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Effects of habitat fragmentation on carabid beetles: experimental evidence

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Summary

1. We tested for effects of habitat fragmentation in a controlled, replicated, field experiment, in south-eastern Australia. Our experimental subjects were eight carabid beetle species, and the carabid assemblage (45 species). Monitoring was by pitfall trapping in forest remnants and in adjacent continuous-forest controls. Remnants were of three sizes (0.25, 0.875, 3.062 ha.). Monitoring commenced 2 years prior to habitat fragmentation. Here we present results for 6 years after habitat fragmentation (4 years for species richness).

2. We tested four hypotheses. Hypothesis one: habitat fragmentation reduces species richness in the remaining remnants. Carabid species richness was not different in habitat remnants compared to continuous forest, neither was carabid richness different for remnants of different sizes, or at monitoring sites close to remnant edges compared to sites in remnant interiors.

3. Hypothesis two: populations decline as a result of habitat fragmentation. Two species of eight were completely isolated on remnants and both declined in abundance on remnants compared to control plots in continuous forest. The other six species responded in various ways, which included relative increases and decreases in abundance and no change, but as they were not completely isolated on remnants, their responses could not be explained by isolation.

4. Hypothesis three: remaining subpopulations decline further on smaller habitat remnants than on larger remnants. Three species responded to remnant size; one was most abundant in small remnants, the second was most abundant in large remnants, and the third was equally abundant in small and large remnants and less abundant in medium-sized remnants.

5. Hypothesis four: populations near to remnant edges decline further than populations in remnant interiors. Two species were more likely to occur in remnant interiors than at edges, whereas three species were equally likely to occur in remnant interiors and at edges.

6. The effects of habitat fragmentation may be the consequence of: (i) isolation; and (ii) habitat modification. In this study, we were able to consider effects of isolation for two carabid species. We tested only one aspect of the habitat modification hypothesis, edge effects. We discuss the possibility that other aspects of habitat modification in remnants may explain some of our results and suggest that this is where future research be directed.

Key-words: edge effects, equilibrium theory of island biogeography, isolation, metapopulation dynamics, remnant size.

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Introduction

The fate of the earth's biological diversity is inextricably linked to the fate of natural habitat and habitat fragmentation is one of the most widespread and

pervasive human activities. Fragmentation reduces the total area of habitat, creates subpopulations of species and isolates those subpopulations from one another, disrupting individual and population behaviour (e.g. Hanski *et al.* 1995; Redpath 1995), the ex-

change of genes between populations (e.g. Sarre 1995a), species interactions (e.g. Aizen & Feinsinger 1994) and ecological processes (Kapos 1989; Saunders, Hobbs & Margules 1991). Understanding the nature and extent of such disruptions is a requirement for managing fragmented landscapes so that they retain biological diversity.

There have been many studies of the effects of fragmentation on the survival or local extinction of species, yet they remain poorly understood (Margules 1996). The overwhelming majority of these studies have been observational, correlating observed distribution patterns or population size with some external variables like fragment size, distance to other populations, habitat variables, etc. (e.g. Harris 1984; Quinn & Harrison 1987; Haila, Hanski & Raivio 1993; Heckert 1994; McCoy & Mushinsky 1994; Sarre 1995b; Sarre, Smith & Meyers 1995; and chapters in Settele *et al.* 1996). Others have been theoretical (e.g. Hanski 1985; Fahrig & Paloheimo 1988; Hanski 1991; Nee & May 1992; Tilman *et al.* 1994; Wissel, Stephan & Zschke 1995; Oostermeijer, Berholz & Poschod 1996; Poethke, Seitz & Wissel 1996). Both observational and theoretical studies are necessary but not sufficient. They give rise to hypotheses which require experimental testing.

Results from observational and theoretical studies to date can be distilled into three intuitively sensible generalizations. The first, from the theory of metapopulation dynamics, suggests that subpopulations created by habitat fragmentation may depend more strongly on immigration for their persistence than populations of unfragmented habitat and therefore have a higher probability of local extinction due to environmental or demographic stochasticity (Hanski 1994). The second generalization, from MacArthur & Wilson's (1967) equilibrium theory of island biogeography, predicts that the number of species on an island (habitat fragment) is a function of island size and distance to the mainland (continuous unfragmented habitat) so that smaller, more isolated fragments retain fewer species than larger, less isolated ones (Diamond 1975; Wilson & Willis 1975; Terborgh 1976). The third generalization, from observation, is that fragmentation modifies physical conditions by, for example, increasing fluxes of wind, water and solar radiation (Saunders *et al.* 1991) and creates habitat edges which are different from habitat interiors (Diamond 1975; Wilson & Willis 1975; Yahner 1988). It seems likely that the responses of species to habitat fragmentation depend, in varying degrees, on a reduction in habitat area, isolation and physical modification.

Manipulative field experiments on habitat fragmentation are labour intensive, time consuming, logistically difficult, and require a commitment of resources that is not easy to obtain (Lovejoy *et al.* 1984; Robinson *et al.* 1992; Margules, Milkovits & Smith 1994; Margules 1996). Without them, however, progress in

understanding the effects of habitat fragmentation will be limited, depending on theory and observation alone. This paper reports some results from a field experiment set up to monitor the responses of species to habitat fragmentation. Carabid beetles were used as experimental subjects to test the specific predictions that: (i) habitat fragmentation reduces species richness; (ii) populations decline as a result of fragmentation; (iii) remaining subpopulations decline further on smaller fragments than on larger fragments; and (iv) populations near the edges of fragments decline further than populations in the interior.

Materials and methods

EXPERIMENTAL DESIGN

The Wog Wog habitat fragmentation experiment is located 17 km south-east of Bombala in south-eastern NSW, Australia (37°04'30"S, 149°28'00"E; Fig. 1). The experiment was established in 1984 and is intended to be an ongoing study with an operating timescale of decades. The experimental design and the rationale for it were described by Margules (1993). Briefly, the experiment was established with three plot sizes: 0.25 ha, 0.875 ha and 3.062 ha; the larger plots were 3.5 times the size of the smaller ones. Each plot size was replicated six times in a randomized block design, giving a total of 18 plots. All six of the blocks (hereafter called replicates) were in continuous *Eucalyptus* forest when the experiment commenced in summer 1984/85. The forest surrounding four of the six replicates was cleared in 1987 and planted to *Pinus radiata*. The resulting 12 plots were retained as fragmented habitat (habitat remnants) in the *P. radiata* plantation. *Pinus radiata* is an alien species which creates a habitat quite inimical to indigenous species (e.g. Ahern & Yen 1977). Unlike *Eucalyptus* forest, the canopy closes, reducing light to the extent that very few plants, sometimes none, are recruited under this canopy. Pine needles form a thick mulch and lower soil pH levels. The other two replicates (six plots) remained in adjacent uncleared continuous forest and now serve as the unfragmented control plots. These controls provide data on the year-to-year dynamics of species in continuous unfragmented habitat for comparison with the experimental remnants.

Within each plot, monitoring sites were stratified in two ways. First, sites were stratified by topography into slopes and drainage lines, because vegetation complexes were found to form an association with these topographical features (Austin & Nicholls 1988; Margules 1993). Second, sites were stratified by proximity to the remnant edge into core zones (the area in the remnant core) and edge zones (the area near to the remnant edge). In the design, topography and proximity to edges were crossed. Thus, each of the 18 plots was divided into four combinations (core slope, edge slope, core drain, edge drain). For each plot,

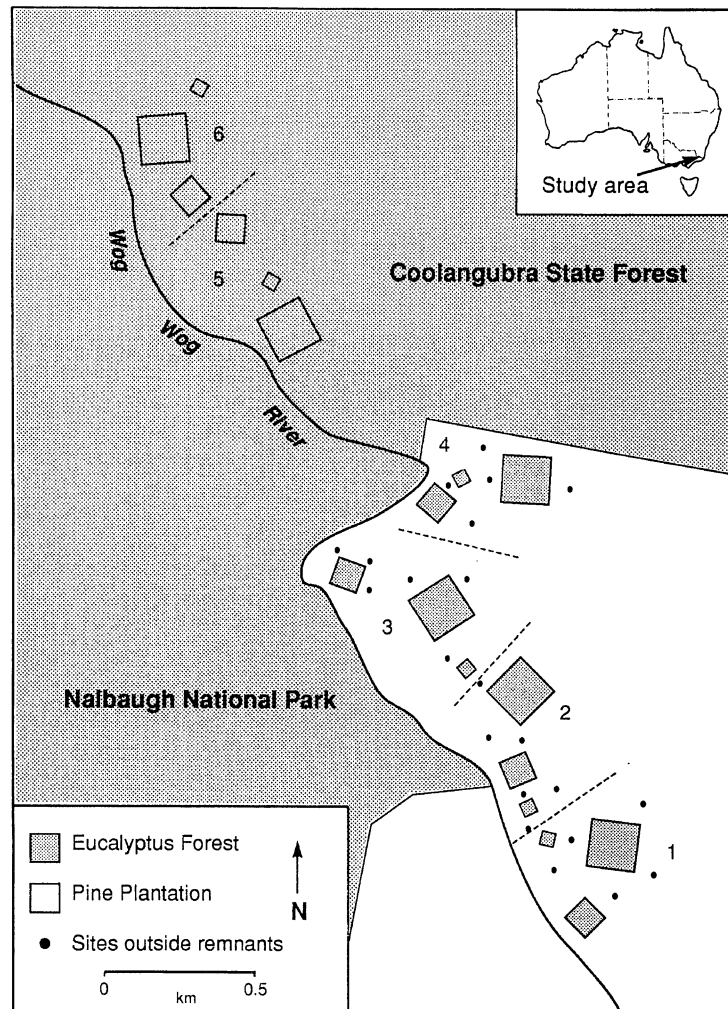


Fig. 1. Map of the experimental site showing forest remnants and control plots in continuous forest. Each dot represents the approximate location of a pair of monitoring sites (a slope site and a drainage-line site) established between the remnants after habitat fragmentation. Reprinted with the permission of the Ecological Society of America.

there were two replicate monitoring sites for each of the four strata, totalling eight sites within each plot and giving a total of 144 sites over the 18 plots. An additional 44 monitoring sites were established in the *Pinus radiata* plantation following clearing around the habitat remnants represented by replicates one, two, three and four. Two permanent pitfall traps were located at each monitoring site. Traps were opened for 7 days four times a year, that is, once during each season. Catches from these traps in the remnants are compared to catches from traps in the controls opened at the same time and for the same duration.

Monitoring commenced in February (summer) 1985. The experimental treatment, forest habitat fragmentation, took place over 9 months in 1987. The pine plantation was established in winter 1988 and by 1992 the pines were ≈ 5 m in height.

A total of 45 carabid beetle species were captured by pitfall trap at the site, as determined by Dr J.F. Lawrence of the Australian National Insect Collection, CSIRO (species are listed in the Appendix). The

effect of habitat fragmentation on the richness of this carabid assemblage was analysed. Also, eight species were chosen for which we determined species-level responses to fragmentation. The eight species chosen accounted for 92% of all carabid individuals trapped at Wog Wog since the study commenced. They were *Notonomus resplendens* (Castelnau), *N. variicollis* (Chaudoir), *N. minimus* Sloane, *N. metallicus* Sloane, *Eurylychnus blagravei* (Castelnau), *Promecoderus* sp. Dejean, *Carenum* sp. Bonelli and *Helluo costatus* Bonelli. Voucher specimens have been deposited at the Australian National Insect Collection, CSIRO Division of Entomology, Canberra.

DATA ANALYSIS

The experimental design is highly structured and requires a sophisticated analysis to incorporate the key features which include: (i) a nested treatment structure applied to both treatments and controls; and (ii) before (baseline) and after treatment data.

Analysis of variance (ANOVA) was first tried, which is well suited to modelling nested data. However, since the data for both species richness and individual species were highly asymmetric, they did not satisfy the assumption of normality required for ANOVA (Day & Quinn 1989). Data transformation was not satisfactory and so ANOVA could not be used. Instead, generalized linear models of two types, Poisson regression and logistic regression, were used (McCullagh & Nelder 1989). For seven species, the data approximated a Poisson distribution so Poisson regression was used. Data for the eighth species, *Carenum* sp., were binary and so logistic regression was used.

Defining the model

The variables that were included as fixed effects in the model are listed below with the reasoning behind their specification:

1. *Fragmentation*: a variable with two levels: (i) fragmented forest and (ii) continuous forest, that tests for the effect of forest fragmentation.
2. *Size within fragmentation*: a term that describes the interaction between fragmentation and size. It has three levels, (i) small; (ii) medium; and (iii) large, and tests for an effect of remnant size nested within the fragmentation treatment.
3. *Topography*: a variable with two levels: (i) slope; and (ii) drainage line. The inclusion of this variable accounts for variation associated with known environmental variation, as indicated by understorey vegetation (Austin & Nicholls 1988).
4. *Edge within fragmentation*: a term that describes the interaction between fragmentation and edges. It has three levels: (i) sites in remnant interiors (inner sites); (ii) sites located at remnant edges (outer sites); and (iii) control sites located in the continuous forest (no edge). This term tests for the effect of edges nested within the effect of fragmentation.
5. *Log of abundance before habitat fragmentation*: a covariate that controls for conditions prior to fragmentation by testing for relationships between patterns in abundance across the experimental site before the treatment was applied and after the treatment was applied.

The experiment has a nested design, therefore the response of a given species must be estimated at three different spatial scales. The scales are (the corresponding strata are in brackets; see Table 1): trapping sites (site stratum), which occur within plots (plot stratum), which occur within replicates (replicate stratum). Ideally, the residual variation would have been estimated for each stratum, as in ANOVA. However, generalized linear models estimate only one error term and this is for the site stratum. To compensate, two additional variables were included in the model to account for the residual variation associated with the

remaining two strata. These variables were considered as analogous to random effects:

1. *Replicate*: a variable with six levels (replicate stratum).
2. *Size within replicate*: a term that describes the interaction between replicate and size (plot stratum). It has three levels: small, medium and large.

These variables were also used to apply an additional check to the biological meaning of both *fragmentation* and *size within fragmentation* effects. When *fragmentation* was significant, the ratio of the mean deviance for *fragmentation* and the mean deviance for *replicate* was calculated. If this ratio equals one, then the fragmentation effect is of the same magnitude as the replicate effect (the spatial variation in abundance across the study site). If the ratio was greater than two, it was considered that the variation resulting from *fragmentation* was much greater than the replicate to replicate variation, and thus that the effect of *fragmentation* was biologically convincing. If the ratio was less than two, although there was a significant effect of *fragmentation* according to the statistical model, it was considered that the effect of *fragmentation* was not biologically convincing. The same protocol was applied when *size within fragmentation* was significant. The ratio of the mean deviance for *size within fragmentation* and the mean deviance for *size within replicate* was calculated and then the procedure was as above.

Model fitting and checking for eight individual species

The process of model fitting and checking is outlined here for individual species. The same procedure was used for carabid richness with some minor differences, which are highlighted in the next section.

The data for each of the eight study species were analysed separately. The response variable for each species was the number of individuals trapped after habitat fragmentation at each pitfall site 1–144, for the sum of years five to eight (spring 1988 to winter 1992; Table 2). The catches for two pitfall traps at each site were combined. Data for years three and four were not included because the clearing and burning associated with the fragmentation treatment, which took place from late summer in year three through to early summer in year four, may have confounded the effects of fragmentation. Years refer to biological years, which, in the southern hemisphere, begin in the spring of one calendar year (September) and end in the winter of the following calendar year (August). Data for years one and two, the prefragmentation data, were included as a covariate, as described above.

First the full model was defined, this included all fixed and random effects, as described above, and the first-order interactions between them. Higher order interaction terms were not included because no biological meaning could be ascribed to them. Each vari-

Table 1. Summary of Poisson regression analysis of the effect of habitat fragmentation on *Notonomus variicollis* at Wog Wog in south-eastern NSW. The significance of a variable was determined by the change in deviance (Deviance) associated with adding or dropping that variable. A variable was considered significant when the change in deviance associated with it exceeded the chi-squared critical value, at $P < 0.05$, for the number of degrees of freedom (d.f.) that the variable conferred. The level of significance is listed in the Probability column. Dot notation represents the interaction between terms

Variable	d.f.	Deviance	Probability
<i>Replicate stratum</i>			
Fragmentation	1	144.52	< 0.005
Replicate (random effect)	4	201.42	< 0.005
<i>Plot stratum</i>			
Size within fragmentation	4	75.46	< 0.005
Size within replicate (random effect)	8	123.07	< 0.005
<i>Site stratum</i>			
Edge within fragmentation	1	4.26	< 0.050
Topography	1	40.93	< 0.005
Fragmentation. Topography	1	3.58	NS
Size within fragmentation. Edge within fragmentation	2	34.37	< 0.005
Size within fragmentation. Topography	2	2.42	NS
Edge within fragmentation. Topography	1	7.01	< 0.005
Log abundance prefragmentation	1	47.89	< 0.005
Residual	117	369.72	
Total	143	1054.65	

Table 2. A summary of the data that were analysed to produce statistical models of the responses of eight carabid species to habitat fragmentation. The data were collected between spring 1988 and winter 1992 from 144 monitoring sites in forest remnants and continuous forest; values represent sums for those four years

Species	Total number of beetles	Total non-zero records	Range per monitoring site	Median per monitoring site	Mean per monitoring site
<i>Notonomus resplendens</i>	2050	143	0–73	11	14.3
<i>N. variicollis</i>	658	106	0–41	3	6.2
<i>Eurylychnus blagravei</i>	185	64	0–19	2	2.9
<i>Promecoderus</i> sp.	176	75	0–9	2	2.3
<i>Carenum</i> sp.	76	48	0–5	1	1.6
<i>N. metallicus</i>	41	24	0–5	1	1.7
<i>N. minimus</i>	22	21	0–2	1	1.1
<i>Helluo costatus</i>	27	23	0–2	1	1.2

able was dropped one at a time, starting with the interaction terms. A variable was considered significant if the change in deviance associated with dropping that variable exceeded the chi-squared critical value, at $P < 0.05$, for the number of degrees of freedom that the variable conferred (McCullagh & Nelder 1989). An example analysis summary table is presented in Table 1. The response of a species to the experiment was considered to be described by the final model, which included only the significant terms. These models are presented in the results section as summary graphs (see Fig. 3).

For the three least abundant species, *N. minimus*, *N. metallicus* and *H. costatus*, there were insufficient data to use the full model as outlined above (Table 2) so the data were summed at the plot level. As a result there was just one datum point for each plot. This

simplified the model because the terms from the site stratum (Table 1) no longer applied.

Any 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.

Carabid richness

The response variable for carabid species richness used data for biological years five and six only because, although the eight individual study species were sorted and identified up to the end of year eight (winter 1992), the other 37 carabid species were only sorted and identified to the end of year six (winter 1990). Poisson regression was used because the data consisted of counts of the number of species. Carabid

richness from years one and two was included as the covariate 'Log of carabid richness before fragmentation'. Otherwise the modelling procedure was the same as for the individual carabid species, as described above. Two analyses were undertaken, each at a different spatial scale. The first looked at species richness per trap site. The second looked at species richness per remnant or control plot.

Results

RESPONSE IN SPECIES RICHNESS

Habitat fragmentation did not alter species richness (Fig. 2a and b). Considered at the site scale (Fig. 2a),

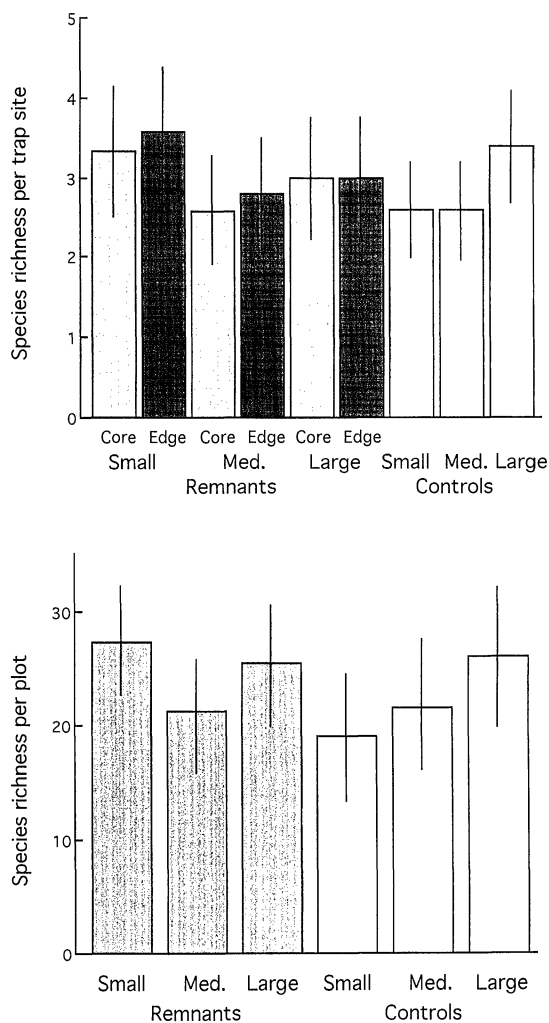


Fig. 2. The effect of habitat fragmentation on carabid species richness at two spatial scales. Graph (a) contrasts the number of carabid species per trap site in core and edge sites, in small medium and large fragments in remnants and continuous forest controls. There was no statistically significant difference in carabid richness between core and edge sites, remnants of different sizes, and remnants and continuous forest controls. Graph (b) contrasts differences in species richness for small, medium and large remnants and small, medium and large control plots in continuous forest. Again there was no significant difference in species richness between different sized plots, or between remnants and continuous forest control plots. Error bars represent 95% confidence intervals.

species richness was not significantly different between sites in habitat remnants and in continuous forest ($P > 0.1$), neither was species richness different between sites in large remnants compared to small remnants ($P > 0.1$), nor at sites at remnant edges compared to remnant interiors ($P > 0.1$). Considered at the plot scale (Fig. 2b), species richness was not significantly different in remnants compared to control plots ($P > 0.2$), or in remnants of different sizes ($P > 0.2$).

However, if species identities are considered, then it can be seen that there has been some change in species composition since fragmentation (Table 3). Of a total of 45 carabid species trapped at Wog Wog, three species were trapped only before fragmentation and 12 species were trapped only since fragmentation occurred. Of the 12 species trapped only since fragmentation, six species were trapped only once and only in the remnants. Little can be said about these species other than that they may not have been trapped before fragmentation because they are rare, or rarely caught in traps. The remaining six species were trapped at least five times each, both in the remnants and the pine monoculture. These species may have been introduced with the pine monoculture.

RESPONSES OF INDIVIDUAL SPECIES TO FRAGMENTATION, REMNANT SIZE AND EDGES

The eight individual species responded to habitat fragmentation in three different ways (Fig. 3). Three species decreased in abundance in remnants compared to continuous forest (*N. resplendens* $P < 0.005$, *N. metallicus* $P < 0.005$, *N. minimus* $P < 0.005$). In contrast, three other species increased in abundance in remnants compared to continuous forest (*N. variicollis* $P < 0.005$, *E. blagravei* $P < 0.005$, *Carenum* sp. $P < 0.005$). Two species, not shown in Fig. 3, did not respond to habitat fragmentation. The probability of occurrence of the first of these, *Promecoderus* sp., at any site across the experiment, was dependent only on its abundance at that site before habitat fragmentation ($P < 0.005$). For the other species, *H. costatus*, there were no significant effects. Two of three species that decreased in abundance, *N. metallicus* and *N. minimus*, were not trapped in the pine monoculture between the remnants (Table 4). Thus, the responses of *N. metallicus* and *N. minimus*, were the only responses that might reasonably have been attributed to isolation.

Of the six species that responded to habitat fragmentation *per se*, only three responded further to remnant size (Fig. 3). *Notonomus resplendens* was estimated to be more abundant in small and large remnants than in medium remnants, and less abundant in all three remnant sizes than in continuous forest plots ($P < 0.005$). *Notonomus variicollis* was estimated to be more abundant in small and large remnants than in medium remnants and continuous forest plots ($P < 0.005$). *Eurylychnus blagravei* was

Table 3. The number of carabid species trapped before and after habitat fragmentation, in remnants and in continuous forest controls. Carabid species richness after habitat fragmentation is presented for the pine plantation matrix, for remnants of different sizes, and for remnant edges and interiors. Note that there are twice as many trap sites in the remnants as in the continuous forest controls

Number of species trapped		Number of species trapped	
Only before fragmentation	3	Pine plantation	31
Only after fragmentation	12	Only caught in pines	9
Before in remnants and continuous forest	25	Never caught in pines	5
Before in remnants	20	Small remnants	23
Before in continuous forest	15	Medium remnants	21
After in remnants and continuous forest	31	Large remnants	19
After in remnants	30	Remnant edges	28
After in continuous forest	19	Remnant interiors	24

estimated to be most abundant in large remnants and more or less equally abundant in small and medium remnants and in continuous forest plots ($P < 0.005$).

Two species responded to changes associated with induced edges. The first of these, *N. variicollis*, was estimated to be more abundant at remnant interior sites than at sites on remnant edges and was predicted to be less abundant in continuous forest than either remnant interiors or edges ($P < 0.05$). The other species, *E. blagravei*, was estimated to be more abundant in remnant interiors than in continuous forest, and least abundant on remnant edges ($P < 0.005$). Three species, *N. resplendens*, *Carenum* sp. and *Promecoderus* sp., were estimated to be equally abundant in remnant interiors and on remnant edges. Three species, *N. minimus*, *N. metallicus* and *H. costatus*, were not tested for edge effects because there were insufficient data (data were summed at the plot level).

Discussion

SPECIES RICHNESS: FRAGMENTATION, REMNANT SIZE AND EDGE EFFECTS

Carabid species richness was not affected by habitat fragmentation, remnant size or edge effects at Wog Wog. These results do not support the prediction that habitat fragmentation reduces species richness, or the prediction that species richness will be reduced more in small compared to large fragments. Similar results have been found in correlative studies of ground-dwelling invertebrates in forest remnants. In these studies (Niemelä *et al.* 1988; Bauer 1989; Usher, Field & Bedford 1993), the results were attributed to colonization of the remnants by species from the surrounding habitat, where species richness was higher. In some cases there was a negative relationship between remnant area and species richness because small remnants were most likely to be invaded (Webb & Hopkins 1984; Halme & Niemelä 1993). At Wog Wog, 12 species that were not trapped before fragmentation, were trapped in the remnants after frag-

mentation. Of these 12, six were trapped only once and thus probably represent species that were not trapped before fragmentation because they are rare. The other six species trapped only after fragmentation were trapped also in the pine monoculture. They may represent introductions from the pines. These six were not enough to alter significantly species richness in the remnants compared to the continuous forest, but if invasions continue, species richness may be altered in the future.

Considerable attention has been paid in conservation biology to the effects of habitat fragmentation on species richness, perhaps because of the influence of the equilibrium theory of island biogeography (MacArthur & Wilson 1967). However, simply counting the number of species provides no information on species composition, and if richness is used as a measure of biological conservation value, may even be misleading because disturbances may favour widespread and abundant species, leading to an increase in richness. In contrast, analysing the responses of individual species is more likely to provide an understanding of the processes that lead to extinction or persistence in fragmented landscapes (e.g. Margules *et al.* 1994).

INDIVIDUAL SPECIES: FRAGMENTATION, REMNANT SIZE AND EDGE EFFECTS

It is difficult to draw convincing general conclusions from field experiments. Quite apart from the practical difficulties of conducting such experiments, general conclusions require repeated experiments to achieve the same results. In this experiment the fragmentation treatment is not replicated, only the size treatment. More experiments are needed elsewhere in the landscape to replicate the fragmentation treatment. Nevertheless, one useful generalization seems to have emerged, and that is that different species respond differently. It is not appropriate to draw conclusions about all species, whether from theory, observation or experimentation.

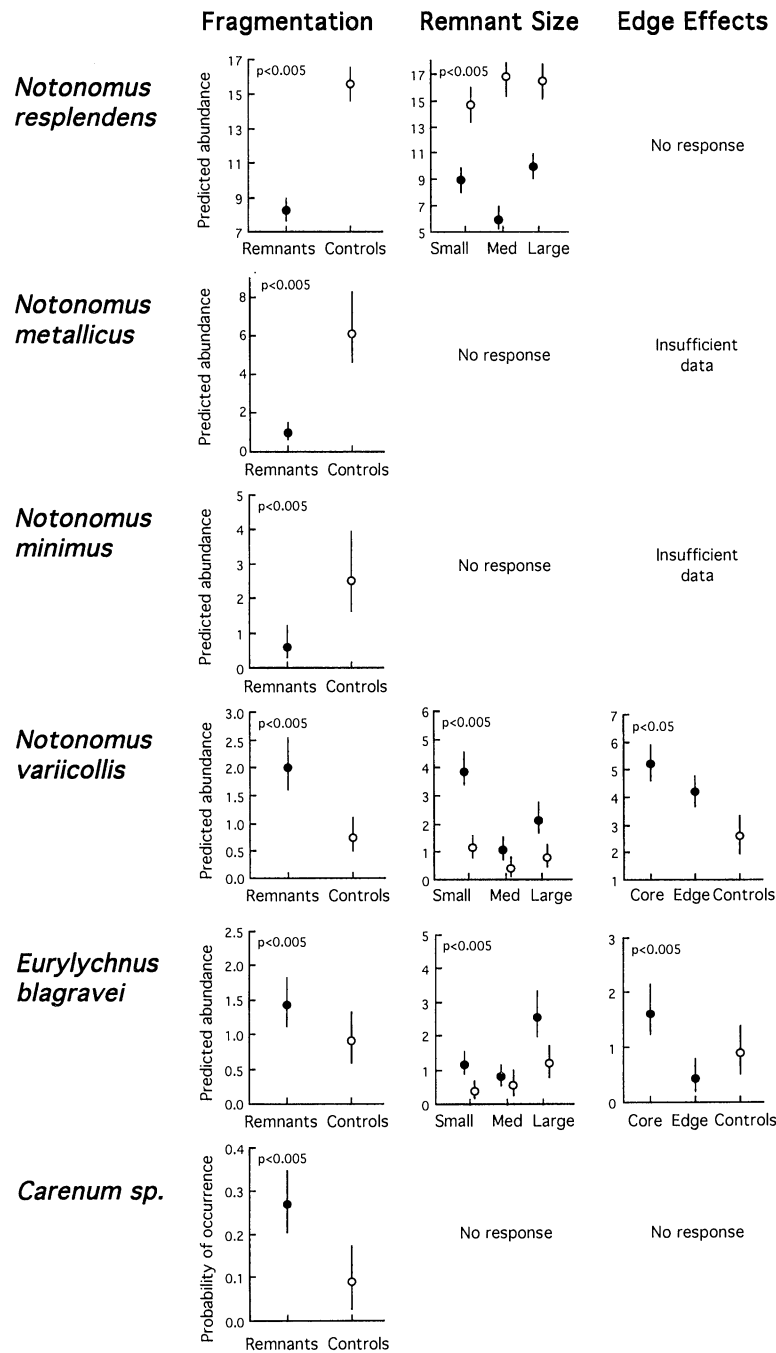


Fig. 3. The responses of carabid species to the Wog Wog habitat fragmentation experiment. Results are presented in table form with species as rows and treatments as columns. The graphs represent abundances estimated from the statistical models per pitfall trap site, of carabid beetles in: (1) habitat remnants and continuous forest controls (column 1); (2) small, medium, and large remnants and small, medium and large plots in continuous forest (column two); (3) remnant cores and edges, and continuous forest controls (column three). Solid circles represent remnants and open circles represent continuous forest controls. ‘No response’ means that there was not a significant response to that treatment. For two species, *Notonomus metallicus* and *N. minimus*, data were pooled at the plot level because there were insufficient data to test for edge effects. Error bars represent 95% confidence intervals. Two species, *Helluo costatus* and *Promecoderus sp.*, are not included here because they did not respond significantly to the experimental treatments.

In discussing these results, declines or increases in abundance are relative to the control plots in continuous forest (Fig. 1). Thus, for example, a species that increased in abundance in the treatments over time actually was considered to have declined if the same species increased significantly more in the

controls. That is, the species had undergone a decline relative to the control plots.

The two species completely isolated, *N. metallicus* and *N. minimus*, both declined in abundance in remnants compared to control plots in continuous forest. While isolation could be responsible for the decline

Table 4. A summary of catches of eight carabid species from pitfall traps in the pine plantation between the *Eucalyptus* remnants. The data were collected between spring 1988 and winter 1992 from 44 monitoring sites

Species	Total number of individuals caught in the pines	No. of sites at which the species was caught
<i>N. resplendens</i>	125	30
<i>N. variicollis</i>	9	5
<i>E. blagravei</i>	2	2
<i>Promecoderus</i> sp.	5	4
<i>Carenum</i> sp.	3	3
<i>N. metallicus</i>	0	0
<i>N. minimus</i>	0	0
<i>H. costatus</i>	2	2

of these populations, it has not contributed to the response of *N. resplendens*, which also declined relative to the controls, as this species was abundant in the pine monoculture and therefore was not isolated on fragments. Either there are resident populations of *N. resplendens* in the pine monoculture, or individuals of *N. resplendens* disperse between the remnants and the continuous forest through the pine monoculture. Thus, it appears that a population need not necessarily be isolated for habitat fragmentation to cause a relative decline. Populations of three other species increased in abundance in the remnants relative to the controls, and populations of two species were not different in the remnants compared to the continuous forest. None of these species were completely isolated on the remnants since all five species were trapped in the pine monoculture. It seems unlikely that the responses of any of these six species are the result of being small and isolated. Alternative hypotheses are therefore needed to explain these results.

No clear messages emerge from the responses to remnant size, as distinct from the responses to fragmentation *per se*. Three of the species that responded to fragmentation showed no response to remnant size. Of the other three, one was almost equally abundant in the small and large remnants and less abundant in the medium-sized remnants, one most abundant in the small remnants and one most abundant in the large remnants. Medium remnants generally had lower abundances than small or large remnants. These results cannot be explained at this time but it is clear that they do not support the prediction that abundance decreases as remnant size decreases.

Only one aspect of the habitat modification hypothesis was tested, that of edge effects. The responses of species to edge effects, and visible changes that can be observed at Wog Wog, suggest that habitat modification may be an important influence. First, two species responded to induced edges. Both were more abundant in remnant interiors than at edges. Three

species were equally likely to occur in the interior and at edges, and there were insufficient data to test the responses of the other three species. It has been predicted that populations near remnant edges are more likely to decline than populations near remnant cores because habitat quality is reduced at the interface of remnants and surrounding habitat (Levenson 1981; Yahner 1988). However, it has also been recognized that a full range of responses to induced edges should be expected, ranging from increasing abundance, through no change, to decreasing abundance, because different species have different habitat requirements (Sisk & Margules 1993). Thus, induced edges may provide habitat that is either more or less suitable for a given species. The results of the present study may reflect the different habitat requirements of the study species.

Second, there are visible modifications to the remnants at Wog Wog and it is possible to see potential links between these modifications and changes in the distribution and abundance of species, given that abiotic factors can regulate ground-dwelling beetle populations (den Boer 1986; Lövei & Sunderland 1996). More light reaches the forest floor in remnants and this is most pronounced at remnant edges and in small remnants. Increased solar radiation could impact on species by raising soil temperature, for example. Many carabids burrow and lay their eggs below the soil surface (e.g. Horne 1992 for *Notonomus* species), so increased soil temperature could affect choice of nest site and alter rate of egg mortality (e.g. Basedow 1994). Greater fluxes of water across the remnants have created significant erosion gullies and caused soil deposition, and have affected the drainage lines of remnants such that they contain more water when it rains, and dry out more quickly when the rain stops compared with the continuous forest. Likely consequences are changes in soil moisture levels and changes in vegetation structure. Both of these factors have been correlated with carabid distributions (Niemelä *et al.* 1988; Gardner 1991; Rushton, Luff & Eyre 1991; Niemelä *et al.* 1992; Holmes, Boyce & Reed 1993). It is possible that modifying the physical environment has altered catches in the pitfall traps by modifying carabid activity patterns, rather than abundance as we have assumed (Southwood 1978). This is a possibility that will need to be investigated in further studies.

The species which declined appear to have done so in response to complete isolation and/or physical changes on habitat fragments or changes to ecosystem processes accompanying fragmentation. Lovejoy *et al.* (1984), Klein (1989) and Bierregaard *et al.* (1992) report similar findings from the Amazon rainforest fragmentation experiment where, for example, forest interior birds and butterflies avoided the lighter, more open conditions in forest fragments, tree mortality increased as a consequence of greater exposure to wind, and lower densities of carrion and dung beetles

were correlated with lower rates of decomposition in rainforest remnants. At Wog Wog, three other species, an amphipod, a scorpion and a frog, have responded in different ways to habitat fragmentation and in these cases also, the most plausible hypotheses link habitat requirements and physical changes to habitat on the remnants (Margules *et al.* 1994; Margules *et al.* 1995). The next step in this ongoing study is to quantify physical modifications to the remnants at Wog Wog in contrast to the continuous forest, and to test whether or not it is possible to link these changes to the responses of species.

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References

- Ahern, L.D. & Yen, A.L. (1977) A comparison of the invertebrate fauna under *Eucalyptus* and *Pinus* forests in the Otway Ranges, Victoria. *Proceedings of the Royal Society of Victoria* **89**, 127–36.
- Aizen, M.A. & Feinsinger, P. (1994) Forest fragmentation, pollination and plant reproduction in a Chaco dry forest, Argentina. *Ecology* **75**, 330–51.
- Austin, M.P. & Nicholls, A.O. (1988) Species associations within herbaceous vegetation in an Australian eucalypt forest. *Diversity and Pattern in Plant Communities* (eds H. Doring, M. Werger & J. Willems), pp. 95–114. Academic Publishing, The Hague.
- Basedow, T.H. (1994) Phenology and egg production in *Agonum dorsale* and *Pterostichus melanarius* (Col., Carabidae) in winter wheat fields of different growing intensity in northern Germany. *Carabid Beetles: Ecology and Evolution* (eds K. Desender, M. Dufrêne, M. Loreau, M. L. Luff & J.-P. Maelfait), pp. 101–7. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Bauer, L.J. (1989) Moorland beetle communities on limestone 'habitat islands'. I. Isolation, invasion and local species diversity in carabids and staphylinids. *Journal of Animal Ecology* **58**, 1077–98.
- Bierregaard, R.O., Lovejoy, T.E., Kapos, V., dos Santos, A.A. & Hutchings, R.W. (1992) The biological dynamics of tropical rainforest fragments. *BioScience* **42**, 856–66.
- den Boer, P.J. (1986) What can carabid beetles tell us about dynamics of populations? *Carabid Beetles. Their Adaptations and Dynamics* (eds P. J. den Boer, M. L. Luff, D. Mossakowski & F. Weber), pp. 315–30. Fischer Verlag, New York.
- Day, R.W. & Quinn, G.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**, 433–63.
- Diamond, J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* **7**, 129–46.
- Fahrig, L. & Paloheimo, J. (1988) Determinants of local population size in patchy habitats. *Theoretical Population Biology* **34**, 194–213.
- Gardner, S.M. (1991) Ground beetle (Coleoptera: Carabidae) communities on upland heath and their association with heathland flora. *Journal of Biogeography* **18**, 281–9.
- Haila, Y., Hanski, I.K. & Raivio, S. (1993) Turnover of breeding birds in small forest fragments: the 'sampling' colonisation hypothesis corroborated. *Ecology* **74**, 714–25.
- Halme, E. & Niemelä, J. (1993) Carabid beetles in fragments of coniferous forest. *Annales Zoologica Fennici* **30**, 17–30.
- Hanski, I. (1985) Single-species spatial dynamics may contribute to long-term rarity and commonness. *Ecology* **66**, 335–43.
- Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* **42**, 17–38.
- Hanski, I. (1994) Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* **9**, 131–5.
- Hanski, I., Pakkala, T., Kuussaari, M. & Lei, G. (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* **72**, 21–8.
- Harris, L.D. (1984) *The Fragmented Forest*. The University of Chicago Press, Chicago.
- Heckert, J.R. (1994) The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* **4**, 461–71.
- Holmes, P.R., Boyce, D.C. & Reed, D.K. (1993) The ground beetle (Coleoptera: Carabidae) fauna of Welsh peatland biotopes: factors influencing the distribution of ground beetles and conservation implications. *Biological Conservation* **63**, 153–61.
- Horne, P.A. (1992) Comparative life histories of two species of *Notonomus* (Coleoptera: Carabidae) in Victoria. *Australian Journal of Zoology* **40**, 163–71.
- Kapos, V. (1989) Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* **5**, 173–85.
- Klein, B.C. (1989) Effects of forest fragmentation on dung and carion beetle communities in central Amazonia. *Ecology* **70**, 1715–25.
- Levenson, J.B. (1981) Woodlots as biogeographic islands in southeastern Wisconsin. *Forest Island Dynamics in Man-Dominated Landscapes* (eds R. L. Burgess & D. M. Sharpe), pp. 13–39. Springer-Verlag, New York.
- Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**, 231–56.
- Lovejoy, T.E., Rankin, J.M., Bierregaard, R.O., Brown, K.S., Emmons, L.H. & van der Voort, M.E. (1984) Ecosystem decay of Amazon forest remnants. *Extinctions* (ed. M. H. Nitecki), pp. 295–325. The University of Chicago Press, Chicago.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McCoy, E.D. & Mushinsky, H.R. (1994) Effects of frag-

- mentation on the richness of vertebrates in the Florida scrub habitat. *Ecology* **75**, 446–57.
- McCullagh, P. & Nelder, J. (1989) *Generalized Linear Models*. Chapman and Hall, London.
- Margules, C.R. (1993) The Wog Wog habitat fragmentation experiment. *Environmental Conservation* **19**, 316–25.
- Margules, C.R. (1996) Experimental Fragmentation. *Species Survival in Fragmented Landscapes* (eds J. Settele, C. Margules, P. Poschlod & K. Henle), pp. 93–110. Kluwer Academic Publishers, Dordrecht.
- Margules, C.R., Milkovits, G.A. & Smith, G.T. (1994) Contrasting effects of habitat fragmentation on the Scorpion *Cercophonius squama* and Amphipod, *Arcitalitrus sylvaticus*. *Ecology* **75**, 2033–42.
- Margules, C.R., Davies, K.F., Meyers, J.A. & Milkovits, G.A. (1995) The responses of some selected arthropods and the frog *Crinia signifera* to habitat fragmentation. *Conserving Biodiversity: Threats and Solutions* (eds R. A. Bradstock, T. D. Auld, D. A. Keith, R. T. Kingsford, D. Lunney & D. P. Sivertsen), pp. 94–103. Surrey Beatty & Sons, Chipping Norton, NSW.
- Nee, S. & May, R.M. (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* **61**, 37–40.
- Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. (1988) The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. *Annales Zoologica Fennici* **25**, 107–19.
- Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. (1992) Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. *Journal of Biogeography* **19**, 173–81.
- Oostermeijer, J.G.B., Berholz, A. & Poschlod, P. (1996) Genetical aspects of fragmented populations: a review. *Species Survival in Fragmented Landscapes* (eds J. Settele, C. Margules, P. Poschlod & K. Henle), pp. 93–110. Kluwer Academic Publishers, Dordrecht.
- Poethke, H.J., Seitz, A. & Wissel, C. (1996) Species survival and metapopulations: conservation implications from ecological theory. *Species Survival in Fragmented Landscapes* (eds J. Settele, C. Margules, P. Poschlod & K. Henle), pp. 81–92. Kluwer Academic Publishers, Dordrecht.
- Quinn, J.F. & Harrison, S.P. (1987) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* **75**, 132–40.
- Redpath, S.M. (1995) Habitat fragmentation and the individual: Tawny owls, *Strix aluco*, in woodland patches. *Journal of Animal Ecology* **64**, 652–61.
- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. & Martinko, E.A. (1992) Diverse and contrasting effects of habitat fragmentation. *Science* **257**, 524–6.
- Rushton, S.P., Luff, M.L. & Eyre, M.D. (1991) Habitat characteristics of grassland *Pterostichus* species (Coleoptera, Carabidae). *Ecological Entomology* **16**, 91–104.
- Sarre, S. (1995a) Mitochondrial DNA variation among populations of *Oedura reticulata* (Reptilia: Gekkonidae) in remnant vegetation: implications for metapopulation structure and population decline. *Molecular Ecology* **4**, 395–405.
- Sarre, S. (1995b) Size and structure of populations of *Oedura reticulata* (Reptilia: gekkonidae) in woodland remnants: implications for the future regional distribution of a currently common species. *Australian Journal of Ecology* **20**, 288–98.
- Sarre, S., Smith, G.T. & Meyers, J.A. (1995) Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. *Biological Conservation* **71**, 25–33.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**, 18–32.
- Settele, J., Margules, C., Poschlod, P. & Henle, K. (1996) *Species Survival in Fragmented Landscapes*. Kluwer Academic Publishers, Dordrecht.
- Sisk, T.D. & Margules, C.R. (1993) Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. *Nature Conservation 3: Reconstruction of Fragmented Ecosystems, Global and Regional Perspectives* (eds D. A. Saunders, R. J. Hobbs & P. R. Erlich), pp. 57–69. Surrey, Beatty & Sons, Chipping Norton, NSW.
- Southwood, T.R.E. (1978) *Ecological Methods*. Chapman & Hall, London.
- Terborgh, J. (1976) Island biogeography and conservation: strategy and limitations. *Science* **193**, 1029–30.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature* **371**, 65–6.
- Usher, M.B., Field, J.P. & Bedford, S.E. (1993) Biogeography and diversity of ground-dwelling arthropods in farm woodlands. *Biodiversity Letters* **1**, 54–62.
- Webb, N.R. & Hopkins, P.J. (1984) Invertebrate diversity on fragmented *Calluna* heathland. *Journal of Applied Ecology* **21**, 921–33.
- Wilson, E.O. & Willis, E.O. (1975) Applied biogeography. *Ecology and Evolution of Communities* (eds M. L. Cody & J. M. Diamond), pp. 522–34. Belknap Press, Cambridge, MA.
- Wissel, C., Stephan, T. & Zschke, S.H. (1995) Modelling extinction and survival of small populations. *Minimum Viable Populations* (ed. H. Remmert), pp. 67–103. Springer Verlag, Berlin.
- Yahner, R.H. (1988) Changes in wildlife communities near edges. *Conservation Biology* **2**, 333–9.

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Appendix

SPECIES LIST

(Species are grouped by tribe).

Bembidiini

Pericompsus sp.*Tachys* sp.*Tasmanitachoide* sp.

Broscini

*Eurylychnus blagravei**Promecoderus* sp.

Harpalini

Amblystomus sp.*Hypharpax peronii**Hypharpax* sp.*Gnathaphanus melbournensis**Lecanomerus* sp.*Lecanomerus* sp.*Amblystomus* sp.*Lecanomerus* sp.*Euthenarus promptus**Euthenarus* sp.*Stenolophus piceus**Amblystomus* sp.*Notiobia* sp.

Helluonini

Helluo sp.

Lebiini

Microlestodes sp.*Demetrída* sp.*Anomotarus* sp.*Anomotarus* sp.*Agonocheila* sp.

Licinini

Lacordairia sp.*Lestignathus* sp.

Odacanthini

Homethes sp.

Pentagonicini

Scopodes sp.

Pseudomorphini

Adelotopus sp.

Psydrini

Mecyclothorax sp.*Mecyclothorax* sp.*Moriodema mcoyei**Amblytelus* sp.

Pterostichini

*Notonomus resplendens**N. minimus**N. metallicus**N. variicollis**Prosopogmus oodiformis**Prosopogmus* sp.*Pseudoceneus* sp.

Scaritini

Carenum sp.*Clivina* sp.*Clivina basalis**Clivina* sp.

Trechini

Trechobembix baldiensis