

Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem

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Summary

1. Species extinction in fragmented habitats is a non-random process described by transient, rather than equilibrium dynamics. Therefore, 'static' approaches focusing on experimentally established spatial gradients of diversity may fail to capture essential aspects of ecosystem responses to species loss.
2. Here we document temporal changes in microarthropod species abundance, biomass and richness during a community disassembly trajectory following experimental habitat fragmentation of a moss-based microecosystem.
3. Habitat fragmentation reduced heterotrophic species richness and community biomass in remnant moss fragments. Extinction was biased towards rare species, and thus occurred initially without significant changes in total community abundance and biomass. Eventual reductions in abundance and biomass were found to lag behind observed declines in species richness.
4. The presence of moss-habitat corridors connecting fragments to a large 'mainland' area coupled with an immigration rescue effect maintained microarthropod richness, abundance and biomass within remnant fragments.
5. Our results indicate that both the order of species loss and the dynamics of remnant populations influence the magnitude and timing of ecosystem-level responses to habitat destruction and isolation.

Key-words: corridors, ecosystem functioning, extinction debt, habitat fragmentation, microarthropods, microecosystem, moss microcosm, secondary biomass, species extinction.

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Introduction

Habitat destruction and fragmentation are regarded as the major causes of species extinction in human-modified landscapes (e.g. Andrén 1994). The loss of inhabitable area, increased isolation and increased edge effects associated with fragmentation initiate a process of community disassembly (Mikkelsen 1993), involving declines in both species abundance and diversity within remnant habitat patches. These community changes might be characterized either by the loss of rare species under the influence of demographic stochasticity (Lawton 1995), or by changes in dominant,

widely distributed taxa, in which persistence may be compromised by low dispersal ability (Nee & May 1992; Tilman, Lehman & Yin 1997a). The order of species loss may thus affect not only community disassembly, but also the magnitude and trajectory of changes in ecosystem properties (Lawton 1994; Sala *et al.* 1996; Grime 1998). Few studies, however, have attempted to integrate the effect of fragmentation-induced extinction dynamics with community- and ecosystem-level processes.

Most experiments relating ecosystem function to changes in species diversity have so far adopted a 'static' approach. Selected ecosystem variables are usually measured across gradients of spatially interspersed diversity treatments, often represented by synthetic communities drawn at random from a given species pool (e.g. Tilman *et al.* 1997b; Hector *et al.* 1999; Lepš *et al.* 2001). Although useful for revealing diversity effects independent of species composition (Tilman

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1997; cf. Huston 1997; Wardle 1999), such protocols might tell us little about the ecosystem changes that accompany diversity loss in fragmented habitats, where extinction is a non-random process dominated by non-equilibrium dynamics. In particular, the identity of species extinctions (e.g. rare vs. dominant; Sala *et al.* 1996; Grime 1998) and the rate at which such extinctions occur can generate non-linear responses (i.e. 'extinction debts'; Kareiva & Wennergren 1995) that are unobservable if spatially structured gradients of fixed diversity levels are used as a surrogate for species loss following fragmentation (Lamont 1995). Furthermore, the abundances of remnant populations are expected to decline in newly fragmented ecosystems (e.g. Didham *et al.* 1998a,b). It is thus likely that transient dynamics initiated by habitat isolation will have important, and possibly delayed, effects upon ecosystem functioning. This temporal aspect of community disassembly has been largely missing from biodiversity–function studies. To date no experimental study has examined the joint trajectories of community disassembly and ecosystem-level properties during postfragmentation time.

Habitat corridors could attenuate population decline and extinction in fragmented landscapes by creating networks of otherwise isolated patches, or by linking small fragments to large 'mainland' areas of continuous habitat (Wilson & Willis 1975; Saunders & Hobbs 1991; Saunders, Hobbs & Margules 1991; Harrison 1994). Unequivocal evidence in support of this idea is still lacking, mainly because few studies have evaluated experimentally the effects of habitat connectivity on isolated multispecies communities (Gilbert, Gonzalez & Evans-Freke 1998; Gonzalez *et al.* 1998; Golden & Crist 1999; Haddad & Baun 1999; Collinge 2000). If, however, by enhancing immigration corridors exert a 'rescue' effect (Brown & Kodric-Brown 1977) that maintains both local and regional species diversity, their presence could also have a positive influence on ecosystem functioning.

In this paper, we report two experiments designed to investigate heterotroph community disassembly in a temperate moss microecosystem. In a first experiment, we examined the dynamics of microarthropod species diversity, abundance and biomass in moss-habitat fragments following partial destruction of the original moss carpet. In a second experiment, we tested the potential for habitat corridors to buffer changes in moss arthropod communities upon fragmentation. A previous corridor experiment (Gilbert *et al.* 1998; Gonzalez *et al.* 1998) showed that networks of interconnected habitat patches are buffered against local extinction and community collapse, as predicted by metapopulation theory (Hanski 1994; Harrison 1994). Here, we asked whether habitat corridors connecting small moss fragments to large, continuous moss habitat, help maintain microarthropod diversity, abundance and biomass within prefragmentation levels. Corridors were manipulated to evaluate their effect on

dispersal, rather than as landscape elements offering extra habitat for extinction-threatened species.

Methods

THE STUDY SYSTEM

Temperate moss ecosystems harbour a high-density, species-rich microfauna of protists, rotifers, tardigrades, nematodes, collembolans and mites (Gerson 1969; Kinchin 1992). Moss carpets occur naturally on rocky substrate and large boulders, forming continuous miniature landscapes that are large compared to the size and dispersal capacity of the organisms that inhabit them. The size, biotic complexity and short generation time of most component taxa, makes them ideal study systems for confronting the practical problems posed by large spatio-temporal scales associated with community responses to habitat fragmentation (Robinson *et al.* 1992; Schmiegelow *et al.* 1997; Didham *et al.* 1998a,b). This study focused on the effect of habitat loss on moss-inhabiting mites (Arachnida: Acarina), a diverse group of organisms including predatory (principally feeding upon other mites and nematodes) and herbivorous species (feeding upon fungi and decaying matter) (Evans, Sheals & McFarlane 1961; Krantz 1978; Kinchin 1992), which account for $\approx 70\%$ of the total arthropod density in this system (Gonzalez 1998). The experiments were conducted in the Derbyshire Peak District, northern England (OS map ref SK 264566). For each experiment, we selected large, flat limestone boulders covered by a mixture of the moss species *Hypnum cupressiforme* (Hedw.), *Thuidium tamariscinum* (Hedw.) and *Tortella tortuosa* (Hedw.).

EXPERIMENTAL DESIGN AND SAMPLING

Experiment 1 was initiated in March 1995. We established two treatments, control and fragmented, in a randomized block design using eight moss-covered boulders. Each replicate boulder contained 12 randomly distributed circular moss fragments, six 20 cm² and six 200 cm² (the slower dynamics of which will not be considered here but details can be found in Gonzalez 2000), and a continuous moss carpet acting as an undisturbed control (minimum area: 50 × 50 cm). The fragmented treatment was created using a template to ensure constancy in fragment area and distance (15 cm) between adjacent fragments. Habitat fragments were created on one half of the boulder by scraping and removing the moss cover; the remaining moss fragments were left surrounded by a 'sea' of bare rock, a habitat considered inhospitable for most mite taxa.

Community responses to fragmentation were monitored over a 12-month period encompassing several generations for the larger predatory mites (equivalent to tens of generations for many of their prey species). Every 2 months, one moss fragment was chosen randomly and removed from each block. Moss samples of

equal area were also removed from the control treatment on each sampling date. This control allowed for seasonal changes in species abundance and diversity (Davis 1981; Schenker & Block 1986). Microarthropods were extracted using a Tullgren funnel (Evans *et al.* 1961). Moss samples were exposed to the heat–light gradient for 72 h; emerging specimens were collected in an alcohol/glycerol/water (7 : 2 : 1) mix and sorted into morphospecies (Evans *et al.* 1961; Krantz 1978; Eisenbeis & Wichard 1987). In total, 133 microarthropod morphotypes were extracted; note that this is likely to be an approximation to the actual species richness. A total of $\approx 98\,000$ individuals were counted and identified, with most (87%) belonging to the Acarina and Collembola.

Experiment 2 was conducted between November 1996 and May 1997. In this case, we chose seven moss-covered boulders and set up four treatments in a randomised block design. Each block comprised a large continuous moss carpet (50×50 cm), hereafter the *mainland* treatment, surrounded by twelve 10-cm² circular moss fragments. These fragments were randomly assigned to each of three treatments differing in degree of connectivity. An *insular* treatment comprised fully disconnected moss fragments. A *corridor* treatment was created by connecting fragments to the mainland area with a 7-cm-long \times 2 cm-wide strip of live moss. A *broken-corridor* treatment, in which corridors were split by a 2–3-cm gap of bare rock, was established to control for the increase in habitat area generated by the presence of corridors. Microarthropods were sampled 3 and 6 months after establishment. At each date, and from each block, we removed one randomly chosen fragment from each treatment, and one equivalently sized sample from the control mainland. Other methodological details followed the protocol for experiment 1.

HETEROTROPHIC DIVERSITY AND BIOMASS

Mites with distinct sets of morphological characters were considered the operational taxonomic entities. Hence, throughout this paper the term species diversity (or richness) will refer to different mite morphotypes. A species was considered locally extinct from a replicate landscape when it no longer appeared in the suite of organisms extracted with the Tullgren funnel. This is necessarily a working definition. Although the extraction efficiency of this system is high, it was very difficult to ascertain for sure whether a species did not occur in a given fragment, or that it was so rare that remaining individuals could not be extracted. Most important for this definition of ‘extinction’ was that control and fragmented landscapes experienced identical extraction regimes.

Mean population abundance (density) and biomass were assessed for all individual morphospecies on each sampling date. We calculated mite species biomass in each moss sample using an empirical relationship

between individual fresh weight and body size (length): $\text{weight} = 0.31 \text{ length}^{3.07}$ ($r^2 = 0.92$, $F_{1,10} = 110.01$, $P < 0.001$) estimated from a subset of mites collected during the first experiment. Biomass values (mg) of individual species were summed to estimate total community biomass within a moss fragment. Heterotrophic biomass (hereafter referred to as community biomass) was used as an integrative parameter of energy flow into trophic levels other than producers.

DATA ANALYSIS

In experiment 1, the effect of fragmentation on arthropod species richness, abundance, and biomass at the patch scale (20 cm²) was evaluated through univariate three-way ANOVA, with treatment (two levels), date (five levels) and block (fixed effect). Biomass and abundance (number of individuals) data were log-transformed before analysis to meet the assumption of normally distributed errors. A statistical model including repeated measures was not appropriate because destructive sampling of moss patches ensured that consecutive measurements were independent. Unplanned pairwise comparisons between the control and fragmented treatments were conducted for each of the last three sampling dates using the Bonferroni *t*-test. This method allows one to keep the experiment-wise error rate at the chosen level ($= 0.05$) while adjusting the significance value for a fixed number of comparisons (Day & Quinn 1989). We then used a conservative significance level ($P < 0.01$) to account for three unplanned tests within each broader ANOVA.

The relation between biomass, abundance and species richness, and in particular the relative contribution of the latter two variables in statistically explaining the dynamics of community biomass over time post-fragmentation was examined through multiple regression using a backward elimination procedure. Logistic regression analysis was conducted to determine whether the probability of extinction of an individual species after 12 months of fragmentation was associated to its local abundance and/or its distributional extent (i.e. proportion of occupied patches) in continuous landscapes. Local abundance and distribution were fitted separately in these logistic regressions.

In experiment 2, effects of isolation and corridors were evaluated using ANOVA models that included the appropriate orthogonal contrasts to test for significant differences in arthropod community structure between ‘connected’ (mainland + corridor) and ‘disconnected’ (insular + broken-corridor) habitat patches, as well as between the treatments within each of these pairings. This analysis tested two main hypotheses: first, isolation decreases arthropod richness, abundance and biomass at the fragment scale; second, corridors prevent community disassembly by facilitating arthropod movement between large, continuous moss carpets and small, otherwise isolated, moss fragments.

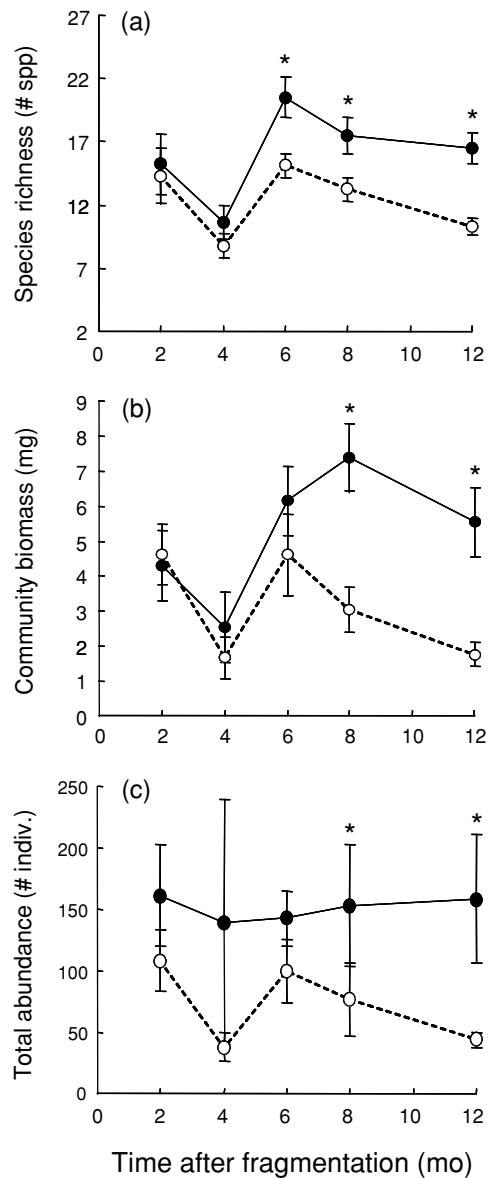


Fig. 1. Changes in mean species diversity (a) species richness, (b) community biomass and (c) total abundance of microarthropods in 20-cm² moss patches extracted from continuous (solid circles) and fragmented (open circles) moss carpets. Vertical bars show ± 1 SEM; asterisks indicate significant treatment effects within dates ($P < 0.01$).

Results

SPECIES DIVERSITY

In experiment 1, moss-habitat fragmentation had a strong effect on mean species richness in remnant fragments (Fig. 1a). Moss fragments contained fewer species of microarthropods than control habitat patches ($F_{1,59} = 16.09$, $P < 0.001$). Microarthropod diversity varied significantly with time ($F_{4,59} = 9.03$, $P < 0.0001$), but there was no significant treatment \times time interaction ($F_{4,59} = 1.19$, $P > 0.30$). After 6 months of study, mean species richness remained consistently higher ($P < 0.01$) in control landscapes than in fragmented ones (Fig. 1a).

HETEROTROPHIC BIOMASS

Fragmentation decreased community biomass in experiment 1 ($F_{1,59} = 12.06$, $P < 0.001$). Mean community biomass changed across sampling dates ($F_{4,59} = 6.82$, $P < 0.0001$), but the treatment by date interaction was not significant ($F_{4,59} = 1.87$, $P > 0.10$). We found only small, non-significant effects of fragmentation on heterotrophic biomass over the first 6 months of study (at 6 months differences were only significant at $P < 0.10$) (Fig. 1b). The negative effect of isolation on community biomass emerged only after eight months, when microarthropod biomass in continuous habitat patches was twice that in remnant fragments (Fig. 1b).

SPECIES ABUNDANCE AND EXTINCTION

In experiment 1, microarthropod abundance showed no temporal trend in patches of continuous habitat, whereas it decreased in habitat fragments (Fig. 1c). This resulted in a significant effect of time after fragmentation ($F_{4,59} = 4.09$, $P < 0.01$; treatment \times time: $F_{4,59} = 0.56$, NS). Habitat fragmentation caused a highly significant reduction in mean microarthropod abundance ($F_{1,59} = 18.88$, $P < 0.0001$), although this reflected differences between control patches and fragments emerging only after 8 months of treatment (Fig. 1c).

Logistic regression revealed that the species suffering extinction in fragmented landscapes had lower population abundance ($\chi^2 = 20.12$, d.f. = 1, $P < 0.001$), and were more narrowly distributed ($\chi^2 = 16.44$, d.f. = 1, $P < 0.001$), than the remaining species (Fig. 2). Thus, the observed decline in total arthropod abundance did not reflect species extinction as provoked by habitat destruction, but a generalized decline in the population density of species persisting within habitat fragments (Fig. 3). Inspection of individual species' changes in density and biomass after 6 months suggests that some early species losses were compensated for by changes in abundance of some remnant species with low biomass in unfragmented landscapes (Fig. 3).

EXTINCTION, COMMUNITY ABUNDANCE AND BIOMASS LOSS

Multiple regression indicated that community abundance (slope = 0.63; SE = 0.11; $P < 0.001$) and species richness (slope = 0.02; SE = 0.01; $P < 0.008$) were both positively and linearly correlated with community biomass, and together explained 65.1% of the variation in community biomass ($F_{2,35} = 35.46$, $P < 0.0001$). However, species richness explained only a small (6.7%) fraction of this biomass variation when the effect of community abundance was accounted for. These results should be interpreted cautiously given that species richness and community abundance were weakly, yet significantly correlated (slope = 0.04; SE = 0.01; $P < 0.01$).

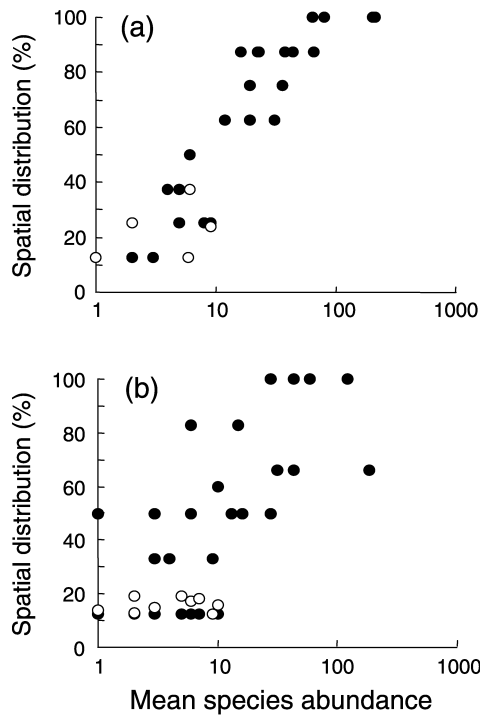


Fig. 2. Patterns of microarthropod extinction in response to fragmentation relative to individual species abundance (mean density per patch, log scale) and distribution (percentage of occupied patches) in continuous moss landscapes, at (a) 6 and (b) 12 months since fragmentation. Local species extinctions are denoted by empty symbols.

This analysis suggests that reductions in abundance and, to a lesser extent, in species richness were both concurrent to postfragmentation changes in heterotrophic community biomass. Indeed, initial reduction

of species richness in moss fragments (25% relative to control patches after 6 months) did not correspond to significant changes in secondary biomass (Fig 1. a,b). By 8 months the mean proportional species loss remained the same, whereas the mean heterotrophic biomass in remnant fragments decreased by 59% below control levels. Finally, 12 months of habitat fragmentation caused a 40% and 68% decline in microarthropod richness and biomass, respectively.

EFFECTS OF CORRIDORS

The presence of corridors ameliorated the negative effects of habitat loss and isolation on arthropod community structure and productivity. In experiment 2, patch isolation decreased mean species richness after six months of treatment (Fig. 4a), as shown by a significant contrast between connected vs. disconnected moss patches ($F_{1,18} = 13.3, P < 0.002$). Species richness did not differ between mainland and corridor treatments ($F_{1,18} = 0.03, NS$), nor between the broken-corridor and insular ones ($F_{1,18} = 0.004, NS$). The insular and broken-corridor treatments contained, on average, 34% fewer species than the corridor and mainland treatments. After 6 months, mean arthropod biomass was significantly higher in connected than in disconnected moss patches ($F_{1,18} = 7.16, P < 0.025$). Insular and broken-corridor patches experienced an average 62% reduction in heterotrophic biomass relative to that in connected patches (Fig. 4b), but did not differ between them ($F_{1,18} = 0.10, NS$). There was also no difference in mean arthropod biomass between mainland and corridor treatments ($F_{1,18} = 0.4, NS$). Overall

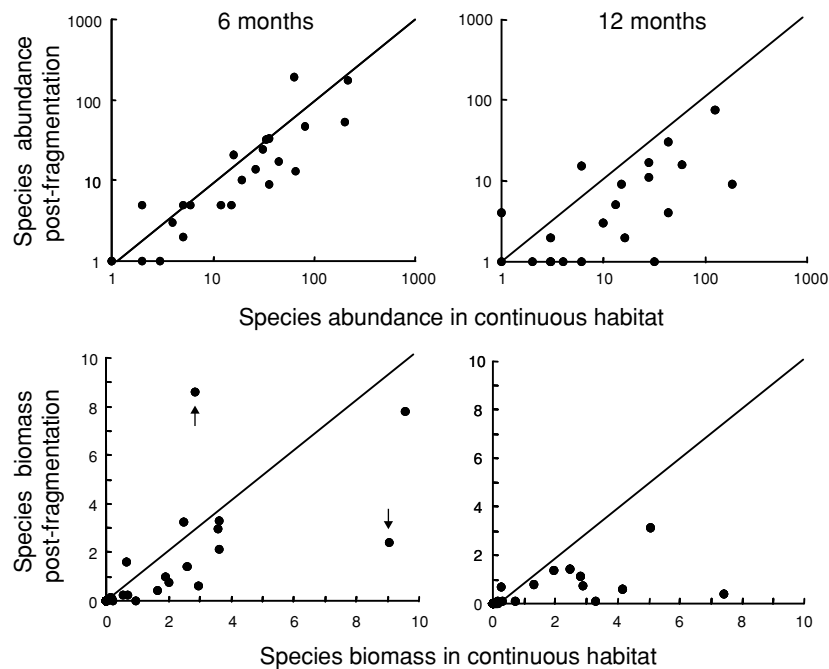


Fig. 3. Effect of moss-habitat fragmentation on total biomass (mg) and population abundance (number of individuals) of individual microarthropod species, after 6 and 12 months of treatment in experiment 1. Arrows highlight compensatory changes (i.e. before and after fragmentation) in dominant species biomass and density. Note that species abundances are plotted on a log scale.

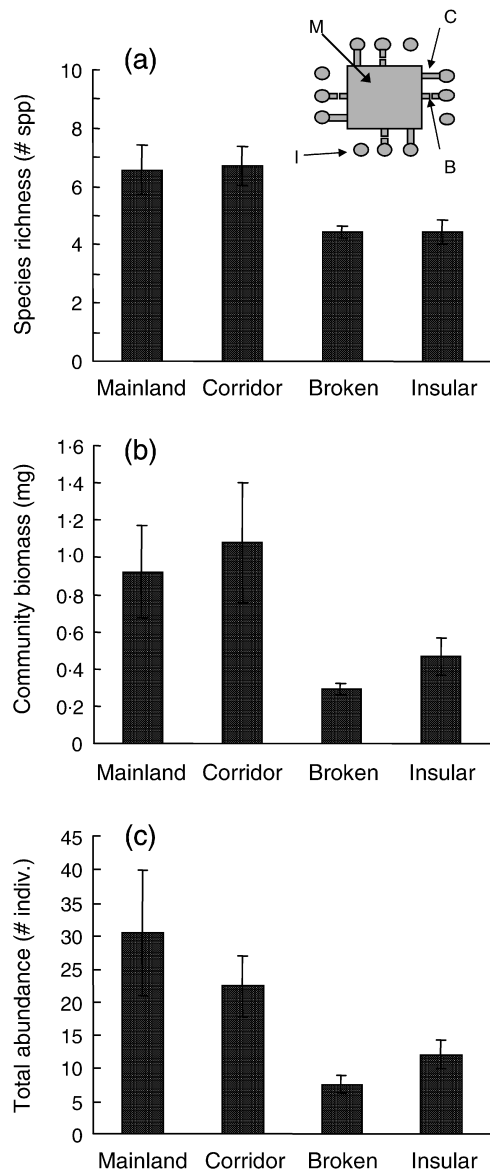


Fig. 4. Effect of isolation and habitat corridors on (a) species diversity, (b) standing biomass and (c) total abundance of moss-living microarthropods in experiment 2. Bars represent means \pm 1 SEM after 6 months of experiment. The inset shows an experimental block with the four treatments: M = mainland, C = corridor, B = broken corridor, I = insular.

microarthropod abundance was 60–80% greater in patches of mainland and corridor treatments than in broken-corridor and insular ones (Fig. 4c; $F_{1,18} = 13.9$, $P < 0.002$). No significant difference in arthropod density was found between connected treatments, nor between disconnected ones ($F_{1,18} = 0.19$ and 1.01 , $P > 0.10$).

Discussion

We have reported the changes in heterotroph community abundance and biomass as species were lost during a community disassembly process triggered by habitat fragmentation. The potential existence of delayed temporal effects inherent in the dynamics of species extinc-

tion may circumscribe the application of previously established conclusions regarding the effects of species loss upon ecosystem functioning. Most previous results have been derived from experiments using 'static' or discrete diversity gradients to approximate the process of species loss. The experimental approach described here differs in several important ways.

First, we did not construct random species assemblages of different richness and composition to mimic diversity loss, but focused on the disassembly of extant animal communities. We thus avoided the assumption that species extinction in human-perturbed ecosystems will follow random pathways insensitive to the abundance (Lawton 1995; Tilman *et al.* 1997a) or trophic position (Mikkelsen 1993; Kruess & Tschardt 1994; Grime 1998; Petchey *et al.* 1999) of constituent species. Secondly, biodiversity experiments have sometimes had unrealistically constrained dynamics because they compared depauperate communities with fixed species-abundance distributions, over time scales that did not allow for relevant population processes (but see Wardle *et al.* 1999; Wilsey & Potvin 2000). Yet studies using terrestrial (Mikola & Setälä 1998; Laakso & Setälä 1999) and aquatic microcosms (McGrady-Steed, Harris & Morin 1997; Petchey *et al.* 1999; Norberg 2000) indicate that population dynamic responses to species removal from the same or adjacent trophic levels can mediate the ecosystem-level effects of diversity and environmental change. We have monitored changes in species abundances through several generations, a key factor in the progressive loss of diversity from fragmented habitats (Lawton 1995; Tilman *et al.* 1997a; Didham *et al.* 1998a,b). Indeed, our results suggest that demographic processes affecting species distribution and local abundance (Gonzalez *et al.* 1998) underpin the relationship between diversity and heterotrophic biomass. Finally, whereas our design did not specifically test for diversity effects (see Tilman 1997), we initiated a disassembly process that addressed more directly the issue of species extinction, and its potential consequences for ecosystems (Lamont 1995; Wardle 1999). Thus, our protocol did not assume, a priori, a causal diversity–biomass relationship, nor was species loss simulated as a series of discrete events (cf. Symstad *et al.* 1998; Wardle *et al.* 1999). Overall, we consider this 'dynamic' approach as complementary to that of studies using spatially structured, random species assemblages.

The fragmentation of continuous moss carpets and subsequent isolation of remnant patches led to a significant decrease in microarthropod species richness. This diversity analysis, as reported in Gonzalez (2000), shows an 'extinction debt' (*sensu* Tilman *et al.* 1997a) that is evident only 6 months after the initial bout of habitat loss. In the present study, logistic regression showed that extinctions predominantly involved species with low abundance and low occupancy in continuous landscapes (Fig. 2). Some of these species were probably predatory mites, a trophic group that appears

sensitive to microhabitat conditions in isolated moss patches (Gilbert *et al.* 1998). The loss of consumers from a food web may have disparate ecosystem-level consequences, according to the functional and numerical responses of the remnant species (Laakso & Setälä 1999; Petchey *et al.* 1999; Norberg 2000) and the duration of observation (Ernest & Brown 2001).

The loss of species from fragmented microecosystems was accompanied by a delayed decrease in the heterotrophic biomass supported by isolated moss fragments. Total biomass was maintained close to control levels in the short term despite a 25% decline in species richness. The lagged effect of isolation on community biomass did not become apparent until eight months since fragmentation (Fig. 1). Furthermore, there is suggestive evidence for some functional redundancy within this decomposer web given by early compensatory changes between numerically dominant microarthropod species (Fig. 3). However, a rigorous test of species redundancy would require knowledge of species traits to demonstrate functional overlap among species sharing the same resource base (Lawton 1994; Grime 1998; Laakso & Setälä 1999; Walker *et al.* 1999; Norberg 2000). In the present study, monitoring the transient dynamics of multitrophic arthropod assemblages allowed us to establish the events linking biomass decline to species loss after fragmentation.

The negligible influence of early, rare species extinctions on community biomass renders explanation of large, but delayed decreases in total biomass difficult to explain by species richness *per se*. Habitat fragmentation caused a concurrent, nearly community-wide reduction in microarthropod abundance that took longer to occur, but was a better predictor of biomass loss than species richness. Such results suggest that analyses of diversity–function relations in disturbed ecosystems should focus on the dynamics of remnant populations, as well as on the process of species diversity loss.

Two well-known effects of habitat fragmentation are the changes in microclimate that result from the increased edge:area ratio of fragments, and the inhibition of dispersal (Saunders *et al.* 1991; Harrison 1994; Didham *et al.* 1998a). In this ecosystem, edge effects increased the frequency of substrate desiccation, the most likely factor altering the abundance and diversity of microarthropods within isolated moss patches (Block 1966; Davis 1981; Schenker & Block 1986; Gonzalez 2000). Furthermore, Vannier (1972) demonstrated that the probability of microarthropod dispersal increases in response to microhabitat drying. Hence, in the absence of adequate dispersal routes, continued exposure to stressful conditions may have increased both within-fragment mortality and movement across large areas of inhospitable rocky substrate. The results of the second experiment, demonstrating the beneficial effects of corridors connecting remnant fragments to large moss carpets, support the above line of reasoning (see also Gonzalez *et al.* 1998).

The presence of corridors helped maintain microarthropod abundance and species richness in otherwise isolated patches (Fig. 4). In contrast, the 'broken' corridors were not effective in preventing the disassembly of these communities. Given that the only difference between the two corridor treatments was a small break in the moss cover (see Fig. 4: inset), it seems unlikely that corridor effects could be explained by differences in available habitat or microclimate conditions, suggesting that dispersal played a major role in the persistence of local microarthropod populations (see also Gilbert *et al.* 1998). The results of the present study are novel in showing that the so-called 'rescue effect' of corridors (Brown & Kodric-Brown 1977) was also important in the maintenance of a measure of ecosystem function (Fig. 4b). The decreased abundance and richness of microarthropods within insular patches presumably reflected changes in moss-substrate quality (Vannier 1972; Davis 1981). By preserving a flow of immigrants from less disturbed habitat, corridors helped avoid such short-term effects being translated into reduced secondary biomass. We therefore hypothesize that dispersal may buffer the ecosystem's capacity for organic matter processing and storage in fragmented habitats.

Although the loss of rare species may not have immediate consequences for community biomass, theory suggests that such extinctions could be important for the longer-term stability of certain ecosystem functions (McNaughton 1977; Frost *et al.* 1995; Tilman 1996; Yachi & Loreau 1999; Loreau 2000). Specifically, if due to environmental fluctuations species change position in the community rank–abundance distribution, in the long term, transiently rare species may be expected to contribute to ecosystem stability (Tilman 1996; Walker, Kinzig & Langridge 1999; Yachi & Loreau 1999). Our experimental results with this moss microecosystem (see also Gonzalez *et al.* 1998) indicate that the persistence of rare species in habitat fragments may strongly depend upon immigration from nearby patches. Thus, they support the broader hypothesis (Tilman *et al.* 1997a; Grime 1998) that disruption of habitat connectivity will not only induce widespread reductions in local abundance and species diversity, but may also increase community variability (e.g. Boulinier *et al.* 1998) thereby impairing the ability of the ecosystem to adjust to future environmental change.

In conclusion, the results of this study emphasize the importance of focusing on community disassembly trajectories when assessing the effect of extinction drivers on ecosystem processes. In particular, we have shown that habitat fragmentation can generate a *functioning debt* – i.e. a delayed alteration in ecosystem attributes driven by the decline of species persisting in remnant patches. Although here species abundance dynamics appeared to dominate postfragmentation changes in heterotrophic biomass, the loss of rare species provided early signs of altered ecosystem functioning. Our results imply that if we are to establish the

consequences of biodiversity loss, more studies linking population dynamic processes to ecosystem function in disturbed landscapes will be needed.

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