



Landscape geometry determines community response to disturbance

Brian M. Starzomski and Diane S. Srivastava

B. M. Starzomski (starzom@zoology.ubc.ca) and D. S. Srivastava, Biodiversity Research Centre and Dept of Zoology, The Univ. of British Columbia, 6270 University Blvd., Vancouver, Canada, BC V6T 1Z4. Present address for BMS: Bamfield Marine Sciences Centre, 100 Pachena Rd., Bamfield, British Columbia, Canada, V0R 1B0.

Ecological communities are impacted by anthropogenic changes in both habitat geometry (i.e. amount, shape, fragmentation and connectivity of habitat) and disturbance regime. Although the effect of each of these drivers on diversity is well-documented, few studies have considered how habitat geometry and disturbance interact to affect diversity. We used a miniature landscape of moss patches to experimentally manipulate both habitat geometry and disturbance frequency on microarthropod communities. Species richness and abundance in local patches declined linearly with disturbance rate in all experimental landscapes, but the speed of this decline (a measure of ecological resilience) depended on the size and connectivity of the surrounding region. Reductions in region size had little effect on community resilience to disturbance until habitat loss resulted in complete loss of connectivity between patches, suggesting a threshold in community response to habitat loss. Beyond this threshold, repeated disturbance resulted in rapid declines in patch species richness and abundance and substantial changes in community composition. These effects of habitat geometry and disturbance on diversity were scale-dependent. Gamma (regional-scale) diversity was unaffected by habitat geometry, suggesting experimental reductions in alpha (local-scale) diversity were offset by increases in beta diversity. There was no effect of body size, abundance, or trophic position in determining species response to disturbance. Taxonomic grouping had a weak effect, with oribatids less affected by drought. We conclude that, in this system, dispersal from the surrounding metacommunity is vital in allowing recovery of local communities from disturbance. When habitat loss and fragmentation disrupt this process, extinctions result. Studies that examine separately the effects of habitat alterations and disturbance on diversity may therefore underestimate their combined effects.

Humans have radically impacted landscapes, both in terms of habitat loss and fragmentation, and in terms of disturbance regime. These changes have all separately been shown to affect ecological communities. For example, local richness is generally reduced by habitat loss (Turner 1995) and, depending on context, is either increased or decreased by habitat fragmentation and by intensified disturbance (Didham et al. 1998, Fahrig 2003). It is not clear, however, how the effects of changed landscape geometry (i.e. the amount, shape and connectivity of habitat) interact with a changed disturbance regime in affecting communities. Recently, Sala et al. (2000) identified such interactions between anthropogenic changes in the environment as the largest source of uncertainty in predicting future loss of

biodiversity. Here we report a study that examines how landscape geometry impacts the ability of communities to recover from disturbance, that is, resilience. Ecological resilience refers to the amount of impact a system can sustain before that system is pushed to an alternate state or domain (Holling 1973). We define a highly resilient community as one which remains near or returns to pre-disturbance levels of species richness, abundance and composition.

Populations in local patches may recover from catastrophic disturbance through immigration from the neighbouring region, via the “rescue effect” (Brown and Kodric-Brown 1977) if populations are merely reduced, or through metapopulation dynamics (Hanski 1999) if populations have gone extinct. Since landscape

characteristics affect the dispersal of organisms (Taylor et al. 1993, Roland and Taylor 1997), a straightforward prediction is that local diversity is strongly affected by the interaction between landscape geometry and disturbance. Less obvious is the direction of the interaction. For example, consider a community where coexistence between competitors is maintained by tradeoffs in species' abilities to compete for resources or colonize new habitat. Reduced connectivity (in this study we explicitly define connectivity as habitat joining two or more patches) may impede the immigration of a dominant competitor into the disturbed area, slowing the process of competitive exclusion and thus increasing local diversity (Nee and May 1992). However, reduced connectivity will also impede immigration of even the good colonizers, and this negative effect on local diversity may override the effects of reduced competition. For example, in protist microcosms, reduced dispersal rates led to lower diversity after disturbance (Warren 1996a). A number of empirical and theoretical results suggest that both positive and negative effects of dispersal on local richness can occur, leading to a unimodal pattern (Mouquet and Loreau 2003, Kneitel and Miller 2003, Cadotte 2006a, 2006b). Reductions in the size of the region surrounding a disturbed patch may also have complicated effects on local diversity. Smaller regions contain fewer species (Rosenzweig 1995). Island biogeography theory therefore predicts that smaller regions will supply fewer new species per unit time to a disturbed patch, leading to a local reduction in species diversity. However, recent theoretical and empirical studies suggest that reductions in regional richness can have either negative or neutral effects on local diversity, with the exact pattern depending on assembly time, trophic rank and dispersal ability of taxa (Mouquet et al. 2003, Fukami 2004, Munguia 2004).

So far, we have considered how landscape geometry and disturbance affect local diversity. However, ecologists are interested in species diversity at multiple spatial scales, typically categorized as local (alpha diversity), regional (gamma diversity) and the turnover in species between local areas in a region (beta diversity). In some scenarios, effects on gamma diversity may simply follow alpha diversity. For example, reduced connectivity between local patches may lead to reductions in both alpha and gamma diversity, as species go extinct first locally (due to reduced rescue effects) and then regionally. Dispersal, however, tends to homogenize communities (Cottenie and De Meester 2004). Thus reduced connectivity could also result in large differences in species composition amongst local patches (high beta diversity), leading to increased gamma diversity. For example, Forbes and Chase (2002) found that reduced dispersal of zooplankton amongst aquatic mesocosms resulted in higher beta and hence higher

gamma diversity. Reductions in region size are predicted to reduce gamma diversity, as smaller regions almost always contain fewer species (Rosenzweig 1995).

Although for clarity we have, in the above, separated the effects of reducing region size and region connectivity, in practice these two effects are tightly coupled. As habitat is progressively lost from a landscape, regions change from intact habitat to interconnected areas to unconnected patches (Simberloff 2000, Fahrig 2003). Landscape models using percolation theory suggest a threshold in loss of connectivity occurs with loss of approximately 40% of the original area (With et al. 1997). In this study we progressively reduce the size of regions around local patches until the patches become completely unconnected. Thus we use a realistic scenario of habitat loss to examine how landscape structure affects community resilience to disturbance. We predict that community resilience will be particularly reduced when enough habitat has been removed to disconnect local patches. Population models predict such thresholds in response to habitat loss (Moilanen and Hanski 1995, Solé et al. 2004), but this question has rarely been empirically studied (Villard et al. 1999).

Reductions in diversity reflect the loss of individual species. Species are likely to differ in their susceptibility to both disturbance and habitat change. Other studies have found differences amongst taxa in extinction risk which correlate with traits such as trophic position, abundance and body size (reviewed by Lawton 1994, Gaston and Blackburn 1995, Rosenzweig 1995). We examine whether species traits and taxonomic affiliation predict responses to our experimental treatments.

The experiment was conducted using the microarthropod community (predominately mites, *Acar*i, and springtails, *Collembola*) within moss patches. The small size of microarthropods (most species <1 mm) results in high diversity within a few cm² of moss, and allows us to address landscape questions at experimentally-tractable scales (Gonzalez 2000, Gonzalez and Chaneton 2002, Hoyle 2004, 2005, Srivastava et al. 2004). We created miniature moss landscapes differing in regional area and connectivity, and subjected local patches in each landscape to a range of simulated drought frequencies. This drought disturbance is similar to the natural drought cycle in moss habitat in coastal British Columbia, where the experiment was conducted.

We test the following hypotheses: (1) landscape geometry affects community resilience to disturbance, where resilience is measured as the return to undisturbed levels of richness, abundance and composition; (2) there is an abrupt change (a threshold) in resilience when habitat loss results in loss of connectivity between local patches, (3) effects of landscape geometry on the

resilience of diversity depend on whether diversity is measured at local or regional scales.

Methods

Study site and system

The experiment was conducted using the community of microarthropods inhabiting a moss (*Polytrichum* and *Bryum* spp.) covered granitic outcrop in the Univ. of British Columbia's Malcolm Knapp Research Forest in Haney, British Columbia, Canada (49.216 N, 122.515 W). The Research Forest is situated at an elevation of 600 m, with forest cover of western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western redcedar (*Thuja plicata*). The microarthropods (predominantly mites, *Acari*, and *Collembola*) inhabiting the moss mats are found in high abundances, and 200 or more morphospecies (hereafter referred to as species) can be found in small areas (less than 20 m², pers. obs.).

In an area measuring 4 × 6 m, experimental moss patches of various shapes and sizes were created by scraping moss and soil from the rock surface until only bare rock was showing between them. In similar moss systems such areas of bare rock constitute effective barriers to movement by soil-dwelling microarthropods (Gilbert et al. 1998).

Experimental design

To simulate different region sizes, 20 circular moss regions were created by scraping continuous moss from rock (Fig. 1). Four different sizes of region (n = 5 replicates per treatment) were created: a large-region treatment (treatment A: 40 cm diameter), a medium-region treatment (B: 28 cm diameter), a small-region treatment (C: with the four local patches, each 10 cm in diameter, with a perimeter of 1 cm-thick moss, and a 2 cm wide moss corridor between regions), and a 'no' region treatment (treatment D), with no connections between local patches. From the original continuous moss carpet, replicated treatments were positioned randomly on the rock surface, with at least 10 cm of bare rock separating each region replicate. A plastic template of each region size was used to ensure the same patch size was created for each replicate. Each region contained within it four 10 cm diameter circular 'plugs' of moss (the local patches for sampling) that were subjected to variable frequencies of disturbance over the course of four months. These plugs constitute a habitat patch of moss embedded within the larger region of moss, and are thus an open community. The total undisturbed area for each of the regions was as follows: A- 942.5 cm², B- 301.6 cm², C- 154.2 cm², D- 0 cm². The response variables were the number of individuals, species richness, and community composition of microarthropods in the moss plugs. All replicates were left

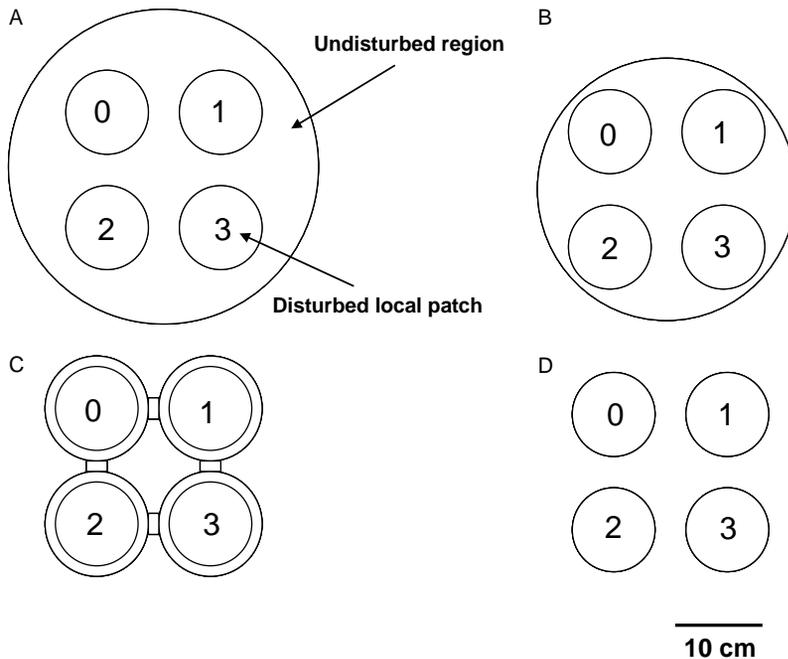


Fig. 1. Experimental design. A = large region, B = medium region, C = small region, D = no region. 0 = not disturbed, 1 = disturbed once/month for 1 month (last 1 month), 2 = disturbed once/month for 2 months (last 2 months), 3 = disturbed once/month for 3 months.

undisturbed for one month prior to the beginning of the disturbance treatments, to allow the communities within the moss to respond to the creation of the region-size treatments.

To simulate different disturbance regimes, each of the four local patches (moss plugs) within the region was subjected to different rates of disturbance over four months, from December 2002 to April 2003. Three disturbance levels were chosen, along with one control (termed disturbance level 0). The moss plug under high disturbance (disturbance level 3) had all microarthropods removed by Tullgren funnel extraction three times over three months (January–March). In the medium disturbance level (disturbance level 2), the moss plug was disturbed once a month for the final two months (February–March), and the low disturbance (disturbance level 1) treatment was disturbed once (in March). For the undisturbed treatment (disturbance level 0), the plug was extracted only at the end of the experiment (April). Every month each 10 cm moss plug was removed from the field, placed in a resealable plastic bag, and transported 60 km to a lab at the University of British Columbia. Each moss plug was then placed in a Tullgren funnel for 36 h. Tullgren funnels use a humidity gradient created by a combination of light and heat (Knudsen 1972) to cause the microarthropods found in the moss to drop into a vial of 70% ethanol, 20% glycerol and 10% water. If a disturbance was being conducted on an individual plug, the 40 W light bulbs of the Tullgren funnels were turned on for 36 h to remove all microarthropods. For the undisturbed treatments, each plug was placed in the funnel, but the light was not turned on. At the end of four months (corresponding to a generation or more for many of the microarthropod taxa, Walter and Proctor 1999), all moss plugs were removed from the field and brought to the lab where microarthropods were removed by Tullgren funnel extraction. While the extraction efficiency of Tullgren funnels is very high, it is likely this efficiency was less than 100%, but consistent for all plugs. All plugs were extracted at the end of the experiment and microarthropods collected. All microarthropods were stored in vials at 4°C until manually sorted under a 60 × dissecting scope. Microarthropods with distinct morphological characteristics were described as individual morphospecies, using various keys (Krantz 1978; unpublished keys provided by the Ohio State University Acarology Summer Program), and identification by experts (D. Walter, H. Proctor, H. Klompen, V. Behan-Pelletier, J. Addison). Descriptions and a key for all the morphospecies found in this study are available on the world wide web at <http://www.zoology.ubc.ca/~srivast/mites>, and a list of the morphospecies is found in Appendix S1.

Analyses

A priori planned comparisons of richness and abundance in regions A, B and C (together) vs D (to look for threshold effects that occur when decreased region size causes fragmentation and loss of connectivity), A and B vs C (to look for effects of increased fragmentation), and A vs B (to look for the effect of region size) were performed using t-tests. A caveat must be mentioned here about covariance between region size and connectivity. When the surrounding region becomes small enough to cease to exist, local patches necessarily become disconnected. Compared to region C, region D has both decreased region size and decreased connectivity. Similar concerns may be raised about the change in edge:area ratio, or area of disturbed moss in this system. We make the point that all these factors co-vary with loss of habitat and regional area in nature; we therefore conservatively interpret our response as affected by both loss of connectivity and region area, rather than being caused solely by one or the other.

To look for trait predictors for differences in response to disturbance, microarthropods were placed in taxonomic groups (collembola, adult and juvenile oribatids, prostigmatids and mesostigmatids). Morphospecies were assigned to a trophic level based on taxonomy and natural history (detritivorous/fungivorous oribatids and collembola were assigned to trophic level 1, small prostigmatid nematode feeders to trophic level 2, arthropod-feeding prostigmatids and mesostigmatids to trophic level 3, and pseudoscorpions, staphylinid beetles, and spiders to trophic level 4; Krantz 1978, Walter and Proctor 1999). For each region treatment, effect sizes for each species' response to disturbance were calculated by taking the natural log of the quotient of the number of individuals present in the three times-disturbed plugs (pooled over all replicates) divided by those present in the undisturbed plugs. Analysis of the effect of body size on response to disturbance used a body size index defined as a species' body length multiplied by body width in millimetres (Davies et al. 2000), divided by 1000.

We cannot assess the effects of abundance on disturbance response in the same way as the other traits because less abundant species (where less abundant species are defined as those with fewer than five individuals) are less likely than common species to be sampled in a post-disturbance plug, simply due to their lower numbers. Such sampling effects, however, should not affect the proportional decline in abundance as disturbance increases. We therefore compared the slopes of the regressions of mean proportion of individuals remaining between the undisturbed and disturbance levels 1, 2 and 3 separately for regions A through D.

Statistical analyses were conducted using NMDS and ANOSIM routines in Primer 5 for Windows (Plymouth Marine Laboratories), t-tests, ANOVA, ANCOVA and linear regression in R version 2.0.1 (R Development Core Team 2004) and PopTools within Microsoft Excel (CSIRO and Microsoft corporation). For NMDS plots, square-root transformed abundance data was first used to construct a Bray-Curtis similarity matrix of region and disturbance levels, then graphed using Hierarchical Agglomerative Clustering.

All microarthropods were measured using a Leica™ MZ16 A stereomicroscope and Auto-Montage 3D reconstruction software (Syncoscopy Corporation).

Results

A total of 26 274 individuals and 163 species were counted in this study; an appendix containing species data can be accessed at the online site (Appendix O15547 at www.oikos.ekol.lu.se).

We calculated the mean alpha richness in the highest disturbance treatment (disturbance level 3), for each region. Planned comparisons of all connected (mean richness across all disturbance level 3 plugs for regions A, B and C) and unconnected (region D) regions showed that connected regions had a higher number of individuals (t-test with unequal variances, $p = 0.043$, $DF = 77$) and species (t-test with unequal variances, $p = 0.024$, $DF = 77$). There was no significant effect of reduced region size on species richness or abundance when patches were connected to each other by at least some habitat (mean richness across all disturbance level 3 plugs for regions A and B vs C) nor when the entire perimeter of the patch was connected to the region (A vs B) (t-tests, all p -values $\gg 0.05$, $DF = 57$). Increased disturbance caused a statistically significant decrease in the number of species (Fig. 2a), though not in the number of individuals (Fig. 2b), across all region size treatments. There was a significant decrease in both richness and abundance in region D (Fig. 3a–b).

Species' abundances increased with fragmentation of the moss habitat. In the undisturbed plug of the unconnected treatment, D, total abundance (mean = 620, $SD = 194$, range = 427 to 863) increased above that seen in the undisturbed local patches of the larger and connected region sizes (A, B, C; mean = 372, $SD = 140$, range 184 to 639). With disturbance, however, abundances within the unconnected treatment were reduced below the levels of the others (Fig. 2b). Species richness and abundance in the smallest region samples (D- the unconnected region) decreased at a much greater rate than those in the connected regions; for species richness the decrease was 2.5 times faster, and for number of individuals, 4 times faster (Fig. 3a–b). To avoid the potential of spatial covariance

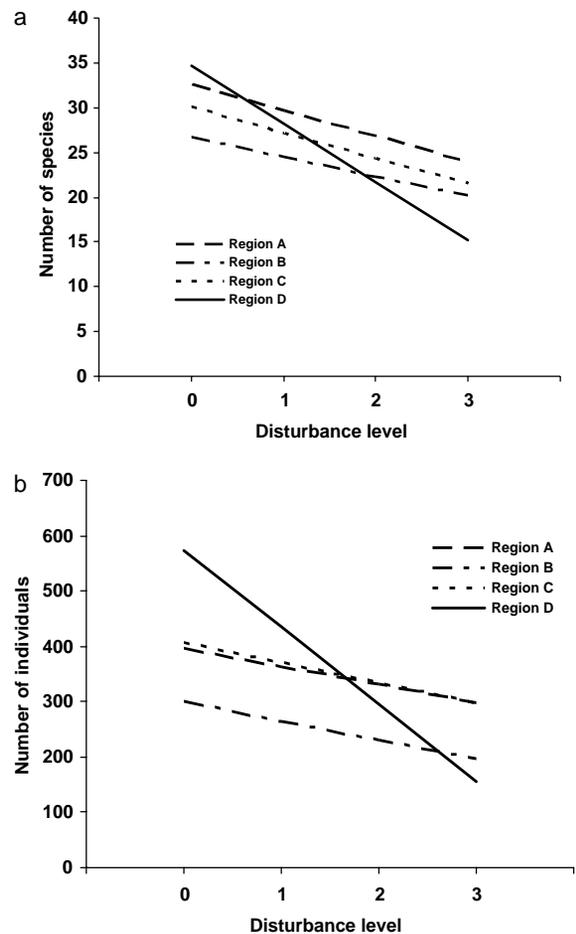


Fig. 2. The relationship between disturbance and species richness (a), and disturbance and abundance (b), as a function of region size. Disturbance measured from 0 (no disturbance) to 3 (highest disturbance), and region size from A (largest region) to D (no region). For species vs disturbance: region A- $y = -2.88x + 35.5$, $R^2 = 0.89$; B- $y = -2.18x + 28.79$, $R^2 = 0.90$; C- $y = -2.84x + 33.04$, $R^2 = 0.90$; D- $y = -6.5x + 41.85$, $R^2 = 0.94$. For individuals vs disturbance: region A- $y = -32.32x + 428.50$, $R^2 = 0.50$; B- $y = -34.78x + 333.26$, $R^2 = 0.70$; C- $y = -36.66x + 446.83$, $R^2 = 0.27$; D- $y = -139.66x + 727.77$, $R^2 = 0.93$. Error bars of slope values are shown in Fig. 3.

in the design (disturbance treatments are nested within the region treatments), the slopes of all species richness vs disturbance regressions were compared in an ANOVA, using one slope parameter per regional replicate ($n = 5$). The richness–disturbance slope of region D was significantly steeper than that of the other regions (region size: $F_{3,16} = 3.71$, $p = 0.03$, only slope for region D significantly different from the regions A, B and C: Fisher's LSD).

Mean community composition (species richness and abundance) changed in response to disturbance,

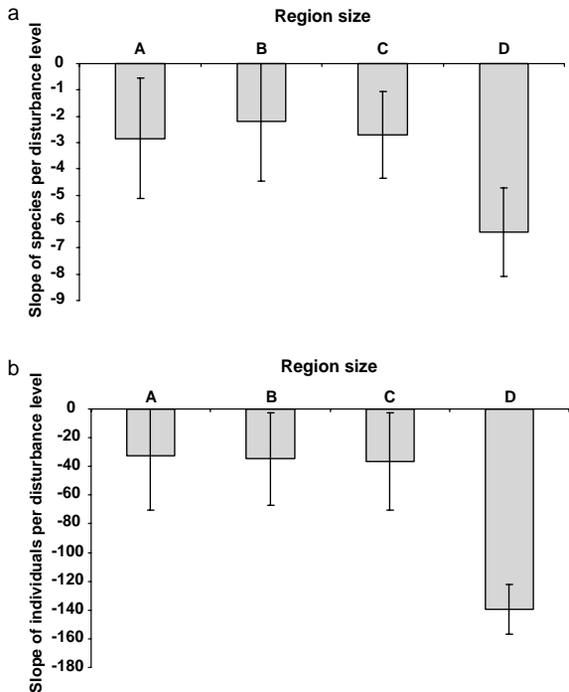


Fig. 3. Mean (\pm SE) of the slopes of disturbance frequency versus species richness per region (a), and disturbance frequency vs abundance per region (b), for region sizes, A (largest region) to D (no region).

especially in the smallest and most fragmented regions (Fig. 4). Undisturbed patches had similar composition regardless of region size. Increasing disturbance frequency lead to greater change in community composition

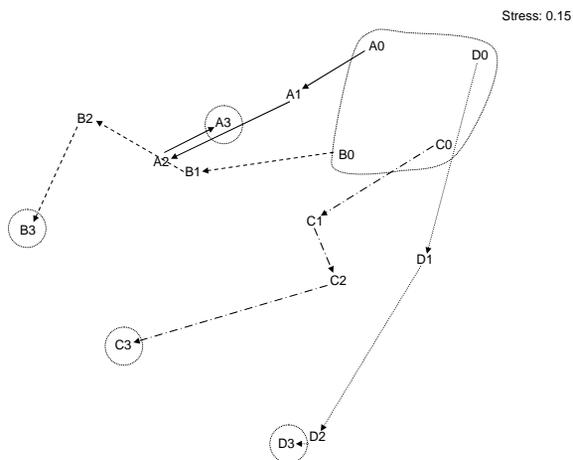


Fig. 4. Ordination (NMDS) plot of all treatment communities, showing mean species richness per treatment. The undisturbed patches are enclosed with a stippled line, and arrows show increasing disturbance frequency. The letter refers to the region size (A largest to D smallest), and the number to disturbance rate (0- no disturbance to 3, 3 times disturbed). Stress = 0.15.

tion (2-way ANOSIM of disturbance frequency and region size: global $R = 0.493$, $p = 0.002$). This can be seen in the paths followed through NMDS space. NMDS plots show the relative community similarity between plots using Bray-Curtis similarities; the plot itself is dimensionless. For example, treatment A0 vs A3 has a relative similarity of 64.33%, and D0 vs D3, 53.39%. Region A communities changed the least in response to disturbance frequency (A0 vs A3), and region D communities changed dramatically, following much longer paths to their end states (D0 vs D3; Fig. 4).

We used a gamma diversity measure similar to that used in type III species-area curves (i.e. we sampled constant areas within regions- the four local patches- and pooled the total of all species in all disturbance treatments within a region; Rosenzweig 1995). There was no difference in gamma diversity between region sizes (ANOVA: $F_{3,16} = 0.585$, $p = 0.63$; Fig. 5).

Various metrics of species identity showed few differences in response to fragmentation and disturbance (Table 1). Oribatids in the connected regions – A, B and C (ANOVA and LSD test) – showed a weaker decline following disturbance compared to other taxa. In region D, there was no difference in numerical response to disturbance amongst all taxa. In fact, for all taxa (save the Oribatid differences just mentioned), none of abundance, body size, or trophic position affected species response to disturbance (Table 1).

Discussion

In any landscape a suite of factors, both biotic and abiotic, work together to structure the community of species found in a local patch (MacArthur 1972, Ricklefs and Schluter 1993, Fahrig 2003). We consider the roles of habitat geometry (particularly amount and

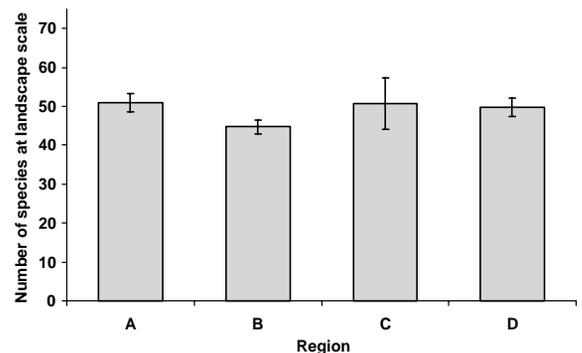


Fig. 5. Gamma diversity across all region size treatments. Gamma diversity is equivalent to the number of species at the landscape scale, or the pooled number of species across all 4 disturbance treatments, within a region. Error bars are ± 1 SE.

Table 1. Trait effects for body size, taxonomic group, trophic position, and abundance, with associated p-values from regressions (continuous variables: body size), ANOVAs (discrete variables: trophic position, taxonomic group) and an ANCOVA (abundance). p-values >0.05 indicate there is no difference in mean abundance for the various traits between disturbance level 0 and 3.

Trait	Region			
	A	B	C	D
Trophic position	0.21	0.75	0.21	0.06
Body size	0.71	0.63	0.31	0.48
Taxonomic group	0.042 ¹	0.005 ¹	0.004 ¹	0.72
Abundance	0.001 ²	0.001 ²	0.15	0.28

¹Oribatids are less likely to decrease in abundance (LSD test).

²Oribatids have higher extinction risk when found at low abundances (<5 individuals) (p = 0.001).

connectivity of habitat) and disturbance in determining the local community composition of moss microarthropods embedded within a larger region of similar, undisturbed habitat.

Our study presents three main conclusions. First, habitat geometry affected the resilience of local communities to repeated disturbance. Local (alpha) diversity was particularly sensitive to disturbance when loss of habitat resulted in patches being disconnected. Second, the effect of habitat geometry and disturbance on species richness was scale-dependent. Although alpha diversity was strongly affected by the experimental treatments, gamma diversity was not. Third, for only one group (oribatids) did body size, taxonomic group, or trophic level of species predict a species' response to decreased region size and fragmentation. We examine each of these conclusions in turn.

Habitat geometry affected the ability of local communities to recover from disturbance. Although alpha diversity decreased in all communities as a result of increased disturbance frequency, the strongest effects were seen in the small, unconnected treatment D. This treatment achieved higher alpha diversity than the connected treatments (A, B, C) in the absence of disturbance, but lower alpha diversity after disturbance. The high diversity in undisturbed patches of unconnected treatment D was likely due to a combination of edaphic edge effects and the reduced ability of microarthropods to disperse across even 1 cm of bare rock (Gilbert et al. 1998, Gonzalez et al. 1998). The edges of the fragmented and unconnected local patches showed signs of drying, and this may have activated aestivating microarthropod stages, or caused the hatching of eggs of dry-season specialists. A fence effect (Krebs et al. 1969, MacArthur 1972), caused by the bare-rock dispersal barrier, may then have confined to the patch species that would normally have dispersed. Many systems show complex edge effects after habitat fragmentation

(Redding et al. 2003, Ries et al. 2004, Harper et al. 2005). Once patches were disturbed, the greater decrease in species richness in unconnected regions was likely due to reduced dispersal between isolated patches, resulting in a decrease in the rescue effect for populations approaching extinction (Brown and Kodric-Brown 1977), as well as decreased immigration of new species. An important question to consider here is from where are the species that are found in the disturbed, disconnected local patches coming? As stated in the methods, the Tullgren funnel disturbance is not 100% effective in removing individuals from the moss. Some microarthropods, for example adult oribatids, may be able resist desiccation. Some eggs may even be stimulated to hatch by the dry-wet cycle of the extraction-rewetting procedure. Thus individuals within the patch may repopulate the disturbed patches. Additionally, individuals may immigrate to the disturbed patch from other moss patches by traversing the bare rock. Low rates of immigration can even occur through deposition from the air ("aerial plankton"). To look at the relative contribution of repopulation vs immigrant individuals (i.e. those that survive the disturbance in situ vs those that recolonise from other sources), we might consider the response of the different species to the disturbance. If recolonists across the rock are the most important, we expect to see highly mobile species, such as many adult mesostigmatid predators. If eggs are desiccant resistant, we expect many juveniles. If desiccant resistant adults repopulate the patch, we would expect many adult oribatids. Our trait analysis, however, shows no dominance of any of these groups in region D following disturbance, suggesting a role for both recolonisation and recovery. Future experiments aimed at disentangling the effects of both recolonisation and recovery would be useful.

Holling (1973) described systems as having low resilience if they have low capacity to rebound from a stressor. We interpret a strong negative effect of disturbance on final community richness and abundance (slope of the lines in Fig. 2a and 2b) as a measure of low resilience. In this study, therefore, the three largest and connected patches have similar resilience whereas patches in the smallest, unconnected regions exhibited lowest resilience (Fig. 3). This suggests that the response of community resilience to habitat loss has a threshold that coincides with loss of connectivity between local patches. Although such thresholds in response to habitat loss are predicted by theory (Moilanen and Hanski 1995, Solé et al. 2004), there are few empirical tests (Villard et al. 1999). We cannot definitively attribute this threshold in resilience to either reductions in region size or loss of connectivity, as both occur simultaneously. We intentionally designed our experimental landscapes to mimic the real-world pattern whereby progressive habitat loss necessarily results

in reduced connectivity. Now that we have demonstrated this threshold, future work is needed to determine the relative importance of regional size and connectivity in causing the threshold.

Several studies have shown conservation benefits of corridors in undisturbed systems, including facilitation of movement (Schmiegelow et al. 1997), maintenance of ecosystem processes (Gonzalez and Chaneton 2002, Levey et al. 2005), and enhancement of species richness in small patches. Our study suggests that corridors may have a further benefit: increased community resilience to disturbance. In a similar moss-microarthropod system, Gonzalez et al. (1998) found corridors prevent local extinctions by maintaining connectivity between patches rather than by increasing region size. Another study using the moss-microarthropod system, however, found no evidence for a difference in species richness between different connectivity treatments, and suggested that corridors connecting patches may be more useful during extreme conditions (Hoyle and Gilbert 2004). Our results confirm the conjecture of Hoyle and Gilbert (2004): changes in habitat geometry have the greatest effect in extreme drought conditions. It appears that on the short-term, at least, fragmented populations can persist if connected to source pools of potential colonizers. This has important implications for conservation: while corridors may not seem a good conservation bargain under ideal conditions, they may become very important to maintaining species on a landscape in the face of extreme or novel conditions such as climate change (Honnay et al. 2002).

The effect of habitat geometry and disturbance on species richness was scale-dependent. While at a given disturbance level, local (alpha) species richness of individual patches differed between experimental landscapes, regional (gamma) diversity did not. This was the result of two patterns. First, alpha diversity in region D was both higher and lower than other regions, depending on disturbance level, so the mean local diversity over all disturbance levels was similar. Second, although treatment A tended to have higher alpha diversity than other regions at nearly every level of disturbance, this was counteracted by reduced turnover in community composition between patches in this treatment (decreased beta diversity; Fig. 4.), resulting in unchanged gamma diversity. The lower beta diversity of treatment A as compared to the smaller regions may reflect the role of dispersal from the species pool in both homogenizing community composition over space and allowing rapid colonization of patches after disturbance. Other experimental manipulations of dispersal have shown scale-dependent effects on diversity (Warren 1996b, Forbes and Chase 2002, Kneitel and Miller 2003, Cadotte and Fukami 2005, Cadotte 2006b). A recent meta-analysis concludes that increased dispersal results in either positive or unimodal effects on

alpha diversity but negative or no effects on gamma diversity (Cadotte 2006a).

Following Davies et al. (2000), we equated larger declines in abundance with increased extinction risk. The finding that neither body size nor trophic position predicted species response to fragmentation is in contrast to that of several studies (Didham et al. 1998, Gilbert et al. 1998, Davies et al. 2000). All taxonomic groups save oribatids decreased in abundance similarly; oribatids increased, or decreased at a lower rate relative to other taxa. This is likely due to the ability of hard-exoskeleton oribatids to withstand some of the disturbances *in situ*. Species lost a similar proportion of their individuals between the undisturbed and greatest disturbance treatments, regardless of their abundance. We might expect that less abundant species would be extirpated first due to stochastic effects associated with their low numbers, but our contrary result may indicate a competition/colonization tradeoff: poor competitors *in situ* (the less abundant species), may in fact be able to recolonise disturbed areas at a faster rate than common species. The short return time of disturbance may not have allowed the community to reach a competitive equilibrium, and thus the low abundance species persisted or recolonized post-disturbance relatively better than the common species. Didham et al. (1998) and Gonzalez and Chaneton (2002) found that extinction was biased toward rare species following fragmentation, though their work did not explicitly disturb local patches post-fragmentation. It appears that in our study, common and rare species are responding to region size and disturbance frequency treatments in a broadly similar manner.

Conclusions

We experimentally examined the interactive effects of habitat geometry and disturbance on local species richness. When considered separately, increased disturbance resulted in lower local richness, whereas increased habitat loss had no effect, or even increased local richness. Simultaneous occurrence of both disturbance and habitat loss resulted in a loss of community resilience that could not be predicted from individual effects, especially a threshold in resilience which coincided with loss of habitat connectivity. While our results do not agree with all studies on the effects of connectivity (Hoyle and Gilbert 2004), they do agree with those studies that include extreme conditions (Gonzalez et al. 1998): intact habitat provides local communities with resilience to disturbances. We consider the maintenance of resilience by means of local patch connectivity to the regional pool of species to be an important conservation investment in managed landscapes.

Acknowledgements – Marc Cadotte, Luke Harmon, Jonathan Shurin, Ross Thompson and Katsky Venter provided valuable comments on earlier versions of this manuscript. The authors thank the Natural Sciences and Engineering Research Council of Canada for funding, and Valerie Behan-Pelletier, Hans Klompen, Heather Proctor, David Walter, Cal Welbourn and the Ohio State Univ. Acarology Summer Program for help in identifying species. Thanks also to the staff of the Malcolm Knapp Research Forest for access to our field site.

References

- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – *Ecology* 58: 445–449.
- Cadotte, M. W. 2006a. Dispersal and species diversity: a meta-analysis. – *Am. Nat.* 168: 913–924.
- Cadotte, M. W. 2006b. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. – *Ecology* 87: 1008–1016.
- Cadotte, M. W. and Fukami, T. 2005. Dispersal, spatial scale and species diversity in a hierarchically structured experimental landscape. – *Ecol. Lett.* 8: 548–557.
- Cottenie, K. and De Meester, L. 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. – *Ecology* 85: 114–119.
- Davies, K. F. et al. 2000. Which traits of species predict population declines in experimental forest fragments? – *Ecology* 81: 1450–1461.
- Didham, R. K. et al. 1998. Beetle species responses to tropical forest fragmentation. – *Ecol. Monogr.* 68: 295–323.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – *Annu. Rev. Ecol. Syst.* 34: 487–515.
- Forbes, A. E. and Chase, J. M. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. – *Oikos* 96: 433–440.
- Fukami, T. 2004. Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. – *Popul. Ecol.* 46: 137–147.
- Gaston, K. J. and Blackburn, T. M. 1995. Birds, body size and the threat of extinction. – *Proc. R. Soc. B.* 347: 205–212.
- Gilbert, F. S. et al. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. – *Proc. R. Soc. B.* 265: 577–582.
- Gonzalez, A. 2000. Community relaxation in fragmented landscapes: the relation between species, area and age. – *Ecol. Lett.* 3: 441–448.
- Gonzalez, A. and Chaneton, E. J. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. – *J. Anim. Ecol.* 71: 594–602.
- Gonzalez, A. et al. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. – *Science* 281: 2045–2047.
- Hanski, I. 1999. *Metapopulation ecology*. – Oxford Univ. Press.
- Harper, K. A. et al. 2005. Edge influence on forest structure and composition in fragmented landscapes. – *Conserv. Biol.* 19: 1–15.
- Holling, C. S. 1973. Resilience and stability of ecological systems. – *Annu. Rev. Ecol. Syst.* 4: 1–23.
- Honnay, O. et al. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. – *Ecol. Lett.* 5: 525–530.
- Hoyle, M. 2004. Causes of the species-area relationship by trophic level in a field-based microecosystem. – *Proc. R. Soc. B.* 271: 1159–1164.
- Hoyle, M. 2005. Experimentally fragmented communities are more aggregated. – *J. Anim. Ecol.* 74: 430–442.
- Hoyle, M. and Gilbert, F. 2004. Species richness of moss landscapes unaffected by short-term fragmentation. – *Oikos* 105: 359–367.
- Kneitel, J. M. and Miller, T. E. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. – *Am. Nat.* 162: 165–171.
- Knudsen, J. W. 1972. *Collecting and preserving plants and animals*. – Harper and Row.
- Krantz, G. W. 1978. *A manual of acarology*. – Oregon State Univ. Bookstores.
- Krebs, C. J. et al. 1969. *Microtus* population biology. – *Ecology* 50: 587–607.
- Lawton, J. H. 1994. Population dynamic principles. – *Proc. R. Soc. B.* 344: 61–68.
- Levey, D. J. et al. 2005. Effects of landscape corridors on seed dispersal by birds. – *Science* 309: 146–148.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. – Princeton Univ. Press.
- Moilanen, A. and Hanski, I. 1995. Habitat destruction and competitive coexistence in a spatially realistic metapopulation model. – *J. Anim. Ecol.* 64: 141–144.
- Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. – *Am. Nat.* 162: 544–557.
- Mouquet, N. et al. 2003. Community assembly time and the relationship between local and regional species richness. – *Oikos* 103: 618–626.
- Munguia, P. 2004. Successional patterns of pen shell communities at local and regional scales. – *J. Anim. Ecol.* 73: 64–74.
- Nee, S. and May, R. M. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. – *J. Anim. Ecol.* 61: 37–40.
- Redding, T. E. et al. 2003. Spatial patterns of soil temperature and moisture across subalpine forest-clearcut edges in the southern interior of British Columbia. – *Can. J. Soil Sci.* 83: 121–130.
- Ries, L. et al. 2004. Ecological responses to habitat edges: mechanisms, models and variability explained. – *Annu. Rev. Ecol. Syst.* 35: 491–522.
- Roland, J. and Taylor, P. D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. – *Nature* 386: 710–713.
- Ricklefs, R. E. and Schluter, D. (eds) 1993. *Species diversity in ecological communities*. – Univ. of Chicago Press.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. – Cambridge Univ. Press.

- Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. – *Science* 287: 1770–1774.
- Schmiegelow, F. K. A. et al. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. – *Ecology* 78: 1914–1932.
- Simberloff, D. 2000. What do we really know about habitat fragmentation? – *Texas J. Sci.* 52: 5–22.
- Solé, R. V. et al. 2004. Habitat fragmentation and biodiversity collapse in neutral communities. – *Ecol. Comp.* 1: 65–75.
- Srivastava, D. S. et al. 2004. Are natural microcosms useful model systems for ecology? – *Trends Ecol. Evol.* 19: 379–384.
- Taylor, P. D. et al. 1993. Connectivity is a vital element of landscape structure. – *Oikos* 68: 571–573.
- Turner, I. M. 1995. Species loss in fragments of tropical rain forests: a review of the evidence. – *J. Appl. Ecol.* 33: 200–209.
- Villard, M. -A. et al. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. – *Conserv. Biol.* 13: 774–783.
- Walter, D. E. and Proctor, H. C. 1999. Mites: ecology, evolution and behaviour. – Univ. of New South Wales Press and CAB Int.
- Warren, P. H. 1996a. Dispersal and destruction in a multiple habitat system: an experimental approach using protist communities. – *Oikos* 77: 317–325.
- Warren, P. H. 1996b. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. – *Oecologia* 105: 132–140.
- With, K. A. et al. 1997. Landscape connectivity and population distributions in heterogeneous environments. – *Oikos* 78: 151–169.

Appendix S1 can be found as Appendix O15547 at www.oikos.ekol.lu.se.