MICROARTHROPOD DIVERSITY AND DISTRIBUTION IN SOUTHWESTERN CANADA

by

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Abstract

Microarthropod diversity patterns were investigated in southwestern British Columbia, Canada. We surveyed soil microarthropods associated with moss carpets on exposed rocky outcrops. Our survey identified 352 morphospecies in 32 sites spanning a 130 km × 60 km area. Previous studies have interpreted strong correlations of species composition with environmental factors as evidence of niche limitation, and strong correlations with spatial factors as evidence of dispersal limitation. Here, we examine 18 ecological variables relevant to either spatial location or environmental aspects of ecological processes, and evaluate their influences on the microarthropod community. We tested whether the relative importance of spatial and environmental factors was concordant between various community attributes including composition, abundance and species richness, and between different taxonomic groups of microarthropods (Oribatida, Mesostigmata, Collembola). We used two different methods (distance-based Mantel and raw data-based ordination methods) to show that spatial variables could not explain composition or compositional turnover for most microarthropod groups, except Collembola. Dispersal limitation of Collembola is surprising given the high dispersal ability of this group. Although environmental factors explained a large amount of spatial variance in composition (raw data-based ordination method) for all microarthropod groups, environmental similarity (distance-based Mantel method) was a poor predictor of compositional similarity for Oribatida and Mesostigmata. Total abundance and species richness could also be explained by combinations of environmental factors, particularly those relating to tree cover and soil-relevant microhabitat variables (i.e, water content/mass, total soil mass and particle mass), but total abundance and richness were

themselves only weakly correlated across space. The most important environmental influences on microarthropod communities were tree cover and water mass, followed by distance-to-sea. At the same time, there was a lot of unexplained variance in the composition of microarthropod communities (especially for species incidences) which could not be explained by the available ecological variables. As richness hotspots were dispersed across different habitats for different taxonomic groups, we suggested that species interactions might be equally important as environmental filtering and spatial autocorrelation in shaping microarthropod community structure, especially for patterns in species incidence.

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Chapter One: General introduction

Ecology is on the way to build fundamental theories. Development of the neutral theory of biodiversity and biogeography in the early 21st century (Hubbell 2001) is one of the important milestones in establishing general ecological principles, just like the foundational milestones of species-area relationship and niche theory were in earlier decades.

However, neutral theory still encounters a lot of difficulties in explaining species diversity patterns across geographic regions and for different taxonomies. Interpretation of species community structure still relies substantially on niche theory. Therefore, a compromise has been proposed to reconcile the struggle between neutral and niche theories (Whitfield 2002; Chase & Myers 2011). Partitioning the spatial variance in species composition into that attributed to niche and neutral processes is one of the possible solutions (Smith & Lundholm 2010).

Variation partitioning can be referred to as constrained partial ordination analysis in numerical ecology (Borcard *et al.* 1992; Meot *et al.* 1998). The method is to use a three-step procedure to identify and separate the contribution of different explanatory variable groups (for example, spatial variables that could be related to neutral dispersal limitation, environmental variables that could be related to niche structuring) to the total variance involved in the response factors.

There are also other possible methods to test the relative importance of niche and neutral processes in creating ecological pattern. For example, path analysis, or its more general form - structural equation modeling - can be powerful in disentangling the relative explanatory abilities of different

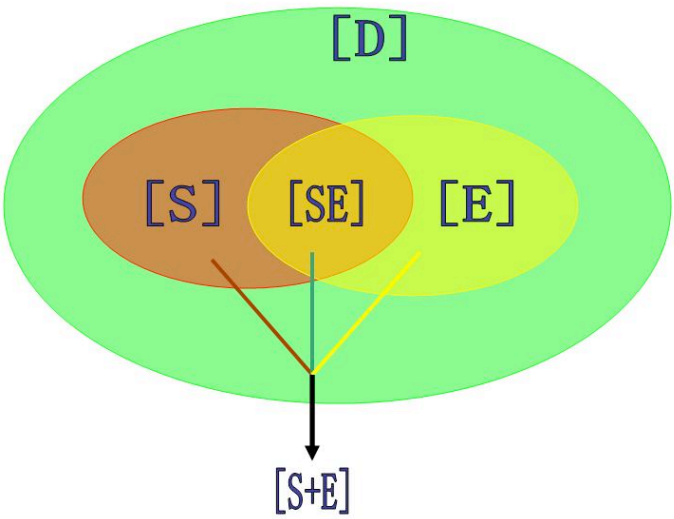
regressors on determining response factors. Structural equation modeling is highly flexible, therefore allowing ecologists to test different hypotheses simultaneously.

Community ecology has benefited from population ecology and population genetics, especially aspects of population dynamic mathematical models (Leibold *et al.* 2004). Currently, these theoretical models have been widely applied in the studies of other subjects, like molecular genetics, molecular ecology and molecular phylogenetics. It is worth mentioning that the Hubbell's neutral theory is also the extension derived from the neutral theory of molecular evolution proposed by Kimura (Kimura 1968, 1983) two decades ago.

Variance partitioning

Variance partitioning technique has been applied in current ecological literature. The merit of the method is that it could allow ones to quantify the relative contribution of each category of explanatory variables to explain the variance of focused objects. In ecological studies, typically the partitioning of variance can be divided into four parts: pure environmental variance, mixed environmental and spatial variance, pure spatial variance and unknown variance (Borcard *et al.* 1992; Meot *et al.* 1998). The objective of dividing such a four-part variance is to attribute community variance to different factors which are derived from the exclusive mechanisms: the niche mechanism and the neutrality mechanism. Fig. 1.1 shows a schematic map of the variance components. When comparing different parts of variance, we could determine the relative strengths of space [S], environment [E], and the interaction [SE] between space and environment on structuring species communities.

Fig. 1.1. A schematic map showing different components that are used in variance partitioning. [E]-pure environmental variance; [SE]-shared variance between environment and space; [S]-pure space variance; [D]-unexplained variance. [S]+[SE]+[E]=[S+E] denotes the total explained variance. [S+E]+[D]=1 totally.



Mite diversity in western coast of Canada

In a recent study, Lindo and Winchester (2009) applied the variance partitioning method to show the relative contribution of spatial and environmental factors in influencing arboreal and terrestrial oribatid mite diversity. This work showed that terrestrial oribatids and arboreal oribatids showed different responses to spatial and environmental variables.

However, it is not clear what the response would be for different mite groups. The main taxonomic

groups of soil microarthropods are Collembola (Insecta), Oribatida (Acari), Mesostigmatida (Acari), and Prostigmata (Acari). We did not attempt to identify prostigmatids because many species are extremely small, and their diverse trophic position makes interpretation of patterns in this group difficult.

Microarthropods could have different forms of dispersal, by either active or passive mechanisms. At local scales, active dispersal should be prevailing. Microarthropods (especially collembolans) crawl very actively above soil substrates or wood surfaces (personal observation). At broad spatial scales, microarthropods could disperse over a long distance via the mechanisms of phoresy and aerial transport.

For example, it is observed that collembolans can actively disperse across long distances as well via passive dispersal mechanisms (Garrick 2002; Hawes *et al.* 2008; Querner & Bruckner 2009). Dispersal vectors could be wind (Farrow & Greenslade 1992), large animals (King *et al.* 1985), water (Moore 2002; Hawes *et al.* 2008) and so on. Therefore, we would expect in general for Collembola, environmental constraints may be more important than spatial constraints, as they could choose to dwell in best habitats through extensive dispersal activities.

By contrast, terrestrial oribatids are wingless, soil-dwelling and cursorial. Oribatids typically have low dispersal abilities (Berthet 1964; Ojala & Huhta 2001; Lindo 2010). There are relatively few examples of passive dispersal of oribatids (Karasawa *et al.* 2005). Thus, we could readily hypothesize that oribatids as a group are dispersed limited and therefore spatially determined (Lindo & Winchester 2009).

For Mesostigmata, we predict intermediate long-distance dispersal abilities as phoresy (and hyperphoresy, (Athias-Binche 1994; Szymkowiak *et al.* 2007)) mechanisms have been well documented in Mesostigmata (Binns 1982; Hunter & Rosario 1988; Houck & O'Conner 1991; Athias-Binche 1994; Szymkowiak *et al.* 2007). For example, in the nest chambers of the dung beetle *Copris lunaris*, it was observed that there were 10 mesostigmata species, which preferentially attach to either the parental or progeny generations of beetles (Masan and Halliday 2009). This kind of behaviour allowed them to undergo long-distance dispersal with the dung beetle.

As we see, one of the most important ecological features for microarthropods is the phoresy mechanism, which has been widely found for Collembola and Mesostigmata. The definition of phoresy is a kind of symbiotic relationship in which one organism transports another organism from a different species to a different location (Walter & Proctar 1999). Thus, this very nature allowed us to hypothesize that both microarthropod groups should be largely environmentally constrained.

From the perspective of diet and trophic positions, different microarthropod groups have different characteristics as well. Oribatid species include over 45000 taxa (Hess 2008), but most of these are specialists. Many oribatids have close associations with soil microflora and plants, particularly fungi, in terms of diets (Wallwork 1983). For example, Phthiracarids only feed on pine materials, while Oppiids only feed on fungal material (Ponge 1991). Although most oribatids are heavily defended against mesostigmatid predation, a few mesostigmata species have developed specialized means of overcoming these defenses. For example, species from the family Bdellidae (Prostigmata) typically feed on insects and oribatids (as an example, see

http://www.zoology.ubc.ca/~srivast/mites/s/AK6.html).

Collembolan species feed on decaying vegetable matter, fungi, lichens etc (http://www.ento.csiro.au/education/hexapods/collembola.html). Sometimes the food bolus could be composed of bacteria with minute fungal and mineral particles (Ponge 1991). Also, faecal material could be a major food source for some Collembola, e.g, *Folsomia manolachei, Isotomiella minor* etc (Ponge 1991). Moreover, animal remains are also commonly found in the guts of Collembola (Ponge 1991). As positioned in lower trophic ranks of food webs, they could be predated by mesostigmatids to some extent.

For Mesostigmatids, typically their diet spectrum is wide since they are situated in the top predator level of microfauna food webs (Buryn and Brandl 1992). They can inject digestive liquid into the prey body and absorb dissolved tissues from the prey (http://soilbugs.massey.ac.nz/acari.php), thus typically they were presumed theoretically and tested experimentally to prefer predating on nematodes, microarthropods and possibly collembolans (Karg 1961; Dunger 1983; Eisenbeigs and Wichard 1985; Buryn and Brandl 1992). Consequently, many mesostigmatid species have the potential to be biocontrol agents. For example, *Lasioseius scapulatus* feeds on nematodes voraciously and substantially reduces the nematode species *Aphelenchus avenae* in laboratory setting (Imbriani and Mankau 1983).

Prostigmata is another extremely large suborder with 136 families (http://soilbugs.massey.ac.nz/acari.php), and many but not all of the species are predators. Many of the species in this group feed on host plants or are parasites of animals. For example, Tetranychoid mites (Prostigmata) use over 1000 plant species as hosts, extracting basic nutrients from the plants to

support their growth and development, leading to the symptoms of chlorosis and white/yellow spots to the host plants (Zhovnerchuk 2006).

Soil microarthropod food webs show differences between wet and dry seasons (e.g., Starzomksi *et al.* 2008). It was found that drought stress could negatively influence mite abundance and richness to a great extent and the food web was largely contracted to a core of persistent species (Lindo *et al.* 2012). Thus, global change could threaten microarthropod diversity, which has not ever been rigorously assessed. As my study covered different areas of Southwestern Canada, part of the field plots were situated at humid coastal areas, while others located at dry interior landscapes. Thus, we would expect some difference when comparing the community abundance and richness of microarthropods across different areas.

From the perspective of life history of microarthropods, their population dynamics showed a great degree of differentiations when one compares different taxonomic groups. For example, oribatids reproduce slowly and their life can span up to 7 years (http://www.massey.ac.nz/~maminor/mites.html; Schatz and Behan-Pelletier 2008). In contrast, collembolans could reproduce quickly and their generation time could be just over 3-5 weeks. Microarthropods have been hypothesized to be largely limited by resources (IIIig *et al.* 2010). As describe above, lower-trophic rank taxonomic groups are specialists (e.g., oribatids), while top-trophic rank mesostigmatids and prostigmatids are generalist predators. Thus, we predicted that resource quality and abundance should be vital to determine the abundance and richness of different taxonomic groups at various areas, instead of predation.

Species distribution modeling

Species niche modeling has been widely applied in ecological studies, for describing suitable niches of species, understanding species' distribution patterns, revealing risk of epidemic diseases outbreak (Peterson *et al.* 2002; Costa *et al.* 2002; López-Cárdenas *et al.* 2005; Costa & Peterson 2012) and prioritizing conservation areas for species (Chen & Bi 2007; Urbina-Cardona & Flores-Villela 2010). There are a lot of species niche modeling methods proposed so far. I introduced some of mathematical algorithms, which will be used in the project to estimate mite diversity and suitable ranges across BC, Canada. The methods include random forest model (RF), classification and regression trees (CART), artificial neutral network (ANN), multivariate adaptive regression splines (MARS), generalized boosting models (GBM), and surface range envelop (SRE). The results of potential suitable distribution ranges of microarthropods in BC of China were presented in Appendix I and Fig. A.1.

Chapter Two: Spatial variance in soil microarthropod communities: niche, neutrality or stochasticity?

Introduction

Understanding spatial patterns in species composition is still a major task in ecological research. Two mutually exclusive mechanisms have been hypothesized to determine species composition patterns in the natural world: neutral and niche processes. Ecological neutral theory posits that local community composition is primarily determined by the combination of limited dispersal, demographic drift, and speciation (Hubbell 2001). Niche theory suggests that species differ in how they interact with the local environment and other community members, and such differences determine community composition (Vellend 2010). Typically, neutral theory predicted that species have "perfectly overlapping niches" (Harpole 2010) or should be functionally equivalent (Hubbell 2006). By contrast, niche theory relaxes this assumption, allowing species to have a variety of niche patterns, either overlapping or non-overlapping. Currently, one of the mainstream themes in community ecology is to combine both niche and neutral processes to explain community structure, and test the relative importance of each component (Cottenie 2005). Since the publication of Stephen Hubbell's neutral theory (Hubbell 2001), ecologists have often interpreted the correlation of species composition with environmental or spatial factors as evidence for, respectively, niche or neutral processes (Gilbert & Lechowicz 2004; Cottenie 2005; Legendre *et al.* 2005). Environmental descriptors define the niche

envelopes of species, while spatial descriptors represent the trait-independent dispersal processes that are so important to neutral dynamics.

One of the main challenges in attributing species turnover to either environmental or dispersal limitation is spatial autocorrelation (Legendre 1993). Spatial autocorrelation is a common phenomenon whereby sites separated by short distances are more similar in species compositions than sites separated by longer distances. Although this pattern is predicted from limited local dispersal, it may also reflect the fact that environmental similarity also decreases with distance between sites (Legendre 1993). To solve this problem, variance partitioning methods (Borcard *et al.* 1992; Meot *et al.* 1998; Peres-Neto *et al.* 2006; Legendre 2007) isolate the environmental-space covariance in order to detect the independent contribution of spatial and environmental factors in explaining variances in community composition. This is achieved either by using multivariate methods to associate community composition with environmental or spatial predictors (raw data-based ordination methods), e.g. Borcard *et al.* (1992), or by examining correlations between community dissimilarity between pairs of sites and either environmental dissimilarity or spatial distance between the same sites (distance-based Mantel methods, e.g. Duivenvoorden *et al.* (2002)). It is worthy to note here, our "distance" method only denotes the Mantel test, but not distance-based ordination methods (e.g., distance-based RDA). Typically, variance in species composition can be divided into four parts: variance explained by pure environmental filtering, variance explained by pure spatial autocorrelation (interpreted as dispersal limitation), co-variation explained concurrently by both environment filtering and spatial autocorrelation, and unknown variance which may be caused by systematic errors, data sampling biases, biological stochasticity and so on. When environment itself is spatially

auto-correlated, we could perform the regression of environment on spatial variables and use the residuals as the representation of true environment signals. However, in practice, we didn't need to do that, because this colinearity between environment and space could be reflected by the "co-variation" part of the total variance. The interpretation of variance partitioning results in terms of separating niche from neutral processes has recently been challenged, due to sensitivity of results to data structure, dispersal rate or model choice (Smith & Lundholm 2010; Gilbert & Bennett 2010; Logue *et al.* 2011), but the separation of fundamental niche constraints from dispersal constraints remains a useful goal in community ecology.

The recent interest in the relative importance of niche and neutral processes in structuring community composition can be contrasted with a much older debate about the relative importance of local conditions versus dispersal from the regional pool in limiting community species richness (Ricklefs & Schluter 1993). However, there is a connection between the two debates. The main environmental factors that constrain the distribution of species are expected to also be relevant to the number of species that can occur at a site, since the maximum local richness is simply the sum of the species whose fundamental niches are compatible with site conditions. Similarly, if the composition of communities is largely limited by dispersal, there may also be spatial patterns in local richness caused by mass effects (species-rich sites will tend to increase the species richness of neighbouring sites, e.g., Peters (2003)). Variance in total species abundance may be attributed to multiple reasons, for example, body size, metabolism or environmental conditions, and indeed neutral theory often assumes a constant total number of individuals in each site (e.g. Hubbell (2001)).

Traits are vital in determining species' responses to surrounding environments as well as their

dispersal ability (Flynn *et al.* 2011). For example, community assembly in tropical forests is determined by the interaction between leaf traits and ambient temperature (Lebrija-Trejos *et al.* 2010). At another side, some works showed traits related to dispersal could determine community patterns and determine the change of community due to habitat loss (Marini *et al.* 2012). Although neutral theory assumes species are identical in dispersal ability, it is clear that differences in dispersal ability between groups of species influence patterns of colonization (Bruna *et al.* 2011; Brederveld *et al.* 2011) and species vulnerability to habitat fragmentation (Schleicher *et al.* 2011). The variance in community composition that cannot be explained by either environmental filtering or (trait-neutral) dispersal has been attributed in part to demographic stochasticity (Shipley *et al.* 2012). However, the influence of demographic stochasticity may also differ between groups of species that have different demographic rates, for example due to different life history traits. Thus, we might expect that groups of species with different traits will differ in the relative importance of environmental constraints, dispersal limitation and demographic stochasticity for community structure. As many ecological traits are phylogenetically conserved (Freckleton *et al.* 2002; Blomberg *et al.* 2003), a simple way to test this idea is to compare different taxonomic groups.

The central questions for the present study therefore are: (1) Is the composition of soil microarthropod communities primarily limited by environmental conditions or by dispersal? (2) Do the environmental or spatial factors that determine composition patterns also determine variance in species richness or total microarthropod abundance? (3) Do taxonomic groups of microarthropods differ in the relative importance of environmental and dispersal limitation? Although two previous studies have used variance partitioning approaches to examine microarthropod composition, both

focused on oribatid mites (Borcard & Legendre 1994; Lindo & Winchester 2009; Caruso *et al.* 2012).To the best of our knowledge, there has been no attempt to examine environmental and spatial determinants of other important microarthropod groups, such as Collembola or Mesostigmata. We begin by discussing some a priori predictions about which microarthropod groups will be more affected by environment or space based on their morphology, dispersal modes (active and passive), behaviour and trophic position. The following paragraphs provide additional details about the different taxonomic groups and their ecological roles for formulating our predictions.

Collembolans are able to jump using a specialized appendage (the fercula), so at the local level they may have higher mobility than mites, which normally move by crawling through the soil matrix. Also, it has been observed that collembolans can disperse long distances via passive dispersal mechanisms (Garrick 2002; Hawes *et al.* 2008; Querner & Bruckner 2009). Known dispersal vectors include wind (Farrow & Greenslade 1992), large animals (King *et al.* 1985), and water (Moore 2002; Hawes *et al.* 2008). Therefore, we would expect collembola to be more environmentally constrained than dispersal limited.

Terrestrial oribatids are wingless, soil-dwelling and cursorial. Oribatids typically have low dispersal abilities at the local level (Berthet 1964; Ojala & Huhta 2001; Lindo 2010). There is limited evidence showing passive dispersal of oribatids (Karasawa *et al.* 2005), although canopy-associated horizontal dispersal may occur (Lindo 2010). Thus, we hypothesize that oribatids are dispersal-limited and therefore their communities should be spatially structured. This hypothesis has been tested and supported by several studies. For example, two studies examined the oribatid mite communities in Canadian landscapes: soil oribatids from Vancouver Island of BC. (Lindo & Winchester 2009) and

moss-associated mites from a lake in eastern Canada (Borcard & Legendre 1994). Recently, another study was carried out on the soil oribatids from Mediterranean beech forest and grassland landscape (Caruso *et al.* 2012). All three studies found that spatial variables were more important than environmental ones in shaping oribatid community structure. Thus, environmental heterogeneity is not as important as spatial limitation for patterning orbiatid communities. However, Lindo and Winchester (2009) did show that arboreal oribatids were strongly affected by environmental filtering as well.

For mesostigmatids, we predicted dispersal ability to be intermediate between oribatids and collembolans. There are a variety of reasons for proposing this hypothesis. First, mesostigmatids are cursorial species, like oribatids, but often larger-bodied, with longer legs than oribatids, so may be better dispersed at local scales. Mesostigmatids could also disperse through passive dispersal modes as collembolans, especially phoresy. Phoresy phenomena are kinds of transportation of one species by another species which typically has higher dispersal ability (Athias-Binche 1994). Phoresy (and hyperphoresy, (Athias-Binche 1994; Szymkowiak *et al.* 2007)) mechanisms have been developed independently in many groups of Acarina, including Prostigmata, Astigmata and Mesostigmata (Binns 1982; Hunter & Rosario 1988; Houck & O'Conner 1991; Athias-Binche 1994; Szymkowiak *et al.* 2007). Additionally, as the predators in the microarthropod communities, many mesostigmatids are generalists, thus facilitating dispersal across habitats to some extent (Beard & Walter 2001; Beaulieu *et al.* 2006; Lindo & Winchester 2009).

Thus to sum up, we hypothesized that collembolans would be environmentally structured given that they are long-distance dispersers, while oribatids should be spatially structured. Mesostigmatans are expected to have an intermediate response to both environment and space.

Materials and methods

Sampling sites

We established 32 sampling sites in Southwestern British Columbia, distributed over an area of 130km×60km (Fig. 1). Sites were selected that fulfilled the following criteria: (1) contiguous with the mainland (islands excluded); (2) flattened large rocky outcrops with > $4m^2$ of moss carpets; (3) easy access: the sites should be adjacent to roads. In each site, we sampled 5 circular soil cones (or cylinders) with diameter = 12cm, including the overlying moss and extending to the underlying continuous rock.

The dispersal scales for microarthropods is quite various, for oribatids, their dispersal is limited, thus, at small distance for example about 1km should be enough for measuring dispersal limitation. However, for other groups, for example, collembolas, they could disperse actively and passively, thus, the distance for quantifying dispersal limitation is much larger than oribatids. Thus, in designing the sampling locations, the 32 sites could have various distances from each other, with a minimum of 3km up to a maximum over 130km.

Environmental variables

We measured latitude and longitude of each site with a GPS to represent spatial location. We also measured 16 environmental variables. (1) Soil depth (code: Depth), which was measured by pushing a ruler vertically into the soil until it reached solid rock surface; Site temperature attributes: Data

loggers (iButtons, Maxim Company, URL: http://www.maxim-ic.com/products/ibutton/) were used to capture the air temperature range for five months (July 24, 2011 to January 9, 2012). The temperature data were then extracted to obtain for each site (2) maximum (MaxTemp), (3) minimum (MinTemp), (4) average (MeanTemp) and (5) variance (VarTemp) over the seasons. (6) Canopy cover (Cover): For 25/32 sites, an observer estimated the cover (in a 1 m^2 square centered at the sampling point) directly at the field sites; these were supplemented for the remaining sites by quantifying the percentage canopy openness for each sampled plot from hemispherical photographs taken 1m above the ground. (7) distance to the closest road (Distance2R), which was calculated as the length of a line, perpendicular to the road and extending from the road to the field site, using GPS (latitude, longitude, elevation) coordinates. (8) Site slope (Slope) was measured by a clinometer along the steepest slope within the sampled patch. (9) Elevation (Elevation) was measured with a GPS. The nearest distance to the sea (10) was calculated by extracting boundary co-ordinates from a boundary map of British Columbia, Canada (http://www.geobase.ca) and calculating the minimum Euclidean distance to the sea for each sampling location.

Additional environmental variables were measured in the lab, including: (11) soil mass (SoilM), the total soil core mass before drying out. (12) Water mass (WaterM): soil cores were stored in plastic sample bags until transported to the lab, where they were immediately weighed, dried out in Tullgren funnels at room temperature for 72 hours and re-weighed. The loss of weight is regarded as the soil water mass. (13) Soil water content (WaterC) was calculated as the ratio of water mass to total sample mass (soil+water). (14) Soil pH (pH): measured at a soil:water ratio of 1:2.5 (wt/wt) using a pH electrode. Specifically, 10 g dried soil derived from the moss patch was added to 25 ml of distilled

water, shaken for 2 min, and then after 30 min settlement, this procedure was repeated again before the pH test. (15) Large particle mass (ParticleM): Stones > 1cm in diameter in the soil core were extracted and weighed. (16) Finally, large particle content (ParticleC) was calculated as the percentage of the sample patch mass due to the stones.

Microarthropod extraction and sorting

Tullgren funnels were used to extract microarthropods from each soil core in the laboratory. The process of microarthropod extraction is also the process to remove water from the samples. In detail, before putting soil cores into the Tullgren funnel, we measured the wet mass of soil core (as the total sample patch mass). After that, we took out the moss patch and put it into the Tullgren tunnel under dimmed 40 W bulbs for extraction lasting 72 hours. The microarthropods were collected in sample jars below the funnel, containing a solution of 70% ethanol, 20% glycerin and 10% water.

The jars containing extracted microarthropods were stored at 4 °C until sorted. Species sorting was carried out at 60x magnification with a dissecting microscope. Morphospecies, the surrogates of taxonomic species, are often effective in overcoming identification difficulties especially for invertebrate identification (Derraik *et al.* 2010) and our morphospecies library has been checked by acarologists. Dr. David Walter checked an earlier version of our library for species lumping or splitting errors, and found a <1% error rate, all of which were corrected. Here, microarthropod morphospecies were identified using the online key which has been established for BC microarthropods by our lab (URL: http://www.zoology.ubc.ca/~srivast/mites/). Possible new morphospecies that were not matched in the species key were recorded, drawn, photographed and

updated to the online key. We did not consider Prostigmata, another common microarthropod group in soils, due to the difficulty in identifying the small individuals of some species (esp. Zerconiidae), and their trophic heterogeneity, which would have complicated interpretation of any environmental effects.

Statistical methods

Multiple regression analysis and stepwise model selection

We performed multiple regression analysis with a model selection procedure to identify the best predictors of microarthropod abundances and richness, both overall and for each of the three taxonomic groups. Since considering all the 18 variables in a full model would leave many variables not significantly correlated with microarthropod community, we performed stepwise model selection to choose the best combination of variables for each functional group. The stepwise model selection procedure chose the best one using AIC method. We performed both backward and forward selection procedures and the results were identical.

Variance partitioning

We used two fundamentally different methods to partition community variance into environmental and spatial components. “Raw data” approaches use ordination to summarize variance in community composition amongst sites to a small number of axes, and then examine the strength of environmental versus spatial predictors in explaining this ordination. “Distance” approaches use Mantel tests to examine how compositional dissimilarity between pairs of sites correlates with either environmental dissimilarity between sites or geographic distance. Thus raw data approaches explain variance in

composition, whereas distance approaches explain variance in compositional dissimilarity (beta-diversity). This distinction has spawned a vigorous and as yet unresolved debate about the better method (Legendre et al. 2008, Tuomisto & Ruokolainen 2008). Gilbert and Bennett (2010) found that none of the available multivariate techniques are able to reflect the underlying variance in composition data accurately. So, instead of only using a single method, we use different methods to see if the results were consistent. We also considered a composition dataset based only on species presence ("incidence-based composition"), as well as one that also included information on local abundance ("abundance-based composition") as dispersal limitation might be more reflected in presence, whereas environmental limitation might be more reflected in abundance.

Redundancy analysis (RDA) or Canonical correspondence analysis (CCA) (Ter Braak 1986) are the most common ordination methods used to investigate the relationship of environmental variables to species composition information (Legendre & Legendre 1998). Either could be employed in the "raw data" methods to perform variance partitioning and examine the relative importance of individual predictors on influencing species distribution and abundance at the communities (Peres-Neto *et al.* 2006); we chose CCA.

Variance partitioning based on redundancy analysis was performed using the 'vegan' package under the R environment (Oksanen *et al.* 2012). As one of our main objectives was to distinguish the relative importance of niche and dispersal mechanisms shaping current microarthropod diversity in communities, we divided the 18 local variables into two categories: space-related and environment-related ones. The space-related variables included the geographic coordinates of the sites. Except for these two variables, the remaining variables were regarded as environmental variables.

Space-related variables only included the geographic coordinates, requiring many fewer degrees of freedom for model-fitting than niche-relevant variables. It has been argued that to address this discrepancy, the number of spatial variables should be expanded (Borcard and Legendre 2002, (Dray *et al.* 2006)). There are several ways to decompose spatial information: by using the eigenvectors derived from the principal coordinate analysis on modified spatial coordinates (PCNM; e.g. (Dray *et al.* 2006), by extracting Moran's eigenvector maps (Griffith & Peres-Neto 2006), or employing a polynomial surface method (Gilbert & Lechowicz 2004). We chose to use the PCNM method as it is most widely used.

To perform PCNM, all the orthogonal principal coordinates (the analysis returned 9 principal axes) were extracted and equally weighted and used to represent space-relevant variables. The variance partitioning analysis was then repeated again by using PCNM-derived spatial variables and the original environmental variables. PCNM-derived spatial variables have been used previously in ecological studies (Gilbert & Lechowicz 2004; Griffith & Peres-Neto 2006; Dray *et al.* 2006).

Finally, the variance attributed to "pure" environmental effects was determined by the remaining 16 environmental variables.

The distance method for variance was based on comparing two distance-decaying patterns, characterizing beta-diversity. The first examined how microarthropod compositional similarity declined as a function of environmental dissimilarity/distances among sites. The second examined how microarthropod compositional similarity declined as a function of geographic distances among sites. Partial Mantel tests were employed to determine the "pure" effects of environment and spatial distance in explaining compositional similarity, as opposed to their joint (covariance-related) effects.

To quantify geographic distances among sites, we calculated the Euclidean distances among the geographic coordinates (latitude/longitude) of the sites. For environmental dissimilarity, we employed the raw 16 environmental variables as input in a principal component analysis (Qian & Ricklefs 2012) and then extracted the first two principal axes as the input to calculate Euclidean distances among sites (Gilbert & Lechowicz 2004). To measure faunal similarity, we employed the classical Sorensen similarity index, which has been widely applied in community ecology studies (Condit *et al.* 2002; Gilbert & Lechowicz 2004).

Results

Microarthropod richness and abundance in Southwestern Canada

Based on the survey, there were 352 microarthropod species in the 32 sites, of which there were 83 collembolan, 132 oribatid and 137 mesostigmatid species. In total we counted 5939 oribatid individuals, 4990 collembolan individuals and 2331 mesostigmatid individuals.

Microarthropod richness and abundance had different spatial patterns across the 32 field sites (Wilcox signed rank test, $p<0.001$). Richness hotspots (Fig. 2.2) for different groups (except collembolans) could be found in either the Coast mountain range or at low elevation inland sites. However, abundance hotspots except for collembolans were only found in the Coast mountain range (Fig. 2.2). Collembolans showed a different spatial pattern to mites, with abundance hotspots across spatially-disparate areas and richness hotspots restricted to the Coast mountain range.

Multiple regression analysis of species diversity and environmental variables

Microarthropod richness and abundance, in sum and for each taxonomic group separately, was related to several environmental and spatial factors through a model selection procedure (Table 2.1). The most common predictor was net water mass (WaterM), which had a negative influence on abundance or richness in 7 out of the 8 reduced models (Table 2.1). Moss was sampled on dry summer days so soil moisture should accurately reflect site conditions, not weather on particular sampling days. Abundance and richness increased with cover (significant predictor in four models), decreased with the net mass of stones in soil cores (three models) but increased with stone mass expressed as a percentage (three models). High elevations had lower collembolan abundances but higher richness of microarthropods overall and oribatids. In particular, there was higher species richness closer to the sea (Oribatida and Collembola) and at westerly longitudes (Mesostigmata). In addition, collembolan richness and abundance were negatively related to temporal variance in temperature (VarTemp), whereas minimum temperature and maximum temperature were negatively and positively associated with collembolan abundance respectively. More importantly, collembolan abundance and richness were both negatively correlated to the proximity of sampling areas to the sea. These results stressed that stable temperature and humidity were very important for collembolan communities. Overall, the two spatial descriptors (Longitude and Latitude) each entered the best regression models 4 times. But their coefficients became statistically significant only in 1 of the 4 richness models respectively (Predator and Oribatid richness), but - as predicted - none of the 4 abundance models (despite entering the selected models).

Additional model comparisons were performed as well to see the influence of disturbance-related

variables, such as minimal distances to the road, but did not substantially change the fit, suggesting the minor contribution of anthropogenic impacts to the variance in the microarthropod richness and abundance. Moreover, the negative influence of net water mass was rarely altered by adding or excluding any other variables.

Variance partitioning of microarthropod community structure

Using the "raw data" method for variance partitioning, we found that environmental factors outperformed spatial factors in shaping microarthropod composition (Fig. 2.3). Specifically, a much larger proportion of compositional variance could be explained by 'pure' environmental variables than by 'pure' spatial factors, especially when we examined species abundance rather than species occurrence. Less variance could be explained in total for species occurrence.

The dominance of environmental factors was also apparent for separate taxonomic groups, and there was little evidence of differences between taxonomic groups in the relative dominance of environment and spatial structuring of incidence-based composition. When composition also included abundances, Collembola tended to be more environmentally structured than Oribatida or Mesostigmata.

Delving further into the environmental predictors of composition, the first principal axis of CCA ordination for abundance-based composition data indicated that microarthropod composition was strongly influenced by variance in temperature (CCA 1 score=-0.7379), maximum temperature (-0.6254), tree cover (0.5095), and soil depth (0.5052; Fig. 2.4). For the second ordination axis, the principal factors correlated with species composition were water content (CCA 2 score=-0.4555),

water mass (-0.3276), soil mass (0.3118), and large particle mass (0.3004). Thus, axis 1 of CCA ordination represented a gradient in temperature and soil microhabitat properties, while axis 2 mainly represented a gradient in soil texture and moisture. The CCA ordination based on incidence data was similar to that for abundance, except that the distance-to-sea was also important. It is not surprising because multiple regression analysis also showed that it could be significantly related to oribatid and collembolan richness.

The distance-based methods for variance partitioning (in fact, that Mantel test is for evaluating the strength and significance of correlation between compositional dissimilarity and environment/space distances) led to very different conclusions than the raw data-based ordination methods. Similarity of both total microarthropod communities and the Collembola subset declined with geographic distance and environmental distance (Table 2.2). However, environmental variables were themselves spatially structured (Fig. 2.5c). Once partial Mantel tests were used to remove the effect of this covariance, only the faunal distance of Collembola communities was correlated with "pure" environmental and/or "pure" spatial distance (Table 2.2; Fig. 2.5). In the partial Mantel tests with Collembola communities, both the correlations of the distances of environment and space were significant (or marginally, $p<0.1$) for abundance-based dataset for all the partial/non-partial situations, but only space was significantly correlated in all the partial/non-partial situations and environment was only significantly (or marginally, $p<0.1$) correlated to the distance of Collembola communities in two of the cases for incidence-based composition dataset (Table 2.2).

Discussion

Are mite communities limited by local environmental conditions or by dispersal?

Our analysis shows that the answer to this question depends on the method used (raw data vs. distance methods for composition) as well as the resolution of the composition data (based on occurrence or abundance). In terms of method, the ordination method for variance partitioning analysis concludes that the environment explains much more variance in composition than space, for all taxonomic groups. By contrast, the distance method concludes that the compositional similarity of mite communities was unrelated to either spatial distance or environmental dissimilarity, except for Collembola (equally correlated with space and environment). The raw data and distance methods ask subtly different questions: the raw data method seeks to explain composition at sites, whereas the distance method seeks to explain compositional dissimilarity (beta diversity) between sites. The debate about which question is most relevant to separating environmental from dispersal limitation is far from resolved (Legendre *et al.* 2005, 2008; Tuomisto & Ruokolainen 2006, 2008; Laliberte 2008). The two methods do agree on some conclusions: (a) much of the variance in composition or compositional dissimilarity remains unexplained by either environment or space (or their covariance), (b) at the scale of this study, space was of minor importance in determining composition or compositional dissimilarity (except possibly for Collembola, despite the fact that they are more dispersive) and (c) incorporating abundance information into species composition generally increases the strength of environmental determinants and decreases the importance of spatial determinants. The latter result is consistent with the strong relationship found between many environmental factors and

total abundance.

The generally minor role of space in determining microarthropod composition suggests that soil microarthropods, at least at the scale of this study, are not very dispersal limited. Many studies have suggested that small-bodied organisms (e.g. bacteria, viruses, zooplankton, diatoms) disperse further than larger bodied organisms, and thus should be primarily environmentally limited (Fenchel & Finlay 2004; Fontaneto 2011; Curini-Galletti *et al.* 2012). This is popularly known as "everything is everywhere, but the environment selects" (Baas-Becking 1934; O'Malley 2007, 2008). However, our conclusion of minor dispersal limitation contrasts with a previous analysis of soil oribatid mites, also conducted in British Columbia and at a similar spatial scale (Lindo & Winchester 2009), which found that both composition and compositional similarity of oribatid mites in forest soils were strongly related to space. Part of this discrepancy may be related to the specialized habitat that we sampled (thin soil horizons on exposed rocky outcrops, overlain by moss carpets) which contrasts to the more common and contiguous habitat of forest soils in the study by Lindo and Winchester (2009). In the same study, oribatid mites in arboreal moss mats were also sampled, and demonstrated weaker effects of spatial distance on compositional dissimilarity.

Do the main taxonomic groups of microarthropods differ in environmental filtering or spatial limitation?

Using the raw data-based ordination methods, collembolan composition was more strongly related than mite composition to environmental variables for abundance, but not incidence data (Fig. 2.3). However, with the distance method, collembolan compositional dissimilarity increased significantly

with spatial distance, using either abundance or incidence data (Fig. 2.5). This was not observed for mites, even when environmental covariance was partialled out (Table 2.2). These partial Mantel test results are contrary to our initial prediction stating that collembolans should be environmentally structured due to long-distance passive transportation abilities.

For mesostigmatas and oribatids, we observed that the compositional patterns of both were principally determined by environmental limitation using ordination-based variance partitioning (Fig. 2.3), however, Mantel tests suggested that neither spatial nor environmental factors could significantly influence the beta diversity of either taxonomic group (Table 2.2). Thus, both methods conclude that collembolan communities are structured somewhat differently than mite communities, although they predict opposite mechanisms for this result. In general, however, it is surprising how homogeneous different microarthropod groups are in their responses to environment and space. Although these groups occupy different trophic levels, have different generation times and body sizes, they perhaps are ultimately all experiencing the same environmental limitations in the form of frequent droughts in thin, exposed soils, and the same dispersal limitations due to their microscopic size.

Why is much of the variance in microarthropod composition unexplained by either environment or space in CCA/RDA-based variance partitioning methods?

A large proportion of the variance in the composition data could not be explained by either environment or space, or their covariance (for abundance data, the unexplained variance ranged from 8.6% to 55%; for richness data, the unexplained variances ranged from 17.2% to 42.2% for different groups). These amounts of unexplained variances were consistent with the variance partitioning

results from other studies on mites and spiders (Lindo & Winchester 2009; Sattler *et al.* 2010), as well as other types of communities (Cottenie 2005).

There are several possible reasons for this unexplained variance. (A). Variance partitioning methods fail to account for species interactions, and it is possible that competitive exclusion or top-down effects have strong influences on community composition (Bengtsson *et al.* 1994; Goldberg 1994; Elmendorf & Moore 2007). (B). Technical aspects of the mite sampling could add observation error, for example, the effects of different sorters (different judgment and expertise); the uncertainties in morpho-species identification and classification; the difficulties of accurate identification of mite species down to the level of species; a single survey season and limited sample sizes. (C). Recent simulations indicate that current statistical methods for CCA/RDA-based variance partitioning might be not accurate since there is a great difference between true and estimated variance (Gilbert & Bennett 2010). (D) The unexplained variance may include aspects of dispersal limitation that do not correlate with spatial distance (e.g. if phoretic dispersal is important), or environmental factors that were not measured. (E) Finally, some parts of the unexplained variance may represent stochasticity in occurrence or abundance, for example due to demographic drift.

Why are the spatial patterns in microarthropod arthropod and richness not congruent?

High species richness of microarthropods was mainly found in two relatively distant regions. Of the 5 most species rich sites, three were located in the Coast mountain range (one near Whistler at 1052m, one near Mt. Seymour at 1376m and the last near Squamish at 436m) and two were at low elevations and inland (one near the west end of the Coquihalla Hwy at 347m and another near Hope at 304m). By

contrast, microarthropod abundance was greatest just south of the Whistler richness hotspot, and low in all other sites, especially in inland sites. This pattern in microarthropods is largely driven by the mites (Oribatida and Mesostigmata); the Collembola show the opposite pattern as we discuss below.

A number of niche models predict that species richness and total community abundance should be tightly correlated. For example, niche models often predict that more species can coexist in areas where there is a greater quantity or variety of resources, both of which decrease interspecific competition and thus permit greater total abundances (Srivastava & Lawton 1998). Other niche models predict negative correlations between abundance and species richness at local scales, for example when high resource availability permits the dominance of a species (e.g. shift from nutrient to light competition in plant communities: see Mayfield & Levine (2010)), or when mortality imposed by disturbance reduces dominance and thus competitive exclusion (Peterson 2011). Neutral models often predict that species richness and total abundance can be spatially decoupled, but only because of the assumption of spatial homogeneity in total abundances (e.g. the zero net sum assumption in Hubbell (2001)) – clearly not the case in our study. Thus the particular pattern of spatial incongruence in our study is unlikely to be explained by a single process; it is more likely to be a combination of different ecological processes operating over the longitudinal gradient from wet mountainous habitat to dry inland habitat.

In our study, oribatid abundance was primarily related to environmental variables – especially tree cover, soil water and content– whereas oribatid richness was additionally related to spatial variables (latitude and distance-to-sea). Moreover, mesostigmata abundance was related to only environmental variables (tree cover and particle mass), while its richness could be additionally related to a spatial

descriptor longitude. All these observations further suggested a decoupling of the underlying ecological processes between abundance and richness. Of particular interest is the increase in total microarthropod and oribatid richness with elevation, in the absence of a corresponding increase in abundance.

All the groups showed a spatial mismatch between abundance and richness patterns (Fig. 2.2). Interestingly, the collembolan pattern is inverse to the pattern for mites. Previous experiments have shown Collembola to be more sensitive to drought than Oribatida and Mesostigmata (Starzomski & Srivastava 2007; Chisholm *et al.* 2011). However, collembolans can also have a burst of reproduction after drought, allowing a fast recovery of abundance (Waagner *et al.* 2011). It is possible that the combined response of collembolans to drought - high mortality followed by rapid reproduction – results in abundant but species poor collembolan communities in British Columbia's dry interior (a community-level bottleneck). An alternative explanation is that low abundance of mesostigmatid predators in interior British Columbia reduces top-down control on their collembolan prey (Meldrum 2012). Note that adult oribatids are largely resistant to mesostigmatid predation, so we would not expect and did not find similar patterns in oribatid abundance.

How does the environment limit microarthropod communities?

Environmental variables were important in explaining both total abundance and species richness of microarthropods, as well as community composition. In general, total abundance and species richness increased with tree cover, but decreased with total water mass. Since tree cover reduces solar incidence, leading to moist soil conditions, together these variables all point to complex relationships

with soil moisture. Similarly, microarthropod composition was most strongly influenced by a gradient in edaphic conditions from warm but variable temperatures far from sea to shaded, moist and deep soils close to sea.

The influence of soil moisture on microarthropod communities is well documented (O'Lear & Blair 1999; Chisholm *et al.* 2011; Peterson 2011; Kardol *et al.* 2011). Soil moisture also changes the resource base of the moss patch food web (Lindo & Gonzalez 2010). In addition, the joint effect of temperature and moisture on microarthropod communities became stronger (Hayward *et al.* 2001).

Taxonomic groups of microarthropods differed in the influence of environmental factors. It has been shown in other studies that warm temperatures can enhance the reproduction and development of temperate collembolans (Martikainen & Rantalainen 1999; Choi *et al.* 2002; Peterson 2011), thus allowing population expansion of the group in the habitats. Interacting with humidity, increasing temperature could affect collembolan diversity (Kardol *et al.* 2011). Our finding that collembolan abundance increases with maximum temperature and – like richness - decreases with temperature variance agrees with some previous reports (Martikainen & Rantalainen 1999; Hayward *et al.* 2001; Uteseny *et al.* 2010; Peterson 2011), strongly indicating that Collembola had higher abundances and species richness in warm, dry, thermally stable conditions. Oribatid abundance was paradoxically negatively related to total water mass of the soil core, but positively related to soil water content. The total water mass of a patch is influenced both by soil depth and soil moisture. Thus in models where both water mass and water content entered the model but had negative and positive effects, respectively, the model may therefore be selecting for shallow but moist soils. Confirming this interpretation, when we replaced water mass by soil depth in such models, the sign of the water

content parameter did not change (although the significance of the parameters was no longer held for the model of mesostigmata abundance).

Conclusions

Microarthropod diversity and distribution in southwestern BC, Canada were investigated. Environmental filtering was the principal determinant in structuring the microarthropod community for different taxonomic groups as evidenced by CCA/RDA-based variance partitioning and multiple regression analysis. However, the role of spatial limitation could not be overlooked (especially for collembolans) as indicated by partial Mantel tests of geographic distance-similarity decaying patterns when compared to the environment-similarity decaying patterns. Multiple regression analysis and stepwise model selection suggested that net water mass and tree cover were two prevalent factors significantly associated with microarthropod richness and abundance (across different functional groups and the whole data sets) with negative and positive influences respectively. As the explained variance was generally low in these variance partitioning analyses, we suggest that the influence of biotic interactions and demographic stochasticity also strongly influences microarthropod communities.

Figures and Tables

Fig. 2.1. Field locations for microarthropod sampling in southwestern British Columbia, Canada. The sampling area covered approximately a 130km by 57km area.

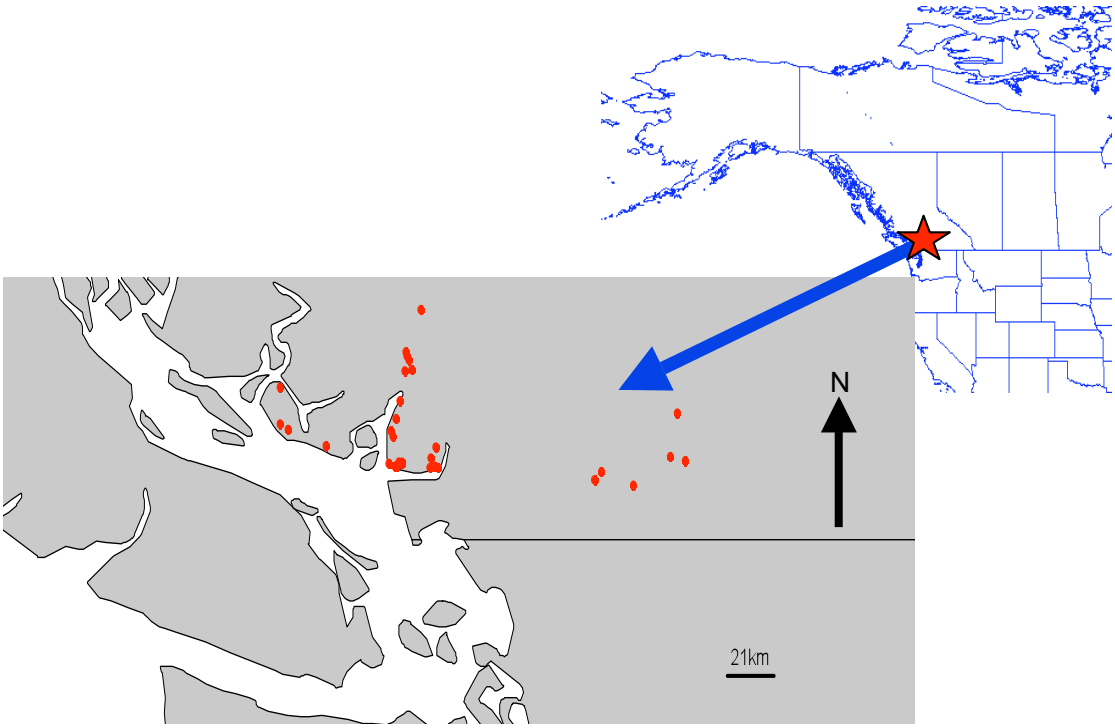


Fig. 2.2. Microarthropod richness and abundance at 32 sites in southwestern British Columbia. Areas of filled red circles are proportional to relative richness or relative abundance. The scale is identical to that in Fig. 2.1.

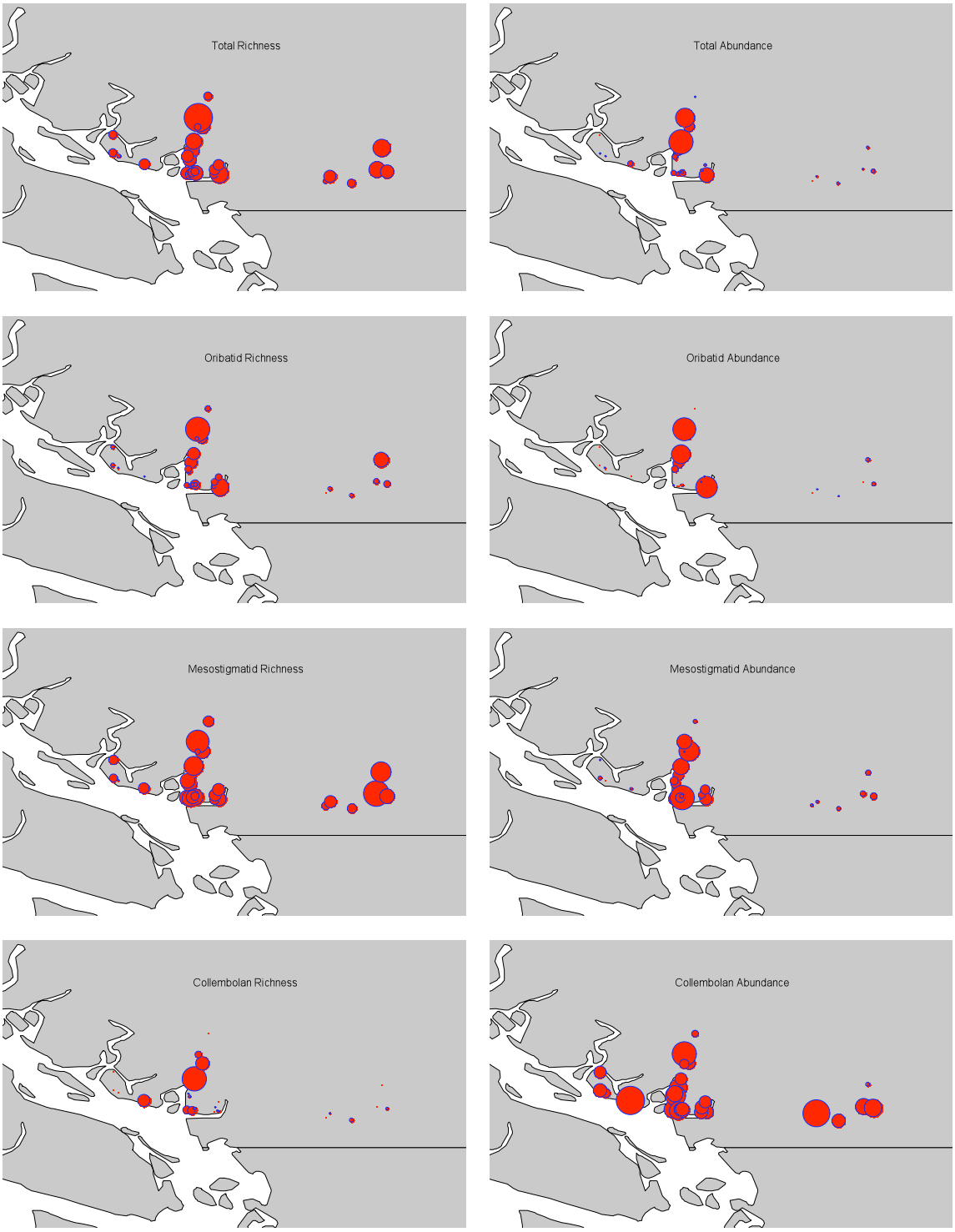
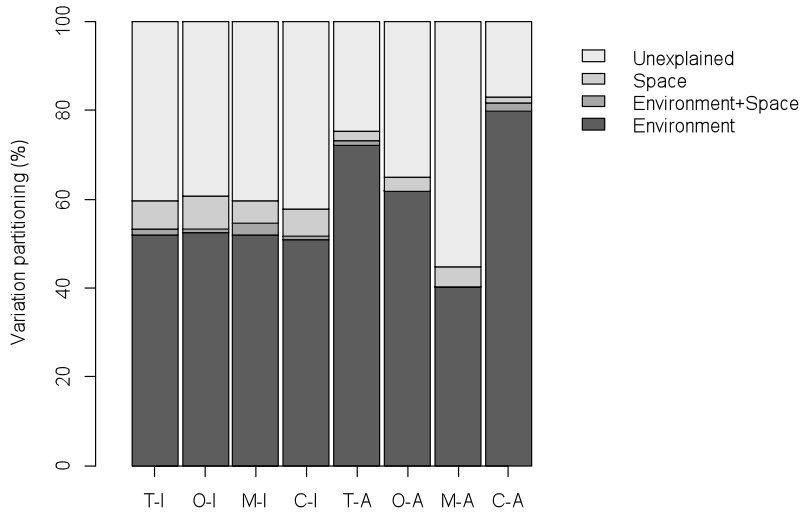


Fig. 2.3. Results of variance partitioning for each of the three microarthropod groups and the microarthropod community as a whole, for both simple/raw (a) and PCNM-derived (b) data sets. Abbreviations: I-incidence; A-abundance; T-total community; O-oribatids; M-mesostigmatids; C-collembolans. "T-I" indicated incidence data for total community, the definitions for other *x*-axis labels of the histograms are similar.

a)



b)

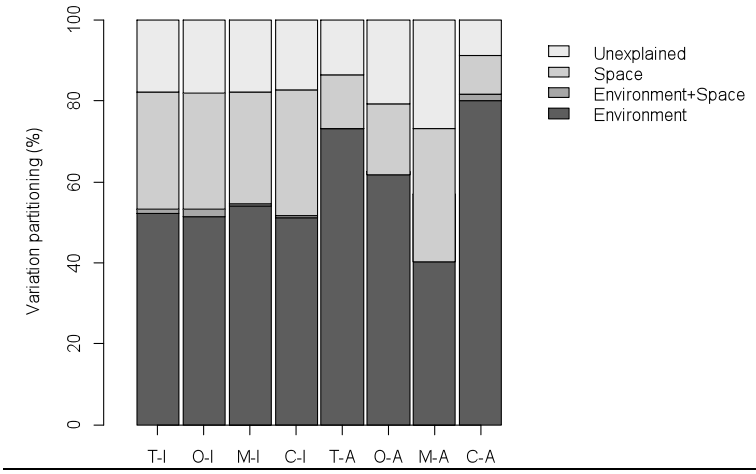
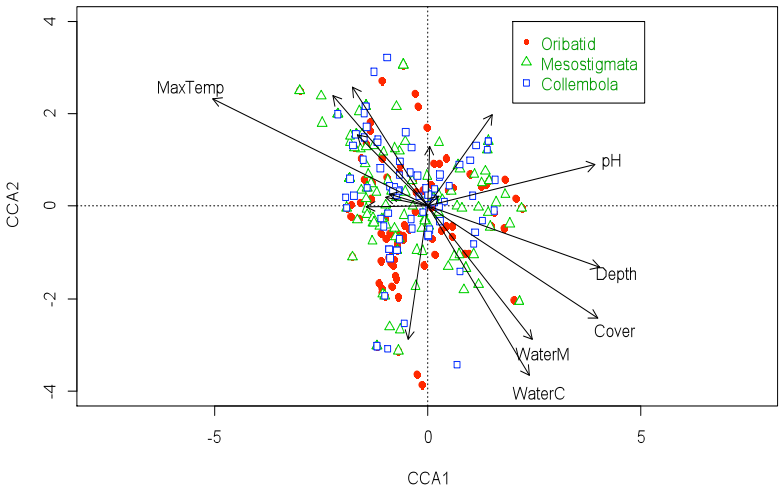


Fig. 2.4. Ordination of microarthropod richness and abundance using canonical correspondence analysis. a) ordination based on abundance data; b) ordination based on incidence data

a)



b)

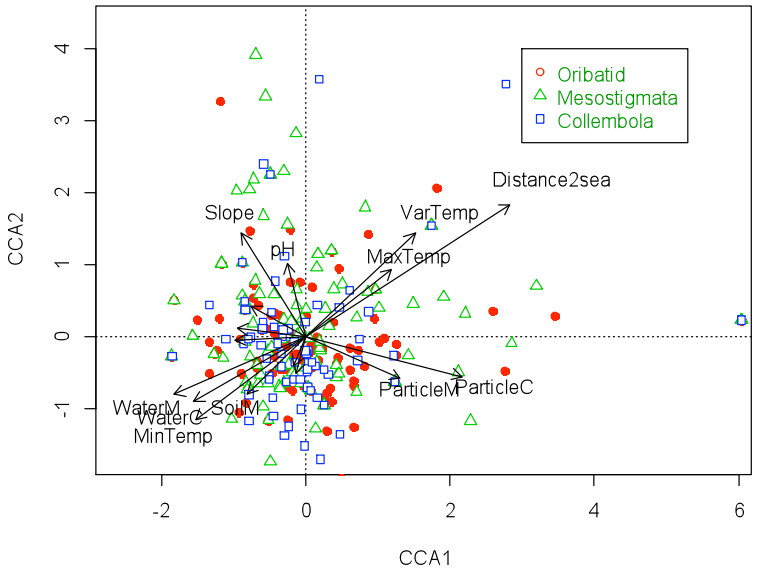
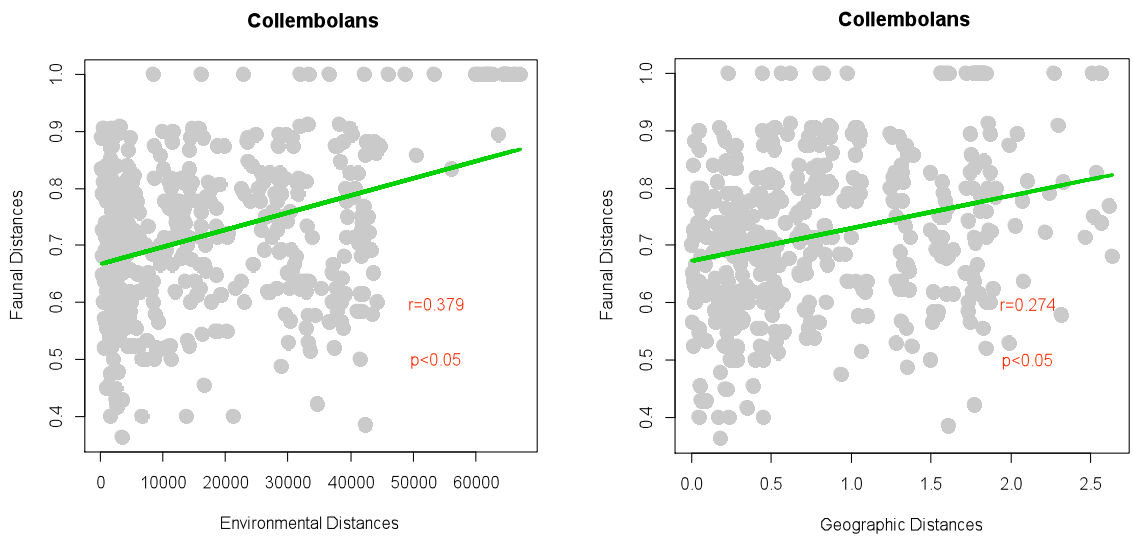
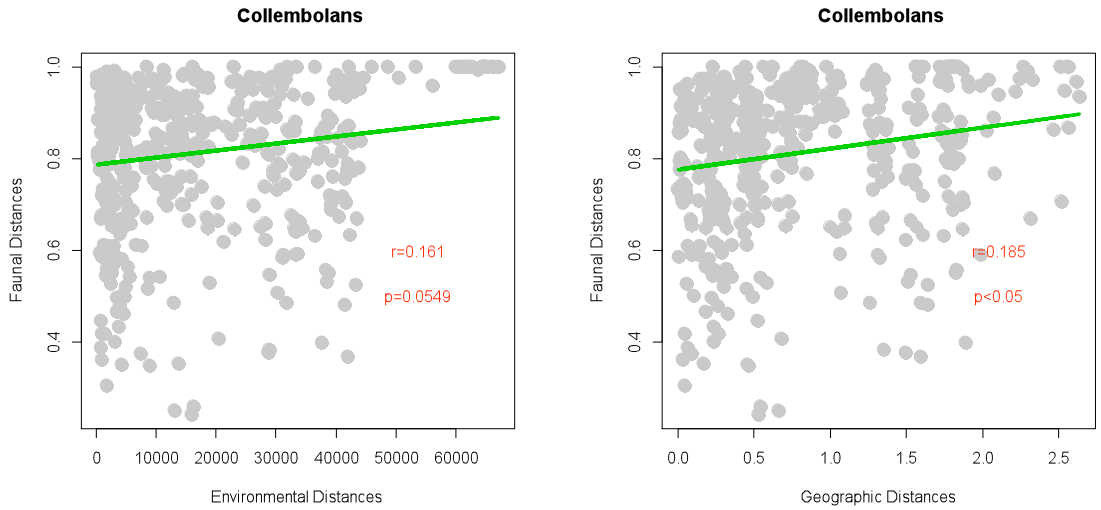


Fig. 2.5. The relationship between geographic distances, environmental distances (both measured by Euclidean distance) and collembolan compositional similarities (measured by Sorensen similarity index) across the 32 sampling sites. Compositional similarity was based either on incidence (a) or abundance (b) data. c) showed the relationship between geographic and environmental distances. All the correlation values (*r*) and significant levels (*p*) were measured by Mantel tests with 20000 permutations.

a) Incidence



b) Abundance



c)

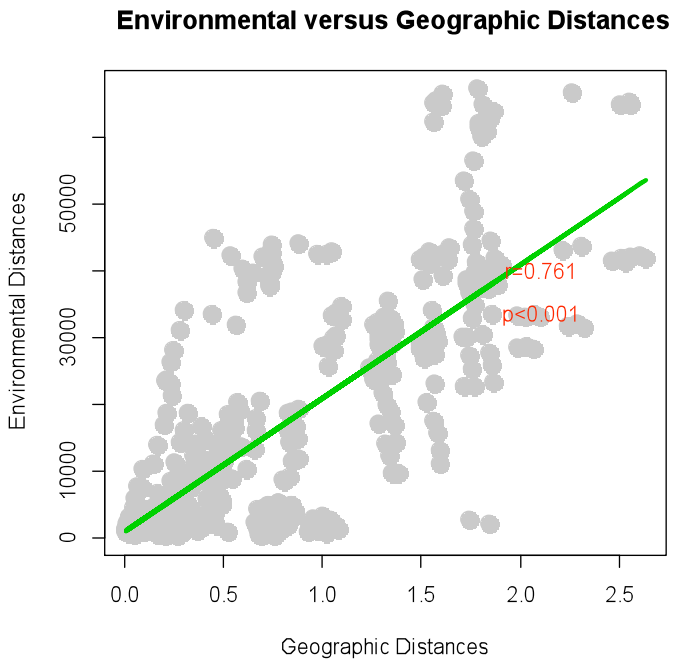

Environmental versus Geographic Distances
Environmental Distances
0
10000
30000
50000
0.0
0.5
1.0
1.5
2.0
2.5
Geographic Distances
r=0.761
p<0.001

Table 2.1. The best multiple regression models describing microarthropod abundance and richness. Models were performed for microarthropods as a whole, as well as different mite functional groups. Only coefficients of significant variables within these best fit models are shown. (Codes for the variables: Cover: tree cover; WaterM: water mass in the moss patches; WaterC: water content; ParticleM: small rock mass (size>1cm) in the moss patches; VarTemp: variance of the temperature time series; MaxTemp: maximum value of the temperature time series; Elevation: elevation of the field site; Latitude and Longitude: geographic coordinates of the field sites).

Items	Significant factors	Coefficient	P values	Best-choice Model	Adjusted-R^2	Model AIC	Model F-statistic (DFs)	Global P value
Total Abundance	Cover	5.890711	0.004988	TotalA ~ Latitude + Slope + Cover + SoilM + WaterM + WaterC + ParticleM + ParticleC + MaxTemp + VarTemp	0.599413	460.5468	5.639(10,21)	0.0004
	SoilM	10.59264	0.007979					
	WaterM	-37.8265	6.31E-05					
	WaterC	2387.984	0.000543					
Oribatid Abundance	Cover	2.951151	0.032562	OribA ~ Latitude + Elevation + Cover + SoilM + WaterM + WaterC + ParticleM + ParticleC + MinTemp	0.514642	438.5605	4.652(9,22)	0.0016
	WaterM	-19.9793	0.00051					
	WaterC	1325.501	0.001206					
Mesostigmata Abundance	Cover	1.027084	0.002582	PredA ~ Cover + WaterM + ParticleM	0.257497	344.706	4.584(3,28)	0.0099
	ParticleM	-2.22007	0.045063					
Collembolan Abundance	Elevation	-0.17646	0.009575	CollA ~ Elevation + Distance2sea + Slpe + SoilM + pH + WaterM + WaterC + ParticleM + ParticleC + MeanTemp + MaxTemp + MinTemp + VarTemp	0.652236	405.867	5.472(13,18)	0.0006
	Distance2sea	-0.00799	0.004376					
	Slope	5.766501	0.024176					
	pH	362.7831	0.003057					
	WaterM	-11.594	0.003308					
	WaterC	669.4723	0.023558					
	ParticleM	-43.4621	0.007827					
	ParticleC	3755.672	0.020298					
	MaxTemp	27.10672	0.00101					
	MinTemp	-69.15	0.004991					
	VarTemp	-215.396	7.62E-05					
Total Richness	Elevation	0.011612	0.033118	TotalR ~ Latitude + Longitude + Elevation + Distance2sea + Slope + Cover + Depth + WaterM + WaterC + ParticleM + ParticleC + MaxTemp + VarTemp	0.47732	260.3585	3.178(13,18)	0.0123
	WaterM	-0.81694	0.001571					
	ParticleC	293.8619	0.049571					
Oribatid Richness	Latitude	36.38537	0.012873	OribR ~ Latitude + Longitude + Elevation + Distance2sea + Cover + WaterM + WaterC + ParticleM + ParticleC	0.513936	229.5475	4.642(9,22)	0.0016
	Elevation	0.007279	0.030405					
	Distance2sea	-0.00073	0.049835					
	WaterM	-0.30299	0.015019					
	ParticleM	-2.10356	0.014834					
	ParticleC	241.702	0.010163					
Mesostigmata Richness	Longitude	-2.87314	0.039411	PredR ~ Longitude + Slope + Cover + WaterM + ParticleM	0.417312	198.5618	5.44(5,26)	0.0015
	Cover	0.094236	0.006653					
	WaterM	-0.16394	0.002109					
Collembolan Richness	Distance2sea	-0.00017	0.040037	CollR ~ Longitude + Elevation + Distance2sea + Depth + WaterM + MaxTemp + VarTemp	0.255825	183.0116	2.522(7,24)	0.0428
	WaterM	-0.15495	0.004778					
	VarTemp	-3.48322	0.014033					

Table 2.2. Correlation of compositional distances with environmental and geographic distances. Results are presented separately for each of the three microarthropod groups as well as the microarthropod community as a whole and are based both on incidence-based and abundance-based composition data sets. The results were generated using partial Mantel tests with 20000 permutations. Significant (or marginally significant, p<0.1) correlations are indicated with boldface.

Correlated variables	Abundance	Correlation	P	Incidence	Correlation	P
Geographic distance	**All data**	**0.1337**	**0.052**	**All data**	**0.161**	**0.058**
	Oribatid	0.95	0.16	Oribatid	0.065	0.253
	Mesostigmata	-0.0123	0.538	Mesostigmata	0.0199	0.4
	Collembola	**0.19**	**0.029**	**Collembola**	**0.274**	**0.003**
Environmental distance with geographic distance partialled out	All data	0.0253	0.4006	All data	-0.07	0.75
	Oribatid	-0.116	0.853	Oribatid	-0.095	0.798
	Mesostigmata	-0.0089	0.552	Mesostigmata	-0.1192	0.878
	Collembola	**0.172**	**0.059**	Collembola	0.1215	0.113
Environmental distance	All data	0.047	0.289	All data	-0.045	0.658
	Oribatid	-0.104	0.83	Oribatid	-0.08	0.77
	Mesostigmata	-0.0056	0.52	Mesostigmata	-0.116	0.853
	Collambolan	**0.22**	**0.018**	Collambolan	0.156	0.082
Geographic distance with environmental distance partialled out	All data	0.1224	0.1	**All data**	**0.165**	**0.054**
	Oribatid	0.1123	0.113	Oribatid	0.084	0.175
	Mesostigmata	-0.0205	0.594	Mesostigmata	0.04	0.337
	Collambolan	**0.148**	**0.064**	**Collambolan**	**0.256**	**0.006**

Chapter Three: General conclusions

Main findings

During my Master's research, I have devoted my time to experimental and statistical aspects of community ecology. Microarthropods inhabiting mosses have been an ideal micro-ecosystem to test ecological theories and address ecologically important questions (Srivastava *et al.* 2004). I studied the microarthropods in moss carpets in southwestern B.C. The species I found are predicted – through ecological niche modeling (Appendix I) – to be largely restricted to habitat in the study area.

My microarthropod survey showed that microarthropods have spatially incongruent patterns of abundance and richness. Furthermore, microarthropod abundance and richness were explained by different subsets of spatial (latitude/longitude) and environmental variables. An extensive model searching procedure determined that there were two principal variables - water soil density and tree cover - that were important in affecting microarthropod abundance and richness patterns, regardless of the taxonomic group (collembolans, oribatids and mesostigmatids). I also compared spatial patterns in composition between microarthropod groups. Only collembolan composition decayed with spatial distance between sites, suggesting dispersal limitation in this group. When collembolan abundance was incorporated into composition measures, compositional similarity also decreased with environmental differences between sites. This conclusion differs from that obtained by

CCA/RDA-based variance partitioning, which concluded that all microarthropod groups were strongly affected by environmental factors, rather than spatial. At the same time, there was a lot of unexplained variance in our microarthropod community (especially for incidence-based data) which could not be explained by the available ecological variables. As richness hotspots were dispersed across different habitats for different taxonomic groups, we suggested that the stochasticity derived from species interactions and demography might be equally important as environmental filtering and spatially-limited dispersal in shaping microarthropod community structure, especially for the richness patterns. We argued that both distance-based Mantel test and ordination-based RDA/CCA should be employed and compared to better uncover the effects spatial and environmental limitations on structuring communities.

Limitations of the thesis

My research definitely possesses some limitations, of which I just discuss two here.

Firstly, the microarthropod survey was only limited to certain areas and restricted to moss-based species, which may not be able to truly indicate microarthropod diversity patterns in Southwestern Canada. As we mentioned previously, the works from tree habitats and from island ecosystems in Southwestern Canada had both congruent and incongruent aspects with my work. Thus, my study could only unravel microarthropod community structure in the region in a particular, but not a holistic view.

Secondly, the study is purely observational, thus not being able to quantitatively assess the roles of different ecological mechanisms on influencing microarthropod diversity. Also, we are only able to

quantify beta diversity of microarthropod species at species level, but not at phylogenetic and functional levels. Phylogenetic diversity has become a dominant theme in current ecological literature, but my work could not determine what the differences are between species diversity and phylogenetic diversity for microarthropods, and what the impacts of space and environment are on determining the phylogenetic diversity of microarthropod assemblages.

Further directions

Variance partitioning in ecology has undergone rapid development and broad applications in the last decade since the seminal work of Borcard *et al.* (1992). However, there is still a seemingly endless debate on the effectiveness and legitimacy of different statistical methods for partitioning community variance. On the basis of my thesis, I argued that first we should clearly understand different parts of the explained variance before we could critically assess the validity and effectiveness of variance partitioning. As shown in my study, negative variance is an incoherent concept from ecological perspective, but could be commonly generated from CCA/RDA-based variance partitioning methods. Thus, we challenge the conventional recognition that the variances should be partitioned into three parts-pure spatial, pure environmental and shared spatial-environmental variances. We hold the belief that it may be better to only consider spatial- and environment-induced variances, but not looking at the shared co-variation, since it is misleading and not really helpful for us to improve our understanding of community variance.

A potential way to reconcile the debate is to develop novel multivariate techniques to powerfully capture different parts of variance. A promising pathway is to integrate the knowledge of

community-level beta diversity and understand its' partitioning (Baselga 2010, 2012). In such a way, we could perform multivariate analysis on each separate part of the beta diversity derived from the community matrix solely against the spatial and environmental variables. Through these multiple steps, we might be able to deeper our understanding of the relationship between beta diversity and the environmental/spatial constraints.

From the prospect of experimental ecology, we have to acknowledge that our field work only cover a small part of the Southwestern areas of Canada. Our knowledge gained from the results thus is largely limited to the coastal areas. However, it would be illuminating survey more field sites, especially when we further compare different landscapes (e.g., islands, coastal lines, interior mainland), habitats (e.g., trees/shrubs, mosses, man-made concrete areas) and spatial scales (e.g., local, national, regional and worldwide). Also, our experiment is purely observational, which has constrained our perception of the interplay of varying ecological mechanisms in determining community patterns. Thus, another pathway for improving our understanding on the relationship of environment and diversity is to perform manipulative experiments including transplantion experiments, control-treatment experiments, and comparison of microarthropod diversity under different environmental conditions (e.g., dry and wet; Chisholm *et al.* (2011)) and so on.

There are inevitably new patterns and uncertainties emerging when ones set up new mite experiments. These unpredictable scenarios would certainly open more ecological questions and challenges. However, they are not impossible to resolve, when one adopts highly-effective microcosm ecosystem models to explore microarthropod communities. Microcosm ecology assumes that a microscopic ecosystem follows similar functional rules as the whole earth (Srivastava *et al.* 2004;

Lindo and Gonzalez 2010). If true, all ecological theories and hypotheses could be addressed without losing generality. Finally, we ascertain that further exploitation of microarthropod diversity patterns at various spatial and temporal scales could help us better understand the functioning and dynamic of the microarthropod metacommunity.

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Appendices

Appendix I: Species richness modeling

We considered whether conditions suitable for the microarthropods found in this study exist in the remainder of the province. Since nutrient (i.e., SoilM, WaterM etc.) and soil-relevant physical variables (for example, aspect, cover etc.) are not possible to include in the distribution modeling, we adopted the environmental variables for British Columbia as a whole extracted from WorldClim database (URL: http://www.worldclim.org). Different variables, including attributes for temperature, precipitation, evaporation and bioclimatic indices were obtained using R scripts.

We performed species niche modeling using six mathematical algorithms (Thuiller *et al.* 2009), including random forest model (RF), classification and regression trees (CART), artificial neutral network (ANN), multivariate adaptive regression splines (MARS), generalized boosting models (GBM), and surface range envelop (SRE). Evaluation of model outputs used 3 metrics: Cohen's Kappa, higher of which indicated that modeling fitting was better; True skill statistics (TSS), values of which ranged between -1 and 1, higher values indicating better models far beyond random models; and areas under the curve (AUC), higher values of which indicated better accuracy of the models.

Environmental data were extracted from WorldClim database, in which temperature-related data (e.g., maximum temperature, minimum temperature), precipitation data, elevation and bioclimatic data were generated. In total there were 68 environmental variables considered in our niche modeling.

Because we have over 350 morphospecies in the study, we focused on estimating regional microarthropod diversity across the province of British Columbia, Canada. Therefore, we used all the

32 sites as the known occurrence records of 352 species and the richness in each site as the entry to perform model running using the 'BIOMOD' package under R environment (Thuiller *et al.* 2009).

Species richness modeling using alternative niche models

After running the models, only three of the six models could generate potential suitable ranges beyond the current sampling plots (CTA, GBM and RF, Fig. A.1). Two models failed to predict potential ranges (SRE and FDA), because they have generated distributional range identical to current sampling sites, therefore being meaningless as well.

Model evaluation suggested that the results simulated by GBM (Cohen's Kappa=0.94; TSS=0.99; ROC=1.0) and RF (Cohen's Kappa=1.0; TSS=1.0; ROC=1.0) were better than CTA model (Cohen's Kappa=0.12; TSS=0.80; ROC=0.9), especially for the case of Cohen's Kappa statistic. Here, higher values the three statistics are, better the models are. So, GBM and RF models have the highest statistical support. Therefore, the combined suitable habitat scenario (the right-bottom sub-plot) was generated by averaging the occurrence probabilities across the geographic boundary predicted by GBM and RF only.

The predicted range scenario suggested that the suitable habitats for microarthropods in this study were limited to humid areas, especially in the southernmost coastal areas of BC. Thus, microarthropods in this study are predicted to be excluded for the areas located at the northeastern and middle part of the province that are typically too dry in the summer and too cold in the winter.

Fig. A.1 Prediction of suitable distribution ranges of mite species in the grid system of BC, Canada based on the presence information of 32 field plots. The last plot was generated by combining the two best models (RF+GBM). Colors from warm red to light grey indicated the occurrence suitability index of mites from high (1) to low (0).