When corridors work: Insights from a microecosystem

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Evidence for a beneficial effect of corridors on species richness and abundance in habitat patches is mixed. Even in a single microecosystem of microarthropods living in moss patches connected by a moss corridor, experiments have had different results (positive and neutral). This paper attempts to provide an explanatory framework for understanding these results. I developed a stochastic individual-based model of the moss—microarthropod microecosystem. Some of the movement parameter values were estimated from two manipulation experiments. Assuming mortality independent of the season, and assuming the corridors merely increase migration rates between patches, only a very weak beneficial effect of corridors was possible in simulations. Incorporating a seasonal pattern to mortality caused some simulated populations to die out, which were then occasionally rescued by migrants from the adjacent patch. Corridors were slightly beneficial if there was little or no immigration from the surrounding matrix. In contrast, corridors were very beneficial in simulations that incorporated lower emigration to the matrix when a corridor was present, even for moderate levels of immigration from the matrix. Thus corridors may reduce the chance of species extinction in patches even when the lifespan of the individuals is long relative to the timescale in question. The beneficial effect in this case can act via two possible mechanisms: seasonal mortality imposing brief periods of high vulnerability to extinction, and the presence of a corridor reducing the rate of emigration to the matrix by encouraging movement along the corridor. Either one or both of these mechanisms may have operated in the study whereby corridors had a beneficial effect, but not in the study whereby corridors did not have a beneficial effect. This work demonstrates that corridor effectiveness is dependent on the species and landscape in question, and that it is important to understand the mechanisms by which corridors function.

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1. Introduction

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) by increasing animal movement rates between habitat patches (Saunders and Hobbs, 1991). However, corridors are controversial (Mann and Plummer, 1995).

Corridors may function by reducing the negative impacts of demographic and environmental stochasticity via the rescue effect (Brown and Kodric-Brown, 1977). Furthermore, they may increase the size of the effective gene pool, thereby reducing inbreeding depression. However, there has been no research on the impact of corridors on emigration from habitat patches (Hudgens and Haddad, 2003): they will be beneficial if they direct migrants through corridors. On the other hand, corridors may increase the chance of extinction by increasing...
genetic uniformity, and by synchronising population dynamics (Earn et al., 2000). Furthermore they may increase the incidence of disease, the movement of invasive species, and disturbance in general (Hess, 1994). Corridors may act as sinks (Amarasekare, 1998; Hudgens and Haddad, 2003) since the quality of the habitat may be poor due to the edge effect, and since individuals may wander unproductively in corridors.

Unfortunately therefore, it is difficult to generalise about the value of corridors (Debinski and Holt, 2000). Instead the effectiveness will probably be specific to the species and landscape in question. Other factors will include the scale of the system relative to the size and dispersal of the species (Berggren et al., 2002), patch isolation and the demographic parameters of the species both in and out of the habitat. The time-scale and nature of the major threat of local extinction (Hudgens and Haddad, 2003), such as sustained population decline or boom-bust cycles, will also be important. It is therefore important to understand the mechanisms by which corridors may be beneficial, perhaps in conjunction with a population model with estimates of rates of movement, birth and death. For example corridors may boost the patch-to-patch migration rate (Haddad, 1999; Tewksbury et al., 2002), perhaps by organisms following corridor edges (Levey et al., 2005), and corridors may increase the rate of immigration from the surrounding matrix by acting as drift-fences, where organisms are intercepted from the matrix and then directed into connected patches (Fried et al., 2005).

Studies of corridor effectiveness are either in the form of controlled experiments (e.g. Burkey, 1997; Schmiegelow et al., 1997; Gilbert et al., 1998; Gonzalez et al., 1998; Haddad, 1999; Collinge, 2000; Berggren et al., 2002; Forbes and Chase, 2002; Mabry and Barrett, 2002; Tewksbury et al., 2002; Hoyle and Gilbert, 2004), or correlational (e.g. Saunders and Hobbs, 1991; Mech and Hallett, 2001; Selonen and Hanski, 2003). Two reviews of the literature (Beier and Noss, 1998; Debinski and Holt, 2000) concluded that most studies support the utility of corridors, and further studies have agreed (e.g. Gilbert et al., 1998; Gonzalez et al., 1998; Mech and Hallett, 2001; Haddad et al., 2003). On the other hand, some studies suggest that corridors may have neutral or even negative effects on species persistence (Burkey, 1997; Collinge, 2000; Forbes and Chase, 2002; Hoyle and Gilbert, 2004), perhaps because dispersers act to synchronise the population dynamics (Burkey, 1997; Earn et al., 2000).

There are great logistic difficulties in designing replicated experiments to test whether corridors increase the rate of migration between habitat patches in the field (Inglis and Underwood, 1992). Hence, a microecosystem approach can be a very practical solution, although extrapolation to communities on a larger scale should be treated with care. The moss—microarthropod microecosystem is a rare example of a field-based microecosystem of wildlife corridors. A large community of microarthropods of different trophic levels live in a small patch of moss and are easily extracted for censusing. Furthermore, the effects of fragmentation on the microarthropod populations can occur in as little as 6 months (Gilbert et al., 1998; Gonzalez et al., 1998).

Gilbert et al. (1998) and Gonzalez et al. (1998) found that connecting patches of moss habitat with moss corridors for 6 months slowed the rate of microarthropod species extinction. Broken corridors of the same total area did not have this effect. The abundance of most species was higher in connected patches (Fig. 1a). Henceforth, I refer to this experiment as the “Positive Study” and the greater species richness and abundance in the complete—compared to the broken-corridor patches as the “corridor effect”. The mechanism behind the corridor effect was not investigated, but the authors suggested that 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. By contrast, Hoyle and Gilbert (2004) did not find...
the corridor effect (Fig. 1b) in a similar study. Henceforth, this experiment is referred to as the "neutral study". Again, the mechanism of corridor function was not investigated.

Here, I aim to account for these contradictory results. This paper is organised as follows. I introduce a mathematical population model (based on Renshaw, 1991) used to analyse the empirical data. The model assumes that a pair of populations are subject to density-dependent births and deaths, and are connected by migration across a corridor. Next I describe two manipulation experiments designed to estimate the movement parameters of the microarthropods. I then use the parameterized model to present two possible explanations for the corridor effect of the positive study, and to suggest why the effect was not found in the neutral study.

2. Materials and methods

2.1. Population model

The model chosen to describe the population dynamics of the microarthropods, based on Renshaw (1991), suits the data practically obtainable on the microecosystem and the questions being addressed in this paper. The model (coded in Visual Basic for Applications, Appendix A) is "structured individual-based": the future abundance of a single microarthropod species in each of two moss patches is simulated, assuming the following density-dependent processes: birth and death, migration between the two patches, emigration from the patches into the surrounding matrix, and immigration from the matrix into the patches. The deterministic form of the model is given by a pair of coupled non-linear differential equations, one for each patch:

\[
\frac{dN_i(t)}{dt} = \beta_i(t)N_i(t) - \delta_i(t)N_i(t) - \mu_i(t)N_i(t) + \mu_j(t)N_j(t) + i_N(t) - e_N(t)N_i(t)
\]

where \(N_i(t)\) is the abundance of a microarthropod species in one patch at time \(t\) and \(N_j(t)\) is the abundance in the other patch. In patch \(i\):

- birth rate: \(\beta_i(t) = \beta_0 - \beta_1N_i(t)\).
- death rate: \(\delta_i(t) = \delta_0 + \delta_1N_i(t)\).
- between-patch migration rate: \(\mu_i(t) = \mu_0 + \mu_1N_i(t)\).
- emigration rate to matrix: \(e_N(t) = e_0 + e_1N_i(t)\).
- immigration rate from matrix: \(i_N(t) = i_0 - i_1N_i(t)\).

where \(\beta_0, \beta_1, \delta_0, \delta_1, \mu_0, \mu_1, e_0, e_1, i_0, i_1\) are constants assumed equal for both patches. It was assumed that \(\mu_0\) and \(\mu_1\) would be greater when the patches were connected with a moss corridor. For biological reasonableness, all parameters were subject to a minimum of zero. The intrinsic capacity of increase is \(r = \beta_0 - \delta_0\).

A Poisson process for the stochastic version of the deterministic equations is assumed (Renshaw, 1991). The time to the next event for each of the ten processes in Eq. (2) is distributed exponentially. For random numbers \(0 < U_j < 1, j = 1, \ldots, 10\), and patches \(i = 1, 2\) (Renshaw, 1991):

\[ -\frac{\ln(U_i)}{\beta_i(t)N_i(t)} \] gives the time to the next birth.
\[ -\frac{\ln(U_i,2)}{\delta_i(t)N_i(t)} \] time to the next death.
\[ -\frac{\ln(U_i,4)}{\mu_i(t)N_i(t)} \] time to the next migration from patch \(i\).
\[ -\frac{\ln(U_i,6)}{e_i(t)N_i(t)} \] time to the next emigration.
\[ -\frac{\ln(U_i,8)}{i_i(t)} \] time to the next immigration.

The next simulated event is the one corresponding to the minimum of these times. The populations in the two patches are then recomputed—either increasing or decreasing by one unit, or remaining unchanged. The algorithm is then repeated: 10 random numbers are generated, the time to the next event is computed, and the populations adjusted, and so on until the maximum time of 6 months (the length of the positive and neutral studies) is reached.

The model assumes the following. First, the time to the next event is exponentially distributed. The death process imposes the simplifying assumption that the mortality rate is independent of age. The duration of migration between patches is assumed to be zero (tested in the second manipulation experiment). Since inter-specific competition data were unavailable, the model is of a single species (see Section 4). Species interactions are allowed for only indirectly by the existence of an equilibrium abundance for each species. Microarthropods are assumed to be reproductively active immediately after birth.

2.2. Microarthropod movement rates

There is very little literature concerning microarthropod movement rates (Norton, 1994). 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, since they are better equipped to deal with predation danger and desiccation (Norton, 1994) than immatures. Berthet (1964) measured movement of Cryptostigmata mites in soil of two to four centimetres per day. Ojala and Huhta (2001) found lower dispersal rates of Collomella (0.5–10 cm per week) than for Cryptostigmata mites (1–20 cm per week) in soil. Unfortunately, it is not possible to observe the microarthropods move, since they are usually buried deep in the moss. Rates of microarthropod migration across the corridor and immigration across the bare rock were obtained indirectly from the first and second manipulation experiments, respectively.

2.2.1. First manipulation experiment

The first manipulation experiment was designed (1) to test whether the rate of migration (\(\mu_0, \mu_1\)) between patches is greater with a connecting corridor than across bare rock, (2) to estimate the density-independent corridor migration rate (\(\mu_0\)) and (3) test for density-dependent corridor migration (\(\mu_1\)).
Each of six replicates consisted of four moss patches (mostly mixtures of *Homalothecium sericeum*, *Brachythecium rutabulum* and *Hylocomium lacunosum* var. *lacunosum* or *Isothecium myosuroides* (Brid.) *var. myosuroides*, as in the neutral study) and one moss corridor (Fig. 2). The moss was collected from the site of the neutral study (see Hoyle and Gilbert, 2004). One patch contained microarthropods, while the remaining patches were cleared of the fauna, by being placed in Tullgren funnels for 48 h. The moss patches were then chosen at random and placed in the arrangement of Fig. 2 in the grounds of the University of Nottingham, and covered with netting to retain moisture. After 1 month, in July 2001, the moss (which was still alive) was removed and placed in Tullgren funnels for 48 h. (which preliminary experiments had shown extracts 98% of all individuals; Hoyle, unpublished data). All emerging microarthropods were collecting in an ethanol/glycerol mixture, and then sorted into the same morphospecies (with advice from experts, see Acknowledgements) as in the neutral study. The microarthropods are commonly found in moss, and vary in size from approximately 0.1–1 mm.

The first test examined whether the abundance of each species varied among the cleared patches. Generalised linear models with Poisson errors corrected for overdispersion, with statistical block as a factor, were performed in “R” (Ihaka and Gentleman, 1996). Two non-orthogonal contrasts were used: (1) between patches C and A, to test whether there was greater movement across the corridor than across the gravel; (2) between patches A and D, to test for migration across the gravel. The second test, for density-dependent migration, proceeded as follows. It was assumed that microarthropods in all patches had arrived from the surrounding environment. Additionally, the fauna in patch A (Fig. 2) had migrated across the gravel from patch B, fauna in patch C had migrated across the corridor from patch B, and fauna in patch B were those originally present, minus those that had emigrated to patches A and C. As a first approximation, double-migrations and mortality over the relatively short duration of the experiment were ignored. The approximate migration rate per species across the corridor over 1 month was then calculated, averaged over all experimental blocks, as

\[
\frac{C_{t=1} - D_{t=1}}{B_{t=0.5}}
\]

where \(A_{t=1}, B_{t=1}, C_{t=1}, D_{t=1}\) are the average abundances of any given species in patches A, B, C and D, respectively, at the end of the 1 month experiment, and

\[
B_{t=0.5} = 0.5 (B_{t=1} + B_{t=0}) \quad \text{and} \quad B_{t=0} = (B_{t=1} - D_{t=1}) + (C_{t=1} - D_{t=1}) + (A_{t=1} - D_{t=1})
\]

are the estimated abundances in patch B half way through and at the start of the experiment, respectively.

If migration is density-dependent then:

\[
\frac{dC(t)}{dt} \propto B(t)(1 + bB(t)).
\]

where \(b\) is a constant.

Hence, assuming little change in B over time, \(C_{t=1}\) is approximately proportional to \(B_{t=0.5} (1 + bB_{t=0.5})\), a quadratic in \(B_{t=0.5}\). Therefore, to test for density-dependent migration, \(C_{t=1}\) was modelled as a quadratic function of \(B_{t=0.5}\). Poisson errors were assumed, again corrected for overdispersion.

The most important finding was that there were more individuals in the connected patch (C) compared to the disconnected patch (A) (Table 1) (binomial test: \(P < 0.0005\)). This suggests that microarthropods move more readily across the moss corridor than across the gravel, i.e. that \(\mu_0\) is greater when a corridor is present. Significance may not have been achieved for some species due to a lack of statistical power. The number of individuals in patch A was sometimes higher and sometimes lower than the number in the completely isolated patch (D) (Table 1), but with no overall trend, suggesting that the gravel was a significant barrier to movement.

Surprisingly, there was only occasionally evidence that the abundance in patch C depended on the abundance in the microarthropod-rich patch (B) (Table 1). Nonetheless, in common with much theory (e.g. Renshaw, 1991), migration was expressed as a rate per individual. The density-independent migration rate (\(\mu_0\)) was estimated to lie in the range 0.05–0.21 for Cryptostigmata mites (Table 2). There was little evidence for density-dependent migration (\(\mu_1\)), hence \(\mu_1\) was set to zero.

### 2.2.2. Second manipulation experiment

The second manipulation experiment was designed to estimate immigration rates from the surrounding environment, and migration rates across corridors of various lengths and widths at three times of the year, at the same site as the neutral study in the peak district, and in the same valley as the positive study.

#### 2.2.2.1. Methods

For the first part (from March to April 2002), within each of nine blocks, eleven treatments (Fig. 3, Table 3) were randomly allocated on the top of the dry-stone wall of the neutral study in the peak district, in the same valley as used in the positive study. The source moss was cut from the mainland moss of the same dry-stone wall, and was randomly allocated...
Table 1 – Estimated migration rates and tests for density-dependent and -independent corridor migration for the most common species and taxonomic groups in the first manipulation experiment

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Morphospeciesa</th>
<th>Corridor migration rate ($μ/0$)</th>
<th>Difference in abundance between patches</th>
<th>Abundance in $C ∝ B^2$</th>
<th>Density-dependence: abundance in $C ∝ B^2$?</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>C &gt; A (one-tailed)</td>
<td></td>
<td>F₁,₄ = 0.36, n.s.</td>
</tr>
<tr>
<td>Cryptostigmata mites</td>
<td>All</td>
<td>0.13</td>
<td>$t_{10} = +6.36^{**} (A &gt; B)$</td>
<td>$t_{10} = +1.38, n.s.$</td>
<td>F₁,₄ = 6.14, n.s.</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.12</td>
<td>$t_{10} = +0.35, n.s.$</td>
<td>$t_{10} = 0.00, n.s.$</td>
<td>F₁,₄ = 0.06, n.s.</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>0.13</td>
<td>$t_{10} = +2.94^* (A &gt; B)$</td>
<td>$t_{10} = +0.87, n.s.$</td>
<td>F₁,₄ = 0.13, n.s.</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>0.11</td>
<td>$t_{10} = +1.71, n.s.$</td>
<td>$t_{10} = −1.35, n.s.$</td>
<td>F₁,₄ = 0.03, n.s.</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>0.14</td>
<td>$t_{10} = +6.20^{***} (A &gt; B)$</td>
<td>$t_{10} = +2.44^* (B &gt; C)$</td>
<td>F₁,₄ = 1.00, n.s.</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.21</td>
<td>$t_{10} = +3.14^* (A &gt; B)$</td>
<td>$t_{10} = +2.15, n.s.$</td>
<td>F₁,₄ = 0.05, n.s.</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>0.13</td>
<td>$t_{10} = +2.10^* (A &gt; B)$</td>
<td>$t_{10} = −1.93, n.s.$</td>
<td>F₁,₄ = 0.05, n.s.</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>0.05</td>
<td>$t_{10} = +0.78, n.s.$</td>
<td>$t_{10} = +0.00, n.s.$</td>
<td>F₁,₄ = 0.05, n.s.</td>
</tr>
<tr>
<td>Mesostigmata mites</td>
<td>All</td>
<td>0.11</td>
<td>$t_{10} = +1.32, n.s.$</td>
<td>$t_{10} = −0.39, n.s.$</td>
<td>F₁,₄ = 0.44, n.s.</td>
</tr>
<tr>
<td>Prostigmata mites</td>
<td>All</td>
<td>0.50</td>
<td>$t_{10} = +1.72, n.s.$</td>
<td>$t_{10} = −1.53, n.s.$</td>
<td>F₁,₄ = 1.73, n.s.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F₁,₄ = 0.05, n.s.</td>
<td>F₁,₃ = 553^{***} (negative density-dependence)</td>
</tr>
<tr>
<td>Collembola</td>
<td>All</td>
<td>0.64</td>
<td>$t_{10} = +1.06, n.s.$</td>
<td>$t_{10} = −5.57^{***} (C &gt; B)$</td>
<td>F₁,₄ = 0.72, n.s.</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.35</td>
<td>$t_{10} = +0.08, n.s.$</td>
<td>$t_{10} = −4.68^{***} (C &gt; B)$</td>
<td>F₁,₄ = 7.94^*</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.07</td>
<td>$t_{10} = +2.30^* (A &gt; B)$</td>
<td>$t_{10} = +1.50, n.s.$</td>
<td>F₁,₄ = 0.21, n.s.</td>
</tr>
</tbody>
</table>

The critical P-value was 0.025 after the Dunn–Sidak correction for non-orthogonal tests.

- Morphospecies descriptions are given in Appendix A.
- *P < 0.05.
- **P < 0.01.
- ***P < 0.005.
Table 2 - Model parameters

<table>
<thead>
<tr>
<th>Purpose of simulation</th>
<th>Initial population</th>
<th>Parameter</th>
<th>( \beta_0 )</th>
<th>( \beta_1 )</th>
<th>( \delta_0 )</th>
<th>( \delta_1 )</th>
<th>( \epsilon_0 )</th>
<th>( \epsilon_1 )</th>
<th>( \mu_0 )</th>
<th>( \mu_1 )</th>
<th>( A )</th>
<th>( \Omega )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Best estimate</td>
<td>42</td>
<td>0.167</td>
<td>0.002</td>
<td>0.042</td>
<td>0.001</td>
<td>29</td>
<td>0.69</td>
<td>0</td>
<td>0</td>
<td>0.14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Seasonal mortality</td>
<td>13</td>
<td>0.448</td>
<td>0.005</td>
<td>0.018</td>
<td>0.005</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>800</td>
</tr>
<tr>
<td>Variable emigration rates</td>
<td>42</td>
<td>0.167</td>
<td>0.002</td>
<td>0.042</td>
<td>0.001</td>
<td>0–29</td>
<td>0–0.69</td>
<td>0</td>
<td>0</td>
<td>0–1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Parameters are described in Section 2.

to the treatments. The moss was mostly *H. sericeum*, *B. rutabulum* and *H. lacunosum var. lacunosum* or *I. myosuroides* (*Brid.* var. *myosuroides*, as in the neutral study and the first manipulation experiment). The first treatment consisted of a single circular patch of diameter 10 cm, which had previously been cleared of microarthropods by the method described previously. All other treatments consisted of two circular patches of diameter 10 cm, with one microarthropod-rich and one cleared patch. A corridor was either absent, or present: when present, the corridor length varied from 0 to 7 cm, and the width from 1.5 to 2.5 cm, and was either microarthropod-rich or cleared. All moss was stuck to the bare rock using glue. A preliminary experiment established that the glue did not significantly reduce microarthropod immigration into the cleared moss (**F**1,12 = 0.15, P > 0.05). Treatments were at least 10 cm apart and at least 10 cm from the remaining "mainland" of moss (as the positive and neutral studies).

The second and third parts also lasted 1 month (June to July 2002 and September to October 2002, respectively). They consisted of just two treatments (Table 3): one isolated cleared patch, and one cleared patch connected to a microarthropod-rich patch by a microarthropod-rich corridor of length 7 cm and width 1.5 cm (treatments 1 and 6 of the first part).

Table 3 - Treatments of the second manipulation experiment

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Corridor length (cm)</th>
<th>Corridor width (cm)</th>
<th>Corridor cleared of microarthropods/not cleared?</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st part</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>One cleared patch</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>0.0</td>
<td>–</td>
<td>No corridor, patches separated by 7 cm</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>1.5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>1.5</td>
<td>Not cleared</td>
<td>–</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>1.5</td>
<td>Cleared</td>
<td>–</td>
</tr>
<tr>
<td>6</td>
<td>7</td>
<td>1.5</td>
<td>Not cleared</td>
<td>–</td>
</tr>
<tr>
<td>7</td>
<td>7</td>
<td>1.5</td>
<td>Cleared</td>
<td>–</td>
</tr>
<tr>
<td>8</td>
<td>7</td>
<td>1.5</td>
<td>Not cleared</td>
<td>Left for 2 months</td>
</tr>
<tr>
<td>9</td>
<td>7</td>
<td>1.5</td>
<td>Not cleared</td>
<td>Left for second month only</td>
</tr>
<tr>
<td>10</td>
<td>7</td>
<td>2.5</td>
<td>Not cleared</td>
<td>–</td>
</tr>
<tr>
<td>11</td>
<td>7</td>
<td>2.5</td>
<td>Cleared</td>
<td>–</td>
</tr>
<tr>
<td>2nd part</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>One cleared patch</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>1.5</td>
<td>Not cleared</td>
<td>–</td>
</tr>
<tr>
<td>3rd part</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>One cleared patch</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>1.5</td>
<td>Not cleared</td>
<td>–</td>
</tr>
</tbody>
</table>

Fig. 3 gives a pictorial representation of the treatments.
The moss species were the same as those in the first manipulation experiment and in the neutral study. All moss patches were removed from the dry-stone wall after 1 month (as the first manipulation experiment) for analysis, except for treatment 8, which was removed after 2 months. The microarthropods were extracted from the moss and sorted into morphospecies as before. The moss was weighed after being placed in the funnels to give the moss dry weight.

All tests were performed on the abundance of all microarthropods, all non-predatory mites, all predatory mites, all Collembola, and the fourteen most common microarthropod species. Treatment and experimental block were implemented as statistical factors and the moss dry weight was a covariate (to correct for differences in patch size), assuming Poisson errors corrected for overdispersion.

The following hypotheses were tested for the first part:

1. Connected patches contain more individuals than disconnected patches due to migration across the corridor: tested by an a priori contrast between treatments 1 and 2 and treatments 3–11.
2. Patches connected by a microarthropod-rich corridor contain more individuals than patches connected by a cleared corridor of the same dimensions due to individuals initially in the corridor migrating across into the cleared patch: treatment 6 versus 7.
3. As 2 for corridors of length 3 cm, width 1.5 cm: treatment 4 versus 5.
4. As 2 for corridors of length 7 cm, width 2.5 cm: treatment 10 versus 11.
5. Patches left for 2 months contain more individuals than those left for just 1 month: treatment 8 versus 9.
6. The narrower the microarthropod-rich corridor the lower the abundance in the patch, due to lower migration rates across the narrower corridor: treatment 6 versus 10.
7. As 6 for cleared corridors of the same dimensions: treatment 7 versus 11.
8. The shorter the cleared corridor, the higher the abundance in the patch, due to higher migration rates across the shorter corridor: treatment 5 versus 7.
9. The greater the corridor length, the lower the abundance in the cleared patch, due to lower migration rates across the longer corridors: regression of treatments 3, 4 and 6.

The Dunn–Sidak correction on these nine non-orthogonal tests gave a critical P-value of 1 – (1 – 0.05)^(9/9) = 0.0057.

Next, the abundance of the same species and groups of species were compared between the two treatments: (1) one cleared isolated patch (treatment 1) and (2) a cleared patch connected to a microarthropod-rich patch by a microarthropod-rich corridor of length 7 cm, width 1.5 cm (treatment 6) for all three parts combined.

2.2.2.2. Results. For both manipulation experiments combined, 38,000 individual microarthropods were counted and sorted into morphospecies (usually genus level, see Appendix A) and a further 15,000 individuals estimated. Most microarthropods belonged to the Acari (69% of individuals, only adults counted) and Collembola (non-predatory, 31%). Within the Acari, 89% of individuals were Cryptostigmata (non-predatory), 1% Mesostigmata (predatory) and 10% Prostigmata (predatory). There were 36 mite morphospecies, 8 Collombula morphospecies and 10 other morphospecies (mostly beetles, spiders, centipedes, millipedes and pseudoscorpions).

At the end of the second manipulation experiment, per moss patch cleared at the start, there were an average of 169 adult Cryptostigmata mites of 7 species, 6 adult Mesostigmata mites of 2 species, 23 Prostigmata mites, 84 Collombula of 3 species, and 3 other microarthropods.

For the tests on the first part of the experiment, none of the hypotheses were accepted for all microarthropod individuals combined (Fig. 3). None of the species or groups of species supported Hypotheses 2, 3 nor 4, which allows us to accept the modelling assumption of instantaneous migration. Additionally, Hypotheses 7 and 8 were never accepted. Only one species (Cryptostigmata morphospecies 5: Appendix A) supported the hypothesis of more individuals in the cleared patch after 2 months compared to 1 month (t98 = 3.20, P < 0.002); one species (Cryptostigmata morphospecies 5 again) supported the hypothesis of more individuals in the cleared patch connected by the wider corridor (t98 = 3.01, P < 0.004); one species (Cryptostigmata morphospecies 8) was actually less abundant in the patches connected versus disconnected from microarthropod-rich patches (t87 = 4.11, P < 0.0001), against expectation; and one non-predatory mite species (Cryptostigmata morphospecies 2), one predatory mite species (Prostigmata morphospecies 2), all predator individuals combined and one Collombula species (morphospecies 1) were more abundant in the cleared patch with increasing corridor length (F1,23 = 9.94, P < 0.005, F1,24 = 16.21, P < 0.0005 and F1,24 = 14.59, P < 0.001, respectively), again against expectation.

There was no significant difference in abundance of any species or group of species between the isolated island and the patch connected by a corridor over the three times of year, except for one predatory species (Prostigmata morphospecies 2) where there were more individuals in the connected than in the isolated patch (F1,47 = 5.96, P < 0.05), and for one non-predatory species (Cryptostigmata morphospecies 8) where there were fewer individuals (F1,47 = 10.00, P < 0.005) with and against expectation, respectively, Fig. 4. In most cases, abundance varied significantly by season in agreement with Norton (1994).

Immigration from the surroundings into a single cleared patch is high: the best estimate of the rate of immigration is 280 microarthropods per month, 164 non-predatory mites, 22 predatory mites, 91 Collombula and 3 other microarthropods. The immigration rate was approximately 29 mites per month (280 microarthropods per month, 164 non-predatory mites, 22 predatory mites, 91 Collombula and 3 other microarthropods). The immigration rate was approximately 29 mites per month (1994).

Demographic parameters were taken from the literature. Most studies of microarthropod longevity are laboratory-based—there are very few field data (Norton, 1994). However, the non-predatory Cryptostigmata probably live surprisingly...
Fig. 4 – Results of all three parts of the second manipulation experiment. There was a significant difference in the logarithm of the abundance of all microarthropods in the cleared patches (open circles) by time of year ($F_{2,46} = 12.44$, $P < 0.00005$) but not by experimental treatment ($F_{1,46} = 0.04$, $P > 0.05$). Error bars show ±1 S.E. Table 3 gives a full description of the treatments.

Table 4 – Tests for seasonality in microarthropod abundance

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Mean abundance in mainland</th>
<th>Significant difference in abundances?</th>
<th>Seasonal/not seasonal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 months (start)</td>
<td>3 months</td>
<td>6 months (end)</td>
</tr>
<tr>
<td>(a) Positive study</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All microarthropods</td>
<td>132</td>
<td>240</td>
<td>298</td>
</tr>
<tr>
<td>All mites</td>
<td>101</td>
<td>195</td>
<td>255</td>
</tr>
<tr>
<td>Mite A</td>
<td>24</td>
<td>33</td>
<td>49</td>
</tr>
<tr>
<td>Mite B</td>
<td>14</td>
<td>29</td>
<td>42</td>
</tr>
<tr>
<td>Mite C</td>
<td>3</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td>Mite D</td>
<td>8</td>
<td>9</td>
<td>14</td>
</tr>
<tr>
<td>All Collembola</td>
<td>29</td>
<td>37</td>
<td>39</td>
</tr>
<tr>
<td>(b) Neutral study</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptostigmata mites</td>
<td>12</td>
<td>262</td>
<td>142</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td>5</td>
<td>$F_{1,43} = 3.12$ n.s.</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>11</td>
<td>$F_{1,43} = 0.02$ n.s.</td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>12</td>
<td>$F_{1,43} = 0.13$ n.s.</td>
</tr>
<tr>
<td>5</td>
<td>134</td>
<td>104</td>
<td>$F_{1,43} = 1.97$ n.s.</td>
</tr>
<tr>
<td>8</td>
<td>22</td>
<td>20</td>
<td>$F_{1,43} = 0.02$ n.s.</td>
</tr>
<tr>
<td>9</td>
<td>74</td>
<td>103</td>
<td>$F_{1,43} = 1.26$ n.s.</td>
</tr>
<tr>
<td>All Collembola</td>
<td>All</td>
<td>328</td>
<td>240</td>
</tr>
</tbody>
</table>

Abundance of the most common mite species and all Collembola combined in the mainland moss in the (a) positive study at the start, intermediate point and end of the experiment and in the (b) neutral study at the start and end of the experiment only.

*a* Species descriptions are not available.

*b* See Appendix A for morphospecies descriptions.

*$P < 0.05$.*

***$P < 0.0005$.***

long in the field—from several months to 2 years (Norton, 1994). Hartenstein (1962) estimated the generation time of the predatory Mesostigmata mite *Pergamasus crassipes* (Mesostigmata morphospecies 5, Appendix A) as about 2–3 months. Some Collembola species have one, and others more than one generation per year (Hopkin, 1997). Assuming Cryptostigmata mites live 12 months in the field at the equilibrium abundance ($K$), then $\delta(K) = 1/12$, since the mean of the exponential distribution is the inverse of the rate parameter. We are forced to estimate the density-dependent mortality rates, given the lack of relevant literature. Assuming the rate at zero abundance is half that at the equilibrium abundance, then $\delta(0) = 1/24$. Solving these simultaneous equations, and assuming an equilibrium abundance of 42 given by the average abundance of mite B in the mainland in the Positive Study, then $\delta_0 = 0.042$ and $\delta_1 = 0.001$. By definition, the birth and death rates are equal at the equilibrium abundance, hence $\mu(K) = \delta(K) = 1/12$. If we similarly assume that the birth rate is twice as great at zero as at the equilibrium abundance, then $\mu(0) = 2/12$. Hence $\mu_0 = 0.167$ and $\mu_1 = 0.002$.

2.4. Simulations

2.4.1. Best estimate parameters

One thousand simulations were performed on the population dynamics of mite B using the best estimate parameters (Table 2), in the two moss patches over 6 months. Given that
there is no independent measure of the emigration rate, $\varepsilon_0$ and $\varepsilon_1$ were initially set to zero. For simplicity, both patches were assumed to be at the equilibrium abundance of 42 at the start of the experiment.

### 2.4.2. Seasonal mortality

Microarthropod populations have often been observed to fluctuate seasonally (Luxton, 1981). There was strong evidence of seasonal variation in mite abundance in the positive but not in the neutral study, and no evidence for seasonal variation in abundance of Collembola in either study (Table 4).

Given the seasonality of mite abundance in the positive study, seasonal mortality rates were assumed (subject to a minimum of zero):

$$\delta^N(t) = \delta_0 \left(1 + A \sin \left(\frac{t\pi}{6} + \Omega\right)\right) + \delta_0 N_i(t).$$  

The intrinsic rate of increase was then:

$$r(t) = \beta_0 - \delta_0 \left(1 + A \sin \left(\frac{t\pi}{6} + \Omega\right)\right)$$  

at time $t$ months, with amplitude $A$ and phase $\Omega$ in both patches. Mortality rates in the two patches are assumed to be in phase.

Then parameter values were chosen (Table 2) in an attempt to recreate the corridor effect of mite B (Fig. 1a). The emigration rate was set to zero as before. Initially, the immigration rate was also set to zero. The instantaneous expected lifespan (calculated as the inverse of the mortality rate for a Poisson process) is long for much of the year (in keeping with the literature), but much shorter for a brief period. One thousand simulations were performed for each migration rate between zero and one (covering the range measured in the first manipulation experiment), and the average final population of the two patches recorded.

### 2.4.3. Variable emigration rates

Microarthropods search for suitable microhabitats as dictated by the demands of various stages of their life history (Norton, 1994). A single moss patch of diameter 10 cm may not encompass a sufficiently large area. Suppose an individual leaves a patch at any instant with a probability that is equal for both the complete- and broken-corridor treatments. For the complete-corridor treatment, suppose further that of this probability, there is a further chance that an individual will migrate across the corridor to the adjacent patch. Then the emigration rate will be lower in the complete- compared to the broken-corridor treatment.

Mite B was chosen to attempt to recreate the corridor effect based on emigration rates depending on the patch connectivity. The birth and death (now not seasonal) rates were best estimates, and the migration rate was varied within a reasonable range. One thousand model simulations were then performed with the density-independent emigration rate varying from zero to 0.3, at three reasonable levels of immigration (Table 2). For simplicity, the density-dependent emigration rate was set to zero.

### Results

#### 3.1. Best estimate parameters

Using the parameter best estimates, the abundance of mite B never fell to zero in either patch for any of the simulations (Fig. 5a), implying that the rescue effect was not relevant. Nevertheless, there was a weak trend of increasing final abundance with increasing density-independent migration rate (Fig. 5b). Furthermore, the magnitude of the corridor effect did not vary greatly for a reasonable range of density-dependent birth and death rates (parameters for which there is neither literature nor empirical data). However, there was very little difference in the simulated final abundance between the connected and disconnected corridor treatments (Fig. 5b) based on the best estimate range of the corridor migration rates. It was impossible to recreate the strong corridor effect of the Positive Study by adjusting either the birth and death rates (to simulate the shorter lifespan of the Mesostigmata and Collembola), or the density-dependent migration ($\mu_1$).

![Fig. 5](image-url) - (a) A single typical simulation of the population dynamics of mite B in two connected patches (shown in black and grey) over 6 months based on best estimate parameters (Table 2). (b) A simulated weak increase in abundance at the end of the experiment (6 months) with increasing migration. The migration rate for the broken-corridor treatment is assumed to be zero and for the complete-corridor treatment between 0.05 and 0.21 (indicated by the area between the dotted lines). Error bars represent 95% confidence intervals.
3.2. Seasonal mortality

When the intrinsic capacity of population increase ($r$) is negative, the abundance generally decreases, and vice versa (Fig. 6). The average final abundance (Fig. 7) and the chance of the occurrence of the rescue effect (Fig. 6) both increased with the migration rate. With some immigration, the rescue effect can occur even at low or zero patch-to-patch migration, so weakening the corridor effect. Although the corridor effect has been recreated, the magnitude of the effect has not (Fig. 7). Further simulations (not shown) demonstrate that the corridor effect is stronger when the mortality rates are out of phase in the two patches, since the rescue effect is more likely to occur.

3.3. Variable emigration rates

Abundance generally falls over time for positive emigration rates. The greater the emigration rate, the greater the rate of decline (Fig. 8), and the lower the average final abundance (Fig. 9). Furthermore, assuming no immigration for simplicity, the model can explain the corridor effect for mite B assuming emigration rates of 0.10 for the complete- and 0.30 for the broken-corridor treatments (Fig. 9). The corridor effect is very insensitive to the patch-to-patch migration rate, but is weakened with increasing immigration (Fig. 9). The important message here is that we can find parameter values that accurately recreate the corridor effect if we assume that the emigration rate depends on patch connectivity.
Two further conditions were necessary for the hypothesis to hold. Firstly, immigration from the surrounding environment must be low so that populations driven to extinction at times of high mortality can be rescued only by migration from the adjacent patch. Immigration was high at the site of the neutral study (second manipulation experiment). Thus although mortality may have been seasonal in the neutral study, any corridor effect was probably negated by high immigration. Secondly, the corridor effect assumes reasonably high migration between patches, higher than measured in the first manipulation experiment. The migration rate in the neutral study may not have been high enough to produce the corridor effect. It would be interesting to measure the immigration and migration rates at the site of the positive study to see whether they fall within the range required by the hypothesis.

The model also assumes that the birth rate increases with reducing abundance. Alternatively, if there is an Allee effect, then the rescue effect may become even more important at times of high mortality. Populations that fall below the Allee threshold may be rescued from extinction by migrants from the adjacent patch, if this is above the threshold (Amarasekare, 1998). The Allee effect has indeed been recorded for mites in the laboratory (Stamou and Asikidis, 1989).

Now I turn to the second mechanism: emigration rates. No empirical studies have measured whether emigration rates to the surrounding matrix are lower for patches connected by a corridor (Hudgens and Haddad, 2003). Such emigration would require that an individual has a reasonable chance of locating the corridor, and prefers to move through the corridor rather than the surrounding matrix. Indeed, corridors have been observed to channel movement (Berggren et al., 2002). When leaving a patch, microarthropods may search in a way that maximizes their chance of finding suitable habitat, perhaps using cues such as pheromone trails (Verhoef et al., 1977). Indeed, microarthropods are able to find conspecifics, since they generally aggregate (Usher, 1975). Alternatively, isolated patches may be drier than connected patches, perhaps due to an exchange of moisture across the connecting corridor. Emigration and death rates may then be higher and birth rates lower in the isolated patch, leading to lower microarthropod abundance and the corridor effect. However there is no evidence that the moisture content of moss patches depends on patch connectivity (Hoyle and Gilbert, 2004). In any case, the corridor effect can be simulated using lower emigration rates for patches connected by a corridor. Immigration need not be very low (contrary to the previous hypothesis), but the corridor would have to hold. Firstly, immigration from the surrounding environment must be low so that populations driven to extinction at times of high mortality can be rescued only by migration from the adjacent patch. Immigration was high at the site of the neutral study (second manipulation experiment). Thus although mortality may have been seasonal in the neutral study, any corridor effect was probably negated by high immigration. Secondly, the corridor effect assumes reasonably high migration between patches, higher than measured in the first manipulation experiment. The migration rate in the neutral study may not have been high enough to produce the corridor effect. It would be interesting to measure the immigration and migration rates at the site of the positive study to see whether they fall within the range required by the hypothesis.

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effect weakens with increasing immigration. The migration rate estimated from the first manipulation experiment again allows for only a weak corridor effect based on the emigration hypothesis. The moss species of the neutral study may have contained more microhabitats than the species of the positive study and hence the emigration rates of the neutral study may have been lower than in the Positive Study. This would imply that the emigration rate hypothesis and hence the corridor effect was relevant only to the positive study. Each patch was connected to two other patches in the positive study, but only one patch in the neutral study. Emigration may then have been much lower in the connected compared to the isolated patches in the positive study, since the microarthropods would have a greater chance of encountering a corridor when dispersing. Other factors could have led to a difference in emigration between the studies include: different times of the year; seasonal movement (second manipulation experiment; Norton, 1994); and as mentioned above, higher overall densities in the neutral study. Thus the strong corridor effect of the positive study could well have been due to a combination of both seasonal mortality and connectivity-dependent emigration rates.

Unfortunately, it is not possible to observe the microarthropods move, since they are usually buried deep in the moss. It was therefore necessary to use the manipulation experiments as an indirect method to estimate the degree of immigration and migration. The first manipulation experiment was conducted not in the field, but under controlled conditions. The estimated migration rates should then be viewed as indications rather than exact values. Although the results of the second manipulation experiment are consistent with those of the Neutral Study, it is surprising that it provided no evidence of migration across the corridor (contrary to the first experiment), and no evidence that cleared patches left for 2 months contained more individuals than those left for 1 month. A pilot study found no evidence that immigration is lower in cleared patches stuck to the rock with glue compared to patches not stuck down. Nevertheless, the carrying capacity may be lower for glued patches compared to patches growing naturally on rock. If so, all the cleared patches in the second manipulation experiment may have reached the carrying capacity (40% of that for patches not glued) after 1 month. This experiment would then be unable to detect any migration that did occur. To test this idea, the experiment could be repeated with the moss sampled after a shorter period, perhaps one week. The second manipulation experiment certainly demonstrated that immigration at the site of the neutral study is high. The seasonal mortality hypothesis (but not the emigration hypothesis) requires low immigration. It would be instructive to measure immigration at the site of the positive study to see whether this was consistent with this hypothesis. To test the emigration hypothesis, it may be possible to trap emigrants by surrounding moss patches with sticky tape. The hypothesis then predicts fewer emigrants from patches connected by a corridor. The seasonal mortality hypothesis could be tested in the following way. The abundance of microarthropods in the mainland moss should be monitored at regular intervals throughout the year. The test of corridor effectiveness as implemented in the positive and neutral studies should be repeated on several occasions. A corridor effect should be anticipated only from those experiments that encompass a period of high mortality and hence low mainland abundance. The phase lag in mortality between adjacent patches could in principal be estimated by recording microarthropod abundance in a small area of moss sampled along a transect of mainland moss at frequent time intervals throughout the year.

All models make important assumptions, so it is important to capture the most relevant processes of the system under study. The model should demand only data that are practically available from experiments. The principle of parsimony should apply to processes for which data are not available. In this case, mortality was assumed constant over the life of an individual, to avoid the need to track each microarthropod, and emigration and migration were initially assumed to be density-independent, even though microarthropods are known to aggregate (Usher, 1975). The following refinements could be added to the model, but I suggest that they would introduce spurious accuracy: allow for mortality in the corridor; assume a finite corridor migration time; assume a non-reproductive juvenile stage; and extend the model to many species at more than one trophic level, since species persistence depends on interaction with other species (Hiltyoa, 2000).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2006.11.008.

REFERENCES


