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LETTER

Connectivity, non-random extinction and ecosystem function in experimental metacommunities

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Abstract

The spatial insurance hypothesis indicates that connectivity is an important attribute of natural ecosystems that sustains both biodiversity and ecosystem function. We tested the hypothesis by measuring the impact of manipulating connectivity in experimental metacommunties of a natural and diverse microecosystem. Isolation led to the extinction of large-bodied apex predators, subsequently followed by increases in prey species abundance. This trophic cascade was associated with significantly altered carbon and nitrogen fluxes in fragmented treatments. The ecosystem impacts were characteristic of a function debt because they persisted for several generations after the initial loss of connectivity. Local extinctions and disruption of ecosystem processes were mitigated, and even reversed, by the presence of corridors in the connected metacommunities, although these beneficial effects were unexpectedly delayed. We hypothesized that corridors maintained grazer movement between fragments, which enhanced microbial activity, and decomposition in comparison to isolated fragments. Our results indicate that knowledge of habitat connectivity and spatial processes is essential to understand the magnitude and timing of ecosystem perturbation in fragmented landscapes.

Keywords

Connectivity, dispersal, metacommunity, ecosystem function, extinction, fragmentation, trophic cascade.

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INTRODUCTION

Many ecosystems are currently undergoing dramatic changes in biodiversity due to habitat fragmentation and land use change (McKee *et al.* 2004). Although the importance of dispersal for the maintenance of biodiversity is well understood (e.g. Amarasekare 2004; Holyoak *et al.* 2005), its importance to ecosystem functioning remains relatively unexplored. For example, weak flows of individuals between habitats may have significant impacts on population production and community stability (Loreau *et al.* 2003). From this perspective, a more complete understanding of the impacts of habitat fragmentation on ecosystems requires the study of the spatial processes that mediate the link between biodiversity and ecosystem functioning (Gonzalez *et al.* 2009).

The multifarious effects of habitat fragmentation initiate a non-random process of community disassembly (Lawton & May 1995). For example, species at higher trophic levels are more prone to extinction following fragmentation because of their larger body size, greater area requirements, lower densities and lower connectance within the food web (Didham *et al.* 1998; Holyoak 2000; Duffy 2003). Over time community disassembly is associated with an initially rapid loss of biodiversity followed by a second, longer-term process of decay or 'relaxation' in residual diversity in the remaining habitat fragments (Borrvall & Ebenman 2006; Tilman *et al.* 1994; Gonzalez 2000; Vellend *et al.* 2006; Kuussaari *et al.* 2009). An extinction debt due to habitat fragmentation has been hypothesized to cause a parallel ecosystem function debt, that is, a long-term alteration in ecosystem attributes driven by the decline and extirpation of species in remnant patches (Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002). The functional consequences of habitat fragmentation are likely to be great and delayed (Didham *et al.* 1996; Laurance *et al.* 1997; Duffy 2003), because non-random extinction and cascading changes in community composition will impact ecosystem processes via changes in food web structure, community compensation and nutrient recycling (Elmqvist *et al.* 2003; Ives & Cardinale 2004; Larsen *et al.* 2005; Gonzalez & Loreau 2009).

Recent metacommunity theory (Loreau *et al.* 2003; Gonzalez *et al.* 2009) asserts that productivity and stability of ecosystem functions are dependent on the rate of dispersal within fragmented landscapes. We tested a prediction from the spatial insurance hypothesis (Loreau *et al.* 2003), that habitat connectivity mediates the magnitude and timing of ecosystem effects in the face of ongoing extinction (Gonzalez *et al.* 2009). We manipulated the connectivity of a moss ecosystem consisting of a diverse decomposer food web, spanning multiple trophic levels. Trophic interactions in detrital systems have a large potential to influence ecosystem processes (Seastedt 1984; Wardle 2002). Microarthropods in detrital systems may not only contribute to nutrient cycling directly by releasing carbon and nitrogen from microbes and other food resources, but also indirectly by stimulating microbial activity in patchy habitats (Bengtsson *et al.* 1993). We induced changes in community structure and extinctions by fragmenting the moss habitat, a process previously shown to generate non-random biodiversity loss in this natural model ecosystem (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002).

We hypothesized that biodiversity loss in the detrital food web would be associated with ecosystem-level consequences (changes in nutrient retention/loss, and gas flux) and that these effects would be mitigated in larger or more connected habitats. Specifically, we tested four hypotheses. First, fragmentation will induce non-random biodiversity loss associated primarily with the extinction of large-bodied top predators (e.g. mesostigmatid mites) (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002). Second, depletion of top predators will cause a corresponding increase in prey abundance due to release from predation. Third, the consequences of this trophic cascade will be demonstrated in a long-term response of ecosystem-level processes in the form of altered nitrogen and carbon dynamics (Setälä *et al.* 1991; Bradford *et al.* 2007). Fourth, connectivity in the form of corridors among habitat patches will maintain diversity and mitigate ecosystem impacts due to non-random extinction. Consistent with these hypotheses, we show that habitat fragmentation can cause large, long-term and delayed changes to ecosystem function, and that habitat connectivity in the form of corridors can mitigate and even reverse these impacts on multiple ecosystem processes in a manner entirely consistent with this theory.

MATERIALS AND METHODS

Moss chamber and experimental design

Experimental microcosms consisted of four metacommunities of varying connectivity: (1) small *island* fragments with no corridors, (2) small fragments with *broken* corridors, (3) small fragments connected by *corridors* and (4) a large *continuous* habitat. These treatments are similar to a design previously used (Gilbert *et al.* 1998; Gonzalez *et al.* 1998) in the field. Microcosms were constructed of 30-mm thick, 240-mm square PVC base with four 70-mm-diameter subchambers in each corner (see Fig. S1). Each subchamber was 60-mm height and had a total volume of 0.23 L. *Island* microcosms consisted of only the four subchambers, whereas strips of moss 77-mm long and 17-mm wide were used to connect subchambers in the *broken* and *corridor* treatments. In the *broken* treatment, the strips were blocked in the middle with a 4-mm thick PVC divider.

Carpets of feather moss (*Thuidium tamariscinum*) and underlying detritus were collected on 12 January 2005 from the surface of large rocks in Derbyshire, England (53°6.4' N, 1°36.4' W). The moss was carefully cut into circles of the same diameter as the subchambers, fresh weighed and placed in the subchambers. Strips of moss were cut to fill the connecting links in *corridor* and *broken* treatments. The *continuous* microcosms were similarly constructed on a 310-mm square base, but the main areas surrounding subchambers were filled with moss; thus these subchambers were not physically separated from the surrounding moss. The total volume of moss in each microcosm treatment was: *continuous* = 967.2 cm^3, *corridor* = 205.9 cm^3, *broken* = 203.1 cm^3, and *island* = 149.6 cm^3, but in all cases measurements were taken from subchamber-sized sections of the moss carpet.

Microcosms were allocated a 30-mm deep Perspex lid (3-mm thick), which fitted tightly along the contours of the subchambers and their corridors. Lids for the *continuous* microcosms, in addition to covering the subchambers, also covered the whole continuous area and included a 30-mm deep Perspex skirt around their edge. Drainage outputs (2-mm diameter) were located at the centre of each subchamber, within the corridor strips and regularly throughout the main area of the *continuous* microcosms. Each subchamber had an air inlet and outlet, fashioned from stainless steel pipe, with a 2-mm internal diameter. Ambient air from outside the laboratory was passed through a pre-filter (to remove particulates) and a 430-L buffer chamber to dampen short-term fluctuations in CO_2 concentration, and humidified to minimize moss desiccation between watering and then delivered to the subchambers at 100 mL min^{-1}.

Each moss-filled experimental microcosm type was replicated five times, placed and maintained in a climate-controlled plant-growth room for 315 days (from 12 January to 23 November 2005). A fully randomized experimental layout was used to eliminate any effect of lighting and airflow on the various treatments. In addition, a set of empty microcosms, one of each treatment type, was used to factor out any perturbation in measured CO_2

concentration values. Microcosms were maintained for the first 16 weeks of the experiment with a diurnal cycle set at 12/12 h (temperature 15 °C/12 °C), after which the diurnal cycle was switched to 14/10 h (temperature 18 °C/15 °C) for the duration of the experiment. The photosynthetically active radiation (PAR) at moss height ranged from 400 to 450 μmol m^{-2} s^{-1}.

Measurement of CO_2 net exchange, dissolved organic carbon and total nitrogen leachate

To obtain a measure of CO_2 net exchange three subchambers of each microcosm had air output drawn from the overall system, whereas the fourth subchamber was linked, via an automated gas sampler, to an infrared gas analyser (IRGA). An automated line-switching device linked to the IRGA allowed each of the 24 microcosms to be regularly sampled for CO_2 exchange every 72 min. A lag time of 3 min was used to make sure that the gas sample reaching the IRGA was not contaminated by the previous sample. In parallel, the IRGA continuously recorded the CO_2 concentration of the input air, sampled from the buffer chamber. The IRGA measurements were regularly checked and the IRGA recalibrated at least once a week. The difference between the input and the output CO_2 concentration was calculated, giving an instantaneous measure of subchamber CO_2 exchange. The values obtained from the moss-free microcosms were used to adjust the values for the microcosms containing moss, and then these adjusted values were summed for each month to obtain an index of CO_2 net exchange for each chamber.

We also measured net losses and gains in dissolved organic carbon (DOC) and total nitrogen (TN). The moss was watered bi-weekly with simulated rainwater containing the following ionic concentrations (mg L^{-1}): 1.56 Na^+, 0.19 Mg^{2+}, 0.56 Ca^{2+}, 0.16 K^+, 0.61 NH_4^+, 2.40 SO_4^{2-}, 1.74 NO_3^-, 2.98 Cl^-. The bi-weekly simulated rainwater solution was delivered as a fine spray equivalent to 5-mm rainfall (=20 mL per subchamber) per application. The throughflow leachate was collected from each of the four subchambers and pooled at the microcosm level, and then frozen until analysis at the end of the experiment. DOC and TN were measured for the leachate using an automated C and N analyser. Net losses or gains were calculated for each microcosm using a mass balance approach for each of the 20 collection dates.

Microarthropod richness and abundance

Microarthropods within moss subchambers were extracted using Tullgren funnels after 315 days and collected directly into vials containing a 7 : 2 : 1 ethanol:glycerol:water ratio over 48 h. The microarthropods were sorted into morpho-species and counted under a dissecting microscope (see Table S1 for faunal groups and counts). Morpho-species were subsequently grouped into five broad taxonomic categories: Collembola, Oribatida (oribatid mites), small fungivorous mites (mostly Prostigmata, some Oribatida), predatory mites (mostly Mesostigmata, some Prostigmata) and other mesofauna (<1% relative total abundance and included Oligochaetes (earthworms), Psocoptera (booklice), Isopoda (wood lice), Thysanoptera (thrips), Diptera (flies) and miscellaneous insect larvae). Microarthropod abundances were log transformed ($x + 1$) prior to analyses. We compared the difference in abundance between *continuous* and fragmented microcosm treatments for each morpho-species, and plotted the difference as a percent change from the *continuous* treatment ([ln(*continuous* – *island* abundance)/ln(*continuous* abundance)] × 100). Extinction due to fragmentation was observed as the number of species found in *continuous* but not in fragmented microcosms at the end of the experiment.

Statistical analyses

We quantified treatment differences in net CO_2 exchange, DOC and TN in leachate measures, and in the microarthropod communities at the end of the experiment. Data for net CO_2 exchange, DOC and TN in leachate were analysed using repeated-measures analysis of variance (RM-ANOVA) in STATISTICA 7 (Statsoft Inc. 2004). We analysed the joint response of microarthropod species richness, density and biomass to the experimental treatments using MANOVA (overall Wilk's lambda and univariate F values given) in STATISTICA 7, because their responses are known to be causally interdependent through resource competition and predator–prey interactions. We focused on overall effects of treatment on nutrient dynamics and faunal diversity, and three sets of planned contrasts reflecting our experimental design: (1) differences between *continuous* (treatment 4) and fragmented landscapes (treatments 1–3); (2) between connected (treatments 3 and 4) and unconnected landscapes (treatments 1 and 2) and (3) a delayed response in nutrient dynamics was tested by comparing treatment effects between connected and unconnected landscapes in the first half of the experiment with the second half of the experiment (midpoint = 150 days). Analyses t values refer to *a priori* contrasts (1 and 2) at one time point; contrast 3 was tested with a single-d.f. F value for a repeated-measures interaction with time.

RESULTS

Microarthropod richness and abundance

Fragmentation had a significant effect on total species richness (Fig. 1d, Wilk's $\lambda = 0.122$, $P = 0.012$) driven

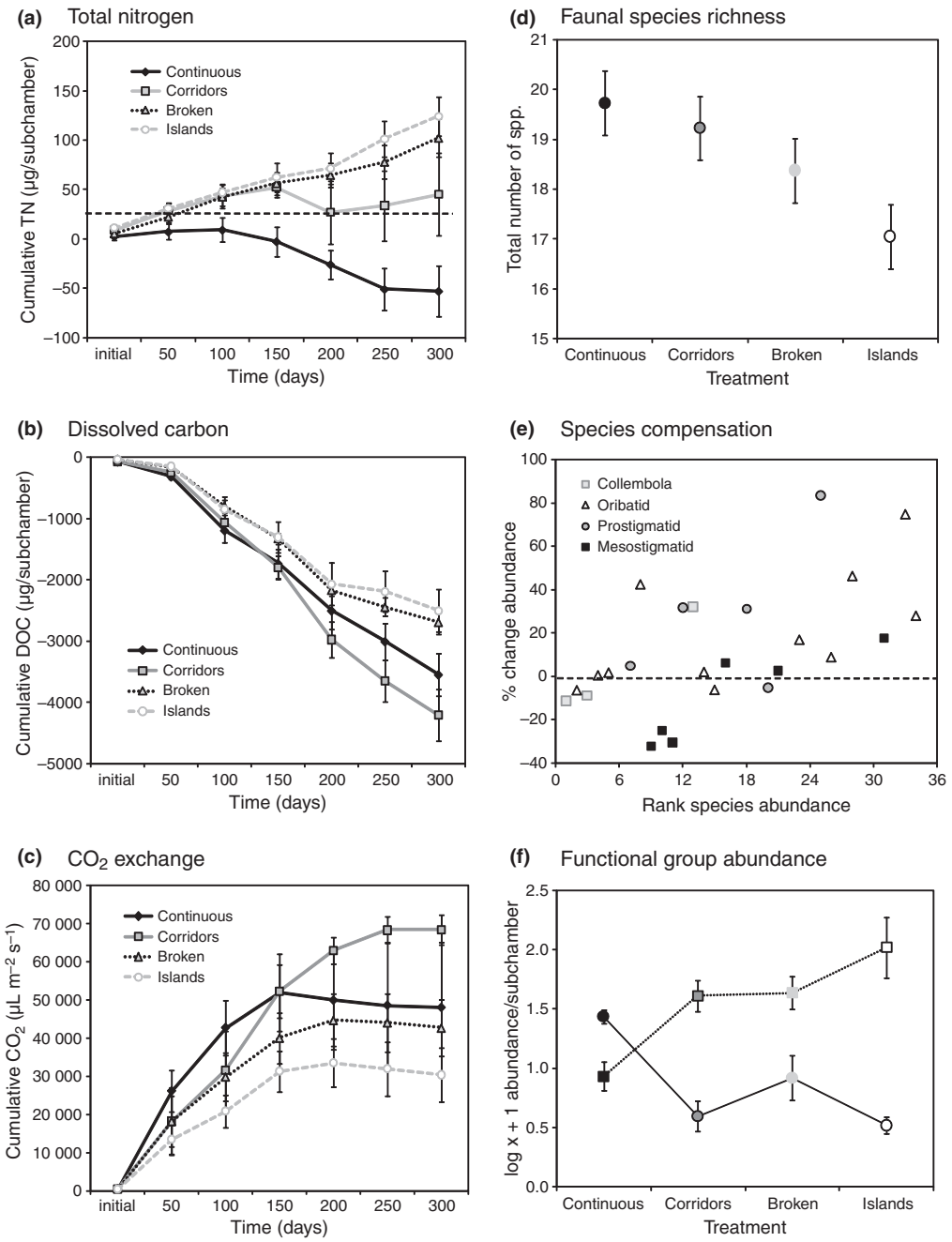

Figure 1 (a) Average cumulative total nitrogen (TN) lost or retained; (b) average total dissolved organic carbon (DOC) lost; (c) average cumulative CO_2 exchange in the four fragmentation treatments over 300 days (values are means ± SE); (d) average total species richness (number of species per moss fragment ± SE) in microcosms differing in extent of fragmentation and connectivity; (e) percent differences in ln(abundance) for *island* relative to *continuous* microcosms, plotted against the rank of species abundance; data shown do not include extinctions; (f) abundance of small fungivorous and large predaceous mites at the end of the experiment (315 days) (values are means ± SE fauna abundance (log x + 1) per microcosm subchamber).

mainly by the extinction of predators in fragmented habitats ($F_{3,16}$ = 11.391, P < 0.001; contrast 1: t = 5.569, P < 0.001; contrast 2: t = 3.659, P = 0.002). Additionally, abundant, large-bodied and predatory organisms (e.g. mesostigmatid mites) decreased in abundance following fragmentation (Fig. 1e), and accounted for seven out of 10 observed

extinctions in the *island* relative to the *continuous* treatments. Fragmentation was also associated with a significantly greater species richness of small fungivorous mites (prostigmatid and oribatid mites) in comparison with the *continuous* treatment ($F_{3,16} = 3.552$, $P = 0.038$; contrast 1: $t = 2.603$, $P = 0.019$).

Total microarthropod densities did not substantially differ among treatments (Wilk's $\lambda = 0.186$, $P = 0.064$), a result that is explained by countervailing shifts in the densities of the major taxonomic groups (see Table S1). In particular, large predatory mite density in the *continuous* treatment was significantly greater than in the fragmented treatments ($F_{3,16} = 11.513$, $P < 0.001$; contrast 1: $t = 5.341$, $P < 0.001$), whereas densities of small fungivorous mites were significantly lower in the *continuous* treatment versus the fragmented treatments ($F_{3,16} = 7.007$, $P = 0.003$; contrast 1: $t = 4.176$, $P < 0.001$) (Fig. 1f). We also observed the same large countervailing shifts in predator and fungivorous mite biomass (see Supporting Information and Fig. S2). Total collembola biomass did not significantly differ amongst treatments ($F_{3,16} = 1.602$, $P = 0.228$). A similar analysis for the Isotomidae (the dominant collembola group representing >75% of collembola biomass) indicated large differences in mean biomass between the *continuous* treatment and the fragmented treatments (see Fig. S3) but these effects were not statistically significant ($F_{3,16} = 1.337$, $P = 0.297$).

CO_2 exchange, dissolved organic carbon and total nitrogen leachate

Habitat fragmentation affected whether there was net release or retention of nitrogen in the microcosms. The most connected treatment (*continuous*) remained in nitrogen balance during the first half of the experiment but then progressively lost nitrogen in the second half while, in contrast, the most fragmented treatments (*broken*, *island*) showed consistent nitrogen gains (Fig. 1a, $F_{3,16} = 7.843$, $P = 0.002$; contrast 1: $t = 4.571$, $P < 0.001$; contrast 2: $t = 3.888$, $P = 0.001$). As predicted, we observed a delay in the onset of differences in nitrogen dynamics and this was related to connectivity. Strikingly the *corridor* treatment diverged from the isolated (*broken*, *island*) treatments after 150 days, and grouped statistically with the *continuous* treatment (Fig. 1a; contrast 3: $F_{1,16} = 13.163$, $P = 0.002$). These results demonstrate that the overall effect of habitat loss and fragmentation caused this detrital system to have net nitrogen uptake, whereas continuous or connected habitats maintained net nitrogen availability. Although the *corridor* treatment responded initially like the fragmentation treatments, the corridors exerted a delayed functional effect that increasingly mitigated the nitrogen net uptake effect of fragmentation.

We observed similar effects of fragmentation on our measures of carbon exchange. All treatments consistently lost DOC during the course of the experiment with the connected treatments (*continuous*, *corridor*) showing significantly greater loss than the unconnected treatments (*broken*, *island*) beyond Day 150 (Fig. 1b, $F_{3,16} = 3.067$, $P = 0.058$; contrast 3: $F_{1,16} = 9.640$, $P = 0.007$). Strong diurnal fluctuations in CO_2 flux confirmed that the moss and decomposer community were physiologically active throughout the experiment. Similar to patterns in DOC, the cumulative ecosystem CO_2 exchange increased through time for all treatments, showing net CO_2 respiration of the decomposer system. A large difference in cumulative CO_2 appeared between *corridor* and *broken* corridor treatment beyond Day 150 and persisted until the end of the experiment. The much larger *continuous* moss treatment behaved like the *corridor* treatment until Day 100 and then attained a plateau. During the experiment, the connected treatments (*continuous*, *corridor*) had a greater cumulative CO_2 respiration than the unconnected treatments (*broken*, *island*), although this effect was not statistically significant (Fig. 1c, $F_{3,16} = 1.738$, $P = 0.199$; contrast 2: $t = 2.074$, $P = 0.055$). Taken together, the DOC and CO_2 data suggest that *continuous* and *corridor* treatments had greater decomposition.

DISCUSSION

We used a species-rich natural microcosm under controlled experimental conditions to demonstrate that habitat loss and fragmentation can induce non-random extinction and affect multiple aspects of ecosystem functioning. The experiment revealed joint community and ecosystem responses to altered habitat connectivity that although predicted by theory has remained largely untested by experiment. Our results indicate that habitat fragmentation impacts ecosystem functions and generates an ecosystem function debt, characterized by a long-term alteration in ecosystem attributes persisting after the occurrence of fragmentation. Most importantly these functional effects on nitrogen and carbon dynamics were partly mitigated by the presence of corridors. In the case of nitrogen a clear recovery occurred after a significant delay (Fig. 1) that represents several generations for some microarthropod groups in this system.

Non-random extinction and ecosystem function

Habitat loss and fragmentation in the moss microcosms led to a significant decrease in microarthropod species richness and corresponding extinctions in primarily large-bodied top predators. The mitigating effects of corridors on species richness were small (*c.* 5% of total richness) compared with other field-based studies (e.g. Gilbert *et al.* 1998; Damschen *et al.* 2006). This is expected because fluctuations in humidity, the main driver of mortality in this system in

the field, were controlled in the experiment, reducing the potential for dispersal-dependent rescue effects.

Fragmentation treatments also showed increased abundance of small fungivorous mites (prey) compared with the *continuous* treatment that had high predator levels, suggesting top–down predatory control of fungivores and prey release under lower predation pressure. Although some detrital food web studies fail to show top–down effects of predators (Mikola & Setälä 1998; Laakso & Setälä 1999), prey abundance can decrease with increased predators (Cole *et al.* 2004; Lenoir *et al.* 2007), and trophic cascades which permeate through three or more trophic levels in detrital food webs are not uncommon (Hedlund & Sjögren Öhrn 2000; Cortet *et al.* 2003). Furthermore, trophic interactions in detrital systems have a large potential to influence ecosystem processes because the abundance and biomass of the microbial and microbivorous communities control energy flow and nutrient cycling (Seastedt 1984).

We hypothesize that the effects of fragmentation on ecosystem functions were due to a trophic cascade linking top–down extinctions and increase in prey abundance and biomass to nutrient dynamics. The non-random loss of top predators resulting in prey population increases is well established. Cascading functional effects of extinctions in soil food webs are expected to significantly alter ecosystem processes from local to global scales (Wolters *et al.* 2000). For example, Cole *et al.* (2004) found that higher predator abundance and corresponding lower prey abundance resulted in lower release of nitrogen from the system.

Trophic effects observed here are entirely consistent with our understanding of detrital system dynamics (Seastedt 1984; Osler & Sommerkorn 2007). The functional effects of the trophic cascade on nitrogen and carbon were likely driven by grazing-stimulated fungal growth and fungal-driven decomposition (Bradford *et al.* 2007), and immobilization of nutrients within prey (grazer) biomass (Setälä *et al.* 1991). Predatory fauna are efficient assimilators of carbon and nitrogen, and excrete a high proportion of the total nitrogen they ingest (Osler & Sommerkorn 2007). In *continuous* microcosms the persistence of predators and a sufficient level of predation on lower trophic levels maintained nitrogen availability (Setälä *et al.* 1991) via high assimilation and release rates (Fig. 2a). Thus over the duration of the experiment net available nitrogen was leached from the *continuous* treatment (Fig. 1a). The extinction of predatory arthropods in the fragmented treatments induced a trophic cascade (Cole *et al.* 2004; Hedlund *et al.* 2004; Lenior *et al.* 2007) that enhanced grazing-stimulated fungal growth and a net uptake and immobilization of nitrogen (Fig. 2b). Microbial grazing by microarthropods can stimulate microbial growth (Seastedt 1984), immobilizing nitrogen within the microbial and/or grazer fauna biomass (Mikola *et al.* 2002). Microbial grazers (small fungivorous prey species) are poor assimilators of nitrogen and release a low proportion of the nitrogen they ingest (Osler & Sommerkorn 2007). Thus over the duration of the experiment net nitrogen uptake was observed in the fragmented treatments (Fig. 1a). Nitrogen dynamics in particular is strongly governed by microbes. The processes of mineralization (nitrogen release) and immobilization (nitrogen uptake) occur simultaneously within detrital systems, with net immobilization occurring when microbial growth is limited by nitrogen.

The ecosystem effects of corridors

Species loss and ecosystem dynamics were mitigated in larger and more connected habitats (*c.* 50% for nitrogen and 100% for dissolved carbon). These results significantly extend previous work showing that habitat corridors can slow extinction and mitigate the community effects of habitat fragmentation (Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002; Tewksbury *et al.* 2002; France & Duffy 2006; Brudvig *et al.* 2009). Although predicted by metacommunity theory (Loreau *et al.* 2003; Gonzalez *et al.* 2009), few experiments have clearly demonstrated the joint community and ecosystem impacts of altered habitat connectivity in naturally complex communities (Didham *et al.* 1996; Gonzalez & Chaneton 2002; France & Duffy 2006) and none have clearly shown the effect on nutrient fluxes.

The delayed TN and DOC dynamics we observed in the *corridor* treatment is a previously unreported ecosystem effect of corridors. Up to day 150, response of the *corridor* treatments was similar to that of the *broken* and *island* treatments, but after Day 150 the trajectory of these treatments showed a distinct change. In the case of DOC *corridor* treatments resembled more the *continuous* treatment, and in the case of TN was intermediate between *continuous* and disconnected treatments. These are striking results given that the only difference between the *corridor* and *broken* corridor treatment was a 4-mm-thick division (5% of corridor length). The delayed corridor effects on nutrients are likely due to spatial dynamics (e.g. movement and dispersal) that we were unable to quantify because microarthropods could only be sampled destructively on one occasion.

Several reasons for the ecosystem effects of corridors can be identified. Corridors likely facilitated the movement of all groups within the metacommunity and movement is known to affect population and ecosystem processes; generally through spatial averaging (e.g. Ives *et al.* 2004; Gonzalez *et al.* 2009) and more specifically through the effects of mobile link species (Lundberg & Moberg 2003). However, research on a grazer-fungus interaction in patchy soil habitats suggests a mechanism by which corridor-facilitated movement may translate into enhanced fungal activity (metabolic

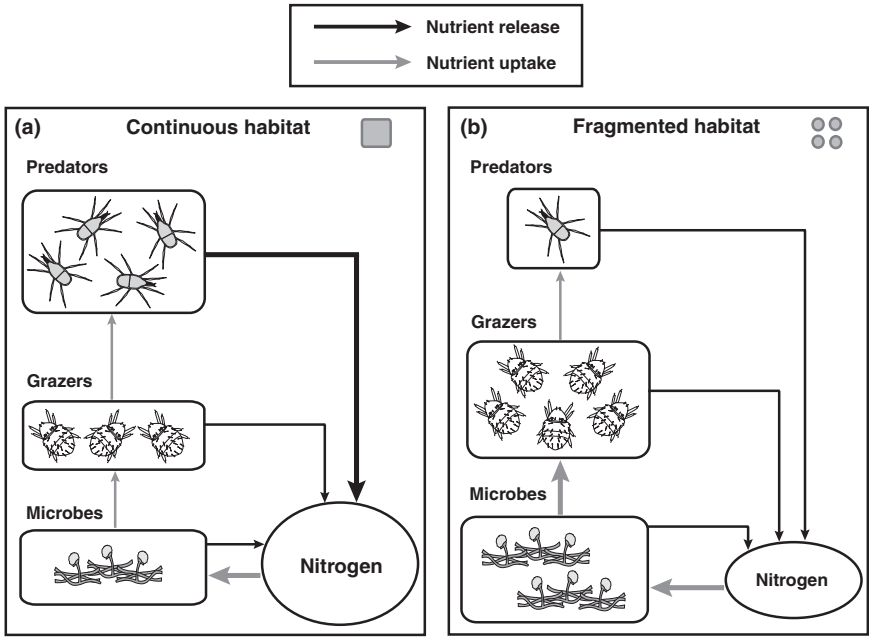

Figure 2 A simplified diagram of the effects of predator extinction due to fragmentation on nitrogen availability in the moss-microarthropod microcosm system. Grey arrows indicate assimilation and subsequent immobilization of nitrogen within the food web. Nitrogen is assimilated through feeding and immobilized within trophic level biomass. Black arrows represent the process of nitrogen release whereby organically bound nitrogen is released as dissolved organic and inorganic nitrogen into the system. Predators are efficient assimilators and release a high proportion of the N they ingest. Grazers are poor assimilators and release a low proportion of the N they ingest. (a) In *continuous* habitats, predators maintain N availability in the system by high assimilation and release rates. Over time nitrogen becomes available for leaching from the system. (b) Following fragmentation and the subsequent loss of predators from the food web, both grazer and microbial biomass increase, immobilizing a greater amount of nitrogen within these trophic levels, and releasing little to the system. Net nitrogen uptake is observed.

and growth rate) and a lagged change in mean nutrient flux (Bengtsson *et al.* 1993).

Bengtsson *et al.* (1993) studied the effect of spatial subdivision on fungal growth using experimental systems of fungal patches connected by corridors of different length (i.e. corridors of 7 cm or 14 cm) grazed by a common fungivorous collembola species *Onychurius armatus*. During a 6-week experiment, they showed that fungi grazed by collembola exhibited enhanced growth (three to fourfold) by subdivision of the mycelium into discrete patches (when compared with a large control patch of equivalent area) and that this effect was strongest for slow-growing fungi when patches were connected by the short corridors (7 cm), whereas the response of fast-growing fungi was greatest with longer corridors (14 cm). Significantly, this effect took several weeks to emerge, and persisted for the duration of the experiment (6 weeks). Bengtsson *et al.* (1993) hypothesized that collembola grazing on distinct patches connected by corridors must spend time travelling between and searching for new fungal resources, and that the re-growth response of the fungi following grazing depends upon the travelling time between patches. Thus spatial fragmentation with corridors modulates grazing pressure to a level more favourable to fungal activity, a spatial mechanism that requires no differences in grazer densities between treatments and is therefore likely at play in our *corridor* treatments. Moreover, the enhanced fungal activity would increase decomposition because fast-growing hyphae are known to produce more extracellular enzymes (Hedlund *et al.* 1991). Taken together the results of Bengtsson *et al.* (1993) may explain why in our experiment DOC loss was greater in the *corridor* treatment than the *continuous* treatment and why this response was lagged.

The results of Bengtsson *et al.* (1993) thus suggest a role for collembola as mobile link organisms (Lundberg & Moberg 2003). Mobile link organisms actively move in the landscape and functionally connect habitats in space and time (e.g. pollinators, predators, seed dispersers). It has been proposed that these species can act as process linkers and may be particularly important for the recovery of ecosystems following disturbance and fragmentation. Although no soil microarthropod groups have been formally identified as mobile links, collembola are common and important dispersers of mycelial fragments and fungal propagules (Lussenhop & Wicklow 1984), which when combined with their grazing effects may partly explain the effects of corridors we observed in the connected landscapes. More detailed experiments on collembola

dispersal in these moss landscapes will reveal the strength of these hypotheses.

CONCLUSION

Habitat loss and fragmentation markedly affected carbon and nitrogen dynamics and this was driven by top–down extinction and the subsequent community compensation amongst prey species. Strikingly, both biodiversity loss and change in ecosystem fluxes were mitigated in the habitats connected by corridors, which were more similar to the *continuous* than to fragmented habitat. A number of important ecological effects are now attributed to habitat corridors and habitat connectivity in general (Crooks & Sanjayan 2006). They can reduce extinction (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002), alter plant and animal interactions (Tewksbury *et al.* 2002), and alter patterns of movement (Haddad & Tewksbury 2005) and spatial biodiversity (Brudvig *et al.* 2009). The novel result shown here is that they can also alter ecosystem processes and mitigate the ecosystem effects of habitat fragmentation. In this experiment, the ecosystem effects of corridors were surprisingly delayed. The temporal effects we observed point to the value of experiments with natural microcosms as a means of bridging theory and field. These results outline the potential implications for studies in conservation biology and agroecology, where debates about corridors point to their costs, but do not evaluate their benefits for ecosystem functioning and services. We conclude that knowledge of habitat connectivity and spatial processes is essential to understand the magnitude and timing of ecosystem perturbation in fragmented landscapes.

AUTHOR CONTRIBUTIONS

A.G., F.G and P.C. designed the experiment, P.S. performed the experiment, collected the data, Z.L. sorted and identified the fauna, Z.L. performed the analyses, Z.L., P.S. and A.G. wrote the paper. All authors discussed the results and commented on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Image of the PVC-based chambers used to maintain the moss microcosms.

Figure S2 The effect of fragmentation on the biomass (mean $mg/m^2 \pm SE$) of large predaceous mites (circles) and small fungivorous mites (squares) at the end of the experiment (315 days).

Figure S3 The effect of fragmentation on the biomass (mean $mg/m^2 \pm SE$) of the dominant collembola group Isotom-

idae (~75% of collembola biomass) at the end of the experiment (315 days).

Table S1 Average density of mesofauna (# individuals / m^2) collected following 315 days incubation in four fragmentation treatment microcosms.

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