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Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks

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Connectivity is critical to the maintenance of biodiversity in fragmented landscapes, but its effects differ depending on the arrangement of linkages within a habitat network. Additionally, heterogeneity in habitat quality within the habitat network can alter patterns of diversity at local and regional scales in the metacommunity. Using a controlled experiment we examined the interactive effects of habitat connectivity, network form (linear vs square), and habitat patch quality on a moss-inhabiting microarthropod community. We fragmented moss habitat while controlling for habitat loss, and altered habitat patch quality by regulating moisture conditions in landscapes differing in patch arrangement. Habitat patch quality had a significant effect on patterns of species richness, extinction, abundance and biomass. The effects of network form on diversity were strongest in heterogeneous landscapes. Gamma and beta diversity were greatest in continuous and linear landscapes. However, linear habitat networks showed marked patch specific edge effects that were detrimental to diversity under heterogeneous conditions. We provide direct evidence that habitat network structure impacts species community properties through mass effects, that are most evident when heterogeneity in habitat patch quality is present within the network. We conclude that habitat quality at the individual patch level and the distribution of high-quality habitat within the network are important factors affecting biodiversity in metacommunities.

Many ecosystems are currently undergoing dramatic changes in biodiversity due to habitat loss and fragmentation due to land use change, pollution, overexploitation, and climate change. Habitat isolation, degradation (or altered habitat quality) and changes in patch configuration (arrangement) are co-occurring processes during land use change. Although the overall effect of habitat loss and fragmentation is often a net loss of biodiversity, separating the co-occurring effects of habitat isolation (connectivity), local habitat arrangement and habitat quality on biodiversity is challenging (Leibold et al. 2004, Gonzalez 2005). Habitat fragmentation is the subdivision, or breaking apart of a large contiguous habitat into smaller, more isolated patches (Fahrig 2003). The effects of fragmentation on diversity, independent of habitat loss, are thought to be mainly related to increased edge effects (Murcia 1995, Didham et al. 1998, Ewers et al. 2007), which can both diminish and enhance habitat quality (Cadenasso et al. 1997), depending upon the spatial configuration of the habitat mosaic. The adverse effects of alterations in habitat configuration may be particularly important in landscapes where habitat quality is highly variable and good quality patches are spatially aggregated (Visconti and Elkin 2009).

Habitat connectivity reverses fragmentation by reconnecting isolated habitat. Theory and experiments indicate that increasing connectivity can maintain local and regional diversity. In particular, connectivity can maintain diversity by promoting the movement or dispersal of individuals among adjacent habitat patches by spill-over or mass effects (Schmida and Wilson 1985, Mouquet and Loreau 2003). Mass effects (also "spatial mass effects" "source/sink dynamics" or "spillover effects") refer to the dynamics that occur among patches due to differences in population density (or mass) in different patches, or asymmetric dispersal due to differences in habitat quality, that can drive patterns of immigration and emigration between local communities. Populations occurring in poor-quality habitat that have low intrinsic rates of growth (sink patches) are maintained through immigration of individuals from good-quality habitat with high intrinsic growth (source patches). This reduces rates of extinction and increases the probability of population persistence (Gilbert et al. 1998, Gonzalez et al. 1998, Fahrig 2003, Ewers and Didham 2006). Furthermore, the condition of a poor-quality habitat may be enhanced by an adjacent high quality habitat (Ries and Sisk 2004), which may boost population numbers and enhance mass effects. This ameliorating effect will be particularly evident in highly connected large habitat networks.

One way to create or maintain connectivity among fragmented habitat patches is through the use of habitat corridors (Gilbert et al. 1998, Haddad et al. 2003). Yet the feasibility of creating corridors and the degree of connectivity that can be created depends on the arrangement of habitat patches within the habitat network (Matisziw and Murray 2009). For example, habitat networks with a high degree of connectivity, such as a landscape of clustered or looped habitat patches are expected to assist dispersal, increase individual patch recolonization rates, and increase regional species persistence (Lefkovitch and Fahrig 1985, Frank and Wissel 1998) compared to more linear networks. Additionally, the number and arrangement of corridors affects the ratio of interior versus peripheral patches which can affect regional species population size (Anderson and Danielson 1997).

Conserving species in increasingly fragmented habitats requires knowledge of the response of species and communities to fragmentation and the spatial distribution of habitat quality within the network (Jordán et al. 2003). In this study we examined the interactive effects of habitat connectivity, network arrangement, and habitat patch quality independently from habitat loss on microarthropod metacommunities in a model moss ecosystem. The use of moss-microarthropod systems (sensu the ''bryosphere'' – Lindo and Gonzalez 2010) has been established in the past decade for addressing ecological theory in community ecology, as the relative body size, generation time and dispersal powers of the populations within these moss systems allow for similar comparisons to macrofauna of real nature reserves. In this study we address whether habitat quality interacts with fragmentation by directly manipulating a known habitat quality response variable (moisture), and we separate the absolute effect of connectivity, using data standardized for ''island'' fragments unconnected to a network.

We tested the following hypotheses: 1) large areas of contiguous patches will maintain greater species richness than an equal area of discrete patches linked by dispersal corridors, as large areas provide increased interior and less edge habitat while allowing greater connectivity and free movement of individuals; 2) the overall habitat quality of a landscape will influence species richness; landscapes with a high proportion of good-quality patches will maintain greater species richness, while an increased proportion of poor-quality habitat patches within the landscape will increase mortality and decrease overall species richness; 3) among networks composed of patches with dispersal corridors, the landscape with the greater number of linked patches and lower number of terminal patches will support a greater number of species; 4) individual habitat patches of poor quality that are adjacent to good-quality patches will maintain species diversity and abundance through the amelioration of habitat quality (large contiguous patches) and mass effects (all network design treatments).

Materials and methods

Study system

The experiment was conducted using a diverse community of microarthropods inhabiting the feathermoss, *Pleurozium schreberi* collected from Schefferville, Quebec, Canada (54°48′N, 66°49′W) in June 2008. This moss is characteristic of the sub-arctic boreal region and is ideal as a model system for fragmentation due to its high diversity of species (predominantly mites) and their relatively small size (100 μm–2 mm) and dispersal capacity compared to the size of moss landscape. Intact carpets of the feathermoss were maintained under greenhouse conditions at 16°C and were misted with water twice daily (20 min each) for three months prior to the start of the experiment. The experiment was performed from October 2008 to January 2009 under the same greenhouse conditions. However, the misting procedure of the previous three months was stopped for the duration of the experiment to allow experimental control of moisture conditions.

Experimental control and design

Landscape-level network arrangements included a continuous area of moss habitat (*continuous*), four moss patches connected by four corridors in a square arrangement (*square*), and four moss patches connected by three corridors in a linear arrangement (*linear*) (Fig. 1). Continuous areas consisted of circular patches 15 cm in diameter, while fragmented landscapes consisted of four circular patches 7 cm in diameter, connected in a square or linear network arrangement through 6×2 cm corridors (Fig. 1). The total surface area of moss in all treatments was equal (ca 180 cm^2), while the amount of edge differed considerably between the *continuous* (47 cm edge) and the fragmented *square* and *linear* treatments (120 and 124 cm edge, respectively). Moss landscapes were inserted within plaster of Paris moulds in individual 20×50 cm greenhouse trays.

A census of the entire initial microarthropod community was conducted prior to the experiment by heat extraction by placing each patch and corresponding corridor (160 total) in Tullgren funnels over water-filled vials for a period of 48 h. This procedure minimized mortality during extraction for the species census. Immediately following extraction, moss patches were weighed and placed within the respective landscapes, while microarthropod richness (to morphospecies) and abundance from each patch plus corridor was recorded on a digitally captured image. All microarthropods were then immediately returned to their source patch within the experiment along with 10 ml of deionised water. Landscapes were maintained within the greenhouse, and randomly rearranged every four weeks to account for minor variation in humidity and light gradients within the greenhouse.

Habitat quality at the landscape level was manipulated and maintained through the addition or denial of water to individual patches (numbered 1–4) within landscapes (Fig. 1). *Wet* treatments were watered daily with 15 ml deionised water to each patch (1 through 4) within the landscape. *Dry* treatments were created through the neglect of watering (patches 1 through 4) over the course of the experiment. In the *heterogeneous* treatment, patch 1 and 2 received daily watering of 15 ml per patch, while patches 3 and 4 remained unwatered. Four replicates of each *continuous, square* and *linear* arrangements were

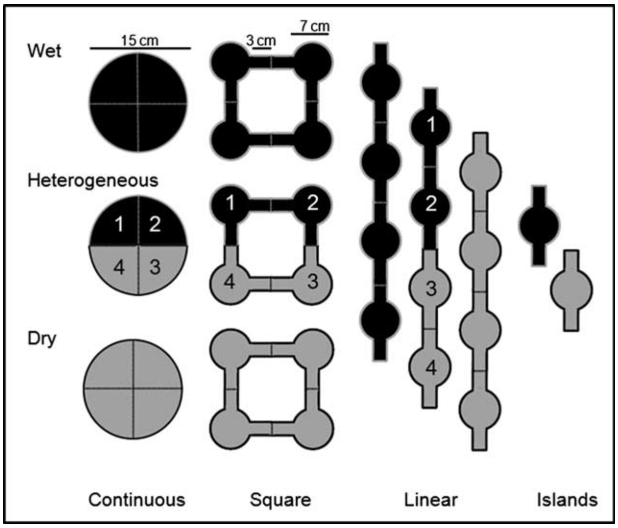

Figure 1. Experimental moss networks and moisture treatments. Black indicates wet habitat, favourable for microarthropods, while grey indicates unfavourable, dry habitat. Landscape-level network arrangements used were unfragmented areas (Continuous), four patches linked by four corridors in a square arrangement (Square), four patches linked by three corridors in a linear arrangement (Linear), and individual "island" fragments serving as negative controls for the effect of connectivity (Islands). Patch numbers are indicated on heterogeneous habitat quality treatments, wet and dry landscapes are similarly numbered (not shown). Dashed lines within landscapes denote patch boundaries for demonstrative purposes and are not physical boundaries.

assigned to each of the three habitat quality treatments (*wet, dry, heterogeneous*), for a total of 36 landscapes. An additional set of negative controls, eight wet and eight dry habitat patches (7 cm in diameter) with two half-corridors (3×2 cm), were created as single (*island*) landscapes (Fig. 1) (surface area $= 50.5$ cm^2, edge $= 34$ cm).

The experimental treatments were maintained for 14 weeks, which is enough time for several generations of most species used in the experiment. At the end of the experiment, each patch and corresponding corridor was weighed, extracted for microarthropods, and re-weighed after extraction to gravimetrically calculate the moisture content of individual patches (moisture content % = (wet weight (g) − dry weight (g)/dry weight (g)) × 100). Microarthropods were extracted into 70% EtOH, and all microarthropods were identified to morphospecies and enumerated under a stereomicroscope. Species richness and abundance were standardized to number of species or individuals per 100 g dry weight (dwt) moss. Microarthropods were grouped into five taxonomic (functional) groups: Oribatida, Prostigmata, Mesostigmata, Collembola, and "Other Microarthropods" (see Supplementary material Table S1 for complete list). Biomass of morphospecies was estimated using average length and width measurements from representative morphotypes of adults and immatures of each species using the original digitized photos and converted to mass (μg) using species density values from Vreeken-Buijs et al. (1998).

Statistical analyses

A two-way repeated measures multivariate analysis of variance (RM-MANOVA, full factorial and fixed effects) was used to compare the species richness of each taxonomic (functional) group under the effect of network arrangement and habitat quality. Individual patches were used as spatial repeated measures within landscapes to observe results at the individual patch-level. Similar tests were performed for abundance and biomass. Moisture content was analyzed using a two-way repeated measures analysis of variance (RM-ANOVA) using patches as spatial repeated measures in order to examine habitat quality treatments and determine moisture as a covariate. Species richness, abundance and biomass data were log transformed ($x+1$) prior to analysis to meet model assumptions, and all analyses were performed in STATISTICA 7.0 (StatSoft 2004).

To test for the effect of connectivity on our measures of species richness, abundance and biomass we standardized the measures of individual patches within habitat networks by dividing wet and dry patches by the average ($n = 8$) taken from the single *island* controls (wet or dry, respectively). Any value greater than one thus indicates that habitat connectivity inflates a given response variable. Treatment differences between the connectivity-standardized measures of total richness was tested using a two-way repeated measures multivariate analysis of variance (RM-MANOVA) using patches as spatial repeated measures as described above.

Using presence/absence data we calculated the alpha (α), beta (β) and gamma (γ) diversity components at the landscape level. Gamma diversity was calculated as the total number of species in each landscape, alpha diversity was calculated as the average number of species per patch within each landscape, and beta diversity was calculated as the average number of species not observed in each patch within a given landscape, as given by the additive equation ($\gamma = \alpha + \beta$) (Lande 1996). A two-way MANOVA was performed on these diversity measures.

Finally, extinction estimates were calculated at the landscape level by comparing the microarthropod richness at the initial versus final sampling times. Extinction was calculated as the percent loss in the number of microarthropod species between initial and final samples at the landscape level. "Other Microarthropods" were excluded as a group in this analysis due to their low occurrence within the landscapes (<2% total abundance). Extinction proportions were arcsine transformed and analyzed using a two-way ANOVA (model I: full factorial and fixed effects).

Results

Habitat heterogeneity

As intended moisture content of the moss was significantly different among the habitat quality treatments and was also influenced by the patch arrangement in the habitat network. The greatest overall moisture was maintained in *wet* networks, followed by the *heterogeneous* and *dry* habitat treatments at the network level ($F_{2,19} = 484.7$, $p < 0.001$). On average, *dry* networks maintained 1.9%

and *heterogeneous* networks 64.6% of the moisture content of *wet* networks, respectively. Overall moisture content was greatest in *continuous* landscapes, followed by *linear* and *square* landscapes ($F_{2,19} = 58.1$, $p < 0.001$).

A significant arrangement-by-habitat quality interaction ($F_{4,19} = 32.6$, $p < 0.001$) revealed that the *heterogeneous continuous* treatment maintained 97.5% of the moisture content of *wet continuous* areas. This was greater than the *heterogeneous square* or *heterogeneous linear* treatments with 45.9 and 46.1% of the moisture content in *wet* landscapes of the same network arrangement, respectively. These trends were best demonstrated at the individual patch level (patch × arrangement × habitat quality interaction $F_{12,57} = 2.4$, $p = 0.013$). Moisture conditions in patches 3 and 4 (dry patches) of *heterogeneous continuous* networks were not significantly different from the adjacent (wet) patches 1 and 2 indicating a wicking effect that ameliorated dry moisture conditions in patches 3 and 4. In contrast, patches 3 and 4 (dry patches) of *heterogeneous square* or *heterogeneous linear* networks had significantly lower moisture content and showed no ameliorating or wicking effect of the adjacent wet patches.

Effects at the network level

A total of 49 morpho-species were present in the experimental networks (Supplementary material Table S1). At the network level, overall habitat quality treatment had a significant effect on species richness as expected; total species richness was 1.5 and 9.0 times greater in *wet* networks, than *heterogeneous* and *dry* networks, respectively (Supplementary material Fig. S1A). Species richness was generally low in all *dry* networks, intermediate in *heterogeneous* networks, and highest in *wet* networks for all groups regardless of the network design.

Measures of the alpha, beta and gamma diversity components for the experimental networks demonstrate a similar significant interaction between network arrangement and habitat quality (Wilk's $\lambda = 0.28$, $p < 0.001$). *Square heterogeneous* treatments had lower alpha, beta and gamma diversity than the *linear* and *continuous heterogeneous* networks (Fig. 2). The main significant effect of network arrangement on diversity measures (Wilk's $\lambda = 0.54$, $p = 0.002$) was driven by alpha diversity rather than gamma diversity (univariate: alpha diversity, $F_{2,27} = 6.0$, $p = 0.007$). *Dry* networks had significantly lower alpha, beta and gamma diversity than *wet* and *heterogeneous* treatments for all network arrangements (main effect: Wilk's $\lambda = 0.05$, $p < 0.001$, univariate: alpha diversity, $F_{2,27} = 149.0$, $p < 0.001$, beta diversity, $F_{2,27} = 32.4$, $p < 0.007$, gamma diversity, $F_{2,27} = 125.0$, $p < 0.001$).

Highest extinction occurred in *dry* networks and lowest extinction occurred in *wet* networks (Fig. 3). There was a significant interaction effect of network arrangement and habitat quality on the level of extinction observed (Wilk's $\lambda = 0.09$, $p < 0.001$). *Square* networks had greater levels of extinction than *linear* and *continuous* networks under wet and heterogeneous conditions, but this trend was reversed under dry conditions (Fig. 3).

Effects at the patch level

The interaction of habitat quality and network arrangement also proved to be an important factor defining patterns of species richness, abundance and biomass at the patch level (Table 1, and Supplementary material Table S2). Species richness in dry patches 3 and 4 of *heterogeneous* networks differed with network design (Fig. 4A). Patches 3 and 4 (dry patches) in *continuous heterogeneous* habitat maintained species richness equal to patches 1 and 2 (wet patches), while in *heterogeneous square* networks, dry patches 3 and 4

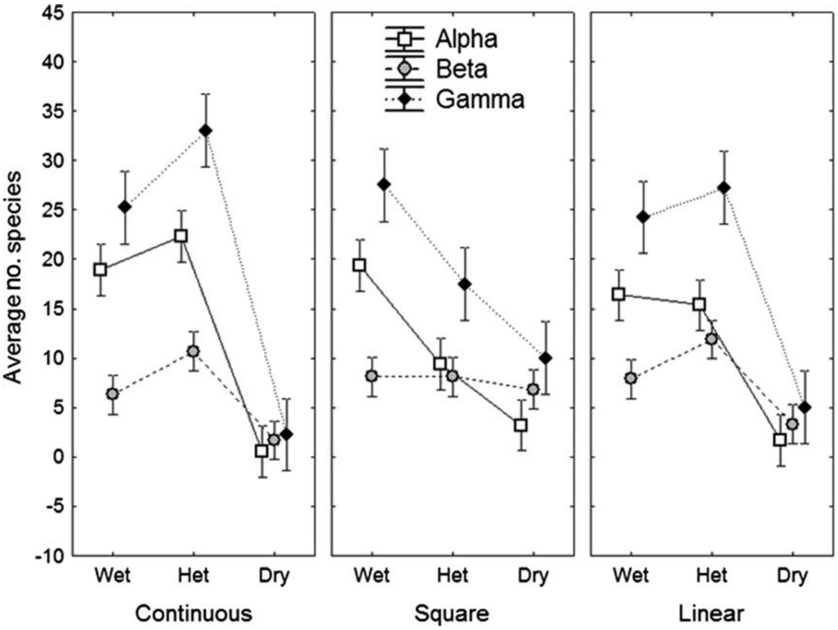

Figure 2. Measures for alpha, beta and gamma diversity (average no. species) calculated from individual habitat patches differing in habitat quality within different network arrangements. Values are means ± two standard errors.

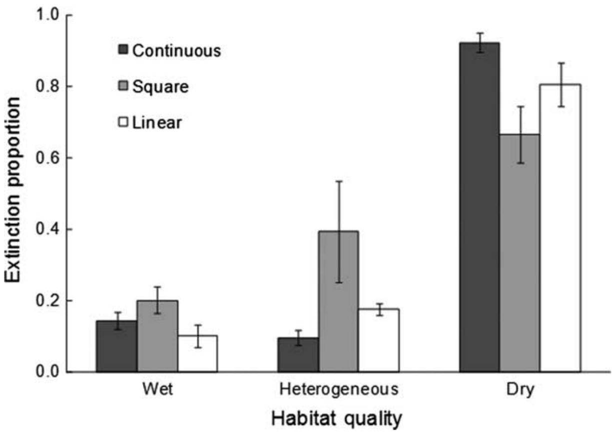

Figure 3. Proportion of landscape-level species extinction that occurred in microarthropods inhabiting greenhouse moss systems differing in habitat patch quality (wet, heterogeneous, dry landscapes) and network arrangement (continuous, square, linear). Extinction was calculated as the proportion of species lost from the initial composition as compared to species present at the end of the 14 week experiment. Values are means ± two standard errors.

were similar to each other, and had reduced species richness compared to wet patches 1 and 2. *Heterogeneous linear* networks had reduced species richness in dry patches 3 and 4, yet patch 3 had significantly greater richness than patch 4 (Fig. 4A). Patches 1 and 2 within the *heterogeneous* networks had total species richness values similar to patches 1 and 2 in *wet* networks for all network designs.

Individual faunal groups generally followed the patterns observed in total species richness, with a significant interaction between network arrangement and habitat quality at the patch level as described above (Fig. 5A, 5B, and Supplementary material Fig. S2A), but richness patterns in patches 3 and 4 of *heterogeneous square* and *heterogeneous linear* networks differed depending on the taxonomic group. Predatory (mesostigmatid) mite species richness in patches 3 and 4 of *heterogeneous square* and *linear* networks had richness values equal to *dry square* and *linear* networks (Fig. 5A) whereas for collembola, which are a potential prey species for mesostigmatid mites, richness tended to be greater in *heterogeneous linear* than *heterogeneous square* networks (Fig. 5B).

The effect of connectivity on total species richness was most apparent in patches 3 and 4 of the *heterogeneous* networks (Fig. 4B) underlying the significant interaction effect of network arrangement and habitat quality at the patch level (Table 1). Dry habitat patches 3 and 4 within *heterogeneous* networks showed a very large positive effect of connectivity on species richness, but only when connected to wet patches, i.e. patches 3 and 4 in *continuous* and *square* network arrangements and only patch 3 in *linear* network arrangements. There was no direct effect of connectivity observed among *wet* networks of different network arrangement (values not significantly different from zero), but connectivity maintained 3 times greater species richness in *dry* networks compared to *island* patches (Supplementary material Fig. S1B).

Patterns in the effect of connectivity on oribatid mite species richness drove trends in total species richness (Supplementary material Fig. S2B), but other faunal groups showed different effects of connectivity. Notably mesostigmatid mite predators and collembola prey species differed in their response to connectivity within dry patches of the *heterogeneous* treatments. Mesostigmatid mites showed a strong effect of connectivity only in patches 3 and 4 of the *heterogeneous continuous* networks, while collembola showed a positive effect of connectivity in patches 3 and 4 of all *heterogeneous* networks (Supplementary material Fig. S3A and B). Trends for species abundances and biomass demonstrated similar patterns to that of species richness for both the unstandardized and standardized data (Supplementary material Table S2).

Discussion

Conserving biodiversity in increasingly fragmented landscapes requires that we not only understand the response of species and communities to isolation, but also the effects of changing habitat quality and habitat network structure (Mortelliti et al. 2010). At present, studies addressing habitat network design rely heavily on theoretical models (Bruinderink et al. 2003, Cabeza and Moilanen 2003) or focus on applied conservation case studies, often addressing the population dynamics of a single species (Hanski et al. 1995). Furthermore, understanding the multiple effects of fragmentation on community dynamics (i.e. habitat configuration with respect to connectivity and network arrangement) has been limited because it is frequently

Table 1. Results of repeated measures multivariate analysis of variance (RM-MANOVA) for treatment effects of network arrangement and habitat quality on species richness of moss-inhabiting microarthropods after 14 weeks following fragmentation. Repeated measures multivariate analysis of variance (RM-MANOVA) on total species richness standardized by island fragment negative controls also given. Individual habitat patches within landscapes are used as repeated measures.

Source of variation ($_{DF}$)	Species richness			Standardized species richness		
	Wilk's λ	F	p	Wilk's λ	F	p
Arrangement $_{(2,\ 27)}$	0.189	4.766	<**0.001**	0.031	17.062	<**0.001**
Habitat quality $_{(2,\ 27)}$	0.028	18.092	<**0.001**	0.016	25.346	<**0.001**
Arrangement × Habitat quality $_{(4,\ 27)}$	0.086	3.322	<**0.001**	0.010	8.802	<**0.001**
Patch $_{(3,\ 81)}$	0.161	2.905	**0.044**	0.008	65.700	<**0.001**
Patch × Arrangement $_{(6,\ 81)}$	0.059	1.722	0.099	0.001	24.381	<**0.001**
Patch × Habitat quality $_{(6,\ 81)}$	0.056	1.789	0.084	0.001	25.068	<**0.001**
Patch × Arrangement × Habitat quality $_{(12,\ 81)}$	0.002	2.205	**0.003**	0.001	11.701	<**0.001**

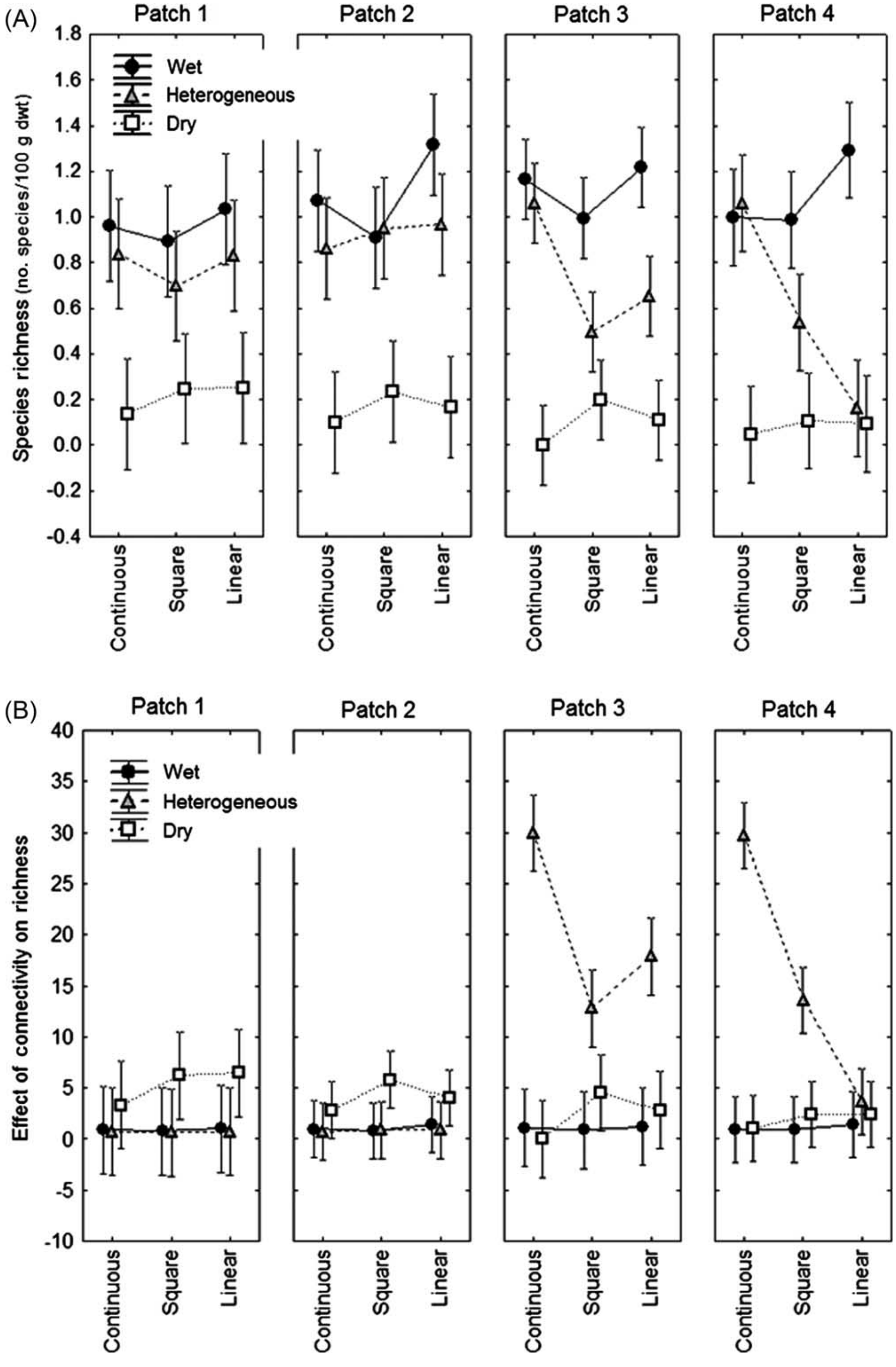

Figure 4. (A) Patch-level patterns of species richness for all microarthropods in greenhouse moss systems (no. species/100 g dry weight moss substrate) differing in habitat patch quality (wet, heterogeneous, dry landscapes) and network arrangement (continuous, square, linear). (B) Patch-level patterns demonstrating the absolute effect of connectivity on species richness. Habitat patch quality treatments (wet, heterogeneous, dry) are designated at the landscape-level. Patches 1–4 were good quality “wet” patches in wet landscapes, patches 1–4 were poor quality “dry” patches in dry landscapes. In heterogeneous landscapes, patches 1 and 2 were good quality “wet” patches while patches 3 and 4 were poor quality “dry” patches. Values are means ± two standard errors.

confounded with habitat composition (i.e. habitat amount and quality) (Ewers and Didham 2006) and habitat loss (Fahrig 2003). In this study we provide experimental evidence that habitat network structure affects species richness, abundance and biomass patterns, at the patch and metacommunity scale, but most strongly when heterogeneity in habitat patch quality is present within the network.

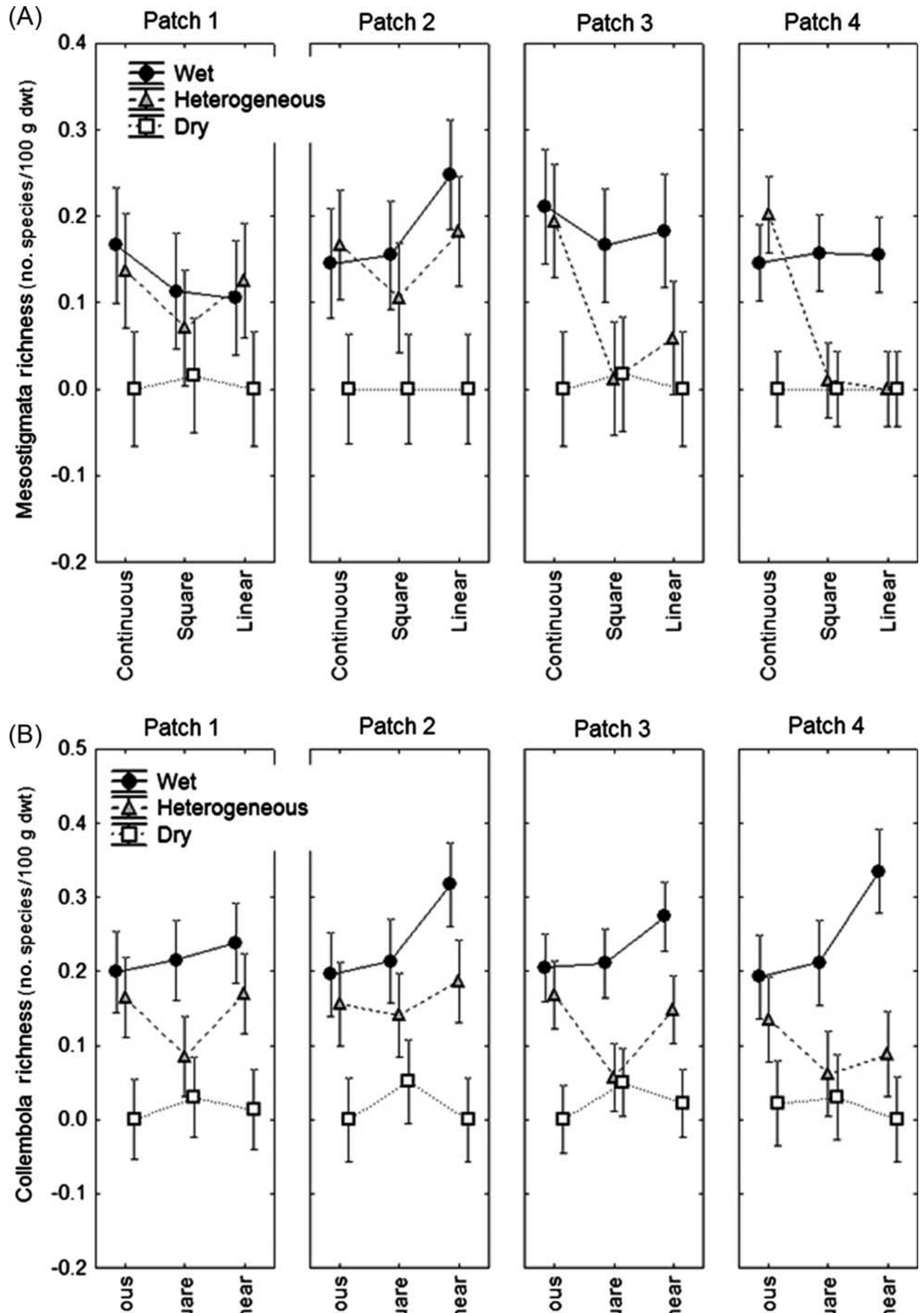

Figure 5. Species richness of (A) predators (Mesostigmata) and (B) their prey (Collembola) in greenhouse moss systems (no. species/ 100 g dry weight moss substrate) differing in habitat patch quality (wet, heterogeneous, dry landscapes) and network arrangement (continuous, square, linear). Habitat patch quality treatments (wet, heterogeneous, dry) are designated at the landscape-level. Patches 1–4 were good quality "wet" patches in wet landscapes, patches 1–4 were poor quality "dry" patches in dry landscapes. In heterogeneous landscapes, patches 1 and 2 were good quality "wet" patches while patches 3 and 4 were poor quality "dry" patches. Values are means ± two standard errors.

The role of habitat quality within the network

Network models in the field of conservation biology have recently revealed the importance of including patch quality as it relates to local population size (Jordán et al. 2003) and local reproductive potential (Minor and Urban 2007). We directly manipulated and controlled moisture conditions at the patch level to create differences in heterogeneity at the landscape level, and found that habitat patch quality had a significant effect on patterns of species richness, abundance and biomass, and on levels of extinction. Overall quality of the network was a critical factor in the level of extinction occurring at the landscape level with dry networks having over 5 times greater number of extinctions than wet networks, and 3.6 times greater number of extinction than heterogeneous networks.

Moisture regimes and humidity of microhabitats are fundamental factors influencing the diversity, abundance and distribution of many microarthropods (Reddy 1984, Siepel 1996, Lindo and Winchester 2008, Lindo et al. 2008), and high levels of extinction were associated with dry and fragmented heterogeneous treatments. Dry networks had the lowest values for all diversity measures indicating communities within these patches were species poor irrespective of the network structure. This is similar to Lindo et al. (2008) who found that drought conditions may act as an environmental filter, producing communities of limited membership and composed of species tolerant to the dry conditions. More generally, the quality of the habitat places limits on population size and population growth rate, both factors that determine population persistence and extinction risk (Root 1998, Thomas et al. 2001, Griffen and Drake 2008).

The role of network design and connectivity

Habitat fragmentation in our study was imposed by changing the number and size of individual habitat patches within a landscape (1 large patch versus 4 small patches), and by manipulating isolation and edge effects based on differences in the degree of connectivity and circumference to surface area ratio. The effects of connectivity in this experiment were striking (Fig. 4B). In keeping with our first hypothesis, large areas of contiguous patches maintained greater species richness than equal area of patches linked by dispersal corridors, but this effect of connectivity was strongest under heterogeneous conditions. The effects of connectivity were also strong in *linear* and *square* networks under heterogeneous conditions, but were also present in *linear* and *square* dry networks. These results suggest that the beneficial effects of connectivity are greatest when spatial heterogeneity is marked. In a large contiguous area, the condition of a poor-quality habitat patch may be enhanced by an adjacent high quality habitat (Ries and Sisk 2004), which we observed in the wicking effect of moisture from wet patches into dry patches under the *heterogeneous continuous* treatment. This ameliorating effect of moisture conditions evident in our connected large habitat areas was not evident in the *heterogeneous square* or *heterogeneous linear* landscapes.

Despite drought conditions, individual habitat patches of poor-quality within fragmented heterogeneous networks adjacent to good-quality patches maintained intermediate species richness compared to poor-quality patches in *dry* landscapes (i.e. patches 3 and 4 in *heterogeneous square* and patch 3 in *heterogeneous linear* networks). Our results support recent metacommunity theory that connectivity becomes more important as overall habitat quality decreases, or when marked habitat heterogeneity occurs (Loreau et al. 2003). Binzenhöfer et al. (2008) found that increased connectivity between patches could even compensate for poor quality habitat in maintaining long-term survival of metapopulations. Both habitat heterogeneity and moderate rates of dispersal among local patches is known to increase species richness (Forbes and Chase 2002, Mouquet and Loreau 2003, Davies et al. 2009), however, most studies cite heterogeneity in resources, rather than heterogeneity in resource availability. The standardized data further demonstrate these effects of adjacency, suggesting that patch arrangement plays an important role in maintaining species richness through source-sink metapopulation and metacommunity dynamics (Pulliam and Danielson 1991, Hanski 1998, Mouquet and Loreau 2003) in particular through mass effects (Schmida and Wilson 1985). Thus the presence of a dispersal corridor as a means to mediate some of the adverse effects of habitat fragmentation may be especially important when patch habitat quality is spatially or temporally heterogeneous across the landscape (see also Matthews and Gonzalez 2007).

Predictive models suggest that organisms should avoid edges adjoining lower quality habitats that offer only supplementary resources, they should show increased density near edges with higher quality habitat or habitat that contains complementary (different) resources, and they should show no response to edges adjoining similar quality habitat that offers only supplementary (similar) resources (Ries and Sisk 2004). Our study shows that despite a strong association of microarthropods with moisture gradients, taxonomic groups responded differently to the interactive effects of heterogeneity and network connectivity. In particular, *heterogeneous linear* networks rarely contained predatory mesostigmatid mites in the dry patches, while collembola were observed in high abundances within dry patches adjacent to wet patches. These differences are likely due to difference in reproductive rate, rather than environmental tolerances or predator:prey dynamics. Fragmentation in the moss system has previously shown to cause non-random extinction of mesostigmatid mites consistent with their being large-bodied, top predators (Gilbert et al. 1998, Gonzalez et al. 1998, Gonzalez and Chaneton 2002, Staddon et al. 2010). However, this study suggests that mesostigmatid mite abundance and richness are directly related to the moisture conditions at the patch level rather than fragmentation per se. Furthermore, connectivity was only shown to be important when it was associated with wicking moisture conditions. In contrast, collembola showed persistence under dry conditions, but only when directly adjacent to wet patches. Thus we attribute the observed patterns predominantly to proximity and mass-effects, specifically source-sink dynamics.

Anderson and Danielson (1997) suggest that peripheral patches such as the terminal patches in linear landscapes are less beneficial to the overall system than interior patches, which can be supported under heterogeneous conditions. However, at the network level, there was no overall difference in species richness or abundance between square and linear networks. Contrary to our predictions, species extinctions were greater in square network arrangements under wet and heterogeneous conditions compared to linear networks. These results may be explained by the quality of the corridors connecting patches. In the case where all corridors are "good" or "poor" quality, Anderson and

Danielson (1997) found negligible difference between square and linear arrangements. But when the quality of the connections among patches is altered, we find scenarios where linear arrangements may maintain greater overall abundance in linear versus square arrangements.

Conclusions

While the effects of fragmentation on metacommunity diversity are only tentatively understood (Forbes and Chase 2002, Gonzalez 2005, Layman et al. 2007, Shulman and Chase 2007, Cagnolo et al. 2009) we conclude that habitat quality at the individual patch level and the proximity of high-quality habitat within the network are important determinants of network biodiversity. These results reinforce the conclusion that habitat heterogeneity within the landscape has a strong influence on patterns of diversity (Trzcinski et al. 1999, Heikkinen et al. 2004) and that it interacts with network configuration to effect diversity and in certain circumstances it may prove to be as important as the effects of isolation and area (Thomas et al. 2001, Fleishman et al. 2002).

We found supporting evidence for several of our hypotheses. Firstly, landscapes with a high proportion of good-quality patches maintained greater species richness, while an increased proportion of poor-quality habitat patches within the landscape increased mortality and decreased overall species richness. We found that large areas of contiguous patches maintained greater species richness than equal area of patches linked by dispersal corridors, this effect was marked and significant under heterogeneous environmental conditions. Lastly, individual habitat patches of poor quality adjacent and connected to good-quality patches maintained species diversity and abundance. This pattern was primarily attributed to the amelioration of habitat quality in large contiguous patches, and through dispersal mediated mass effects in fragmented but connected networks. Only one of our four hypotheses was not supported in this study – square arrangements would have greater species richness than linear arrangements due to a greater number of linked patches and lower number of terminal patches – however, experimental manipulation of corridor quality in concurrence with network designs outlined by Anderson and Danielson (1997) may elucidate the mechanistic explanation of these results.

Our results have implications for reserve design because they point to the synergism between connectivity and habitat quality. Improving landscape connectivity to facilitate species dispersal is the most commonly identified recommendation to mitigate negative impacts of climate change on biodiversity (Heller and Zavaleta 2009). However, for species to be able to respond to climate change via dispersal to new habitats, two conditions must be met: high-quality habitats must exist and individuals must be able to reach them reliably. Management of habitat connectivity, network arrangement, and habitat patch quality will be essential for the conservation of biodiversity in the future.

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