine matrix (not isolated) by the number of times that it was caught in the fragments (standardized for trapping effort). Group 1 (not shown) was never captured in the pine matrix, i.e., these species were completely isolated (ratio = 0, $n = 21$). Group 2 was captured less often in the pine matrix than in the fragments, and group 3 was captured more often in the pine matrix than in the fragments. Note the log scale in the Group 3 x -axis (used to retain resolution between ratios 1 and 5).

mentation ($n = 69$; $P < 0.001$; Fig. 4a). Further, when we tested only those species that were isolated on fragments ($n = 21$), the rarest species declined most ($P = 0.008$; Fig. 5). When we tested only the 16 species that declined, there was also a significant relationship between natural abundance and response to fragmentation ($n = 16$; $P < 0.001$; Fig. 6). Species that were captured ≤ 10 times in the two years before fragmentation occurred in fragments at 25% of their abundance in the continuous forest. In contrast, species that were caught ~ 100 times before fragmentation occurred in fragments at 80–90% of their abundance in continuous forest.

Isolation.—Those species that were isolated on fragments declined in abundance in fragments compared to continuous forest controls. Species that were semi-isolated (less abundant in the pine matrix than in fragments) were equally abundant in fragments and continuous forest, whereas species that were not isolated increased in abundance in fragments compared to continuous forest ($P = 0.001$; Fig. 4b).

Among the 16 species that declined most, there was no relationship between how much a species declined and its degree of isolation ($P = 0.09$; Fig. 6, Table 1). Species that were completely isolated on fragments did not decline any more or less than did species that were not isolated, suggesting that populations can decline for reasons other than being small and isolated.

Many species were only slightly affected by fragmentation (abundance changed to 80–120% of abundance in controls; $n = 33$). Among these species, the degree of isolation ($P < 0.001$) was significant in predicting how a species would respond to fragmentation (Table 1, Fig. 6); on average, isolated species declined slightly to 93% of their abundance in continuous forest.

Body size.—Beetle body size was not correlated with the responses of beetles to fragmentation ($P = 0.513$, Fig. 4). Further, among isolated species, body size was not correlated with response to fragmentation ($P = 0.091$; Table 1, Fig. 5). There was no relationship between body size and abundance ($F_{1,68} = 0.61$; $P = 0.44$).

Trophic group.—There was no significant difference between the responses to fragmentation of beetles that were detritus and dead-wood feeders, herbivores, and predators ($P = 0.07$; Fig. 4d), when we considered all 69 species. There was no difference in response to fragmentation for different trophic groups among isolated species ($P = 0.739$; Table 1, Fig. 5). However, among 16 beetle species that declined after fragmentation, predators declined significantly more ($P = 0.009$) than did detritus and dead-wood feeders. In fragments, predators occurred at 30% of their abundance in the continuous forest, whereas detritus and dead-wood feeders occurred at 75% of their abundance in the continuous forest. Only one of the 16 species that declined was a herbivore, so it was not considered. Further, among 33 species that were only affected slightly by fragmentation (with abundances in fragments changing to between 80% and 120% of their abundance in controls), predators declined slightly to $\sim 95\%$ of their abundance in continuous forest ($P = 0.017$; Fig. 6).

Species that increased

For species that increased in fragments to $>120\%$ of their abundance in continuous forest, there were no relationships between how much a species increased and its degree of isolation ($P = 0.329$), trophic group ($P = 0.168$), natural abundance ($P = 0.22$), or body size ($P = 0.584$; Fig. 6, Table 1). In contrast to the analysis in which all species were considered together, species that were abundant in the pine matrix did not increase any more than did species that were not very abundant in the matrix. Also, species that occurred naturally at high abundances did not increase any more than did species that occurred at low abundances.

Is response to fragmentation related to taxonomic grouping?

The responses of beetle species to fragmentation were not related to their family placement ($P = 0.6$; $df = 15$, variance ratio = 0.87). In the two largest families, Carabidae and Staphylinidae, species responses ranged from declines to increases. Most other families showed a range of responses, but contained too few species for us to draw conclusions.

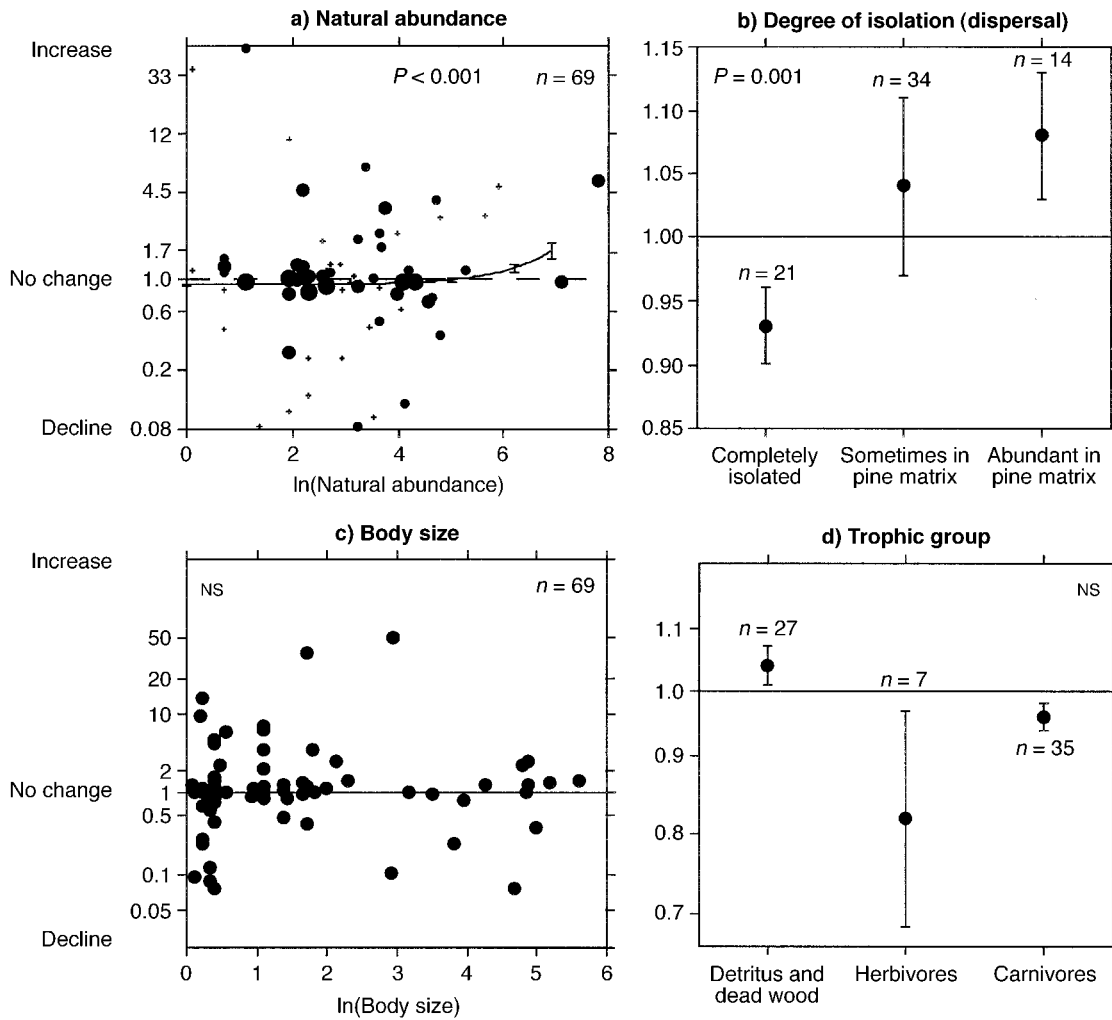


FIG. 4. Traits of species correlated with their responses to experimental forest fragmentation. A species' response (plotted on the y-axes) to fragmentation was calculated as $\log_e(\text{mean abundance in fragments}/\text{mean abundance in controls})$. Here, values have been back-transformed so that 1.15 represents an increase of 15% times in populations in fragments compared to continuous forest, and 0.85 represents a decline of 15% in populations in fragments compared to continuous forest. The y-axis is on a natural-log scale. The responses were correlated with traits using multiple regression. P values are given for the final model for which only the significant variables were fitted (adjusted $R^2 = 0.54$, slope for natural abundance = 0.0006). Natural abundance was not logged for the analysis but is logged here so that the detail for the smaller values can be seen. Error bars represent ± 1 SE.

DISCUSSION

In the face of increasing human impacts, a major goal of conservation biology is to provide principles by which biological diversity can be preserved. The ability to categorize species as to their risk of extinction may be a powerful tool for conservation biologists because it provides a basis for preventative management. We considered the responses of 69 beetle species to fragmentation in relation to four traits that have been linked theoretically to extinction risk.

Natural abundance

We have experimentally confirmed theoretical predictions that rare species and small populations are

most likely to decline following fragmentation, and are therefore likely to be at greatest risk of extinction (MacArthur and Wilson 1967, Leigh 1981, Goodman 1987). Species that occurred at low densities declined in fragmented forest compared to continuous forest, and those species that occurred at the lowest densities declined the most. As far as we know, only one other study has experimentally tested for a relationship between low abundance and extinction risk. In an experimentally fragmented grassland, 18 of 21 species of plant that occurred at low abundance went extinct (Robinson and Quinn 1988).

Two points are worth noting about our finding. First, it has been suggested that rare species may do better

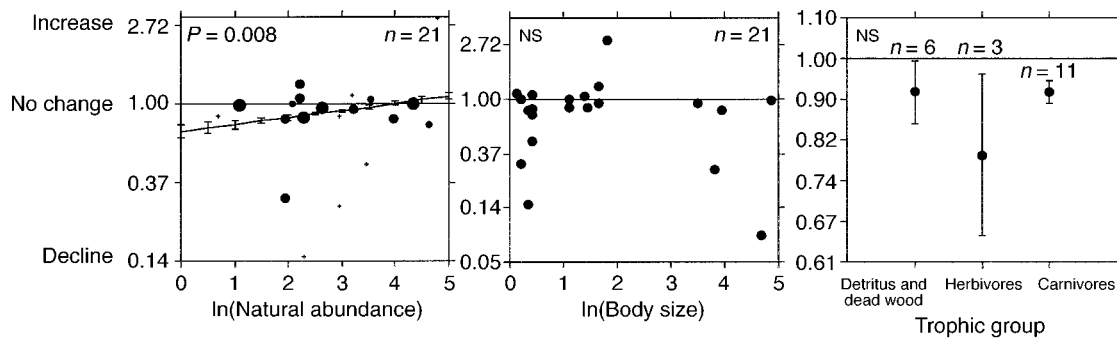


FIG. 5. Traits of isolated species ($n = 21$) correlated with their responses to experimental forest fragmentation: natural abundance, body size, and trophic group. A species' response to fragmentation was calculated as $\log_e(\text{mean abundance in fragments}/\text{mean abundance in controls})$. Here, values have been back-transformed so that 2.72 represents an increase of 2.72 times (172%) in abundance in fragments compared to continuous forest, and 0.14 represents a decline of 86% in abundance in fragments compared to continuous forest. These responses were correlated with traits using multiple regression. P values are given for the final model for which only the significant variable was fitted (adjusted $R^2 = 0.59$, slope for natural abundance = 0.09). Natural abundance was not logged for the analysis but is logged here so that the detail for the smaller values can be seen. Error bars represent ± 1 SE.

when isolated on fragments because they are preadapted to life as small, isolated populations, in contrast to species that were once widespread and abundant (Kunin and Gaston 1993, Lawton 1994). This hypothesis follows from evidence that abundance and range size are persistent, rather than labile, characteristics of species in evolutionary time (Jablonski 1987, Ricklefs and Latham 1992). Although we have no information about range size, our study did not support this hypothesis; we found that species with low abundance that became isolated by fragmentation, tended to decline more than abundant species. Second, in recent theoretical work, Tilman et al. (1994) predicted that good competitors that tend to be *abundant* species are most at risk of extinction in a fragmented landscape because they also tend to be poor dispersers. Our finding did not support this prediction, first, because abundant species that became isolated were less affected than rare species, and second, because the most abundant species tended to increase and did not become isolated.

Isolation

Habitat fragmentation caused declines in populations of species that were isolated on fragments, a finding supported by other fragmentation studies in which movement through or presence in the matrix was measured (Klein 1989, Diffendorfer et al. 1995, Sarre et al. 1995, Stouffer and Bierregaard 1995b). By our definition, to be completely isolated on a fragment, two conditions were necessary: (1) the species did not occur in the matrix, i.e., it was a habitat specialist in the sense that it was a specialist of eucalypt habitat; and (2) the species did not disperse between fragments. Given that roughly one-fourth of our 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 the 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. Then, an alternative explanation is that habitat specialists declined because the quality of their habitat on fragments was reduced.

In contrast to isolated species, species present in the matrix were mostly unaffected by fragmentation. Extending our definition, species can be non-isolated in two ways: (1) species may move freely through the matrix between fragments, but do not inhabit the matrix; or (2) populations inhabit the matrix so that, even if individuals move only relatively small distances, the overall effect is a mixed population at the between-fragment or landscape scale. This second scenario probably applies to the 14 species that were more abundant in the matrix than in the fragments (Fig. 4b), and that increased in abundance in the fragments compared to the continuous forest. These species probably perceive the matrix as better quality habitat than the fragments, resulting in a net flow of individuals from the matrix into the fragments. Thus, our results suggest that, depending on a species' perception of the quality of the matrix habitat, a landscape that is fragmented to one species may be continuous to another (see Diffendorfer et al. 1995, Stouffer and Bierregaard 1995a, Ingham and Samways 1996).

Body size

We found no relationship between body size and population decline. This places our finding among the large body of literature that has reported a range of findings including positive, negative, and no relationship between extinction risk and body size (e.g., Terborgh and Winter 1980, Pimm et al. 1988, Soulé et al. 1988, Burbidge and McKenzie 1989, Laurance 1991, Rosenweig and Clark 1994, Angermeier 1995, Gaston and Black-

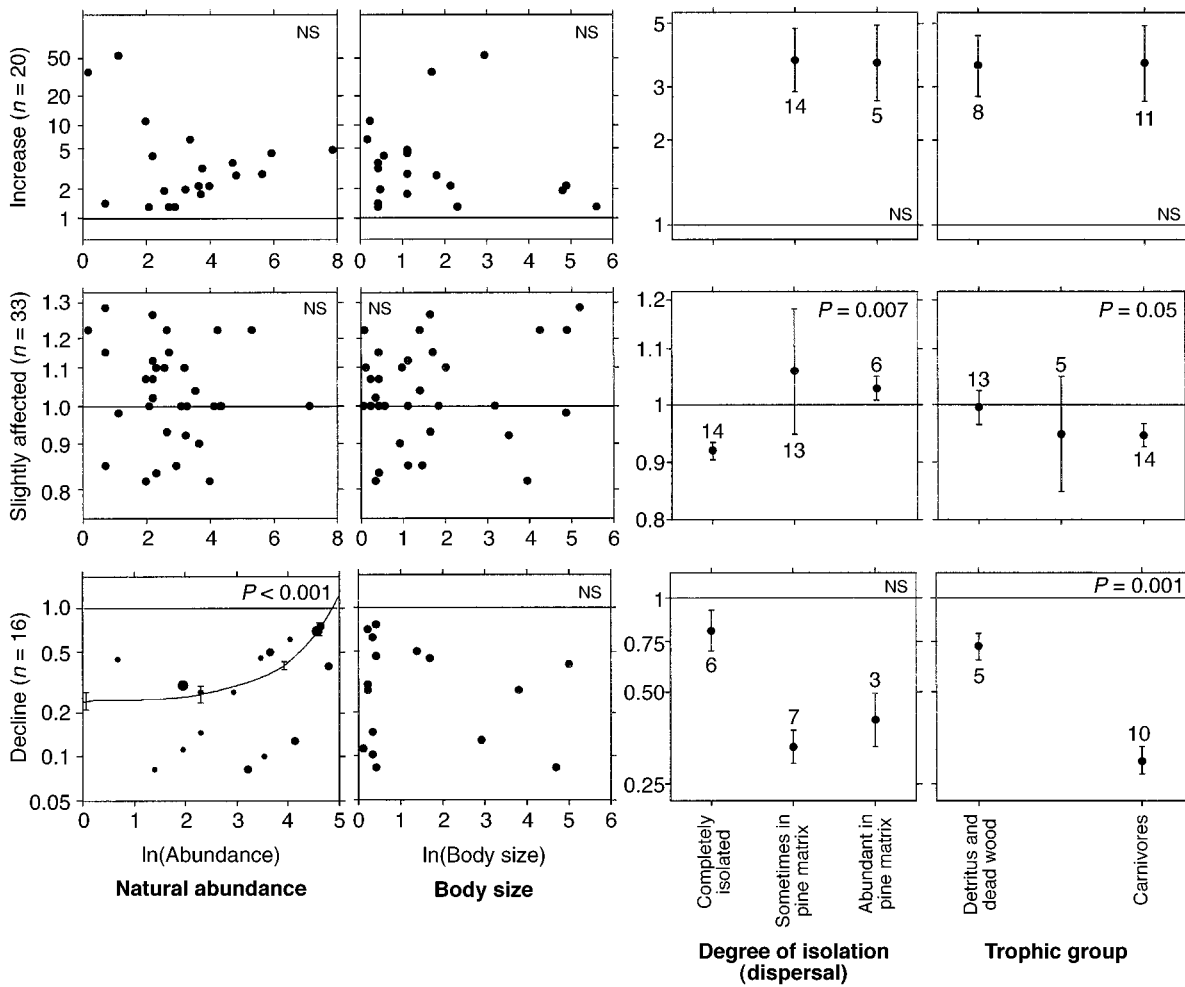


FIG. 6. Traits of species correlated with their responses to experimental forest fragmentation: isolation, body size, trophic group, and natural abundance, grouped by response (increase, slight increase or decline, decline). A species' response to fragmentation was calculated as $\log_e(\text{mean abundance fragments}/\text{mean abundance controls})$. Here, values have been back-transformed so that 5 represents an increase of 5 times (400%) in abundance in fragments compared to continuous forest, and 0.25 represents a decline of 75% in abundance in fragments compared to continuous forest. These responses were correlated with traits using multiple regression. *P* values are given for the final model for which only the significant variables were fitted. Details for the three analyses are: (1) increase, adjusted $R^2 = 0.19$; (2) slight increase/decline, adjusted $R^2 = 0.54$; and (3) decline, adjusted $R^2 = 0.78$; slope for natural abundance = 0.01. Natural abundance was not logged for the analyses but is logged here so that the detail for the smaller values can be seen. Error bars represent ± 1 SE.

burn 1996*b*; for review, see Gaston and Blackburn 1996*a*). Mammals and birds have been the focus of most studies. That a clear pattern has failed to emerge is perhaps not surprising, given the complexity of the relationship between extinction risk and body size.

Body size is linked to extinction risk, not directly, but because it is correlated with three variables (abundance, population fluctuations, and population growth rate) that are correlated with extinction risk. However, the relationships between body size and these variables are uncertain. First, the relationship between body size and abundance has received much attention that reveals no clear pattern (Blackburn et al. 1992, 1993, 1994, Cotgreave 1993, Blackburn and Gaston 1994, Gaston and Blackburn 1995, 1996*a, c, d*, Cyr et al. 1997).

Recent evidence suggests that the spatial scale of the study may be crucial. Studies at local spatial scales rarely find a relationship between body size and abundance, whereas studies at regional scales often find negative linear relationships (Blackburn and Gaston 1997). This may help to explain our result, as our study was at a local scale and there was no relationship between abundance and body size. Second, the relationship between population fluctuations and extinction risk is also contentious (McArdle and Gaston 1993). Some theory assumes that populations of large-bodied taxa fluctuate less than populations of small-bodied taxa, and therefore predicts that large species are less likely to fluctuate to extinction (reviewed in Pimm 1991). On the other hand, others argue that neither

TABLE 1. Summary table of five multiple regression analyses of beetle response to experimental fragmentation as a function of trophic group, degree of isolation, natural abundance, body size, and first-order interactions between these variables. Variance ratios and probabilities for the full models are shown here.

Variable	df	Variance ratio	Probability
All beetle species ($n = 69$)†			
Trophic group	2	3.03	0.070
Isolation	2	7.82	0.001
Natural abundance	1	19.53	<0.001
ln(Body size)	1	0.43	0.513
Trophic group \times Isolation	4	2.41	0.061
Natural abundance \times Trophic group	2	0.33	0.720
ln(Body size) \times Trophic group	2	0.29	0.752
Natural abundance \times Isolation	2	1.98	0.150
Natural abundance \times ln(Body size)	1	1.94	0.170
ln(Body size) \times Isolation	2	0.55	0.580
Residual	49		
Total	68		
Species isolated on fragments ($n = 21$)‡			
Trophic group	2	0.31	0.739
ln(Natural abundance)	1	11.04	0.01
ln(Body size)	1	3.50	0.091
ln(Natural abundance) \times Trophic group	2	1.72	0.228
ln(Body size) \times Trophic group	2	0.20	0.822
ln(Natural abundance) \times ln(Body size)	1	0.01	0.910
Residual	10		
Total	19		
Species that declined in abundance in response to fragmentation ($n = 16$)§			
Trophic group	1	38.24	0.009
Isolation	2	5.97	0.090
Natural abundance	1	54.96	0.005
ln(Body size)	1	0.42	0.564
Trophic group \times Isolation	0		
Natural abundance \times Trophic group	1	0.96	0.400
ln(Body size) \times Trophic group	1	0.30	0.621
Natural abundance \times Isolation	2	4.63	0.121
Natural abundance \times ln(Body size)	1	1.05	0.381
ln(Body size) \times Isolation	1	4.34	0.129
Residual	3		
Total	14		
Species that were only slightly affected by fragmentation ($n = 33$)			
Trophic group	2	5.88	0.017
Isolation	2	22.26	<0.001
Natural abundance	1	2.52	0.138
ln(Body size)	1	3.24	0.097
Trophic group \times Isolation	4	0.26	0.898
Natural abundance \times Trophic	2	16.80	<0.001
ln(Body size) \times Trophic	2	0.05	0.954
Natural abundance \times Isolation	2	15.24	<0.001
Natural abundance \times ln(Body size)	1	9.03	0.011
ln(Body size) \times Isolation	2	0.33	0.726
Residual	12		
Total	31		
Species that increased in abundance in response to fragmentation ($n = 20$)			
Trophic group	1	2.29	0.168
Isolation	1	1.08	0.329
Natural abundance	1	1.77	0.220
ln(Body size)	1	0.33	0.584
Trophic group \times Isolation	1	0.30	0.596
Natural abundance \times Trophic	1	0.00	0.948
ln(Body size) \times Trophic	1	0.19	0.673
Natural abundance \times Isolation	1	0.87	0.377
Natural abundance \times ln(Body size)	1	0.53	0.488
ln(Body size) \times Isolation	1	1.06	0.333
Residual	8		
Total	18		

Note: Probabilities for the final models, containing only the significant variables, are given in Figs. 4–6.

† The first analysis was for the response of all 69 species to fragmentation (see Fig. 4); the other four analyses examine subsets of this group.

‡ See Fig. 5.

§ See Fig. 6.

empirical evidence nor logic supports this theory (Schoener and Spiller 1992, Tracy and George 1992), and that fluctuations are only likely to lead to extinction when populations are unrealistically small (Chesson 1991). Third, because small species recover faster from low numbers than do large species, they could be at lower risk of extinction (Goodman 1987, Pimm et al. 1988). On the other hand, large body size is also associated with high longevity, which could also lower extinction risk (Pimm et al. 1988).

Finally, the action of these variables in combination probably contributes to the fuzziness of the body size vs. population decline relationship. That is, positive correlations between body size and extinction risk due to population abundance and rate of recovery (Cotgreave 1993, Lawton 1994), are offset by the negative correlation between body size and extinction risk due to population fluctuations (Pimm 1991).

Trophic group

Contrary to the predictions of theory, species at higher trophic levels did not decline in abundance in habitat fragments more than did species at lower trophic levels. The predicted greater vulnerability of species at higher trophic levels is due to unstable population dynamics and vulnerability to fluctuating environments. Thus, despite our result, we expected that we might see declines at higher trophic levels, at least among species with populations that had become small and isolated on fragments. Isolated predators were no more vulnerable than herbivores or detritus feeders. However, among species that declined, predators declined the most.

Only a few empirical studies have linked extinction risk and trophic group, and their results have been mixed. In laboratory microcosms of protozoa and bacteria, prey went extinct more often than predators (Lawler 1993). For small mammals in boreal forest fragments, the proportion of predators declined with decreasing species richness, but the proportion of insectivores remained constant and the proportion of herbivores increased (Patterson 1984). In a study incorporating data from five different surveys of vertebrates and plants, there was no tendency for species in one trophic group to go extinct more often than any other (Mikkelsen 1993). Perhaps these results are mixed because other traits also determine extinction risk (Lawton 1994). For example, species at higher trophic levels are often large in body size, but populations of large species are thought to fluctuate less, and therefore, to be less extinction prone (Pimm 1991). Conversely, species at higher trophic levels are usually the taxa with the lowest population densities and, thus, the highest risk of extinction (Gard 1984).

What is different about the extreme cases?

We expected that the species with the most extreme responses to fragmentation, both increases and de-

clines, might have unique traits. However, we found that there was nothing special about these species, at least for the four traits that we considered. Of three species that showed a 10-fold decline in abundance in fragments compared to continuous forest, two were predators, one fed on fungal spores, one was large, two were small, their natural abundances ranged from low to high, one was a carabid, and two were staphylinids. The only trait shared by all three was isolation.

Important considerations

Four final points warrant discussion. First, two of our findings suggest that we may need to examine processes other than population dynamics, such as habitat modification, when considering extinction risk in fragmented landscapes. (1) Not all species that declined were isolated on fragments. Indeed, some were quite abundant in the matrix. This suggests that species can be at risk in fragmented landscapes for reasons other than having small, isolated populations. (2) There were no correlations with traits for species that increased in abundance, and there was high variance in the response of these species, suggesting that species increase in abundance for a range of reasons. It is possible that both results can be explained if habitat on fragments has changed (Lovejoy et al. 1986, Saunders et al. 1991) to poorer quality habitat for species that declined and better quality habitat for species that increased. Although there is empirical evidence that habitat modification affects the biota of fragmented landscapes (e.g., Lovejoy et al. 1984, Bierregaard et al. 1992, Robinson et al. 1992, Aizen and Feinsinger 1994), there is, as yet, no theoretical framework for evaluating the effects of habitat modification and how they interact with population dynamics. We are currently collecting data to test the habitat modification hypothesis at Wog Wog.

Second, many species did not decline in abundance, none of the 69 species went extinct in the fragments, and slightly more species increased in abundance than declined. These results suggest that habitat fragmentation may not lead to loss of diversity in the short term, but rather to changes in community structure. Similar to other habitat fragmentation experiments, the results reported here are for a relatively short period postfragmentation, when population and community dynamics are likely to be transient. It is possible that the declines recorded will eventually become local extinctions and that changes in species composition will result in further extinctions through biotic interactions, as the species that become more abundant have more influence on community dynamics. These predictions need to be tested in long-term experiments and in landscapes that have been fragmented for long periods.

Third, it was not necessary to examine fragment size or edge effects to address the theory or the four hypotheses considered in this study. However, size and edge effects are important when considering, more

broadly, the effects of fragmentation on species and communities (Klein 1989, Mills 1995, Didham et al. 1998). We will consider their impacts in future work examining the effects of fragmentation on the beetle community.

Fourth, although the sample size of 69 species is large, it may not be representative of the 655 species captured. The sample probably represents the most trappable species, excluding those with low vagility and low numbers. The problem of how to assess impacts on rare species is one faced by all ecologists wishing to use inferential statistics. Nevertheless, the rarest species that we considered was still quite rare, captured just 40 times in five years of sampling. We believe that our sample of 69 species is appropriate for addressing the questions that we have posed, because the answers are relative rather than absolute.

CONCLUSIONS

We draw four conclusions: rare species were at greater risk of extinction; isolated species were also more at risk; body size was not correlated with extinction risk; and trophic group was correlated with extinction risk, but only for species that declined, among which predators declined most.

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