Experimentally fragmented communities are more aggregated

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Summary

1. I investigated the effect of habitat fragmentation on species richness, aggregation and community dominance and composition for predators and non-predators at two spatial scales. Two independent experiments were considered, both using a microecosystem of microarthropods inhabiting moss patches.

2. In the study at a larger spatial scale, species richness was lower in the more fragmented habitats, due possibly to the lack of a metapopulation ‘rescue effect’. In the smaller-scale study, species richness was again lower in the fragmented habitats, but did not depend on whether a connecting moss ‘corridor’ was complete or broken. Fragmentation affected predators more than non-predators in both studies.

3. The degree of aggregation both within and among habitat patches was greater in the fragmented species-poor communities, especially for predators. Theory suggests that lower migration in the fragmented communities may either (a) lead to greater aggregation and lower species richness simultaneously, or (b) greater aggregation, leading to increased dominance and hence lower species richness.

4. There was no clear association between community dominance and species richness.

5. Community composition was affected by fragmentation in both studies, but knowledge of trophic level and mite developmental stage was insufficient to predict these effects.

Key-words: dominance, extinction, metapopulations, microcosms, species richness.

Introduction

Levin (1992) has argued that ‘the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology’, and Crawley (1997) that ‘the most important differences that affect the interpretation of species richness are: (i) the relative abundance of the different species, (ii) the degree of aggregation of the species and (iii) the degree to which the spatial distributions of the species are correlated’. Species richness and relative abundance are well studied by ecologists, but much less is known about aggregation and its effects in a metacommunity. The widely recognized ‘species dominance’ relationship, based largely on empirical observation, is that species richness decreases with increasing species dominance, i.e. with an increase in unevenness in species abundances (Armesto & Pickett 1985; Crawley 1997). Furthermore, species richness depends greatly on the spatial distribution of species (Connell 1971; Crawley 1997; Ney-Nifle & Mangel 1999).

There is very little theory concerning the effects of dominance and spatial aggregation on species richness (He & Legendre 2002). Nevertheless, there are two alternative ways in which we can think of a causal connection between these factors in a metacommunity context. A recent approach (Hubbell 2001) suggests that the level of migration among local habitats (among other factors) in a metacommunity determines the degree of species richness, dominance and aggregation. If the migration rate is low, some species become highly abundant, and potentially monodominant. The lower the migration rate the lower the species richness (at the local scale) and the greater the community dominance and aggregation of individual species. Conversely, abundance and spatial distribution may
control species diversity (He & Legendre 2002), suggesting that in order to understand species diversity, we should look for processes that influence the abundance and spatial distribution of species. If a mechanism can make species abundances more even, or their spatial distribution more regular, this is likely to contribute to species coexistence. In fragmented habitats, reduced mobility should increase aggregation and probably competition for limited resources, leading to increased community dominance, and hence a reduction in species richness (Huston 1979). Models by He & Legendre (2002) predicted a decrease in species richness with increasing species dominance, and increasing species aggregation. If a species is aggregated, the occupancy should be less than under a random distribution, and the greater the aggregation, the lower the occupancy. Thus the same result (an association between low species richness, high dominance and high aggregation and vice versa) is predicted in a variety of different ways.

These predictions were supported by analysis of data from a tropical rain forest community (He & Legendre 2002) and from microarthropod aggregation (Berthet & Gerard 1965). Furthermore, connecting subpopulations has been observed to reduce the degree of aggregation of individual species both among patches (Forney & Gilpin 1989; Forbes & Chase 2002), due to migration smoothing differences in abundance, and within patches (Bjornstad, Andreassen & Ims 1998), where connectivity may change the nature of dispersal. A study cited widely as showing a negative relationship between dominance and species richness is that of Bazzaz (1975) on plants of old-field sites in Illinois. As succession increased species richness over 40 years, the slope of the rank–abundance curve decreased. However, this study does not demonstrate such a relationship because dominance is relative, not absolute, and Bazzaz did not adjust his curves for the increases in species richness.

Individuals of most species are seldom distributed randomly in space (Hartenstein 1961; Crawley 1997; He & Legendre 2002), but are either regular or aggregated, the latter being typically observed (Taylor 1961; Greig-Smith 1983). In practice, populations of all species are distributed patchily at some scale or another. Furthermore, there may be more than one scale of aggregation (Greig-Smith 1979; Usher & Booth 1986): for example, a smaller reproductive pattern (e.g. seeds germinating near a parent plant) and a larger scale of pattern dependent on environmental influence (e.g. microtopography). For highly mobile animals (e.g. birds), empty pockets on an island can be colonized rapidly: for such species, the entire island is effectively a single population. But for many groups of organisms, such as soil organisms, mobility even within modest-sized islands may be low. For these species, it makes sense to imagine all but very small islands as metapopulations of local populations coupled by limited dispersal (Holt 1992).

There are many methods of estimating the degree of spatial aggregation (see Bartlett 1975; Greig-Smith 1983). The negative binomial distribution has been found to fit many data particularly well (Hassell 1978; Taylor, Woiwood & Perry 1979), including soil microarthropods (Hartenstein 1961; Berthet & Gerard 1965), and also allows covariates to be included. The variance of the Poisson (random) and negative binomial (aggregated) distributions can be described by $\phi\mu$, where $\phi$ is the ‘scale parameter’ equal to 1 and $1 + (\mu/\theta)$, respectively. This demonstrates that the variance decreases as $\theta$ increases, and as $\theta \to \infty$, the negative binomial tends to the Poisson distribution. The negative binomial distribution may then be used both to adjust for overdispersion and to test for differences in the degree of aggregation expressed by $\theta$.

The negative binomial distribution used to describe spatial aggregation can arise in several different ways (Anscombe 1950; Waters & Hensen 1959). First, if the mean of a Poisson distribution varies randomly among samples, under certain conditions a negative binomial distribution results (Pielou 1969). The distribution of oribatid mites in the soil (Berthet & Gerard 1965) appears to arise according to this mechanism. Second, a negative binomial distribution is also produced if the presence of one individual affects the chance that another will also occur there (due perhaps to aggregation pheromones: Verhoef, Nagelkerke & Joosse 1977). In particular Taylor & Taylor (1977), developed a mechanism expressed by the so-called ‘delta’ function, based on a fitness-maximizing balance between density-dependent repulsion and attraction behaviour. It is not possible, therefore, to attribute a single cause to aggregation, because there are several mechanisms that may give rise to the negative binomial distribution. Random dispersal direction is generally assumed in metapopulation models, e.g. the Levins’ model (Levins 1969, 1970), but dispersing individuals of some species prefer to settle on habitat patches occupied by conspecifics (Smith & Peacock 1990). Ray & Gilpin (1991) showed that conspecific attraction lowered occupancy within a metapopulation at equilibrium, but Tyutyunov et al. (1996) suggested the existence of a growth-rate threshold, below which aggregation is favoured, and above which conspecific repulsion is advantageous.

I present the first study of the connection between habitat fragmentation, species richness and aggregation and community dominance by trophic level. Two experiments use the moss–microarthropod microecosystem: a new experiment using 4 cm$^2$ quadrats from 79 cm$^2$ patches (the ‘small-scale’ study) and a reanalysis of the data of Gilbert, Gonzalez & Evans-Freke (1998) and Gonzalez et al. (1998) (using undivided 79 cm$^2$ patches, the ‘large-scale’ study). In the large-scale study, species richness was greater in mainland than in fragmented moss patches after 6 months. Additionally, connecting patches of moss habitat with moss ‘corridors’ slowed the rate of microarthropod species dispersal (Holt 1992).
extinction, with predators benefiting more than non-predators. Broken corridors of the same total area did not have this effect. Gilbert et al. (1998) and Gonzalez et al. (1998) suggested that the corridors facilitated the dispersal of microarthropods between the habitat patches, maintaining species richness by the metapopulation ‘rescue effect’ (Brown & Kodric-Brown 1977), and that the scale of fragmentation and dispersal distance of the microarthropods were likely to be appropriate for the metapopulation concept to apply. Experimental tests of population dynamic processes have often used laboratory microcosms because of their tractability and short time-scales of change, e.g. Burkey (1997). The two most important hypotheses at each spatial scale were: (1) the degree of aggregation and (2) community dominance both increase with fragmentation. In addition (3) community composition is affected by fragmentation and (4) predators are less aggregated than non-predators.

Methods

STUDY SYSTEM

The moss–microarthropod microecosystem is particularly suitable for testing these predictions. It occurs naturally in the field in both continuous and fragmented states, thus experimental fragmentation merely reproduces patterns that occur naturally. It is practical for several reasons: it is relatively quick and cheap to set up several replicates of each treatment, and contains a large community of easily extracted microarthropods at different trophic levels. Furthermore, microarthropods are known to have an aggregated distribution in moss (see Discussion).

SMALL-SCALE STUDY: EXPERIMENTAL DESIGN

Methods for the large-scale study have already been published (Gilbert et al. 1998). At the start of the small-scale study, a metal template was used to cut nine replicate sets (blocks) of two treatments: complete- and broken-corridor (Fig. 1) from continuous moss (Isothecium myosuroides (Brid.) var. myosuroides) growing on nine large boulders in Snowdonia (UK, OS map ref. SK 625507), leaving bare rock in between. The third treatment was an area of mainland moss, left undisturbed until the end of the study (Fig. 1). It was assumed that any differences in microarthropod community composition between the two corridor treatments (of equal area) would be due only to a reduced migration rate between patches for the broken-corridor treatment. The bare rock was considered to be a relatively inhospitable environment for the majority of the moss taxa, restricting (but not eliminating) movement among patches. Treatments were at least 10 cm apart and at least 10 cm from the remaining ‘mainland’ of moss, to minimize migration across the rock. The moss was removed from the boulders after 6 months (as Gilbert et al. 1998; Gonzalez et al. 1998) either as whole patches, or as 2 × 2 cm ‘quadrats’ (Fig. 1) to investigate aggregation at this small spatial scale. Ideally all moss would be removed in quadrats, not as whole patches. However, this was not possible due to resource constraints.

When sampled, the moss was placed in Tullgren funnels for 12 h (by which time, approximately 95% of individuals were extracted) and all emerging animals were collected in an ethanol/glycerol mixture, and then sorted into morphospecies (using Krantz 1978) and identified with help from relevant experts (see Acknowledgements). Mite larvae were divided into just two groups: Cryptostigmata and Mesostigmata, as they are difficult to identify to species level (Roy Norton, personal communication). The Tullgren funnel technique is well known to be efficient at extracting adult but not juvenile mites (Roy Norton, personal communication). Nevertheless, mite larvae were counted because they constituted a large proportion of all mite individuals (9% of all Cryptostigmata and 29% of all Mesostigmata), and the extraction efficiency of larvae (and adults) will be roughly constant among samples because moss quadrats were approximately the same size. Samples were weighed both before and after being placed in the funnels to give the wet and dry moss weights.

In total, 35 000 microarthropods were counted and sorted into 53 morphospecies (usually genus level, corresponding closely to the species list of Hoyle & Gilbert 2004). Most microarthropods belonged to the Acari (47%...
Fragmented populations are more aggregated

of individuals) and Collembola (non-predatory, 62%). Within the Acari, 79% of individuals were Cryptostigmata (non-predatory), 2% Mesostigmata (predatory) and 19% Prostigmata (predatory). In the rest of this paper the term ‘species’ refers to the morphospecies.

SMALL-SCALE STUDY: SPECIES RICHNESS AND ABUNDANCE AND COMMUNITY DOMINANCE

For the small-scale data set, species richness at the scale of a complete patch was compared between the three treatments (Table 1, Test A) for the following variables: all microarthropods combined, all non-predatory adult mites, all predatory adult mites and all Collembola, modelled by quasipoisson errors in ‘R’ (Ihaka & Gentleman 1996; Crawley 2002), with the residual deviance reduced by including the nuisance covariate moss dry weight (to allow for differences in moss quadrat depth and unintended small differences in quadrat area) and the nuisance factors experimental block and ‘moss patch divided into quadrats/not divided’. For the patches divided into quadrats, species richness at the level of a patch was calculated by combining the constituent quadrats. Model simplification was performed by backward elimination from the maximal model to the minimum adequate model, and factor significance was assessed by a $\chi^2$ test of the increase in deviance after factor deletion. When treatment was significant, orthogonal contrasts tested for a difference between: (1) the complete- and broken-corridor patches; and (2) the mainland and the combination of the other two treatments. Abundances for the above four taxonomic groups were analysed similarly (Table 1, Test B), but this time using negative binomial errors (function ‘glm.nb’, library ‘MASS’) rather than Poisson, as the data were overdispersed. Mainland patches might have been wetter than the two corridor patches (and hence more species rich), as the latter would be more exposed to the drying effect of wind: moss wet weight was therefore compared between the three treatments, assuming normal errors, with moss dry weight as a covariate and experimental block as a factor in an analysis of covariance (Table 1, Test C).

Difference in dominance between the fragmentation treatments was assessed by analysis of variance, with treatment and block as factors, assuming normal errors (Table 1, Test D). Dominance was measured by the evenness index

$$\frac{1}{n} \sum_{i=1}^{n} \frac{1}{p_i}$$

(Simpson 1949),

where $n$ is the species richness and $p_i$ the proportion of all microarthropod individuals of species $i$ per moss patch. The test was applied separately to all microarthropod species, non-predatory and predatory mite species. The index allows for comparisons of dominance among communities of differing species richness.

An alternative test of dominance differences uses rank–abundance plots, which lose less information than the evenness index. Hence relative rank–abundance graphs, displaying abundances for all species, were plotted for the two data sets. Relative abundances were calculated by dividing the abundance of each species in a treatment by the total number of individuals in the treatment, and relative ranks by dividing the rank for each species by the species richness in that treatment. Given that the slope of rank–relative abundance graphs generally decrease with increasing species richness (Tokeshi 1999), it is preferable to plot relative rank against relative abundance. Thus relative rank–abundance graphs allow visual comparison of the dominance of communities varying in species richness by standardizing species richness (as in the variant of the Simpson evenness index, above) and abundance for each community: the steeper the graph, the more dominant the community. The shapes of the relative rank–abundance curves were compared by testing for differences in the relative-rank linear and quadratic terms between the three fragmentation treatments by analysis of covariance (Table 1, Test E). These statistics were computed separately on the rank–abundance plots of all microarthropod species, non-predatory and predatory mite species (to be consistent with the analysis of the Simpson index).

SMALL- AND LARGE-SCALE STUDIES: AGGREGATION

The main series of tests were on the differences in the degree of aggregation, as measured by $\theta$ (estimated by maximum likelihood) of the negative binomial distribution, among the treatments (Table 1, Tests F). For the small-scale study, two contrasts were performed: complete- vs. broken-corridor treatments; and complete- and broken-corridors treatments combined vs. mainland treatment. The variables tested are shown in Table 2a. Likelihood ratio tests were used to see whether two separate $\theta$-values were a better fit than one $\theta$-value common to both groups (B. Ripley, personal communication). Complete- vs. broken-corridor, and complete + broken-corridor vs. mainland contrasts were tested in this way, allowing for the treatment main effect and all treatment interactions as appropriate. Significance was assessed by $\chi^2$ with 1 d.f. In the second contrast, the two corridor treatments were combined because there was generally no significant difference in $\theta$ and individual abundance between these treatments (see Results). In all cases, the models included main effect and interaction terms for moss dry weight and experimental block to reduce the residual deviance.

The same procedure was followed for the large-scale data, except using three, not two tests (Table 1, Test G). The first test was exactly as before, but the second and third tests compared the broken-corridor and mainland
Table 1. Summary of the statistical tests

<table>
<thead>
<tr>
<th>Test ID</th>
<th>Scale</th>
<th>Response</th>
<th>Explanatory variable</th>
<th>Nuisance variables</th>
<th>Test statistic</th>
<th>Errors</th>
<th>Orthogonal contrasts</th>
<th>No. of observations</th>
</tr>
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<tbody>
<tr>
<td>A</td>
<td>Large</td>
<td>Species richness: All microarthropods Non-predatory mites Predatory mites Collembola</td>
<td>Treatment</td>
<td>Moss dry weight, block, patch divided/not divided</td>
<td>$\chi^2$</td>
<td>Quasi-poisson</td>
<td>Complete- vs. broken-corridor, mainland vs. above</td>
<td>44</td>
</tr>
<tr>
<td>B</td>
<td>Large</td>
<td>Species abundance: All microarthropods Non-predatory mites Predatory mites Collembola</td>
<td>Treatment</td>
<td>Moss dry weight, block, patch divided/not divided</td>
<td>$\chi^2$</td>
<td>Negative binomial</td>
<td>Complete- vs. broken-corridor, mainland vs. above</td>
<td>44</td>
</tr>
<tr>
<td>C</td>
<td>Large</td>
<td>Moss wet weight</td>
<td>Treatment</td>
<td>Moss dry weight, block</td>
<td>$F$</td>
<td>Normal</td>
<td>Complete- vs. broken-corridor, mainland vs. above</td>
<td>44</td>
</tr>
<tr>
<td>D</td>
<td>Large</td>
<td>Dominance</td>
<td>All microarthropods Non-predatory mites Predatory mites</td>
<td>Treatment</td>
<td>Block</td>
<td>Simpson evenness index</td>
<td>Complete-corridor vs. mainland, broken-corridor vs. above</td>
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</tr>
<tr>
<td>E</td>
<td>Large</td>
<td>Rank–abundance</td>
<td>All microarthropods Non-predatory mites Predatory mites</td>
<td>Treatment, rank</td>
<td>Block</td>
<td>$F$</td>
<td>Complete- vs. broken-corridor, mainland vs. above</td>
<td>170</td>
</tr>
<tr>
<td>F</td>
<td>Small</td>
<td>Aggregation parameter ($\theta$) of species abundance</td>
<td>Several (Table 2a)</td>
<td>Treatment</td>
<td>Moss dry weight, block</td>
<td>$\chi^2$</td>
<td>Negative binomial</td>
<td>Complete- vs. broken-corridor, mainland vs. above</td>
</tr>
<tr>
<td>G</td>
<td>Large</td>
<td>Aggregation parameter ($\theta$) of species abundance</td>
<td>Several (Table 2b)</td>
<td>Treatment</td>
<td>Block</td>
<td>$\chi^2$</td>
<td>Negative binomial</td>
<td>Complete- vs. broken-corridor, mainland vs. broken, mainland vs. complete</td>
</tr>
<tr>
<td>H</td>
<td>Small</td>
<td>PCs 1, 2 and 3 of species abundance</td>
<td>Several (Fig. 4)</td>
<td>Treatment, moss wetness</td>
<td>Moss dry weight, block, quadrat</td>
<td>$F$</td>
<td>Normal</td>
<td>Complete- vs. broken-corridor, mainland vs. above</td>
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<tr>
<td>I</td>
<td>Large</td>
<td>PCs 1, 2 and 3 of species abundance</td>
<td>Several</td>
<td>Treatment</td>
<td>Block</td>
<td>$F$</td>
<td>Normal</td>
<td>Complete-corridor vs. mainland, broken-corridor vs. above</td>
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</table>
Table 2. Maximum likelihood estimates of the aggregation parameter θ of the negative binomial distribution by fragmentation treatment and maximum-likelihood tests for differences in θ for the (a) small-scale and (b) large-scale studies. Lower values of θ correspond to greater aggregation. Trophic level and species composition data for the morphospecies in the large-scale study is unavailable. †Indicates comparison not significant after the Dunn–Šidák multiple comparison correction. §in (a) see morphospecies descriptions in Hoyle & Gilbert (2004), in (b) descriptions not available. ¶Comparisons are displayed graphically (Fig. 3)

(a) Small-scale study

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Morphospecies§</th>
<th>Developmental stage</th>
<th>Trophic level</th>
<th>Broken corridor θ (SE)</th>
<th>Complete corridor θ (SE)</th>
<th>Mainland θ (SE)</th>
<th>θ comparisons</th>
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<td></td>
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<td></td>
<td>B (SE)</td>
<td>C (SE)</td>
<td>M (SE)</td>
<td>Complete vs. broken corridor</td>
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<td>All</td>
<td>Adult</td>
<td>Both</td>
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<td>2·26 (0·28)</td>
<td>3·52 (0·44)</td>
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<td>Cryptostigmata</td>
<td>7</td>
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<td>1·74 (1·07)</td>
<td>0·94 (0·31)</td>
<td>3·22 (1·68)</td>
<td>2·19 (0·79)</td>
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</tr>
<tr>
<td></td>
<td>9</td>
<td></td>
<td>1·05 (0·24)</td>
<td>1·46 (0·41)</td>
<td>2·11 (0·31)</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>12†</td>
<td></td>
<td>0·88 (0·13)</td>
<td>0·78 (0·12)</td>
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<td>NS</td>
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<td></td>
<td>21</td>
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<td>0·96 (0·46)</td>
<td>2·03 (2·27)</td>
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<td>NS</td>
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<tr>
<td>Mesostigmata</td>
<td>1</td>
<td>Predatory</td>
<td>2·02 (6·18)</td>
<td>10·54 (9·98)</td>
<td>1·41 (1·69)</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td>16·54 (21·96)</td>
<td>4·64 (12·77)</td>
<td>12·04 (9·59)</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>Prostigmata</td>
<td>–</td>
<td></td>
<td>0·67 (0·11)</td>
<td>0·62 (0·12)</td>
<td>0·89 (0·17)</td>
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<tr>
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<td>Non-predatory</td>
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<td>4·88 (1·34)</td>
<td>4·24 (1·06)</td>
<td>C &gt; B*</td>
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<tr>
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<td>0·47 (0·31)</td>
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<tr>
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<tr>
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<td>1·71 (0·21)</td>
<td>2·01 (0·26)</td>
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(b) Large-scale study

<table>
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<th>Taxonomic group</th>
<th>Morphospecies§</th>
<th>Experimental treatment</th>
<th>θ comparisons</th>
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<td></td>
<td></td>
<td>Broken corridor θ (SE)</td>
<td>Complete vs. broken corridor</td>
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<tr>
<td></td>
<td></td>
<td>C (SE)</td>
<td>M (SE)</td>
</tr>
<tr>
<td>Microarthropods</td>
<td>All</td>
<td>19·80 (4·86)</td>
<td>NS</td>
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<td>Mite</td>
<td>A</td>
<td>10·41 (6·70)</td>
<td>NS</td>
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<td></td>
<td>B</td>
<td>3·22 (0·94)</td>
<td>NS</td>
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<tr>
<td></td>
<td>C</td>
<td>5·50 (1·59)</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>4·53 (2·21)</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>15·68 (10·57)</td>
<td>NS</td>
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<tr>
<td></td>
<td>F</td>
<td>3·17 (1·06)</td>
<td>NS</td>
</tr>
<tr>
<td>Collembola</td>
<td>A</td>
<td>6·00 (4·74)</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>12·39 (5·04)</td>
<td>NS</td>
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</table>
treatments and the complete-corridor and mainland treatments, respectively. A complete + broken-corridor combined vs. mainland treatment test was not performed, as Gilbert et al. (1998) and Gonzalez et al. (1998) have already shown that the microarthropod abundances of the two corridor treatments differed significantly. This would then tend to reduce θ in the combined broken- and complete-corridor model due to an inflated variance, and so lead to an incorrect comparison with θ from the mainland treatment. Dunn–Šidák corrections were applied to these non-orthogonal tests. The variables tested are shown in Table 2b.

**SMALL- AND LARGE-SCALE STUDIES: COMMUNITY COMPOSITION**

To investigate the correlations in the spatial distribution between the microarthropod species (see Crawley 1997) at the quadrat scale (4 cm²), a principal components analysis was performed (Table 1, Test H) on the correlation matrix (giving equal weight to each species) of the quadrat abundances of the most common species to reduce the data to its main uncorrelated axes of variation. The analysis was performed on the residuals of each variable after the main effects of the nuisance covariate moss dry weight and factors experimental block and quadrat position were removed. Any correlations between species abundances caused by these nuisance variables would be of no interest, and would mask the correlations of real interest (due to treatment and moss wetness). To avoid pseudoreplication, mean principal component scores per habitat patch were modelled in an analysis of variance by experimental treatment with orthogonal contrasts, assuming normal errors. A randomization test assessed whether the correlations between the variables were significantly greater than zero (and hence that the principal component axes do not represent random noise). For each of 10 000 simulations, the observations for each of the groups of species were shuffled randomly and independently, and proportions from the 10 000 simulations. Similarly, a principal component analysis was performed on the most common mite and Collembola species from the large-scale data set (Table 1, Test I).

**Results**

In the small-scale study, over all treatments and blocks, there was an average of 249 adult Cryptostigmata individuals of nine species per 10 cm-diameter patch, seven adult Mesostigmata individuals of three species, 60 Prostigmata individuals of two species, 495 Collembola individuals of two species, and three other microarthropod individuals of two species.

In the small-scale study, the average number of microarthropod species was significantly greater in the mainland compared to the two corridor treatments, but there was no difference between the broken- and complete-corridor treatments (Table 3). The same pattern was followed for the predatory mites, but not for the non-predatory mites, nor for the Collembola. Additionally, there was no significant difference in individual abundance for all species combined nor for Collembola nor for all predatory mites. However, there were more adult Cryptostigmata mites in the mainland, and within the predatory mites there were more Mesostigmata in the mainland. Moss wet weight did not vary significantly between the treatments (Table 3).

In the large-scale study, species richness was greater in the mainland and complete-corridor patches compared to the broken-corridor patch after 6 months (Gilbert et al. 1998; Gonzalez et al. 1998). Additionally, the mainland was more species-rich than the complete-corridor treatment. Predators benefited proportionally more from connectivity than non-predators.

| Table 3. Small-scale study comparisons of (a) species richness and moss wetness and (b) abundance, between: (1) complete- and broken-corridor patches (2) mainland and corridor patches. *** P < 0.005 |
|---|---|---|---|---|
| **Taxonomic group** | **All microarthropods combined** | **Non-predatory mites** | **Predatory mites** | **Collembola** | **Moss wetness** |
| (a) Species richness | | | | | |
| Complete-(CC) vs. broken-corridor (BC) | t_{52} = 0.31 NS | $\chi^2_{1} = 4.10$ NS | $t_{53} = 0.61$ NS | $\chi^2_{1} = 2.02$ NS | $F_{2,31} = 2.16$ NS |
| Mainland (M) vs. CC and BC | M > CC + BC (20.1 > 17.0) | M > CC + BC (3.5 > 2.0) | t_{53} = 4.52*** | |
| (b) Abundance | | | | | |
| Complete-(CC) vs. broken-corridor (BC) | $\chi^2_{1} = 3.25$ NS | z = 0.85 NS | $\chi^2_{1} = 1.19$ NS | $\chi^2_{1} = 0.35$ NS | |
| Mainland (M) vs. CC and BC | M > CC + BC (274 > 243) | z = 3.35*** | | | |
Fragmented populations are more aggregated.


Table 4. Tests of dominance based on rank–abundance curve fitting and on the Simpson evenness index. *P < 0·05, **P < 0·01, ***P < 0·005

<table>
<thead>
<tr>
<th>Study</th>
<th>Taxonomic group</th>
<th>Rank–abundance term</th>
<th>Linear</th>
<th>Quadratic</th>
<th>Simpson index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small-scale</td>
<td>All microarthropods</td>
<td>F_{2,163} = 5·04**</td>
<td>F_{2,163} = 0·28 NS</td>
<td>F_{2,41} = 1·20 NS</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mainland least dominant</td>
<td></td>
<td>F_{2,30} = 1·64 NS</td>
<td>F_{2,30} = 0·73 NS</td>
<td>F_{2,30} = 2·15 NS</td>
</tr>
<tr>
<td></td>
<td>Predatory mites</td>
<td>F_{2,35} = 0·94 NS</td>
<td>F_{2,35} = 0·98 NS</td>
<td>F_{2,35} = 7·74</td>
<td></td>
</tr>
<tr>
<td>Large-scale</td>
<td>All microarthropods</td>
<td>F_{2,138} = 2·01 NS</td>
<td>F_{2,138} = 3·22*</td>
<td>\text{Mainland most dominant}</td>
<td>\text{Broken-corridor least dominant}</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>t_{88} = 5·27***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 2. All microarthropods species rank abundance for the three fragmentation treatments from the (a) small-scale and (b) large-scale studies. In (a) there is some evidence that the mainland community is the least dominant, and in (b) the broken-corridor community is the most dominant (Table 4).

COMMUNITY DOMINANCE

The results of the dominance tests were mixed (Table 4). For all microarthropod species, in the small-scale study rank–abundance analysis suggested that the mainland was the least dominant community (Fig. 2), but the Simpson index did not confirm this. Conversely, in the large-scale study, rank–abundance analysis suggested that the broken-corridor treatment was the most dominant (Fig. 2), whereas the Simpson index indicated the reverse. There was no evidence for difference in dominance of the non-predatory mites, and only the Simpson index indicated that the mainland community was most dominant for the predatory mites.

AGGREGATION

In the small-scale study (Table 2a), \( \theta \) was often significantly greater (aggregation lower) for the mainland (higher species richness) than for the two corridor treatments (lower species richness), but rarely differed significantly between the two corridor treatments (similar species richness). In the large-scale study (Table 2b), \( \theta \) was often significantly greater (aggregation lower) in the complete-corridor and mainland treatments (higher species richness) compared to the broken-corridor treatment (lower species richness), but rarely differed between the mainland and complete-corridor treatments. Figure 3 shows abundance histograms by treatment for all microarthropods combined and for the most common mite species, for the small-scale study only. Assuming that \( \theta \) follows a normal distribution with means and standard errors given in Table 2a, the total predatory adult mites were more aggregated than the total non-predatory mites for the mainland (\( z = 2·06, P < 0·05 \)) and broken-corridor treatments (\( z = 1·97, P < 0·05 \)), but not for the complete-corridor treatment (\( z = 1·53, P > 0·05 \)). Total non-predatory mite adults were more aggregated than total non-predatory mite larvae for the complete-corridor treatment (\( z = 2·73, P < 0·01 \)), but not for either the broken-corridor (\( z = 1·67, P > 0·05 \)), nor for the mainland treatment (\( z = 1·25, P > 0·05 \)). Aggregation did not vary significantly between the predatory mite adults and larvae for any treatment.
Figure 4 gives the eigenvalues, proportion of the total variance and loadings for the first two principal components (PC) from the small-scale study. The randomization tests on the first two axes both gave significance values of less than 0.001, implying that these axes do not represent random noise. The loadings of PC1 are all of the same sign, suggesting that all species covaried (even after the effects of moss dry weight, quadrat position and statistical block were removed), although rather weakly, as the eigenvalues were low. The signs of the loadings of PC2 and PC3 (not shown) vary among the species, but there appears to be no general pattern in terms of trophic level. Experimental treatment explained a significant proportion of the scores for PC1 ($F_{2,24} = 11.4, P < 0.001$) and PC2 ($F_{2,24} = 3.80, P < 0.05$), but not for PC3 ($F_{2,24} = 0.68, P > 0.05$). The PC1 and PC2 orthogonal contrasts between the complete- and broken-corridor treatments were not significant ($t_{24} = 0.89, P > 0.05$ and $t_{24} = 1.00, P > 0.05$, respectively), but the contrasts between the two corridor treatments combined and the mainland treatment were significant ($PC1, t_{24} = 4.50, P < 0.0001$, with lower scores for the mainland: $PC2, t_{24} = -2.57, P < 0.05$, with higher scores for the mainland). The lower (more negative) PC1 scores for the mainland (Fig. 4) correspond to higher (positive) residuals for all species tested compared to the two corridor treatments, reiterating the previous finding that species abundances are generally greater for the mainland treatment. Mainland scores along PC2 were more extreme than the corridor treatments, more positive for species with positive loadings and more negative for species with negative loadings. This interesting result suggests that fragmentation affects species to differing degrees (Fig. 5).

The first principal component for the large-scale data also varied significantly by degree of fragmentation ($F_{2,64} = 81.2, P < 10^{-15}$), again reflecting differences in species abundances by treatment. The second axis also varied significantly by treatment ($F_{2,64} = 3.64, P < 0.05$), with no difference between the mainland and complete-corridor treatments ($t_{64} = 0.43, P > 0.05$), but a significant difference between these treatments combined and the broken-corridor treatment ($t_{64} = 2.10, P < 0.05$).
**Discussion**

The most important finding of this paper is that microarthropods in fragmented communities, which suffer reduced species richness, are more aggregated both within and among habitat patches (Fig. 5), in agreement with theoretical (Connell 1971; Crawley 1997; Ney-Nifle & Mangel 1999; Hubbell 2001; He & Legendre 2002) and empirical studies (Berthet & Gerard 1965; Forney & Gilpin 1989; Bjornstad et al. 1998; Forbes & Chase 2002; He & Legendre 2002). The results of the tests of dominance depended on the exact definition of dominance. Overall, there was no clear connection between community dominance and species richness for either predatory or non-predatory species, against theory (Huston 1979; Hubbell 2001; He & Legendre 2002), and contrary to other empirical studies (Bazzaz 1975; Armesto & Pickett 1985; Crawley 1997). Multivariate analysis of abundances in both experiments were affected significantly by fragmentation, implying that fragmentation does have an impact on the relative abundances of the species. We can imagine the 2 × 2 cm quadrats within a patch as separate subpopulations connected by migration in the sense of Holt (1992) and Hubbell (2001). Migration rates between these subpopulations are presumably not altered according to whether the patch is connected to the adjacent patch. However, the immigration rate into any given subpopulation is likely to be greater in connected patches, due to immigration from the connected patch (or from the surrounding moss in the case of the mainland treatment). Although an examination of the theory of Hubbell (2001) in relation to fragmentation has not yet been explored fully, in such cases Hubbell (2001) predicts a lower degree of aggregation and community dominance at the scale of the quadrat and the patch. Alternatively, causality may differ: changes in the level of aggregation and/or dominance may influence species richness (He & Legendre 2002). Regardless of the cause, the main message here is that as habitats are lost after fragmentation and species (especially predators) become more rare, they may also become more aggregated.

Potentially, the effect of fragmentation on aggregation could have been explained by differences in moss wetness: lower overall moss wetness could cause the moisture to aggregate in particularly sheltered microsites, leading to greater microarthropod aggregation. However, this explanation is not valid, because moss wetness did not vary by treatment (data available for the small-scale study only). Migration in the mainland and across the complete corridor in the large-scale study may act to even out differences in the populations in adjacent patches, hence accounting for lower microarthropod aggregation in these treatments at the spatial scale of a patch. However, attractive density-dependent migration (Smith & Peacock 1990) may reverse this effect. In the mainland, microarthropods are relatively free to move between microhabitats, thus smoothing their spatial distribution; but in fragmented patches movement is presumably restricted, perhaps resulting in greater aggregation.

Aggregation of microarthropods has been found before (Berthet & Gerard 1965; Usher 1971; Usher & Booth 1986), also at multiple scales of aggregation.

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**Fig. 5.** Summary of the most important results of this paper, displaying the relationships between fragmentation, species richness, aggregation, community dominance (measured by the Simpson index and rank–abundance curve fitting) and community composition (measured by principal component analysis). *P < 0.05, **P < 0.005 and †data are insufficient or unavailable. #see Gilbert et al. (1998) and Gonzalez et al. (1998).**
Little is known about microarthropod dispersal
would reduce or abolish any metapopulation effect. Microarthropod communities. A high rate of dispersal
could exceed more slowly than in the large-scale study. Community relaxation (species richness reduction over time
after fragmentation: Diamond 1972) was merely proceeding more slowly than in the large-scale study.

Dispersal across the bare rock would clearly influence the impact of moss habitat fragmentation on the
microarthropod communities. A high rate of dispersal would reduce or abolish any metapopulation effect.

The species richness of predators in the small-scale study was more affected by fragmentation than species
richness overall, as theory predicts (Diamond 1984; Schoener 1989). Although I did not find this in a previous experiment (Hoyle & Gilbert 2004), it was a feature of the large-scale study. Possibly because of the rescue effect (Brown & Kodric-Brown 1977), in the small-scale study the mainland moss was more species-rich than the islands, as others (Gonzalez & Chaneton 2002) and the large-scale study (Gilbert et al. 1998; Gonzalez et al. 1998) found, but unlike my own previous experiment (Hoyle & Gilbert 2004). The small-scale result cannot be due to moisture differences because this was included as a covariate (and was non-significant). As previously (Hoyle & Gilbert 2004), but unlike these other experiments, I found no difference in species richness between the complete- and broken-corridor treatments. Hoyle & Gilbert (2004) gave several possible explanations for this discrepancy (e.g. studies used different moss species, different locations, and ran at different times of the year) but did find some evidence for the beginnings of the beneficial effect of the corridor on species richness, suggesting that community relaxation (species richness reduction over time
after fragmentation: Diamond 1972) was merely proceeding more slowly than in the large-scale study.

Dispersal across the bare rock would clearly influence the impact of moss habitat fragmentation on the
microarthropod communities. A high rate of dispersal would reduce or abolish any metapopulation effect. Little is known about microarthropod dispersal (Norton 1994; Ojala & Huhta 2001), but it must at least be restricted in the microecosystem, because the unfragmented community was more species-rich in both studies. Dispersal of Cryptostigmata mites may be due to seeking of food or favourable oviposition sites by gravid females (Norton 1994) and is probably restricted primarily to adults, as they are better equipped to deal with predation danger and desiccation (Norton 1994) than immatures. Berthet (1964) observed movement of Cryptostigmata mites in soil
using radioactive tagging and estimated a rate of 2–4 cm day$^{-1}$. Ojala & Huhta (2001) found lower dispersal
rates of Collembola (0.5–10 cm week$^{-1}$) than for Cryptostigmata mites (1–20 cm week$^{-1}$) in soil.

Multivariate analysis at the smaller spatial scale revealed that predators and non-predators tended to
covary, albeit weakly (Usher & Booth 1986), implying no clear niche separation between these groups. Interestingly, multivariate analysis for both experiments indicated that the species-rich, less fragmented communities were subtly different from the species-poor, more fragmented communities. In the mainland community of the small-scale study the second principal component axis revealed two main groups, each consisting of five species. Species abundance within each group was positively correlated, whereas abundance between groups was negatively correlated. There was no such community separation in either the broken- or complete-corridor patches. Greater migration in the mainland community may have enabled the two groups to separate spatially. Both groups of species contained predatory and non-predatory microarthropods, hence the niche separation could not have been due simply to predator/non-predator interactions. Furthermore, we might expect the species in the two groups to be more aggregated in the mainland community, given the niche separation. However, this was not confirmed by the analysis of aggregation, as measured by the aggregation parameter of the negative binomial distribution. Indeed, some of the species were actually less aggregated. Further investigation into the cause of the partitioning is required.

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References

more aggregated


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