# Species richness of moss landscapes unaffected by short-term fragmentation

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Theory predicts that habitat fragmentation and varying corridor length and width will affect animal populations in adjoining habitat patches due to varying migration rates. Previous work on the moss/microarthropod microcosm showed that connecting moss patches with moss corridors maintained species richness and individual species abundance. By contrast, in this study there was little evidence for differences in species richness between landscapes of varying connectivity and corridor length and width. The  $\gamma$  diversity, the cumulative species richness of entire connected systems, followed the same pattern. Similar non-significant results were obtained for species abundance. Contrary to a previous study, I found no evidence that populations of predators were more affected by fragmentation than non-predators. Since this experiment ran during temperate environmental conditions and the previous be more useful in reducing species extinction during extreme environmental conditions.

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Habitat loss and isolation pose perhaps the most serious threat to biological diversity (Kareiva et al. 1993). Habitat corridors have been proposed as a means of reducing the negative effects of habitat isolation (Diamond 1975), and are a practical option for conservation managers to implement. Corridors are predicted to increase animal movement rates between habitat patches, reducing the probability of species loss (Saunders and Hobbs 1991). However, the lack of empirical evidence concerning the effectiveness of corridors has led to much debate about their usefulness (Mann and Plummer 1995). Indeed, there are very few field experimental data supporting the prediction that corridors maintain species richness (Simberloff et al. 1992). However, there is some observational evidence that animals use corridors (Saunders and Hobbs 1991, Haas 1995, Tewksbury et al. 2002). It is likely that the impact of corridors on populations will depend on the scale of the system relative to the size and dispersal abilities of the species

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(Hanski et al. 1996) and the degree to which patches are isolated. Note that migration between patches in the absence of corridors is not required to be zero, but merely sufficiently restricted to affect patch population dynamics. Most critics agree that if corridors promote migration between habitat patches then the extinction rate is reduced (Simberloff et al. 1992). A more contentious question is whether corridors allow such migration (Simberloff et al. 1992).

The equilibrium theory of island biogeography and metapopulation dynamics form the theoretical basis for understanding the effectiveness of corridors. Island biogeography theory suggests that the shorter and wider the corridor, the greater the migration rate between habitat patches increasing the probability that populations will be "rescued" from extinction (Brown and Kodric-Brown 1977, modelled by Tischendorf and Wissel 1997). However, individuals may wander unproductively in wider corridors (Soule and Gilpin 1991) and

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poor quality corridors may act as sinks (Henein and Merriam 1990). Predators may be more susceptible to extinction after fragmentation due to their greater movement (Schoener 1989). Some experiments have agreed with this prediction (Burkey 1997), but others have not (Mikkelson 1993).

Most corridor studies have been observational, (Haas 1995), but there have been a few controlled experiments (Forney and Gilpin 1989, Burkey 1997, Gilbert et al. 1998, Gonzalez et al. 1998, Forbes and Chase 2002, Gonzalez and Chaneton 2002, Tewksbury et al. 2002). In a review of the literature, Beier and Noss (1998) concluded that most studies support the utility of corridors. On the other hand, some studies suggest that corridors may have neutral or even negative effects on species persistence (Burkey 1997). Forbes and Chase (2002) found that connectivity in a zooplankton community had no effect on local ( $\alpha$ ) species diversity, but reduced regional  $(\gamma)$  diversity, and increased the proportional similarity of local populations. Warren (1996) and Gilbert et al. (1998) found the opposite effect on  $\gamma$ diversity, possibly because the habitat patches used by Warren (1996) and Gilbert et al. (1998) were relatively homogeneous (Forbes and Chase 2002).

In microarthropod communities inhabiting moss patches, Gilbert et al. (1998), Gonzalez et al. (1998) and Gonzalez and Chaneton (2002) found that connecting patches of habitat slowed down the rate of species extinction. Broken corridors of the same total area did not have this effect. They suggested that the corridors facilitated the dispersal of microarthropods between the habitat patches, maintaining the distribution and abundance of species through the rescue effect, and that the scale of fragmentation and dispersal distance of the organisms were likely to be appropriate for the metapopulation concept to apply. The  $\gamma$  diversity, the species richness of the entire connected system was higher than in the fragmented system. Finally, the proportion of predator species declined significantly in disconnected as compared to connected treatments.

I chose to use a similar moss/microarthropod microcosm to study the effects of connectivity and varying corridor width and length on species richness. It is a rare example of a field-based microcosm of wildlife corridors, and it is an effective system for several reasons. It is relatively quick and cheap to set up several replicates of each treatment. A large community of microarthropods, at different trophic levels, live in a small patch of moss and are easily extracted. Finally, the effects of fragmentation on the microarthropod populations have repeatedly been shown to occur after just six months (Gilbert et al. 1998, Gonzalez et al. 1998).

### Material and methods

Six experimental blocks of treatments were set up between February and May 2001. Within each block

eight treatments (Fig. 1) were replicated and randomly allocated to the moss on the top of a dry stone wall near Cromford in the Peak District (Derbyshire, UK; OS map reference SK 285572), in the same valley as used by Gilbert et al. (1998), Gonzalez et al. (1998) and Gonzalez and Chaneton (2002). All treatments consisted of two circular patches, 10 cm  $\emptyset$ . A corridor was either absent, broken, or present. When present, the corridor length varied from 0 cm to 14 cm, and the width from 1.5 cm to 2.5 cm (Table 1).

The moss species were mostly *Homalothecium sericeum*, *Brachythecium rutabulum* and *Hypnum lacunosum* var. *lacunosum*. I partly cleared the moss to the bare rock in order to set up the experimental treatments. A metal template and a scalpel were used to cut out the shapes of the treatments from the mainland moss. The bare rock was considered to be a relatively inhospitable environment for the majority of the moss taxa. Treatments were at least 10 cm apart and at least 10 cm from the remaining "mainland" of moss and were removed from the dry stone wall after six months for analysis (as Gilbert et al. 1998). When sampled, the moss was placed in a Tullgren Funnel for 48 h and all emerging animals



Fig. 1. (a)  $\alpha$  diversity and (b)  $\gamma$  diversity of log(number of microarthropod morphospecies) by landscape treatment ( $\pm$  1 s.e.).

Table 1. Experimental treatments.

Treatment	Corridor length (cm)	Corridor width (cm)	Notes
1	0	1.5	
2	3	1.5	=
3	7	1.5	_
4	7	2.5	_
5	14	1.5	_
6	N/A	N/A	No corridor, patches separated by cm
7	7	1.5	Corridor broken in middle, gap of cm
8	7	1.5	Cut from mainland moss at end of experiment

were collected into an ethanol/glycerol mixture, and then sorted into morphospecies (Krantz 1978). This technique is well known to be efficient at extracting adult but not juvenile mites (R Norton, pers. comm.). Samples were weighed both before and after being placed in the funnels to give the wet and dry moss weights.

In total, 69,000 individual microarthropods were counted and sorted into morphospecies (usually genus level, see Appendix), and a further 138,000 individuals were estimated. Most microarthropods belonged to the Acari (63% of individuals, only adults counted) and Collembola (non-predatory, 37%). Within the Acari, 86% of individuals were Cryptostigmata (non-predatory), 2% Mesostigmata (predatory) and 12% Prostigmata (predatory). There were 50 mite morphospecies, 12 Collembola morphospecies and 32 other morphospecies (mostly beetles, spiders, centipedes, millipedes and pseudoscorpions).

Tests were performed on the number of species per moss patch ( $\alpha$  diversity) and per pair of patches ( $\gamma$ diversity) and on the number of individuals for all microarthropods, all non-predatory mites, all predatory mites and all Collembola. Analyses were implemented using the statistical package "R" (Ihaka and Gentleman 1996). The logarithm of the response variable was modelled as an analysis of covariance with two factors, treatment type and experimental block and with one covariate, the dry weight of the moss patches. In all cases, the log transformation of the response variable was adequate to stabilise the variance of the residual errors and to normalise the residual errors. Hence normal errors were used.

The following hypotheses were tested;

 Connected patches have more species and individuals per species than disconnected patches, since the rescue is assumed to be relevant only for the connected patches. This was tested by an a priori contrast between treatments 1, 2, 3, 4, 5, 8 and treatments 6, 7.

- 2) Short-corridor patches have more species and individuals per species than long-corridor patches, since the rescue effect is more likely to occur in the short-corridor treatments, where the probability of migration between patches is assumed to be greater. This was tested by a regression of corridor length, using treatments 1, 2, 3 and 5.
- 3) The wide-corridor patches have more species and individuals per species than the narrow-corridor patches, for the same reason as above. This was tested by a contrast between treatments 3 and 4.
- 4) The mainland patches have more species and individuals per species than the average of the other patches, a basic assumption of island biogeography. This was tested by a contrast between treatment 8 and all the other treatments.

The Dunn-Sidak correction was used, since the contrasts were non-orthogonal (Sokal and Rohlf 1995).

I hypothesised that the different treatments may be of varying wetness according to their connectance and shape. The wetness of a moss patch might then influence the distribution of the resident microarthropods.

The four tests above were repeated, with the wet weight of the moss patch as the first response variable and the wet weight of the corridor as the second response variable and with the dry weight as a covariate and the date of moss removal and the treatment as factors.

The same tests were performed on the ratio of the density of microarthropods in the corridor to the density of microarthropods in the adjoining patches. The density was defined as the number of microarthropods in the corridor or patch divided by the dry weight of the corridor or patch. There were five response variables involving the total number of microarthropods, Cryptostigmata, Mesostigmata, Prostigmata and Collembola.

A Levene test was performed on the log-transformed data to test for the equality of coefficients of variation (Sokal and Braumann 1980) in the population sizes of the two patches in the two patch treatments. Response variables were chosen as the nine most common Cryptostigmata mites and the two most common Collembola species. We might expect the coefficient of variation to be greater for the broken corridor treatment and the larger and narrower corridor treatments, since the migration rate between patches should be lower for these treatments.

Finally, rank abundance graphs were plotted for the average of the connected treatments (treatments 1, 2, 3, 4, 5, not including the mainland treatment) and fragmented treatments (treatments 6 and 7) separately, in an attempt to highlight differences in community structure. Differences in the linear and quadratic terms were tested by ANCOVA.

## Results

On average, over all treatments and blocks there were 10 adult Cryptostigmata species, 3 adult Mesostigmata species, 484 adult Cryptostigmata individuals, 9 adult Mesostigmata individuals, 73 adult Prostigmata individuals, 314 Collembola individuals and 8 other micro-arthropod individuals per moss patch.

For species richness, none of the hypotheses were accepted, except that that mainland treatment for all morphospecies combined had fewer species than the average of the other treatments for the  $\alpha$  (12% fewer,  $t_{244} = 3.653$ , P < 0.001) and  $\gamma$  diversities (10% fewer,  $t_{106} = 2.573$ , P = 0.011) and the non-predatory (Cryptostigmata) mite  $\alpha$  diversity for the mainland was significantly lower (by 10%,  $t_{249} = 2.740$ , P = 0.007) than for the average of the other treatments. The graphs of the logarithm of the number of microarthropod species against treatment are shown for the  $\alpha$  and  $\gamma$ diversities (Fig. 1a, b). For the total number of individuals per patch, none of the hypotheses were accepted for all morphospecies combined, for non-predatory (Cryptostigmata) mites, for predatory (Mesostigmata and Prostigmata) mites or for Collembola (Fig. 2). In virtually all these tests, the response variable increased with increasing patch dry weight. In addition, there was often a highly significant block effect in the analysis of covariance.

For the patch wetness, none of the hypotheses, apart from the corridor width hypothesis, were accepted. There was evidence (by 28%,  $t_{231} = -2.75$ , P = 0.006) that the patches in the wide corridor treatment (treatment 4) were wetter than the patches in the narrow corridor treatment (treatment 3). Surprisingly, the mainland patches were not significantly wetter ( $t_{231} = 0.624$ , P = 0.533, n.s.) than the average of the other patches. None of the hypotheses for the corridor wetness were accepted.

For the test of the ratio of densities of microarthropods in the corridor to the density of microarthropods in the adjoining patches, none of the hypotheses were accepted after the Dunn-Sidak adjustment. The average ratio for all microarthropods combined was 0.91, for Cryptostigmata mites 0.93, for Mesostigmata mites 0.69, for Prostigmata mites 0.38 and for Collembola 1.02. Since most of these values are less than one, it might appear that the corridors contain proportionally fewer microarthropods. Only three tests for differences in coefficients of variation were significant after the Dunn-Sidak correction. For Cryptostigmata morphospecies 5 the coefficient of variation for the narrower corridor treatment (treatment 3) was 62% greater than for the wider corridor treatment (treatment 4),  $t_{195} =$ 3.323, P = 0.001. For Cryptostigmata morphospecies 7 the coefficient of variation for all unconnected two patch treatments (treatments 6 and 7) combined was 55% greater than for all the connected two patch treatments (treatments 1, 2, 3, 4, 5 and 8) combined),  $t_{195} = -3.297$ , P = 0.001. For Cryptostigmata morphospecies 11 the coefficient of variation for the longer corridor treatments (treatments 3, 4 and 5) combined was 53% greater than for the shorter corridor treatments (treatments 1 and 2) combined,  $t_{195} = -2.801$ , P = 0.006.

#### Discussion

The most important finding of this experiment is that there is no difference in species richness between the broken and connected landscape treatments for all microarthropods combined and for non-predatory (Cryptostigmata) mites alone, the species richness of the mainland was significantly lower than for the average of the other treatments. Both results contrast sharply with the results of Gilbert et al. (1998). Gonzalez et al. (1998) and Gonzalez and Chaneton (2002). However, the rank abundance analysis suggests that rare species became rarer in isolated systems, indicating the beginning of the process of relaxation. The mainland result may have been due to the influence of soil in the samples. The mainland moss appeared to have more soil than the moss in the other treatments, perhaps because the soil in the other treatments was more easily eroded during the experiment. The soil in the Tullgren funnels may then have reduced the microarthropod extraction efficiency and an independent experiment supports this interpretation.

I can suggest several possible reasons for the discrepancy between my results and those of the above two workers. Perhaps most importantly, my experiment ran during temperate environmental conditions, whereas the previous experiments ran during more extreme weather conditions (A. Gonzalez pers. comm.), perhaps increasing mortality rates of the microarthropods (Siepel 1996). The rescue effect may then have been more important in arresting species extinction in the previous studies. Note that the generation times of the microarthropods are actually quite long relative to the duration of the experiment (six months). In temperate forest soils, the development time of most Cryptostigmata species is probably several months to over one year (Norton 1994). Barker (1969) found the mean generation time of the Mesostigmatid mite Hypoaspis aculeifer (Canestrini) to be three to four weeks in the laboratory. Hartenstein (1962) reported four to five generations a year for the Mesostigmatid mite Pergamasus crassipes (Linnaeus) (a species found in my study). Christiansen et al. (1992) suggested a generation time of about one month for most Collembola species in the laboratory; but some species are univoltine (one generation per year) and others are mutivoltine (more than one generation per year, Hopkin 1997). Next, I used different moss species. I



chose Homalothecium sericeum, Brachythecium rutabulum and Hypnum lacunosum var. lacunosum, whereas the previous studies used Hypnum cupressiforme, Thuidium tamariscinum and Tortella tortuosa. My experiment ran at a different time of year to Gilbert et al. (1998) and Gonzalez and Chaneton (2002) and ran for a shorter period than Gonzalez et al. (1998). Note that microarthropod dispersal rates may depend on the season and on the life stage (Norton 1994). My experimental blocks spanned several rocks on a dry stone wall, whereas previous studies allocated all treatments in a block to a single boulder. Gilbert et al. (1998) found on average far fewer microarthropods per moss patch, suggesting a different type of microarthropod community. Finally, the previous studies used four patches per treatment in a square design, whereas I used just two patches.

Furthermore I found no significant difference in the  $\gamma$  diversity amongst the treatments (except for the mainland treatment), and there was no evidence that the predators (Mesostigmata and Prostigmata mites) were especially affected by fragmentation, both contrary to Gilbert et al. (1998). The general lack of significance of the regression of corridor length against species richness and species abundance could be explained by the

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opposing effects of the rescue effect (negative effect) and corridor habitat area (positive effect).

The block effect confounded spatial and temporal variation, since the blocks were sited in different physical locations and were set up and removed at different times. The highly significant block effects are to be expected, since there is much evidence for seasonal fluctuations in mite and Collembola communities (Mitchell 1977).

The lack of significant differences in the wetness among treatments suggests that the microclimates of the patches are reasonably similar. Consequently, if this result was common to the previous studies, it seems unlikely that their fragmentation results were due to differing microclimatic conditions of connected versus broken treatments.

The lack of significant differences in the densities of microarthropods in the various corridor types suggests that the corridors are equally attractive habitats for the microarthropods. It does not appear that the narrower and longer corridors contain proportionally fewer microarthropods, as one might expect. However, the microarthropod extraction efficiency of the Tullgren funnels may depend on the size of the moss sample, i.e. the proportion of extracted microarthropods in a sample of moss may be greater or less for a corridor compared to a patch.

If the movement of microarthropods between patches was significantly higher in the connected, short and wide corridors, we might expect to find a lower coefficient of variation in these treatments. Indeed we did find some evidence for this. However, generally, there was no significant difference in the coefficients of variation of microarthropod populations between corridor treatments (contrary to Forney and Gilpin 1989). This may question the movement assumption. Berthet (1964) measured the movement of Cryptostigmata mites in soil using radioactive tagging and observed the high rates of about two to four centimetres per day, but rates of movement may be different over rock surfaces and in moss.

Dispersal of Cryptostigmata mites may be due to seeking of food or favourable oviposition sites by gravid females (Norton 1994). Mite dispersal is probably restricted primarily to adults, since they are better equipped to deal with predation danger (Norton 1994) and desiccation (Mitchell 1977) than immatures. Relatively large epigeic Collembola are more efficient dispersers than edaphic species (Ojala and Huhta 2001). Ojala and Huhta (2001) found lower dispersal rates of Collembola (0.5–1 cm per week) than for Cryptostigmata mites (1–2 cm per week) in soil.

Hanski and Simberloff (1997) warn against assuming metapopulation dynamics in any system with patchiness at any spatial or temporal scale. They give the following definition of a metapopulation; "populations are spatially structured into assemblages of local breeding populations and migration among the local populations has some effect on local dynamics, including the possibility of population reestablishment following extinction". To test whether the moss/microarthropod system really does have discrete local breeding populations, it would be necessary to follow the movements of individual microarthropods in the moss patches. We could then see the extent to which the microarthropods stay in the moss patches, and the extent to which they migrate to other areas. Hanski and Simberloff (1997) define a Mainland-Island metapopulation as: "System of habitat patches (islands) located within dispersal distance from a very large habitat patch (mainland) where the local population never goes extinct". We may describe the microarthropod/moss system as a Mainland-island metapopulation. The moss patches are surrounded by a relatively inhospitable habitat (bare rock), but within dispersal distance from a very large habitat patch (surrounding moss).

In conclusion, there was no evidence that corridors between habitat patches slowed the rate of microarthropod species extinction relative to habitat patches without corridors. This contrasts with the results of Gilbert et al. (1998), Gonzalez et al. (1998) and Gonzalez and Chaneton (2002). In addition, there was no evidence that species richness and numbers of individuals per species were reduced for treatments with longer and narrower corridors. Surprisingly, there was some evidence that there were fewer species in the mainland treatment than in the other treatments, but this was probably due to differing microarthropod extraction efficiencies between the treatments.

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# Appendix: Microarthropod morphospecies descriptions

Morphospecies	Species identified	
	Cryptostigmata	
1	Ceratoppia bipilis (Peloppiidae = Ceratoppiidae) (Hermann)	
2	Chamobates borealis (Chamobatidae) (Trägårdh)	
	Chamobates cuspidatus (Chamobatidae) (Michael, 1884)	
	Minunthozetes pseudofusiger (Mycobatidae) (Schweizer, 1922)	
3	Phthiracarus longulus (Phthiracaridae) (C L Koch)	
4	Sphaerozetes piriformis (Sphaerozetes) (Nicolet)	
5	Tectocepheus sarekensis (Tectocepheidae) (Trägårdh, 1910)	
6	Eueremaeus (possibly oblongus) Eremaeidae (C L Koch)	
7	Quadroppia quadricarinata virginalis (Oppiidae) (Lions, 1982)	
8	Hermannia gibba (Hermanniidae) (C L Koch)	
9	Achipteria nitens (Achipteriidae) (Nicolet, 1855)	
10	Carabodes marginatus (Carabodidae) (Michael, 1884)	
	Carabodes labyrinthicus (Carabodidae) (Michael)	
11	Oribatula tibialis (Oribatulidae) (Nicolet, 1855)	
12	Dissorhinaornata (Oppiidae) (Oudemans)	
	Ramusella Ramusella cf. Assimilis (Oppiidae) (Mihelcic, 1950)	
	Suctobelba trigona (Suctobelbidae) (Michael)	
13	Camisia horrida (Camisiidae) (Hermann)	
14	Oribatella berlesei (Oribatellidae) (Michael)	
15	Porobelba spinosa (Damaeidae) (Sellnick, 1920)	
16	Caleremaeus monilipes (Caleremaeidae) (Michael)	
17	Euzetes globulus (Euzetidae) (Nicolet)	
18	Chamobates schuetzi (Chamobatidae) (Oudemans)	
19	Damaeus clavipes (Damaeidae) (Nicolet)	
	Damaeus Damaeus cf. Riparius (Damaeidae) (Nicolet, 1855)	
20	Xenillus tegeocranus (Xenillidae) (Michael)	
21	Carabodes willmanni (Carabodidae) (Bernini, 1975)	
22	Odontocepheus elongatus (Carabodidae) (Michael, 1879)	
23	Trichoribates trimaculatus (Ceratozetidae) (C L Koch)	
24	Phthiracarus nitens (Phthiracaridae) (C L Koch)	
25	Phthiracarus montanus (Phthiracaridae) (Perez-Iñigo)	
Plus eight unidentified morphospecies.		
	Mesostigmata	
1	Paragamasus integer (Parasitidae) (Bhattacharryya, 1963)	
	Paragamasus schweizeri (Parasitidae) (Bhattacharryya, 1963)	
2	Zercon zelawaiensis (Zerconidae) (Sellnick, 1944)	
3	Geholaspis longispinosus (Macrochelidae) (Kramer, 1876)	
	Geholaspis mandibularis (Macrochelidae) (Berlese, 1904)	
4	Paragamasus robustus (Parasitidae) (Oudemans, 1902)	
5	Pergamasus crassipes (Parasitidae) (Linnaeus, 1758)	
	Pergamasus longicornis (Parasitidae) (Berlese, 1906)	
	Pergamasus septentrionalis (Parasitidae) (Bhattacharyya, 1963)	
6	Cosmolaelaps claviger (Laelapidae) (Berlese, 1883)	
7	Uropoda (Cilliba subgenus) sp. (Uropodidae)	

	Prostigmata
Bdellidae (species unknown)	
Eupodidae (species unknown)	

Holoparasitus inornatus (Parasitidae)

Uropoda misella (Uropodidae)

Holoparasitus calcaratus (Parasitidae) (Koch, 1839)

Eupodidae (species unknown) Eupodidae (species unknown) Cryptognathidae (species unknown)

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1 2 3 Appendix (Continued)

Morphospecies

Species identified

Plus four unidentified morphospecies

	Collembola
1	Pseudoisotoma sensibilis (Isotomidae) (Tullberg)
2	Xenylla boerneri (Hypogastruridae) (Axelson)
3	Orchesella villosa (Entomobryidae) (Geoffroy)
	Tomocerus minor (Entomobryidae) (Lubbock)
4	Neanura muscorum (Hypogastruridae) (Templeton)
5	Entomobrya nivalis (Entomobryidae) (Linnaeus)
6	Dicyrtomina minuta (Sminthuridae) (O. Fabricius)
	Lepidocyrtus curvicollis (Sminthuridae) (Bourlet)

Plus six unidentified morphospecies