



Corridors maintain species richness in the fragmented landscapes of a microecosystem

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Theory predicts that species richness or single-species populations can be maintained, or at least extinctions minimized, by boosting rates of immigration. One possible way of achieving this is by establishing corridors of suitable habitat between reserves. Using moss patches as model microecosystems, we provide here probably the first field experimental test of the idea that corridors can reduce the rate of loss of species, and therefore help to maintain species richness. Connecting patches of habitat with corridors did indeed slow the rate of extinction of species, preserving species richness for longer periods of time than in disconnected habitat patches. The pattern of γ -diversity, the cumulative species richness of entire connected systems, is similarly higher than that of fragmented systems, despite the homogenizing effects of movement. Predators are predicted to be more susceptible to fragmentation because of their greater mobility and smaller population sizes. Our data are consistent with this prediction: the proportion of predator species declined significantly in disconnected as compared with connected treatments.

Keywords: conservation; extinction; metapopulations; island biogeography; microcosms; γ -diversity

1. INTRODUCTION

Conservation biologists frequently advise the establishment of corridors to connect isolated reserves (Saunders & Hobbs 1991; Harris & Scheck 1991; Meffe & Carroll 1994; Noss 1994; Harris 1996), based on various theoretical rationales (Wilson & Willis 1975; Harrison 1994; Lynch *et al.* 1995; Hanski *et al.* 1996). The potential cost of creating a connected system of reserves can be huge (Mann 1995; Mann & Plummer 1995), but surprisingly there are virtually no field experimental data supporting the major theoretical prediction that species richness is maintained, or losses minimized (Nicholls & Margules 1991; Simberloff *et al.* 1992; Hobbs 1992; but see Schmiegelow *et al.* 1997). Almost the only field data suggesting that corridors actually work in promoting migration between patches, or slowing the rate of extinction of populations, consist of observations that some organisms do indeed sometimes use corridors (e.g. Saunders & Hobbs 1991; Beier 1993; Haas 1995; Dunning *et al.* 1995; Downes *et al.* 1997*a,b*); experimental results are very few, and largely laboratory based (Ims & Stenseth 1989; Holyoak & Lawlor 1996; Burkey 1997; but see Schmiegelow *et al.* 1997). In contrast, there has been a great deal of theory associated with the idea that corridors between habitat patches might offset some of the deleterious effects of habitat fragmentation, principally loss of species richness (Saunders & Hobbs 1991; Harrison 1992; Lindenmayer & Nix 1993; Hill 1995). The suggestion is that species richness or single-species populations can be maintained, or at least extinctions minimized, by boosting rates of immigration via the establishment of corridors of suitable habitat between reserves. Despite some obvious negative possibilities such as enhanced

disease transmission (Simberloff *et al.* 1992; Hess 1994), the consensus is that corridors are beneficial.

Rather little theory exists on the relationship between food webs and habitat patchiness (Cohen & Newman 1991; Pahl-Wostl 1993; Holt 1996). What there is predicts that certain types of species are more susceptible than others in the fragmentation process, with predators, large species and habitat specialists (all correlates of rarity) apparently being extinction prone (Diamond 1984; Schoener 1989; Cohen & Newman 1991; Tracy & George 1992). There is some evidence for and against these predictions: the proportion of carnivores amongst boreal mammals of montane fragments in the USA declines with decreasing species richness (Patterson 1984); many parasitoids 'failed to colonize' small patches of experimentally established plants where their hosts had colonized, leading to relatively fewer predators on smaller patches (Kruess & Tschardt 1994); and top predators suffer extinction in isolated microcosms (Wright & Coleman 1993; Burkey 1997). In contrast, no such differences in extinction susceptibilities were detected in a variety of data sets from 'natural experiments' (Mikkelsen 1993). Differential dispersal abilities, with predators generally better than non-predators, mean that the presence of corridors may help predator populations more than those of non-predators in avoiding the extinction consequent upon insularization. The only experimental tests of this idea used laboratory microcosms: Holyoak & Lawlor (1996) confirmed that moderate levels of dispersal maximized persistence and predator abundance, whereas Burkey (1997) found, surprisingly, that top predators died out more rapidly in connected as opposed to disconnected systems.

More sophisticated approaches suggest that such differential effects may be difficult to demonstrate. Cohen &

Newman (1991) suggested that because food chain length increases only slowly with the number of species in a web, and that the number of species in a habitat increases only logarithmically with habitat area, there should only at most be a weak link between area and food chain length. Holt (1996) predicted an increasing effect of area on the number of species in higher trophic ranks, but that the effect might be difficult to detect. A deeper understanding of what makes a species vulnerable to extinction is considered vital to efforts to solve the biodiversity crisis by applying ecological principles (Simberloff 1988; Ehrlich 1993).

We use here an experimental microecosystem, island-like patches of moss containing diverse communities of microarthropods, to test experimentally the idea that corridors can reduce the rate of loss of species, and therefore help to maintain species richness. We predicted that connecting patches of habitat with corridors would slow rates of extinction of these microarthropods, retaining species richness for longer than in isolated habitat patches. We further predicted that predators would suffer disproportionately in the extinction process, but corridors would help them more than non-predators because of their better movement.

2. METHODS

Rates of extinction are too slow in large-scale systems to be useful experimentally (see Schmiegelow *et al.* 1997), and therefore we used a small-scale moss ecosystem as a microcosm (de Ruiter *et al.* 1995; Moore *et al.* 1996). Moss patches are ideal systems for experiments of this sort because they are easy to manipulate, contain an easily sampled, well-known, diverse community of microarthropods at high to very high densities (Gerson 1969; Corbet & Lan 1974; Eisenbeis & Wichard 1987; Kinchin 1992), and occur naturally in patches which are large relative to the size and dispersal powers of the populations that live in them (which may make their microarthropod communities good models for the macrofauna of real nature reserves). Experimental tests of insular processes have often used such microcosms because of their tractability and the short time-scales of change. For example, studies of colonization have used ciliates (Henebry & Cairns 1980; Robinson & Dickerson 1987; Have 1987; Azovsky 1988), fungi (Wildman 1987), lichens (Armesto & Contreras 1981) and marine invertebrates (Schoener & Schoener 1981). Studies of extinction have used protozoa (Dickerson & Robinson 1985, 1986; Warren, 1996; Burkey 1997); studies of relaxation, soil nematodes (Wright & Coleman 1993); and studies of turnover, protozoa (Cairns *et al.* 1969) and fungi (Kinkel *et al.* 1987).

We set up a field experiment in which we manipulated habitat connectivity, while allowing for the inevitable increase in area that connections bring with them. There has been some discussion in the literature about an appropriate design (Nicholls & Margules 1991; Inglis & Underwood 1992; Lindenmayer & Nix 1993); we deliberately chose to consider connections between already fragmented habitats, rather than connections between fragments and a large mainland. We chose six large, flat limestone rocks, originally continuously covered in moss (mainly *Hypnum cupressiforme*, *Thuidium tamariscinum* and *Tortella tortuosa*), near Wirksworth in the Peak District (Derbyshire, UK; OS map reference SK 264566). In October–November 1995, five circles (each 10 cm in diameter) were sampled from the continuous moss of each rock before clearance to give data on the initial

species richness of the 'mainland' of moss. Then we partly cleared the moss to the bare rock (assumed to be a relatively inhospitable environment for the majority of moss taxa) in order to set up four experimental fragmentation treatments, each consisting of four circular islands 10 cm in diameter. Island centres were placed at the corners of a square of side 17 cm (i.e. islands were separated 7 cm from each other); treatments were at least 10 cm apart on each rock, and at least 10 cm from the remaining 'mainland' of moss. Fragmentation treatments (cf. figure 1) were (i) mainland (four circular samples (diameter 10 cm) taken from the surrounding matrix of continuous moss), (ii) corridor (four islands connected along the sides of the square by corridors 7 cm long by 1 cm wide), (iii) broken corridor (as the corridor treatment, but corridors split in the middle and separated by a gap of 5 cm—this controls for the increased area of the corridor treatment) and (iv) insular (no corridors present). We therefore had four replicate islands per treatment, with all four treatments replicated on each of six rocks. As in real nature reserves, the 'inhospitable' habitat between islands is probably a partial rather than an absolute barrier to movement; there is very little evidence about the dispersal abilities of microarthropods (see Schenker & Block 1986).

Treatments were removed from each rock after six months for analysis; this time-period is equivalent to several generations of most of the fauna in the moss. We also had samples from three months to compare the time-course of the relaxation process, but results from these are only briefly reported here. When sampled, each 10-cm island (a 'sample') was placed in a Tullgren funnel for 48 h and all emerging animals collected into alcohol, identified to major group (using, amongst other reference works, Evans *et al.* (1961), Krantz (1978) and Eisenbeis & Wichard (1987)), and sorted to morphospecies. In all samples, 30 000 individuals were counted and identified; most belonged to the Acari (32% of species) and Collembola (23%). In addition, species were classified as predators (prostigmatid and mesostigmatid mites, spiders, pseudoscorpions) or non-predators (cryptostigmatid mites, collembolans, beetles, etc.). Further details will be published elsewhere (A. Gonzalez, unpublished data). All mean values cited here in the text are given with standard errors.

In the first analysis, the average species richness (square root transformed) of the four 10-cm islands of each treatment on each rock was the dependent variable in an analysis of variance (ANOVA), implemented using GLIM4 (Francis *et al.* 1993; Crawley 1993). Using orthogonal contrasts, we tested the *a priori* prediction that connected treatments (mainland + corridor) would retain more species than the disconnected treatments (broken + insular): then within these pairings we tested for differences in species richness between mainland versus corridor, and broken versus insular.

We then calculated the proportion of predators among the species present, and used this as the dependent variable in a second similar ANOVA. Proportions were not arcsin transformed because the transformation worsened the fit to the normal distribution. Again, using orthogonal contrasts, we tested the *a priori* prediction that connected treatments (mainland + corridor) would retain a higher proportion of predators than the disconnected treatments (broken + insular), followed by the mainland versus corridor and broken versus insular contrasts.

We repeated these analyses using γ -diversity as replicates, i.e. treating the cumulative species richness of all four 10-cm islands in any one treatment on each rock as a single replicate. Finally, we also ran similar ANOVA on the square root transformation of the total number of individuals per replicate.

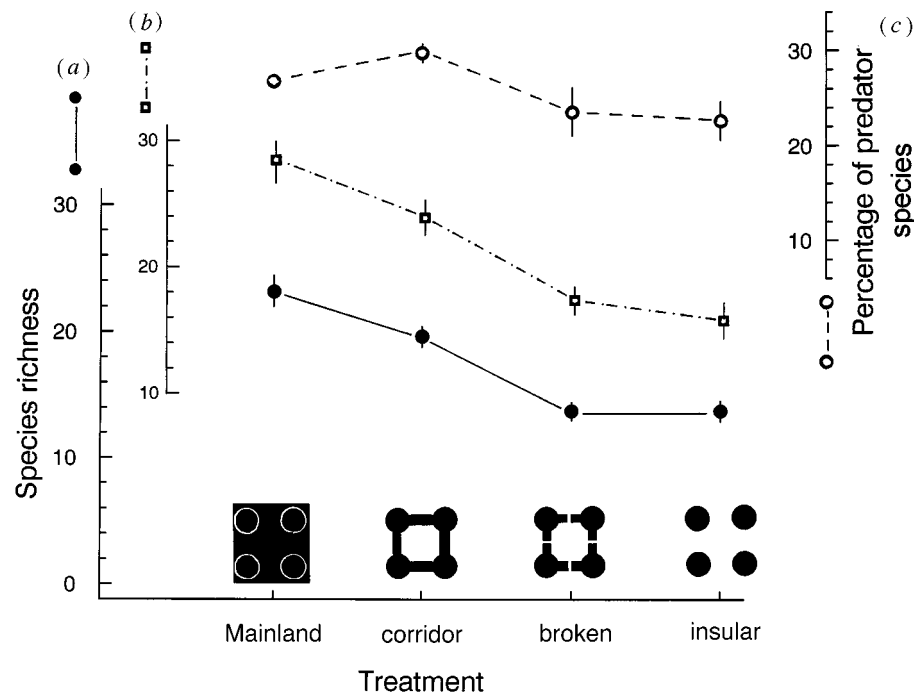


Figure 1. The effect of connectivity treatments on diversity in experimental moss islands. Figures are plotted as means \pm one standard error. (a) Filled circles and solid lines (main left-hand y-axis): local species richness of individual 10-cm islands. The *a priori* contrast between connected (mainland + corridor) and disconnected (broken + insular) systems is highly significant (see table 1). (b) Empty squares and dot-dashed line (left offset y-axis): γ -diversity (species richness of the unit of all four 10-cm islands). The *a priori* contrast between connected (mainland + corridor) and disconnected (broken + insular) systems is highly significant (see text). (c) Empty circles and dashed lines (right-hand y-axis): the percentage of the species richness that consists of predators. The *a priori* contrast between connected (mainland + corridor) and disconnected (broken + insular) systems is highly significant (see table 2).

3. RESULTS

There was an overall rise in background species richness between the initial (18.6 ± 1.4 , $n=30$) and six-month (23.2 ± 1.2 , $n=24$) mainland samples. This was probably a

Table 1. *The effect of fragmentation treatments on species richness of microarthropods in moss patches*

(The effect on species richness (the dependent variable, square-root transformed) of fragmentation (a treatment factor with four levels) replicated on different rocks (a block factor with six levels) was assessed using an analysis of variance with normally distributed errors, implemented using GLIM4 (see Crawley 1993). The treatments were: mainland, corridor, broken corridor and insular. Using *a priori* orthogonal contrasts, we tested the impact of connected treatments (mainland + corridor) versus disconnected treatments (broken corridor + insular), and then mainland versus corridor, and broken corridor versus insular.)

source	d.f.	SS	MS	F	p
fragmentation	3	5.38	1.79	28.11	0.001
connected versus disconnected	1	5.02	5.02	79.68	<0.001
mainland versus corridor	1	0.36	0.36	5.71	<0.05
broken versus insular	1	0.02	0.02	0.31	n.s.
rocks	5	4.01	0.80	12.7	0.01
residual	15	0.94	0.063		
total	23	10.34			

seasonal effect, an interpretation supported by intermediate values for some three-month background samples (20.7 ± 0.9 , $n=24$). There were significant effects of 'treatment' (table 1): most of the effects of the treatments were contained in the contrast between connected and disconnected treatments and, in addition, the corridor treatment had significantly fewer species than the mainland (see table 1). This result is further supported by the samples taken at three months, where broken-corridor and insular treatments had already lost species compared to the background. Between three and six months, the background moss gained in species richness (by 2.5 species; see above); the corridor treatment lost 3.5 species, but the broken-corridor samples lost 6.5 species, and the insular samples 4.8 species. The magnitude of the treatment effects on species richness were considerable (figure 1); compared with the continuous moss (the mainland treatment), islands with corridors lost an average of 15.5% of their species, whereas the disconnected islands (broken + island treatments) lost almost 41%. As no differences existed between broken-corridor and insular treatments, islands with broken corridors therefore behaved like islands without corridors: there was no detectable effect on species richness of the small amount of extra area entailed by this treatment. This implies that it is movement that is creating the observed pattern.

The number of individuals per island likewise increased seasonally, from the initial mainland islands (132 ± 14 , $n=30$), to three-month (234 ± 12) and mainland (297 ± 12) samples at six months. The mean number was strongly affected by fragmentation treatments ($F_{3,15} = 33.6$, $p < 0.001$), and 77% of the sum of squares was accounted for by the

Table 2. *Effect of fragmentation treatments on the proportion of predators among microarthropods in moss patches*

(The effect on the proportion of species that were predators (the dependent variable) of fragmentation (a fixed treatment factor with four levels) replicated on rocks (a random block factor with six levels) was assessed using an analysis of variance with normally distributed errors, implemented using GLIM4 (see Crawley 1993). Proportions were not arcsine transformed because without it the fit to the normal distribution was improved. The treatments were: mainland, corridor, broken corridor and insular. Using *a priori* orthogonal contrasts, we tested for the impact of connected treatments (mainland + corridor) versus disconnected treatments (broken corridor + insular), and then mainland versus corridor, and broken corridor versus insular.)

source	d.f.	SS	MS	F	p
fragmentation	3	203.35	67.8	11.56	0.0002
connected versus disconnected	1	185.37	185.37	31.63	<0.0002
mainland versus corridor	1	14.19	14.19	2.42	n.s.
broken versus insular	1	3.79	3.79	0.64	n.s.
rocks	5	13.19	8.63	1.47	n.s.
residual	15	88.0	5.86		
total	23	334.5			

connected versus disconnected contrast ($F_{1,15}=77.3$, $p \ll 0.001$). The mean numbers of individuals in mainland islands was more than 50% greater than in corridor islands (182 ± 16), and about three times greater than in broken-corridor (86 ± 7) or insular samples (113 ± 10).

The proportion of predators declined significantly between connected and disconnected treatments (see figure 1), since the contrast was highly significant, accounting for 91% of the treatment sum of squares (see table 2). Furthermore, the broken versus island contrast was not significant, confirming the important result that broken corridors are ineffective. In this system, therefore, there is strong evidence that predators were more sensitive to the impact of fragmentation and its amelioration by corridors than were non-predators.

In the analysis of γ -diversity (see figure 1), there was also a significant effect of fragmentation treatment on larger-scale species richness (ANOVA with Poisson errors, $\chi^2=28.1$, 3 d.f., $p < 0.001$), virtually all of which lay in the contrast (connected versus disconnected contrast, $\chi^2=25.4$, 1 d.f., $p < 0.001$). All the fragmented treatments lost species relative to the background (see figure 1). There was a significant difference in γ -diversity between just the corridor and the broken treatments ($\chi^2=6.1$, 1 d.f., $p < 0.02$). Analysis of the number of individuals (square root transformed) gave similar results. There were no overall differences between treatments in their proportion of predators (ANOVA with normal errors, $F_{3,20}=0.11$, n.s.), nor in the specific contrast between connected and disconnected treatments ($F_{1,20}=0.24$, n.s.).

4. DISCUSSION

'The ecological value of . . . corridors is disputed by some of the discipline's leading researchers. . . . wildlife

corridors have quietly become one of the most important battlegrounds for conservation, with major development projects and the future of valuable nature preserves at stake' (Mann & Plummer 1995). Some think that corridors 'hold more promise for the management of the diversity of life than any other management factor except stabilization of the human population' (Keith Hay of the Conservation Fund, reported by Mann & Plummer (1995)), whereas others such as Dan Simberloff (Simberloff *et al.* 1992) remain much more cautious or sceptical of the rationale behind the use of corridors. One of the main reasons for this dispute is the total lack of experimental data supporting the role of corridors in maintaining biodiversity. Our results demonstrate experimentally that in the moss-island microecosystem, intact corridors do indeed slow down the process of extinction following fragmentation. The obvious difference between intact and broken corridors means that the extra area in corridors is not important; this in turn implies that restriction of movement is the key to understanding the dynamics of the experiment.

We interpret this as indicating that in this moss microecosystem, the interpatch movement that may be maintained by the existence of corridors may allow small extinction-prone populations to persist longer than those existing in the unconnected fragmented landscapes. Harrison (1994) reviewed evidence for metapopulation behaviour, and concluded that the conditions leading to the maintenance of an extinction-migration balance are probably rather unusual in nature: it is possible that the relative sizes of islands, corridors and taxa in our microecosystems were conducive to obtaining a corridor effect. We think that dispersal to adjoining patches on the scale of the experiment probably ameliorated the localized population crashes via a rescue effect, and that the absence of corridors precluded this process, resulting in permanent extinction. We therefore predict that the population impact of corridors will depend on the scale of the island-corridor system relative to the size and dispersal powers of species (Harrison 1994; Hanski *et al.* 1996), thus affecting species differentially and predictably. The extent to which these results can be scaled up to macroscale ecosystems needs to be investigated—small mammals in patches of woodland might be a suitable macroscale analogue of our experiment. Further experiments using this very suitable microecosystem could manipulate the relative sizes of islands and corridors to explore this further. Despite the effectiveness of corridors, however, they only slowed the extinction process, rather than preventing it altogether. It is unclear from the present experiment what the more long-term (>6 months) outcome of fragmentation with corridors might have been, and hence whether the equilibrium number of species in the fragmented landscape with corridors would have been higher than in the totally fragmented landscape. The observation of fewer species in the connected landscape when compared with the mainland suggests that long-term persistence may only be achieved by connection to an extinction-buffered mainland.

The larger-scale γ -diversity (the species richness of the four islands treated as a single replicate) is interesting in the context of whether many small islands accommodate more species than the same area as a single large island

(the SLOSS debate: Higgs 1981; Baz & Garcia-Boyer 1996; Boecklen 1997). Having corridors and hence allowing movement might affect this because movement might increase the homogeneity of species composition across connected islands. This idea predicts that the local per-island species richness may be greater than the equivalent disconnected system, but the cumulative species richness for the whole connected system might be lower. However, our data show that, like local species richness, the γ -diversity of connected systems is greater than that of disconnected ones, and there is no evidence of reduced diversity caused by homogenizing movement.

The differential impact of fragmentation on predators is a result predicted to a greater or lesser extent by theory (Cohen & Newman 1991; Holt 1996). The simplest explanation is that the generally greater movement of predators means that corridors are more important to them. Our result supports the body of theory proposing top-down community disassembly (Schoener 1989). More work focused on this issue is clearly required. The moss microecosystem could also be used to test other important related issues, such as the prediction that habitat fragmentation and loss should cause biased extinction of superior competitors (Tilman *et al.* 1994, 1996).

In conclusion, our results support current predictions about the likely effects of corridors; in our moss microecosystem, corridors between isolated habitats slowed the rate of extinction of species relative to fragmented habitats without corridors. We found strong support for the idea that predators suffer more than non-predators, and benefit more from corridors. The data also suggest that the cumulative species richness of entire connected systems is also higher than that of fragmented systems. We think more emphasis needs to be placed on the important effects of the larger scale at which processes can operate, which is present when corridors are implemented; we will explore these in a further paper.

We thank Howard Mace for help with a pilot study (done with A.G. at Nottingham); Paul Murphy for help with mite identification; Jack Rieley for identifying the mosses; Robert Dean for logistical help; and Tom Day and John Lawton for comments on the manuscript. A.G. was supported by a NERC studentship. We thank three anonymous referees who made important improvements to an earlier version, including the suggestion of analysing γ -diversity.

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