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The beetles at Wog Wog: a contribution of Coleoptera systematics to an ecological field experiment

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Abstract. In this brief review we outline the contribution of Dr J. F. Lawrence to a major long-term field experiment in the southeast forests of NSW that examines the effect of habitat fragmentation on beetles. Dr J. F. Lawrence identified and curated the beetle fauna, which proved to be a significant and long-term commitment. The beetle data set has since provided great insight to the complex effects of habitat fragmentation. In addition, the size and quality of the data set mean that, on an international level, it is a major inventory of beetle diversity in a temperate *Eucalyptus* forest, in its own right. Here we outline Dr J. F. Lawrence's contribution and summarise the main features of the beetle data set and our findings about the impacts of fragmentation on the beetle fauna.

Introduction

The Wog Wog habitat fragmentation experiment is a long-term field experiment, established in 1985, to quantify the effects of habitat fragmentation on plants and animals, and in particular invertebrates (Margules 1993). Soon after the experiment began, Dr J. F. Lawrence became involved in the identification and inventory of the beetle fauna, which later proved to be a significant and long-term commitment. The beetle data set has since provided great insight into the complex effects of habitat fragmentation. In addition, the size and quality of the data set mean that it is a major inventory of beetle diversity in its own right. Thus, it will continue to be a significant resource that can be used to address both ecological and systematic questions.

This brief review: (*1*) outlines the experimental design and sampling of beetles; (*2*) summarises the main features of the beetle data set, putting the significance of the inventory effort in an international context; and (*3*) summarises our findings about the impacts of fragmentation on the beetle fauna.

Materials and methods

The Wog Wog habitat fragmentation experiment is located in southeastern Australia (37°04′30″S, 149°28′00″ E; Fig. 1), in 80–100 year old native *Eucalyptus* forest. The experimental design and rationale were described by Margules (1993). Briefly, it consists of three plot sizes: 0.25 ha, 0.875 ha, and 3.062 ha. Four replicates of each plot (fragment) size became habitat fragments when the surrounding *Eucalyptus* forest was cleared during 1987 and planted to *Pinus radiata* for plantation timber in winter 1988. Two replicates of each plot size remain in uncleared continuous forest, and serve as unfragmented control plots. Data were collected for a period of two years prior to the fragmentation treatment for all plots.

Within each plot, monitoring sites are stratified by both topography (slope or drainage line) and proximity to the fragment edge (edge or interior). There are two monitoring sites in each of the four strata. Thus, there are eight sites within each plot and a total of 144 sites over the 18 plots. Following clearing, an additional 44 monitoring sites were established in the *P. radiata* plantation between the habitat fragments.

Trapping technique

Two permanent pitfall traps are located at each site. Each trap consists of a plastic cup, 9 cm in diameter and 10 cm deep, inserted into a polyvinyl chloride sleeve, sunken flush with ground level. A 60-cm long, 5-cm high, galvanised iron drift fence sits along the edge of the cup and a galvanised iron roof, 20 cm by 20 cm, covers the cup, flush with the drift fence. We use a preservative fluid consisting of 70 % ethylene glycol, 29.75 % ethanol and 0.25 % formalin. Traps are opened for seven days four times a year, once during each season. Between sampling, traps are closed and remain in place. Monitoring commenced in February 1985.

Specimen identification

Beetle specimens were identified to species level by Dr J. F. Lawrence up until winter 1991 (July), that is, for two years pre-fragmentation through five years post-fragmentation (a total of seven years), for four samples per year. All species were allocated a voucher number and can be recognised to species level. Specimens have been lodged at the Australian National Insect Collection, CSIRO Entomology, Canberra.

Results

Over seven years, 57 989 individual beetles were captured and identified, representing 669 species from 58 families. More than half of these species (343) were trapped only once or twice, while six species were trapped over one thousand times each (Fig. 2). The incidental captures may represent

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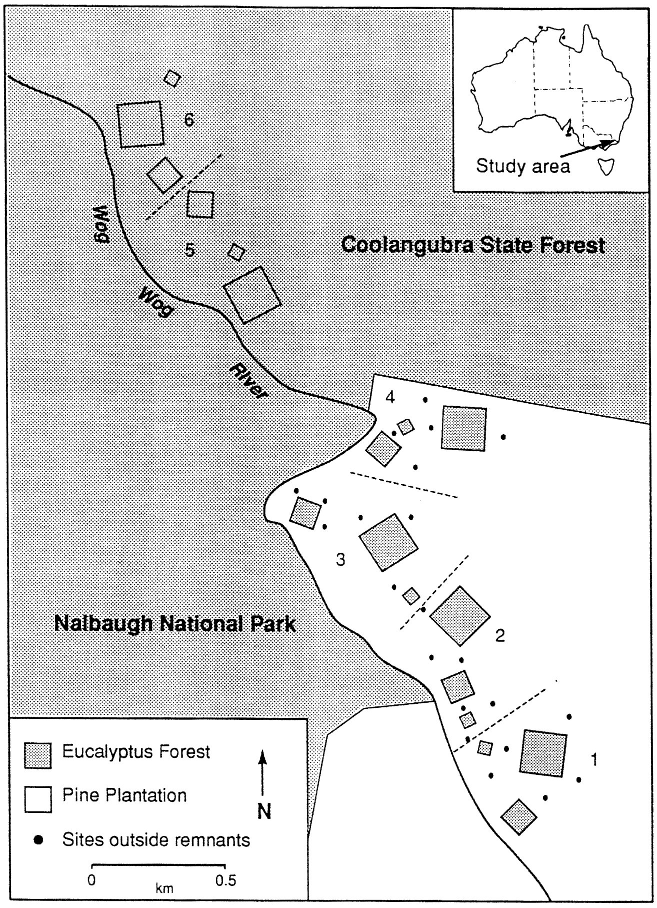

Fig. 1. Map of the experimental site showing eucalypt forest fragments and control plots in continuous forest. Each dot represents the approximate location of a pair of monitoring sites (a slope site and a drainage-line site) established in the pine matrix between the remnants after habitat fragmentation. Fragments are separated by a minimum of 50 m.

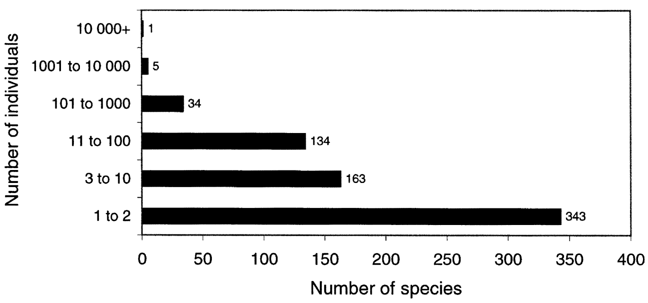

Fig. 2. Histogram of the number of beetle species caught at Wog Wog by the number of individuals of each species caught. For example, 342 species were only captured one or two times, while 34 species were captured between 101 and 1000 times.

species that are either rare, are not habitually ground dwelling, are 'tourists' (just passing through), or move little and are therefore unlikely to fall into pitfall traps. The most specious family was Staphylinidae with over 200 species. Although all species have been assigned a voucher number and can be recognised as morphospecies, 511 are undescribed at the species level and 134 are undescribed at the genus level. A comprehensive description of the data set is in preparation (J. F. Lawrence, personal communication).

Our main findings regarding the responses of both the beetle community and individual beetle species to fragmentation can be summarised as follows.

Initially, we tracked the responses of individual species to fragmentation and discovered that not all species responded to fragmentation in the same way. Some species declined in abundance in fragments compared with continuous forest, others increased in abundance, and some species were not affected by fragmentation (Davies and Margules 1998). This was illuminating because theory has been interpreted to predict that individual species will decline and species richness will be reduced as a result of fragmentation (MacArthur and Wilson 1967; Levins 1969).

We then explored which species declined and which species increased as a result of fragmentation, by testing for relationships between traits of species and declines in abundance. We tested five hypotheses derived from theory (Diamond *et al.* 1987; Hanski 1994; Lawton 1994; Gaston and Blackburn 1996; Pimm and Lawton 1997) and discovered that: (*1*) species that were naturally rare were more likely to decline than abundant species; (*2*) species isolated on fragments were more likely to decline than species that were not isolated; (*3*) body size was not correlated with response to fragmentation, although theory predicts that it could be (Gaston and Blackburn 1996); (*4*) predators declined most severely, whereas detritivores tended to increase in abundance; and (*5*) taxonomically related species did not respond in the same way to fragmentation (Davies *et al.* 2000).

We also investigated the response of the whole beetle community to fragmentation. Edge effects drove the changes that we observed in beetle relative abundance, species composition and species richness. Species richness increased slightly at fragment edges, while species composition and relative abundance became most different from the continuous forest controls at small fragment edges, but remained similar to the continuous forest controls in the interiors of large fragments (Davies *et al.* in press). These edge effects were driven by habitat modification on fragments. This finding contrasts with current theory, which tries to explain the effects of fragmentation through biogeographic factors such as isolation and distance to the next nearest populations (Hanski 1994). In addition, the *Pinus radiata* matrix between fragments provided alternative habitat for some species, which then increased in occurrence in fragments compared with continuous forest. However, the matrix did not act as a source of novel invading species.

Species turnover was reduced in fragments compared with continuous forest. Thus, one effect of fragmentation was to stabilise community dynamics in fragments (Davies *et al.* in press). This is a finding, which, on the face of it, might seem counterintuitive. Populations in habitat fragments are more exposed to factors that might be expected to increase population fluctuations and, therefore, turnover, as some species go locally extinct and are replaced by others. Clearly new theory will have to be developed to explain this result.

In summary, some traits (i.e. being rare, isolated and predatory) put species at greater risk of extinction. Local processes (edge effects) rather than regional processes (dispersal) had the greatest impact on beetle community dynamics. The pine matrix appeared to have the potential to influence persistence on fragments by allowing some species to become more abundant there and thus boost populations within fragments.

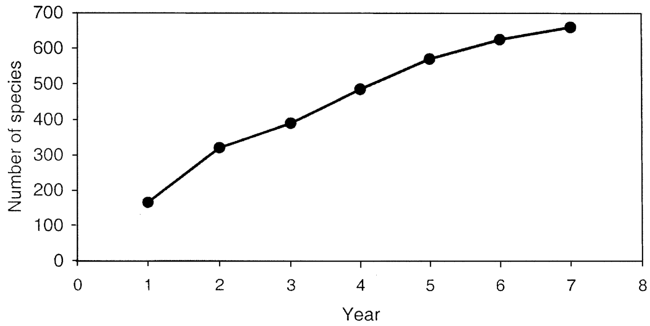

Fig. 3. Species accumulation curve.

Discussion

The Wog Wog beetle data set is significant when compared to other large sampling efforts of biodiversity in other parts of the world (Table 1). There are two important features. First, we have trapped a large number of beetle species. This is particularly notable given that our study site is temperate whereas most other studies considered are tropical, where more species can be expected. Second, the Wog Wog beetle data set is multi-temporal. In contrast with the studies reviewed (Table 1), most of which sampled for one year or less, the Wog Wog beetle data set covers 28 sampling periods over seven years. This multi-temporal aspect of the data has two benefits. First, we are much more likely to have sampled all of the ground-dwelling species that inhabit the study area. In fact, a species accumulation curve illustrates that the rate of increase in the number of species sampled had started to level off after about six years (Fig. 3). Second, by following beetle diversity through time we gain much greater insight into the complexities of the beetle responses to fragmentation.

For ecologists there is tremendous benefit in such a large data set with so many species representing such great functional diversity. It allows us to make robust tests of ecological theory, which are rare, and consequently allows us to attempt robust generalisations beyond invertebrates.

John Lawrence's contribution, through the identifications and base-line biological data, has been critical to this project and to ongoing work. The ecological work described would not have been possible without the quality and depth of taxonomic input and life history data provided by John. In conclusion, we believe that fragmentation studies have significantly greater meaning with the level of systematics input that John contributed to the Wog Wog beetle data set.

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Table 1. Some recent major invertebrate biodiversity inventories

Author	Number of species	Habitat sampled	Period sampled
Wog Wog, Lawrence *et al.* (unpublished data)	669 beetles	Temperate eucalypt forest, ground-dwelling fauna, Australia	7 years (ongoing)
Didham *et al.* (1998)	993 beetles	Rainforest, leaf-litter fauna, Brazil	5 months
Basset *et al.* (1996)	391 herbivorous beetles	Rainforest, Papua New Guinea	1 year
Basset and Novotny (1999)	779 herbivorous insects	Fig trees, Papua New Guinea	2 years
Kruger and McGavin (1998)	492 insects	Acacia canopy, tropical savannah, Tanzania	3 weeks
Stork (1991)	3059 arthropods	Rainforest canopy, Borneo	2 weeks
Recher *et al.* (1996)	976 arthropods (east Australia), 683 arthropods (west Australia)	Eucalypt forest canopy, Australia	1 year
DeVries *et al.* (1997)	130 butterflies (fruit-feeding)	Rainforest, Ecuador	1 year

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