Traits explain community disassembly and trophic contraction following experimental environmental change

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Abstract

Many ecosystems are currently undergoing dramatic changes in biodiversity due to habitat loss and climate change. Responses to global change at the community level are poorly understood, as are the impacts of community disassembly on ecosystem-level processes. Uncertainties remain regarding the patterns of extirpation and persistence under single vs. multiple forms of environmental change. Here, we use a trait-based and food web approach to examine the effects of experimentally changing moisture, temperature and habitat ‘openness’ on a functionally important group of microarthropods associated with a boreal forest floor bryosphere (detrital moss) system. Overall, the outcome of community disassembly was mediated by the correlation between our environmental factors and species traits, particularly body size. Minor increases in summer temperatures maintained greater species richness, whereas drought stress had a significant negative effect on community-level abundance and richness. These effects were reflected in modifications to the community-wide body-size spectra. Habitat openness alleviated biodiversity loss in the larger-bodied species of the most abundant taxonomic group, but did not fully mitigate the effects of drought. The most striking result of this experiment was an overall contraction of the food web among persistent species under drought stress (i.e. those not extirpated by environmental change). These results suggest that major changes in boreal microarthropod community structure are likely to occur in response to common forms of global change. Moreover, the contraction in trophic structure even amongst tolerant species suggests that ecosystem function within the bryosphere can be altered by environmental change.

Keywords: biodiversity loss, body size spectra, climate change, community disassembly, habitat fragmentation, natural abundance stable isotopes, traits, trophic space

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Introduction

Habitat fragmentation and climate change jointly affect biodiversity directly and indirectly, by modifying interactions between persistent species (Gonzalez et al., 2011). Anthropogenic change, such as habitat loss and fragmentation, has been shown to induce nonrandom extinction (Didham et al., 1998; Holt et al., 1999; Holyoak, 2000; Duffy, 2003; Staddon et al., 2010) and the attrition of species interactions (Borrvall & Ebenman, 2006): a process termed community disassembly. Recently changes in climate variables, such as temperature and moisture, have been identified as key factors exacerbating the negative effects of habitat loss on biodiversity (Mantyka-Pringle et al., 2012). It is now recognized that interactions between multiple stressors may lead to nonadditive outcomes (Vinebrooke et al., 2001; Brook et al., 2008; Darling & Côté, 2008), yet the rate and scale of biodiversity loss due to the effects of climate change and habitat fragmentation are not well understood. There is therefore a clear need to understand how communities and ecosystems will respond to rapid cumulative environmental change of different types.

It has been suggested that species loss during community disassembly is trait-mediated (Zavaleta et al., 2009), and may be predictable if knowledge of the functional traits involved in the response to environmental change is available. Trait-based approaches can predict patterns of extinction and persistence, because the distribution of trait values can affect the potential of a population to persist or perish under a set of environmental conditions (Norberg et al., 2001; Webb et al., 2002). For example, extinction risk under habitat loss and fragmentation is associated with traits such as high trophic position, large body size and poor dispersal ability (Didham et al., 1998; Gonzalez & Chaneton, 2002; Cardillo, 2003). However, traits involved in the response of a species to one environmental stressor may not be relevant in responding to others: e.g.
dispersal traits in fragmented landscapes vs. drought tolerance in the response to climate change. Furthermore, when selective extinctions occur during community disassembly, changes in species abundances, composition and the nature of interspecific interactions are expected to impact ecosystem processes through changes in community trophic structure, biomass and nutrient assimilation rates (Larsen et al., 2005). Species that persist following community disassembly may have significantly altered ecological roles (Layman et al., 2007b). Body size as a general morphological trait can predict species loss and be related to trophic transfer efficiency, as it is often correlated with many other functional traits and demographic processes (Woodward et al., 2005). The body size spectrum (BSS), which represents the relationship between body size and abundance (or biomass), has been suggested as an integrative measure of community structure (Woodward et al., 2005) and a good indicator of ecological change (Petchey & Belgrano, 2010).

Few experiments have sought to identify the traits associated with species extinctions and persistence, or examined the subsequent effects on community trophic structure. Here, we use a bryophyte-microarthropod detrital system (the bryosphere sensu Lindo & Gonzalez, 2010) as a natural model system to experimentally test the effects of combined global change factors on biological communities. The bryosphere is a species-rich system with a detrital food web spanning multiple trophic levels, and is easy to manipulate in the field. In addition, shifts in bryosphere microarthropod communities have direct effects on the microbial components of detrital systems which perform carbon and nitrogen cycling, and have resolute and long-term consequences for ecosystem functioning in boreal and temperate forests. We examine the effects of increased temperature, drought stress and habitat ‘openness’ on soil microarthropod traits and community disassembly. Following 2 years of treatment we: 1) assessed the biodiversity (species abundance, richness); 2) correlated species-specific traits with temperature, drought and openness treatments to describe the process of community disassembly; and 3) described changes in community-level patterns of persistent species trophic functioning. We predicted communities under drought stress would experience species loss (extirpation) associated with specific traits related to drought tolerance, but that increased ‘openness’ would mitigate species loss through immigration from the external habitat matrix. At the community-level, we expected shifts in body size spectra and changes in the trophic space of persistent species associated with changes in resources and species interactions following community disassembly.

Materials and methods

Study system

Our experimental field site was located in the subarctic-boreal forest region near the town of Schefferville, in northern Quebec, Canada (54°48’ N, 66°49’ W). This area is characterized by short, cool summers and long, cold winters with mean monthly temperatures ranging from −24 °C in January to 12 °C in July (Environment Canada, 2011). The growing season at Schefferville is short (100–120 days), with frequent cloud cover (Lechowicz & Adams, 1978). The mean annual precipitation is 823 mm with 408 mm in the form of rain (Environment Canada, 2011). The area is a transitional zone between boreal forest and tundra with typically well-drained, nutrient-poor podzolic (Brunisols) soils (Moore, 1980). The dominant tree species is black spruce [Picea mariana (Mill.) B.S.P.] with patches of white spruce [Picea glauca (Moench) Voss] and tamarack [Larix laricina (Du Roi) Koch]. The understory is patchy and contains dwarf birch (Betula glandulosa Michx.) and Labrador tea (Ledum groenlandicum Oeder.). The ground cover is nearly continuous with the feathermoss Pleurozium schreberi [(Brid.) Mitt.]; infrequently, the moss species Ptilium crista-castrensis (Hedw.) and Hylocomium splendens (Hedw.) occur. Patches of Reindeer lichen [Cladonia alpestris (L.) Rabh.] are common in nearby areas.

The experimental area was composed of eight replicate sites (blocks) within a 2.4 hectare area. Our site development and sampling occurred in contiguous areas of P. schreberi. Within each site, replicate plots were created on the forest floor in 2007 for destructive sampling in 2008 and 2009. Plots consisted of individual patches of P. schreberi moss that were either contained within 115 cm wide hexagonal open-topped chambers (OTC) or left under ambient conditions. Within the chamber treatments, the OTCs created a strong moisture gradient by acting as a rain shadow at the periphery of the chamber (effectively 25 cm wide) while the area in the middle of the OTC received precipitation similar to ambient conditions. The effect of the OTC increased the temperature at the soil surface by an average of 0.5 °C over the year, driven mainly by a 2 °C increase in daily maxima during the summer months.

Moss patches (12.5 cm diameter × 9 cm deep) were cut from the surrounding matrix, placed in plastic plant pots, then exposed to one of four treatments: 1) outside of the OTC under ambient conditions (ambient), 2) within the inner area of the OTC (inner), 3) at the outer periphery of the OTC (outer), or 4) at the outer periphery of the OTC but open to the surrounding moss habitat by two, 3 cm wide openings on each side (corridors). We use the ambient moss patches as a control to explore the effects of temperature, moisture and ‘openness’ on community disassembly: differences between ambient and inner-chamber patches test the effect of temperature (contrast 1), differences between inner-chamber patches and outer-chamber patches test the effect of drought (contrast 2) and differences between outer-chamber patches with and without corridors test the effect of openness in the presence of drought (contrast 3).

Moss patches were collected during the peak dry period (August) following 1 and 2 years in the field. Microarthropods
were extracted from the moss using Tullgren funnels over 48 h into 75% EtOH, then identified and enumerated. Moss samples were weighed prior to and immediately following extraction to gravimetrically calculate the moisture content of individual patches (moisture content % = [(wet weight (g) – dry weight (g))/dry weight (g)]*100). Microarthropod abundance and species richness were standardized by dry weight (dwt) of substrate sampled, and are expressed as the number of individuals or number of species per gram dry weight respectively. Body mass of each species was estimated using average length and width measurements from representative types of adults and immatures converted to mass (μg) using Caruso & Migliorini (2009).

We characterized the species in our samples according to 26 trait states related to life history and morphological characteristics. Traits hypothesized to be relevant in coping with environmental change were considered a priori (Supporting Information Table S1). Body size was measured from body mass calculations; desiccation tolerance was categorized from Spearman rank coefficient (r) of the correlation between species abundance and moisture content at the patch level. Sclerotization (or mineralization) of the cuticle was categorized based on body colour and hardness. Species were grouped into seven feeding guilds (algivores, fungivores, detritivores, lichenivores, herbivores, omnivores and predators), two reproductive modes (asexual-parthenogenetic, sexual) and three levels of taxonomic uniqueness. Taxonomic uniqueness was binned as three categories dependent on the number of known species in a family: low diversity (<3), moderate (3–15) and high diversity (>15). Life history traits were assigned at the genus and species level for oribatid mites and at the family level elsewhere based on the literature and personal communication with taxonomic experts.

A subset of ten species from 2009 ambient and outer-chamber samples were analysed for natural abundance 15N/14N and 13C/12C stable isotopes. Species were selected on the basis of being consistently present in both ambient and outer patches with a biomass that allowed accurate stable isotopic analysis. Individuals were handpicked from ethanol into tin capsules and dried at 60 °C for 24 h. Samples were weighed and stored in a desiccator until analysed. Each sample consisted of 1–450 individuals pooled from each patch to obtain sufficient biomass for analyses. The same ten species from replicate ambient and outer patches were analysed. Samples were shipped to the UC Davis Stable Isotope Facility for analysis of 13C and 15N isotopes using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The final delta values are expressed relative to international standards V-PDB (Vienna PeeDee Belemnite) and Air for carbon and nitrogen respectively. The stable isotopes of ten species were compared between ambient and outer treatments, using six metrics (Layman et al., 2007a): δ15N range (NR), δ13C range (CR), total area (TA), mean distance to centroid (CD), mean nearest neighbour distance (NND) and standard deviation of nearest neighbour distance (SD NND). All metrics were calculated in R version 2.14.1 (R Development Core Team, 2011).

Statistical analyses

Moisture content was analysed using a two-way analysis of variance (ANOVA) with treatments crossed by year. A two-way multivariate analysis of variance (MANOVA) was used to compare the species richness and abundance of taxonomic groups among treatments and years (overall Wilk’s λ and univariate F values given) in STATISTICA 7.0 (StatSoft, Inc., 2004). Standardized microarthropod abundances, per g dry weight of substrate, were log transformed (x + 1) prior to analyses. We focused on overall effects of temperature, drought and openness on abundance and richness using a planned contrast that reflected our experimental design: (1) differences between ambient and inner-chamber patches (temperature), (2) differences between inner-chamber patches and outer-chamber patches (drought) and (3) differences between outer-chamber patches with and without corrals (openness).

We use the body size spectra (BSS) as an integrative measure of the microarthropod community structure (Woodward et al., 2005) due to the metabolic underpinnings of the body size scaling, and the relationship between body size and numerous species traits (Woodward et al., 2005). The log-log relationship between average standardized abundance of each species and their body size was analysed by quantile regression using the package ‘quantreg’ (Koenker, 2005) in R version 2.14.1 (R Development Core Team, 2011). The 75th quantile was used for the regression as it eliminated spurious results due to nonabundant species being present or absent, thus examines the BSS relationship in the most abundant species. We tested a null hypothesis of equal slopes across all treatments by comparing a series of nested models using a Wald test (Bassett & Koenker, 1982): a full model that allows slopes and intercepts to vary across treatments, a model with a single slope (equal across treatments) and different intercepts for each treatment and a simple model with a single slope and intercept (no treatment effect). Nested models are compared with the full model, such that a rejection of the null hypothesis (P < 0.05) indicates that the extra terms in the full model not included in the nested model are not equal, and therefore represent the data more accurately.

We use two methods to link the traits of the bryofaunal species to our environmental treatment variables: RLQ analysis (Dolédec et al., 1996) and fourth-corner analysis (Legendre et al., 1997; Dray & Legendre, 2008). The RLQ analysis consists of a multivariate ordination of species abundance data (L) constrained by species trait data (Q) and environmental data (R), whereas fourth-corner analysis quantifies and tests the correlation between the variables in Q and R. A total of 32 patches and 25781 individuals belonging to 110 species were included in the analysis (Table S1). Three separate ordinations of the R, L and Q tables were performed prior to the RLQ analysis. The species abundance matrix L (I × J) containing the number of individuals in each species (J) occurring in each sample (I) was analysed by correspondence analysis (CA). The environmental variables (table R) and species traits (table Q) were analysed using principal component analysis (PCA), with row weights and column weights of table L respectively. The sites and species scores (or coordinates) from the species CA are used to link the R and Q tables, as sites are shared by R and L.
and species are shared by Q and L. Moisture content was binned into five moisture categories while dummy variables were used for other environmental treatment variables; all species trait states were expressed as dummy variables. A single inertia analysis (RLQ analysis) was conducted on the cross-matrix of tables R, L and Q. The statistical significance of the relationship between the environmental attributes (R) and species traits (Q) was assessed by comparing 999 Monte Carlo permutations of the rows of tables R and Q with the total inertia in the RLQ analysis (Dolédec et al., 1996). Fourth-corner analysis (Legendre et al., 1997; Dray & Legendre, 2008) was used to quantify and test the relationship between environmental variables and species trait states. The fourth-corner statistic corresponds to a Pearson product-moment correlation measuring the link between species abundances, environmental treatment variables and species traits. The RLQ and fourth-corner analyses were conducted using the ade4 package (Chessel et al., 2004) in R version 2.14.1 (R Development Core Team, 2011).

**Results**

As expected, moisture content of the moss patches was significantly different among the environmental climate treatments ($F_{3,24} = 35.10, P < 0.001$), with a significantly greater moisture occurring in the ambient and inner-chamber patches compared with the outer-chamber patches with or without corridors (contrast 2: $t = 7.44, P < 0.001$) (Fig. 1a); there was no difference in moisture between the 2 years of sampling ($F_{1,24} < 0.01, P = 0.990$).

Moisture content had an overwhelming effect on species abundance and richness. Overall bryofaunal abundance was significantly greater in wetter (ambient and inner-chamber) patches (Wilks $\lambda = 0.223, F_{18,54.2} = 2.11, P = 0.018$) than dry outer and corridor patches (Fig. 1b); univariate statistical results for treatment effects on abundance are summarized in Table 1. Overall species richness at the individual patch level was significantly affected by both year (Wilks $\lambda = 0.522, F_{6,54.2} = 2.90, P = 0.035$) and environmental treatment (Wilks $\lambda = 0.128, F_{18,54.2} = 3.23, P < 0.001$). Species richness results differ qualitatively from patterns observed in species abundances, whereby the inner-chamber patches had significantly greater species richness than the two dry outer-chamber patch treatments (outer, corridors), but the ambient treatment patches were not significantly different from either set of treatments and had intermediate overall species richness (Fig. 1c). At the individual taxonomic group level, all groups had significantly greater richness under inner-chamber vs. ambient (contrast 1) and outer drought conditions (contrast 2), whereas the dominant taxonomic group, the oribatid mites, also demonstrated significantly greater species richness within dry corridor patches compared with the dry, but isolated, outer patches (contrast 3) (Table 1). The year effect was driven by a significant reduction in the number of collembolan species collected per patch in 2009 ($F_{1,24} = 10.88, P = 0.003$).

Quantile regression on the body size spectra (BSS) revealed that species abundances declined significantly with body size (overall regression equation: log
Table 1 Univariate results of MANOVA test for standardized taxonomic group abundance and species richness. A priori contrast results are given demonstrating a significant individual effect of increased temperature (contrast 1: ambient vs. inner), drought stress (contrast 2: inner vs. outer), or habitat openness (contrast 3: outer vs. corridor); nonsignificant results not shown.

<table>
<thead>
<tr>
<th></th>
<th>Abundance</th>
<th>Temperature (1)</th>
<th>Drought (2)</th>
<th>Openness (3)</th>
</tr>
</thead>
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<tr>
<td></td>
<td>$F_{(3, 24)}$</td>
<td>$P$</td>
<td>$t$</td>
<td>$P$</td>
</tr>
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<td><strong>Abundance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>--</td>
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</tr>
<tr>
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<td>3.85</td>
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<tr>
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<td>&lt;0.001</td>
<td>--</td>
<td>4.99</td>
</tr>
<tr>
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<td>&lt;0.001</td>
<td>--</td>
<td>4.06</td>
</tr>
<tr>
<td>Others</td>
<td>4.22</td>
<td>0.016</td>
<td>--</td>
<td>3.51</td>
</tr>
<tr>
<td><strong>Species richness</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oribatida</td>
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<td>&lt;0.001</td>
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</tr>
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<td>Prostigmata</td>
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<td>$t = -2.58$, $P = 0.016$</td>
<td>4.99</td>
</tr>
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Fig. 2 The relationship between the average standardized abundance of each microarthropod species with body size (log-log scale) for all species within ambient, inner (temperature), outer (drought) and corridor (openness) treatments. Lines show the 75% quantile regression for each treatment.

(abundance) = 1.60–0.30 log (mass); (intercept: $P < 0.001$, slope: $P = 0.001$)) (Fig. 2). Although dry outer patches demonstrated a steeper slope (-0.46) than other treatments (ambient = -0.34; inner = -0.31, corridor = -0.31), this relationship was not significantly different among treatments ($F_{(3, 432)} = 0.22$, $P = 0.883$). Similar to results of manova for the overall abundances, abundance values represented by the intercept of the BSS relationships (log-log scale) were significantly different among wet (ambient = 1.91, inner = 2.06) and dry (outer = 1.36, corridor = 1.38) treatments ($F_{(6,432)} = 5.63$, $P < 0.001$); abundance was slightly, although nonsignificantly, increased under warming (inner) conditions compared with ambient (Fig. 2).
of the variation in the RLQ analysis of the trait data reveals an interesting subset of species that are highly desiccation tolerant despite being small-bodied (0-5 g) and not sclerotized. The fauna associated with this group comprised five species of small prostigmatid mites in the families Tydeidae and Eupodidae. Permutation tests reveal numerous correlations between environmental variables and species trait states that were significantly different from random (Fig. 3c). None of the species traits correlated with ambient vs. chamber treatments per se at the plot level; however, many traits were significantly positively or negatively correlated with the effects of the OTC, in particular moisture content of the patches as dictated by patch arrangement within the chambers (Fig. 3c). The highest correlation \( (R = 0.45, P < 0.001) \) was between highly desiccation-tolerant species and dry habitat patches.

The trophic space of persistent species within outer-chamber treatments demonstrated a distinct vertical contraction of the diet \( (\delta^{15}N \text{ range}) \) compared to trophic space of the same species under ambient conditions (Fig. 4). Community trophic metrics \( \delta^{15}N \text{ range}, \text{total area, average distance to nearest neighbour and the standard deviation of nearest neighbour distances, all decreased in outer-chamber treatments compared with ambient conditions, whereas} \ \delta^{13}C \text{ and distance-to-centroid values increased (Table 3).}

### Discussion

Nonrandom community disassembly has been shown in response to habitat fragmentation (Gonzalez et al., 1998; Staddon et al., 2010), where extinction risk is often associated with higher trophic position, larger body size and smaller local population densities. Our data suggest that specific correlates of extinction associated

| Table 2 | Comparison of variation explained (%) by RLQ analyses with variation explained in the separate analyses of three matrices \( (R \text{ matrix: environment} \times \text{site}; \ L \text{ matrix: species} \times \text{site}; \ Q \text{ matrix: species} \times \text{trait}) \). In the separate analysis, the environmental variables and species traits were analysed using principal component analysis (PCA); the species abundances were analysed by correspondence analysis (CA).
<table>
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<th>Separate analyses</th>
<th>% variance explained by axis 1</th>
<th>% variance explained by axis 2</th>
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<td>L/CA</td>
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<td>Q/PCA</td>
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<tr>
<td>RLQ analysis</td>
<td>% variance explained by axis 1</td>
<td>% variance explained by axis 2</td>
</tr>
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<td>57.6</td>
</tr>
<tr>
<td>L/RLQ</td>
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</tr>
<tr>
<td>Q/RLQ</td>
<td>81.0</td>
<td>83.1</td>
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</table>

Fig. 3 The results of RLQ analysis indicating associations along the first two axes between (a) environmental descriptors and (b) microarthropod species traits. (c) Fourth-corner correlations between species trait states (rows) and environmental variables (columns) at the patch level. White boxes indicate no significant correlation, grey boxes indicate significant negative relationship, black boxes indicate significant positive relationship.
with drought are different from those associated with habitat loss in the moss-microarthropod system. We found that some of the smallest fauna in our experiment persisted under drought conditions, despite possessing traits not usually associated with drought tolerance, and that habitat openness mitigated some species loss under drought conditions. Thus, a combination of species-specific environmental tolerances combined with differential dispersal abilities of species appear to have contributed to the nonrandom patterns of microarthropod community composition in our experimental habitats.

The OTCs produced a strong moisture gradient among moss patches associated with their position within the chambers. Drought stress had an overwhelming effect on bryofauna communities after 1 and 2 years in the field. Moisture content of the moss habitat was the biggest explanatory variable in our measures of bryosphere faunal abundance, where patterns of abundance in all groups followed moisture gradients. The strong negative effect of drought was also evident in our measures of species richness; yet habitat openness to the surrounding matrix partially mitigated this effect, at least in the dominant taxa. Habitat connectivity has been shown to increase the ability of communities to recover from perturbation through recolonization events (Gonzalez et al., 1998; Starzomski & Srivastava, 2007), and even mitigate the negative ecosystem-level effects of fragmentation (Staddon et al., 2010). Dispersal from surrounding habitats may become increasingly important as the overall habitat quality decreases, such as under drought stress. Immigration from adjacent high-quality (moist) areas may have boosted species richness and increased long-term survival of metapopulations (Gonzalez & Chaneton, 2002; Binzenhoefer et al., 2008), although no effect of the corridor treatment was observed for patterns of abundance. Chisholm et al. (2011) found that despite extreme drought conditions in an experimental bryosphere system, poor-quality drought patches adjacent to high-quality wet patches maintained species richness through mass effects driven by dispersal. While corridor patches were within the drought-stress peripheral zone of the OTC, as was the moss matrix immediately surrounding the corridor patches, good-quality moist habitat conditions existed within 10 cm, allowing colonists with the ability to disperse to access the corridor patches.

Abundance generally declines with increasing body size and an efficient transfer of energy is characterized by a shallow negative slope in body size spectra (BSS). Although the slope of the BSS was nonsignificantly different among treatments, the dry outer habitats demonstrated a steeper negative slope that points to a less efficient transfer of energy among these food webs (Sheldon et al., 1972; Petchey & Belgrano, 2010). This supports the idea that changes in basal resources, possibly alterations in the microbial portion of the food web, had cascading bottom-up effects on microarthropod consumers. For example, Mulder & Elser (2009) found that steeper size spectra slopes were associated with changes in nutrient status of grassland soils, in particular decreases in carbon and nitrogen availability. Furthermore, there is some indication that the steeper BSS slope under drought stress is mitigated in corridor

![Fig. 4](https://example.com/image.png)

**Fig. 4** Average (± SE) delta $^{13}$C and delta $^{15}$N values for the same ten microarthropod species collected in ambient and outer-chamber (drought) treatments. Shown is convex hull area of community within ambient (dashed line, shaded) and outer-chamber treatments (black line). Data points outside of the convex hull area are moss-detrital samples for the two treatments.

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Community-wide stable isotope metrics associated with Fig 4. Stable isotopes of ten microarthropod species were explored using six community-wide metrics: [δ$^{15}$N range, δ$^{13}$C range, total area based on convex hull, mean distance to centroid, mean nearest neighbour distance (NND) and standard deviation of nearest neighbour distance (SD NND)] as described in Layman et al. (2007a) for ambient and outer treatments</th>
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<tbody>
<tr>
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<td>δ$^{15}$N range</td>
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<tr>
<td>Ambient</td>
<td>15.43</td>
</tr>
<tr>
<td>Outer</td>
<td>7.21</td>
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</tbody>
</table>

treatments, as increased abundances of larger-bodied species relative to outer patches resulted in a shallower BSS slope.

Our trait-based approach explained a significant proportion of the community response. We found that the bryofaunal assemblage could be roughly divided into four trait-based groups responding to changes in environmental treatments. First, a group of small, unsclerotized, Prostigmatid mites was tolerant to the drying effects of the outer-chamber patches; when all other groups of fauna were extirpated from the drought patches, these Tydeid and Eupodid mites persisted. The second group was drought intolerant, asexual, mainly Oribatid mites (Oppiidae, Suctobelbidae, Tectocephidae) and the third group was medium-sized detritivores that demonstrated a unimodal relationship with moisture. Drought conditions are known to act as an environmental filter, producing progressively nested communities composed of species tolerant to dry conditions (Lindo et al., 2008). Although all species had significantly reduced abundances under drought conditions, a particular subset of the fauna consistently persisted, albeit in low abundances.

Changes in overall richness and abundance were positively and significantly associated with moisture availability within habitat patches (see also Siepel, 1996; Frampton et al., 2000; Tsiafoulia et al., 2005; Lindo & Winchester, 2008; Kardol et al., 2011). However, the fourth trait group, found among the corridor treatments representing ‘openness’ of the fragmented system under drought conditions, demonstrated dispersal-related traits. Habitat openness increased species richness under drought-stress conditions, due to the presence of well-sclerotized, sexual species in the high-diversity and derived families of Mycobatidae and Ceratozetidae (Acarida: Oribatida). We have yet to fully explain this result. The higher level of sclerotization may have increased these species ability to resist desiccation, but these species were not present in dry outer patches that restricted fauna movement. Nevertheless, the significance of sexual reproductive mode and high-diversity taxa in association with habitat openness was unanticipated. Lindberg & Bengtsson (2005) found that sexual microarthropod species were less impacted by drought stress than asexual species, but asexual species were able to recover faster than sexual species. Sexual species are thought to have an advantage in unstable and limited resource conditions, whereas asexual species are thought to have greater colonization and growth rates (Bell, 1982; Norton, 1994). Moreover, sexual species may be more dispersive on average than asexual species, as sexual species need to seek mates, or in this case spermatophores. However, there is currently no evidence that sexual and asexual bryosphere microarthropods differ in their dispersal capability.

Elevated temperature under nondrought conditions in the inner patches as compared to the ambient patches also increased the number of species present. We posit that changes in the microbial community under wet, warmed conditions could have elicited this response. Shifts in microbial community composition under elevated temperature have been reported (Zogg et al., 1997; Gray et al., 2011) with functional implications for nutrient dynamics and potential cascading effects through the detrital food web (Wardle et al., 1999). Decreases in richness and abundance in the outer treatments may have been further exacerbated by correlations among drought and temperature tolerances (Siepel, 1996; Blankinship et al., 2011), yet it was difficult to disentangle these effects given the strong effect of drought stress and lack of drought-without-warming treatments. The effects of experimental warming and altered precipitation on soil biota have been equivocal (Blankinship et al., 2011) and other components of the bryosphere community are likely more impacted by drought stress than microarthropods (e.g. enchytraeids; Maraldo & Holmstrup, 2009). Climate warming and changes in precipitation regimes are expected to have direct impacts on soil organisms and consequently ecosystem-level processes such as nutrient and energy fluxes (Swift et al., 1998; Wardle et al., 1998; Hunt & Wall, 2002).

Species which persist following environmental change have altered ecological roles as seen in our measures of trophic space and the community-level contraction in diet. Stable isotopic analysis revealed that the same species differed in δ13C and δ15N under ambient conditions vs. following 2 years of summer drought. At the community level, this lead to a decrease in the range of δ15N indicating that trophic position was reduced in some species and increased in others. This trophic contraction suggests a long-term consequence of community disassembly as stable isotopes are integrative measures of trophic feeding over space and time. We posit that changes in resource availability and associated bottom-up responses, as suggested through the analysis of the body size spectra, explain both downward and upward shifts in trophic position. Results such as this further corroborate that it is not only species loss, but also the functional roles of the species that persist, which will dictate how ecosystem function will alter under global environmental change scenarios.

There is a growing body of scientific literature recognizing and addressing community and ecosystem responses to multiple, interacting elements of global change (Travis, 2003; Darling & Côté, 2008), yet the
number of experiments which study multiple stressors is small compared with single-stressor experiments (Rustad, 2008). Evidence for interactive effects of climate (drought) and habitat openness in this study was taxon dependent at the family level, which resulted in divergent trait-based responses within the Oribatid mite suborder, and the overall assemblage. In this study, a trait-based approach has advanced our understanding of how environmental change can alter community structure. We found that harsh environmental conditions (drought stress) initiate a process of community disassembly that differs from other habitat alterations such as fragmentation or habitat loss, but that the combination of species-specific environmental tolerances and spatial constraints (dispersal capabilities) of the landscape ultimately interact to structure community composition. A trait-based approach may help us form an understanding of the community disassembly process under different environmental conditions, and identify previously unknown relationships, such as that between sexual reproduction, high within-group taxonomic diversity and dispersal/corridor use. The next step to extend this framework of community disassembly and biodiversity loss is to link changes in community-level trait distributions to ecosystem-level processes and ecosystem function (Lavorel & Garnier, 2002). As demonstrated by changes in trophic space of persistent species under drought stress, we predict that ecosystem-level processes are affected by observed changes in species trait distribution via community trophic structure, biomass and nutrient assimilation rates.

Acknowledgments

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Supporting Information

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

Table S1. Species and trait states for the bryosphere microarthropod community at Schefferville, Québec. Species standardized average abundances (no. individuals per g dwt moss) are given for each experimental treatment. Standard errors in parentheses.

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