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3

Kanon und Gigue Violinen mit Generalbaß.

Kanon.

Johann Pachelbel

(1629 - 1704)

Bearbeitet von Max Seiffert.

Violino I *Violino I. (♩ = 96)*

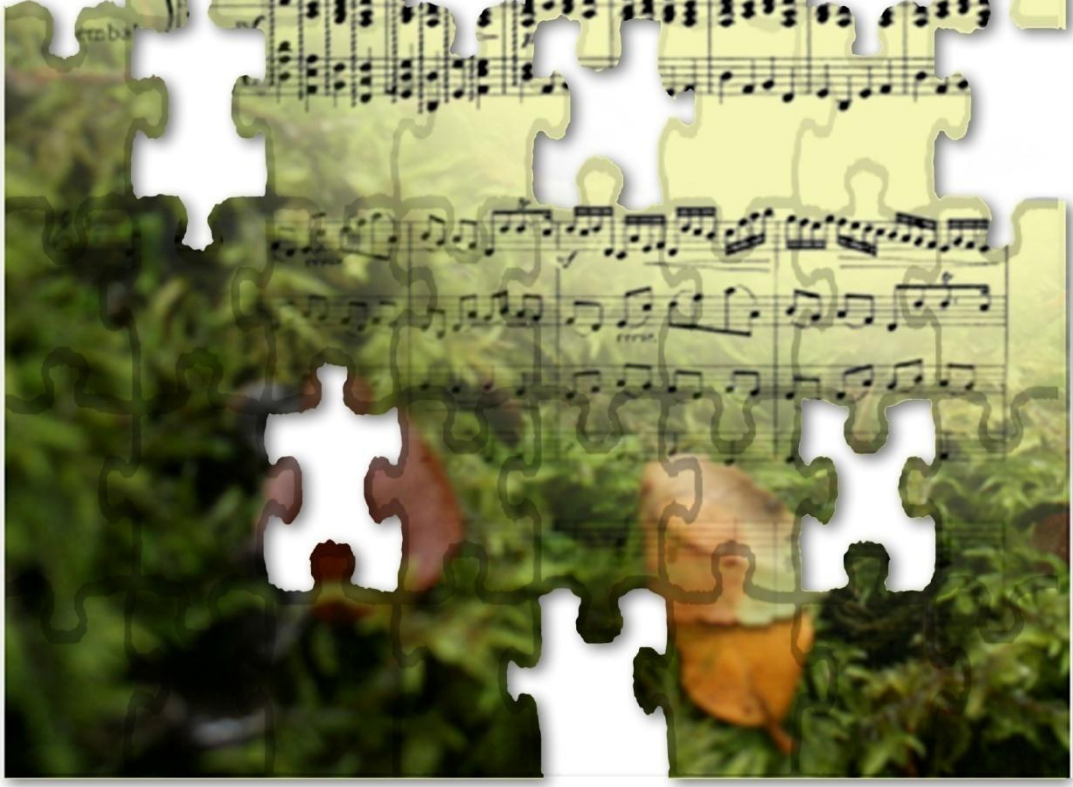
Violino II *pizz.*

Violino III *pizz.*

Viola *pizz.*

Violoncello

Violoncello *Sostenuto. (♩ = 16)*



Preface

In musical terms, a canon is a piece that is constructed through the layering of a single melody upon itself, with each layer commencing at a different time. Variations on this theme have been developed but, in all cases, the final compositions are progressions of harmonies that result from an interdependence between the voices over the course of the piece. The study of ecological communities is to me a search for the sheet music of natural systems. Such searches are guided by the notion that complex, internally-congruent systems can be generated when a suite of players adhere to a similar set of rules. Although this is certainly true of musical masterpieces such as Pachelbel's Canon in D, the notion is likely to be a simplification of natural systems. It is also a necessary simplification.

In search for the sheet music

Design by Giselle and Vanessa Perdomo
Pachelbel Canon's sheet music from
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Moss photo by Giselle Perdomo



**Understanding community and food web dynamics in the
moss-microarthropod model ecological system:
temporal variability and combined experimental habitat fragmentation and
climate change**

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Germinaciones*

Algunas son sólidas, oscuras, renuentes a la violencia
del retoño. Otras se extienden para abrazar el
aire, con vocación irrevocable al vuelo.
Algunas duelen un poco porque clavan sus raíces en los
nervios y desatan tormentas eléctricas. De su
llovizna apenas retenemos una fracción que se
entierra en la carne.
Son vastos los territorios de la vida, secretas la mayoría
de las germinaciones.
Los nombres del azar no explican nada.

Elementos
Pedro Borges

***Germinations**

Some are solid, dark, renounce the violence of
sprouting. Others extend themselves to hug the
air, with an irrevocable vocation to flight.
Some hurt as they dig their roots in nerves and release
electrical thunderstorms. From the rain we
retain merely a fraction that buries itself in the
flesh.
The territories of life are vast, the majority of
germinations secret.
Labels on randomness explain nothing.

Elements
Pedro Borges
Translation by Giselle Perdomo

This thesis is dedicated to the unsung heroes of mite taxonomy,
and to all who, without presumptions or racket,
make good things possible.

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Abstract

There is a clear crisis in the maintenance of global biodiversity worldwide. Climate change and widespread habitat loss, degradation and fragmentation are exerting strong, landscape-scale pressures on biodiversity. Negative impacts of these stressors are seen at all levels of biological organization, but studies at the level of community and food webs are relatively rare. This is in large part due to the large spatial and temporal scales at which food webs operate. Natural microcosms (food webs operating at small spatial scales) have been used to experimentally approach complex theoretical and applied questions in ecology, and have provided many important insights to date. In particular, moss micro-arthropod communities have been used extensively for the study of the effects of habitat fragmentation. Here, we used this ecosystem in a replicated, manipulative experiment to study the combined effects of warming and habitat fragmentation on community and food web structure. In order to do this, we developed tools to estimate diet of Oribatid mites, which were one of the most abundant and diverse taxa in the food web. Stable isotope techniques and analysis of mouthpart morphology allowed us to describe a food web for a moss-microarthropod ecosystem from south eastern Australia. The food web comprised over 100 taxa organized into a suite of feeding guilds: herbivores, fungivores, detritivores, lichenivores and predators. The speciose nature of the system is a strength, and the challenge of dealing with the taxonomy, data storage and food web analysis was met by development of a publicly available taxonomy database/tool, and a food web analysis package. We described temporal variation in a suite of food web attributes across one summer and winter. We found marked differences in food web structure between sampling occasions, with patterns suggestive of temperature- and humidity-driven changes in resource availability. To test the generality of food web structure in our system as compared to other ecosystems, food web attributes

were compared to those of a large compilation of food webs from around the world. Comparison revealed similarities in food web structure to other communities across a range of spatial scales and ecosystems. Dissimilarities were also found and discussed. We concluded that the moss-microarthropod system provides an adequate model for achieving a deeper understanding of processes in community ecology. Our experiments assess the assembly of moss-microarthropod communities after an extreme high-temperature event, against a back-drop of altered climate, and in the context of habitat fragmentation. Data provide initial indications that isolated habitats may be more susceptible to negative impacts of warming than less isolated habitats. Variability of responses among replicate landscapes was considerable, with some being relatively resilient. Future understanding of the underpinnings of this resilience could point to management options for resisting rapid environmental change. Our results highlight the value of dispersal in disturbed landscapes and of disturbance-buffered communities in the face of climate change. Given the importance of synergies between disturbances as drivers of biodiversity loss, and considering the paucity of data assessing the combined impacts of climate change and habitat fragmentation on food webs, further research must be carried out in this area. This could build and draw on the model system we have validated for that purpose, enabled by the suite of new tools generated here.

General Declaration

In accordance with Monash University Doctorate Regulation 17/ Doctor of Philosophy and Master of Philosophy (MPhil) regulations the following declarations are made:

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes no original papers published in peer reviewed journals and one unpublished publication. The core theme of the thesis is effects of climate change and habitat fragmentation on biodiversity. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Sciences at Monash University under the supervision of Paul Sunnucks and Ross Thompson.

The inclusion of co-authors in Chapter 1 reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of Chapter 1, my contribution to the work involved the following: I had the original idea, contacted relevant experts, collected Australian samples, carried out the stable isotope analyses, measured and weighed specimens, carried out procedure to extract and measure chelicerae, analysed the data and was the main author of the paper.

Thesis chapter	Publication title	Publication status*	Nature and extent of candidate's contribution
1	Resolving food webs in mite-dominated systems	In review	85% - see above for details

I have / have not (circle that which applies) renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Signed:



Date:04-01-12.....

Acknowledgements

Plants need soil, sunshine, pollinators, water. Fruits are not their own.

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General Introduction

There is a clear crisis in the maintenance of biodiversity worldwide (MEAB 2005; Wake & Vredenburg 2008; Fonseca 2009; Barnosky *et al.* 2011; Doerr *et al.* 2011). This crisis has been generated in large part by landscape-scale disturbances such as habitat loss, degradation and fragmentation (Sala *et al.* 2000; Foley *et al.* 2005; Swift & Hannon 2010). Rapid climate change constitutes a significant additional stressor to ecological systems (Parmesan 2006; Lindenmayer *et al.* 2010). Although positive feedbacks between threats to biodiversity can significantly increase species extinction risks (Brook *et al.* 2008; Laurance & Useche 2009), the interaction between habitat loss and climate change has to date received relatively little attention. At the community level, our understanding of these stressors is poor because our knowledge of the critical processes that underpin the assembly and disassembly of ecological communities remains poor. The large spatial and temporal scales of operation of communities of general interest have limited our capacity to carry out experiments and to gain insights into these complex ecological processes. I briefly review the individual impacts of climate change and habitat fragmentation, then consider interactions between them, and explore the need for model ecological systems to make progress in understanding this critical harmful synergy in global environmental change.

Habitat loss, degradation and fragmentation

Vegetation clearance can result in habitat loss, degradation and fragmentation. Consequently, species in remnant patches are confronted with reduced, more isolated habitats and novel ecological boundaries (Ewers & Didham 2006). Although distinguishing among the effects of loss, degradation and isolation can be difficult (Fahrig 2003; Hodgson *et al.* 2009), and despite the fact that what constitutes suitable habitat

often differs between species, it is widely recognized that landscape alteration constitutes a severe threat to biodiversity (Sala *et al.* 2000; Foley *et al.* 2005; Swift & Hannon 2010). Negative impacts on species arise from deterministic effects on species' biology, habitat and resources, as well as from increased susceptibility to stochastic demographic and genetic processes (reviews in Fahrig 2003; Fischer & Lindenmayer 2007). Effects on species biology can include increased stress (Janin *et al.* 2011), altered breeding patterns and decreased breeding success (Kurki *et al.* 2000; Zarette *et al.* 2000), altered foraging behaviour and success (Goverde *et al.* 2002; Haapakoski & Ylönen 2010) and decreased dispersal success (Stow *et al.* 2001; Coulon *et al.* 2010). The loss of species from ecological communities can result in bottom-up and top-down extinction cascades through food webs, as well as in extinctions through the breakdown of consumer-mediated coexistence (reviewed in Ebenman & Jonsson 2005; Soulé *et al.* 2005; Borrvall & Ebenman 2006). Community disassembly in fragmented habitats has been linked to declines in top-predators (Terborgh *et al.* 2001; Staddon *et al.* 2010). The larger area requirements, larger body size and lower densities of species at higher trophic levels can often increase their extinction proneness (Duffy 2003). In fragmented habitats, indirect effects on top-predator species have been shown to arise via the loss of resource diversity and the consequent niche-breadth collapse (Layman *et al.* 2007). Altered disturbance regimes and increased exposure and susceptibility to invasive species can also significantly alter community structure in fragmented habitats (Laurance 2004; Didham *et al.* 2007; Malhi *et al.* 2008). Alterations in community and food web structure arising from differences in habitat size and degree of isolation have been shown to affect important ecosystem functions such as nutrient cycling (Wardle *et al.* 2003a; Staddon *et al.* 2010). There have been important reviews of the individual and combined effects of habitat loss, degradation and fragmentation (reviewed in Haila 2002; Fahrig 2003; Ewers & Didham 2006; Fischer & Lindenmayer 2007). Although many questions remain, it is

clear that these landscape alterations exert significant pressure on individuals, populations, communities, food webs and ecosystems.

Climate change

Projections of the magnitude of anthropogenic change of the Earth's climate vary across geographic regions and among carbon emission scenarios. However, it is unlikely that temperatures will cease to increase in the coming decades even if global carbon emissions are stabilised (IPCC 2007). Increases or decreases in mean precipitation, depending on the geographic region, are also projected (Boulanger *et al.* 2007; IPCC 2007; Feng *et al.* 2011). Amplified climate variability and as well as increased frequency of extreme climatic events (e.g. droughts, heatwaves) have been recorded, and are projected to increase further (Easterling *et al.* 2000; IPCC 2007).

The negative impacts of climate change on species and ecosystems are not merely threats in a distant future. Such negative impacts have already occurred on virtually all taxonomic groups and in most continents (reviewed in Walther *et al.* 2002; Parmesan 2006; Fischlin *et al.* 2007). A meta-analysis of 866 peer-reviewed articles relating to impacts on biota that could be attributable in whole or in part to climate change found that by far most observations relate to phenological changes, i.e., changes in the timing of biological events (Parmesan 2006). Altered phenology can be seen for example in changes in the timing of spring events (Menzel *et al.* 2006), altered hibernation patterns (Visser 2010), asynchrony between flower and pollinator emergence, and mismatches in predator-prey populations (Visser & Both 2005; Parmesan 2006; Post & Forchhammer 2008). However, effects of climate change are diverse. Other impacts can arise through alteration of sex ratios (Mitchell & Janzen 2010), inhibition of dispersal (Massot *et al.* 2008), loss and fragmentation of suitable climate space (Rahel *et al.* 1996) and decreased breeding success (Visser *et al.* 2006; Huang & Pike 2011).

To survive rapid climate change, species must either adapt to new conditions or migrate to suitable climates, typically at higher latitudes or altitudes. An excellent review of mechanisms that can give rise to differences in species' capacity to adapt to climate change has been made by Somero (2010), with a specific focus on data from ectotherms. Adaptation to new climatic conditions requires functional genetic diversity, which may be naturally absent for many taxa under many conditions (Hoffmann & Sgro 2011). Rising temperatures have been shown to reduce genetic diversity in populations (Balint *et al.* 2011), and in the tropics, where species richness is highest, species may already be living at the limits of their physiological tolerances and thus be highly vulnerable to change (Kellermann *et al.* 2009). As invasive species tend to be better able to tolerate a broad range of climatic conditions, novel climates may place them at competitive advantage (Rahel & Olden 2008). Migration of vulnerable species to higher altitudes requires the existence of higher-altitude habitat within their dispersal capabilities. Endemic species of landscapes with little topographical variation, e.g. the Australian continent, can be at increased risk from climate change (Lindenmayer *et al.* 2010). Species that specialize in high altitude or latitude habitats may also be at increased extinction risk (Scriber *et al.* 2002; La Sorte & Jetz 2010).

Communities, food webs and ecosystem function have also been shown experimentally and through correlative studies to be affected by changes in temperature. Effects of climate change on species richness, total biomass and/or community structure have been recorded for marine plankton (Hays *et al.* 2005), reef systems (Holbrook *et al.* 1997; Johnson *et al.* 2011), arctic tundra plants (Chapin *et al.* 1995; Kittel *et al.* 2011), arid and semi-arid desert fauna and flora (Brown *et al.* 1997; Jimenez *et al.* 2011; Miranda *et al.* 2011), grassland soil fauna (Briones *et al.* 2009), intertidal and subtidal fauna (Barry *et al.* 1995; Dijkstra *et al.* 2011) and mountain butterflies (Wilson *et al.* 2007), among others. Effects on communities may be mediated by changes in trophic

relationships and food web structure (Petchey *et al.* 1999; Tylianakis 2009; Beveridge *et al.* 2010; Petchey *et al.* 2010; Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). In sum, there is a globally-coherent, strong body of literature indicating that the Earth's biological systems have already been impacted and will continue to be significantly impacted by anthropogenic changes in climate (Parmesan & Yohe 2003; Parmesan 2006; Fischlin *et al.* 2007).

Interaction between climate change and habitat loss, degradation and fragmentation

A wealth of calls has been made for the study of the interaction between climate change and habitat alteration as a necessary tool for the adequate assessment of threats to biodiversity and for the subsequent development of effective conservation strategies (Laurance 1998; Kappelle *et al.* 1999; Opdam & Wascher 2004; Ewers & Didham 2006; Brook *et al.* 2008; Leimu *et al.* 2010; Lindenmayer *et al.* 2010; Driscoll *et al.* 2011). A number of recent reviews have detailed the impact of different elements of climate change (e.g. drought, increased temperature, increased fire frequency) combined with habitat modification (loss, degradation, and/or fragmentation) on biodiversity (Opdam & Wascher 2004; Leimu *et al.* 2010).

Synergies between climate change and the modification of habitats can be expected to arise through a diversity of mechanisms. Mechanisms that restrict adaptation to or persistence under new climates are classified below as “adaptation constraints”. Those that limit the tracking of suitable climates at higher altitudes or latitudes are classified as “movement constraints”.

- *Adaptation constraints (Figure 1a)*

Although migration has allowed the persistence of species under past climate change, the current rates of change may necessitate adaptation in many organisms (Jump & Penuelas 2005). Endogenous and exogenous factors can limit the extent to which species are able to persist under new climatic conditions. A crucial endogenous limitation arises from the fundamental evolutionary limit to adaptation that is imposed by the quantity of relevant functional genetic diversity the species possess. Habitat fragmentation can increase the risk of extinction under climate change by resulting in loss of the adaptive genetic diversity required for sufficient adaptation to new climatic conditions (Hill *et al.* 2006; Joubert & Bijlsma 2010). Assessments of the negative impacts of fragmentation on plants have shown that impacts can transcend generations. For example, decreased germination success was found under drought conditions for plants from fragmented habitats (Pias *et al.* 2010). There are also important interactions between organism life histories and the time over which climate change occurs. Long life-cycles, coupled with significantly low reproductive success in fragmented habitats, can place plants whose low colonisation capabilities confine them to remnant habitat patches at increased risk of extinction under climate change (Honnay *et al.* 2002).

Exogenous factors can limit species’ capacity to persist under new conditions even where endogenous ones do not pose significant limitations. Habitat fragmentation can result

in trophic niche breadth collapses, whereby the range of resources that a consumer can access are greatly reduced (e.g. Layman *et al.* 2007), and this can be exacerbated by the effects of climate change. Mac Nally *et al.* (2009) reported severe decreases in bird breeding associated with decreased Eucalypt flowering during recent droughts in Australia, a stressor that is compounded by habitat loss through forest woodland clearing. Piessens *et al.* (2009) showed that in fragmented habitats, extreme weather events from which plants may be able to recover can nonetheless result in population extinctions in dependant butterflies.

Other exogenous effects linking habitat fragmentation and climate change can arise from an increase in the edge-to-area ratio in smaller, remnant habitats. In fragmented forests, edges may facilitate penetration of invasive species (Harper *et al.* 2005; Laurance & Useche 2009). This increases the vulnerability of these habitats to migrating invasive organisms colonizing from lower latitudes and altitudes as they track suitable climatic conditions. Edge effects may also be relevant in the context of fire as a threatening process. This is thought to be the case of the Amazon rainforest. The coupling of increased deforestation and increasing surface temperatures may result in a troubling self-reinforcing habitat loss mechanism in this region (Laurance 1998; Cochrane 2001; Laurance & Williamson 2001; Laurance 2004; Laurance & Useche 2009). Fragmented forests are drastically more vulnerable to fire than unfragmented ones and climate change may increase fire frequency (Laurance 2004). Climate-induced habitat loss, degradation and fragmentation exacerbate pre-existing unfavourable landscape conditions generated through vegetation clearance (Malhi *et al.* 2008; Peres *et al.* 2010).

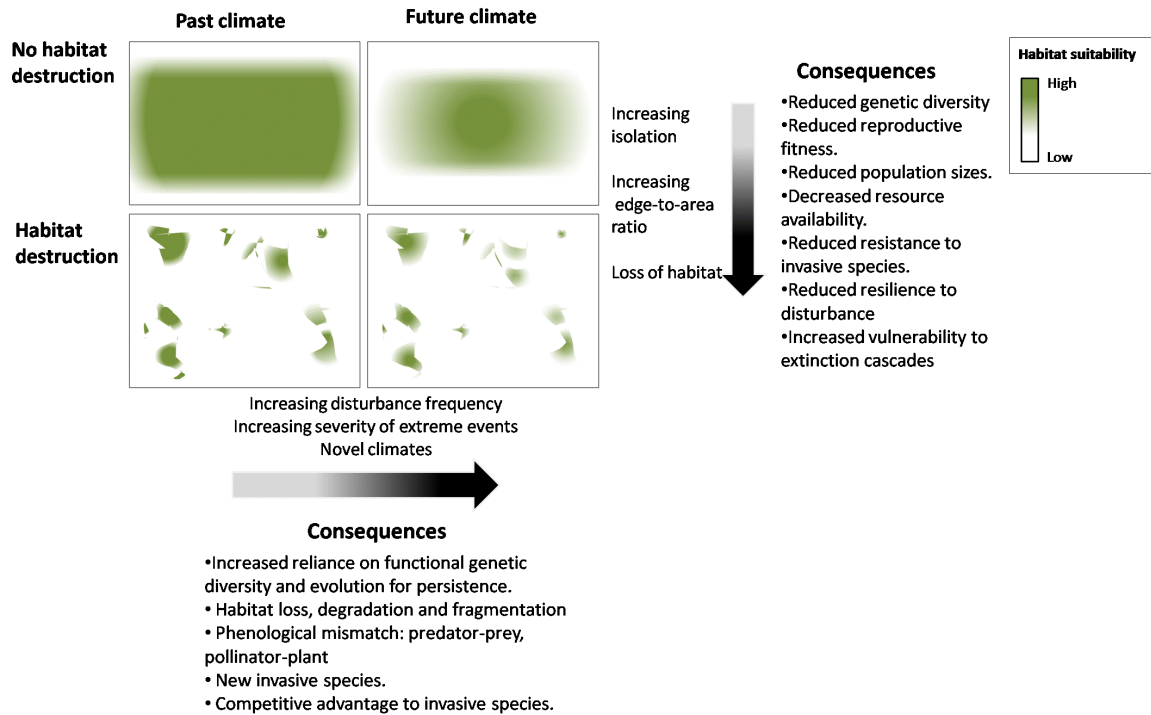


Figure 1a. Graphical summary of the reasons for concern regarding exacerbation of the impacts of one landscape-scale disturbance (climate change) through the impacts of another (habitat loss, degradation and fragmentation) – “adaptation constraints”.

Effects of habitat fragmentation and climate change on hypothetical landscapes are shown.

Habitat loss, degradation and fragmentation may in itself result from climate change, as changes in temperature or rainfall patterns (a) make previously suitable habitat uninhabitable (e.g. high-altitude specialist species), and/or (b) intensify edge-effects (e.g. increases propensity or frequency of devastating fires). Refer to text for details.

- *Movement constraints (Figure 1b)*

In order for migration to be a viable strategy for coping with rising temperatures, several conditions need to be met: (a) suitable climates (typically at higher altitudes and latitudes) need to exist, (b) suitable habitats need to exist at those locations, (c) species need to be able to migrate to these suitable habitats and (d) need to be able to compete with the species that are there. Although many range expansions of organisms tracking suitable climates have been reported (reviewed in Parmesan 2006) it is obvious that the criteria above will not be met ubiquitously. With increasing isolation between habitat patches, fulfilling criterion (c) will become increasingly difficult. Therefore, for species with limited tolerance to rising temperatures and little adaptive potential, the capacity to cope with climate change is inherently linked to the amount, quality and fragmentation of the habitat. For species which are unlikely to be limited by dispersal, such as plants with wind-dispersed seeds, loss of suitable habitat destinations can become the limiting factor for persistence under climate change (Schwartz 1993; Schwartz *et al.* 2001). Poor colonizing ability may also limit the viability of seeds that land in suitable habitats (Honnay *et al.* 2002). Finally, even organisms that have successfully migrated and established elsewhere may still face threats to their persistence due to small population size, metapopulation dynamics and habitat alterations.

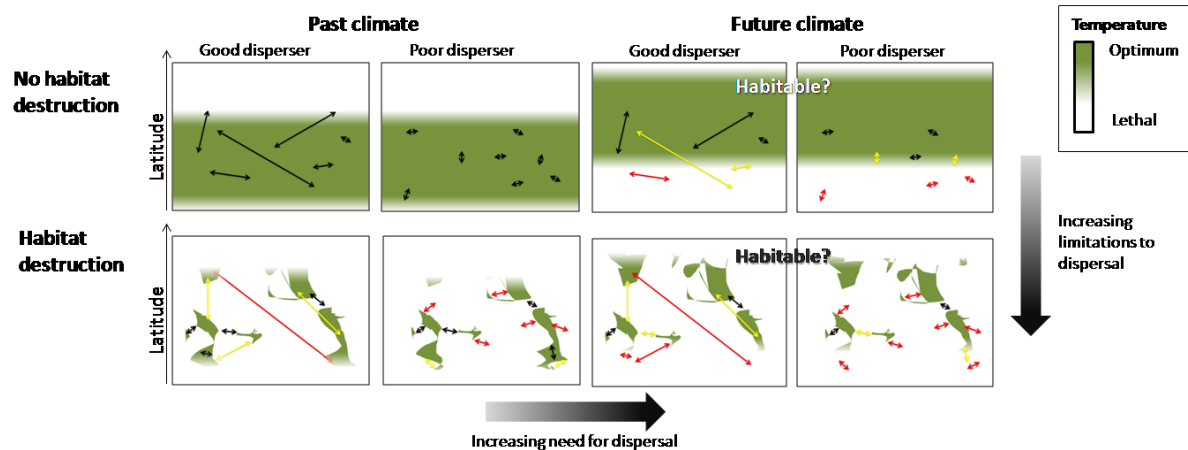


Figure 1b. Graphical summary of reasons for concern regarding exacerbation of the impacts of one landscape-scale disturbance (climate change) through the impacts of another (habitat loss, degradation and fragmentation) – “movement constraints”. The effects of habitat fragmentation and climate change on hypothetical landscapes inhabited by species of differing dispersal capabilities are represented. Arrows in landscapes represent available dispersal pathways, with black arrows representing realized dispersal, yellow arrows representing reduced dispersal and red arrows representing blocked dispersal. Climate change shifts the location of optimal temperatures towards higher latitudes and altitudes, increasing the need for dispersal to enable species persistence. Habitat fragmentation reduces connectivity in landscapes, limiting migration to higher latitudes. New regions where temperature is optimal may or may not be habitable to species, depending on their competitive abilities and availability of resources.

- Trends in the literature

I have reviewed a comprehensive body of literature discussing the interaction between climate change and habitat fragmentation loss, degradation and fragmentation, and found four trends of note. The first is that most of the available research has been carried out

at the species level, with little information relating to species interactions, ecological communities and food webs. Second, a considerable proportion of studies directly measure or manipulate only one of the threats and then proceed to infer conceptually the importance of the second within that context. The importance of the interaction is considered but not directly assessed. Third, experimental and correlative field studies are scarce.

Thirty-one of the 33 studies reviewed suggest that extinction risk from climate change may be higher in more fragmented habitats, or conversely, that the impacts of fragmentation may be more pronounced in landscapes subjected to climate change. A single study (Warren *et al.*, 2001) suggested that climate change would result increased risk in some taxa but reduced effects of fragmentation in others; reduced effects were suggested via increased dispersal of ectothermic, habitat generalists (Warren *et al.* 2001). An additional two studies (Thomas *et al.* 1999; 2001) suggesting a reduced effect of fragmentation with rising temperatures also targeted ectothermic animals, suggesting that increased dispersal capabilities and increased habitat availability due to increased temperature could counteract negative effects of habitat alterations (Thomas *et al.* 1999; Thomas *et al.* 2001). Studies of endotherms are much rarer than those of ectotherms, but all four reviewed described increased negative effects of climate change when paired with fragmentation (Appendix, Table 1). From the available data, it is clear that there are reasons for concern regarding potential synergy between climate change and habitat fragmentation, and that there is an urgent need for research that assesses their combined effects on food webs.

Table 1. Publication trends in surveyed articles that assess the interaction between climate change and habitat loss, degradation and fragmentation. Numbers reflect the count of published articles falling into each category. Studies were classified as conceptual if they are reviews of the literature or discuss the interaction between climate and

fragmentation without directly measuring one of these stressors. Studies of more than one species are considered community studies only if interactions between species are quantified or taken into consideration. Studies of communities are taken as food web studies only if trophic interactions between species are quantified or taken into consideration. * Totals don't equal the sum of the sub-categories where studies encompassed more than one subcategory. For details of on each of the articles, refer to the Appendix.

		Type of study				Total
		Conceptual	Mathematical modeling	Correlative	Experimental	
Scale of study	Species	8	12	2	1	22*
	Community	10			2	12
	Food web	2		2	1	5
Total		16*	12	4	3	34

Model systems in the study of complex ecological processes

Model systems are a common tool in many areas of biology, and significant progress in understanding complex phenomena has been gained through them (Meinke *et al.* 1998; Schneider 2000; Gibson 2005). We face landscape-scale disturbances of complex ecosystems, yet our understanding of the critical processes that underpin the assembly and persistence of ecological communities remains poor. The effects of landscape-scale stressors can be very difficult to study due to the large spatial and temporal scales at which many communities of interest operate. Microcosms have been proposed as model systems through which to experimentally address theoretical and applied questions in ecology. Many different microcosms have been used to date, and their suitability for a given study can depend on the question being addressed (Srivastava *et al.* 2004; Reiss *et al.* 2010). Invertebrate food webs in pitcher plants and treehole communities have contributed to our understanding of the effects of basal resources on biodiversity and of the interactions between population dynamics and food web structure (Kitching 1987; Pimm & Kitching 1987; Kitching 2000). Important insights into the links between biodiversity, island attributes and ecosystem processes have been obtained using soil communities (Wardle *et al.* 1997; Wardle *et al.* 2003a; Wardle *et al.* 2003b). Many other examples exist, and their contributions have been reviewed (Lawton 1995; Srivastava *et al.* 2004; Reiss *et al.* 2010). Although microcosms have generally been criticized for not truly resembling larger scale ecosystems (Carpenter 1996; Schindler 1998), counter-arguments are strong, and are becoming increasingly persuasive (Ives *et al.* 1996; Srivastava *et al.* 2004; Reiss *et al.* 2010; Drake & Kramer 2011).

The term “bryosphere” has been used to describe the small-scale ecosystem composed of mosses and associated fauna (Lindo & Gonzalez 2010). The bryosphere’s food

webs are diverse taxonomically, in life history strategies (Houck 1994; Siepel 1994), dispersal abilities and modes (Krantz 2010), relative sizes (Walter & Behan-Pelletier 1999; Osler & Beattie 2001), behaviour (Walter & Proctor 1999) and phenology (Krantz 2010). The system has been used to gain important ecological insights into the effects of habitat fragmentation and habitat corridors on complex communities (Gonzalez *et al.* 1998; Starzomski & Srivastava 2007; Staddon *et al.* 2010). Nonetheless, working with these communities is not without its challenges. Difficulties in the assessment of the diets of micro-arthropods have traditionally restricted the capacity to monitor food web structure in this system (but see simplified food web study by Staddon *et al.* 2010). This has limited the extent to which results from the ecosystem have been interpretable within the larger context of food web ecology. Owing to these technical challenges, some reticence over the use of microcosms, and the relatively recent appreciation of the likely major importance of strong interactions among habitat alteration and climate change, there has been no previous attempt to combine studies of increased temperature and fragmentation on moss-microarthropod communities.

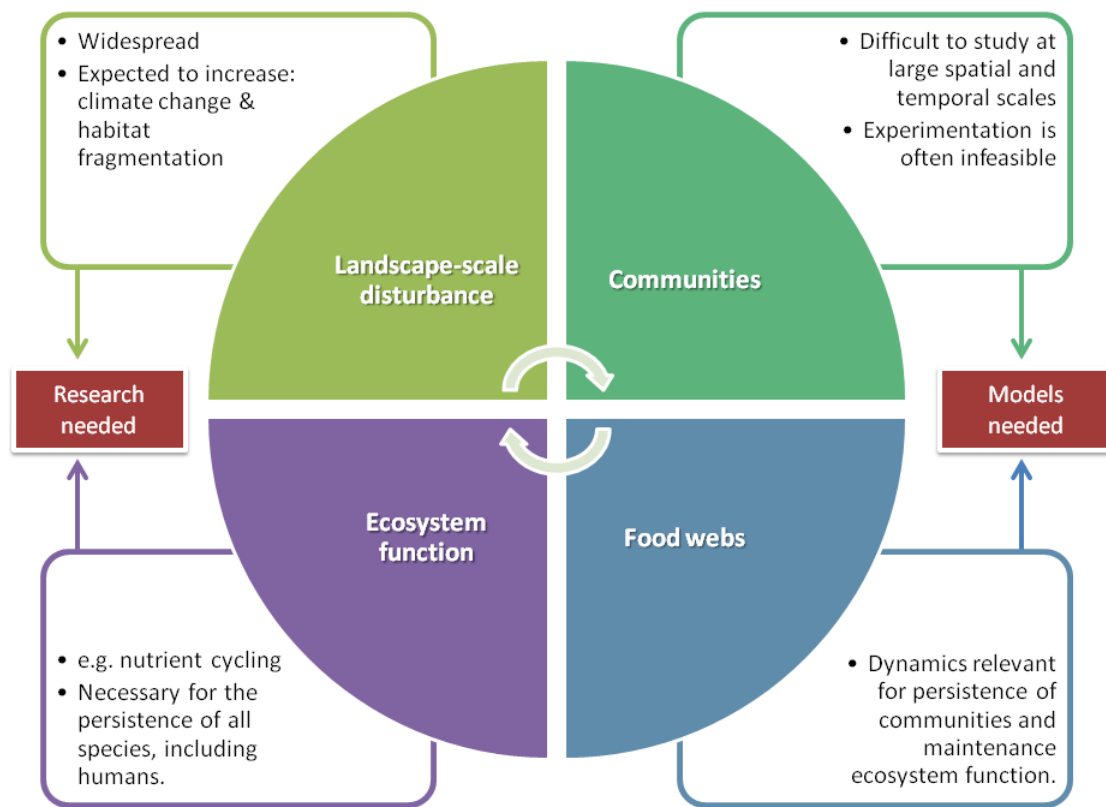


Figure 3. General conceptual framework of this thesis. Landscape-scale disturbances represent considerable threats to biodiversity. Their effects can be felt at all levels of biological organisation, from individuals in populations to ecosystems. The study of the effects on communities and food webs can be hindered by the large spatial and temporal scale at which these operate. Natural model systems can help approach theoretical and applied questions such as these, and thereby help identify the mechanistic links between disturbance, community dynamics, food web dynamics and ecosystem function.

General Aim

This study aims to use the moss-microarthropod ecosystem as a model for understanding the combined effects of climate change and habitat fragmentation on food webs.

- *Specific Aims*
- To facilitate the study of the moss food web by developing tools to estimate the diet of oribatid mites (Chapter 1)
- To facilitate comparisons between large numbers of food webs by developing free, customisable and expandable software for the visualization and analysis of food webs (Chapter 2)
- To describe a moss food web and contribute to the understanding of natural variability in the ecological community and food web structure in this system (Chapter 3)
- To assess the suitability of moss communities as model systems (Chapter 4)
- To assess the effects of climate, habitat isolation and their interaction on a moss community and food web structure (Chapter 5)

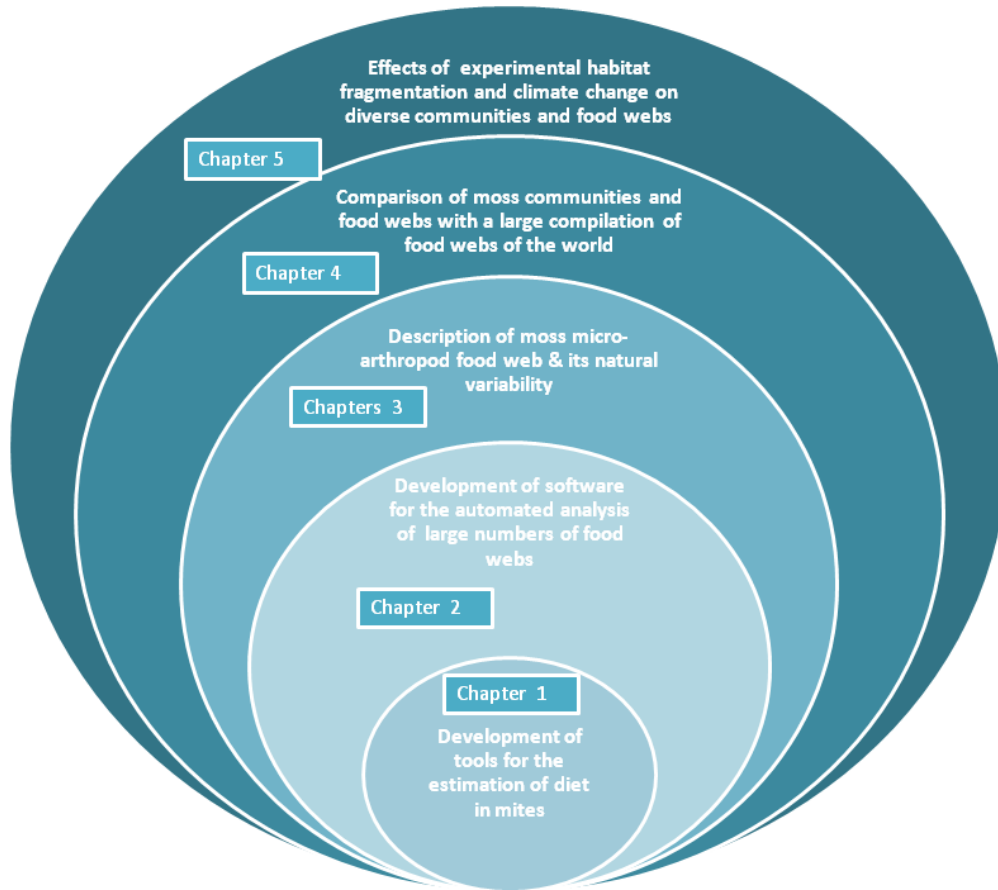


Figure 3. Graphical index of the thesis. The work is divided into five chapters, each addressing a specific aim of the thesis (refer to text). The chapters are ordered such that in the first two, data and tools necessary for the following three are presented. The final chapter describes results from experiments on microarthropod communities subjected to habitat fragmentation and climate change. The data are interpreted within the of the natural seasonal variability in the microecosystem (Chapter 3) and having assessed the degree to which moss microarthropod resembles food webs resemble those that operate at larger temporal and spatial scales (Chapter 4).

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Appendix – Review of studies on the combined impacts of climate stress and habitat modification.

Table 2. Review of studies assessing or discussing combined impacts of climate stress and habitat modification. Studies are classified as conceptual if they are reviews of the literature or discuss the interaction between climate and fragmentation without directly measuring one of these stressors. Studies of more than one species are considered community studies only if interactions between species are quantified or taken into consideration. Studies of communities are taken as food web studies only if trophic interactions between species are quantified or taken into consideration.

Reference	Type of climate stress	Type of habitat modification	Approach to the study of interaction between stressors				Scale of study			Impact
			Conceptual	Mathematical modeling	Correlative	Experimental	Species	Community	Food web	
Opdam and Wascher, 2004 (review - climate-fragmentation interaction)	Warming, changed rainfall, extreme weather	Loss, degradation and fragmentation	✓				Multiple			Species specific. Some increased risk, some decreased risk.
Laurance 1998, Laurance and Williamson 2001, Cochrane 2001, Laurance 2004, Malhi et al. 2008, Laurance and Useche 2009	Warming, reduced rainfall, increased fire frequency	Loss, degradation and fragmentation	✓					Amazon forest		Self-reinforcing habitat loss mechanism due to increased fire frequency and susceptibility.
Hill et al. 2006	Unspecified. Warming?	Loss and fragmentation	✓				Butterflies			Increased extinction risk
Chen et al 2011	Temperature increase	Loss and fragmentation	✓				Butterflies			Species specific. Some increase risk, some decreased.
Joubert and Bijlsma, 2011	Warming	-	✓				<i>Drosophila melanogaster</i>			Increased extinction risk
Honnay et al. 2002	-	Fragmentation	✓				Forest plants			Increased extinction risk, altered assemblage structure.
Ewers and Didham 2006 (review - fragmentation)	Warming, extreme weather	Loss, degradation and fragmentation	✓				Multiple			Increased extinction risk
Brook et al., 2008 (review - synergies and extinction)	Fire, drought, warming	Loss, degradation and fragmentation	✓				Multiple	✓	✓	Increased extinction risk, altered community structure, cascading effects through food web.

Table 2 continued

Reference	Type of climate stress	Type of habitat modification	Approach to the study of interaction between stressors				Scale of study			Impact
			Conceptual	Mathematical modeling	Correlative	Experimental	Species	Community	Food web	
Jump and Peñuelas, 2005 (review - climate, fragmentation)	Warming, changes in water availability	Loss, degradation and fragmentation	√					Plant assemblages	Loss genetic diversity, altered community structure, decreased resilience.	
Travis <i>et al.</i> 2003	Warming	Loss of percentage habitat in landscape		√				Non-specific	Increased extinction risk	
Vos <i>et al.</i> , 2008				√				√	Increased extinction risk	
Schwartz <i>et al.</i> 2001	Unspecified. Warming?	Loss and fragmentation		√				Forest plants	Increased extinction risk	
Warren <i>et al.</i> 2001	Warming	Fragmentation		√				Butterflies	Fragmentation reduces positive effects of warming. Only habitat generalists with good dispersal benefit. Specialists placed at increased extinction risk.	
Hill <i>et al.</i> 2002	Temperature and humidity	Loss, degradation and fragmentation		√				Butterflies	Increased extinction risk	
Stefanescu <i>et al.</i> 2004	Temperature & rainfall differences	Land-use types		√				Butterflies	Increased extinction risk	
Jetz <i>et al.</i> , 2007	Warming	Loss, degradation and fragmentation		√				Birds	Increased extinction risk	
Thomas <i>et al.</i> 2001	Warming	Loss, degradation and fragmentation		√				Butterflies	Climate increases amount of suitable habitat, decreases isolation. Decreased extinction risk.	
Thomas <i>et al.</i> , 2001	Warming	Loss, degradation and fragmentation		√				Bush crickets	Climate enhances dispersal capacity, reducing habitat fragmentation. Decreased extinction risk.	
Thomas <i>et al.</i> , 1999	Warming	Loss and fragmentation		√				Grasshopper Butterfly Ant Lizard	Climate increases amount of suitable habitat, decreases isolation. Decreased extinction risk.	

(continued)

Table 2 continued.

Reference	Type of climate stress	Type of habitat modification	Approach to the study of interaction between stressors				Scale of study			Impact
			Conceptual	Mathematical modeling	Correlative	Experimental	Species	Community	Food web	
Mac Nally et al., 2009	Drought and warming	Habitat loss, degradation and fragmentation			√			Eucalypts and avifauna	Increased avifauna extinction risk	
Rubidge <i>et al.</i> 2011	Temperature and rainfall change	Change in plant community structure			√			3 sp. of chipmunk	Species specific. Climate or climate and vegetation structure predict species' range.	
Mora <i>et al.</i> 2007	Warming	Fragmentation				√	Rotifers		Increased extinction risk	
Lindo and Winchester, 2007	Humidity decrease, temperature decrease	Habitat size and isolation				√		Soil communities	Low richness. Nested community structure.	
Starzomski and Srivastava, 2007	Drought frequency	Habitat size and connectivity				√		Moss microarthropods	Loss of habitat and connectivity reduces community resilience to drought. Decreased α diversity, increased β diversity, unaffected γ . Trophic position does not generally determine species response.	
Total number of studies:			14	10	2	3	17	10	3	

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This manuscript has been submitted to Soil Biology and Biogeochemistry. Text, tables and figures are as provided to the journal. Some changes from what was submitted to the journal have been incorporated into the final version of this thesis, following suggestions from the examiners. These changes are not reflected in the published manuscript (Perdomo *et al.* 2012), as it was approved by the journal before the examiner's evaluations were received and taken into consideration. Figures and tables have been embedded into the text for ease of reading. Formatting has been modified to adhere to thesis standard.

Chapter 1: Resolving food webs in mite-dominated systems

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Abstract

Mosses provide habitat for microarthropod communities that are dominated in abundance and richness by mites. Although these systems are used as experimental models to address questions of relevance to general ecology, and despite the fact that they are also of relevance to key, ecosystem-wide functions such as nutrient cycling rates, the trophic relationships that underpin these functions are poorly resolved. The complexity of the moss habitat matrix and the small size of its residents have hampered progress in the determination of diets. We use stable isotope analysis of moss communities and present tools that allow for more in-depth studies of food web structure in mosses and soils than are currently available. We test in mites for the first time the association between mouthpart morphology and isotope signatures. Isotopes capture the diet of mites under field conditions and over a longer time-span than traditional, snapshot measures of diet such as gut contents analyses. Our data suggest that cheliceral morphology can be used as a first inexpensive and quick filter for estimation of dietary preference in mites, with ambiguous trophic relationships resolved through isotope analyses. This work provides new information and tools for the study of mite-dominated food webs.

Keywords: Acari, Oribatida, isotope, C₁₃, N₁₅, chelicerae, food web, moss

Introduction

Mosses provide habitat for microarthropod communities that are dominated by mites, and in particular oribatid mites (Lindo & Gonzalez 2010). Mosses have been shown to be of relevance to key, ecosystem-wide functions such as nutrient cycling rates (Turetsky 2003),

and these systems have been used as experimental models to address questions of relevance to general ecology (Gonzalez *et al.* 1998; Starzomski & Srivastava 2007; Staddon *et al.* 2010). Despite this importance and these applications, the trophic relationships that may underpin such functions are still poorly resolved. This lack of detailed knowledge restricts our understanding of how these systems operate and limits our predictive capacity with regards to the effects of disturbances and of major environmental stressors such as climate change. Developing tools to estimate measures of food web structure in these systems, such as species richness per guild and total biomass, is of clear importance.

Many techniques have been applied to the study of dietary preferences in mites, each with notable strengths and weaknesses (Appendix 4). Determination of diet has traditionally been hampered by mites' small size and the difficulty of carrying out field observations. Researchers attempting to determine mite diets through gut content analysis can report a large proportion of "indeterminate material" (Fashing 1998). Where contents of the gut are identifiable, it can be unclear if the ingested items would eventually have been assimilated into biomass or excreted undigested. It is also doubtful that the snapshot nature of gut content surveys reflects longer-term dietary preferences. Although laboratory experiments of food choice have provided insights into dietary preferences of certain mite species, they are fraught with difficulty in supplying the appropriate choices and quantifying food consumption (e.g. Schneider & Maraun 2005), and they may not reflect feeding preferences in the field.

Stable isotope techniques have recently enabled useful, time-integrated measurements of field diet in mites (Schneider *et al.* 2004; Pollierer *et al.* 2009), and have allowed the assignment of oribatid mites to feeding guilds. However, the minimum mass of mites required to perform these studies, as well as their cost, limit the number of species that can be subjected to such analyses. Most studies using the moss-microarthropod system as a model

encounter more than 100 mite morphospecies, and family or even genus are equivocal proxies for diet where the diet of species of the same family or genus is actually known (Schneider *et al.* 2004). While an association between mite mouthpart morphology and diet has been suggested (Krantz & Lindquist 1979) and studied (Kaneko 1988; Buryn & Brandl 1992), the data with which to compare the morphology has suffered from the pre-isotope limitations described above. Additionally, a detailed understanding of cheliceral functional morphology has only recently become available through synchrotron technologies (Heethoff & Norton 2009). Here we integrate the information that has become available through these new techniques in order to assess whether cheliceral morphology is associated with long-term, field preferences in diet as indicated by isotope signatures. We carry out stable isotope analysis of moss communities in concert with analysis of mite chelicerae, and present tools that allow for more in-depth studies of food web structure in mosses and soils than are currently available.

Methodology

Two sample sets were used to study (a) isotope signatures of moss faunal communities, and (b) the association in mites between position on the food web and cheliceral morphology. Specifications of the samples used can be found in Table 1.

Table 1. Summary of invertebrate material examined and the analyses performed on it.

The stable isotope analysis on German mites was carried out by Schneider et al. (2004)

Country of origin	Habitat type	Taxon	Number of morphospecies	Analyses performed	
				Cheliceral shape	Stable isotopes
Australia	moss	Arachnida			
		Acari - Oribatida	11	√	√
		Acari - Mesostigmata	2	√	√
		Acari - Prostigmata	1		√
		Pseudoscorpiones	1		√
		Aranae	1		√
		Insecta			√
		Coleoptera	3		√
		Homoptera	1		√
		Collembola	9		√
		Crustacea			
		Isopoda	1		√
		Onychophora	1		√
		Germany	litter	Arachnida	
Acari - Oribatida	12			√	√*

- *Stable isotope analysis*

Moss (*Dicranoloma billiardieri*) samples were collected in July 2009 in the Yarra Ranges National Park, Victoria, Australia (37°29' S 145°49' E, 800 m, permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria, Australia). This site is a cool temperate rainforest dominated by Mountain Ash (*Eucalyptus regnans*) and Myrtle Beech (*Nothofagus cunninghamii*) trees. Fauna was extracted into 70% ethanol using Tullgren funnels and stored. The fauna included velvet worms, pseudoscorpions, slaters, spiders, springtails and mites (Table 1). Samples were sorted to morphospecies and oven-dried for 24-48 hours at 60°C. In order to obtain the minimum mass required for analysis (0.01mg), 10 to 41 individuals per mite morphospecies were necessary. Samples were weighed after drying and sent for isotope analysis by Griffith University. Isotope content was analysed using a continuous flow-isotope ratio mass

spectrometer (Europa Tracermass and Roboprep, Crewe, England). Ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were expressed as the relative per mill (‰) difference between the sample and conventional standards (PeeDee Belemnite carbonate and N_2 in air), where $\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000(\text{‰})$, $X = ^{13}\text{C}$ or ^{15}N and $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Potential basal resources for the food web (fern fronds, Mountain Ash leaves, Myrtle Beech leaves and bark in different stages of decomposition, moss, lichen, fungus) were analysed in the same facility after being washed with distilled water, oven-dried and pulverized with a Retsch Mixer Mill MM301.

Estimation of the proportion of the sampled food sources that were likely to account for the isotope signature of non-predatory species was carried out by fitting Bayesian mixing models to the signatures using the package SIAR (Parnell *et al.* 2010) in R Statistical Package (RDCT 2009). Models were run 30,000 times, without priors for the proportion of food sources and with no isotope concentration dependence. Mean and standard deviation of the isotope signatures for moss, bark, litter (all species pooled) and lichen were used for modeling. Due to the lack of replication of the fungal signature, the standard deviation of the litter signatures was assigned to this resource. The rationale for this is that variability in the signature of litter could be expected to affect the variability of the signature of the fungi that consume it. Furthermore, the variability in the signature of the litter was the largest of the sampled basal resources of the fungi (see Figure 3); assuming its variability for the fungi is a conservative approach for the analysis conducted. Variability in the signature of the potential food sources leads to uncertainty in the estimation of diet of the consumers (Parnell *et al.* 2010).

Two sets of trophic enrichment factors (TEFs) were fitted separately in order to determine the effect of changing these on the estimation of proportions of food sources in the diets. TEFs indicate the difference in the isotope value of a consumer relative to its food

source. The first set of TEFs considered in this study (Figure 1, left) was based on the enrichment factors considered applicable for other food webs (Post 2002). The second set of TEFs used (Figure 1, right) takes into consideration observations by Pollierer et al. (2009), who found that the cellulose component of litter was highly enriched in ^{13}C relative to other components. The authors proposed that the large differences observed in ^{13}C signatures between bulk litter samples and all the soil fauna sampled could possibly be accounted for by selective digestion and assimilation of carbon from cellulose. Low ^{15}N enrichment was also reported in that study.

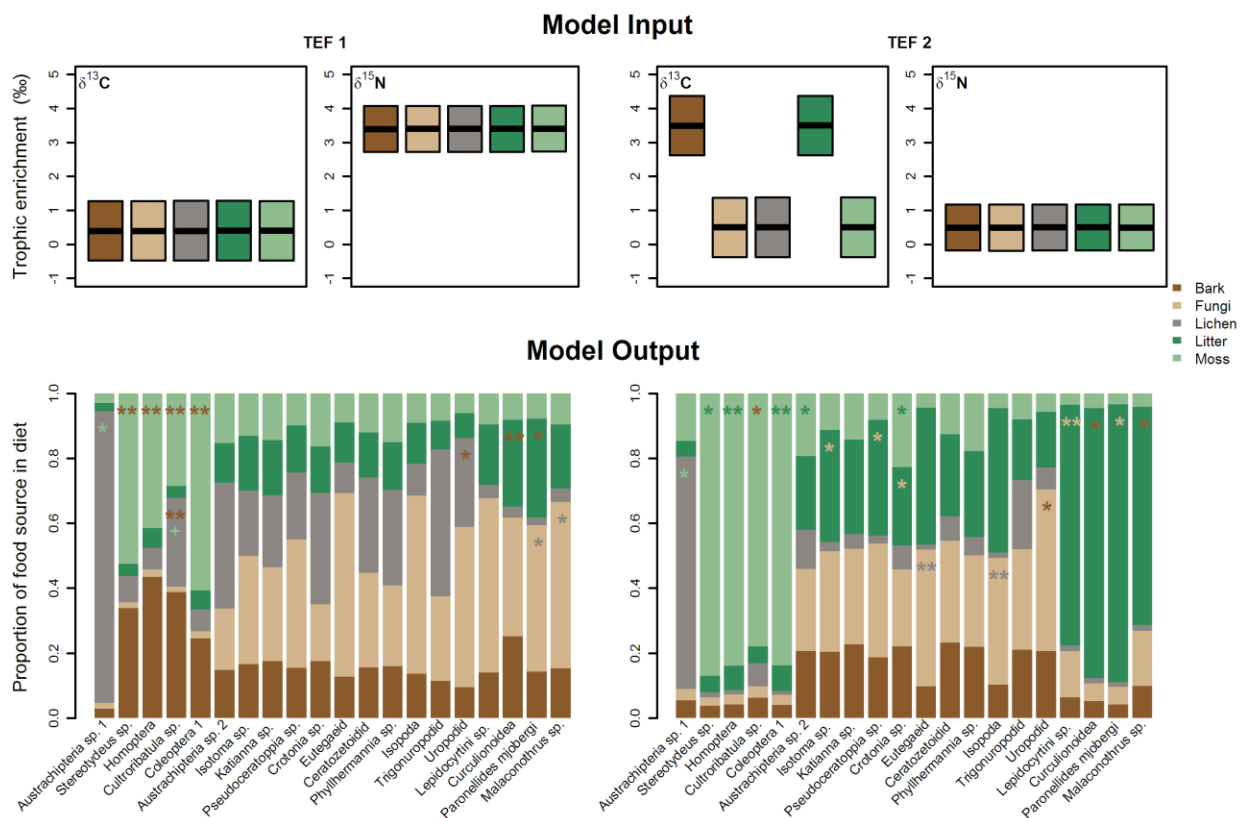


Figure 1. Two sets of trophic enrichment factors (TEF1 and TEF2) used in Bayesian modeling, and resulting estimated proportion of food sources in non-predatory species' diets. Symbols inside the bars indicate correlation between the estimated proportions of food sources. Positive correlation: "+". Negative correlation with index smaller than -0.7: "**". Negative correlation with index between -0.5 and -0.69: "*".

- *Cheliceral measurements*

The following oribatid mite species were collected from the study site where Schneider et al. (2004) carried out their isotope determination (Göttinger Wald, Germany): *Paradamaeus clavipes*, *Hypodamaeus riparius*, *Nothrus palustris*, *Chamobates voigtsi*, *Chamobates cuspidatus*, *Chamobates borealis*, *Oribatula tibialis*, *Hypochthonius rufulus*, *Platynothrus peltifer*, *Tectocephus velatus*, *Amerus troisii*, *Achipteria coleoptrata* and a phthiracarid species. The feeding guilds reported in that paper via stable isotope analysis were used to compare with cheliceral dimensions. Their guilds were: secondary decomposer (predominantly feeding on fungi and partly on litter), primary decomposer (predominantly feeding on litter little colonized by fungi and bacteria), and carnivores/scavengers/omnivores. An additional eleven oribatid morphospecies were used for this analysis from the Australian samples collected for this study as described above; feeding guilds were ascribed on the basis of the isotopic signature determined here.

Mites were dehydrated and placed on a microscope slide with double-sided tape to facilitate extraction of chelicerae using fine tweezers under a stereoscopic microscope. Dehydration was achieved by washing the specimens in 90% ethanol for 5 minutes, 95% for 5 minutes, 100% for 15 minutes twice, and dry 100% ethanol for 15 minutes. Extracted chelicerae from one to five specimens were placed on microscope slides and cleared of internal tissue by adding 80% lactic acid and heating at ~60°C for 15 minutes. Cleared chelicerae were photographed at 40x with a compound microscope and measurements were taken from the images using Motic Images Plus (Motic China Group Co. LTD).

Cheliceral dimensions taken are outlined in Figure 2. Potential of the first-class lever formed by the movable digit to crush food items against the principal segment (Heethoff & Norton 2009) was estimated as the ratio between maximum height of the movable digit (MH)

and its length (ML) (Figure 2), under the assumption that taller digits (per unit length) were likely to have a longer distance from the fulcrum to the levator tendon attachment (effort arm) than sleeker digits. The bouquet shape of the levator muscle that lifts the movable digit and occupies most of the principal segment (Heethoff & Norton 2009) complicates the estimation of the cross-sectional area of this muscle and therefore of its capacity, especially where only a two-dimensional image is available (as in Figure 2). We estimated this cross-sectional area as the square of the maximum height of the principal segment (PH^2).

Statistical analyses were performed in the software package R, using the base package Stats (RDCT 2009). Principal components analysis (PCA) was carried out on all five cheliceral measurements. Species' scores along principal component axes two and three (PC2 and PC3) were used to perform single factor analyses of variance with feeding guild as a predictor variable (the lichenivorous guild was not included as it was represented by a single morphospecies). Tukey's post hoc tests were performed to compare scores among feeding guilds. PC1 scores were not used as the axis was constructed with negative loadings of similar magnitude for all measurements, suggesting scores would be highly influenced by variability in size rather than shape.

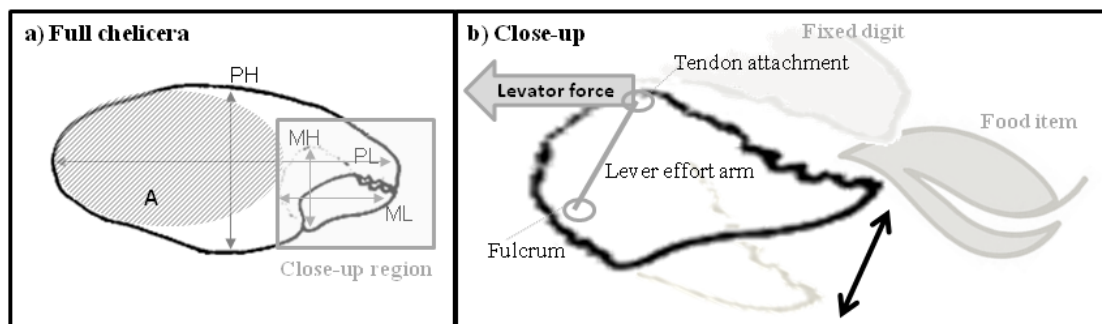


Figure 2. a) Cheliceral measurements used in this study. PL: principal segment length. PH: principal segment height. ML: Movable digit length. MH: Movable digit height. A: shaded area, area available for the levator muscle of the movable digit. **b) Schematic representation of cheliceral functional morphology** (based on Heethoff & Norton 2009).

Results

- *Stable isotope analysis*

Groups of potential food sources for the faunal communities in moss differ in their isotope signatures, with lichens being severely depleted in ^{15}N and enriched in ^{13}C , moss, litter and bark being relatively high in ^{15}N and low on ^{13}C , and the fungus being relatively high for both isotopes (Figure 3). Moss signatures were lower in ^{15}N than those of litter. The fauna spans 14.4 ‰ $\delta^{15}\text{N}$ and 9.5 ‰ of $\delta^{13}\text{C}$, with most taxa presenting ^{13}C signatures more than 3.5 ‰ higher than those of plants. The nitrogen signatures of one mesostigmatid (*Gamasellus* sp.) and one oribatid mite (*Lanceoppia* sp.) were as high as that of assumed top predators in the system (velvet worms, pseudoscorpions, spiders). Carbon and nitrogen signatures of *Austrachipteria* congenics differed markedly, with one species presenting a signature intermediate between lichen and litter/bark/moss, and another similar to that of

fungi. The carbon and nitrogen signatures of the prostigmatid mite (*Stereotydeus* sp.) were similar to that of moss.

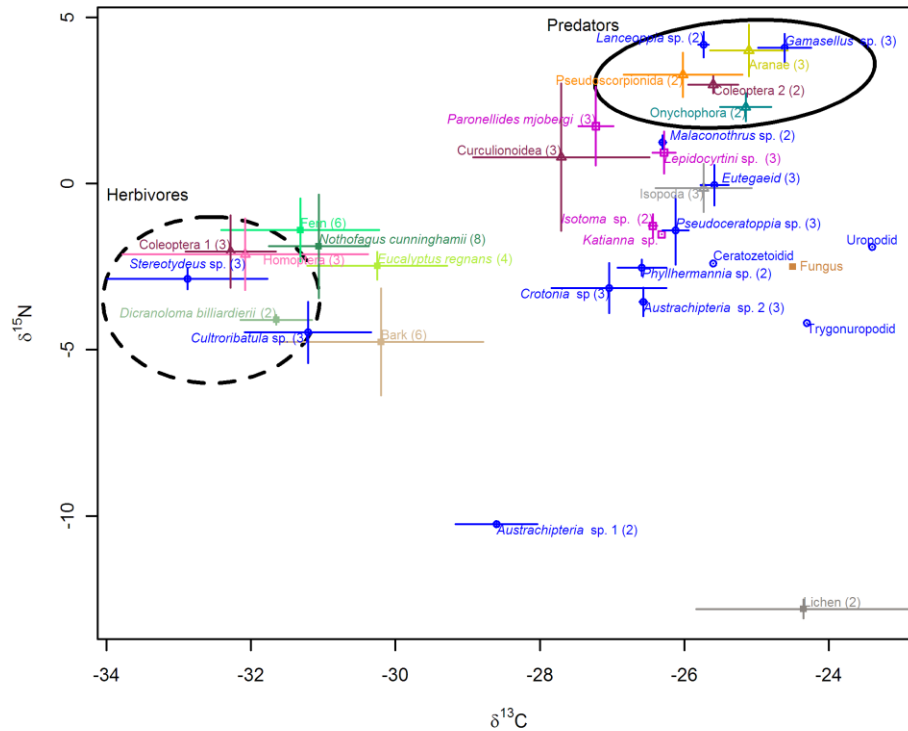


Figure 3. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of moss dwelling fauna and its potential basal food sources. Blue: mites. Violet: collembolans. Other colours indicate other animal taxa and food sources.

The estimated proportion of litter in non-predatory mite species' diets was higher when trophic enrichment of carbon from this source was fitted as having a mean of 3.5 rather than of 0.5 (TEF set 2 vs 1, Figure 1). Conversely, the estimated proportion of lichen and fungi in the diet was higher with TEF set 1 than 2. Overall differences in diet among four groups of species were found, and these were maintained regardless of change in trophic enrichment factors. The diets estimations of *Stereotydeus* sp., *Cultroribatula* sp., Coleoptera 1 and Homoptera changed considerably with a change in trophic enrichment factors. The TEF set with a mean 3.4‰ enrichment of nitrogen (compared to 0.5 ‰) resulted in lower

estimated proportions of moss in diets, and higher proportions of bark, a source with a less-enriched nitrogen signature. There was evidence of a strong negative correlation between the estimated proportion of bark and moss in the diets using TEF1; bimodal distributions in the estimated proportions for the sources were found (data not shown). These negative correlations indicate that diet estimation iterations that included one food source tended to exclude the other in order to explain the species' isotope signature, i.e. the sources were found to be interchangeable. Strong negative correlations were also found between litter and moss for known herbivorous taxa (Homoptera, Coleoptera) using TEF2.

- *Association between mouthpart morphology and isotope signatures in oribatids*

A large proportion of the variability in cheliceral shape (85%) was accounted for along a single axis (PC1). This axis had negative loadings of similar magnitude for all measurements, suggesting scores along it would be highly influenced by variability in size rather than shape (e.g. chelicerae of similar shape would receive differing PC1 scores if they were of a different size).. PC2 and PC3 captured 10 and 5% of the variability respectively, and loadings of the variables differed in magnitude and sign. Feeding guild is associated with cheliceral morphology (ANOVA on PC2, $F_{2,19}=11.715$, $p<0.001$; Tukey's post-hoc $p<0.05$ except between primary and secondary decomposers; ANOVA on PC3, $F_{2,19}=9.22$, $p<0.05$; Tukey's post-hoc $p<0.05$ except between carnivores and secondary decomposers). Removal of mesostigmatid mites from the analysis (reduction of the sample size in the carnivorous guild to three) reduced the variability explained by PC2 and PC3 to 5 and 2% respectively. Significance of comparisons using PC2 scores was unaltered. PC3 scores were not significantly different across guilds without mesostigmatids in the analysis.

Leverage and estimated cross-sectional area of the levator can be used in conjunction to differentiate between guilds with higher accuracy than each measure would provide independently (Figure 4). Carnivorous/omnivorous/scavenger mites have chelicerae that have a low leverage index and little space for levator muscles. Primary decomposers generally have chelicerae with a high leverage index, and an estimated cross-sectional area smaller than $2000 \mu\text{m}^2$. The pthiracarid mite is an exception to this general pattern, with its chelicerae showing the second largest area of all species. Chelicerae of secondary decomposers (feeding mostly on fungi) generally have a large cross-sectional area (higher than $2000 \mu\text{m}^2$) and a leverage index between 0.5 and 0.7. A correlation between the estimated levator cross-sectional area and mite body size was found (Appendix 1, Figure 1, $p < 0.05$, $R^2 = 0.3752$). Leverage did not show an association with logarithm of body size (Appendix 1, Figure 2, $p = 0.67$).

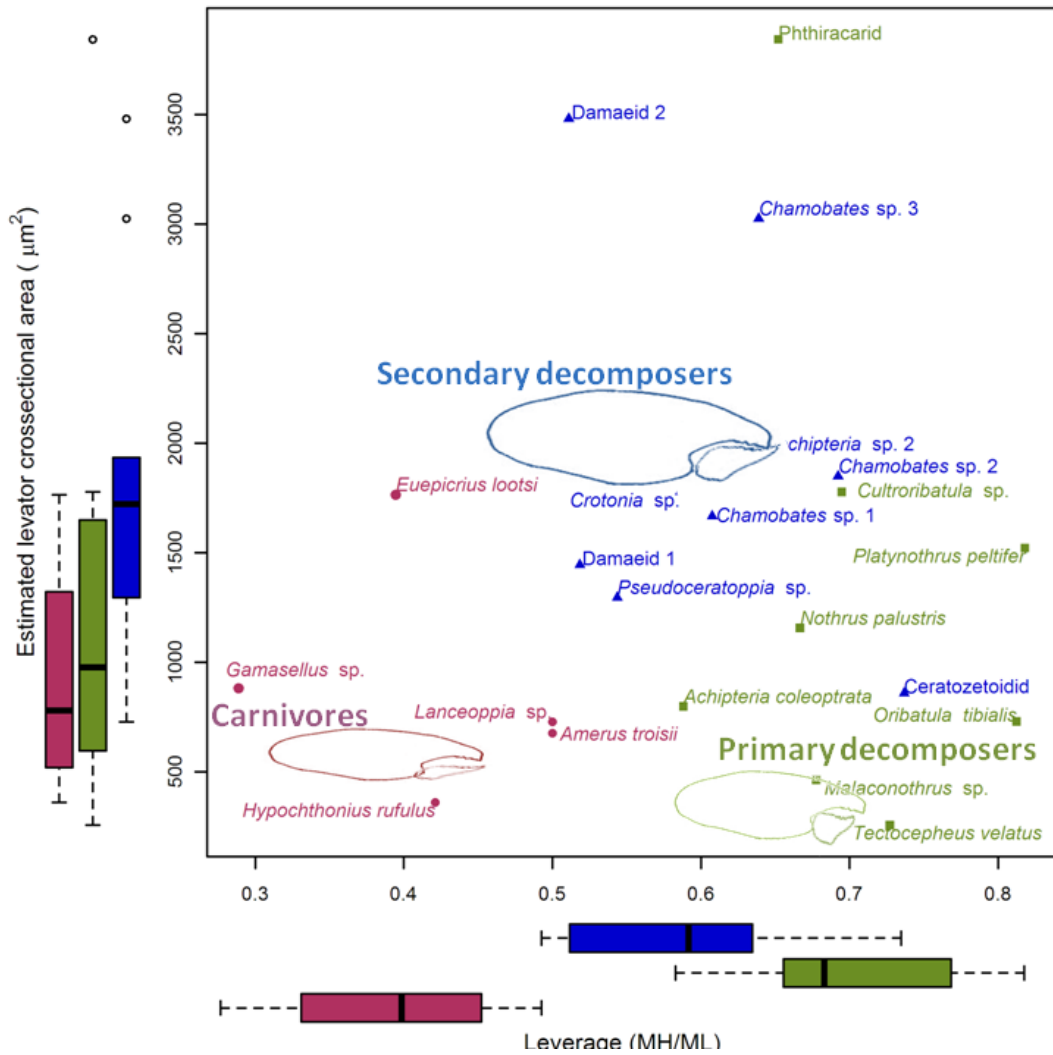


Figure 4. Relationship between feeding guilds and cheliceral measurements. Boxplots represent median, 25th and 75th percentiles, range and outliers of values in each axis. Primary decomposers: feed predominantly on litter. Secondary decomposers: feed predominantly on fungi.

Discussion

Bryophytes can play important roles in key, ecosystem-wide functions such as nutrient cycling rates (Turetsky 2003). Despite some functional understanding of moss

ecosystems (Lindo & Gonzalez 2010), and the use of moss microarthropod food webs as ecological models (Gonzalez *et al.* 1998; Starzomski & Srivastava 2007; Staddon *et al.* 2010), food web structure has not been described in detail due in part to insufficient information about the diet of an abundant and diverse taxon: oribatid mites. This is also largely true for soil food webs, which are characterized by a similar fauna (but see Berg *et al.* 2001 for a highly resolved soil food web). The lack of more detailed information on these food webs is largely due to the many challenges associated with determination of the diet of the diverse and understudied community of microarthropods that inhabit these habitats. Here we provide the first stable isotope study of a moss food web and expand on available tools to assess diets in oribatid mites, an abundant and diverse taxon in the system.

- *Trophic levels in moss communities*

The use of stable isotopes to trace the flow of both carbon and nitrogen in the moss system suggests that most of the fauna sampled does not feed directly on moss. The range of carbon and nitrogen signatures in this study is similar to that found in soil communities (Schneider *et al.* 2004; Pollierer *et al.* 2009), and suggests a food web with more than one basal resource and trophic level. The presence of oribatid mites across the range of isotope signatures confirms results of previous work (Schneider *et al.* 2004) indicating that these mites should not be pooled into just one detritivorous guild.

Detailed studies of trophic enrichment of ^{13}C and ^{15}N are not available for most moss-dwelling organisms and this can hamper further interpretation of the ranges. We have shown that use of different trophic enrichment factors can change estimations of diet generated by mixing models, and that the adoption of enrichment levels often applied to non-soil foodwebs can result in estimations that are not consistent with what is known about the basic biology of some taxa present in moss (e.g. Homoptera). In contrast, the adoption of high enrichment

values of carbon from litter and bark, combined with low enrichment of nitrogen from all sources, produced results which were more consistent with the known natural history of the consumers. This provides support for Pollierer *et al.*'s (2009) suggestion that cellulose in litter may be selectively assimilated, and suggests that trophic enrichment in moss systems may be more similar to those in soils rather than other systems. We propose that TEF2 is more likely to allow accurate estimation of food webs in moss systems than TEF1. In order to gain additional insight into the proportion of food sources in the diets of soil- and moss-dwelling taxa via the isotope techniques presented here, further work assessing enrichment levels for different sources and taxa is recommended.

Although the use of mixing models to estimate proportion of food sources in the diet is common (e.g. Bugoni *et al.* 2010; McClellan *et al.* 2010; Dodge *et al.* 2011), they have not to our knowledge been applied in studies of soil or moss food webs to date. One of the advantages of their use is the transformation of isotope signatures (represented in δ -space, ordinations that are potentially specific to particular locations) into more biologically relevant estimations of dietary compositions (occurring in p-space and thus potentially generalisable across locations) (Parnell *et al.* 2010). However, this technique necessitates comprehensive sampling of potential food sources in order to produce reliable results. The large negative correlation indices found in this study between litter and moss for known herbivorous taxa (Homoptera, Coleoptera) using TEF2 indicate that diet estimation iterations that included one food source tended to exclude the other. This reflects that the model could not determine with precision which of the sources was most likely to account for the signature of the fauna. It is likely that the absence of signatures of live plants other than moss in our study accounts for this. Nonetheless, results indicating that a live plant source is the major component of the diet of herbivorous mesofauna provide support for our estimations of

herbivory in the microfauna for which little information was previously available (e.g. *Stereotydeus* sp., *Cultroribatula* sp.).

We did not determine isotope composition of bacterial films in this study or perform extensive sampling of fungal hyphae. Variability around the fungal signature was however fitted into the mixing models, and fungal feeding has been reported and extensively studied in mites (Maraun *et al.* 2003; Schneider *et al.* 2004; Schneider & Maraun 2005). It is therefore likely that the ^{13}C and ^{15}N enriched signatures we observed correspond at least in part to feeding on this resource. Additionally, there was a high degree of concordance between the morphology and taxonomic groupings of the taxa that we classified as fungivores, and those classified as fungivores independently in Schneider *et al.* (2004), further suggesting that our isotopically-enriched mites do in fact rely on fungi as a food source. Finally, correct estimation of herbivorous diet for known herbivores (e.g. Homoptera) provides a measure of confidence in our diet estimations.

- *Assembling food webs in mite-dominated communities*

Assembling food webs requires the determination of the roles of members of a community in terms both of their feeding preference and of the amount of mass that each member species contributes to its respective guild (Cohen *et al.* 1993a). In moss food webs, the most abundant and diverse taxon is oribatid mites. The biomass contributed by each species to the food web can be readily estimated via simple measures of body size (Appendix 2), but the assignment of a species to a particular feeding guild is more complex. Here we provide evidence that cheliceral morphology of oribatids is associated with the time-integrated measures of diet that can be obtained through stable isotope analyses. Furthermore, we provide a plausible mechanism explaining this association by assessing the

morphological data in light of information that has recently become available about the way in which cheliceral muscles operate.

Considering the general locations of the movable digit lever, its fulcrum and the tendon attachment (Figure 2), we propose that for a given length of movable digit (“ML”), it is likely that the taller the digit (larger “MH”) the longer the effort arm of the lever. The longer the effort arm, the more force can be applied at the tip of the chelicera. In accordance with this, our data show that species that rely on litter (primary decomposers) have relatively tall digits (higher MH to ML ratio, i.e. higher leverage). Conversely, where the relative ML length is greater, higher speeds of closing the chelicerae can be achieved, which would be advantageous for catching fast-moving prey. As expected, a lower leverage is found in carnivorous species. Species relying on fungi (secondary decomposers) show leverage values in between those of predators and primary decomposers. Similar observations were made by Kaneko (1988), who found that species classified via gut-content analysis as macrophytophagous (i.e. feeding predominantly on higher plant matter) generally had an MH/ML ratio higher than 0.6, and microphytophagous species (i.e. feeding on predominantly on fungal hyphae and spores) had a ratio lower than 0.6. Our work expands on this original observation by considering stable isotope signatures, incorporating species classified as carnivorous and estimating cross-sectional area of the levator muscle to further differentiate between guilds. The positive correlation found between body size and estimated levator cross-sectional area suggests that differences in body size could at least in part drive the patterns shown here for the levator muscle; conversely, the lack of such a correlation for leverage confirms the expectation that this index is not affected by the size of the species.

Previous studies have suggested that one limitation of the application of stable isotopes in the study of mite-dominated communities is that enrichment of ^{15}N could possibly occur through the preferential consumption of fungi that grow on decomposing animals,

rather than from direct consumption of the animals themselves (Schneider *et al.* 2004). We show here that the morphology of chelicerae of ^{15}N -enriched oribatid mites studied is different from that of fungivorous ones and more similar to that of predatory mesostigmatid mites. This suggests not only that these oribatids are likely to be carnivorous but also highlights that cheliceral shape can provide additional insights into the dietary preferences of these organisms. Type one levers with long effort arms can be expected to be slower than those with shorter effort arms. The finding that ^{15}N enriched species have the slimmest (i.e. likely fastest) chelicerae suggests carnivory in these species may occur through predation rather than scavenging. Furthermore, the difference found in cheliceral morphology between species that had been assigned to different guilds via isotope analysis provides strength to the arguments that isotopic composition accurately distinguishes between groups of species that preferentially feed on different food sources in the field.

Although the association between morphology and isotope signature did not apply to all of the species studied, the observed discrepancies between guilds attributed via isotope analysis and the expectations of feeding preference based on mouthpart morphology are interesting and can provide focus for further work. For example, the phthiracarid mite studied had a cross-sectional area uncharacteristic of other primary decomposers, and its estimated leverage is intermediate between these two groups. The isotopic signature for this species (from Schneider *et al.* 2004) was also intermediate between decomposer groups. One possible explanation for these intermediate values is that the species relies on both resources, but this requires further investigation. The power to detect these discrepancies is valuable for focusing efforts of dietary preference determination on controversial species. Considering the abundance and diversity of oribatid mites in mosses and the considerable value of understanding food web dynamics in this model ecological system, we propose that where economic resources are limited, cheliceral morphology can be used as a good measure for

separation of oribatid mites into three feeding guilds: carnivore, primary decomposer and secondary decomposer, and that species displaying morphological borderline values can be targeted for isotope analysis. Although some species may be allocated to guilds that would not correspond to the guilds assigned by isotopic signature, here we have shown that these techniques are in large part in accordance with each other.

The study of food web dynamics can significantly enhance our understanding of nutrient cycling and energy fluxes in ecosystems (DeAngelis 1992; Massol *et al.* 2011). Biomass and species richness per guild are fundamental attributes of food webs, and have major impacts on properties such as stability in the face of disturbance (Ings *et al.* 2009; Rooney & McCann 2012). Owing to difficulties in estimating diets of a speciose component of soil and moss food webs (oribatid mites, Appendix 4), describing food web structure has remained difficult. Here we have developed tools that can help estimate oribatid diets, thereby making in-depth studies of soil and moss food webs more feasible. We show that stable isotopes and cheliceral measurements can be used in conjunction or separately, to provide estimations of oribatid diets that likely to reflect diet under field conditions. Although isotope studies are feasible, they may prove too expensive and/or laborious to perform on a considerable proportion of the species present in a given system. Furthermore, precision in diet estimation through this method is negatively affected by the scarcity of information available on the trophic enrichment of carbon and nitrogen in these systems. The cheliceral measurement method described here is recommended for food web studies, as it is quick and inexpensive, requiring only three measures to be taken from the chelicera (moveable digit height and width, and fixed digit height) to allocate species to one of three categories: predator, primary decomposer and secondary decomposer.

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Appendices

- *Appendix 1 – Association between body length and cheliceral measurements*

Methods

Body size estimation methods are described in detail in Appendix 2. Body length was selected from these measures for comparison with the cheliceral measurements described in the body of the manuscript. Only Australian morphospecies were used in this analysis.

Results

No association was found between body length and leverage (Figure 2). Cross-sectional area increases with the logarithm of body length, but 63% of the variability in area is not explained by increases in body length.

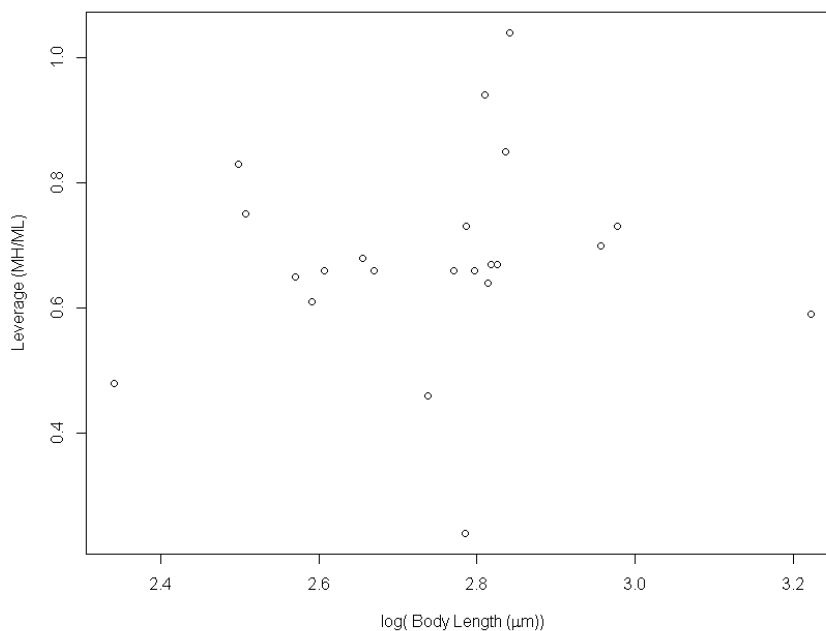


Figure 2. Relationship between moveable digit leverage and body length.

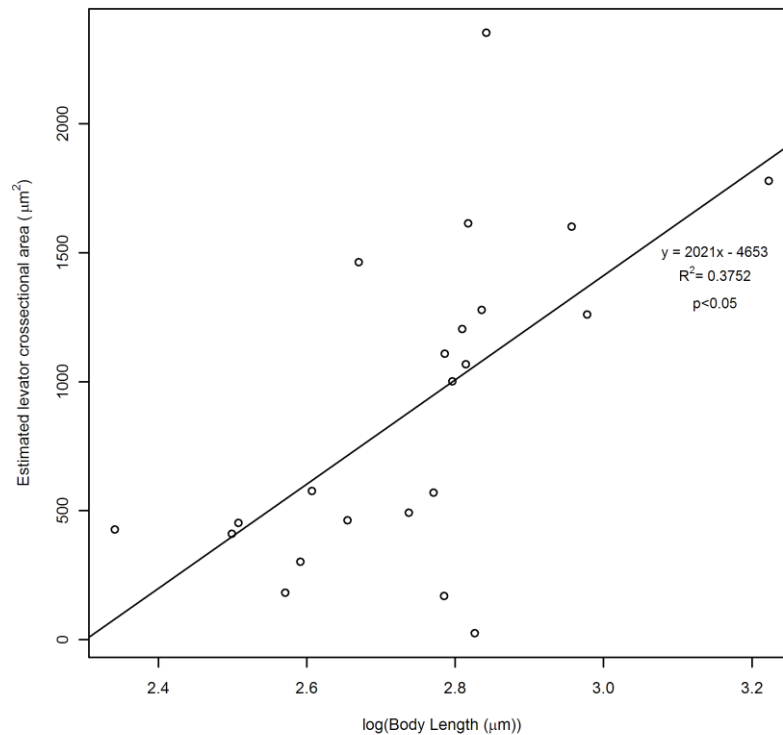


Figure 3. Relationship between estimated cross-sectional area of the levator muscle and body length.

- *Appendix 2 – Association between weight and body-size*

Methods

To evaluate the association between biomass and basic measures of size, 23 Australian mite morphospecies (18 oribatids, two prostigmatids and three mesostigmatids) were weighed using a Sartorius MC5 electronic microbalance after being air-dried for three minutes. One to seven individuals were used per weighing per species for accurate measurement. Measures of body size were taken from scanning electron micrographs of morphospecies of two to five individuals per morphospecies and the average of the

measurements was used for calculations. Ventral area was estimated by multiplying notogastral length by the maximum notogastral width. Volume was estimated by multiplying ventral area by maximum height. Body length was measured as the length of the opisthosoma for mesostigmatid and prostigmatid mites (section of the body containing all legs, excludes gnathosoma), and from the anterior-most point of the prodorsum to the posterior-most point of the notogaster in oribatids.

Results

Weight bears a close linear relationship with basic size measurements on logarithmic scales ($R^2 > 0.83$, $p < 0.05$ for all size estimates) (Figure 4). Incorporation of width and height into the estimates of size increases the amount of explained variability in weight.

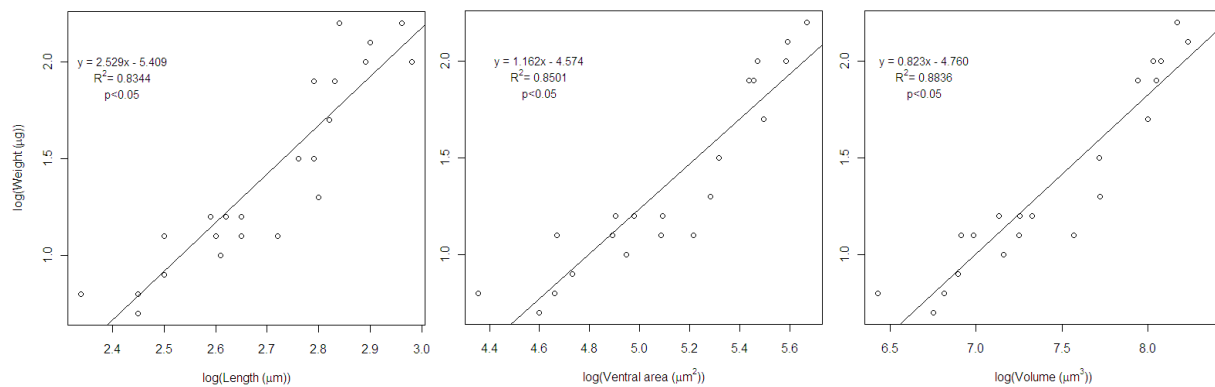


Figure 1. Relationship between weight mite morphospecies and basic measures of size.

- *Appendix 3 – Principal components analysis data*

Table 1. Construction of the principal components axes from cheliceral measurements. Loadings of the variables are shown for all five axes. The percentage variability explained by the axes is for 85, 10, 5, 0 and 0 for axes 1 to 5 respectively.

	PC1	PC2	PC3	PC4	PC5
Fixed digit length	-0.463	-0.132	-0.553	0.644	-0.218
Fixed digit height	-0.459	0.425	0.184	-0.317	-0.689
Movable digit length	-0.399	-0.81		-0.426	
Movable digit height	-0.454		0.719	0.408	0.329
Levator muscle area	-0.457	0.38	-0.376	-0.368	0.608

- Appendix 4 – Benefits and drawbacks of different methods of estimating mite diets

Table 1. Benefits and drawbacks of different methods of estimating mite diets.

Method	Benefits				Drawbacks		Studies using Oribatid taxa	Reviewed by
	Assesses preferences in the field	Assesses assimilation	Integrates across time	Others	Many individuals required	Others		
Food choice experimentation				Controlled conditions allow for direct experimentation and comparison of specific food items.		Experimental conditions may affect feeding behaviour. Not all food choices can be provided. Feeding may be difficult to quantify due to the size of the organisms.	Mitchell and Parkinson, 1976 Maraun <i>et al.</i> , 1998 Kaneko <i>et al.</i> , 1995 Hartenstein <i>et al.</i> , 1962 Schneider and Maraun, 2005 Jacot 1930, 1936, 1939 Riha 1951	-
Gut contents analysis	✓				✓	Ingested material may be difficult to identify. Identifiable material may represent the least digestible rather than the frequently digested.	Chamberlain <i>et al.</i> , 2006 Haubert <i>et al.</i> , 2009 Reuss <i>et al.</i> , 2005 Remén <i>et al.</i> , 2010 Forsslund 1938	-
Enzyme activity analysis	✓	✓			✓	Can require many individuals. Enzyme of the ingested organisms can be confused as enzymes used for digestion.	Siepel and De Ruiter-Dijkman, 1993 Luxton, 1972 & 1979 Zinkler, 1970	-
Fatty acid composition	✓	✓	✓		✓			Ruess and Chamberlain, 2010
Stable isotopes	✓	✓	✓		✓	Expensive. Cannot distinguish between foodsources with similar isotopic signatures. Precise food sources (e.g. specific fungi) cannot be identified. More details in Maraun et al 2011.	Schneider <i>et al.</i> , 2004 Pollierer <i>et al.</i> , 2009 Scheu and Falca, 2000 Erdmann <i>et al.</i> , 2007 Fischer <i>et al.</i> , 2010 Bokhorst <i>et al.</i> , 2007 This study	Maraun et al., 2011 Tiunov, 2007 Ponsard & Arditì, 2000
Cheliceral dimensions	✓	✓	✓	Inexpensive		Precise food sources (e.g. specific fungi) cannot be identified.	Kaneko, 1988 This study	-

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- *Appendix 5 – Oribatid families per feeding group*

Table 1. Oribatid families present in the four feeding groups studied.

	Family	Genus
Predator	Ooppiidae	<i>Lanceoppia</i>
	Hypochthoniidae	<i>Hypochthonius</i>
Primary decomposer	Tectocepheidae	<i>Tectocepheus</i>
	Malaconothridae	<i>Malaconothrus</i>
	Phthiracaridae	
	Oribatulidae	<i>Oribatula</i>
	Achipteriidae	<i>Achipteria</i>
	Nothridae	<i>Nothrus</i>
	Camisiidae	<i>Platynothrus</i>
	Astegistidae	<i>Cultroribatula</i>
Fungivore	Pelopiidae	<i>Pseudoceratoppia</i>
	Austrachipteridae	<i>Austrachipteria</i>
	Chamobatidae	<i>Chamobates</i>
	Damaeidae	
	Crotoniidae	<i>Crotonia</i>
Lichenivore	Austrachipteridae	<i>Austrachipteria</i>

Chapter 2: *food web*: an open-source program for the visualisation and analysis of compilations of complex food webs.

Abstract

Food webs represent the trophic interactions between consumers and resources as a ‘map’ of trophic links, and can meaningfully quantify ecological processes. As the study of food webs evolves so does the need for analytical software. Several programs for the analysis of food web structure exist. Researchers are likely to profit most from programs that calculate the largest number of commonly used parameters, produce output in standard food web ecology language, can be readily modified and updated by the scientific community, and can be used free of charge. Here we have developed a program for the analysis of food webs that calculates twelve commonly used basic measures of food web structure, employs food web language in the code and output, translates between a few common food web formats, can handle food webs consisting of multiple levels, and can automate the analysis for a large number of webs. The program produces 3 dimensional graphs of high-quality that can be rotated and enlarged as needed by the user. *food web* will be provided free of charge to the scientific community and will be embedded inside a commonly used statistical tool (R Statistical Package). The rationale for calculation of parameters and for producing the plots is provided here, along with the code for R.

Introduction

Food webs represent the trophic interactions between consumers and resources as a ‘map’ of trophic links. The first of these maps was described by Camerano (1880) followed by a detailed depiction of the food web of a North American lake (Forbes 1887). A number of descriptions of food webs followed from across terrestrial and aquatic ecosystems, including an early detailed food web from Bear Island (Summerhayes & Elton 1923), as well as more generalized diagrams of energy flow (Lindeman 1942). The development of food web research has been described in a number of reviews (Pimm *et al.* 1991; Dunne 2006). An initial emphasis on the stability of food webs (e.g. May 1972), was replaced by the search for general patterns of food web attributes (e.g. Pimm *et al.* 1991), and the environmental correlates of those attributes (e.g. Briand 1983). This led to the compilation of the first food web databases (Cohen 1989), growing to a recent update including over 200 published food webs (Cohen 2010). The variable quality of early data led to considerable criticism of food web ecology (Paine 1988a; Strong 1988; Polis 1991), and an ongoing effort to describe food webs which were taxonomically detailed, inclusive of all groups, and took a rigorous approach to detecting trophic links (Dunne 2006).

Topological maps of feeding interactions in food webs have been widely criticized due to their low levels of taxonomic resolution and the lack of standard criteria for collection, description and attribution of trophic links (e.g. Paine 1988b; Cohen *et al.* 1993). Those criticisms are valid, and caution must be applied in interpreting patterns observed in topological food webs. However studies using well resolved food webs have shown that they can meaningfully quantify ecological processes such as invasion, and changes in productivity and disturbance (Hall & Raffaelli 1991; Martinez 1991; Woodward & Hildrew 2001;

Thompson & Townsend 2005). Other studies have shown a relatively high tolerance to the abstraction of food webs even into relatively simple binary matrices (Dunne 2006). Food webs provide additional information that supplements information on patterns of biodiversity, and represents a simple approach, albeit an imperfect one, to integrating fluxes of energy with information on species richness.

A suite of food web attributes have emerged and become well established in the literature and have clear biological interpretations (Table 1). These include: measures of diversity overall and in different functional or trophic groups, measures of density of trophic links (connectance, linkage density), measures of web shape (prey:predator ratios) and vertical dimensions (chain length). More recently other network attributes have been applied to the analysis of food webs (e.g. Chen *et al.* 2008), although their relationship to biological parameters is yet to be well established.

As the study of food webs evolves so does the need for analytical software. A number of programs are available for the calculation of food web attributes, each with relative strengths and weaknesses (Table 2). Researchers are likely to profit most from programs that calculate the largest number of commonly used parameters, produce output in standard food web ecology language, produce useful graphs, can be readily modified and updated by the scientific community, and can be used free of charge. This combination of traits is not currently available in the analytical software we have surveyed.

Table 1. Food web attributes and their biological meaning.

Food web attribute	Biological meaning
Taxa richness (S)	Number of biological taxa (nodes) in the food web (Hall & Raffaelli 1993)
Number of trophic links (L)	Number of links (edges) between taxa (Hall & Raffaelli 1993)
Link density (=L/S)	Number of links per taxa measure of dietary specialisation across the food web (Hall & Raffaelli 1993) (Hall & Raffaelli 1993)
Connectance (C) (= L/(S ²))	Proportion of potential trophic links that do occur. An indication of degree of inter-connectivity in a food web, typically 0.05-0.15 (Hall & Raffaelli 1993)
Number of omnivores	Number of species that feed on more than one trophic level (Hall & Raffaelli 1993)
Mean chain length	Average number of links found in a food chain across a food web. Food chains lengthen with higher energy supply (Hall & Raffaelli 1993)
Maximum chain length	The maximum number of links found in any food chain in a food web. Food chains lengthen with higher energy supply (Hall & Raffaelli 1993)
Number of basal taxa (b)	The number of taxa which do not consume any other taxa (Hall & Raffaelli 1993)
Number of intermediate taxa (i)	The number of taxa which are both consumed by, and consume, other taxa (Hall & Raffaelli 1993)
Number of top taxa (t)	The number of taxa which are not consumed by any other taxa (Hall & Raffaelli 1993)
Prey:predator (= b+i/t+i)	A measure of food web 'shape' high values are more triangular, low values are more 'square in shape (Hall & Raffaelli 1991)

Table 2. Food web analysis tools: capabilities and limitations.

	License required	Translates formats	Point-&-click interface	3D imaging capabilities	Multiple trophic levels	Food web specific	Open-source code	All indices in Table 1 calculated	Automated reading
Pajek		√	√		√				
UCINET	√		√		√				
Bipartite						√	√		
Network 3D	√		√	√	√	√		√	
NetIndices					√	√	√		
<i>food web</i>		√		√	√	√	√		√

The food web package for R: description of the analytical approach

The *food web* package for R Statistical Software was created for the three dimensional representation of trophic links in complex food webs, and for the calculation of frequently used parameters of network structure from a large number of food webs. The program performs calculations on symmetrical binary, predator-prey matrices. In these matrices, all species present in the food web must be represented, including basal resources. The values along the column of a given species represent the presence (value = 1) or absence (value = 0) of a feeding link. The program was created in modules encompassing the different steps required to produce the final output. Details of the input and output of each module are shown in Table 3.

food web can run iteratively through the network calculations for many food webs, and add the output as rows to a single, comma delimited file (.csv). It can also be used on single food webs. Most of the complex calculations are performed by the module “Trophic levels” (details below). The module “Metrics” calculates additional basic measurements and adds the complete set (i.e. those of “Trophic levels” and those of “Metrics”), to the .csv file. If the iterative process is used, the row corresponding to a food web will be labeled in the .csv file with the name of the *food web*’s input file. The workflow of the *food web* package from the input file to the output file can be seen in Figure 1.

- *Asymmetrical predator-prey matrices*

To accommodate for asymmetrical predator-prey matrices, the module “Asym to sym” was written. It detects whether all species in the rows are present in the columns and adds all-zero columns to the end of the matrix for species that are not represented. Each column label corresponds to the species name. It then performs the equivalent process for

rows, i.e., detects whether species in the columns are absent from the rows and adds an all-zero row for the missing species. Finally, the matrix is ordered such that column 1 represents the same species as row 1.

Table 3. Inputs and outputs of the food web package.

Module	Input	Output
Trophic levels.R	Binary, symmetrical predator-prey matrix	Total number of species Connectance Trophic level of each species Prey averaged trophic position for omnivores Fraction herbivory Fraction omnivory Fraction top predator Fraction basal species Predator:prey ratio Number of trophic levels <i>Species lists</i> Trophic positions from which each omnivore species feeds Intraguild predators
Plot network.R	Output from "Trophic levels.R" module. Colours to be used in the plot Radius of the trophic level circles	Three dimensional, coloured network representing trophic links among all species in the food web.
Asym to sym. R	Folder in which the files are located Asymmetrical, binary predator-prey matrix	Symmetrical, predator-prey matrix of the kind used by "Trophic levels.R"
List to sym. R	Asymmetrical binary predator-prey matrices Species richness per guild	Binary, symmetrical predator-prey matrices
Matrix to string.R	Binary predator-prey matrix	String format foodweb (i.e. species links list) .csv file containing all parameters calculated for read networks
Metrics.R	Folder in which results file should be created Data generated by "Trophic levels. R"	List of badly formatted files
Food web central. R	Range of values in the names of the food web files.	Excel spreadsheet as generated by Metrics.R

Preparatory work



Calculations

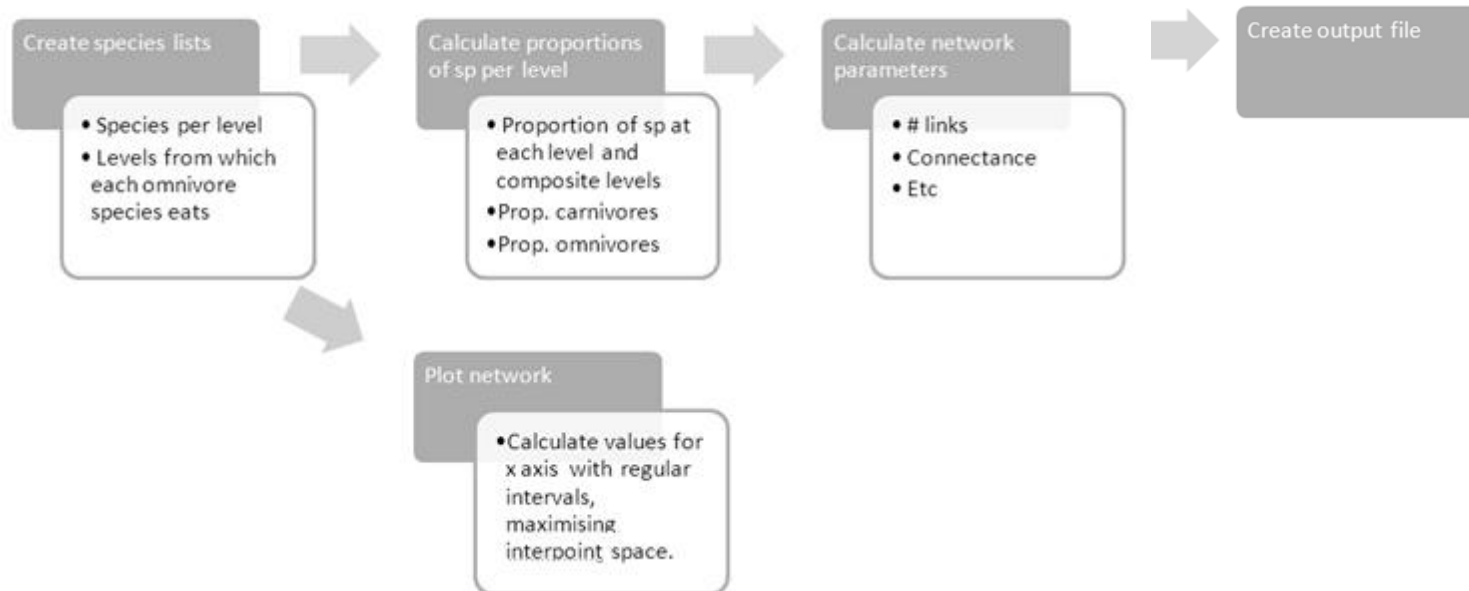


Figure 1. Workflow for the *foodweb* package.

- *Richness per guild lists*

For food webs in which only species richness per guild is known (such as chapters 2 and 5), the program can generate a symmetrical binary predator-prey matrix. Currently this is functional only for the case of the food webs in chapter 2 and 5 but will be made generalisable. The module that performs this is the List to sym.R module.

- *Matrix format to string format translation*

Some network analysis software (e.g. Pajek (Batagelj & Mrvar 1998)) require input files in the form of a list of the links between pairs of species. The module “Matrix to string.R” can be used to convert symmetrical binary matrices into such lists.

- *Trophic levels module*

Trophic levels

We denote as trophic level of a species an integer that reflects the distance of that species to the basal resource; consumption of a resource separates the consumer from the resource by one unit (Thompson *et al.* 2007). Trophic levels of species are stored in a row at the bottom of the food web matrix that has been imported. The assignment of trophic levels from a binary matrix proceeds as follows. Trophic level zero is assigned to basal species, that is, any species that does not consume any other species (i.e. has an all-zero column). After this, an iterative process begins, where any species that consumes level zero species is assigned to level one. Then, any species consuming species on level one is assigned the level two, and so on up the food chain. Once the iterative process finishes, a species will have been assigned a trophic level that is one above the highest level of any of the species that it consumes. A maximum of eight levels are considered possible in this iterative process in

order to enhance performance. This can be changed if needed but none of the food webs considered in this study exceeded that number of trophic levels (see chapter 3).

The number of trophic levels in the food web is calculated as the number of distinct elements in the row containing the trophic levels of the species. This output is used by the network plotting module.

Omnivory and trophic position

For species that feed on different trophic levels (omnivores), trophic position is calculated. Trophic level equals one plus the level of the consumed species that is highest on the food chain, whereas the trophic position reflects the average of the levels of all the consumed species. Calculation of the trophic position is done by creating a duplicate of the original food web matrix, called “by.levels”, where the trophic level of the prey is represented. The trophic position of an omnivorous species is then recorded as the average of the values in its column. This calculation is the equivalent of the ‘prey-averaged’ technique of (Williams & Martinez 2004). An omnivore is therefore defined after Thompson *et al.* (2007) as any species with a non-integer trophic position. Trophic position is stored in a second, additional row in the original food web matrix. A table showing each omnivorous species in the food web as well as the species it feeds on is created at this point and the number of rows in this table is taken as the number of omnivores in the food web. This table can be used to verify that the calculations are being made correctly.

Intraguild predation

Intraguild predation is detected when a species consumes species at its same trophic level. This is recorded in a third additional row to the imported food web. The number of species that engage in intraguild predation is calculated. A table specifying the trophic

position at which intraguild predation occurs is generated, and can be used to verify that the calculations are being made correctly.

Fraction of basal, herbivorous, intermediate and top species

Fractions are calculated relative to the total number of species in the food web. Basal species are those in level zero; herbivorous: those at level 1, top: those at the highest level (i.e. taxa which are not consumed by any other taxa included in the food web), intermediate: those that are neither basal nor top (after Pimm 1982).

Connectance, linkage density and predator:prey ratios

Total number of links is calculated as the sum of all cells in the original food web matrix. Connectance (Pimm 1982) is that number divided by the square of the total number of species. The calculation used here takes the number of links found to occur as a proportion of all links, assuming that all taxa can feed on all other taxa. As such it differs from the calculation used by Jaarsma *et al.* (1998) which modifies the connectance formula to ignore links which are considered impossible (e.g. basal taxa such as plants feeding on predators). Linkage density (Pimm 1982) is calculated by dividing the total number of links by the number of species. The predator prey ratio (Hall & Raffaelli 1991) is calculated by dividing the total number of species that are either intermediate or basal by the total number that are either basal or intermediate.

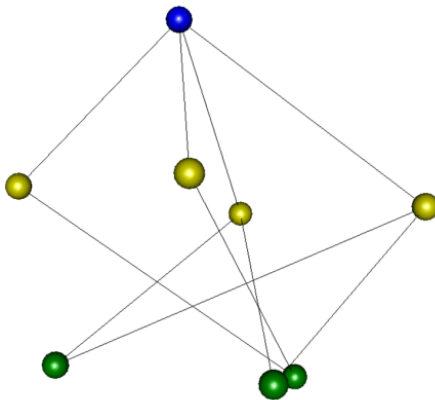
- *Network plot*

The position on the y axis is taken from the trophic level of the species. Positions on the x and z axis are calculated such that spheres are equally spaced along a circumference of radius r , which is to be specified by the user. Equal spacing is created by dividing the circle into as many sections as there are species in the level. This is achieved by dividing the

degrees spanned within the circumference (i.e. 360°) by the number of species in the trophic level (resulting angle is shown in Figure 2 as α). The coordinates of a point on the circumference are calculated on the basis of the radius of the circumference and the internal angle ($360^\circ/n$) created by the sectioning of the circle (Figure 2).

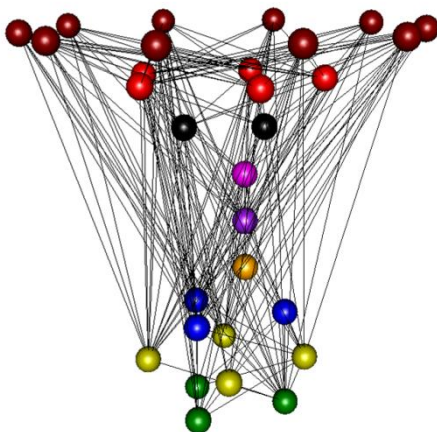
Examples of analysed food webs

- *Example 1: simple food web from Menge and Sutherland (1976)*



Richness	8
Number of links	10
Connectance	0.16
Link density	1.25
N° trophic positions	3
Fraction of omnivores	0.00
Fraction of basal species	0.38
Fraction of intermediate species	0.50
Fraction of top species	0.13
Fraction of herbivorous species	0.50
Prey to predator ratio	1.40

- *Example 2: complex food web from Polis (1991)*



Richness	37
Number of links	216
Connectance	0.16
Link density	5.84
N° trophic positions	9
Fraction of omnivores	0.62
Fraction of basal species	0.24
Fraction of intermediate species	0.73
Fraction of top species	0.03
Fraction of herbivorous species	0.11
Prey to predator ratio	1.29

The food web matrices used to analyse the examples above were obtained from the GlobalWeb food web repository (Thompson, unpublished).

Conclusion

We have produced an analytical tool that facilitates the analysis of large numbers of food webs and produces high quality, customizable 3d graphs. Twelve commonly-used metrics of food web structure can be calculated but others, such as those relating to food chain length, are currently being developed. The strength of this program lies not only in its current capabilities but also in the open-source nature of the code and the imbedding of it inside a commonly used, powerful community-built statistical tool (R Statistical Package).

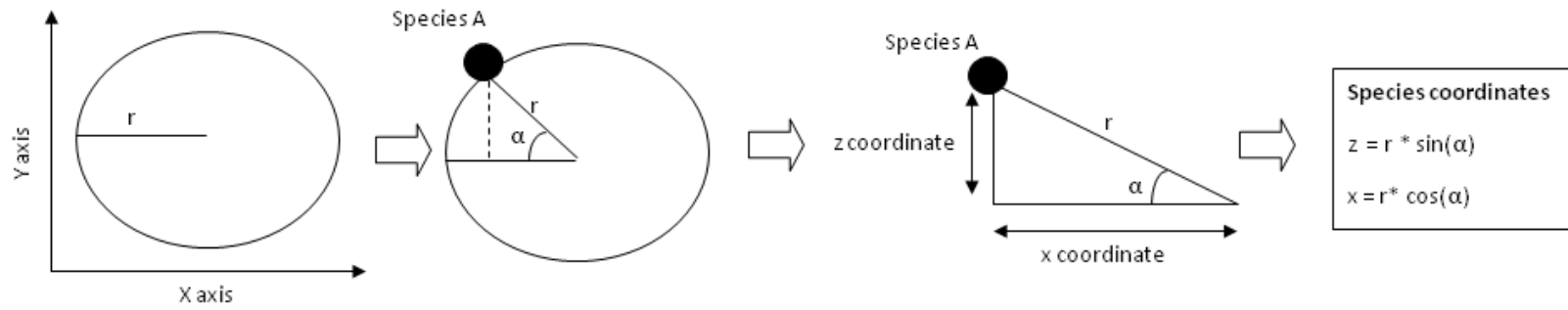


Figure 2. Calculation of the coordinates of a species along the x and z axes.

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Appendix – Food web package scripts

The code presented here was written for R Statistical Software. For information on how the code was developed and how it can be used to analyse food webs, refer to Chapter 2. Syntax highlighting is used below for ease of reading. Green text is explanatory text, it does not affect the running of the code. Commands are highlighted in blue, numbers in red, strings in grey.

- *Foodweb central. R*

```
# For reading and analysing multiple files in GlobalWeb
for (i in 1:213) {
  setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Scripts/Supermodel")
  source("Asym to Sym.R")
}
```

```

    setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Scripts/Supermodel")
    source("Trophic levels.R")
    setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Scripts/Supermodel")
    source("Metrics.R")
    rm(list = ls(all = TRUE))
}

# For reading and analysing from richness per guild lists
setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Main experiment/Food web")
vect <- read.table('samples.csv', header=T, sep=',', row.names=1,
colClasses=numeric())

for (patch in row.names(vect)) {
  name=patch
  setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Main experiment/Food web/Binary matrices")
  foodweb <- read.table(paste(patch, ".csv", sep=""), header=FALSE,
sep=',', colClasses=numeric())
  setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Scripts/Supermodel")
  source("Trophic levels.R")
  setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Scripts/Supermodel")
  source("Metrics.R")
  #rm(list = ls(all = TRUE))
}

```

- *Trophic levels. R*

```

S <- ncol(foodweb)

#Set level=0 for all resources
for (sp in 1:S) {
  if (sum(foodweb[1:S, sp])==0) {
    foodweb[S+1, sp] <- 0
  }
}

#Assign integer trophic levels
for (level in 1:8) { #for each trophic level above basal
resource, stopping at 4
  for (sp in 1:S) { #for each species
    #check if it eats any of the species one level
below it
    for (resource in which(foodweb[S+1,]==level-1)) {
      if (foodweb[resource, sp]==1 &
foodweb[sp,resource]==0) { # if it does,
        foodweb[S+1,sp] <- as.numeric(level)
#assign the current level
        break
      }
    }
  }
}
}

```

```

#Omnivory
## Create a matrix where the trophic _level_ of the prey is
represented
## i.e. multiply each column by a vector with the trophic _level_
of each species
## note: in order to differentiate between "feeds on level zero"
and "doesn't feed on this species"
## I multiply by (trophic level + 1), turn remaining zeros into NA,
then subtract 1
by.level <- sweep(foodweb[1:S,], MARGIN=1,
as.vector((foodweb[S+1,]+1), mode="numeric"), FUN="*")
is.na(by.level[by.level==0]) <- TRUE #sets all values that are
zero to NA
by.level <- sweep(by.level[1:S,], MARGIN=1, 1, FUN="-")
#subtracts one in order to get back the original level

#Record trophic position in row S+2
for (sp in 1:S) {
  if (sum(foodweb[1:S,sp])==0) {
    foodweb[S+2,sp] <- 0
  } else {
    foodweb[S+2,sp] <- (sum(by.level[,sp],
na.rm=TRUE)/sum(foodweb[1:S,sp]))+1
  }
}

## Create a table specifying the species at each trophic position
levels.l <- data.frame(TrophicLevel = character(0), S=integer(0),
sp= character(0))
for (level in unique(t((foodweb[S+2,]))) {
  levels.l <- rbind(levels.l, cbind(level,
length(which(foodweb[S+2,]==level)), paste(which(foodweb[S+2,]==level),
collapse=",")))
}
names(levels.l) <- c("Trophic position", "S", "Species")

## Create a table specifying which trophic position each species
feeds on
#Create a matrix where the trophic _positon_ of the prey is
represented
# i.e. multiply each column by a vector with the trophic position
of each species
by.position <- sweep(foodweb[1:S,], MARGIN=1,
as.vector((foodweb[S+2,]+1), mode="numeric"), FUN="*")
is.na(by.position[by.position==0]) <- TRUE #sets all values
that are zero to NA
by.position <- sweep(by.position[1:S,], MARGIN=1, 1, FUN="-")
#subtracts one in order to get back the original level

omn.l <- data.frame(Predator=integer(0), PredTrophPos=integer(0),
Prey=integer(0))
for (sp in which(foodweb[S+1,]!=foodweb[S+2,])) {
  omn.l <- rbind(omn.l, cbind(sp,
formatC(foodweb[S+2,sp],digits=2, format="f", drop0trailing=TRUE) ,
paste(formatC(as.numeric(na.omit(unique(by.position[,sp])), digits=2,
format="f", drop0trailing=TRUE), collapse=",")))

```

```

    }
    names(omn.l) <- c("Species", "Trophic position", "Prey(s) '
position")
    omn <- nrow(omn.l)

    ## Intraguild predation
    # Tag carnivorous species by placing a 1 in row S+3

    for (sp in 1:S) {
      if (sum(foodweb[(which(foodweb[S+1,-
(sp)]==foodweb[S+1,sp])),sp])>0) {
        foodweb[S+3,sp] <- 1
      } else {foodweb[S+3,sp] <- 0}
    }

    crnv <- sum(foodweb[S+3,])

    temp <- sweep(foodweb[S+3,], MARGIN=2, as.vector((foodweb[S+2,]),
mode="numeric"), FUN="*")
    is.na(temp[temp==0]) <- TRUE #sets all values that are zero to NA
    foodweb[S+3,] <- temp

    #Create a table specifying the trophic position at which intraguild
    predation occurs

    crnv.l <- data.frame(TrophicPosition = character(0),
S.carn=integer(0), sp= character(0))
    for (level in na.omit(unique(t((foodweb[S+3,]))))) {
      if (level != 0) {
        crnv.l <- rbind(crnv.l, cbind(level,
length(which(foodweb[S+3,]==level)), paste(which(foodweb[S+3,]==level),
collapse=", ")))
      }
    }
    names(crnv.l) <- c("Trophic position", "# carnivorous sp.",
"Carnivorous species")

    #Fractions of species

    # Number of basal species
    Basal = sum(colSums(foodweb[1:S,])==0)

    # Number of top species
    Top = length(which(foodweb[S+1,]==max(foodweb[S+1,])))
    Top.l = which(foodweb[S+1,]==max(foodweb[S+1,]))

    # Number of intermediate species
    Int = S - Basal - Top

    # Number of herbivores
    Herb = length(which(foodweb[S+1,]==1))

    • Metrics.R

    ## Total number of links
    L <- sum(foodweb[1:S,])

    ## Connectance

```



```

C <- L/(S^2)

## Average number of links ("linkage density")
AL = L/S

## Put indices in a vector

indices <- vector(length=12)
indices <- cbind(name,S, L, C, AL, omn/S, crnv/S,
length(unique(as.numeric(foodweb[S+1,]))),
Basal/S, Int/S, Top/S,
Herb/S, (Basal+Int)/(Top+Int))
colnames(indices) <- c("Web ID", "Species richness", "Total # Links",
"Connectance", "Link density", "Frac omniv", "Frac carniv",
"Total # trophic positions", "Frac basal",
"Frac intermediate", "Frac top", "Frac herbiv", "Prey:Predator")

setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Seasons")
write.table(indices, file = "First.csv", append=TRUE, quote=FALSE,
sep=",", col.names=TRUE, row.names=FALSE)

```

- *Plot network.R*

```

# Transfore 360 degrees into radians
deg <- 360*pi/180

#Create a matrix to store coordinates of the points and their colour
net.plot <- matrix(nrow= S, ncol=4)
colnames(net.plot) <- c("x", "y", "z", "colour")
net.plot[,2] <- t(foodweb[S+1,])

colour.code <- cbind("green4", "yellow3", "blue", "orange", "purple")
colnames(colour.code) <- unique(t((foodweb[S+1,])))
radius.code <- cbind(4,4,4,6,4)
colnames(radius.code) <- unique(t((foodweb[S+1,])))

for (level in unique(t((foodweb[S+1,]))) {
  n <- length(which(net.plot[,2]==level))
  r <- radius.code[which(colnames(radius.code)==level)]
  x <-as.vector(r*(cos(seq(0, deg, len = n+1))))
  net.plot[which(net.plot[,2]==level),1] <- x[-(length(x))]
  z <-as.vector(r*(sin(seq(0, deg, len = n+1))))
  net.plot[which(net.plot[,2]==level),3] <- z[-(length(z))]
  net.plot[which(net.plot[,2]==level),4] <-
colour.code[which(colnames(colour.code)==level)]
}

plot3d(net.plot[,1],net.plot[,3], net.plot[,2], type="s",
col=net.plot[,4], size=2, box=FALSE, axes=FALSE, xlab="", ylab="", zlab="",
aspect=TRUE, top=TRUE)

for (sp in 1:S) {
  for (prey in intersect(which(foodweb[1:S,sp]==1),
which(foodweb[S+1,]!=foodweb[S+1,sp]))) {

```

```

        lines3d(c(net.plot[sp,1],net.plot[prey,1]),
c(net.plot[sp,3],net.plot[prey,3]), c(net.plot[sp,2],net.plot[prey,2]),
cex=0.1)
    }
}

```

- *Asym to sym.R*

```

#Import the foodweb
setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Supermodel/R Thompson GlobalWeb/Food Web Matrices/")
foodweb <- read.table(paste("WEB", i, ".DAT", sep=""), header=F)
name=paste("WEB", i, ".DAT", sep=")

# Add adequate row and column names & record ID of the foodweb
non.basal.sp <- ncol(foodweb)
foodweb[1,1] <- 9999
colnames(foodweb) <- foodweb[1,]

#find species mentioned in rows that don't have a corresponding
column
row.names(foodweb) <- foodweb[,1]
no.col <- as.vector(setdiff(row.names(foodweb), colnames(foodweb)))
#no.col <- no.col[no.col!=9999]

#Add the column with all zeros and the corresponding species number
for (i in no.col) {
    foodweb <- cbind(foodweb, as.numeric(c(i,rep(0,
times=nrow(foodweb)-1))))
    colnames(foodweb)[(which(no.col==i) + non.basal.sp)] <- i
}

#find species mentioned in columns that don't have a corresponding
row
no.row <- as.vector(setdiff(colnames(foodweb), row.names(foodweb)))

#Add the row with all zeros and the corresponding species number
for (i in no.row) {
    foodweb <- rbind(foodweb, as.numeric(c(i,rep(0,
times=ncol(foodweb)-1))))
    row.names(foodweb)[nrow(foodweb)] <- i
}

foodweb <- foodweb[-(1),-(1)]
foodweb <- foodweb[,order(as.numeric(colnames(foodweb)))]
foodweb <- foodweb[order(as.numeric(row.names(foodweb))),]

if(any(foodweb[,] < 0)) {
    setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Supermodel/GlobalWeb Analysis")
    write.table(name, file = "Problem.csv", append=TRUE, quote=FALSE,
sep="," , col.names=FALSE, row.names=FALSE)
    next
}

```

- *Matrix to string.R*

```

setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Main experiment/Community")

matrix <- read.table('Testing.csv', header=T, sep=',')

S = nrow(matrix)
foodweb <- rbind("Foodweb")
link = ""
for (PredatorID in 1:S) {
  for (PreyID in 1:S) {
    if (matrix[PreyID, PredatorID] == "1"){
      link = paste(PredatorID, PreyID)
      foodweb <- rbind(foodweb, link)
    }
  }
}

write(foodweb[2:nrow(foodweb),], file = "foodweb.csv", append=FALSE)

```

- *Food chains.R – work in progress*

```

setwd("C:/Documents and Settings/perdomo.MONASH/My Documents/R/Data
entry/Supermodel")
foodweb <- read.table('Foodwebmatrix-19-09-11.csv', header=F,
sep=',', colClasses=numeric())
S <- ncol(foodweb)

## Strategy: create a matrix that reflects the number of paths of
each species to the
## basal resource. There are direct paths (flowing from level to
level, stored in row one of fcn.l) and indirect paths.
## Indirect paths occur through carnivory within trophic groups
(stored in row 2)
## And through trophic queue jumping (stored in row 3)
## The sum of all possible paths to the basal resource from the
species that are not predated
## upon is the number of food chains in the food web.

#Step 1 - direct paths # Find number of direct paths (paths that go
from a level to the one directly below it)
# For a given consumer species (column):
# Find only those prey species (rows) where the trophic level (stored
in row S+1 of the prey's column) is level directly below the one being
considered by the loop
# Find the number of paths each of the prey species have to the basal
source
# Set the number of paths of a consumer species as the sum of the
paths of its preys

# Create a vector of S positions, all zeros.
paths.l <- vector(length=S)

```

```

paths.l[1:S] <- 0

# Set the value in paths.l for basal resources to 1 (relevant for the
procedure below)
paths.l[which(foodweb[S+1,]==0)] <- 1

# add the numer of chains of the prey present in the previous level
# for calculation purposes, exclude paths created via carnivory
(hence the need for exclude.carniv vector below)

trophic.levels <- unique(t(foodweb[S+1, ]))
exclude.carniv <- vector(length=S)

for (level in trophic.levels[-(1),]) { #in each trophic level
except the basal one
  #potential.prey <- which(foodweb[S+1,]==level-1)
  exclude.carniv[1:S] <- 1
  exclude.carniv[which(foodweb[S+1,]==level)] <- 0
  for (sp in which(foodweb[S+1,]== level)){ #and each species in
the level
    #multiply the paths.l vector by the consumer species
column
    #add the values in the resulting vector
paths.l[sp] <- sum(foodweb[1:S,sp] * paths.l *
exclude.carniv)
    #set carnivores to zero?
    #Set the number of chains of the species as the sum of
the chains of its preys
  }
}

fcn.l <- matrix(nrow=3, ncol=S)
fcn.l[1,] <- paths.l
#Step 2 - indirect paths#
# Carnivory # Find the number of chains occurring
through carnivory

include.carniv <- vector(length=S)
level=1
length(which(foodweb[S+1,]== level))

for (level in trophic.levels[-(1),]) { #in each trophic level
except the basal one
  #potential.prey <- which(foodweb[S+1,]==level-1)
  include.carniv[1:S] <- 0 # set all values to zero
  include.carniv[which(foodweb[S+1,]==level)] <- 1 #set values
for the species in the level to 1
  for (sp in which(foodweb[S+1,]== level)){ #and each species
in the level
    include.carniv[which(foodweb[S+1,]==level)] <- 1
    include.carniv[sp] <- 0
    #multiply the paths.l vector by the consumer species
column
    #add the values in the resulting vector
fcn.l[2,sp] <- sum(foodweb[1:S,sp] * paths.l *
include.carniv) #- paths.l[sp]
    #set carnivores to zero?
    #Set the number of chains of the species as the sum of
the chains of its preys

```

```

    }
  }

  fcn.l[2,which(foodweb[S+1,]==0)] <- 0

  # Queue jumping # Find the number of queue-jumping paths (i.e paths
  created by trophic queue-jumpers)
  for (level in trophic.levels[-(1:2)]) { #in each trophic level
  except basal and herbivore
    exclude.carniv[1:S] <- 1
    exclude.carniv[which(foodweb[S+1,]==level)] <- 0
    for (sp in which(foodweb[S+1,]!=foodweb[S+2,] &
  foodweb[S+1,]==level)){ #and omnivorous species in that level
      fcn.l[3,sp] <- sum(foodweb[1:S,sp]*(fcn.l[2,]+fcn.l[1,])*
  exclude.carniv)
      # set its number of indirect paths as second row of values
  to the sum of the links of its prey it jumped to
    }
  }

  final.count <- sum(tcn.l[which(rowSums(foodweb[1:S,])==0)])

```

- *List to sym.R*

```

setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Seasons")
vect <- read.table('Food web for network - 08-11-11.csv', header=T,
sep=',', row.names=1, colClasses=numeric())

for (patch in row.names(vect)) {
  resources=4
  S=sum(vect[patch,])
  foodweb <- matrix(nrow=S+resources+1, ncol=S+resources)
  foodweb[,1:4] <- 0 #set cells of basal resources to zero
  foodweb[1,] <- c("moss", "litter", "lichen", "fungi",
    rep("Detritivore",
times=vect[patch,"Detritivore"]),
    rep("Fungivore", times=vect[patch,"Fungivore"]),
    rep("Lichenivore",
times=vect[patch,"Lichenivore"]),
    rep("Predator", times=vect[patch,"Predator"]),
    rep("Herbivore", times=vect[patch,"Herbivore"])
  )
  foodweb[2:3,4] <- 1 # set trophic link between fungi and its
  'prey', i.e. moss and litter

  #create a matrix with the vectors corresponding to each guild
  vectors <- matrix(nrow=S+resources, ncol=length(colnames(vect)))
  colnames(vectors) <- colnames(vect)
  vectors[,which(colnames(vectors)== "Detritivore")] <- c(0,1,0,0,
  rep(0, S)) #create a vector for column of detritivores
  vectors[,which(colnames(vectors)== "Lichenivore")] <- c(0,0,1,0,
  rep(0, S)) #create a vector for column of detritivores
  vectors[,which(colnames(vectors)== "Fungivore")] <- c(0,0,0,1,
  rep(0, S)) #create a vector for column of detritivores

```

```

    vectors[,which(colnames(vectors)== "Herbivore")] <- c(1,0,0,0,
rep(0, S)) #create a vector for column of detritivores
    vectors[,which(colnames(vectors)== "Predator")] <- c(0,0,0,0,
rep(1, times=sum(vect[patch,])))

    #Populate binary foodweb matrix
    for (guild in colnames(vect)) {
      for (sp in 1:(S+resources)) {
        if (foodweb[1,sp]==guild) {
          foodweb[2:nrow(foodweb),sp] <-
vectors[,which(colnames(vectors)==guild)]
        }
      }
    }
    foodweb <- foodweb[-(1),]

    setwd("C:/Documents and Settings/perdomo.MONASH/My
Documents/Results/Seasons/Binary matrices")
    write.table(foodweb, file = paste(patch, "08-11-11.csv", sep=""),
append=FALSE, quote=FALSE, sep="," , col.names=FALSE, row.names=FALSE)

}

```

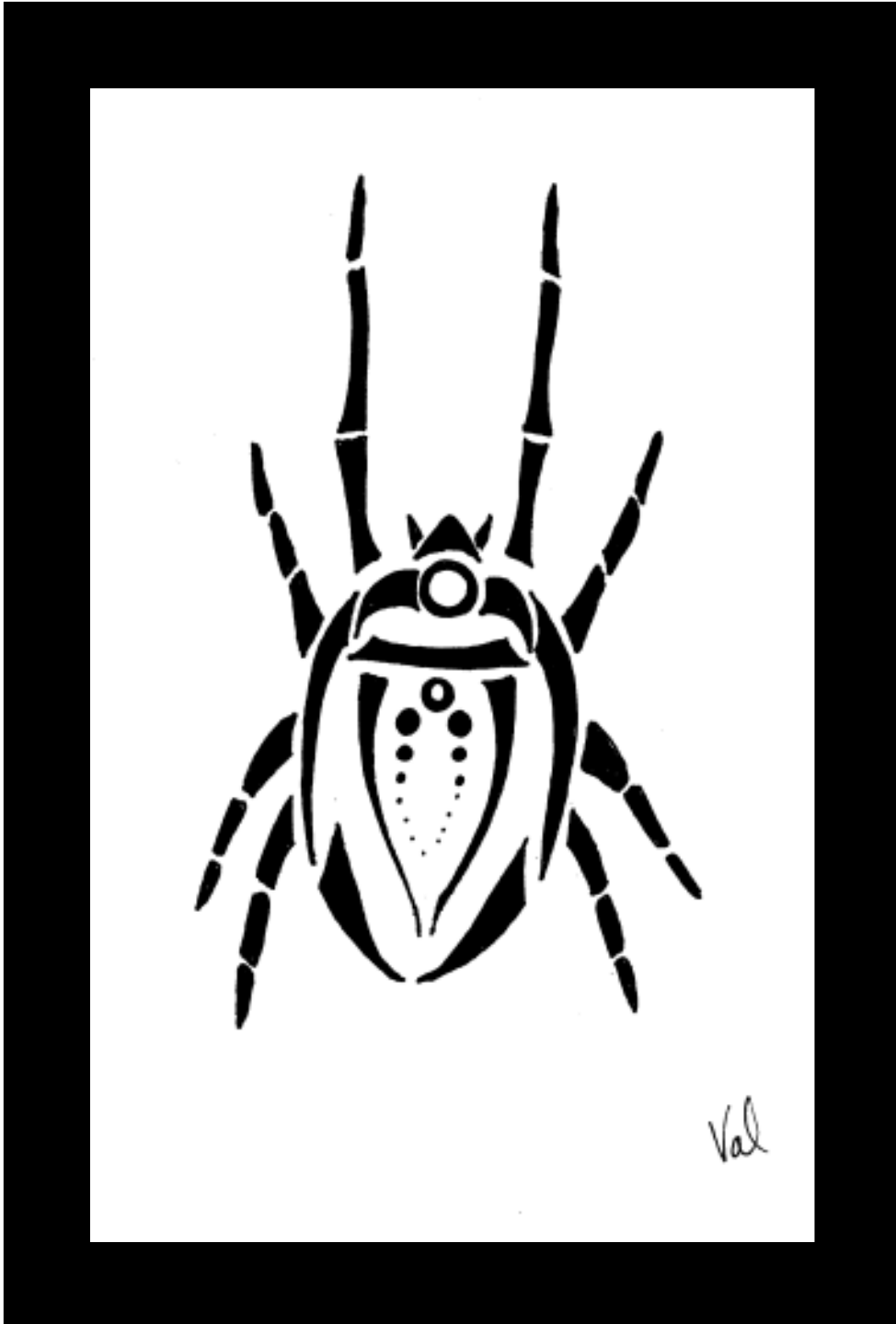
“It is clearly necessary to have a list of the animals in different habitats before one can proceed to study the more intricate problems of animal communities”

John Elton, 1927

“So many mites, so little time”

Barry O’Connor, 2011

Curator - Museum of Zoology - University of Michigan



Chapter 3: Assembling the toolbox to study the moss-microarthropod food web

Abstract

Mosses are key ecological players in many ecosystems, and the microecosystem they form is considered to hold high potential as a model system through which to test theoretical and applied questions in ecology. The study of the communities that inhabit mosses poses significant challenges to researchers, owing to the small size of the fauna and its considerable diversity. It is therefore not surprising that basic data on the structure of the food web and its variability in time is scarce. In this study we aim to; (a) expand the knowledge base and the tools available for the study of moss micro-arthropods, (b) describe the structure of moss micro-arthropod food webs, and (c) present preliminary data on temporal variability in community and food web structure in this model system. We present results of moss microarthropod surveys conducted during summer and winter in an Australian temperate rainforest. We describe taxonomic composition of moss communities and develop tools to record, store, manage and share these data efficiently. Higher densities of microarthropods were found in winter than summer, but there were no differences in species richness. Marked differences in the community structure were driven by changes in species identity as well as abundance. We present abundance, richness and biomass per guild of a moss food web consisting of the following functional feeding groups: herbivores, fungivores, detritivores, lichenivores and predators.. Biomass, abundance and richness of detritivores was higher in summer than winter, and the opposite was true of fungivores. We suggest that these changes may be driven by resource availability. This body of work contributes to the study of moss microarthropod communities and to their development as model systems.

Introduction

Moss-microarthropod systems have been championed as critical components of biodiversity as well as model systems to understand global change processes (Lindo & Gonzalez 2010). However a number of basic, key questions about moss food webs remain outstanding. What does the food web look like? How does it vary temporally? This information is needed to allow comparison of results among moss studies, and for the translation of their results into the broader context of food web ecology. A recent review of what is known of the moss food web draws nearly all of its information from studies of soil communities (Lindo & Gonzalez 2010). This emphasis reflects the scarcity of information on moss food webs, but nonetheless resource availability and microhabitat characteristics may differ between soils and mosses (Kausrud *et al.* 2008; Salmane & Brumelis 2008).. Thus more work on moss microarthropod community ecology is needed to gain a clearer understanding of the natural history of this system so that it can be effectively applied in an experimental context.

The most current representation of the moss food web is based on that seen in a short-grass prairie (Hunt *et al.* 1987; Lindo & Gonzalez 2010). This food web is detrital, and microarthropods form a part of the following guilds: detritivore, bacteriovore, fungivore, herbivore, omnivore, and predator. As estimation of diets of one of the most abundant and diverse members of the food web, oribatid mites, has remained difficult, (reviewed in Chapter 1). In the Lindo and Gonzalez (2010) food web relative abundance, richness and biomass in the functional feeding groups is not parameterized. Such attributes are relevant for understanding food web dynamics and nutrient cycling in the system.

Temporal changes in the availability of basal resources can be important drivers of food web structure, including in a seasonal context (e.g. Tavares-Cromar & Williams 1996;

Thompson & Townsend 1999; Berg & Bengtsson 2007). In nearly all ecosystems, the majority of primary production is not consumed, but rather passes to detritus and enters the animal compartment via bacteria and fungi (DeAngelis 1992). Although parallel, bacterial and the fungal channels of energy flow can be connected at the top of the food web by predators consuming organisms from both channels (Hunt *et al.* 1987). Basal resources in detrital food webs, such as those present in mosses and soils, can be expected to react differently to changes in environmental conditions. These differences provide an opportunity to study food web dynamics under changing basal resource conditions, a topic of increasing interest as episodic, uncharacteristic climatic events create unusual pulses of resource abundance (Ostfeld & Keesing 2000).

Temporal variability in community composition has been recorded in studies of the moss-microarthropod system, and an increase in fungivorous taxa during winter has been suggested, based on personal observations, as a possible driver of such differences (Starzomski *et al.* 2008). Temporal changes in community structure may be driven by direct sensitivity of organisms to environmental conditions, by indirect impacts on food sources and/or competitors, or by a combination of these. Ponge's (1991) study of fungal and arthropod faunal succession during decomposition of needles in a forest floor suggests that microarthropod community structure may be resource dependent, at least with regards to the section of the food web reliant on fungi as a basal resource. Long-term experimental studies of forest soil microarthropod communities suggest that both quantity and quality of litter may impact community composition (Berg & Bengtsson 2007). Bottom-up effects on arthropod communities associated with grasslands have also been shown to be important drivers of community composition (Cole *et al.* 2005). Given the importance of understanding patterns and processes in ecological communities, especially those affected by changing temperatures,

and considering the potential of moss communities as model systems for theoretical and applied ecological studies, the aims of this study were to:

- a) expand the knowledge base and tools available for the study of moss micro-arthropods.
- b) generate basic information on the structure of moss micro-arthropod food webs
- c) present preliminary data on the temporal variability in community and food web structure in this model system.

Methods

- *Data collection*

Circular moss patches (*Dicranoloma* sp.) 10 cm in diameter were collected in cool temperate rainforest in the Yarra Ranges National Park, Victoria, Australia (37°29'13"S 145°49'59"E, 800 m, Permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria). The sampling area was approximately 400m²; samples were separated from each other by at least 5 metres. Average day-time temperature around the site is 8°C in winter and 20° in summer; annual rainfall is 1020 mm (Bureau of Meteorology, station code: 86050). Twenty moss patches were collected in winter (May 2009) and again in summer (January 2010). These sampling occasions are referred to below as occasion 1 and 2, respectively. Tullgren funnels (Tullgren 1918) were used to extract fauna, and specimens were stored in 70% ethanol until sorting. Microarthropods were sorted to morphospecies on the basis of morphological characters used in Hunt *et al.* (1998), Krantz and Walter (2010), and Diane Srivastava's research group website (University of British Columbia, Canada, <http://www.zoology.ubc.ca/~srivast/mites/key.html>).

- *Taxonomic identification*

A public-access, communal online library was created to track taxonomic keys of mites efficiently and in a collective fashion via international collaboration (see Appendix 1 for details).

Scanning electron micrographs were taken of a subset of the morphospecies. Dehydration of the specimens was carried out by washing them in 90% ethanol for 5 minutes, 95% for 5 minutes, 100% for 15 minutes twice, dry 100% ethanol for 15 minutes and dry 100% acetone for 15 minutes. Specimens were subsequently transferred onto a glass dish and left to dry overnight. Specimens were mounted on aluminium stubs and sputter-coated with gold for 160 seconds at 25 volts in an atmosphere of argon using a Baltec SCD 005. Imaging was performed in a Hitachi S570 scanning electron microscope at 10 kv. Images were acquired digitally using the program 'Spectrum'. The imaging was carried out in the Monash University MicroImaging facilities. Micrographs and/or one to seven preserved individuals of abundant morphospecies or those contributing to differentiation among samplings were sent for expert taxonomic identification or validation of identification (see Acknowledgements for details). Family richness in the study was compared to that of four similar studies of moss systems found in the literature.

- *Data and specimen storage and management*

A relational database was created using Microsoft Access® to record, store and link species data with data on moss patch species abundance generated in this chapter and in Chapter 5. The relational database developed has the capacity to store, link, rearrange, display and reformat large amounts of data of different types. The system significantly reduced the time spent recording data, minimized chances for errors during data input, and centralized all data input, storage and output to a single file. Morphospecies information

currently stored in the database is the following: stable isotope signatures, cheliceral dimensions, body size, weight, systematics, image catalog and some taxonomic traits. This information is linked to tables storing species abundance data per moss patch from the present chapter and from Chapter 5. Results from SIMPER analysis (see below) are also stored in the database, making future analysis linking species trait information with changes in abundance between seasons possible (see ‘SIMPER with Traits’ Query). A User’s Guide has been developed in order to aid in extraction and input of data (Appendix 3). The amount and type of information available varies among morphospecies.

A voucher specimen collection was generated and stored in Ross Thompson’s laboratory at Monash University. It contains 103 morphospecies of mites and 10 of collembolans, as well as a number of other arthropods and onychophorans (see *Taxonomic diversity in the moss-microarthropod system* below). Mite specimens were also lodged in specimen libraries administered by Matthew Colloff (oribatids) and Bruce Halliday (mesostigmatids) at CSIRO - Entomology, Canberra. Penelope Greenslade (University of Ballarat, Australia) received and identified specimens of collembolans.

- *Data analysis*
- *Community composition*

Morphospecies richness and total abundance per morphospecies were calculated for each sample, and species abundance curves were constructed. As a measure of the shape of the curves, evenness was calculated by dividing Shannon’s diversity by the natural logarithm of species richness (Pielou 1975; Jost 2007). Two-tailed t tests were used to compare the means of richness, total patch abundances and evenness among samplings. Density was calculated by dividing total abundance by the area in the moss patch. Analyses were performed in R Statistical Package (R Core Development Team 2009).

Analysis of similarity (ANOSIM) was used (Clarke 1993) to assess whether there were significant changes in species composition through time. Abundances were transformed using logarithm (x+1), and a distance matrix generated using Bray-Curtis similarities. The process SIMPER (Clarke & Warwick 1994) was then used to identify the morphospecies contributing the most to differences between sampling occasions. Analyses were performed in PRIMER-E (Clarke & Gorley 2006).

- *Food web description*

All adult bdellid, labidostomatid and mesostigmatid (except uropodine) mites were assigned to the Predatory guild, as they are known to prey on collembolans, eggs, juveniles and soft-bodied mites (Krantz & Walter 2010). Hypogastrurid collembolans were also assigned to this guild based on stable isotope findings suggesting that collembolans from this family may be carnivorous, preying on eggs of other collembolans and/or ingest tardigrades and rotifers (Chahartaghi *et al.* 2005). This information, and the fact that some predatory mites have been shown to feed on eggs and juveniles of other predatory mites, suggests intraguild predation occurs in our moss system (Shipp *et al.* 2010). Guild assignment for remaining taxonomic groups was carried out on the basis of the isotope signature analysis in Chapter 1. This resulted in five guilds: lichenivore, herbivore, fungivore (i.e. secondary decomposer), detritivore (i.e. primary decomposer) and predator.

Where isotope data were not available, mouthpart morphology analysis was used to assign oribatid morphospecies to guilds. Preparation of specimens for mouthpart morphometrics was carried out as in Chapter 1; Oribatid morphospecies with a moveable-digit leverage index smaller than 0.55 were assigned to the Predator guild, those with leverage higher than 0.65 were assigned to the Detritivore guild, and the rest to the Fungivore guild. Taking into consideration that soft-bodied immature mites are vulnerable to many

predators and few predators are known for heavily sclerotised adults (Norton 1994), all soft-bodied mites (nymphs and the few unsclerotised adults) were assigned to the generalised “Prey” guild. Morphospecies for which no feeding guild information was available were classified into an “Unknown” category. The biomass in this category was not large relative to that in the rest of the food web (see Results section). Biomass per individual was estimated from the average body length of the morphospecies using the formula $\log(\text{Weight}(\mu\text{g})) = \log(\text{Length}(\mu\text{m})) \times 2.529 - 5.409$, following Appendix 2 of Chapter 1.

Species that were abundant and/or large were targeted for estimation of diet. The proportion of the biomass that these morphospecies represented relative to the total biomass was large (see below); hence, although our description of the food web may be incomplete, it is nonetheless relatively thorough.

Abundance, richness and biomass per guild were calculated to assess differences in food web structure. Each attribute was analysed separately. Abundances and biomass were $\log(x+1)$ transformed, converted into Bray-Curtis similarities and used in ANOSIM as above. SIMPER analyses were carried out with small (mites) and large (hypogastrurid collembolans) predators considered separately. A range of food web attributes were calculated using the software developed in Chapter Two. Attributes calculated were: proportion of top, intermediate, herbivorous, and basal species, total number of links, mean number of links per species, connectance, total number of trophic positions and prey to predator ratio. Multivariate analysis of variance was carried out on these attributes collectively using Euclidean distance to assess effects of sampling time on food-web structure. Analyses were implemented in PRIMER-E and its add-on software PERMANOVA (Clarke & Gorley 2006; Anderson *et al.* 2008).

Results

- *Species data and the moss-microarthropod database*

Scanning electron micrographs of 77 morphospecies were produced, with images of ventral, dorsal, lateral and/or anterior views of one or more specimens per morphospecies. Additional higher-magnification images of morphological features were taken where relevant. A total of 730 scanning electron micrographs are provided in the CD attached to this thesis, and specifications for each image (morphospecies name, angle of view, region of interest, etc.) are lodged in the Moss-microarthropod database ('Photo Registry' table and associated queries). Images of the chelicerae measured are provided and logged, along with the measurements.

- *Taxonomic diversity in the moss-microarthropod system*

A total of 2554 individuals were counted from 129 morphospecies of mites and 11 morphospecies of collembolans (Table 1). After the sub-order Oribatida (Acari, Acariformes, Sarcotiformes), the second most speciose sub-order was Monogynaspida (Acari, Parasitiformes, Mesostigmata). In total, 6 collembolan and 27 acarine families were identified. Compared to similar studies the total number of microarthropod families was high, especially considering that the number of individuals sorted here is an order of magnitude smaller than that of other studies used for comparison (Table 2). Forty-five percent of families reported in our study were not reported in other studies (Table 2. Appendix 2 for details). Only one genus was identified in most families, with exceptions in Ologamasidae (Mesostigmata; 5 genera), Isotomidae (Collembola; 3 genera) and Entomobryidae (Collembola; 3 genera) (Table 1). The number of mite nymph morphs was smaller than the number of adult morphospecies. No collembolan juveniles were recorded. Seven

morphospecies represented approximately half of the individuals counted in the January sample, and ten morphospecies represented that proportion in the May specimens (Table 3). Macroarthropods (>3 mm) found in the samples (not represented in species counts) included: *Astrochthonius australis* (Pseudoscorpionidae, Chthoniidae), *Micropholcomma caeligenum* (Aranae, Micropholcommatidae), members of the Triaenonychidae family (Opiliones), dipterans, copepods, isopods, hemipterans, coleopterans, hymenopterans and onychophorans.

Table 1. Microarthropod taxon richness in the moss communities. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park. One to seven individuals were subject to expert taxonomic identification (see Acknowledgements).

	Taxon richness			Genus names
	Families	Genera	Morphospecies	
Acari	27	28	131	
<u>Mesostigmata</u>	4	10	38	
Ologamasidae		5	12	<i>Gamasellus, Gamasiphis, Euepicrius, Athiasella, Hiniphi</i>
Parasitidae		1	2	<i>Pergamasus</i>
Uropodidae		3	8	<i>Uropoda, Oplitis, Castriidinychus</i>
Trachytidae		1	1	<i>Acroseius</i>
Nymphs			4	
Unidentified adults			11	
<u>Criptostigmata</u>	20	17	66	
Scheloribatidae		1	3	<i>Scheloribates</i>
Galumnidae		1	3	<i>Galumna</i>
Eutegaeidae		1	2	<i>Neoseutegaeus</i>
Crotoniidae		1	1	<i>Crotonia</i>
Charassobatidae		1	1	<i>Charassobates</i>
Austrachipteridae		1	2	<i>Austrachipteria</i>
Carabodidae		1	4	<i>Austracarabodes</i>
Phthiracaridae			6	
Euphthiracaridae		1	2	<i>Oribotritia</i>
Nothridae		1	1	<i>Novonothrus</i>
Malaconothridae		1	1	<i>Trimalaconothrus</i>
Hermannidae		1	1	<i>Phyllhermannia</i>
Pedrocortesellidae			1	
Astegistidae		1	2	<i>Cultroribatula</i>
Otocephidae		1	3	<i>Pseudotocephus</i>
Pelopiidae			1	<i>Pseudoceratoppia</i>
Archeonothridae		1	2	<i>Stomacarus</i>
Neotrichozetidae		1	1	<i>Neotrichozetes</i>
Oribatellidae		1	1	<i>Oribatella</i>
Oppiidae		1	6	<i>Lanceoppia</i>
Nymphs			10	
Unidentified adults			12	
<u>Prostigmata</u>	3	1	14	
Penthalodidae		1	1	<i>Stereotydeus</i>
Labidostomatidae			1	
Bdellidae			5	
Nymphs			2	
Unidentified adults			5	
Unidentified			13	
Collembola	6	10	9	
Hypogastruridae		1	1	<i>Ceratophysella</i>
Isotomidae		3	3	<i>Folsomia, Isotoma, Acanthomurus</i>
Entomobryidae		3	2	<i>Paronellides, Lepidocyrtini</i>
Neelidae		1	1	<i>Neelides</i>
Sminthuridae		1	1	<i>Sphaeridia</i>
Katiannidae		1	1	<i>Katianna</i>
Total	33	38	140	

Table 2. Comparison of microarthropod families identified in studies of moss communities. Published studies identifying a large number of microarthropod families extracted from moss were considered for comparison with the present study. Identified families are indicated in Appendix 1. Families reported in only one study are counted as ‘endemic’ families. The country where research was carried out is indicated.

	Starzomski and Srivastava 2007	Hoyle and Gilbert 2004	Staddon <i>et al.</i> , 2010	Milne and Short 1999	This study
N° of families identified	24	30	21	13	33
Percent 'endemic' families	33	27	10	31	45
N° of individuals counted	26,274	69,000	Not specified	Not specified	2,554
N° families / n° individual	9.13E-04	4.35E-04			1.29E-02
Country	Canada	England	England	Australia	Australia

Table 3. Microarthropods species representing approximately 50% of the abundance in moss samples collected on two occasions. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park in May 2009 (winter) and January 2010 (summer). One to seven individuals were sent to for expert taxonomic identification (see Acknowledgements).

	Sampling 1 - May	Sampling 2 - January
Species representing a cumulative 50% of community	2 sp. <i>Scheloribates</i> sp. (Oribatida – Scheloribatidae) <i>Gamasellus</i> sp. (Mesostigmata – Ologamasidae) <i>Ceratophysella</i> sp. (Collembola – Hypogastruridae) oribatid nymphs possibly of <i>Phyllhermannia</i> sp. <i>Neotrichozetes cf. spinulosa</i> (Oribatida – Neotrichozetidae) <i>Trimalacoноthrus</i> sp. (Oribatida – Malaconothridae) 2 unidentified Prostigmatids 1 unidentified Mesostigmatid	<i>Lanceoppia</i> sp. (Oribatida - Oppiidae) <i>Scheloribates</i> sp. (Oribatida - Scheloribatidae) <i>Trimalacoноthrus</i> sp. (Oribatida – Malaconothridae) <i>Ceratophysella</i> sp. (Collembola – Hypogastruridae) <i>Lepidocyrtini</i> sp. (Collembola – Entomobryidae) <i>Stereotydeus</i> sp. (Prostigmata – Penthalodidae) nymphs of <i>Neotrichozetes cf. spinulosa</i> (Oribatida – Neotrichozetidae)

- *Community structure*

Cumulative morphospecies richness was similar on the two sampling occasions (102 occasion 1, 105 occasion 2) with the same sampling effort applied. The shape of the cumulative richness curves did not appear to have reached an asymptote, indicating that the number of species recorded for the site would likely increase with further sampling (Figure 1). There was no significant difference in species richness per moss patch between the two sampling occasions ($t: -0.88$, $df: 38$, $p=0.39$, Figure 2). Estimated density was considerably higher for the first sampling (1 individual per cm^2) than the second (0.6 per cm^2) ($t:-2.26$, $p=0.03$, Figure 1), and for both samplings, the cumulative estimate of density varied little after 12 moss patches had been sampled (Figure 1). Species abundance curves were found to be broadly similar in shape on both sampling occasions, although the first twenty morphospecies ranked in order of abundance represented a larger proportion of the abundance on the first sampling occasion than on the second. Accordingly, a statistically significant difference in evenness in the communities was detected, with communities from the first sampling more uneven than those from the second (Figure 2, mean evenness in sampling 1 0.82 ± 0.11 , sampling 2 0.89 ± 0.08 , Student's $t= 2.47$, $df= -38$, $p=0.02$).

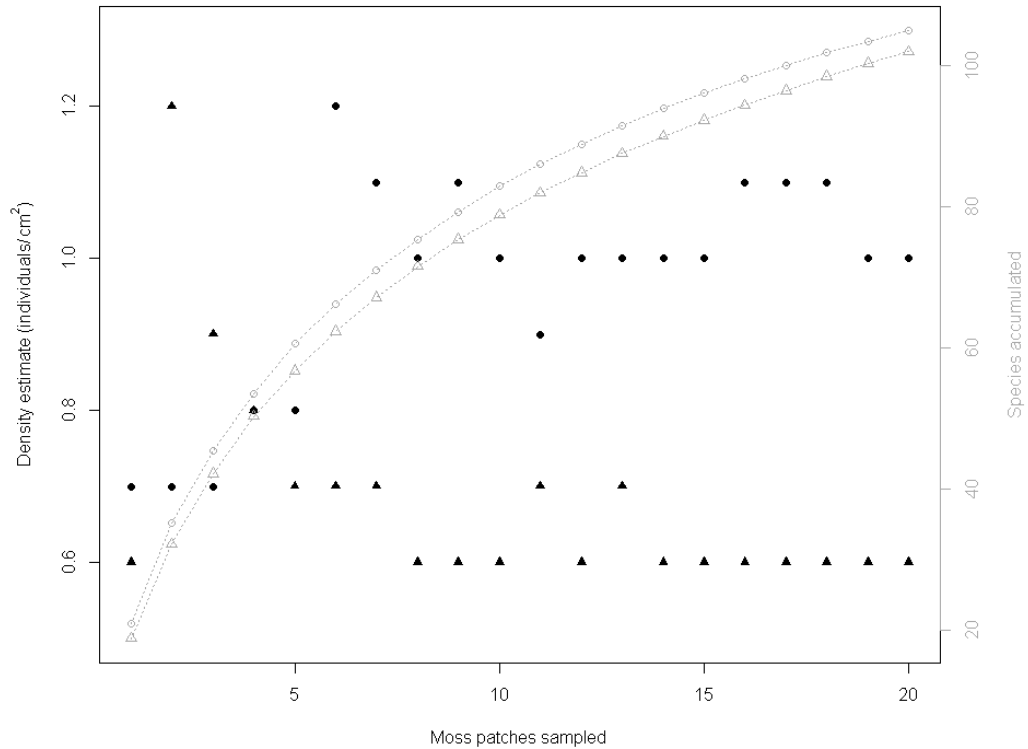


Figure 1. Density estimation (black) and species accumulation curves (grey) of moss microarthropods. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park (permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria) in May 2009 (winter) and January 2010 (summer). Samples from the first sampling are shown as circles, and from the second as triangles. Species accumulation curves were generated through random resampling 999 times using PRIMER-E.

Patterns of community composition, described as patterns of abundance by taxa or presence/absence of taxa, differed markedly between sampling occasions (Figure 3). These differences were significant when abundances of the morphospecies were considered, as well as when only presence or absence data were considered (ANOSIM $p=0.01$ in both cases, Global R 0.499 and 0.496 respectively).

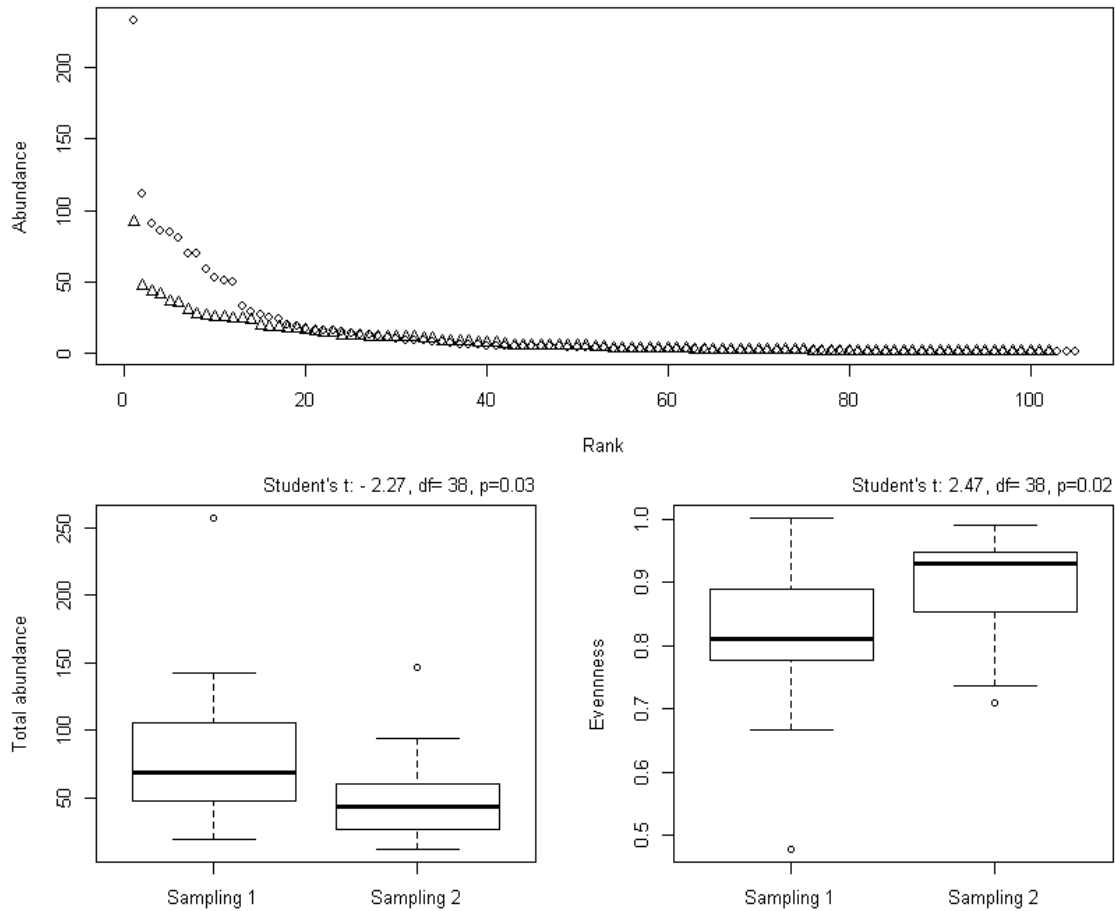


Figure 2. Above: Species abundance curves displayed by sampling occasion (all moss patches pooled). Sampling 1 (May) shown in circles, sampling 2 (January) shown in triangles. Below: Distribution of the univariate descriptors of the species abundance curves, displayed by sampling occasion. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park (permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria) May 2009 (winter, $n=20$) and January 2010 (summer, $n=20$).

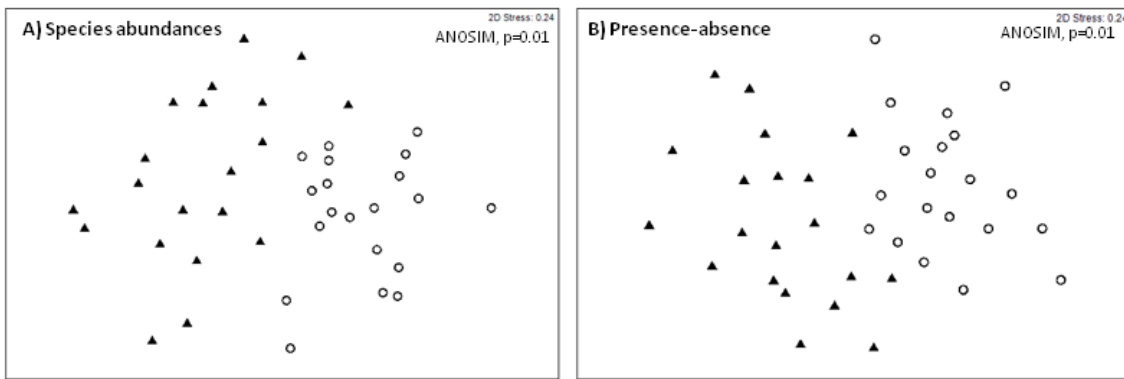


Figure 3. Differences in the structure of microarthropod communities (non-metric multidimensional scaling) between the two sampling occasions. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park in May 2009 (winter, n=20) and January 2010 (summer, n=20). Sampling 1 (May) shown in circles, sampling 2 (January) shown in triangles. A: species abundances (Bray-Curtis similarities using $\log(\text{abundance} + 1)$ data), B: presence-absence data.

- *Food web structure*

Herbivores (*Stereotydeus* sp., Penthalodidae - Prostigmata, *Cultroribatula* sp. Astegistidae - Oribatida) and lichenivores (*Austrachipteria* sp. 1, Austrachipteridae, Oribatida) were in relatively low abundance, and exhibited low species richness compared to other guilds (Figure 4). *Trimalacoethrus* sp. (Oribatida – Malaconothridae) and one of the *Schelorbitates* sp. (Oribatida – Schelorbitidae) dominated abundance in the detritivore guild. The most abundant fungivore morphospecies were *Austrachipteria* sp. 2 (Oribatida - Austrachipteridae), the collembolans *Isotoma* sp., *Katianna* sp., *Sphaeridia* sp. and oribatid mite nymphs believed to be *Phyllhermannia* sp. The most abundant predators in the system were *Gamasellus* sp. (Mesostigmata – Gamasidae), *Lanceoppia* sp. (Oribatida – Oppiidae), and *Ceratophysella* sp. (Collembola – Hypogastruridae). Two other as yet unidentified mesostigmatid mites were also in relatively high abundance. Small predators (mesostigmatid

mites) were more abundant in summer than winter, and large predators (hypogastrurid collembolans) showed the opposite trend (SIMPER analysis separating predator guild by size).

There were significant differences in food web structure between sampling occasions (Figure 5). The relative importance of a guild as a driver of the differentiation depended on whether richness, abundance or biomass was used as a metric of study, (Table 4, Figure 6). There was higher diversity and abundance of fungivores on the first sampling occasion, but no major changes in biomass. Herbivores and Predators drove differentiation in terms of biomass and abundance but their contribution to differentiation in richness was minor. Higher abundance and biomass of large, soft-bodied predators (hypogastrurid collembolans) in the first samples coincided with higher availability of Prey at that time. Smaller, hard-bodied predators (mesostigmatid mites) were in higher abundance, richness and biomass on the second sampling occasion, as were detritivores. Biomass of lichenivores was also higher in the second set of samples.

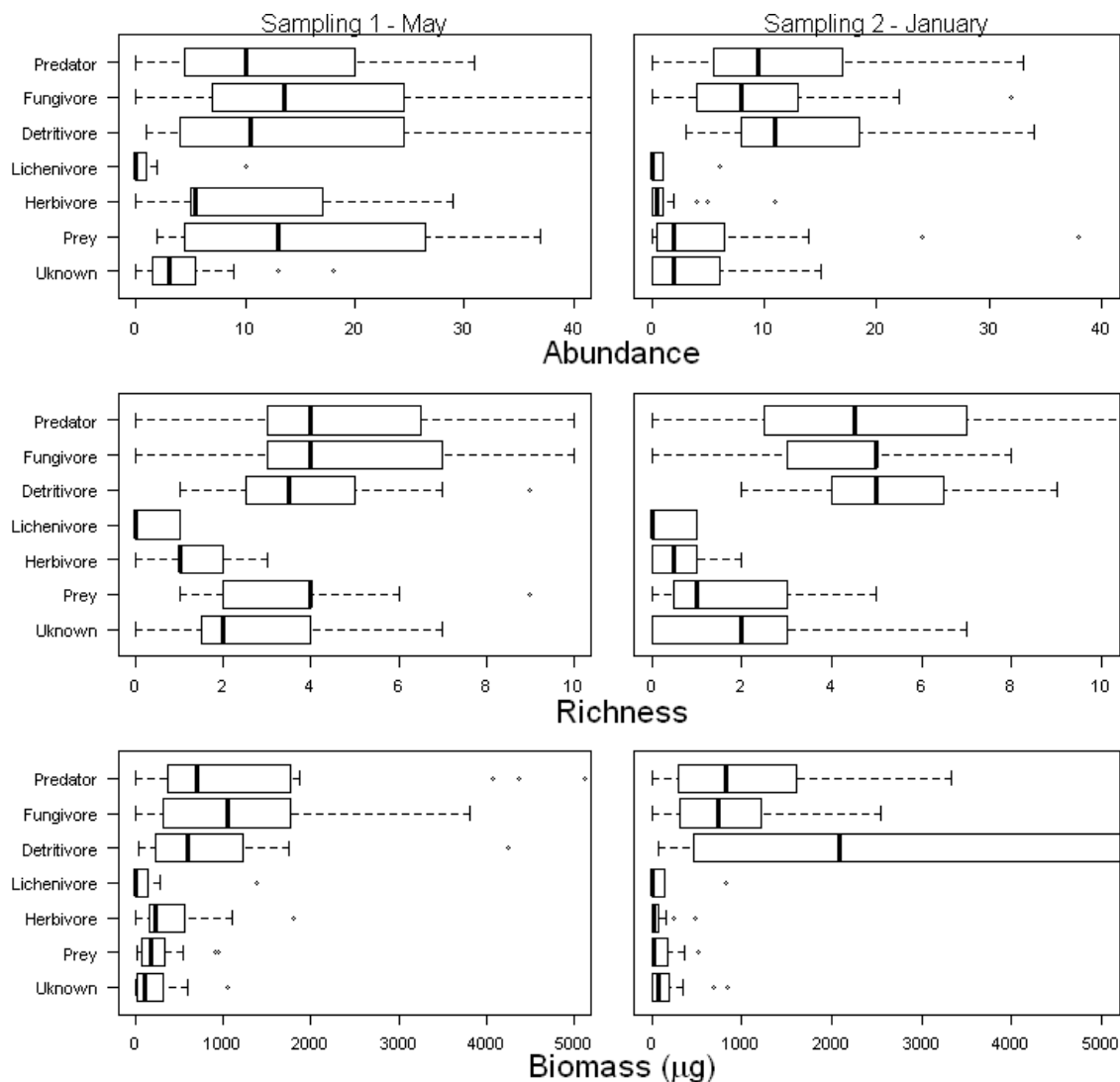


Figure 4. Distribution of abundance, richness and biomass per moss patch across feeding guilds and sampling occasions. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park in May 2009 (winter, n=20) and January 2010 (summer, n=20). Assignment to feeding guilds was carried out through isotope analysis, cheliceral morphology analysis and search of published literature. Plots indicate means with boxes showing inter-quartile ranges and whiskers indicating 95% confidence intervals.

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Food web network attributes (see Chapter 2 for details) did not vary significantly between sampling occasions (ANOSIM, $p=0.37$; see Appendix 2 for comparison of the distribution of individual network attributes).

Table 4. Summary of differences in food web structure between sampling occasions.

Three metrics were used independently to compare food web structure seasons between the two sets of samples: log transformed biomass, log transformed abundance and richness. For each metric, the contribution of each guild to the food web structure dissimilarity between the two times is shown. Contribution to dissimilarity was calculated via SIMPER analysis in PRIMER E. The percent contribution of a guild to the dissimilarity in a given metric is indicated; the sampling occasion the value appears in denotes the occasion in which the value of the metric was high, relative to the value in the other set of samples.. The total number of species in the guild is provided for reference.

	Total richness	Drivers of dissimilarity					
		Sampling 1 - May			Sampling 2 - January		
		Biomass	Abundance	Richness	Biomass	Abundance	Richness
Predators	33			23	11	14	
Fungivore	19				11	14	19
Detritivore	23	12	12	17			
Lichenivore	1	14					
Herbivore	3				21	21	7
Prey	24				16	21	16
Unknown	37				16	13	15

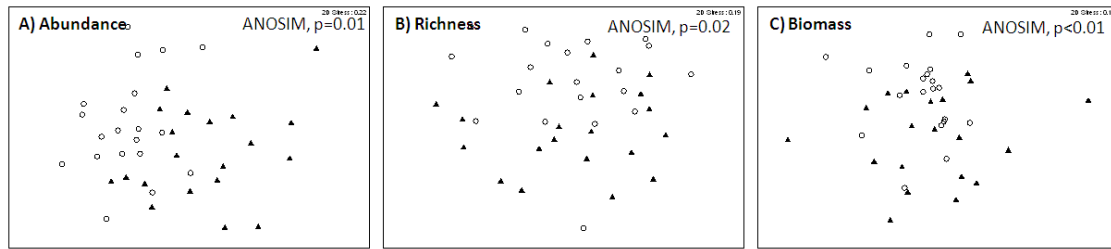


Figure 5. Non-metric multidimensional scaling (Bray-Curtis distances) ordination of food web structure. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park (permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria) in May 2009 (winter) and January 2010 (summer). Assignment to feeding guilds was carried out through isotope analysis, cheliceral morphology analysis and search of published literature. For each moss patch, abundance, richness and biomass in the guilds was calculated. Multivariate analyses of changes in the structure of the food webs was carried out considering abundance (a), richness (b) and biomass (c) separately (see Table 2). Sampling 1 (May) shown in circles, sampling 2 (January) shown in triangles.

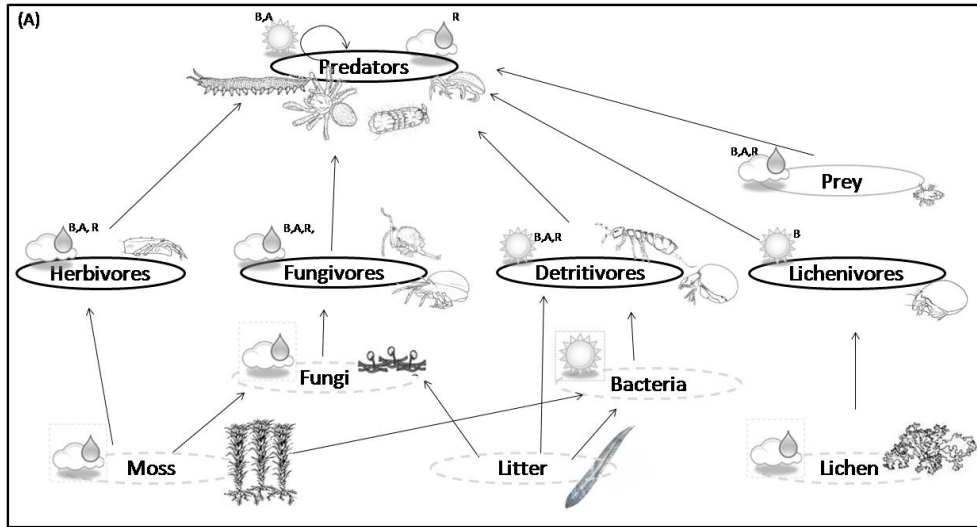


Figure 6. Connectedness food web of the moss microecosystem. Food web parameterized in this study. Assignment to feeding guilds was carried out through isotope analysis, cheliceral morphology analysis and published literature (refer to Methods for details). As distinction between bacteriovores and detritivores was not possible using cheliceral morphology, we follow terminology used in Chapter 1 and denote as “Detritivore” all taxa relying on the comminution of litter to gain access to food resources. Mite taxa are present in all functional feeding groups. Collembola are present in the predatory, fungivorous and detritivorous groups. Spiders, pseudoscorpions and onychophorans are present in the predatory compartment. Continuous lines denote availability of data from this study; dashed lines denote data and associations in the literature. The sun icon indicates that biomass, richness and/or abundance was(were) found to be higher in the January sampling; the cloud denotes that these were higher in May. Superscript indicates the metric differed between sampling occasions (B: biomass, A: abundance; R: richness; details in Table 4). Where components of the food web were not parameterized in this study, sun and cloud symbols represent what may be expected on the basis of the literature. Arthropod line-drawings from <http://www.zoology.ubc.ca/~srivast/mites/key.html>

Discussion

The voucher specimen collection, scanning electron micrographs of morphospecies, expert validation of taxonomic identification, compilation of taxonomic keys and the development of relational database for the management of this information have centralized and significantly increased the amount of data available on the micro-arthropod communities present in moss systems. This can be expected to increase our capacity to study these communities effectively.

High species richness has often been argued as one of the strengths of the moss micro-ecosystem as a model for ecology (Starzomski & Srivastava 2007; Lindo & Gonzalez 2010). We highlight that richness occurs not merely at the species level, but can be found at family level as well, and note that the families reported in mosses show deep evolutionary divergence (Maraun *et al.* 2004; Dabert *et al.* 2010a; Dabert *et al.* 2010b; Krantz & Walter 2010).

- *Food web structure in the moss micro-arthropod system*

By overcoming difficulties in the assessment of the diet of micro-arthropods, we have presented a parameterized food web of a moss model microecosystem and provided a more detailed description than has previously been possible. Our food web is highly resolved and temporally explicit, and can be added to the few available in the literature of this kind. This addresses calls for more highly resolved food webs to be described from a diversity of systems in order to approach fundamental questions in food web ecology (Cohen *et al.* 1993; Ings *et al.* 2009).

Our study suggests that food web structure in the moss-microarthropod system varies to some degree through time, and we hypothesise that these differences may be due at least in

part to changes with season. A higher abundance of fungivores was seen in the sampling during May/winter, and higher abundance of detritivores was seen in January/summer. This is consistent with changes in resource availability driven by increases in bacterial activity and decreased fungal activity, which can in turn be driven by increased temperature and decreased humidity (Winkler *et al.* 1996; Eaton *et al.* 2011). Experimental results of warming of soil communities report a switching to a fungal driven food web with increased temperature (Briones *et al.* 2009), and an increase in fungivores was also observed by Starzomski *et al.* (2008), in a warming experiment on moss food webs. The fact that the opposite pattern was observed in our study may be due to interactions between humidity and temperature. Humidity has important influences on the sensitivity of soil organic matter decomposition to temperature (Latter & Heal 1971; Couteaux *et al.* 1995; Giardina & Ryan 2000; Melillo *et al.* 2002). We suggest that relatively low humidity experienced the moss patches in our study may be a limiting factor for fungal processes. Environmental conditions can have deterministic effects on microarthropod community structure. Experiments using suspended soils along the environmental gradient created by different heights along forest trees have indicated that microarthropod community structure can respond to environmental tolerances of individual species (Lindo & Winchester 2007). Comparisons of oribatid mite communities within and among mangrove forests have shown that communities separated by 500 km can be more similar to each other than those separated by centimeters along different heights of a tree, owing to microhabitat conditions (Karasawa & Hijii 2004). Physical and chemical characteristics of microhabitats within moss carpets have been shown to affect the vertical distribution of mite species (Usher & Booth 1984). Here we have shown temporal changes in community composition and food web structure. However we can not determine whether those changes are due to effects of environmental tolerance and separation of temporal niches, or trophic interactions within the community. Nevertheless, it suggests that

the moss-microarthropod food web is sensitive to seasonal changes, possibly via changes in climatic conditions.

Another potential driver of changes in community composition of prey taxa is ‘top-down’ effects of predation. It is possible that higher temperatures in summer may increase attack and feeding rates in larger predators, thereby increasing their viability and decreasing populations of prey and of the smaller predators. Some support for this is available in the literature (Ji *et al.* 2007), although the relationship between invertebrate predator attack rates and energetic efficiency at different temperatures is complex (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011).

- *Limitations and future challenges*

Despite presenting a finer resolution of food web structure than is common for studies of microarthropod communities, our study did not consider the bacteriovore and omnivore guilds described in the food web model for mosses proposed by Lindo and Gonzalez (2010). If there are oribatids that consume litter to gain access to bacterial films and others that do so to gain access to components of the litter itself, our mouthpart morphometry approach to dietary estimation in this group likely fuses, into the “Detritivore” guild, all species that rely on litter consumption for feeding (detritivores and bacteriovores). Whilst this may be a simplification, it is technically very difficult to avoid, and the reliance on a common resource, albeit for different ultimate gains, provides some support to expectations that changes in litter availability or quality could impact both groups in relatively similar ways. Similar issues have been discussed at length in the stream ecology literature as the ‘cracker or peanut butter’ hypothesis (Cummins 1974), disputing whether litter is consumed for its own nutritional value (the ‘cracker’) or the value of the associated biofilm (the ‘peanut

butter'). To this point it has not been possible to clearly differentiate between these different roles of litter consumption in streams or in terrestrial systems such as the one studied here.

Mouthpart morphometrics currently cannot aid in distinguishing omnivorous or lichenivorous mites from others, and so it is possible that we have underestimated the proportion of these in the communities. Lichenivory was detected in only one out of the 24 taxa studied via stable isotopes in this moss system however (Chapter 1), suggesting that the proportion of lichenivores is likely to be low.

Information on taxonomy and basic biology of microarthropod species is often limited (e.g. it is estimated that 90% of Australian mites are yet to be described, Halliday 2001). Hence, some trait-based comparisons of changes in community structure that could aid in explaining seasonal variability (e.g. comparisons based on the life history strategies) are currently not feasible. Nonetheless, genetic approaches that provide measures of phylogenetic distance between morphospecies can be obtained in the absence of other knowledge on the morphospecies, and could be used as proxies for composites of traits. Deep phylogenetic trees are available for oribatids (e.g. Maraun *et al.* 2004); we suggest that incorporation of evolutionary signal may add important insights to the analysis of data from this microcosm (Davis *et al.* 2010).

It would be interesting to assess whether the size of individuals within predatory morphospecies is larger in warmer months relative to colder ones. We have only noted that predatory morphospecies in the January samples were larger than those in found in May. Although we did not measure size of the morphospecies in each sampling occasion, the specimens are stored in the laboratory and issues of intraspecies temporal variability in size could be investigated.

The sampling of faunal communities reported here was carried out in a single year and it is not possible to distinguish temporal variability due to non-seasonal factors from

those due to seasonal variability. Our findings for mosses are consistent with seasonal variability seen in microarthropod communities from soils (Wallwork 1959; Luxton 1981; Stamou & Sgardelis 1989). Marked inter-seasonal differences in experimental moss communities have also been reported previously (Starzomski *et al.* 2008). The responses of the food web were consistent with expectations that can be made on the basis of differential availability of food sources, which are likely to be driven at least in part by seasonal variation. The intention of this study was not to describe seasonal variability in detail, but rather to describe the natural food web as a basis for the later experimental work. It has also served to show the response of these communities to changes in environmental conditions which are likely to be driven at least in part by seasonal changes in temperature and humidity. Variability in response to those drivers forms an important basis for the utility of this study system in climate change experiments.

Conclusions

Despite the limitations described above, our results suggest that temporal changes in community structure in this system may be profound, and are possibly driven by basal resource availability. We suggest that our methods could aid in addressing the important challenge of understanding long-term resilience in mite communities, by providing more detailed insights into the food web structure. The possible role of temperature in structuring of the food web poses an opportunity for testing a range of hypotheses in moss communities experimentally and/or through field surveys. For example, hotter and drier climatic conditions may favour the flow of matter through processes accelerated by heat (here, detritivory) over processes vulnerable to low humidity (here, herbivory and fungivory). It is also possible that changes in community and food web structure are larger where variability

in temperature is more pronounced, or that intraguild diversity and dietary niche breadth can buffer the effects of disturbances on food web structure. Finally, the apparent sensitivity of the moss community to climatic factors, combined with the feasibility of experimentation on habitat connectivity, presents ecologists with opportunities to address the question of potential interactions between two of the most important threats to biodiversity: climate change and habitat fragmentation. Given the importance of synergies between drivers of species loss (Brook *et al.* 2008), and the difficulties in addressing the question of combined effects of climate change and habitat fragmentation on communities at large scales, we suggest that the moss-microarthropod system may be ideally suited for experimentation in this important area.

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Appendices

- *Appendix 1 – Microarthropod families*

A public-access, online library was created using citeulike.org to track taxonomic keys of mites in a collective fashion via international collaboration. The site functions as a communal online reference manager. A group was created within this site and given the name “Mite Taxonomy” (<http://www.citeulike.org/group/13748>). Researchers likely to have large collections of taxonomic references were contacted directly and asked to join. All researchers contacted thus far have agreed to contribute to the collective library. The library currently contains references to 291 taxonomic keys, mostly for oribatid mites from around the world. This was made possible by generous contributions from acarologists from Argentina (Natalia Fredes) and Brazil (Aníbal Oliveira), as well as by my own efforts. Other researchers from Canada, US and Ukraine have yet to contribute to the collective library. The availability of the tool is yet to be publicized via the worldwide acarology email list.

Considering the challenges inherent in identifying moss microarthropods even where taxonomic keys are available, we have put together a list of families known to occur in moss communities (Table 1). We have chosen to include in this compilation studies that explicitly focus on moss communities and have provided taxonomic identifications from a sizeable sampling effort in different parts of the world.

Table 1. Microarthropod families identified in studies of moss communities. Published studies identifying a large number of microarthropod families extracted from moss were considered for comparison with the present study. Identified families are indicated in Appendix 1.

Family	Starzomski and Srivastava 2007	Hoyle and Gilbert 2004	Staddon et al 2010	Milne and Short 1999	This study
Achipteriidae	√	√	√		
Archeonothridae					√
Astegistidae					√
Austrachipteridae					√
Bdellidae		√	√	√	√
Brachychthoniidae	√		√		
Caleremaeidae		√			
Camisiidae		√		√	
Carabodidae		√			√
Cepheidae	√				
Ceratoppiidae		√		√	
Ceratozetidae	√	√	√	√	
Chamobatidae		√			
Charassobatidae					√
Crotoniidae				√	√
Cryptognathidae		√			
Damaeidae	√	√	√		
Entomobryidae		√			√

(continued)

Table 1. *Continued.*

Eremaeidae		✓			
Erythraeidae				✓	
Euphthiracaridae	✓				✓
Eupodidae		✓	✓	✓	
Eutegaeidae					✓
Euzetidae		✓			
Galumnidae	✓				✓
Gustaviidae	✓				
Haplozetidae	✓				
Hermaniellidae	✓				
Hermaniidae					✓
Hermanniidae		✓			
Hypogastruridae		✓			✓
Isotomidae		✓	✓		✓
Katiannidae					✓
Labidostomatidae					✓
Laelapidae		✓			
Laelaptidae	✓				
Liacaridae	✓				
Lohmannidae				✓	
Macrochelidae		✓			
Malaconothridae					✓
Mycobatidae		✓	✓		
Nanhermaniidae				✓	
Nanorchestidae	✓				
Neelidae			✓		✓
Neoliodidae	✓				
Neotrichozetidae					✓

Table 1. *Continued.*

Nothridae				√	√
Ologamasidae	√				√
Oppiidae	√	√	√		√
Oribatellidae		√			√
Oribatulidae		√	√	√	
Otocephidae					√
Palaeacaridae				√	
Parasitidae	√	√			√
Pedrocortesellidae					√
Pelopiidae					√
Penthalodidae					√
Phthiracaridae		√	√		√
Rhagidiidae	√		√		
Scheloribatidae	√				√
Sminthuridae		√	√		√
Suctobelbidae	√	√	√		
Tarsonemidae			√		
Tectocephidae	√		√		
Trachytidae					√
Trhypocthoniidae	√			√	
Tydeidae			√		
Uropodidae					
Veigiadae	√				
Xenillidae					
Zerconidae	√				

- *Appendix 2 – Network attributes, by sampling period.*

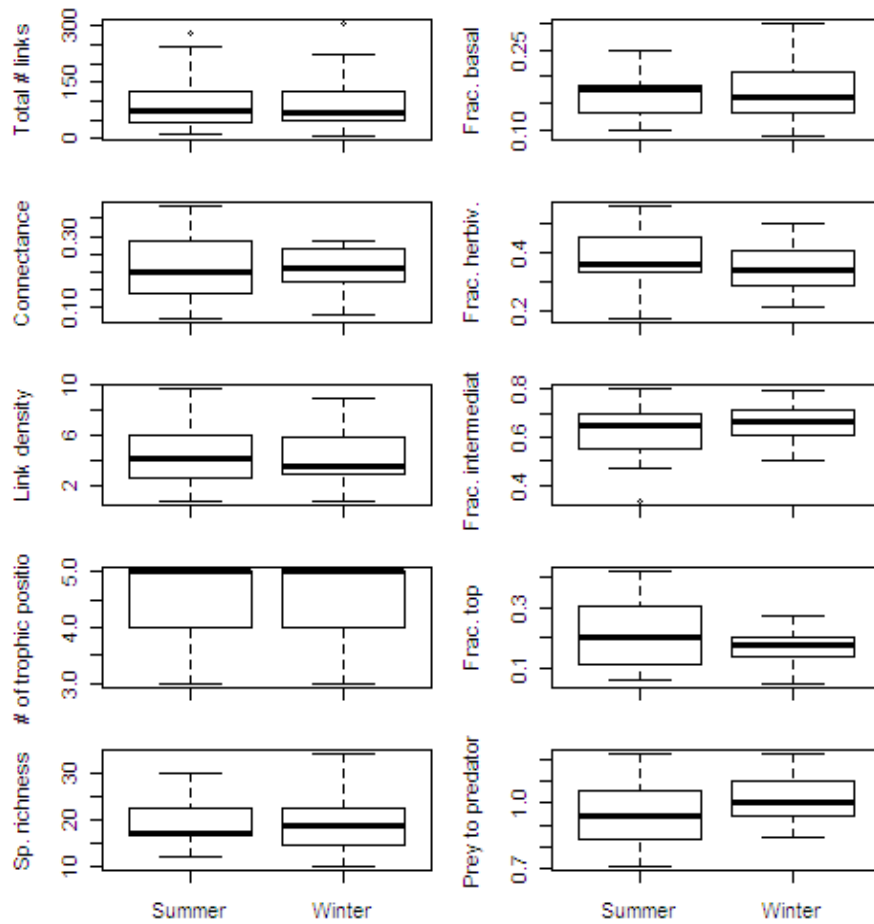


Figure 1. Distribution of moss food web network attributes, shown by season.

Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park in May 2009 (winter, n=20) and January 2010 (summer, n=20). Assignment to feeding guilds was carried out through isotope analysis, cheliceral morphology analysis and published literature. The food web attributes analysed were: proportion of top, intermediate, herbivorous, and basal species, total number of links, mean number of links per species, connectance, total number of trophic positions and prey to predator ratio. See Chapter 2 for calculation details. Summer samples in triangles, winter in circles.

- *Appendix 3 – Body size distribution in the moss microarthropod food web.*

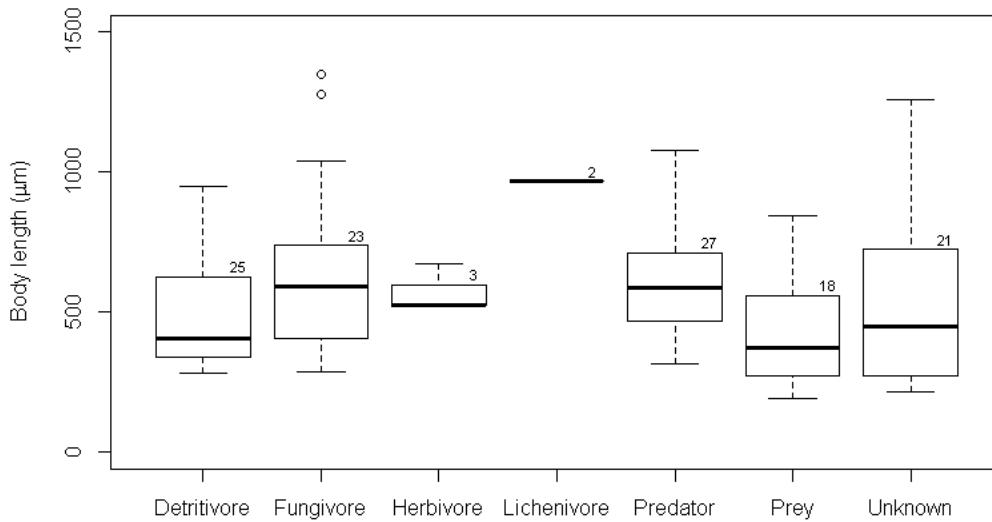


Figure 1. Body sizes in the guilds of the moss food web. Microarthropods were extracted from moss patches collected in the Yarra Ranges National Park (permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria) in May 2009 (winter) and January 2010 (summer). Assignment to guilds was carried out through isotope analysis, cheliceral morphology analysis and published literature literature search. Plots indicate means with boxes showing inter-quartile ranges and whiskers indicating 95% confidence intervals. Numbers on top of plots indicate species richness.

“Unlike population dynamics, I doubt that we could ever build a useful, practical model of an assemblage of even ten or twenty species (never mind hundreds of species) for management purposes. An alternative view, of course, is that I (and others) simply lack the imagination and courage to try.”

John Lawton, 1999

“There are worlds out there even more weird than those created by Ben Okri, and, as serious, unimaginative biologists we ignore them at our peril.”

John Lawton, 1998

Chapter 4: Building the case for moss-microarthropods as an experimental system in community ecology – comparisons with food webs from other systems

Abstract

Natural model systems have been proposed as a tractable way to experimentally address relevant questions in ecology. The moss microarthropod system has been suggested as a model system for community ecology, owing to the diverse nature of the fauna, relatively complex food-web structure and the small spatial scales at which it operates. These attributes make it a tractable system for experimentation. However the question of to what extent moss microarthropod communities and food webs resemble that of larger scale systems has not been addressed comprehensively. Difficulties with taxonomy and limitations in the study of mite diets have restricted the extent to which the food webs have been able to be compared to other, larger-scale, communities. Here we have used the tools and information from Chapters 1, 2 and 3 to assess to what degree the food web structure of moss-microarthropod communities resembles that of other ecological communities. Despite the need for more information on diet specialization of the large number of predatory species, comparison with a compilation of 209 food webs revealed similarities in food web structure to other communities across a range of spatial scales and ecosystems. Dissimilarities were also found and are discussed. We conclude that the moss-microarthropod system provides an adequate model for achieving a deeper understanding of processes in community ecology.

Introduction

As we face the current global crisis in biodiversity, our understanding of the critical processes that underpin the assembly and persistence of ecological communities remains poor. Despite decades of endeavour, it has been argued that community ecology is ‘a mess’: a loose collection of case studies relying on patterns and explanatory laws so contingent on circumstance that even the use of looser terms such as “rules” or even “widely observable tendencies” can seem overly optimistic (Lawton 1999). It has additionally been argued that ecology has failed to solve core environmental problems (Hansson 2003). In part this can be attributed to the failure to understand clearly the dynamics of the processes that maintain biodiversity in the quantifiable ways needed for prediction (Simberloff 2004).

Understanding of these processes has been hindered by: (a) the large number, diversity and interacting nature of environmental factors expected to affect communities; (b) the idiosyncratic nature of the responses of member species to those environmental factors; (c) the complexity of species-to-species interactions influencing relative abundances; and (d) the spatial scale at which some communities operate, which can make experimentation infeasible.

Bridging the gaps between detailed descriptions of individual systems and generalisable understanding of processes can be facilitated by the use of biological models. Studies of genetic processes have been greatly facilitated by understanding of the *Drosophila* model system (Schneider 2000), plant developmental biology has utilized *Arabidopsis* as a model (Meinke *et al.* 1998), and more recently, the three-spined stickleback has been named a ‘supermodel’ for studying evolutionary processes (Gibson 2005). Model systems have been proposed as a means to address theoretical and applied questions in ecology experimentally (Lawton 1995; Kitching 2000; Srivastava *et al.* 2004; Reiss *et al.* 2010; Drake & Kramer

2011). Many different microcosms have been used to date, and their suitability can depend on the question being addressed (Kitching 2000; Srivastava *et al.* 2004; Reiss *et al.* 2010). These models have provided useful insights into ecological processes. For example, the invertebrate food webs found in pitcher plants and treehole communities have contributed to our understanding of the effects of basal resources on biodiversity and of the interactions between population dynamics and food web structure (Kitching 1987; Pimm & Kitching 1987; Kitching 2000). Important insights into the links between biodiversity, island attributes and ecosystem processes have been obtained through the use of soil communities (Wardle *et al.* 1997; 2003). Model systems have greatly contributed to our understanding of a range of ecological patterns and processes (Ives *et al.* 1996; Reiss *et al.* 2010).

Trophic interactions and food web network structure are thought to provide a mechanistic link between organisms, community dynamics and ecosystem function (Cohen *et al.* 1990; Dunne 2006; Ings *et al.* 2009). Food webs have been proposed as a way to represent ecological communities and summarise them as a set of informative attributes. The topology of networks of trophic interactions can be quantified in many ways. These include measures of overall diversity, and diversity in functional and trophic groups, as well as measures of density of trophic links (connectance, linkage density), measures of web shape (prey:predator ratios) and vertical dimensions (chain length). Although criticism of maps of trophic interactions have been raised on the basis of lack of a standardized methodology for collection, description and attribution of trophic links (e.g. Paine 1988; Cohen *et al.* 1993), studies using well- resolved food webs have been able to quantify ecological processes such as invasion, and changes in productivity and disturbance (Hall & Raffaelli 1991; Martinez 1991; Woodward & Hildrew 2001; Thompson & Townsend 2005). Studying the effects of climatic disturbance on ecological communities has proven challenging, in part because of the difficulty of carrying out experiments (Dawson *et al.* 2011). Despite this, there

is a clear role for experimentation using model systems to enhance our understanding of the effects of climate and climatic extremes on community and food web structure (Van der Putten *et al.* 2010). However a case needs to be made to show that the structural attributes of a chosen system for experimentation are consistent with the broad patterns seen across other communities, in order for any general inference to be possible based on experimental results. In particular, model systems need to be sufficiently diverse to be representative of the complexity of other natural systems, and to be not atypical in food web structure. Food web network structure can affect the system's responses to disturbance (Ings *et al.* 2009). For example in freshwaters, inverted biomass pyramids have been observed and are thought to be dynamically unstable and are uncommon among ecosystems more generally (Wang *et al.* 2009). Should the moss-microarthropod ecosystem show similar structure, it would be indicative that its response to experimental treatments would be of more limited generalisability across food webs. Therefore this chapter seeks to describe the structure of the moss-micro-arthropod food web and compare it with that seen in other systems.

Methods

- *Food web data for mosses*

Data for mosses correspond to those described in detail in Chapter 3. January and May data were pooled for the purpose of the present analysis. Due to the scarcity of detailed information about feeding preferences of the members of our moss food web, we have assumed that predatory species in the moss consume (nymphs of) all species. Our food web is hence maximally connected.

- *Selection and classification of other food web studies*

All available data (209 food webs) in the GlobalWeb food web repository (Thompson, unpublished) were used in the comparative analysis of food web structure. Studies represent a diversity of systems, scales and geographic regions (Table 1 and Appendix 3). As network attributes could be expected to differ across ecosystems, geographic region and publication date, studies were categorised to facilitate comparison with the moss food webs. Geographic region was categorised as temperate, tropical or polar. Given that (a) the resolution with which food webs are described can impact metrics of food web structure (Thompson & Townsend 2000), and (b) this resolution has increased over the years, date of publication was categorized as old (published before 1990) or recent (published during or after 1990). Recognition of the need of taxonomic resolution in the study of food webs gained importance around that time, and a call for higher resolution was made by influential scientists following a review of the state of food web science (Cohen *et al.* 1993). The cutoff point was been placed at 1990 in an attempt to distinguish between food webs described in time periods where emphasis on taxonomic resolution differed. In this chapter, ecosystem type was separated into terrestrial, marine, freshwater and ice; food webs used as microcosms (moss, pitcher plants) were not allocated.

Table 1. Number of published food webs used in this study, shown by category. A large compilation of published food webs was used to compare with the moss food web network structure. As network attributes could be expected to differ across ecosystem, geographic region and publication date, studies were categorised to facilitate comparison with the moss food webs. Given that (a) the resolution with which food webs are described can impact metrics of food web structure (Thompson & Townsend 2000), and (b) this resolution has increased over the years, date of publication was categorized as old (published before 1990) or recent (published during or after 1990). Food webs published before 1990 were classified as “old” and those published after 1990 were classified as “recent”.

Category	# of food webs
<i>Date of publication</i>	
Old	182
Recent	27
<i>Ecosystem type</i>	
Freshwater	71
Marine	53
Terrestrial	71
Ice	3
Pitcher plant	10
Moss	1
<i>Geographic region</i>	
Temperate	169
Tropical	18
Polar	3

- *Food web attributes*

Food webs in GlobalWeb are coded as binary matrices, where 1 denotes the presence of a trophic link and zero denotes its absence (Cohen *et al.* 1990). Due to scarcity of information, data on the strength of trophic links, relative abundance of species and species’ characteristics (e.g. size) for most studies, these data were not included in the analyses. All food web attributes were calculated from the matrices using the *food web* package for R Statistical Software (Chapter 2). The food web attributes analysed were: total species

richness (S), proportion of top, intermediate, herbivorous, basal and cannibalistic species, total number of links (L), mean number of links per species, connectance (C), total number of trophic positions and prey:predator ratio.

- *Statistical analyses*

Food web attributes sensitive to the assumption of maximal connectivity (connectance, link density, total number of links, fractions of cannibalistic and of omnivorous taxa) were considered separately from those not expected to be sensitive to it (species richness, fractions herbivorous, basal or intermediate, number of trophic levels and prey: predator ratio). These sets of attributes are referred to below as link-dependent attributes and link-independent attributes respectively. Given the considerable effect of maximal connectivity on link-dependent attributes, only the link-independent attributes were used to compare the moss food web with other food webs. As species richness reported was associated with date of publication, this attribute was also excluded from comparison. Final comparison was carried out using the following attributes: fraction herbivorous, fraction basal, fraction intermediate, number of trophic levels and prey:predator ratio.

Analysis of variance was carried out on each attribute, with date (for link-dependent attributes) or ecosystem type (for link-independent) as a predictor variable. Attributes that consisted of proportions were arcsine-transformed prior to analysis. Where significant differences were detected in the ANOVAs, Tukey's post-hoc tests were used for pairwise comparisons. These analyses were performed in R Statistical Package (R Development Core Team 2012). Considering the potential for correlations between attributes, multivariate analyses were performed to assess variation of all the attributes jointly. Values of all attributes were $\log(x+1)$ transformed and a dissimilarity matrix among food webs on the basis of Euclidean distances was created. Analysis of Similarity (ANOSIM, Clarke 1993),

was performed on the matrix, to detect effects of geographic region, date of publication and ecosystem type on overall food web network structure. Principal components analysis was used to determine which network attributes contributed most the variability in multivariate space.

To assess the extent to which food web structure in the studied categories was distinct, discriminant analysis was performed. The data for this analysis were the scores of the food webs along axes created through canonical analysis of principal coordinates (CAP). CAP finds axes through multivariate space such that scores along these axes are the best at discriminating among pre-defined categories in the data (Anderson *et al.* 2008). Pre-defined categories for this analysis were constructed taking both ecosystem and date into account, i.e. the following categories were considered: “old terrestrial”, “recent terrestrial”, “old freshwater”, “recent freshwater”, “old marine”, “recent marine”, “old polar ice”, and “old pitcher plants”. There were no recent polar ice or pitcher plants studies in the dataset. Distinctiveness of groups was determined by the leave-one-out procedure, where a food web was removed from the data set, CAP space was calculated, the food web was placed in the created CAP space and allocated the group to whose centroid it was closest. All analyses were performed in PRIMER-E (Clarke & Gorley 2006) and its add-on software PERMANOVA+ (Anderson *et al.* 2008).

Results

When all network attributes were considered, the moss food web was found to be considerably different from all other food webs in the database (ANOSIM, Global $R=0.068$, $p<0.05$, Figure 2a), with pairwise tests between mosses and other ecosystems significant for comparisons with marine ($R=0.958$, $p<0.05$), freshwater ($R=0.88$, $p<0.05$) and terrestrial

systems ($R=0.984$, $p<0.05$). In all but one of the link-dependent attributes (i.e. those sensitive to our assumption of maximal connectance in the moss food web: total number of links, link density, connectance, fraction of cannibals, fraction of omnivores), values from the moss food web were considerably higher than those of the rest of the food webs (Figure 2b). The fraction of omnivores was high but the overall ANOVA results comparing ecosystems were not significant ($F_{5,203}= 2.01$, $p=0.08$), and the difference between moss and other studies was not as large as in the rest of the link-dependent attributes (Figure 2b). Fraction of omnivores can be expected to be less sensitive to the assumption of maximal connectance than the other attributes, as the assessment of omnivory depends on the presence or absence of links to different trophic levels irrespective of the number of times this occurs.

Species richness reported in “recent” studies was considerably higher than that reported in “old” studies, and richness in moss was within the range of that of recent studies (ANOVA, $F_{2,206}=178.4$, $p<0.05$, Figure 2c). When attributes sensitive to the assumption of maximal connectance and to major differences in overall taxonomic resolution were excluded from the comparison, the moss food web was found to be similar to old terrestrial food webs (Figure 2d). Significant differences in food web structure were found among ecosystem types (link- and resolution-independent attributes, ANOSIM, Global R: 0.053, $p=0.001$), with all pairwise tests between mosses and other ecosystems being non-significant. A considerable proportion (86%) of the differences could be represented in two dimensions (Figure 3, PC1 captures 57%, PC2 29%), predominantly reflecting values of prey:predator ratio and number of trophic positions (Figure 3, insert on top right box).

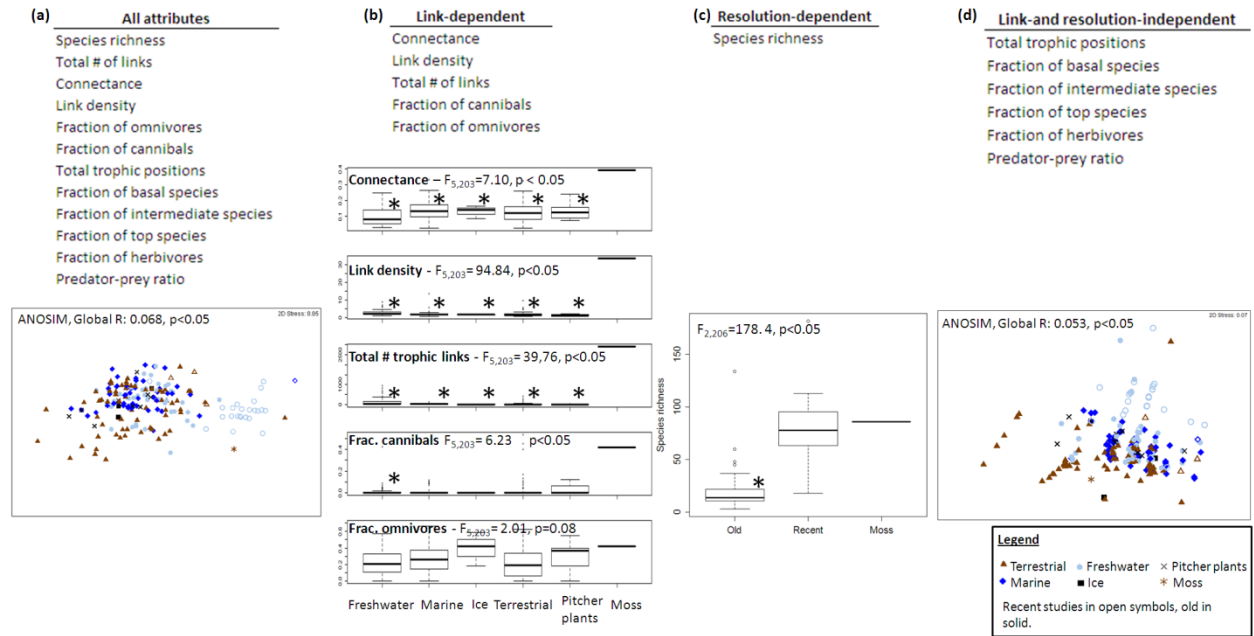


Figure 2. Comparison of moss network attributes with those of a range of published food webs (Appendix 3). Non-metric multidimensional scaling (Euclidean distances) using all network attributes (a) and only link- and resolution-independent ones (d). Plots of link-dependent (b) and resolution-dependant (c) attributes indicate means with boxes showing inter-quartile ranges and whiskers indicating 95% confidence intervals. Results of analysis of variance in each attribute are shown. Where ANOVAs were significant, a star indicates significant ($p < 0.05$) pairwise comparison with the moss food web network. For details on calculation of network attributes see Chapter 3.

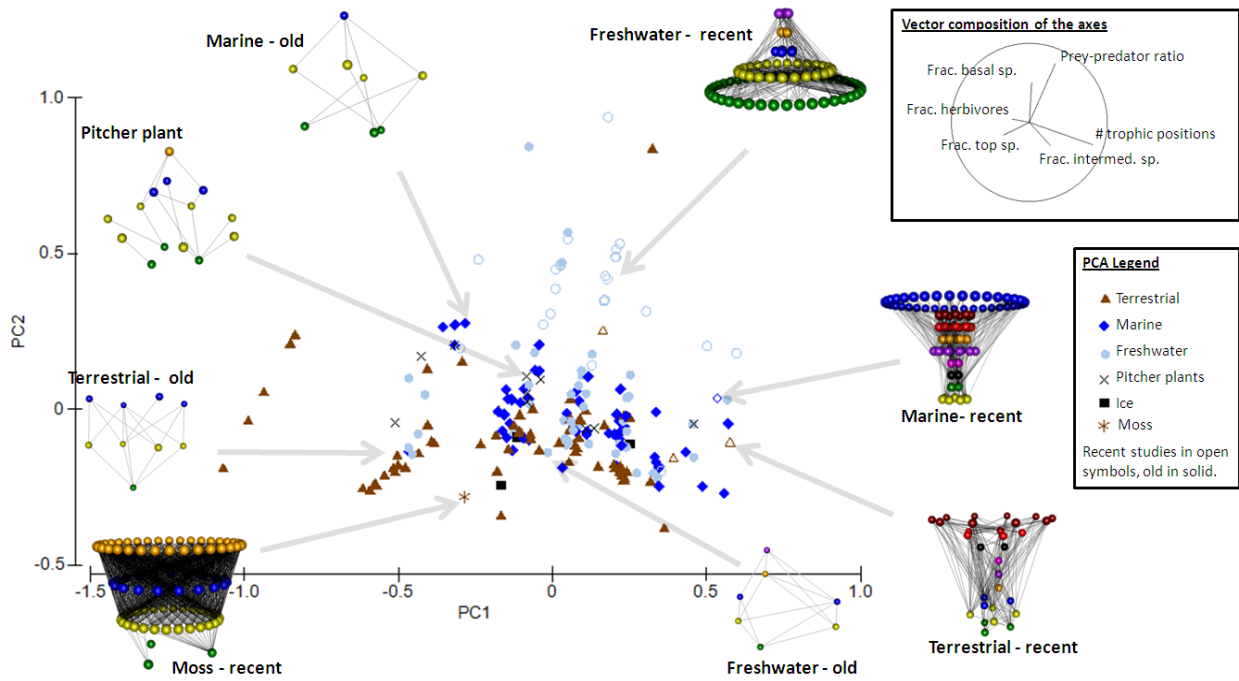


Figure 3. Principal components analysis of link- and resolution-independent attributes for a range of food webs previously published (see Appendix 3) and the moss-microarthropod food web from this study. Studies were classified as “old” if they were published before 1990, and as “recent” otherwise. Principal component axes one and two captured 57% and 29% of the variability respectively. Vector composition of the axes is shown in the upper right box. For each attribute, the direction of the vector indicates the direction of increase in magnitude of the attribute; the length of the vector indicates the attribute’s relative contribution to the construction of the axes. A selection of network plots are overlaid to illustrate diversity of network structures in the compilation across ecosystems and publication date. Arrows indicate the network plot that is provided.

Prey:predator ratios were positively correlated with the proportion of basal species, and negatively correlated with the proportion of top species (Figure 3, vector composition). The moss food web showed considerably lower prey:predator ratios than most other published food webs, associated with a high fraction of top species and a low fraction of basal ones (Figures 3 and 4). The low fraction of basal species reflects the small number of basal resources in the food web (moss, lichen and detritus), and the low taxonomic resolution with which these were described.

The most distinctive group in the dataset was recently-published freshwater food webs (discriminant analysis, leave-one-out allocation success: 78% compared to a null expectation of 13%). The next most distinctive group was old terrestrial systems (allocation success of 52%). The moss food web was allocated to this group. All link- and resolution-independent attributes of the moss food web were within the 95% confidence interval of terrestrial food webs (Appendix 2).

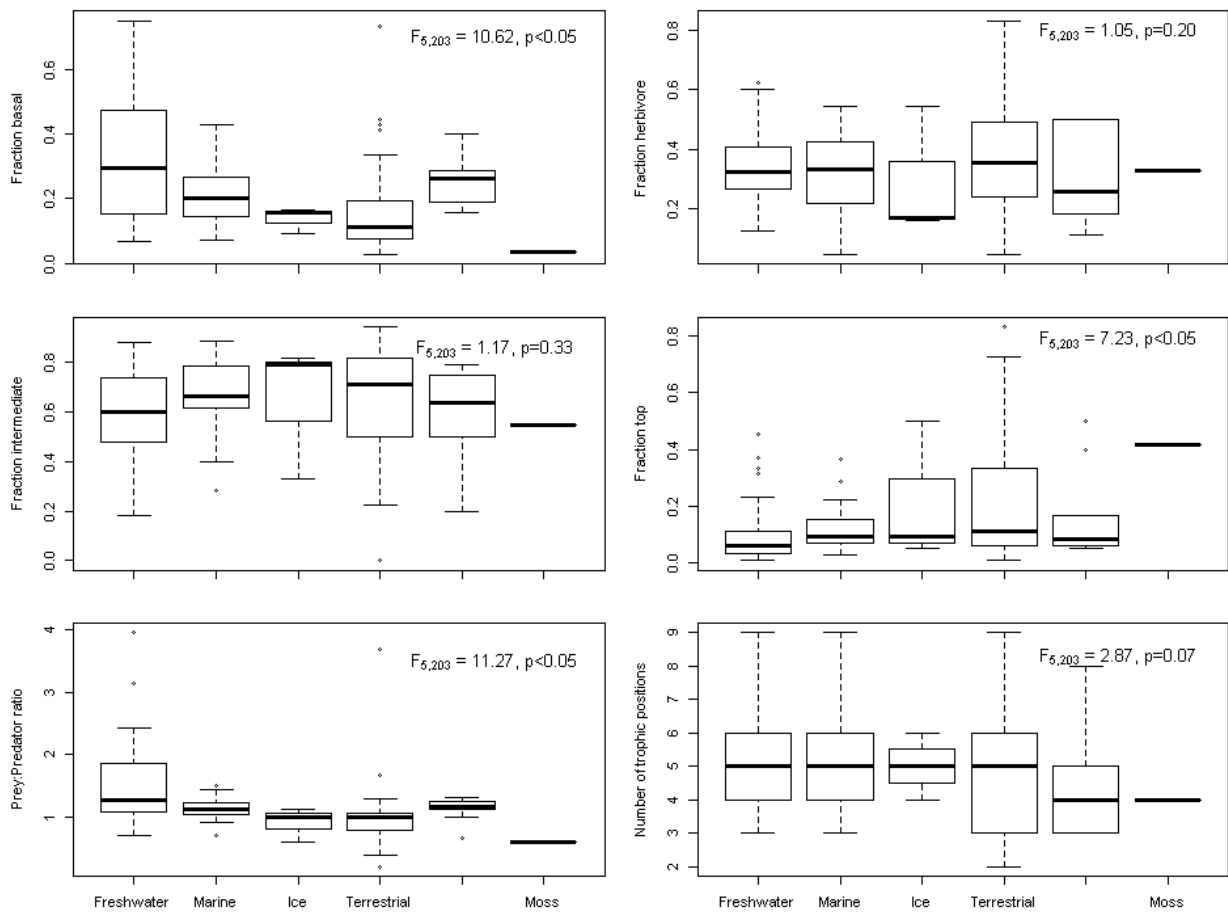


Figure 4. Link- and resolution-independent network attributes for a range of food webs previously published (see Appendix 3) and the microarthropod food web (moss) from this study, divided by ecosystem type. Plots indicate means with boxes showing interquartile ranges and whiskers indicating 95% confidence intervals. Proportion data were arcsine transformed prior to analysis. For detail on calculation of network attributes see Chapter 3. Analysis of variance results shown in top right. In cases where ANOVA results were significant, pairwise comparison performed between mosses and other ecosystem types were not.

Discussion

Our results comparing food web structure in the moss-microarthropod system with those from a large compilation of published food webs suggested that the structure of the moss food web was broadly comparable to that of published terrestrial food webs. The moss food web was within the 95% confidence interval for terrestrial food webs for all of the attributes unaffected by the resolution with which the food web is described. When these attributes are considered together, terrestrial food webs display a distinctive food web network topology, compared to all other ecosystem types, and the moss food web network displays a structure that is most similar to this terrestrial network structure.

These results suggest that structurally the moss-microarthropod food web does resemble a suite of food webs described to date. However, the comparison does underscore the difficulties involved in cross-system comparisons of food web structure. Taxonomic resolution in the description of food webs affects not only species richness but also at least some of the indices relating to the number of links in the food web. This has been shown through the modification of the resolution of food webs initially described with high taxonomic effort (Hall & Raffaelli 1991; Thompson & Townsend 2000). Here we have shown that differences in taxonomic resolution in old versus recent studies are dramatic, underscoring the point that much care must be taken in considering richness as a food web attribute in datasets that contain a large cross-section of publishing dates. By removing species richness and indices dependent on the number of links in the network, we have revealed food web structure differences among ecosystems. Of importance in the context of the current work was the fact that the moss food web resembles that of other terrestrial food

webs, and thus may be a spatially and temporally tractable experimental system for community ecology.

We have described the micro-arthropod component of the moss food web with high taxonomic resolution, and the basal resource compartment only coarsely. It is possible that this unevenness, and not a fundamental difference in the moss food web relative to others, accounts for the relatively low prey:predator ratio in our data. This change would not be new, and would paralleled by stream studies, where food web structure was greatly changed when basal components (diatoms and algae) were subjected to higher levels of taxonomic resolution (Thompson & Townsend 2000). The relatively high fraction of top predators also affects prey:predator ratios, and we propose that this speciose predatory compartment may indeed be a reflection of the structure of the system. We based assessment of top predators on our stable isotope study (Chapter 1) indicating that spiders, pseudoscorpions and velvet worms feed at the same level as predatory mites. However, in many other studies, pseudoscorpions have been placed above predatory mites in soil food webs (e.g. Scheu 2002), and if we were to follow such studies, our top species compartment would be considerably smaller than we have presented here. Further work investigating the relative position of these taxa within the moss food web is warranted, as triangularity of food webs (measured by prey:predator ratio) has been associated with their stability (Neutel *et al.* 2002).

The assumption of maximal connectance within our food web (i.e. the assumption that predators consume nymphs of all species in the community) resulted in a food web structure unlike that of the other food webs studied. It is clear through comparison with the compilation of food webs that the lack of knowledge on dietary specialization of predators in this food web is a significant gap. Given the current state of the study of mites (e.g. it is estimated that at the current rate, 400 years of sustained effort in mite taxonomy would be required to describe all Australian mites (Halliday 2001)), it is highly unlikely that this

knowledge gap will be filled with biological studies in the short term. Nonetheless, the most abundant predatory species can be targeted in an effort to gauge trophic levels and prevalence of omnivory, and thereby gain a better understanding of the system. Stable isotope techniques have a short history in the study of mite diets, although they have significant potential (e.g. Chapter 1, review in Maraun *et al.* 2011). Despite most of the isotope studies on large numbers of mite species having been carried out on Oribatid mites, the technique can be applied to all taxonomic groups. Maraun *et al.* (2011), indicate that a stable isotope study of gamasid mites has been carried out by B. Klärner but is currently unpublished. Given that cheliceral morphology in Mesostigmatid mites can be broadly correlated with consumption of different types of prey (Büryn & Brandl 1992), we propose that a study linking isotope signature and cheliceral morphology in Mesostigmatid mites in a way similar to Chapter 1, could help expand knowledge from a few mites species to encompass a more widespread understanding of the diet within the predatory compartment. Such an understanding would enhance our ability to compare moss food webs to those from other ecosystems.

- *Moss microarthropod communities – potential for experimental manipulations*

One of the useful features of moss microecosystems is the feasibility of experimental manipulation of habitat size and connectivity. Many studies have been carried out to date performing such habitat modifications (Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002; Starzomski & Srivastava 2007; Staddon *et al.* 2010) and measuring impacts on species loss, community composition, food web structure and rates of nutrient cycling. These results could be challenged if moss-microarthropod food webs were particularly simple (small numbers of species, low diversity within trophic levels) or structurally very different from other food

webs. Our results here suggest that this is not the case, and reinforce the potential to generalize from the findings of those experimental studies to other ecosystems.

While the moss-microarthropod system is very tractable for experimentally studying a number of ecological processes, it does have some limitations. The moss community used for microcosm studies is composed entirely of invertebrate fauna, and thus may respond to drivers such as temperature in a different way to food webs dominated by vertebrates. Although a mechanistic understanding of the relationship between body size, metabolic rate and environmental temperature has been difficult to obtain (Kolokotronis *et al.* 2010; White 2010; Ehnes *et al.* 2011), it is clear that invertebrates can increase their activity at temperature ranges that would produce the opposite effect in endothermic animals, and that the relationship between metabolic rate and body size can be expected to differ among these groups (Farrell-Gray & Gotelli 2005; White *et al.* 2007). Therefore, where the effects of reduced activity due to temperature stress are of interest in experiments using the moss-microarthropod system, the thermal constraints of the fauna need to be taken into consideration when setting experimental temperatures. In cases where the object is to study the effects of temperature on an assemblage of species that differ in their sensitivity to temperature, it is possible that no special consideration need apply.

In regard to food web structure, the moss-microarthropod food web was characterized by a high proportion of predatory species. This may make the moss food web less vulnerable to the loss of predatory species than food webs with higher prey:predator ratios (more triangular shape) (Neutel *et al.* 2002; Wang *et al.* 2009). Analysis of the compilation of food webs suggests that marine and freshwater food webs appear to have higher prey:predator ratios than do terrestrial food webs. The moss microarthropod food webs more closely resembled terrestrial food webs in the compilation, which tended to have lower prey:predator

ratios. It appears based on our single moss food web, that these systems may more closely approximate terrestrial food webs than they do freshwater or marine ones.

Table 2. Similarities and differences between the moss microecosystem and larger-scale ecological systems.

Similarities	Differences
Skewed distribution of species abundances.	Size
Overall structure of food web network*	Generation time
Diversity of species, dispersal capabilities, reproductive modes, life history traits, sensitivity to temperature, etc.)	Ectothermia
Subject to environmental variability	Dormancy
	Invertebrate taxa

* Relative to terrestrial food webs

- *Limitations and conclusions*

To the best of our knowledge, this is the first study to describe the structural attributes of the moss microarthropod food web. The intention here was to illustrate the broad structural character of the food web, and to place it in the context of other described food webs. We cannot determine whether similarity in food web structure is due to the same underlying ecological processes in the different systems. Multiple processes can account for patterns in the structure of ecological communities (Vellend 2010). The difficulty of disentangling the processes which underlie structural patterns in food webs is well known, and is one of the reasons that using model communities has proven so powerful. One of the significant contributions of model systems lies in the possibility of submitting recognisable natural patterns in structure to rigorous experimental tests about ecological processes. It is clear that

the moss microarthropod food web shares many structural characteristics with other described food webs,

Our comparison with other food webs has identified some intriguing generalities in food web structure between ecosystem types. These have to some degree been discussed previously (Hillebrand *et al.* 2009) and it is not the intention of this chapter to discuss those differences. The important points for the current study is that the moss microarthropod food web appears structurally to resemble other terrestrial food webs, and more closely than it does aquatic food webs. This is consistent with some of the conclusions of Hillebrand *et al.* (2009) who have discussed the basis for differences in structure between terrestrial and aquatic food webs. Our results suggest that, as more detailed food webs are described, there will be considerable opportunity to explore the factors that underpin structural differences between food webs from different ecosystem types.

We are aware that our description of the moss microarthropod food web is limited to a single location. It is not a definitive representation of this food web, nor is it intended to be. Rather the intention is to describe the structure of this food web as the basis for its use as an experimental model in Chapter 5. Whether the food web network structure of moss microarthropod communities is similar across geographic regions is unknown. Further work is needed to assess variability in network structure in time and space in this system. Such a comparison would be of interest, but it is not the intention to conduct it here.

General conclusion

Whilst we share the concerns expressed by some ecologists regarding reliance on micro- or mesocosms to the detriment and exclusion of all larger-scale studies (Carpenter 1996; Schindler 1998), we believe microcosms are useful and necessary tools for the study of

the dynamics of complex multi-species assemblages. Many studies using microcosms have revealed important insights for ecology (reviews in Lawton 1995; Kitching 2000; Srivastava *et al.* 2004; Reiss *et al.* 2010). Moss microarthropod food webs are sufficiently diverse to incorporate trophic complexity, but are also tractable for community ecology experiments.

Acknowledgements

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Appendices

- *Appendix 1 – Comparison of link- and resolution- dependent food web network attributes between moss and other terrestrial food webs*

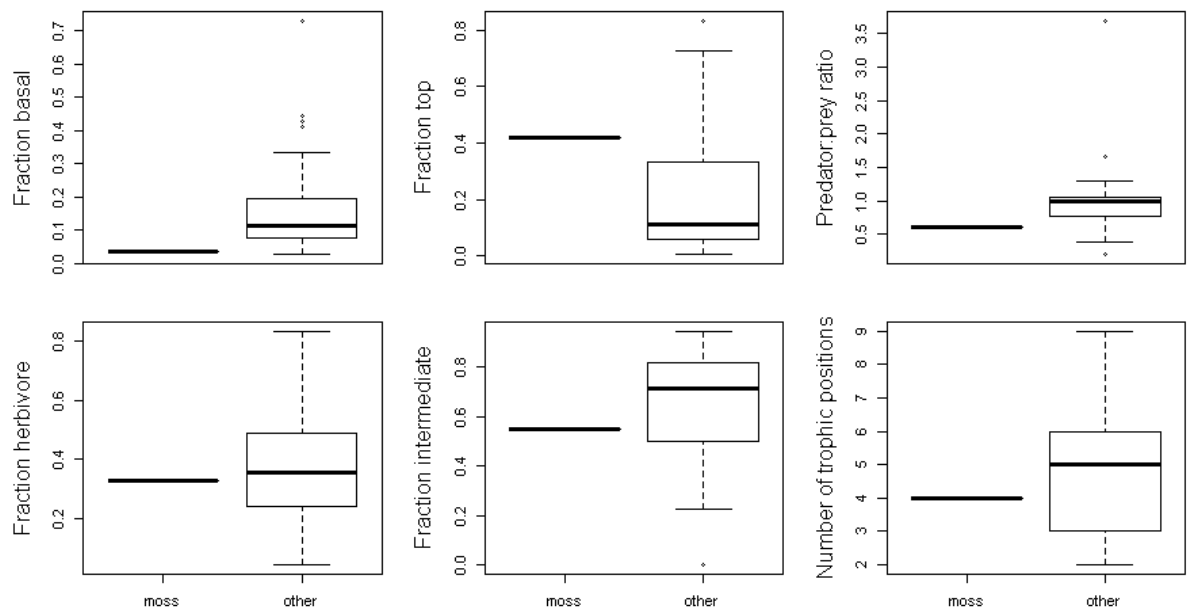


Figure 1. Link- and resolution-independent network attributes for a range of food webs previously published (see Appendix 3) and the microarthropod food web (moss) from this study. Plots indicate means with boxes showing inter-quartile ranges and whiskers indicating 95% confidence intervals.

- *Appendix 2 – Comparison of food web network attributes by region of study.*

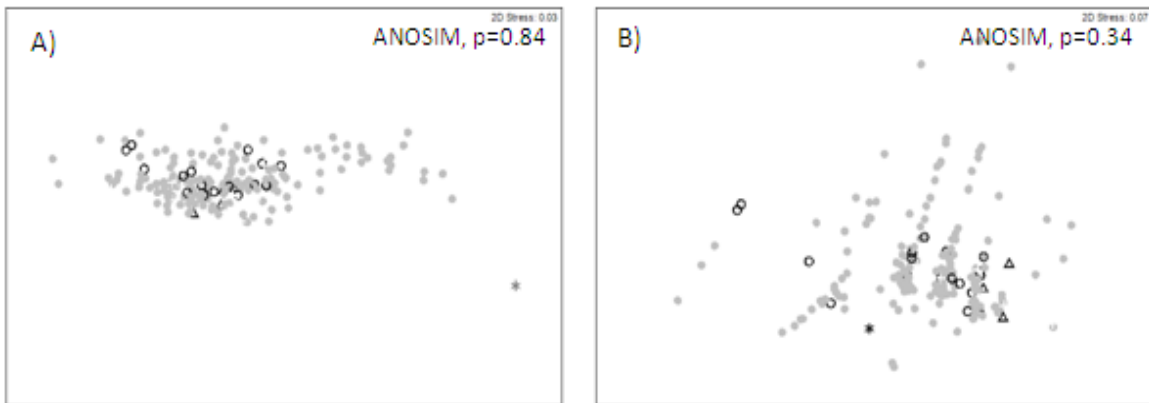


Figure 1. Comparison of food web network attributes by region where the study was carried out. Non-metric multidimensional scaling (Euclidean distances) ordination of attributes of food webs previously published (see Appendix 3) and the moss-microarthropod food webs (moss-recent) from this study. Panel A): all network attributes taken into consideration (total species richness, proportion of top, intermediate, herbivorous, basal and cannibalistic species, total number of links, mean number of links per species, connectance, total number of trophic positions and prey to predator ratio. Panel B): only link- and resolution-independent attributes considered (proportion of top, intermediate, herbivorous, basal and cannibalistic species, total number of trophic positions and prey:predator ratio). For both panels, light-grey circles indicate studies from temperate regions, dark grey circles denote tropical ones, black circles are from polar regions. Moss network represented by a star.

- *Appendix 3 – References of food web studies used*

Table 1. References of all food web matrices contained in the GlobalWeb database

(Thompson unpublished). Food web number refers to the number in the database for food webs 1-213. Numbers from 500 onwards were assigned temporarily for the purposes of the thesis. Those food webs are yet to be assigned a number in the database.

Food web #	Reference
1	(Qazim 1970)
2	(Day 1967)
3	(Woodwell 1967)
4	(Johnston 1956)
5	(Teal 1962)
6	(MacGinitie 1935)
7	(Kremer & Nixon 1978)
8	(Nixon & Oviatt 1973)
9	(Kitching & Ebling 1967)
10-13	(Menge & Sutherland 1976)
14-15	(Walsh 1967)
16	(Copeland <i>et al.</i> 1974)
17	(Hiatt & Strasburg 1960)
18	(Niering 1963)
19	(Brooks & Deevey 1963)
20	(Knox 1970)
21	(Patten & Finn 1979)
22	(Summerhayes & Elton 1923)
23-26	(Bird 1930)
27	(Varley 1970)
28	(Paviour-Smith 1955)
29	(Dunbar 1953)
30	(Mackintosh 1964)
31-32	(Petipa <i>et al.</i> 1970)
33	(Fryer 1959)
34	(Jones 1949)
35	(Mninshall 1967)
36	(Walsh 1967)
37	(Clarke <i>et al.</i> 1967)
38-39	(Fryer 1959)
40	(Harrison 1962)
41	(Parin 1970)
42	(Vinogradov & Shushkina 1978)
43	(Rosenthal <i>et al.</i> 1974)
44	(Yáñez-Arancibia 1978)
45	(Tilly 1968)

46	(Patten & 40-co-authors 1975)
47	(Harris & Bowman 1980)
48-49	(Simenstad <i>et al.</i> 1978)
50	(Nybakken 1982)
51	(Dexter 1947)
52-53	(Paine 1980)
54	(Briand 1985)
55-56	(Milne & Dunnet 1972)
57	(Yáñez-Arancibia 1978)
58	(Smirnov 1961)
59	(Twomey 1945)
60-61	(Rasmussen 1941)
62	(Summerhayes & Elton 1923)
63	(Jones 1950)
64	(Cummins <i>et al.</i> 1966)
65	(Tsuda 1972)
66	(Mann <i>et al.</i> 1972)
67	(Carlson 1968)
68	(Morgan & McLusky 1972)
69	(Saldanha 1980)
70	(Kemp <i>et al.</i> 1977)
71	(Sorokin 1972)
72	(Baril 1983)
73	(Schiemer <i>et al.</i> 1982)
74	(Brown 1964)
75	(Pechlaner <i>et al.</i> 1972)
76	(Schiemer 1979)
77	(Riedel 1962)
78	(Burgis <i>et al.</i> 1972)
79	(Sarvala 1974)
80	(Sarvala 1974)
81	(Hatanaka 1977)
82	(Ohm & Remmert 1955)
83	(Aulio <i>et al.</i> 1981)
84	(Wilbur 1972)
85	(Mizuno & Furtado 1982)
86	(Hogetsu 1979)
87	(Bradstreet & Cross 1982)
88	(Kuusela 1979)
89	(Hartley 1948)
90	(Shure 1973)
91	(Kitazawa 1977)
92	(Swan 1961) (Pattie & Verbeek 1966; Pattie & Verbeek 1976)
93	
94	(Brown 1971)

95	(Brown 1975)
96	(Osmolovskaya 1948)
97	(Dunaeva & Kucheruk 1941)
98	(Holm & Scholtz 1980)
99	(Howes 1954)
100	(Sharma 1980)
101	(Ohm & Remmert 1955)
	(Shushkina & Vinogradov
102	1979)
103	(Petipa 1979)
104	(Menge & Sutherland 1976)
105	(Edwards <i>et al.</i> 1982)
106	(Glynn 1965)
107	(Peterson 1979)
108	(Hewatt 1937)
109	(Castilla 1989)
110-113	(Dexter 1947)
114	(Marshall 1982)
115	(Koepcke & Koepcke 1952)
116	(Hurlbert <i>et al.</i> 1972)
117	(Zaret & Paine 1973)
118	(Blindloss <i>et al.</i> 1972)
119	(Mann <i>et al.</i> 1972)
120	(Moriarty <i>et al.</i> 1973)
121	(van Es 1977)
122	(Nixon & Oviatt 1973)
123	(Harris & Paur 1972)
124	(Collins <i>et al.</i> 1976)
125	(Landry 1977)
126	(Larsson <i>et al.</i> 1978)
127-128	(Beaver 1979)
129	(Morley <i>et al.</i> 1981)
130	(Odum & Heald 1975)
131-135	(Beaver 1985)
136	(Bradshaw 1983)
137	(Corker 1984)
138-139	(Kitching 1983)
140	(Seifert & Seifert 1979)
141-142	(Seifert & Seifert 1976)
143-144	(Kitching 1988)
145-148	(Rejmanek & Stary 1979)
149	(Force 1974)
150	(Hopkins 1984)
151	(Richards 1926)
152	(Whittaker 1984)
153-154	(Mayse & Price 1978)

155-167	(Askew 1975)
168-178	(Hawkins & Goeden 1984)
179	(Robinson 1953)
180-183	(Savely 1939)
184	(Beaver 1972)
185	(Chapman & Sankey 1955)
186-187	(Cornaby 1974)
188	(Jirón & Cartín 1981)
189-194	(McKinnerney 1978)
195-196	(Schoenly & Reid 1983)
197	(Mohr 1943)
198	(Schoenly 1983)
199	(Valiela 1969)
200-201	(Valiela 1974)
202	(Allan 1982)
203	(Collins <i>et al.</i> 1976)
204	(Fryer 1959)
205	(Hildrew <i>et al.</i> 1985)
206	(Jones 1949)
207	(Koslucher & Minshall 1973)
208	(Minckley 1963)
209	(Mninishall 1967)
210	(Percival & Whitehead 1929)
211-212	(Ricker 1934)
213	(Badcock 1949)
500-503	(Thompson & Townsend 2003) Thompson and Townsend
504-508	unpublished
509	(Thompson & Townsend 2004) Thompson and Townsend
510-511	unpublished
512-521	(Thompson & Townsend 2004)
522	(Thompson <i>et al.</i> 2005)
523	(Thompson & Townsend 2004)
524	(Thompson & Townsend 2003)
525	(Warren 1989)
526	(Woodward & Hildrew 2001)
527	(Hawkins <i>et al.</i> 1997)
528	(Polis 1991)
529	(de Ruiter <i>et al.</i> 1995)
530	(Schoenly 1983)
531	(Martinez 1991) (Goldwasser & Roughgarden
532	1993)
533	(Hall & Raffaelli 1991)

Table 2. Food webs used for comparison with the moss food web, and their network parameters. Food web number refers to Table 1. Network parameters were calculated with the program developed in Chapter 2. Food webs with identical values in all parameters were removed from calculations. Hence, not all food webs in Table 1 are represented in Table 2.

Food web #	Ecosystem type	Date	Richness	# links	Connectance	Link density	Frac. Omn.	# troph pos	Frac. Bas.	Frac. Int.	Frac. Top	Frac. Herb.	Prey to Pred.
1	marine	old	9	18	0.222	2.000	0.222	5	0.222	0.667	0.111	0.444	1.143
2	marine	old	15	26	0.116	1.733	0.133	4	0.200	0.733	0.067	0.467	1.167
3	marine	old	24	34	0.059	1.417	0.208	4	0.167	0.667	0.167	0.417	1.000
4	marine	old	13	26	0.154	2.000	0.615	5	0.154	0.769	0.077	0.154	1.091
5	marine	old	7	6	0.122	0.857	0.000	3	0.429	0.286	0.286	0.286	1.250
6	freshwater	old	25	44	0.070	1.760	0.320	7	0.080	0.880	0.040	0.280	1.043
7	marine	old	20	34	0.085	1.700	0.150	5	0.150	0.800	0.050	0.250	1.118
8	freshwater	old	15	25	0.111	1.667	0.400	5	0.267	0.667	0.067	0.267	1.273
9	freshwater	old	10	16	0.160	1.600	0.100	4	0.200	0.700	0.100	0.300	1.125
10	marine	old	5	6	0.240	1.200	0.000	3	0.400	0.400	0.200	0.400	1.333
11	marine	old	8	10	0.156	1.250	0.000	3	0.375	0.500	0.125	0.500	1.400
12	marine	old	13	26	0.154	2.000	0.154	4	0.231	0.615	0.154	0.538	1.100
13	marine	old	13	29	0.172	2.231	0.154	4	0.231	0.615	0.154	0.462	1.100
14	freshwater	old	8	10	0.156	1.250	0.125	4	0.125	0.750	0.125	0.375	1.000
15	freshwater	old	9	11	0.136	1.222	0.111	4	0.111	0.778	0.111	0.556	1.000
16	marine	old	14	20	0.102	1.429	0.143	4	0.286	0.643	0.071	0.286	1.300
17	marine	old	14	23	0.117	1.643	0.214	6	0.214	0.714	0.071	0.214	1.182
19	freshwater	old	17	32	0.111	1.882	0.176	5	0.118	0.824	0.059	0.176	1.067
20	ice	old	19	30	0.083	1.579	0.421	6	0.158	0.789	0.053	0.158	1.125
21	marine	old	10	21	0.210	2.100	0.600	7	0.300	0.600	0.100	0.200	1.286
25	terrestrial	old	25	39	0.062	1.560	0.160	5	0.120	0.840	0.040	0.440	1.091
27	terrestrial	old	22	39	0.081	1.773	0.364	5	0.182	0.682	0.136	0.273	1.056
28	marine	old	45	49	0.024	1.089	0.089	4	0.156	0.644	0.200	0.422	0.947
29	marine	old	22	35	0.072	1.591	0.364	6	0.091	0.818	0.091	0.136	1.000
30	marine	old	14	32	0.163	2.286	0.357	7	0.071	0.857	0.071	0.143	1.000
31	marine	old	14	51	0.260	3.643	0.643	7	0.143	0.786	0.071	0.214	1.083
32	marine	old	14	52	0.265	3.714	0.643	7	0.143	0.786	0.071	0.214	1.083
33	freshwater	old	33	52	0.048	1.576	0.303	5	0.152	0.788	0.061	0.485	1.107
34	freshwater	old	12	27	0.188	2.250	0.333	5	0.333	0.583	0.083	0.333	1.375
35	freshwater	old	13	36	0.213	2.769	0.538	5	0.154	0.615	0.231	0.308	0.909

36	freshwater	old	22	38	0.079	1.727	0.273	5	0.364	0.591	0.045	0.318	1.500
39	freshwater	old	37	75	0.055	2.027	0.216	4	0.135	0.730	0.135	0.405	1.000
41	marine	old	19	52	0.144	2.737	0.579	9	0.105	0.842	0.053	0.053	1.059
42	marine	old	16	44	0.172	2.750	0.625	9	0.313	0.625	0.063	0.063	1.364
43	marine	old	21	41	0.093	1.952	0.381	6	0.190	0.762	0.048	0.333	1.176
44	marine	old	12	29	0.201	2.417	0.417	6	0.250	0.667	0.083	0.333	1.222
45	ice	old	11	20	0.165	1.818	0.182	4	0.091	0.818	0.091	0.545	1.000
46	freshwater	old	19	68	0.188	3.579	0.474	9	0.368	0.579	0.053	0.158	1.500
47	freshwater	old	27	50	0.069	1.852	0.296	6	0.111	0.778	0.111	0.185	1.000
48	marine	old	13	20	0.118	1.538	0.308	6	0.231	0.692	0.077	0.308	1.200
49	marine	old	12	20	0.139	1.667	0.167	5	0.250	0.667	0.083	0.333	1.222
50	terrestrial	old	14	23	0.117	1.643	0.286	4	0.143	0.643	0.214	0.500	0.917
51	marine	old	25	46	0.074	1.840	0.320	6	0.160	0.800	0.040	0.400	1.143
52	marine	old	22	35	0.072	1.591	0.136	4	0.091	0.818	0.091	0.409	1.000
53	marine	old	22	31	0.064	1.409	0.000	3	0.091	0.545	0.364	0.545	0.700
54	marine	old	15	22	0.098	1.467	0.267	5	0.267	0.667	0.067	0.467	1.273
55	marine	old	12	18	0.125	1.500	0.000	4	0.083	0.750	0.167	0.333	0.909
56	marine	old	12	16	0.111	1.333	0.083	4	0.083	0.833	0.083	0.333	1.000
57	marine	old	9	19	0.235	2.111	0.444	6	0.333	0.556	0.111	0.222	1.333
58	freshwater	old	18	22	0.068	1.222	0.278	8	0.278	0.667	0.056	0.222	1.308
59	terrestrial	old	30	66	0.073	2.200	0.267	5	0.200	0.767	0.033	0.367	1.208
60	terrestrial	old	33	69	0.063	2.091	0.182	4	0.152	0.697	0.152	0.394	1.000
61	terrestrial	old	9	11	0.136	1.222	0.222	4	0.222	0.556	0.222	0.444	1.000
62	terrestrial	old	12	13	0.090	1.083	0.083	5	0.250	0.667	0.083	0.500	1.222
63	freshwater	old	18	75	0.231	4.167	0.278	5	0.278	0.611	0.111	0.389	1.231
64	freshwater	old	19	28	0.078	1.474	0.105	3	0.105	0.526	0.368	0.526	0.706
65	freshwater	old	16	43	0.168	2.688	0.125	3	0.125	0.563	0.313	0.563	0.786

66	freshwater	old	10	18	0.180	1.800	0.400	5	0.300	0.600	0.100	0.300	1.286
67	freshwater	old	21	62	0.141	2.952	0.333	7	0.095	0.857	0.048	0.333	1.053
68	freshwater	old	22	32	0.066	1.455	0.182	5	0.182	0.727	0.091	0.318	1.111
69	marine	old	29	73	0.087	2.517	0.345	7	0.138	0.828	0.034	0.379	1.120
70	marine	old	14	28	0.143	2.000	0.357	4	0.143	0.643	0.214	0.286	0.917
71	freshwater	old	16	32	0.125	2.000	0.438	8	0.188	0.750	0.063	0.125	1.154
72	freshwater	old	17	32	0.111	1.882	0.412	6	0.294	0.647	0.059	0.235	1.333
73	freshwater	old	10	15	0.150	1.500	0.200	4	0.400	0.400	0.200	0.300	1.333
74	terrestrial	old	21	36	0.082	1.714	0.429	5	0.095	0.857	0.048	0.476	1.053
75	freshwater	old	9	14	0.173	1.556	0.444	5	0.333	0.556	0.111	0.222	1.333
76	freshwater	old	14	17	0.087	1.214	0.286	5	0.214	0.643	0.143	0.357	1.091
77	freshwater	old	13	24	0.142	1.846	0.231	6	0.231	0.692	0.077	0.231	1.200
78	freshwater	old	16	27	0.105	1.688	0.375	6	0.125	0.813	0.063	0.375	1.071
79	freshwater	old	21	29	0.066	1.381	0.286	6	0.143	0.810	0.048	0.238	1.111
80	freshwater	old	27	70	0.096	2.593	0.222	6	0.185	0.778	0.037	0.296	1.182
81	marine	old	12	19	0.132	1.583	0.500	5	0.083	0.750	0.167	0.250	0.909
82	marine	old	10	14	0.140	1.400	0.100	6	0.200	0.700	0.100	0.300	1.125
83	freshwater	old	25	67	0.107	2.680	0.360	5	0.160	0.800	0.040	0.440	1.143
84	freshwater	old	12	23	0.160	1.917	0.417	6	0.167	0.750	0.083	0.250	1.100
85	freshwater	old	27	49	0.067	1.815	0.370	6	0.296	0.630	0.074	0.222	1.316
86	marine	old	16	37	0.145	2.313	0.375	7	0.125	0.813	0.063	0.188	1.071
87	ice	old	12	20	0.139	1.667	0.583	5	0.167	0.333	0.500	0.167	0.600
88	freshwater	old	16	42	0.164	2.625	0.188	3	0.250	0.438	0.313	0.438	0.917
89	freshwater	old	18	32	0.099	1.778	0.222	5	0.222	0.722	0.056	0.333	1.214
91	terrestrial	old	10	13	0.130	1.300	0.300	5	0.200	0.700	0.100	0.200	1.125
92	terrestrial	old	18	18	0.056	1.000	0.000	4	0.167	0.722	0.111	0.444	1.067
93	terrestrial	old	26	70	0.104	2.692	0.346	4	0.038	0.731	0.231	0.385	0.800
94	terrestrial	old	12	19	0.132	1.583	0.417	6	0.250	0.583	0.167	0.250	1.111
95	terrestrial	old	10	12	0.120	1.200	0.300	5	0.200	0.700	0.100	0.400	1.125

96	terrestrial	old	9	16	0.198	1.778	0.111	3	0.111	0.444	0.444	0.444	0.625
97	terrestrial	old	11	17	0.140	1.545	0.182	4	0.182	0.727	0.091	0.273	1.111
98	terrestrial	old	17	39	0.135	2.294	0.353	6	0.235	0.706	0.059	0.294	1.231
99	terrestrial	old	48	138	0.060	2.875	0.229	5	0.188	0.750	0.063	0.354	1.154
100	terrestrial	old	22	59	0.122	2.682	0.500	6	0.227	0.727	0.045	0.227	1.235
101	marine	old	6	5	0.139	0.833	0.000	3	0.333	0.500	0.167	0.500	1.250
102	marine	old	9	27	0.333	3.000	0.667	8	0.222	0.667	0.111	0.111	1.143
103	marine	old	23	133	0.251	5.783	0.783	9	0.174	0.652	0.174	0.043	1.000
104	marine	old	27	62	0.085	2.296	0.222	6	0.074	0.889	0.037	0.444	1.040
105	marine	old	10	22	0.220	2.200	0.300	6	0.200	0.700	0.100	0.400	1.125
106	marine	old	37	79	0.058	2.135	0.351	6	0.135	0.838	0.027	0.405	1.125
107	marine	old	10	14	0.140	1.400	0.100	4	0.200	0.700	0.100	0.500	1.125
108	marine	old	14	20	0.102	1.429	0.357	4	0.286	0.500	0.214	0.357	1.100
109	marine	old	21	57	0.129	2.714	0.238	5	0.143	0.810	0.048	0.476	1.111
110	marine	old	13	23	0.136	1.769	0.154	4	0.231	0.692	0.077	0.538	1.200
111	marine	old	19	36	0.100	1.895	0.263	4	0.211	0.579	0.211	0.368	1.000
112	marine	old	14	17	0.087	1.214	0.286	4	0.286	0.643	0.071	0.357	1.300
113	marine	old	11	12	0.099	1.091	0.182	4	0.364	0.545	0.091	0.273	1.429
116	freshwater	old	7	15	0.306	2.143	0.571	5	0.143	0.714	0.143	0.286	1.000
118	freshwater	old	14	22	0.112	1.571	0.286	6	0.357	0.571	0.071	0.214	1.444
121	marine	old	12	30	0.208	2.500	0.583	6	0.250	0.667	0.083	0.167	1.222
122	marine	old	9	8	0.099	0.889	0.111	4	0.222	0.556	0.222	0.444	1.000
123	terrestrial	old	134	416	0.023	3.104	0.112	5	0.731	0.261	0.007	0.157	3.694
124	freshwater	old	11	16	0.132	1.455	0.455	3	0.364	0.182	0.455	0.182	0.857
125	marine	old	9	15	0.185	1.667	0.333	5	0.333	0.556	0.111	0.111	1.333

126	freshwater	old	27	48	0.066	1.778	0.111	4	0.333	0.593	0.074	0.407	1.389
127	pitcher	old	16	18	0.070	1.125	0.125	4	0.188	0.750	0.063	0.500	1.154
128	pitcher	old	14	16	0.082	1.143	0.214	4	0.214	0.714	0.071	0.500	1.182
130	pitcher	old	14	17	0.087	1.214	0.357	8	0.286	0.643	0.071	0.143	1.300
131	pitcher	old	19	35	0.097	1.842	0.368	5	0.158	0.789	0.053	0.263	1.125
132	pitcher	old	18	42	0.130	2.333	0.500	5	0.167	0.778	0.056	0.111	1.133
133	pitcher	old	8	10	0.156	1.250	0.375	3	0.250	0.250	0.500	0.250	0.667
134	pitcher	old	11	19	0.157	1.727	0.545	4	0.273	0.636	0.091	0.182	1.250
135	pitcher	old	5	6	0.240	1.200	0.400	3	0.400	0.200	0.400	0.200	1.000
136	pitcher	old	6	6	0.167	1.000	0.000	3	0.333	0.500	0.167	0.500	1.250
137	pitcher	old	11	14	0.116	1.273	0.182	4	0.273	0.636	0.091	0.455	1.250
138	terrestrial	old	9	7	0.086	0.778	0.000	2	0.333	0.000	0.667	0.667	0.500
140	terrestrial	old	7	8	0.163	1.143	0.000	2	0.429	0.000	0.571	0.571	0.750
141	terrestrial	old	9	8	0.099	0.889	0.000	2	0.444	0.000	0.556	0.556	0.800
143	terrestrial	old	12	14	0.097	1.167	0.000	3	0.250	0.667	0.083	0.667	1.222
144	terrestrial	old	11	9	0.074	0.818	0.000	2	0.273	0.000	0.727	0.727	0.375
145	terrestrial	old	13	15	0.089	1.154	0.000	3	0.077	0.462	0.462	0.462	0.583
146	terrestrial	old	25	28	0.045	1.120	0.000	3	0.080	0.400	0.520	0.400	0.522
147	terrestrial	old	12	11	0.076	0.917	0.000	3	0.083	0.333	0.583	0.333	0.455
148	terrestrial	old	13	13	0.077	1.000	0.000	3	0.077	0.308	0.615	0.308	0.417
149	terrestrial	old	8	15	0.234	1.875	0.250	4	0.125	0.625	0.250	0.125	0.857
150	terrestrial	old	9	13	0.160	1.444	0.444	6	0.111	0.778	0.111	0.111	1.000
151	terrestrial	old	23	48	0.091	2.087	0.087	5	0.087	0.870	0.043	0.435	1.048
152	terrestrial	old	23	26	0.049	1.130	0.087	5	0.043	0.913	0.043	0.043	1.000
155	terrestrial	old	16	48	0.188	3.000	0.625	5	0.063	0.438	0.500	0.188	0.533
156	terrestrial	old	14	21	0.107	1.500	0.000	3	0.071	0.357	0.571	0.357	0.462
157	terrestrial	old	7	12	0.245	1.714	0.429	5	0.143	0.714	0.143	0.429	1.000
158	terrestrial	old	3	2	0.222	0.667	0.000	3	0.333	0.333	0.333	0.333	1.000
159	terrestrial	old	8	8	0.125	1.000	0.125	4	0.125	0.750	0.125	0.375	1.000
160	terrestrial	old	14	35	0.179	2.500	0.500	6	0.071	0.857	0.071	0.214	1.000
161	terrestrial	old	12	32	0.222	2.667	0.583	7	0.083	0.833	0.083	0.250	1.000
162	terrestrial	old	11	25	0.207	2.273	0.455	6	0.091	0.818	0.091	0.273	1.000
163	terrestrial	old	9	9	0.111	1.000	0.111	3	0.111	0.222	0.667	0.222	0.375
165	terrestrial	old	6	7	0.194	1.167	0.333	4	0.167	0.500	0.333	0.333	0.800

166	terrestrial	old	11	15	0.124	1.364	0.000	4	0.091	0.818	0.091	0.273	1.000
168	terrestrial	old	36	77	0.059	2.139	0.111	6	0.028	0.944	0.028	0.306	1.000
169	terrestrial	old	37	74	0.054	2.000	0.108	6	0.027	0.946	0.027	0.324	1.000
170	terrestrial	old	13	22	0.130	1.692	0.231	6	0.077	0.846	0.077	0.231	1.000
171	terrestrial	old	9	17	0.210	1.889	0.333	6	0.111	0.778	0.111	0.222	1.000
172	terrestrial	old	12	19	0.132	1.583	0.333	6	0.083	0.833	0.083	0.167	1.000
173	terrestrial	old	9	21	0.259	2.333	0.333	6	0.111	0.778	0.111	0.111	1.000
174	terrestrial	old	12	19	0.132	1.583	0.250	6	0.083	0.833	0.083	0.167	1.000
175	terrestrial	old	12	29	0.201	2.417	0.333	6	0.083	0.833	0.083	0.083	1.000
176	terrestrial	old	19	32	0.089	1.684	0.211	6	0.053	0.895	0.053	0.263	1.000
177	terrestrial	old	24	42	0.073	1.750	0.125	6	0.042	0.917	0.042	0.250	1.000
178	terrestrial	old	9	11	0.136	1.222	0.111	5	0.111	0.778	0.111	0.222	1.000
179	terrestrial	old	9	13	0.160	1.444	0.111	4	0.111	0.778	0.111	0.444	1.000
184	terrestrial	old	20	49	0.123	2.450	0.100	3	0.050	0.750	0.200	0.750	0.842
185	terrestrial	old	32	62	0.061	1.938	0.344	4	0.031	0.938	0.031	0.313	1.000
188	terrestrial	old	27	47	0.064	1.741	0.037	3	0.037	0.593	0.370	0.593	0.654
189	terrestrial	old	18	23	0.071	1.278	0.333	3	0.056	0.500	0.444	0.500	0.588
190	terrestrial	old	8	9	0.141	1.125	0.000	3	0.125	0.625	0.250	0.625	0.857
191	terrestrial	old	27	72	0.099	2.667	0.185	5	0.037	0.926	0.037	0.630	1.000
192	terrestrial	old	6	5	0.139	0.833	0.000	2	0.167	0.000	0.833	0.833	0.200
193	terrestrial	old	21	40	0.091	1.905	0.190	3	0.048	0.667	0.286	0.667	0.750
194	terrestrial	old	3	2	0.222	0.667	0.000	2	0.333	0.000	0.667	0.667	0.500
195	terrestrial	old	25	64	0.102	2.560	0.320	4	0.080	0.880	0.040	0.480	1.043
196	terrestrial	old	14	30	0.153	2.143	0.357	3	0.071	0.500	0.429	0.500	0.615
198	terrestrial	old	28	37	0.047	1.321	0.000	3	0.036	0.786	0.179	0.786	0.852
203	freshwater	old	15	43	0.191	2.867	0.000	3	0.067	0.600	0.333	0.600	0.714
204	freshwater	old	33	54	0.050	1.636	0.303	5	0.152	0.788	0.061	0.485	1.107
205	freshwater	old	24	91	0.158	3.792	0.208	5	0.167	0.792	0.042	0.625	1.150
206	freshwater	old	29	105	0.125	3.621	0.138	4	0.241	0.690	0.069	0.483	1.227
207	freshwater	old	32	140	0.137	4.375	0.156	4	0.531	0.438	0.031	0.313	2.067
208	freshwater	old	11	30	0.248	2.727	0.545	5	0.182	0.636	0.182	0.182	1.000
209	freshwater	old	24	94	0.163	3.917	0.458	7	0.125	0.750	0.125	0.375	1.000
210	freshwater	old	60	185	0.051	3.083	0.117	5	0.117	0.817	0.067	0.550	1.057
211	freshwater	old	34	72	0.062	2.118	0.088	4	0.588	0.382	0.029	0.324	2.357
212	freshwater	old	23	30	0.057	1.304	0.043	3	0.696	0.261	0.043	0.261	3.143
500	freshwater	recent	86	3000	0.406	34.884	0.419	4	0.035	0.547	0.419	0.326	0.602

501	freshwater	recent	105	343	0.031	3.267	0.210	8	0.457	0.533	0.010	0.314	1.825
502	freshwater	recent	58	126	0.037	2.172	0.155	5	0.483	0.500	0.017	0.345	1.900
503	freshwater	recent	71	148	0.029	2.085	0.141	3	0.535	0.310	0.155	0.310	1.818
504	freshwater	recent	78	268	0.044	3.436	0.103	4	0.410	0.577	0.013	0.436	1.674
505	freshwater	recent	78	241	0.040	3.090	0.231	5	0.321	0.667	0.013	0.423	1.453
506	freshwater	recent	71	155	0.031	2.183	0.169	4	0.394	0.563	0.042	0.437	1.581
507	freshwater	recent	69	187	0.039	2.710	0.101	5	0.478	0.507	0.014	0.362	1.889
508	freshwater	recent	49	110	0.046	2.245	0.082	3	0.306	0.571	0.122	0.571	1.265
509	freshwater	recent	79	240	0.038	3.038	0.051	4	0.468	0.519	0.013	0.418	1.857
510	freshwater	recent	58	117	0.035	2.017	0.086	4	0.517	0.448	0.034	0.397	2.000
511	freshwater	recent	85	227	0.031	2.671	0.082	4	0.518	0.471	0.012	0.400	2.049
512	freshwater	recent	107	966	0.084	9.028	0.271	9	0.467	0.514	0.019	0.234	1.842
513	freshwater	recent	86	353	0.048	4.105	0.081	5	0.581	0.407	0.012	0.337	2.361
514	freshwater	recent	96	634	0.069	6.604	0.208	6	0.490	0.490	0.021	0.281	1.918
515	freshwater	recent	98	629	0.065	6.418	0.082	5	0.592	0.398	0.010	0.296	2.425
516	freshwater	recent	78	375	0.062	4.808	0.090	5	0.538	0.423	0.038	0.333	2.083
517	freshwater	recent	113	832	0.065	7.363	0.106	5	0.566	0.425	0.009	0.319	2.286
518	freshwater	recent	92	423	0.050	4.598	0.033	4	0.750	0.239	0.011	0.207	3.957
521	freshwater	recent	87	375	0.050	4.310	0.092	4	0.575	0.402	0.023	0.322	2.297
523	freshwater	recent	95	565	0.063	5.947	0.105	5	0.568	0.421	0.011	0.326	2.293
524	freshwater	recent	109	708	0.060	6.495	0.073	5	0.523	0.468	0.009	0.404	2.077
528	terrestrial	recent	37	216	0.158	5.838	0.622	9	0.243	0.730	0.027	0.108	1.286
529	terrestrial	recent	25	128	0.205	5.120	0.240	8	0.160	0.800	0.040	0.600	1.143
530	terrestrial	old	30	290	0.322	9.667	0.800	9	0.100	0.567	0.333	0.133	0.741
531	freshwater	recent	18	38	0.117	2.111	0.333	7	0.111	0.833	0.056	0.167	1.063
532	terrestrial	recent	46	218	0.103	4.739	0.326	5	0.413	0.565	0.022	0.261	1.667
533	marine	recent	182	2456	0.074	13.495	0.258	9	0.368	0.577	0.055	0.330	1.496
moss	terrestrial	recent	86	3000	0.406	34.884	0.419	4	0.035	0.547	0.419	0.326	0.602

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“In the midst of this unprecedented period of spending Earth’s natural bounty, however, it is time to check the accounts. That is what this assessment has done, and it is a sobering statement with much more red than black on the balance sheet. (...) In many cases, it is literally a matter of living on borrowed time.”

Millennium Ecosystem Assessment 2005

(global warming could) "...result in mass mortality of coral reefs globally, one sixth of the Earth's ecosystems being transformed and about one quarter of known species being committed to extinction."

International Governmental Panel on Climate Change 2007

“The interaction between climate change and habitat destruction could be disastrous”

JMJ Travis, 2003

Chapter 5: Experimental warming and habitat isolation modify food web structure in a naturally diverse model ecological system

Abstract

Predicted changes in climate include increased severity and frequency of extreme climatic events. To manage landscapes, an understanding of the processes that allow recovery from these extreme events is required. Understanding these landscape-scale processes of community assembly and disassembly is hindered by the large scales at which they operate, not least because of the logistical impediments to conducting experiments in such systems. Model systems provide a means of studying landscape-scale processes at tractable scales. Here, we apply a manipulation experiment to assess the combined effects of temperature and habitat-patch isolation on assembly of moss microarthropod communities after a high-temperature event. We show that community assembly depends on temperature and on degree of habitat isolation. Community composition in habitat fragments appears to have been influenced by the source pool of recolonising fauna, highlighting the value of dispersal in disturbed landscapes and the potential for habitat connectivity to buffer communities from the effects of climate change. Heated communities were heavily dominated in abundance by two species. We did not detect an impact of treatments on predator abundance or diversity, although we did find differences in predator community composition. We show the importance of incorporating temperature manipulations into studies of the effect of fragmentation on diverse communities, to address this little-studied interaction of threats to biodiversity. Results from our study indicate that isolated and heated communities can be more severely impacted than those impacted by either factor alone.

Introduction

The capacity of ecological communities to recover from extreme events, and the rate at which they do so, is closely linked to the process of community assembly. Contrasting models of assembly of ecological communities have been proposed, which attribute different degrees of importance to dispersal, resource availability, competition, and environmental conditions, among other factors, as determinants of community structure in time and space (Diamond 1975; Tilman 1982; Hubbel 2001; Choi 2004; Thompson & Townsend 2006). As extreme climatic events become more frequent and severe, the need to understand when and to what extent different factors determine the trajectory of assembling communities becomes more pressing (Easterling *et al.* 2000; Scheffer & Carpenter 2003; Smith 2011). This is especially so given (a) the unprecedented degree, and increasing rate of habitat fragmentation due to human activities, (b) the background of rapidly changing environmental conditions under which extreme climatic events are occurring, and (c) the potential for dispersal limitation and harsh environmental conditions to negatively reinforce each other (Opdam & Wascher 2004; Leimu *et al.* 2010). The planning of effective ecological conservation programs under a changing climate demands that we understand better the process of community assembly at the landscape level (Choi 2004) in the face of these dual stressors.

Experimental studies on ecological communities are notoriously difficult to implement. The large spatial and temporal scales at which communities of general interest operate can significantly hinder progress in understanding key processes such as the assembly and disassembly of ecological communities, the stability of food webs and the relationship between biodiversity and ecosystem function. Model systems in ecology have provided tractable ways to approach such complex questions, and have to date provided

many useful insights (reviewed in Lawton 1995; Kitching 2000; Srivastava *et al.* 2004; Reiss *et al.* 2010). In particular, moss-microecosystems present a level of tractability and complexity superior to many other model systems (Chapter 4, Lindo & Gonzalez 2010). These communities have been used extensively for the study the effects of habitat loss and fragmentation, showing that dispersal limitation impacts both the disassembly and assembly of ecological communities (Appendix 3).

One major focus in the study of the impacts of habitat fragmentation on food webs has been the effects on the predatory compartment. This emphasis is based on the importance of predators for foodweb dynamics (Terborgh *et al.* 2001; Borrvall & Ebenman 2006) and expectations that predators may be more vulnerable to loss of habitat connectivity than other guilds (Schoener 1989; Duffy 2003). Results of studies on the relative vulnerability of predators have been equivocal in moss microarthropod communities (Gilbert *et al.* 1998; Hoyle & Gilbert 2004; Starzomski & Srivastava 2007; Staddon *et al.* 2010). However these studies have focused on predator abundances, rather than species composition within the predator communities. Significant differences in relative body sizes and other species traits can underlie species differences in dispersal capacity (Jenkins *et al.* 2007). These differences can in turn be expected to result in differential vulnerability to fragmentation within the predator guild, as dispersal among patches can enable population persistence (Brown & Kodric-Brown 1977; Hanski *et al.* 1996; Gilbert *et al.* 1998; Gonzalez *et al.* 1998). It is important to investigate whether an apparent insensitivity of the predator guild to fragmentation in terms of abundance and richness masks shifts in predator species composition. The predatory compartment of moss-microarthropod communities is species-rich relative to many large-scale food webs (Chapter 4), and given that predator diversity can dampen trophic cascades (Finke & Denno 2004), shifts in predator composition could determine the moss microarthropod food web's response to disturbance.

The structure of food webs can also be affected by another major landscape-scale disturbance: climate change. Much research has been carried out to understand the impacts of climate change on individual species, but considerably less is known about effects on species interactions, multi-species assemblages and food webs, especially in the context of community assembly (Gilman *et al.* 2010; Walther 2010). Species' responses to temperature do not occur in isolation, and the response of one species can be altered substantially by its interactions with others. Predators can ameliorate impacts of climate change on ecological communities by reducing fluctuations in prey dynamics that would otherwise follow from unusually strong bottom-up forces (Sala 2006). The response of plant communities to warming can depend on the presence or absence of herbivores (Post & Pedersen 2008). Predators have been shown to be at increased risk under increasing temperature in microcosm food webs, with small, temperature-driven changes in trophic interactions of predators causing large impacts on community structure (Sanford 1999) and ecosystem function (Petchey *et al.* 1999). Trophic interactions can be more important than direct effects on species in determining population dynamics in assembled microbial ecosystems (Beveridge *et al.* 2010). Taken together, these and many other studies indicate that temperature can have effects on entire ecological communities beyond those expected from impacts on individual species (Myserud *et al.* 2001; Walther *et al.* 2002; Jiang & Kulczycki 2004; Burkett *et al.* 2005; Harmon *et al.* 2009; Walther 2010; Kordas *et al.* 2011).

Although the potential impact of habitat loss and climate change independently on species and communities have been studied extensively (Table 1 and thesis introduction), in many cases it is the synergistic interactions between these threats that are likely to pose the most significant threat (Brook *et al.* 2008; Driscoll *et al.* 2011). Such interactions have been the subject of a very small number of empirical studies, although there have been repeated calls for more work in this area (Laurance 1998; Kappelle *et al.* 1999; Opdam & Wascher

2004; Ewers & Didham 2006; Brook *et al.* 2008; Lindenmayer *et al.* 2010; Driscoll *et al.* 2011). Synergies between climate change and the modification of habitats can be expected to arise through a diversity of mechanisms (thesis introduction, Opdam & Wascher 2004; Leimu *et al.* 2010). In particular, habitat loss, degradation and fragmentation can affect species' capacity to move through the environment to track suitable climatic conditions, although the individual dispersal and thermal traits of organisms are likely to have a major influence on impacts (Thomas *et al.* 1999; 2001; Warren *et al.* 2001).

Table 1. Selected effects reported in the literature of increasing temperatures and habitat loss, degradation and fragmentation.

Stressor	Mitigating species attributes	Selection of negative impacts reported in the literature			
		Species	Community	Food web	Ecosystem
<i>Climate change</i>	Good dispersal capabilities (range expansion)	Decreased genetic diversity	Decreased species richness	Loss of top predators	Altered nutrient cycling
	High functional genetic diversity (adaptation)	Decreased reproductive fitness	Altered structure	Increased triangularity	
	Wide trophic niche (adaptation)	Decreased food resource	Decreased total biomass	Predator:prey phenological mismatch	
	Wide optimal temperature range (tolerance)	Altered mutualistic relationships	Increased vulnerability to invasive species.		
	Short reproductive cycle (tolerance)	Altered sex ratio			
	Dormancy possible (tolerance)	Habitat loss, degradation and fragmentation			
		Range contraction			
		Increased extinction risk			
<i>Habitat loss, degradation and</i>	Good dispersal capabilities (tolerance)	Decreased genetic diversity	Decreased species richness	Loss of top predators	Altered nutrient cycling
	Wide trophic niche (tolerance)	Decreased reproductive fitness	Altered structure	Loss of intraguild diversity	
	Small area requirements (tolerance)	Decreased food resource	Increased vulnerability to invasive species.	Trophic extinction cascade	
	Short reproductive cycle (tolerance)	Niche width collapse			
	Widespread distribution (tolerance)	Increased extinction risk			

This research will assess the combined effect of increasing temperatures and habitat isolation on a diverse community, addressing a major knowledge gap in existing empirical studies. We use experimental manipulation of the moss microarthropod model ecological system to assess the effect of habitat fragmentation and increased temperature on community assembly following an extreme high-temperature event. We hypothesize the following:

Climate response

1. Given the variability of species' temperature tolerances, and the susceptibility of trophic interactions to warming, increased temperature will alter the relative abundance of species, and modify food web structure.
2. Direction of change will track that seen in comparisons of winter communities to those of summer (Chapter 3).

Fragmentation response

3. Isolation will affect community structure. Similarity to faunal source communities will decay with increasing distance from the source.
4. Predator richness, biomass and/or abundance will be lower in more isolated patches.
5. Predator community composition will be affected by fragmentation.

Interaction between climate and fragmentation

6. The severity of the effects of climate will be positively correlated with the level of isolation the habitat patch is subjected to.
7. Relative to communities experiencing ambient or field temperatures and low levels of isolation, communities subjected to high isolation and higher temperatures will show:
 - a. decreased α diversity
 - b. more skewed distributions of species abundances (i.e. lower evenness)
8. Species losses and declines will be non-random with respect to trophic guild. Predators will be more susceptible to the combined effects of disturbances. This will result in more triangular food webs (higher prey:predator ratios).

Methods

- *Collection of samples*

Moss patches (*Dicranoloma* sp.) were collected in the Yarra Ranges National Park, Victoria, Australia (37°29'13"S, 145°49'59"E, 800 m, permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria). The site is situated in a cool temperate rainforest dominated by Mountain Ash (*Eucalyptus regnans*) and Myrtle Beech (*Nothofagus cunninghamii*) trees. Average difference between maximum and minimum temperatures within a day in the site range from 8 to 15° Celsius. Average day-time temperature around the site is 8°C in winter and 20° in summer. A site near the town of Monbulk, Victoria (37°, 52'57"S, 145°23'07"E, 327 m), approximately 45 km away from the collection site was used for the experimental set-up. This site is situated in a small clearing of cool temperate rainforest of similar composition to the collection site, is at a similar altitude and has a similar temperature regime (data not shown).

- *Experimental set-up*

The experimental set-up was constructed as follows: wooden pallets were placed on the ground and tarpaulin was used to cover them. A 2 cm layer of sand was placed on the tarpaulin, and substrate warmers (Adloheat Horticultural Products Pty Ltd, Berwick, Victoria, Australia) were placed on top of the sand, with a second 2 cm layer of sand on top of the warmers. Each substrate warmer consisted of high-resistance heating wires arranged 10 cm apart in plastic mesh. When buried under 2 cm of sand this produced an even heat at the sand surface (data not shown). A 1 metre-wide barrier of plastic was laid on the ground surrounding the set-up and a 4 cm wide barrier of Tanglefoot Pest Barrier (Contech Enterprises Inc., Victoria, BC, Canada) was applied to its edge to exclude crawling insects.

Shade cloth (90% interception) was used to create a roof (1.5 m tall) and walls for the set-up, mimicking conditions under a shaded forest canopy. Air and rainwater could penetrate this cloth.

Moss patches were configured into a series of “landscapes” on top of the upper sand layer. The configuration of the landscapes (Figure 1) was the following: a circular moss patch (30 cm in diameter, hereafter “mainland”) was taken directly from the field and placed in the centre of each landscape. Smaller circular patches (10 cm in diameter, hereafter “satellites”) collected haphazardly were placed at three different distances from the mainland: 0 cm (herein “d1”), 1 cm (“d2”), and 15 cm (“d3”). There were four replicate patches at each distance treatment. Satellite patches were subjected to an initial drought event (24 hr Tullgren-funnel extraction) (Tullgren 1918) before being placed in the set-up. The procedure uses a light, heat and humidity gradient created by a light source to extract microarthropods. Efficiency is high after 24 hrs, although it may not reach 100% (see Appendix 1 for efficiency over time using larger moss patches). A total of nine landscapes were constructed. Five were left at ambient temperature (landscapes 1-5). Landscapes 6 and 7 were subjected to heating treatment “+6°C”, representing 6 degrees Celsius above ambient. Landscapes 8 and 9 were subject to treatment “+11°C”, representing 11 degrees Celsius above ambient. Local temperature was used as the ambient baseline for heating and was measured automatically at 2 minute intervals on site. Each treatment was applied as an increment above the ambient temperature, maintaining natural patterns of variability. The experiment ran for 3 months, starting in winter. Average temperature during the day in the moss collection site was 8°C in winter to 20°C in summer (Bureau of Meteorology, station code: 86050). At the end of the experiment, all moss patches were subjected to Tullgren funnel extraction for 24 hours and fauna was stored in 70% ethanol until sorting. Microarthropods were sorted to

morphospecies. One to seven individuals of abundant morphospecies were sent for expert taxonomic identification.

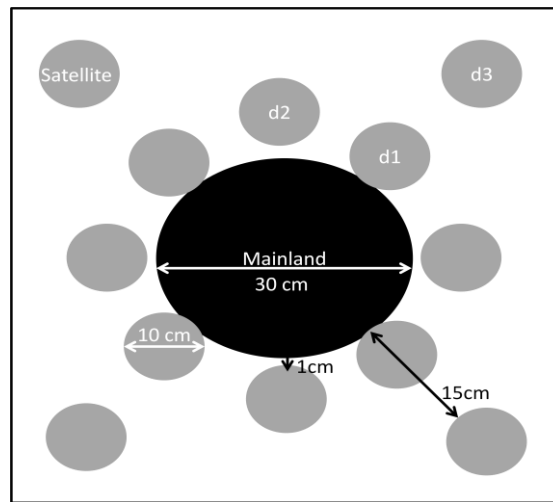


Figure 2. Configuration of the experimental moss landscapes. A circular moss patch (“mainland”) was taken directly from the field and placed in the centre of each landscape. Smaller circular patches (“satellites”) were placed at three different distances from the mainland: 0 cm (“d1”), 1 cm (“d2”), and 15 cm (“d3”). Satellite patches were subjected to an initial drought event, by subjecting them to a 24 hr Tullgren-funnel extraction, before being placed in the set-up. A total of nine landscapes were constructed.

- *Statistical analyses*

The experiment was analysed as a split-plot: replicate landscapes (random factor, $n_{\text{tot}}=9$) were assigned to climate treatments (fixed factor, three levels: ambient, +6°C and +11°C). Fragmentation (fixed factor, three levels: d1, d2 and d3) was replicated within the landscapes (four replicates per fragmentation treatment per landscape). Five landscapes were left at ambient temperature. Each climate treatment was applied to two landscapes.

Community structure

Evenness in the distribution of abundances of species in each sample was calculated as Shannon's diversity divided by the natural logarithm of species richness. Considering the potential for correlation between the variables, evenness, total abundance (log-transformed) and species richness, were analysed jointly to test for similarity in general structure among communities. A similarity matrix was constructed with these data and the CLUSTER and SIMPROF (similarity profile) routines in PRIMER-E (Clarke & Gorley 2006) were used to assess for significant structure in the data set. SIMPROF is a randomisation test for detecting structure in *a priori* undefined groups within a dataset. As the test detected significant and hierarchical structure within the dataset, we focused on the highest ranking significant clustering of groups of samples to assess which community structure attributes differentiated the major clusters in the dataset. As evenness was found to drive clustering, and landscape identity determined response of the communities, effects of fragmentation on evenness within the landscapes was assessed via analyses of variance (ANOVA) performed in R Statistical Software (R Core Development Team, 2009). Evenness, log-transformed abundance and richness were also analysed (independently of each other) via generalised linear mixed effects models (Gaussian errors, split-plot design as stated above), with landscape identity, climate treatment, fragmentation level and fragmentation by climate

interaction as predictor variables. Analyses were performed with the “lme4” package of the R Statistical Software (Bates *et al.* 2011; R Development Core Team 2011). Differences of more than two AIC units were considered to indicate significant differences in model fits. Models with the fewest predictors and lowest AIC were considered the best fit.

Effects of landscape identity, climate and isolation on community structure were assessed via permutational multivariate analysis of variance (PERMANOVA) for split-plot designs, performed in PRIMER-E, using its the add-on software PERMANOVA+ (Anderson *et al.* 2008). Species abundances were $\log(x+1)$ transformed and then standardized by the maximum abundance in the patch. Bray-Curtis dissimilarity was used. Communities from the temporal dynamics study in Chapter 3 were added to multidimensional scaling plots of the experimental samples to provide comparison.

Food web structure

Species were assigned to one of five different guilds on the basis of stable isotope signatures, cheliceral dimensions or reviews of available literature: detritivore, fungivore, lichenivore, herbivore and predators (for details see Chapters 1 and 3). Biomass per individual was estimated from the average body length of the morphospecies using the formula $\log(\text{Weight}(\mu\text{g})) = \log(\text{Length}(\mu\text{m})) \times 2.529 - 5.409$, following Appendix 2 of Chapter 1.

Effects of landscape identity and treatments on food web structure (abundance, richness and biomass per guild) were assessed via PERMANOVA for split-plot designs as above. Abundance, richness and biomass were analysed separately, guilds were analysed together. Abundance and biomass were $\log(x+1)$ transformed and then standardized by the maximum value in the patch. SIMPER (Clarke & Warwick 1994) was used to determine which guilds contributed most to differentiation. Food webs from the experimental set up

were also compared to field data from Chapter 3. Differences in species composition of predatory guild among treatments was assessed using species presence-data. A matrix of Euclidean distances among communities was constructed and effects of treatments were assessed via PERMANOVA as above.

Results

- *Community structure*

A total of 21,272 individuals were counted from 188 morphospecies of mites and 11 of collembolans. Models with landscape identity as the sole predictor variable of abundance, richness and evenness were the best fit (Table 2).

Table 2. Model fit comparison using Akaike Information Criterion (AIC) for microarthropod community evenness as predicted by the experimental treatments. Generalised linear mixed effects models were used, with evenness (Shannon's diversity divided by the natural logarithm of species richness) as a predicted variable, and landscape (L, random factor), fragmentation (F, fixed), climate (C, fixed) and the climate-fragmentation interaction (C:F, fixed) as predictors. Grey shading indicates the best fit models.

Model	d.f.	AIC		
		Evenness	Total Abundance	Richness
L	3	-110.63	1296.6	705.19
C+L	5	-110.12	1297.4	708.43
F+L	5	-109.15	1298.1	708.08
C+F+L	7	-108.67	1298.8	711.32
C+F+C:F+L	11	-103.56	1304.5	716.17

On the basis of similarity in species richness, total abundance and evenness jointly, two major clusters of communities could be recognised (Figure 2). The majority of the communities grouped into one of these clusters, characterized by higher evenness and lower abundance than the second cluster. Abundance and evenness were found to be negatively correlated along the axis that explains most of the variability in the data, and patch species richness was not a driver of difference between the clusters or treatments (Figure 2). The second cluster was made up of 10 aberrant moss patches, characterised by considerably low values of evenness and high total abundances. Most of these patches are from landscape 9, which was subjected to the +11°C treatment, and only one patch was from a landscape left at ambient temperature. The patch from Cluster 2 that was most dissimilar to patches in Cluster 1 was subjected to both the highest temperature treatment and the highest degree of isolation.

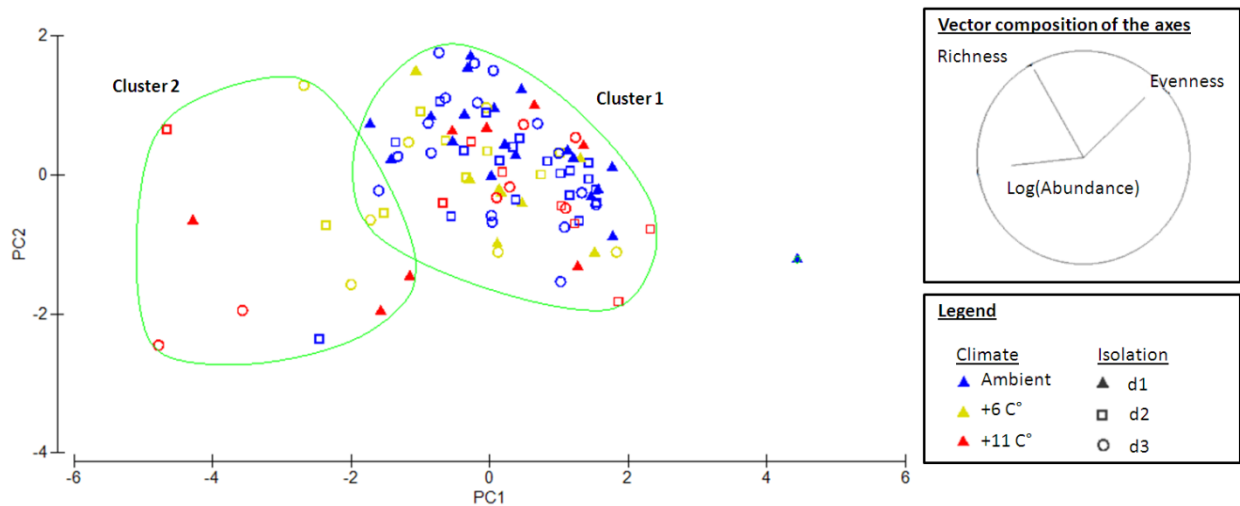


Figure 2. Comparison of moss microarthropod community structure from fragmented landscapes subjected to experimental heating. Dissimilarity with respect to species richness, total abundance (log-transformed) and evenness was used in a CLUSTER/SIMPROM analysis. Principal components space is used to display dissimilarities in structure among the communities, with highest ranking significant clustering detected with SIMPROM indicated by the green circles. Variables were normalised to provide equal weighting in the analyses. Euclidean distance was used. PC1 explains 71% of the variation, PC2 27%. Vector composition on the right displays original variable vectors, with direction of change indicated by the line; the length of the line represents the variable's relative contribution to the construction of the principal components axes.

As landscape identity was important in determining the degree to which evenness in the patches was affected by the treatments (Figure 3), generalizations about effects on evenness cannot be made. In landscape 7 (+6°C), patches furthest away from the mainland were significantly more uneven (had more skewed species abundance distributions) than other patches in the landscape (ANOVA, $F_{2,8}=5.05$, $p<0.05$), but this pattern was not found in landscape 6 (also +6°C, ANOVA, $F_{2,9}=1.20$, $p=0.34$). Evenness in landscape 8 (+11°C) was comparable to levels found in landscapes left at ambient temperature, landscape 9 (also

+11°C) had communities with very skewed species abundance distributions (low evenness). The considerably skewed species distributions in patches from this landscape were caused by unusually high relative abundances of collembolans, in particular *Isotoma* sp. and *Sphaeridia* sp.

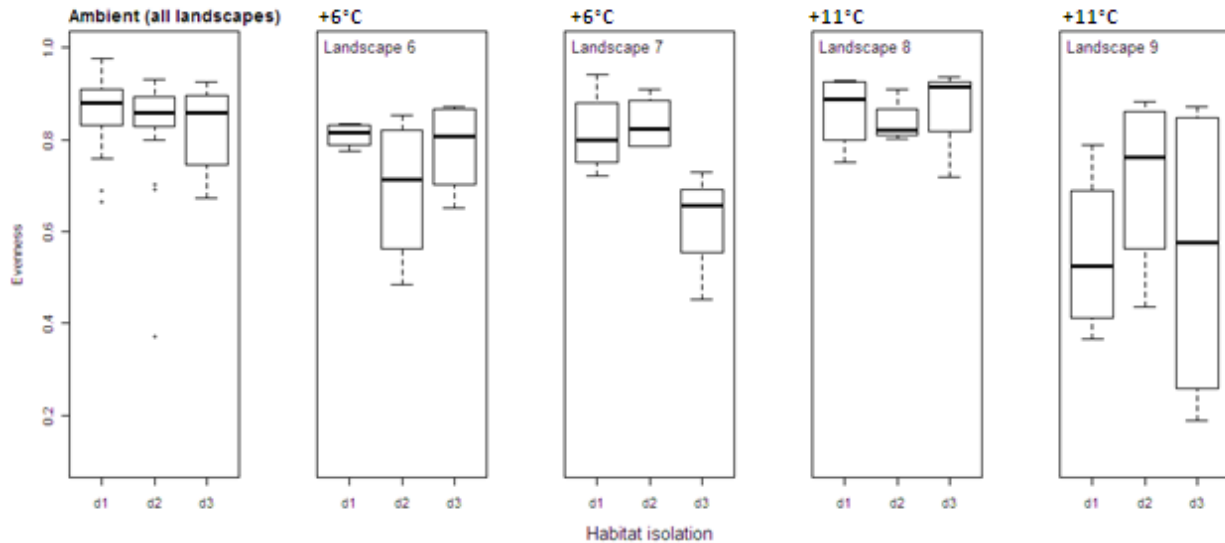


Figure 3. Effect of climate, habitat isolation and landscape identity on the evenness of the distribution of species abundances in moss microarthropod communities. Moss landscapes were subjected to different temperature treatments and fragmentation treatments (see Figure 1). Results shown are for satellite patches. Evenness in the distribution of species abundances was calculated by dividing Shannon's diversity by the natural logarithm of species richness.

Temperature treatments had a significant effect on community structure of the moss landscapes (PERMANOVA, $p=0.01$, Figure 4a). Communities left at ambient temperatures were more similar to winter communities than the heated communities were (Figure 4d).

There were significant effects of landscape identity (PERMANOVA, $p < 0.01$) and degree of isolation (PERMANOVA, $p < 0.05$) on community structure at ambient temperatures. The mainland of landscape 8 (+11°C) was more similar to ambient mainlands than to heated mainlands (Figure 4b and 4c). Use of data on community structure allowed prediction of the patch's isolation treatment with an accuracy of 53, 58 and 70% for patches from distances 1, 2 and 3 respectively (ambient treatment, discriminant analysis using scores along axes from canonical analysis of principal coordinates, Figure 5). These rates are above what could be obtained by chance alone (33%). No effects of isolation on community structure were detected in the heated landscapes.

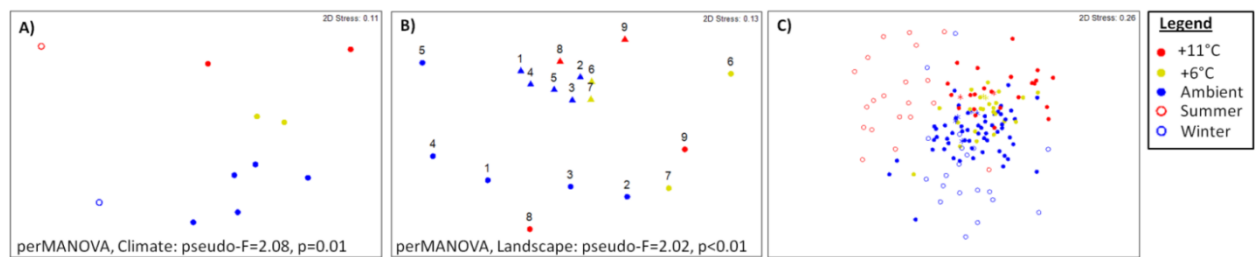


Figure 4. Multi-dimensional scaling ordinations of moss communities. Moss landscapes (Figure 1) were subjected to three different climate treatments with replicate levels of fragmentation. Landscapes left at ambient temperature are represented in the plots as light-grey empty symbols. Those subjected to +6 °C are shown in dark grey solid symbols and those subjected to +11°C are shown in black. Numbers represent different landscapes. A) Centroids of the landscapes and from the seasonal study (Chapter 3). B) Centroids of satellite and mainland patches per landscape. Mainlands are represented by circles, satellites by triangles. D) Individual moss patches in the experiment (circles) and from the seasonal study described in Chapter 3 (triangles, summer in black, winter in grey).

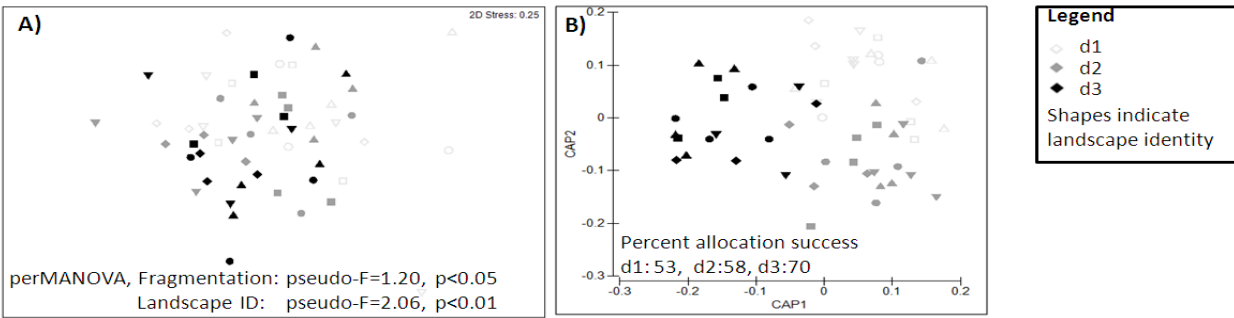


Figure 5. Effects of patch isolation on moss microarthropod communities in fragmented landscapes left at ambient temperature. Symbols represent landscapes identity. (A) Multi-dimensional scaling ordination (Bray-Curtis distance). (B) Principal axes generated through canonical analysis of principal coordinates. Percent success in allocation of patches to their fragmentation treatment using discriminant analysis (leave-one-out procedure) is indicated.

- *Food web structure*

Climate had a significant effect on food web structure (abundance per guild) (Figure 6, PERMANOVA, $p < 0.05$). Food webs from both landscapes subjected to $+11^{\circ}\text{C}$ were considerably different from the others in the study, driven largely by low detritivore and prey abundances in the most heated landscapes relative to ambient and $+6^{\circ}\text{C}$ (SIMPER analysis, cumulative 39% of differences represented by the two functional feeding groups).

Differences between food webs at ambient temperature and those subjected to $+6^{\circ}\text{C}$ were driven by lower abundances of herbivores and prey in $+6^{\circ}\text{C}$ (SIMPER analysis, cumulative 37% of similarity represented).

No significant effects of temperature treatment were found in intraguild diversity or biomass. Richness, abundance and biomass of predators were not affected by the treatments (Figure 7), nor was prey:predator ratio. Species composition in the predatory compartment

responded to the climate treatments (Figure 7a, PERMANOVA, $p < 0.01$) and to fragmentation treatments (ambient treatment only, PERMANOVA, $p < 0.05$).

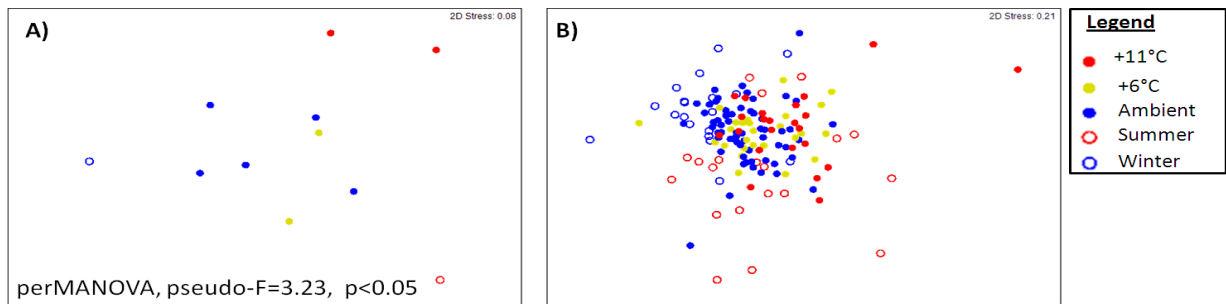


Figure 6. Multi-dimensional scaling ordinations of moss food webs (log-transformed abundance per guild). Moss landscapes (Figure 1) were subjected to three different climate treatments containing replicated levels of fragmentation. A) Centroids of the landscapes and field communities from Chapter 3. B) Individual moss patches in the experiment (full circles) and patches from the seasonal study described in Chapter 3 (empty circles, summer in red, winter in blue).

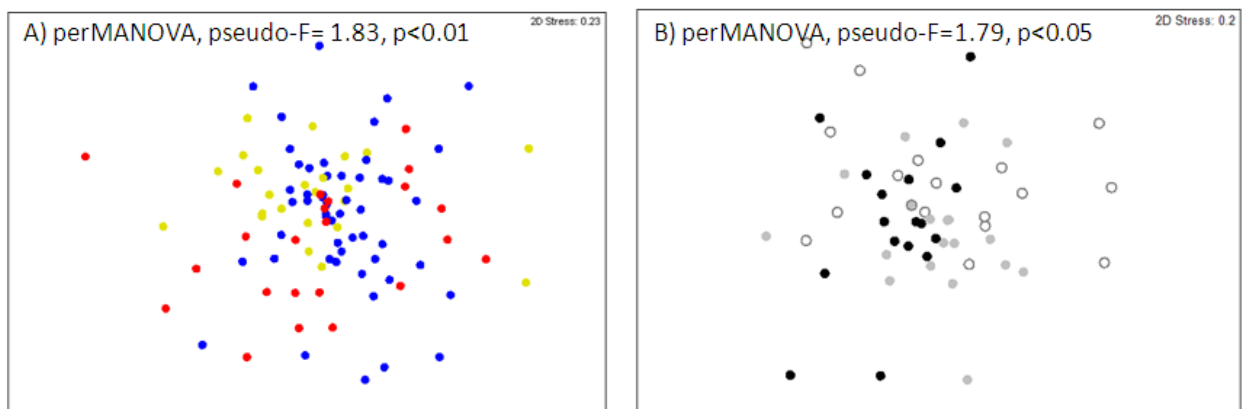


Figure 7. Multi-dimensional scaling ordinations of the predator communities in mosses (presence-absence data) across climate treatments (a) and fragmentation treatments at ambient temperature (b).

Discussion

In previous studies of the effects of warming, treatments have often been applied that increase temperatures to stable, higher means (e.g. Petchey *et al.* 1999). This does not mimic natural variation in temperature, and confounds an increase in mean temperature with a reduction in temperature variability. Studies that have maintained variability in temperature in warmed treatments have maintained variability typical of current climatic conditions (e.g. Briones *et al.* 2009). Yet globally, increases in mean temperatures are predicted to be associated with increased frequency of extreme events (Easterling *et al.* 2000), with profound impacts on communities. While there is a small body of literature describing community-level impacts of warming, and a larger group of studies on assembly after extreme events, ours is the first to describe the assembly of a community after an extreme event, against a back-drop of altered climate, and in the context of habitat fragmentation.

The similarity we found among satellite communities within landscapes, and between satellites and their respective mainlands, suggests a role for dispersal from undisturbed regions in structuring communities after an extreme thermal/moisture event. This is consistent with theoretical expectations from island biogeography and metapopulation theory (MacArthur & Wilson 1967; Hanski 1999), and large-scale experiments on community assembly on islands (Simberloff 1969; Simberloff & Wilson 1970). Although a role for dispersal in preventing community disassembly has been reported extensively using the moss microarthropod system (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002; Staddon *et al.* 2010), our work and that of Starzomski and Srivastava (2007) shows that it can also be relevant in community assembly. Furthermore, our work underscores the

value of undisturbed communities in the recovery of regions impacted by an extreme climatic event (Taberlet & Cheddadi 2002; Shoo *et al.* 2011).

Areas that are buffered from negative impacts of climate have allowed the persistence of species through past changes in climate (Médail & Diadema 2009). Given current and predicted changes in climatic conditions, many calls have been made for the protection of areas that may provide such refugia and help maintain populations and ecological communities (Noss 2001; Taberlet & Cheddadi 2002; Shoo *et al.* 2011). In our experiment, the heated satellite communities that were close to a mainland that was little affected by warming (landscape 8) were better able to cope with warming than satellites subjected to the same heating treatment but whose mainland was severely impacted by heat (landscape 9). Some communities in landscape 9, in particular those subjected to high levels of isolation, showed highly skewed distributions of species abundances. The evenness values in these (e.g. 0.2, 0.3) were markedly lower than those reported for communities left at ambient and for field communities (overall mean: 0.85, standard deviation: 0.1, Chapter 3). Our data therefore provide some experimental support for the landscape-scale value of disturbance-buffered habitats in the face of climate change.

Landscape identity had a strong effect in moderating the impacts of climate and isolation treatments, reducing our capacity to detect treatment effects and interactions. Satellite patches within landscapes resembled each other more than patches from other landscapes, despite having been collected and assigned to landscapes in a haphazard fashion. This is most likely to be due to dispersal from a common source inside the landscape and/or dispersal among satellite patches within the landscapes. A one centimetre gap in habitat corridors is considered to have restricted microarthropod dispersal in other moss studies (e.g. Gonzalez *et al.* 1998; Starzomski & Srivastava 2007). We suggest that our barrier to dispersal may be less hostile than that reported in those studies, as sand can retain more

moisture and provide more opportunities for refuge to dispersing microarthropods than does bare rock. Our results lend support to theoretical and empirical studies showing that dispersal among habitat patches can help homogenize landscapes (Brown & Kodric-Brown 1977; Clarke *et al.* 2008; Laliberte & Tylianakis 2010).

Changes in trophic interactions following increases in temperature can threaten the persistence of ecological communities (Sanford 1999). Studies of aquatic microbes in microcosms have been used to provide experimental evidence of this for communities consisting of up to 16 species (Petchey *et al.* 1999). Here we show that food web structure in a natural, species-rich food web can also respond to experimental warming. In comparison to data on community structure, data on the structure of the food web were more difficult to interpret within the context of temporal variation in the system. On the basis of data from Chapter 3, we expected that heated landscapes would have a higher proportion of detritivores/microbivores in heated landscapes than ambient ones. The opposite occurred. We suggest several possible explanations for this. One is that most taxa in that functional feeding group (oribatid mites) are slow dispersers (Krantz & Walter 2010). If increased temperatures did increase availability of their food source, through increased bacterial activity, lack of dispersal capacity could have prevented access to this increased food resource. A second explanation is that decreased humidity could have rendered the litter too hard to consume (Wallwork 1958). It is also possible that the extreme nature of the temperature treatments applied in the experiment may have resulted in different outcomes to the more gradual and lower intensity effects of seasonal change.

The source of fauna present in isolated moss patches that have been subjected to Tullgren funnel extraction can be difficult to elucidate (Starzomski & Srivastava 2007). Our data on the similarity of satellites to their mainlands suggest that dispersal through relatively hostile matrix can at least partially account for it. Monitoring heated, more severely isolated

moss communities over time, in a fashion similar to that carried out for fragmented moss landscapes by Gonzalez and Chaneton (2002), could provide additional insights into the interacting effects of dispersal ability and functional feeding groups in determining food web responses to fragmentation.

The shifts we report in species composition within the predatory compartment in response to both temperature and fragmentation are of note. They occurred without detectable changes in overall predator abundance or richness, parameters that have traditionally been used to assess effects of treatments on predators in this system (e.g. Gilbert *et al.* 1998; Hoyle & Gilbert 2004; Staddon *et al.* 2010). This suggests that focusing on those parameters alone may fail to detect relevant impacts of disturbance on the moss microarthropod food web.

- *Limitations of the study*

Heating treatments in this study were harsh, although a 6 degree increase in temperature is not beyond the bounds of some predicted changes in climate over the next century (Meinshausen *et al.* 2009). Although moss microarthropod communities routinely experience temperature changes of 8 to 15°C within a day at the collection site (Bureau of Meteorology, station code: 86050), our increases of 6 and 11°C likely stressed these communities, particularly over time, as winter passed. Our 11 degree treatment represents a major perturbation, and is the equivalent of a pronounced and extended heat wave or drought. Nevertheless, our results clearly show that temperature can have significant impacts on the process of community assembly. Future studies testing the degree to which that is subject to the magnitude of increase in temperature relative to ambient are warranted.

The hostile matrix separating habitat patches in our experimental set-up differs from that seen in large-scale, fragmented landscapes in that, in the latter, the matrix is often

habitable by at least some species. Edge effects can in part be driven by those species (e.g. Lacerda *et al.* 2009). Such processes were not considered in this experiment. While fragmentation treatments with very inhospitable intervening habitat are harsh, they are not unrealistic. Fragmentation of aquatic habitats along river networks that dry to pools, patches of vegetation embedded in urban landscapes and rainforest remnants within agricultural matrices all represent natural cases where intervening habitat between patches are extremely hostile.

In our experiments the entire landscapes were warmed, leaving no habitat at suitable temperatures for species to migrate to. In large-scale landscapes, suitable climatic conditions may exist at higher altitudes or latitudes, and it is the restriction of migration to these that can result in a negative interaction between climate change and habitat fragmentation (Opdam & Wascher 2004; Leimu *et al.* 2010). Our experiment considers a scenario in which migration to suitable climates is not possible.

Although the assignment of morphospecies to guilds was carried out more rigorously here than in many previous studies, our procedure does not take into consideration niche breadth, omnivory or diet-switches. All of these would render our assignments to functional feeding groups less precise. The size and diversity of the moss fauna, coupled with the scarcity of data and the equivocal nature of assignment of guilds on the basis of family or genus information (Schneider *et al.* 2004) make more rigorous assignments difficult to implement. In Chapter 3 we have shown that the procedure used for guild assignment can increase our understanding of the moss food web in the context of temporal dynamics, and we have applied the same method here.

Future work and final conclusion

We suggest future work using the moss-arthropod system to assess interactions between habitat fragmentation and climate change is likely to be fruitful and important. Given marked differences in species composition and food web structure between samplings (Chapter 3), it would be interesting to assess whether performing similar experiments taking summer communities as a starting point would produce different results. Furthermore, given indications from our data that in this system, climate-buffered faunal sources can be important in maintaining communities at the landscape scale, research that investigates the basis of resistance to climate stressors (species richness? habitat size? evenness in community compositions?) may provide important insights in the face of increasing climate stressors on ecological communities (IPCC 2007).

The moss microarthropod system is a valuable model for experimentally approaching complex theoretical and applied questions in ecology. To date, studies using the system have contributed diverse and important insights for a better understanding of the role of landscape connectivity in preventing the disassembly of ecological communities (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez 2000; Gonzalez & Chaneton 2002; Starzomski & Srivastava 2007; Staddon *et al.* 2010). We have shown that the incorporation of temperature into these studies can add relevant insights, and can help address the important, little-studied question of interactions between two major landscape-scale disturbances: climate change and habitat fragmentation.

Our results show that assembly after a catastrophic event in the moss microarthropod community depends on habitat connectivity, temperature and the source of recolonising fauna. In a climate future dominated by increased frequency of extreme events, communities are may comprise a resistant core of species with high resistance to extreme events, and a

shifting cast of species assembling based on dispersal traits. Understanding the rules for community assembly in such a dynamic environment requires detailed studies that reconcile ‘extreme event’ and ‘warming’ studies into single experiments, taking into account the highly fragmented nature of most ecosystems. Studies of small-spatial-scale communities consisting of taxa with diverse thermal tolerances, dispersal and life-history traits are likely to be highly informative in predicting effects of altered climates on already fragmented natural ecosystems.

Acknowledgements

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Appendices

- Appendix 1- Microarthropod extraction efficiency over time.

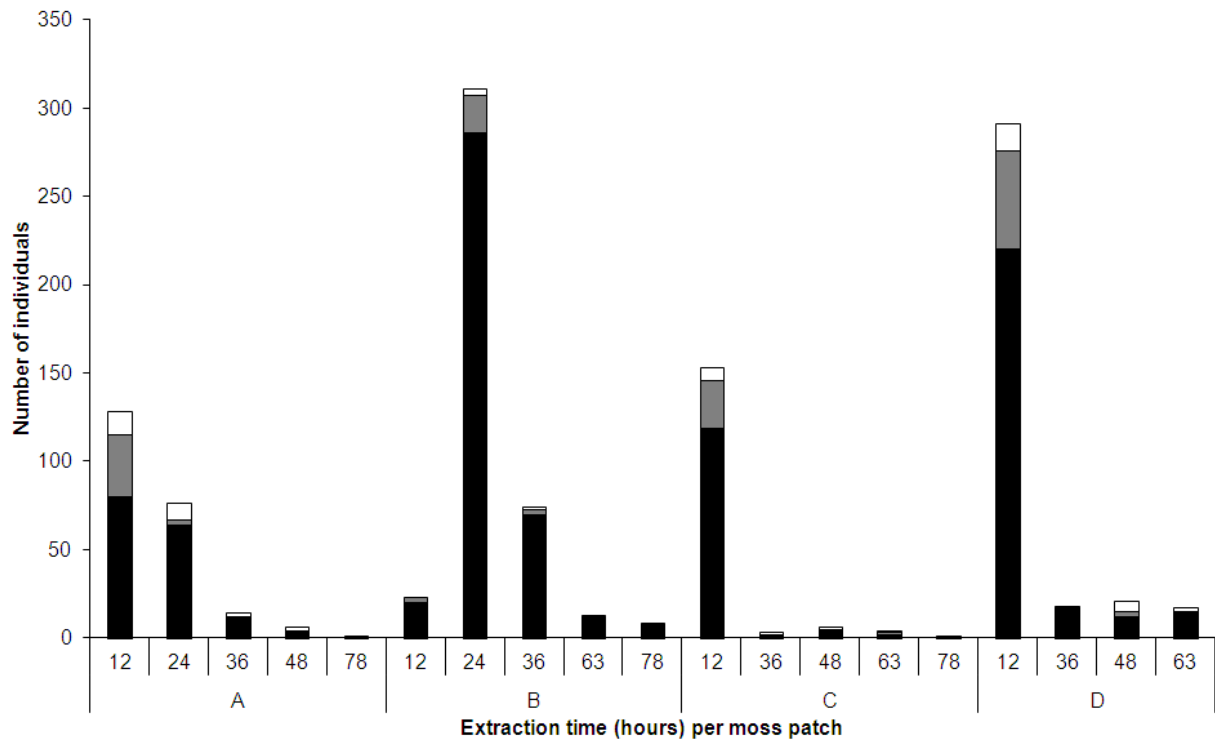


Figure 1. Number of microarthropod individuals extracted from four mosses patches (20 cm²) over time. Black bars represent mites, grey springtails and white other arthropods.

- *Appendix 2 – Temperature differences produced by the heating mats.*

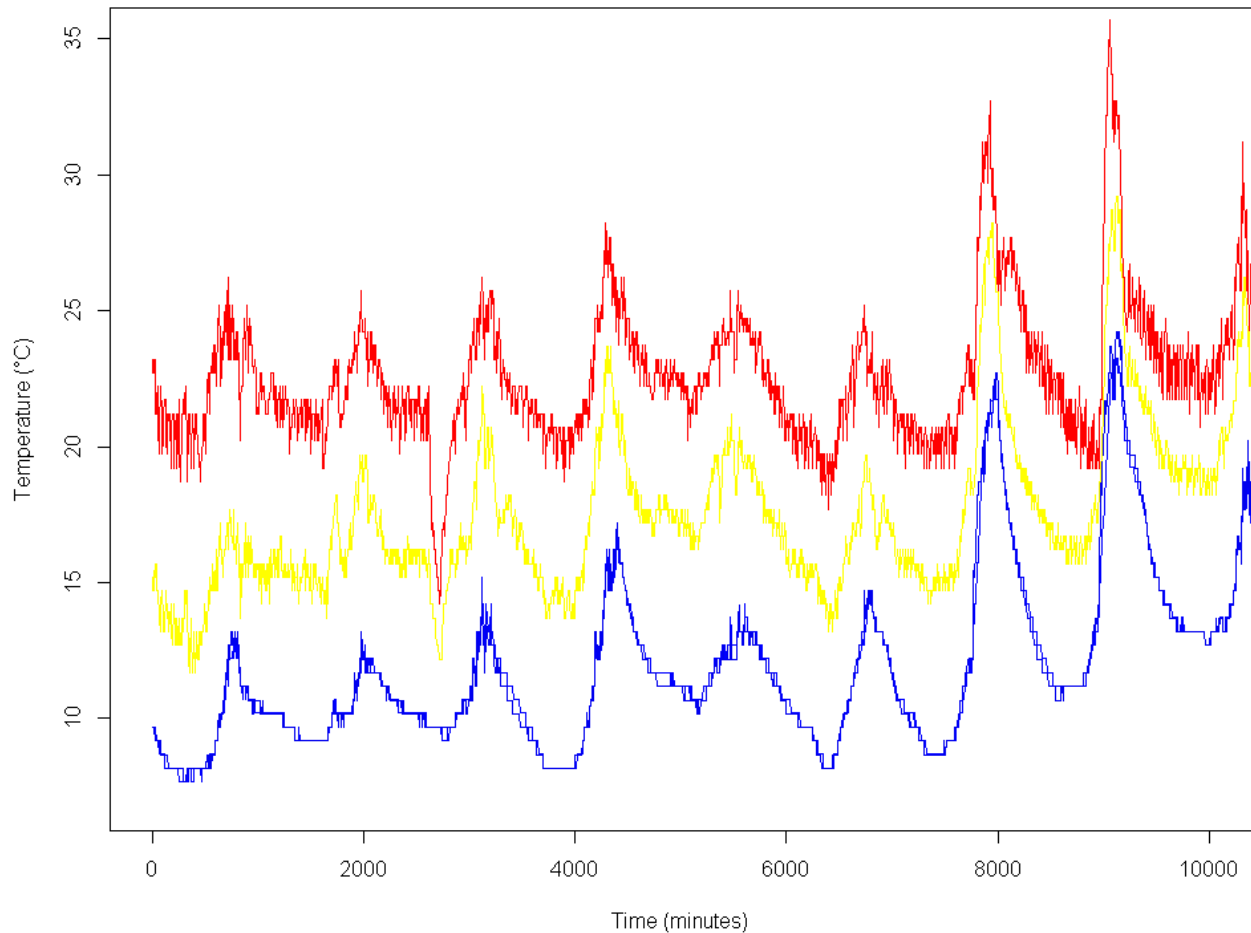


Figure 1. Temperature differences produced by the heating mats under field conditions.

IButtons were placed beside the moss landscapes and made to collect data every five minutes to examine functioning of the heating devices. A subsection of the data, spanning approximately one week, is presented, illustrating the close tracking of changes in ambient temperature by the mats. Blue: ambient, yellow: +6 °C, red: +11 °C.

- *Appendix 3- Review of experimental studies that use moss-microarthropod communities*









Studies on fragmented moss landscapes have provided much-needed data confirming that habitat corridors between otherwise isolated habitat patches can prevent or slow down the process of disassembly of complex communities, and that increased dispersal among

habitat patches is most likely responsible for this result (Gilbert *et al.* 1998; Gonzalez *et al.* 1998). This ‘rescue effect’ of corridors corresponds well with theoretical expectations based on island biogeography theory (Brown & Kodric-Brown 1977). However, effects of connectivity on species richness can be scale-dependent. Although local species richness (α diversity) may be higher in more connected landscapes, low turnover between habitat patches (β diversity) created by a homogenizing effect of dispersal can result in lower regional diversity in connected landscapes (γ diversity). These scale-dependencies have been shown in moss communities (Starzomski & Srivastava 2007) as well as in larger-scale systems (Clarke *et al.* 2008). Furthermore, studies using moss communities have also experimentally shown that increased connectivity can not only prevent community disassembly, but also maintain ecosystem function, as measured by nutrient cycling and total heterotrophic biomass (Gonzalez & Chaneton 2002; Staddon *et al.* 2010). Such studies have helped address criticisms about the conservation value of habitat corridors, raised partially on the basis of a lack of empirical data to support claims that corridors could help reduce species extinction risk (Simberloff *et al.* 1992).

Not all studies on fragmented moss communities have detected significant effects of isolation: non-significant results at the level of α and γ diversity have been obtained, possibly because connectivity may be more important where climatic conditions are more extreme, given that in those cases dispersal may be more important for the maintenance of population sizes (Hoyle & Gilbert 2004). Support for these suggestions has been provided by subjecting moss landscapes with different levels of fragmentation (isolation and surrounding-habitat size) to differing frequencies of intensive droughts (Starzomski & Srivastava 2007). Communities from isolated habitats were less resilient (less able to recover from high frequency, high intensity droughts) than those in more connected habitats. This is an

important piece of evidence showing the potential for an interaction between the loss of habitat connectivity and (episodic) unfavourable climatic conditions. We highlight this study as the only one we have found that experimentally tests the interaction between habitat fragmentation and elements of climate change using complex natural communities.

Table 1. Review of studies performed on moss-microarthropod communities.

Study	Treatments	Design	α diversity	β diversity	γ diversity	Total abundance	Total biomass	Community structure	Food web structure
Gonzalez <i>et al.</i> , 1998	Unfragmented, fragmented, fragmented with corridors, and fragmented with pseudocorridors.		↓						
Gilbert <i>et al.</i> , 1998	Unfragmented, fragmented, fragmented with corridors, and fragmented with pseudocorridors.		↓		↓				Predators more susceptible than non-predators.
Gonzalez and Chaneton, 2002	Unfragmented, fragmented, fragmented with corridors, and fragmented with pseudocorridors. Time	 ↓ preferentially species with low abundance and small distribution	↓		?	↓ only after 8 months	↓ only after 6 months		
Hoyle and Gilbert, 2004	Unfragmented, fragmented, fragmented with corridors of differing length and width, and fragmented with pseudocorridors.		N.S.		N.S.	N.S.			N.S. (predators)
Hoyle 2005	Unfragmented, fragmented, fragmented with corridors of differing length and width, and fragmented with pseudocorridors.		N.S.			N.S.			
Stazoski and Srivastava, 2007	Region size and connectivity. Disturbance frequency.		↓	↑	N.S.	↓ when disturbed with drought		✓	
Staddon <i>et al.</i> 2010	Unfragmented, fragmented, fragmented with corridors of differing length and width, and fragmented with pseudocorridors.								✓
This study	Levels of isolation Temperature		N.S.			N.S.		✓	✓

General Discussion

Landscape-scale disturbances have caused severe, negative and likely irreversible impacts on biodiversity world-wide (Sala *et al.* 2000; Parmesan & Yohe 2003; MEAB 2005). In order to help reduce or ameliorate impacts of disturbances, ecologists must rise to the considerable challenge of gaining a better understanding of the principles governing the assembly and disassembly of ecological communities. Community ecology has been criticised for failing to produce information that can help solve core environmental problems (Hansson 2003) and for not quantifying the dynamics of the processes that maintain biodiversity in the ways needed for prediction (Simberloff 2004). Many obstacles have hindered this endeavour, including the large spatial and temporal scales at which many communities operate.

Microcosms (food webs operating on small spatial scales) have helped experimentally to address theoretical and applied questions in ecology and provided many useful insights (Lawton 1995; Ives *et al.* 1996; Kitching 2000; Srivastava *et al.* 2004; Reiss *et al.* 2010; Drake & Kramer 2011). In particular, the moss-microarthropod model has been used extensively for the study of the effects of habitat loss and fragmentation on the associated microarthropod communities (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez 2000; Gonzalez & Chaneton 2002; Hoyle 2004; Hoyle & Gilbert 2004; Hoyle 2005; Starzomski & Srivastava 2007; Staddon *et al.* 2010). Feasibility of manipulation of the habitat, high species richness and short generation times are often highlighted as useful attributes of the system (Gonzalez *et al.* 1998; Hoyle & Gilbert 2004; Starzomski & Srivastava 2007; Staddon *et al.* 2010). In light of these and other characteristics, calls have been made for the use of moss microarthropod communities in addressing ecological questions (Lindo & Gonzalez 2010).

Challenges inherent in working with the system should not be underestimated however, and the extrapolation of the results from the system to larger-scale ones needs to be validated.

A total of 20,000 mite species have been estimated for Australia alone, and not surprisingly, there are more undescribed mite species than described ones (Halliday 2001; Krantz & Walter 2010). Taxonomy of very small organisms can be challenging and time-consuming. This is especially so where reference collections, compilations of taxonomic keys, high resolution images and a short-list of likely candidates are not at hand. We have created these for a moss system and made them available for future researchers. We expect that these, along with the Moss Microarthropod Database created and the expert-validated identification of common taxa, will greatly facilitate future work in this model community.

Another challenge inherent in working with mites is the estimation of diets. This is necessary if detailed food web information is to be used in the system to obtain a better understanding of community dynamics in the face of disturbance. We have tackled this problem by combining new techniques in the estimation of mite diets (stable isotope analysis, Schneider *et al.* 2004; Maraun *et al.* 2011) with more established methodologies (Kaneko 1988; Buryn & Brandl 1992), to develop an inexpensive and quick diet assessment tool that can be applied to a large number of mite taxa. Through its use, we have been able to provide a detailed description of the moss food web, significantly improving on previous descriptions (Lindo & Gonzalez 2010). The highly-resolved food web we provide is temporally explicit, and can be added to the small number of existing food webs that include temporal variability (e.g. Closs & Lake 1994; Tavares-Cromar & Williams 1996; Thompson & Townsend 1999).

Our studies on the basic structure of the moss food web have allowed us to explore the degree to which this food web resembles that of larger-scale systems. Using a large compilation of food webs studies from around the world, we have been able to identify the ways in which the moss food web does and does not structurally resemble larger-scale webs.

The data we present provide some validation of the use of moss microarthropod communities as models in disturbance ecology, as food web structure can mediate communities' responses to disturbance (Wilsey & Potvin 2000; Ings *et al.* 2009; Wittebolle *et al.* 2009). Additionally, the comparison allowed for the identification of an attribute of the moss food web that may render it more robust to disturbance than other food webs, namely, relatively low prey to predator ratios (Finke & Denno 2004). These comparisons were made possible by our development of “*foodweb*”, a software package that is now embedded in a commonly used, free statistical tool, the R Statistical Software (R Development Core Team 2011). We expect this package will be of great use to food web ecology researchers.

Our field experiment combined the effects of climate change and fragmentation in a factorial design. We found that temperature affects community and food web structure in this system, but that the magnitude of those effects can depend on the original community and the potential for dispersal of the fauna. This provides two novel insights. Firstly, it appears that some aspects of community structure can provide resilience to the effects of climate change, even within one metacommunity. Secondly, dispersal traits are key drivers that determine community responses to changing climate, particularly when fragmentation also occurs. The integration of traits into future studies of food web assembly and disassembly due to changing climates and changed landscapes is critical.

The study of temporal variability in food web structure provided an important reference point to evaluate changes in community structure in the experimental study. We showed that, while food webs did shift towards the summer food webs when warmed, some aspects of community and food web structure appeared to be entirely novel. This supports the contention that rapid and extreme warming of the type predicted under climate change may generate novel food webs. These food webs have unknown interactions with key ecosystem processes and their dynamics are as yet unstudied.

We have identified several lines of future research. Further exploration of community and food web effects of synergies between climate change and habitat fragmentation is critical, and can be facilitated by the use of model systems such as that used here. Research is needed in this area to understand the potential consequences for biodiversity and ecosystem function, of changing climates in already fragmented landscapes. Having shown here the potential for relatively extreme climatic change to alter food webs, future studies should consider effects of milder temperature treatments. We also illustrated the effects of the starting community on the experimental outcomes. There is a need for future research to explore the effects of treatments starting at different times of the year, and to understand how existing spatial variability in community composition may affect food-web responses to warming.

The temporal variability in food-web structure reported here warrant further attention. We suggest that seasonal surveys of moss microarthropod communities should be replicated both in time and space, and that these surveys be coupled with studies of fungal and bacterial activity in the system. This would help clarify whether patterns reported here respond to seasonal dynamics driven by resource availability, like those reported in other systems (e.g. Thompson & Townsend 1999). A better understanding of the relationship between temperature, humidity, rates of organic matter decomposition, relative abundance and activity of fungi and bacteria, and food web structure is likely to contribute to the important debate regarding potential feedbacks between soil organic matter decomposition and climate change (Couteaux *et al.* 1995; Davidson & Janssens 2006).

Research is needed to describe better the predatory compartment of the moss food web. Do predatory mites feed at the same level as spiders, pseudo-scorpions and velvet worms? Our stable isotope results indicate that they do, but these results are not in line with some descriptions of soil food webs (e.g. Scheu 2002). An additional, relatively species-poor

second level of predation in the food web would change our perception of its topology considerably. Research is also needed into the dietary niche breadth of the predators. These data would allow for a more accurate representation of the food web network, and better understanding of expectations of stability in the face of disturbance.

The work presented here represents a contribution to the growing body of food webs that include detailed information on traits in the trophic network. Traits were critical in this study both for understanding trophic relationships (cheliceral morphology) and interpreting community responses to the experimental treatments (dispersal traits). Including additional information on traits in food web studies is critical in order to understand the dynamics of changes in food web structure when subjected to disturbance, and in order to interpret likely functional consequences of changes in food web structure. In an applied context such as that illustrated here, trait information (particularly on dispersal-related traits) will provide insight into the likely tolerance of food webs and parts of food webs to anthropogenic disturbances such as habitat fragmentation and changing climate.

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Prologue

Números

Tienen un número preciso las hojas de los
árboles. No son innumerables los peces
del mar, ni las olas, ni las ráfagas de
viento que recorren la tierra.

Podrían contarse los besos y los litros de sudor
derramados en el amor. Existe un número
finito que indica las veces en que alguna
persona quiso irse, renunciar a lo
concreto, entregarse a los grises.

Esos números existen, pueden tallarse en piedra,
y son inútiles.

Pedro Borges - *Elementos*

Numbers

There is a precise number of leaves on trees.
Neither the fish in the sea, nor the waves
nor the gusts of wind that travel the earth
are innumerable.

Kisses and litres of sweat dripped in love could
be counted. There is a finite number that
indicates the number of times a person
wished to leave, renounce the concrete,
surrender to the greys.

Those numbers exist, can be carved in stone and
are useless.

Pedro Borges – *Elements*
Translation by Giselle Perdomo

Considerando en frío, imparcialmente

Considerando en frío, imparcialmente,
que el hombre es triste, tose y, sin embargo,
se complace en su pecho colorado;
que lo único que hace es componerse
de días;
que es lóbrego mamífero y se peina...

Considerando
que el hombre procede suavemente del trabajo
y repercute jefe, suena subordinado;
que el diagrama del tiempo
es constante diorama en sus medallas
y, a medio abrir, sus ojos estudiaron,
Desde lejanos tiempos,
Su fórmula famélica de masa...

Comprendiendo sin esfuerzo
que el hombre se queda, a veces, pensando,
como queriendo llorar,
y, sujeto a tenderse como objeto,
se hace buen carpintero, suda, mata
y luego canta, almuerza, se abotona...

que el hombre procede suavemente del trabajo
y repercute jefe, suena subordinado;
que el diagrama del tiempo
es constante diorama en sus medallas
y, a medio abrir, sus ojos estudiaron,
Desde lejanos tiempos,
Su fórmula famélica de masa...

Considerando también
que el hombre es en verdad un animal
y, no obstante, al voltear, me da con su tristeza en la cabeza...

Examinando, en fin,
sus encontradas piezas, su retrete,
su desesperación, al terminar su día atroz, borrándolo...

Comprendiendo
que él sabe que le quiero,
que le odio con afecto y me es, en suma, indiferente...

Considerando sus documentos generales
Y mirando con lentes aquel certificado
que prueba que nació muy pequeñito...

le hago una seña,
viene,
y le doy un abrazo, emocionado.
¡Qué más da! Emocionado... Emocionado...

Cesar Vallejo – *Poemas Póstumos I*

Considering calmly, impartially

Considering calmly, impartially,
that man is sad, coughs and, however,
is pleased in his coloured chest;
that the only thing he does is make himself up of days;
that he is a working mammal and combs himself...

Considering
that man proceeds smoothly from work
and becomes boss, sounds subordinate;
that the diagram of time
is constant diorama on his medals
and, half opened, his eyes studied,
from distant times,
his starving formula of mass...

Understanding without effort
that man is left, sometimes, thinking,
as if wanting to cry,
and, subject to lying like an object,
becomes a good carpenter, sweats, kills
and then sings, has lunch and buttons up...

Considering also
that man is in truth an animal
and, regardless, when he turns he hits me on the head with his sadness...

Examining
his found pieces, his toilet,
his desperation, when finishing an atrocious day, erasing it...

Understanding
that he knows I love him
that I hate him with affection and that I am, in sum, indifferent to him...

Considering his general documents
and looking with glasses at the certificate
that proves that he was born very little...

I signal to him,
he comes,
and I hug him, excited.
What can you do! Excited... Excited...

Cesar Vallejo – *Posthumous poems I*
Translation by Giselle Perdomo