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Diversity and drivers of oribatid mites (Acari: Oribatida) in boreal peatlands

Carlos Rafael de Araujo Barreto, *The University of Western Ontario*

Supervisor: Lindo, Zoë, *The University of Western Ontario*

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Abstract

Boreal peatlands are important ecosystems for carbon cycling, storing 1/3 of the world's terrestrial carbon in only ~3% of the globe, making them a key component of potential mitigation strategies in response to global climate warming. Experiments have shown that warming can affect plant and microbial communities in ways that potentially shift peatlands from carbon sinks to sources. Soil food webs, including the microarthropod community, are key in carbon cycling but are relatively understudied both in peatlands and under experimental warming. My research capitalized on a large-scale experimental field manipulation of warming in two contrasting peatland sites in Northern Ontario, and addressed: 1) the diversity of oribatid mites in Canadian peatlands, 2) factors that drive litter decomposition and oribatid mite communities, by examining different microhabitats, 3) how these communities shift under experimental warming, and 4) the carbon flux in the soil food web, using energetic models for natural and warmed conditions. My published synthesis of oribatid mites in peatlands of Canada updates the species records from 71 to 186 species. I also show that peatland oribatid mite communities are driven by soil moisture and temperature, and that responses to warming are species- and site-specific. Oribatid mite community composition is driven by interactions between temperature and moisture, and dependant on peatland type, leading to the conclusion that oribatid communities follow a species sorting metacommunity paradigm driven by environmental filters. Models of carbon flux suggest that compositional changes in the soil food web under warming will significantly alter carbon cycling and potentially the carbon storage potential of peatlands. Using field experiments alongside modelling approaches for soil fauna, my research provides a comprehensive view of the role of peatland microarthropods and their relation to ecosystem processes under environmental changes. My work is also novel because soil systems are often treated as a 'black box' in global change carbon models; thus, my work is the first to link changes in peatland soil biodiversity to carbon storage and release.

Summary for Lay Audience

Peatlands are wetland ecosystems with a high-water table that are important for carbon cycling because of a large organic soil layer composed of partially decomposed plant material called peat. In the boreal zone, peatlands store 1/3 of the world's terrestrial carbon, but only occupy ~3% of the globe. This ability to store high amounts of carbon in relatively small areas confer boreal peatlands the property of acting as a key component of mitigation strategies in response to global climate warming. This is because by storing more carbon than releasing carbon, less carbon is then in the atmosphere to drive higher temperatures. Different microbial, animal and plant species inhabit peatlands, and they are also involved in this carbon storage ability. Studies have shown that higher temperatures can change the plant and microbial types that dominate peatlands, and this change can thus alter the carbon cycle, but studies demonstrating how warming will affect peatland invertebrates are scarce. My thesis focuses on oribatid mites, which are small arachnids related to spiders, but are involved more directly in carbon cycling. I describe their diversity in two contrasting peatland sites in Northern Ontario, and show that oribatid mites of peatlands in Canada are more diverse than we thought, the fauna includes specialist as well as generalist species, and also that species that reproduce asexually tend to dominate. Using a climate change experiment in both sites, I show that warming and warming-induced moisture reduction have variable effects on oribatid mite communities that depend on species and peatland type. I then confirm that moisture has a more important influence on oribatid mite communities than plant litter type when assessing the oribatid mite fauna in litterbags. Finally, I use food web energetic models to show that changes in oribatid mite community composition caused by warming and warming-induced moisture reduction are suggested to alter the carbon cycling and potentially the carbon storage potential of peatlands.

Co-Authorship Statement

Chapters contained within this thesis are either published or planned manuscripts in peer-reviewed journals.

Chapter 2 (https://doi.org/10.11158/saa.26.5.4) was envisioned by both Dr. Zoë Lindo and Carlos Barreto; both authors contributed to the sampling and identifications, CB performed sample processing and data analysis. The material in Chapter 2 has been published in the Journal Systematic & Applied Acarology as open access and theses are written with non-commercial purposes.

Chapter 3 (https://doi.org/10.1080/11956860.2017.1412282) was conceived and initiated by ZL; CB and ZL contributed to identifications, and CB performed sample processing and data analysis. The material in Chapter 3 has been published in the Journal Écoscience, which allows me to use a version of my article in my thesis. Specifically, the copyright transfer states:

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Chapter 4 (https://doi.org/10.1016/j.pedobi.2021.150772) was conceived and initiated by ZL and Dr. Brian Branfireun in collaboration with the Ministry of Northern Development, Mines, Natural Resources (OMNMNRF); CB and ZL contributed to the sampling, identifications, and CB performed sample processing and data analysis. The journal Pedobiologia (Elsevier) states in its copyright FAQ section:

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Chapter 5 (in preparation for publication) was envisioned by ZL and CB in collaboration with Dr. Robert Buchkowski; CB collected the data (that partly also stemmed from the work of Caitlyn Lyons and Devdutt Kamath), and CB and RB analysed the data.

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"So...my main question for you would be whether you are willing to change taxonomic groups and work on soil mites? If so, then I see no reason why the BRACE project would not have room for you." "...but I will be very clear, that I can only fund students working on soil fauna. Please let me know how you feel about that.". And this is how I ended up doing my Ph.D. with Dr. Lindo. Little did they know that I would have no issues learning a new group such as the oribatid mites, and more, that I would follow their own steps. I have a very long list of things I must thank them for, but I will summarise this by saying I am thankful for them believing in me. Dr. Lindo took the risk of bringing in an international Ph.D. student with neither a M.Sc. degree nor a similar research background to be part of their team, when, on paper, I was not a fit and other PIs would not have considered me. They gave me my once in a lifetime opportunity and I will never forget this. Dr. Lindo has everything a supervisor who roots for their students should have. I felt really worthy under their supervision.

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Chapter 1

1 General Introduction

1.1 Boreal peatlands

Peatlands are defined as wetlands with organic soils over 40 cm deep that are often dominated by *Sphagnum* mosses or graminoids and can be classified into bogs or fens, depending on whether they receive water exclusively from precipitation (i.e., disconnected from groundwater sources), or are hydrologically connected to groundwater (i.e., they have a fluctuating water table), respectively (National Wetlands Working Group, 1997). A third peatland type includes swamps, which can be dominated by trees and shrubs and have water rich in dissolved minerals – although swamps can also be characterised by minimal or no peat accumulation (National Wetlands Working Group, 1997). Globally, peatlands are rare (Global Environment Centre and Wetlands International, 2008), covering ~3% of the globe (Gorham, 1991), with most peatlands present in the Northern Hemisphere, and the majority within the boreal zone (Frolking et al., 2011).

Although covering a relatively small fraction of the Earth's area, peatlands are globally important carbon stores (Beaulne et al., 2021; Frolking et al., 2011; Harenda et al., 2018; Hugelius et al., 2020) that contain at least 550 Gt of carbon in their peat (i.e., partially decomposed plant matter) (Global Environment Centre and Wetlands International, 2008), which constitutes about 1/3 of the world's terrestrial C (Limpens et al., 2008), making them major global C carbon sinks. Specifically, in Canada, peatlands cover ~13% (1,136,000 km^2) of the landscape (Tarnocai et al., 2011) with the vast majority in the boreal and subarctic ecozones, and are estimated to store 147 Gt carbon

(Tarnocai, 2006, 2009), which represents 59% of Canada’s stored soil organic carbon (Tarnocai and Lacelle, 1996). This ability to store carbon in soils is most evident in boreal zones, where a combination of abiotic factors such as low temperatures, waterlogging and acidic conditions slow decomposition rates which allows for higher accumulation of organic matter in peatlands compared to other ecosystems (Moore et al., 2007).

1.2 Oribatid mites of peatlands

The ability of peatlands to store carbon is also dependent on biotic aspects, including the activity and diversity of plant, microbial, and soil invertebrate fauna communities. At the same time, these deep accumulations of organic soil horizons provide habitat and food resources for a myriad of soil biodiversity. Among the soil invertebrate fauna of boreal peatlands are the dominant group of oribatid mites (Arachnida: Acari: Oribatida) (Figure 1.1). Oribatid mites inhabit almost all terrestrial environments, and often as the dominant, or most abundant arthropod group, and occur in high densities (local abundance commonly over 100,000 ind. per m^2) and species richness (~11,000 named species in > 170 families with local diversity up to 150 species; Subías (2021)) in most soils and other organic-rich detrital systems like moss-dominated habitats, giving them the common name of moss mites (Norton and Behan-Pelletier, 2009). Oribatid mites are well represented in terms of diversity in wetlands such as peatlands (e.g., Chapter 2; Lehmitz, 2014; Lindo, 2015; Markkula et al., 2019; Minor et al., 2019; Seniczak et al., 2019), although studies on their ecology and taxonomy are not as abundant in Canada as they are in Europe, for example.

Oribatid mites are small arachnids (most 300–700 μm) that exhibit *K*-style life history traits, including low reproductive output and long-life spans (on average 1–2 years) (Norton and Behan-Pelletier, 2009). Evolutionarily, their long lives have selected for defences like protective setae and structures, camouflage, cuticular hardening and defensive strategies like glands and diverse body shapes that allow them protection from predators (Norton and Behan-Pelletier, 2009; Peschel et al., 2006). Overall, reproduction in oribatid mites is predominantly sexual, with indirect fertilization and oviposition occurring in most species (Norton and Behan-Pelletier, 2009). However, an estimated 8–9% of species reproduce by obligate thelytoky (i.e., asexual; female parthenogenesis) (Cianciolo and Norton, 2006), which is highly unusual in most animal groups as pointed by Bell (1982), for instance, who estimated parthenogenetic species to represent only 1% of all insect species. Particularly, oribatid mites have been noted to be better represented by parthenogenetic species in peatlands compared to the oribatid mite fauna in other ecosystems (Behan-Pelletier and Bissett, 1994; Maraun et al., 2019), both in terms of number of parthenogenetic species and total proportional abundance, which might be related to a lower efficacy of free-standing spermatophores produced by males in wet habitat like peatlands (Norton and Palmer, 1991), and/or to resources being plentiful and easy to access in peatlands (Maraun et al., 2019).

Most oribatid mite species are particle-feeding saprophages (i.e., they consume dead plants and animals) and mycophages (i.e., they consume fungi) (Norton and Behan-Pelletier, 2009), but some species have been shown to feed on *Sphagnum* mosses, on protozoans, and on nematodes (Lehmitz and Maraun, 2016). The feeding habits of oribatid mites combined with their dominance in soils make them essential for ecosystem processes such as decomposition, nutrient cycling, and carbon transformation in high-carbon storage ecosystems like peatlands, where they are part of the detrital food web (Figure 1.2).

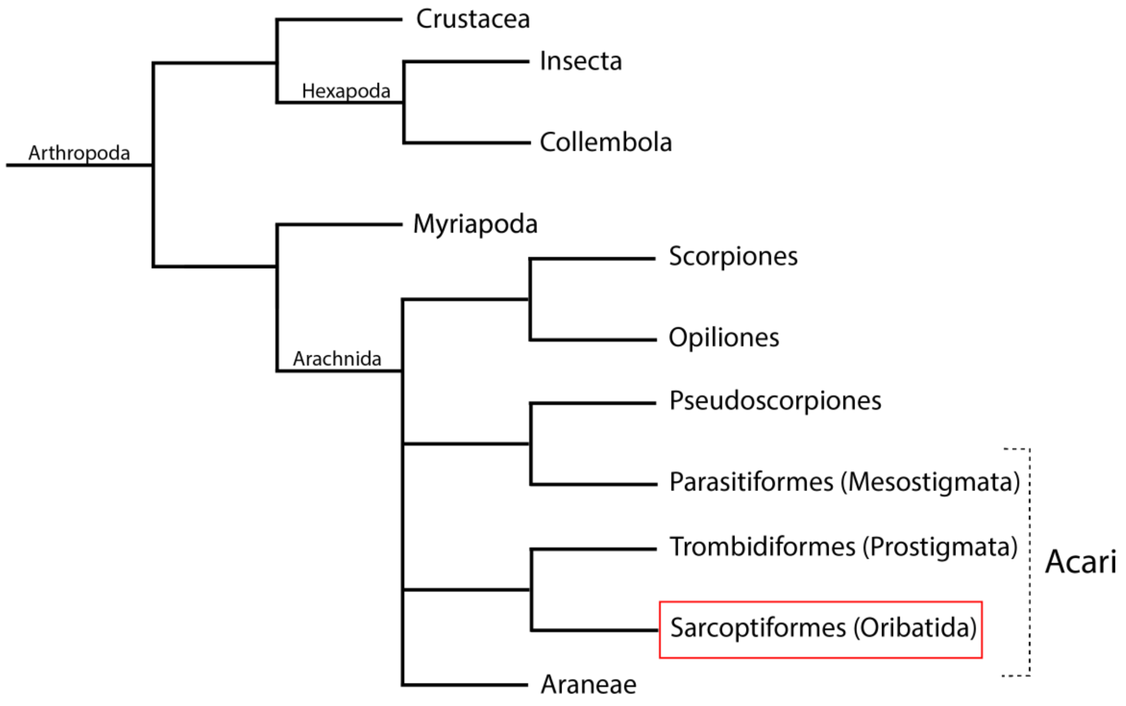

Figure 1.1 Simplified depiction of the relationship between main arthropod groups with focus on mites (Acari).

Phylogenetic tree adapted from Dabert et al. (2010), Giribet and Edgecombe (2013), Kjer et al. (2016), Sanggaard et al. (2014), and Shultz (2007). Only the main groups are presented here. Oribatida is part of the Sarcoptiformes (in red); Astigmata is included in Oribatida and not shown.

1.3 Detrital food webs

Food web models are a visual representation of the feeding relationships among members within a community (Brose and Scheu, 2014; Moore and de Ruiter, 2012), and can be conceptualized as interaction networks, where species or functional groups are nodes, and the feeding relationships are directional links representing the flow of nutrients and energy. In soil systems like peatlands, detritus (i.e., dead organic matter) is the basal source of carbon and other nutrients which stems mostly from inputs of vegetation (i.e., litter) (Odum and Biever, 1984) and is the foundation of soils both as a habitat for soil organisms (Moore et al., 2004), but also as the source of nutrients for microbes and plants through decomposition. In addition to decomposition, recycling of nutrients, and carbon storage also occur in soil systems, with much of detritus remaining and accumulating in soils, which leads to active carbon storage/sequestration in peatlands (Adl, 2003; Fierer et al., 2009).

In detrital food webs, soil microbes (bacteria, fungi) are the primary decomposers (i.e., consumers) of detritus, alongside root exudates that serve as the basal resource for all soil consumer trophic groups. Microbial consumers, or secondary decomposers, include microfauna (e.g., nematodes) and mesofauna (mostly microarthropods, e.g., springtails and mites), which are fed upon by predacious microarthropods, usually mesostigmatid mites (Acari: Mesostigmata), but also spiders and centipedes (Lawrence and Wise, 2017). Most oribatid mite species are then considered secondary decomposers in detrital food webs from feeding on fungi (Figure 1.2).

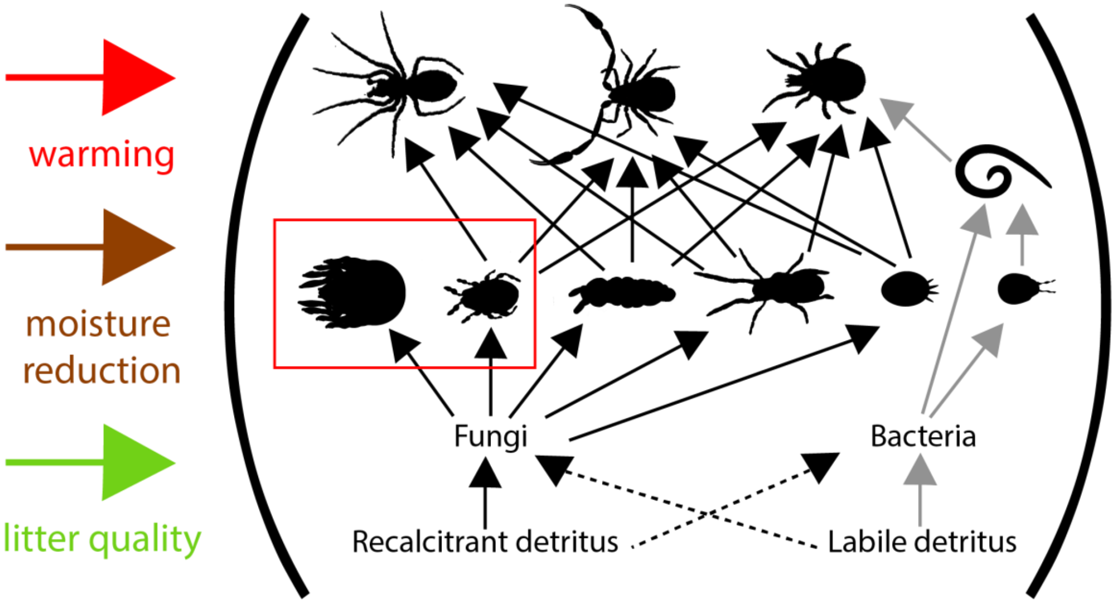

Figure 1.2 Simplified soil food web showing feeding relationships, fungal and bacterial energy channels, and abiotic factors expected to affect biomasses, diversity, energy and/or topology.

From left to right: spiders, pseudoscorpions and mesostigmatid mites are predators; nematodes are omnivores (feeding on two different trophic levels: bacteria and protists); non-edible oribatid mites (highly sclerotized, protected species), edible oribatid mites (non or weakly sclerotized, no protections and small-bodied species), springtails, prostigmatid mites, astigmatid mites and protists (all considered secondary decomposers for feeding on fungi or bacteria); fungi feeding predominantly on recalcitrant low-quality detritus, and less on labile high-quality detritus; and bacteria vice-versa. The subdominant feeding option is represented by the dashed lines. The fungal channel is represented by black and the bacterial channel by grey arrows. The red box highlights the oribatid mites.

Species richness at each of these trophic levels is exceedingly high (Wall and Virginia, 2000), yet feeding groups are often depicted as broadly classified taxonomic groups with similar feeding efficiencies, rates of production, and predation. However, trophic interactions can occur within and between the consumer groups (Garvey and Whiles, 2017), with omnivory (feeding at multiple trophic levels) more common in detrital systems than other types of food webs (Digel et al., 2014). Detrital food webs also demonstrate separated flows of energy (pathways or energy channels) that stem from either bacterial or fungal consumers that differ in detrital substrate use (labile vs recalcitrant detrital sources), and support different levels of trophic diversity (low vs high), and cycle nutrients at different rates (fast vs slow, respectively) (Bardgett and Wardle, 2010; Coleman et al., 1983; Strickland and Rousk, 2010; van der Heijden et al., 2008) (Figure 1.2).

While these dual energy channel web topologies are shown to confer stability (Rooney et al., 2006), different factors can influence food web configurations. On the one hand, predation (or consumer) pressure may exert a measurable response on their prey (or resource), potentially affecting species richness, abundance or productivity (Power, 1992) through ‘top-down’ effects (Barton et al., 2009; Lang et al., 2014). On the other hand, warming-induced increases in resource (or prey) availability can benefit consumers (or predators) through ‘bottom-up’ effects (A’Bear et al., 2013; Antiqueira et al., 2018). Both top-down and bottom-up processes can propagate beyond the next trophic link (i.e., a trophic cascade (Carpenter et al., 1987)), which can destabilize food webs and affect mid-trophic level groups like oribatid mites. Alternatively, when mid-trophic level groups are disproportionately affected by environmental change, they can affect both higher and lower tropic groups (A’Bear et al., 2014; Barton et al., 2009; Lang et al., 2014). These effects on food web community composition and/or biomass may have consequences for carbon flux because carbon is the energetic currency of food webs; carbon is consumed via feeding, assimilated into biomass (both growth and reproduction) and used in metabolic processes like respiration, or returned to the environment as unconsumed, egested or dead matter (Moore and de Ruiter, 2012) before moving to the next trophic level through predation. Ultimately, the fate of these carbon transformations is of high importance in peatlands, given their high capacity of storing soil organic matter.

1.4 Climate warming effects on peatlands

Climate warming is predicted on the order of 1.5-8ºC in the next 50-100 years (IPCC, 2013, 2018) depending on latitude and other factors. The effects of climate warming may have broad consequences for species distributions, species physiology (e.g., metabolic processes like production (Malhotra et al., 2020), reproduction (Lindo, 2015), metabolic demands (Wyatt and Rober, 2019), enzymatic inefficiencies (Reczuga et al., 2017)), and species interactions (Jassey et al., 2015). The consequences of such warming-induced changes are novel communities (Lyons et al., 2020), reconfigurations/rewiring of food webs (Jassey et al., 2013), and altered carbon and nutrient cycling (Briones et al., 2014; Carrera et al., 2009). In boreal peatlands, the widely held viewpoint is that climate warming will decrease carbon storage potential and potentially release stored soil carbon to the atmosphere due to changes in belowground communities.

Warming experiments in peatlands have shown cascading effects from aboveground to belowground communities that affect ecosystem-level processes.

Specifically, this involves vegetation shifts from low-nutrient mosses towards more degradable vascular plants (Dieleman et al., 2015; Fenner et al., 2007), with decreases in moss cover (Lyons et al., 2020) and increase in phenolics associated with sedge root growth (James, 2020) coinciding with more labile carbon availability (Dieleman et al., 2017, 2016) in peat-soils, greater microbial activity (Asemaninejad et al., 2017), faster decomposition rates (Dieleman et al., 2016), homogenization of fungal communities favouring recalcitrant decomposers (Asemaninejad et al., 2018) and increased CO_2 (Bragazza et al., 2012; Briones et al., 2014; Tian, 2019) and CH_4 (Tian, 2019) emissions. In other systems, it is indicated that biotic interactions within the soil food web can significantly alter patterns of carbon storage (Maynard et al., 2017); however, soil systems and soil biodiversity are currently not explicitly considered in global climate models. In addition, the effects of climate warming on peatland detrital food webs have not been investigated to date.

Nonetheless, climate warming can directly and indirectly affect peatland oribatid mite communities through increased metabolism — as per the metabolic theory of ecology — and through changes in the abiotic environment and biotic interactions. Changes in plant and microbial communities can also affect other trophic levels like the secondary decomposer oribatid mites through trophic cascades. Specifically, global change factors such as warming are anticipated to increase productivity of lower trophic groups in detrital food webs through bottom-up processes and cascades often favouring small-bodied species (Brose et al., 2012; Lindo, 2015), while warming often disproportionately affects top trophic levels creating top-down cascades (Lang et al., 2014; Meehan et al., 2021). In soil systems, increased productivity of microbes and their consumers (e.g., oribatid mites) are anticipated to accelerate decomposition and increase rates of nutrient cycling (Kardol et al., 2010; Ngai and Srivastava, 2006; Wagg et al., 2014), increasing carbon release from soil stocks and reducing overall soil carbon sequestration potential (Tarnocai, 2006). In other words, ultimately, warming is predicted to shift northern peatlands from carbon sinks to carbon sources because of changes in soil biodiversity (Bragazza et al., 2016; Hugelius et al., 2020; Ise et al., 2008), with potential catastrophic consequences to life on earth as early as in the next century (IPCC, 2018).

1.5 Thesis objectives and rationale

In this thesis I investigate the diversity and drivers of oribatid mite communities in two fen sites located in northern Ontario, Canada. My specific objectives were to:

1) Characterise the oribatid mite fauna in both a *Sphagnum* moss dominated (SF) and a *Carex* sedge dominated (CF) site, and update the checklist of oribatid mites of Canadian peatlands (Chapter 2).
2) Determine the drivers of oribatid mite communities and litter decomposition for three prevalent peatland plant functional types in hummock and hollow microtopological systems in the SF (Chapter 3).
3) Compare oribatid mite community under warming to ambient temperature plots in both SF and CF using univariate and multivariate analyses (Chapter 4).
4) Model the flux of energy (carbon) in the soil food web of both SF and CF under ambient and warmed conditions (Chapter 5).

I characterised the oribatid mite community of the SF and the CF, since both fens differ in vegetation, nutrient status, and hydrology. For that, I identified oribatid mites sampled over six years. I then used the species list I generated combined with published literature to update the checklist of oribatid mites of Canadian peatlands, last updated more than 25 years ago (Behan-Pelletier and Bissett, 1994).

Because hummock-hollow microtopologies are evident in the SF, I determined the drivers of oribatid community composition and litter decomposition for three prevalent peatland plant functional types differing in litter quality (*Sphagnum* mosses, *Chamaedaphne* shrub and *Carex* sedges) using litterbags deployed in hummocks and hollows for one year.

I compared the oribatid mite community under warming to ambient temperatures in both SF and CF in a large-scale field warming experiment over four years. I used open-top chambers (OTCs) and belowground active warming to warm half of the plots and compare the oribatid communities under both warmed and ambient conditions.

Lastly, I modeled the energy in peatland soil food webs of both SF and CF using carbon as an energy unit. I link differences in oribatid mite and other soil microarthropod communities between fens to the amount of energy being cycled. I also compared energy fluxes under control and warmed conditions in both fens, which help predict larger ecosystem changes caused by climate warming.

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Chapter 2

2 Checklist of oribatid mites (Acari: Oribatida) from two contrasting boreal fens: an update on oribatid mites of Canadian peatlands

2.1 Introduction

Oribatid mites (Acari: Oribatida) are commonly the dominant group of arthropods in terrestrial soils (Norton and Behan-Pelletier, 2009) and are well represented in terms of diversity in wetlands such as peatlands (bogs and fens) (Behan-Pelletier and Bissett, 1994; Belanger, 1976; Chapter 4; Lehmitz, 2014; Lindo, 2015). Despite their importance, peatlands and other wetland systems are understudied with respect to oribatid mite fauna in Canada compared to other habitat types, and it has been more than 25 years since Behan-Pelletier and Bissett (1994) published data on the taxonomy and ecology of oribatid mites of Canadian peatlands. In that study, the authors listed 71 species (49 genera and 34 families) across four categories of peatland habitats (aquatic, mesic, xeric, epigeal). They also noted that parthenogenetic species are better represented in peatlands than in the general ‘soil-dwelling’ oribatid mite fauna, which was also recently noted in Maraun et al. (2019).

Since that work, only a handful of studies have directly examined oribatid mites in Canadian peatland habitats (bogs and fens) (Behan-Pelletier, 1997; Chapter 3; Chapter 4; Lindo, 2015; and Markkula and Kuhry, 2020 for subfossil), described species from Canadian peatlands (Behan-Pelletier and Eamer, 2003; Behan-Pelletier and Walter, 2013; Norton and Behan-Pelletier, 2007; Walter and Latonas, 2013), or provided records from non-specific *Sphagnum* moss habitats (McAdams et al., 2018; Meehan et al., 2020). In the United States recent studies of oribatid mites in peatland and/or *Sphagnum* moss habitats only include Donaldson (1996), Norton and Behan-Pelletier (2007), and Walter and Latonas (2013). The work of Belanger (1976) is still the most comprehensive study documenting 44 species in a *Sphagnum*-dominated fen in New York State, of which 25 species had been previously recorded from European peatlands. In Europe, however, oribatid mites in peatlands have been and continue to be much more intensively studied (Borcard and Matthey, 1995; Borcard and Vaucher-von Ballmoos, 1997; George et al., 2017; Ivan et al., 1997; Ivan and Călugăr, 2003; Juan-Ovejero et al., 2019; Laiho et al., 2001; Lehmitz, 2014; Lehmitz et al., 2020; Lehmitz and Maraun, 2016; Markkula, 2014; Markkula et al., 2019; Melekhina et al., 2015; Minor et al., 2019, 2016; Mumladze et al., 2013; Seniczak et al., 2020, 2019, 2016; Sidorchuk, 2008; Starý, 2006). In addition, subfossil oribatid fauna from European peatlands are also thoroughly investigated (Cañellas-Boltà et al., 2012; Karppinen et al., 1979; Markkula, 2020, 1986; Markkula et al., 2018).

The data of Behan-Pelletier and Bissett (1994) was derived primarily from Marshall et al. (1987) and Behan-Pelletier (1989), and the examination of specimens housed in the Canadian National Collection of Insects, Arachnids and Nematodes sampled from peatland sites in the Canadian provinces of Ontario, Quebec, Alberta, New Brunswick, and Newfoundland. In this study I updated this list of the oribatid mite community of Canadian peatlands. My objectives were to: 1) characterise the oribatid mite fauna in two boreal peatlands: a nutrient-poor fen dominated by *Sphagnum* spp. mosses, and an intermediate nutrient level fen dominated by *Carex* spp. sedges using samples collected over five years, and 2) update the checklist of oribatid mites of Canadian peatlands using the species found in my sites, and also published work since

1994; this is data mainly derived from Behan-Pelletier and Lindo (2019), which includes Alberta Biodiversity Monitoring Institute data and other published literature. For the data I collected from two sites in Ontario, I predicted higher number of species and diversity in the *Sphagnum*-dominated fen because the *Sphagnum*-dominated fen has greater vascular plant and moss species richness, and higher heterogeneity in its landscape (e.g., hummock/hollow topography) compared to the *Carex* spp. fen site. In addition, there is greater saprophytic fungal biomass due to the to lower litter quality of *Sphagnum* spp. as the main saprophytic fungal resource (Lyons and Lindo, 2020), which would translate into higher number of individuals of oribatid mites in the *Sphagnum*-dominated fen. Thus, the *Sphagnum*-dominated fen should provide greater food resources and habitat for oribatid mite communities compared to the *Carex*-dominated fen.

2.2 Material & Methods

2.3 Study area

This study was conducted in two fen sites near White River, northern Ontario, Canada (48.21°N, 85.21°W). These sites integrate a large boreal peatland complex that has been studied by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry for the past 17 years. The two sites are approximately 2 km apart and experience a continental climate strongly influenced by the proximity of Lake Superior, with a mean annual temperature of 2.1°C and precipitation of 980 mm (~40% as snow). Temperatures can reach –40°C in the winter (ave. January temperature –14.2°C) and rarely exceed 30°C in the summer (ave. July temperature 14.7°C); the growing season is 70–100 days (see Webster and McLaughlin (2010) for a full site description).

Although in the same area, the two fens differ in terms of nutrient status, water table depth and dominant vegetation. The *Sphagnum*-dominated fen (hereafter SF) is a 4.5 ha nutrient-poor fen (pH ~4.1) covered by mixed *Sphagnum* (*Sphagnum angustifolium* (C.E.P. Jensen ex Russow), *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum girgensohnii* Russ., *Sphagnum magellanicum* Brid.) and other mosses (*Dicranum polysetum* Sw., *Pleurozium schreberi* (Michx.) Trevis), but also include sedges (*Carex disperma* Dewey, *Carex magellanica* Lam./*Carex oligosperma* Michx., *Carex pauciflora* Lightf.), and abundant shrubs such as leatherleaf (*Chamaedaphne calyculata* (L.) Moench), and Labrador tea (*Rhododendron groenlandicum* Oeder). Among shrubs, species such as bog rosemary *Andromeda polifolia* L. (Ericaceae) and bog laurel (*Kalmia polifolia* Wagenh.) are also present. Sparse trees (e.g., tamarack (*Larix laricina* (Du Roi) K. Koch), speckled alder (*Alnus incana* (L.) Moench) and black spruce (*Picea mariana* (Mill.) B.S.P.)), herbs (e.g., round-leaved sundew (*Drosera rotundifolia* L.), false toadflax (*Geocaulon lividum* (Richardson) Fern.), threeleaf false lily of the valley (*Maianthemum trifolium* (L.) Sloboda), narrowleaf cow wheat (*Malampyrm lineare* Desr.) and purple pitcher plant (*Sarracenia purpurea* L.)), and small ground cover such as creeping snowberry (*Gaultheria hispidula* (L.) Muhl. ex Bigelow), lowbush blueberry (*Vaccinium angustifolium* Aiton), small cranberry (*Vaccinium oxycoccos* L.) are also common for this site. The SF is bounded by mixed-wood forest and borders on a small lake. The water table at the SF is ~30 cm below the peat surface, depending on relative position considering the hummock-hollow topology that exists (see Asemaninejad et al., 2017); total peat depth is approximately 104–127 cm.

On the other hand, the *Carex*-dominated fen (hereafter CF) is a 10.2 ha mostly open fen surrounded by mixed-wood forests, with two small streams tributaries on its edges, and with an intermediate nutrient status (pH ~ 5.4). The water table at this site is considerably higher than the SF, and it is not uncommon to have several centimeters of standing water at the surface for several months of the year. The CF is dominated by *Carex* species (*Carex lasiocarpa* Ehrh / *Carex oligosperma* Michx., *Carex stricta* Lamb.) and the shrubs bog rosemary (*Andromeda polifolia* L.) and sweetgale (*Myrica gale* L.). Other common plants in the SF include leatherleaf (*Chamaedaphne calyculata* L. Moench), bog willow (*Salix pedicellaris* Pursh), and *Sphagnum angustifolium* (C.E.P. Jensen ex Russow) that is typically associated with sweetgale. Occasional records of bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) P.Beauv.), wild strawberry (*Fragaria virginiana* Duchesne), marsh cinquefoil (*Comarum palustre* L.) and bog St. John's wort (*Triadenum fraseri* (Spach) Glea.) have also been listed for the CF (Lyons et al., 2020). The total peat depth in the CF is ~60 cm.

2.3.1 Sampling design

To assess the oribatid fauna of these peatlands, peat soil samples (ave. 8.52g ± 0.26g SE dry weight (dwt)) were collected in August 2015 (five samples/fen), June 2017 (16 samples/fen), June 2018 (18 samples/fen), June 2019 (16 samples/fen), August 2019 (16 samples/fen) and June 2020 (16 samples/fen), totalling 174 samples. Soil samples were placed in plastic bags and kept cool until return to the laboratory. Within 72 hours of collection, samples were extracted using Tullgren funnels over three days into 75% EtOH using a low wattage (25W) bulb. Following microarthropod extraction, all oribatid mites (Acari: Oribatida), as the dominant group in my samples (72.13% of all microarthropods) were morphotyped under a stereomicroscope (Nikon SMZ 745T). Representative individuals were slide mounted in Hoyer's medium and identified to the family and genus level under a compound microscope (Nikon Eclipse Ni) using keys in Norton and Behan-Pelletier (2009) and literature provided by The Ohio State University Summer Acarology course. Final species level identifications were made using primary literature and confirmed where possible against reference material.

2.3.2 Descriptive statistics

For each soil sample, I quantified the standardised oribatid mite species richness (# of species / g dwt) and calculated species diversity of adults (as Shannon's diversity (H')). Shannon's diversity index was calculated for oribatid mites sampled from peat soil following the equation:

$$H' = -\sum Pi \times lnPi$$

Where P_i is the proportional abundance of the ith species.

I compared those univariate measures between fen types using a one-way Analysis of Variance (ANOVA) using functions within the base package and "vegan" package (Oksanen et al., 2019) in R statistical program (R Core Team, 2020). In addition, to investigate if my sampling effort was satisfactory, species accumulation curves for both fens were generated in the order samples were collected, and rarefied with 1000 permutations of samples in random order using the function {specaccum} in the "vegan" package in R. True species richness for each fen was also estimated using Chao, Jackknife 1, Jackknife 2, and Bootstrap estimators within the function {poolaccum} also in the "vegan" package.

Lastly, to determine whether the overall oribatid mite community composition differed between fens, I used a one-way permutation multivariate ANOVA (PERMANOVA) based on Bray-Curtis dissimilarity, and results were visualized using a non-metric multidimensional scaling (NMDS) ordination. The Bray-Curtis matrix consists of pairwise distances (i.e., dissimilarity) between each oribatid mite community (i.e., in each peat soil sample), and communities that are more similar to one another are plotted close together. Dissimilarity in oribatid communities was tested for significant differences between fen by comparing the distribution of dissimilarities using 1000 permutations using the function {adonis} in the “vegan” package. All analyses use an alpha of 0.05, and final plots were created in R with “ggplot2” package (Wichkam, 2016).

2.3.3 Update on Oribatida of Canadian peatlands

I updated the checklist of the oribatid mite species of Canadian peatlands with all species identified in this chapter, all the species records published in the previous checklist for Canadian peatlands (Behan-Pelletier and Bissett, 1994), and in the checklist of oribatid mites of Canada (Behan-Pelletier and Lindo, 2019) that includes all literature up to 2019. A few addional species were added based on a Web of Science literature search using the key words ‘Canada’, ‘oribatid*’, and ‘peatland’, ‘bog’ or ‘fen’. For species listed in Behan-Pelletier and Lindo (2019), I included all species found in one of the following habitats: peatland, bog, fen, *Sphagnum* moss (including non-specified peatland habitat), wetland, understory of Labrador tea (*Rhododendron* (Ledum) *groenlandicum*), temporary bog pool, *Sphagnum* area in swamp, and bog tundra.

2.4 Results

2.4.1 Oribatid mite fauna

In total, 80 species of oribatid mites distributed in 33 families were collected from the two fen sites near White River, ON (Appendix A). Standardised species richness ($F_{1,172} = 298.57$, $P < 0.001$) and species diversity ($F_{1,172} = 223.00$, $P < 0.001$) were significantly higher in the SF (ave. richness = 3.85 ± 0.32 SE; ave. diversity H' = 2.45 ± 0.02 SE) compared to the CF (ave. richness = 1.23 ± 0.14 SE; ave. diversity H' = 1.66 ± 0.04).

In total, at the SF site I collected 69 species from 22,252 sampled adult individuals, of which 29 were unique to that site, and eight collected as singletons (i.e., one individual). The two most abundant species at the SF were the cosmopolitan *Tectocepheus velatus* Trägårdh, 1910 and *Oppiella nova* (Oudemans, 1902), followed by two known peatland species, *Malaconothrus mollisetosus* Hammer, 1952 and *Eniochthonius mahunkai* Norton and Behan-Pelletier, 2007. The estimated total species richness for the SF is between 74–85 species and new species records were still being added in the last year of sampling (Figure 2.1A) suggesting there are likely more species that were not collected.

At the CF I collected 51 species from 7,273 adult individuals of which 11 were unique to that site and not found in the SF, and four were singletons (*Cultroribula divergens* Jacot, 1939, *Liochthonius* sp., *Nothrus borussicus* Sellnick, 1928, *Trhypochthoniellus setosus canadensis* Hammer, 1952). The two most abundant species at the CF were *Tyrphonothrus maior* (Berlese, 1910) and *Mainothrus badius* (Berlese, 1905), which contributed to >50% of all individuals collected at that site. The estimated richness for the CF is between 57–71 species, and several new species records were added in the last year of sampling at this site also (Figure 2.1B), suggesting there are more species that were not collected. Combined richness estimates for both these sites are 86–105 species.

In total, 40 species were shared between SF and CF sites (Figure 2.2A), but overall composition was significantly different between the two sites ($F_{1,172} = 105.55$, $P = 0.001$) (Figure 2.2B). Notably, of the 40 shared species, 15 species were dominant (i.e., >10× more abundant) in the SF, of which five species had only one individual found in the CF (*Acrotritia ardua* (C.L. Koch, 1841), *Carabodes granulatus* Banks, 1895, *Hoplophorella thoreaui* (Jacot, 1930), *Nothrus monodactylus* (Berlese, 1910), *Sellnickochthonius zelawaiensis* (Berlese, 1910)). On the other hand, there were four species in the CF that, although found in the SF, were more dominant in CF (*Anachipteria* sp., *Limnozetes guyi* Behan-Pelletier, 1989, *T. maior, Liochthonius sellnicki* (Thor, 1930)).

2.4.2 Update on Oribatida of Canadian peatlands

Behan-Pelletier and Bissett (1994) originally listed 71 species of oribatid mites for peatlands in Canada; I found 140 species recorded from peatland habitats (including those 71) with some listed as subfossils in the updated list of oribatid mites of Canada by Behan-Pelletier and Lindo (2019). These checklists combined with my work presented in this chapter expand the number of oribatid mites in Canadian peatlands to 186 species (Appendix A). From those, only 35 species are common to Behan-Pelletier and Lindo (2019) and Appendix A.

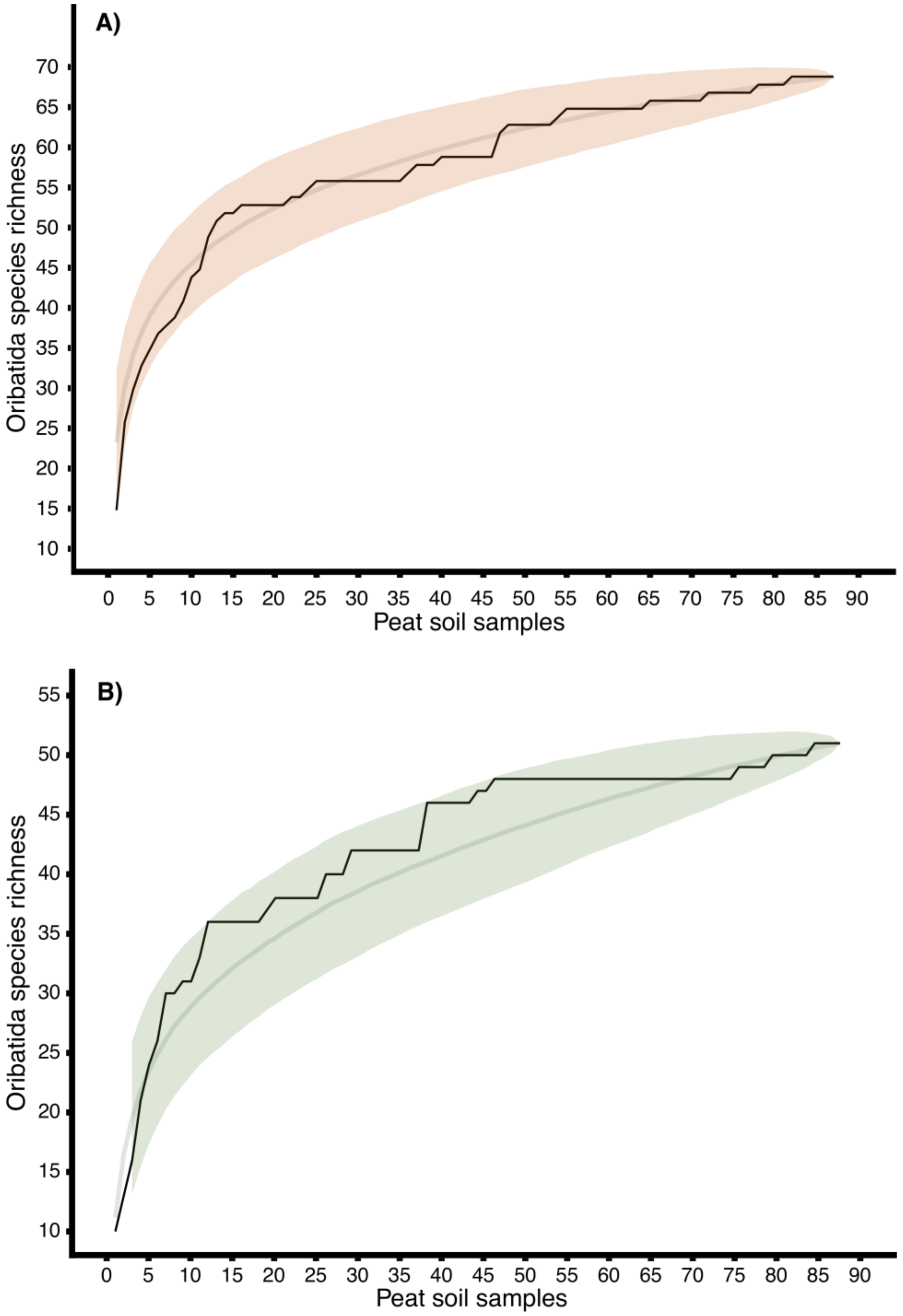

Figure 2.1 Species accumulation curves. A) *Sphagnum*-dominated fen oribatid mite species B) *Carex*-dominated fen oribatid mite species.

Collector curves are in black sampling effort over time on the X-axis (left to right 2015–2020). Rarefied accumulation curves (grey and brown/green) are plotted from means and standard deviation of 1000 permutations of samples in random order.

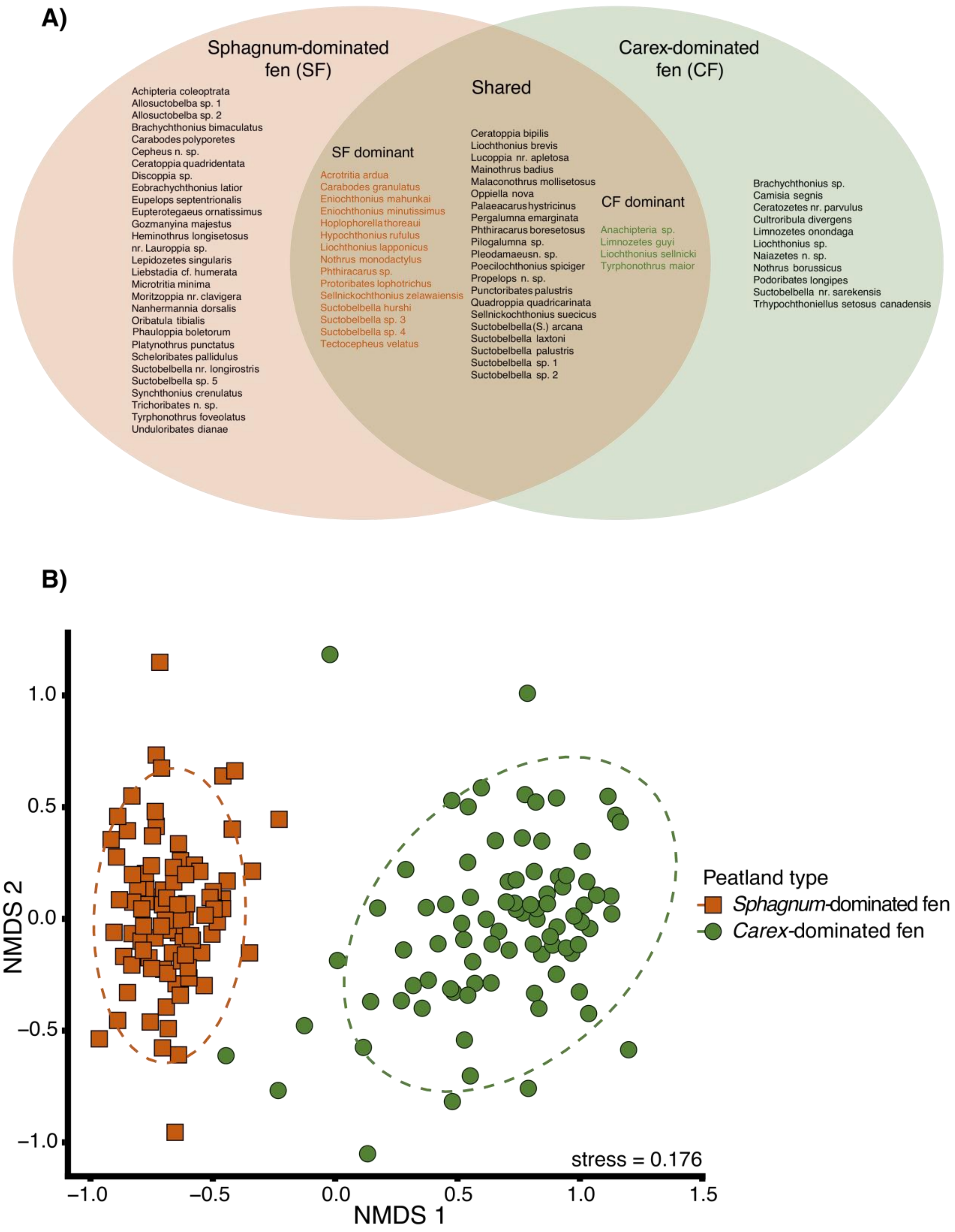
A)
Sphagnum-dominated fen (SF)
Achipteria coleoptrata
Allosuctobelba sp. 1
Allosuctobelba sp. 2
Brachychthonius bimaculatus
Carabodes polyporetes
Cepheus n. sp.
Ceratoppia quadridentata
Discoppia sp.
Eobrachychthonius latior
Eupelops septentrionalis
Eupterotegaeus ornatissimus
Gozmanyina majestus
Heminothrus longisetosus
nr. Lauroppia sp.
Lepidozetes singularis
Liebstadia cf. humerata
Microtritia minima
Moritzoppia nr. clavigera
Nanhermannia dorsalis
Oribatula tibialis
Phauloppia boletorum
Platynothrus punctatus
Scheloribates pallidulus
Suctobelbella nr. longirostris
Suctobelbella sp. 5
Synchthonius crenulatus
Trichoribates n. sp.
Tyrphonothrus foveolatus
Unduloribates dianae
SF dominant
Acrotritia ardua
Carabodes granulatus
Eniochthonius mahunkai
Eniochthonius minutissimus
Hoplophorella thoreaui
Hypochthonius rufulus
Liochthonius lapponicus
Nothrus monodactylus
Phthiracarus sp.
Protoribates lophotrichus
Sellnickochthonius zelawaiensis
Suctobelbella hurshi
Suctobelbella sp. 3
Suctobelbella sp. 4
Tectocepheus velatus
Shared
Ceratoppia bipilis
Liochthonius brevis
Lucoppia nr. apletosa
Mainothrus badius
Malaconothrus mollisetosus
Oppiella nova
Palaeacarus hystricinus
Pergalumna emarginata
Phthiracarus boresetosus
Pilogalumna sp.
Pleodamaeusn. sp.
Poecilochthonius spiciger
Propelops n. sp.
Punctoribates palustris
Quadroppia quadricarinata
Sellnickochthonius suecicus
Suctobelbella (S.) arcana
Suctobelbella laxtoni
Suctobelbella palustris
Suctobelbella sp. 1
Suctobelbella sp. 2
CF dominant
Anachipteria sp.
Limnozetes guyi
Liochthonius sellnicki
Tyrphonothrus maior
Carex-dominated fen (CF)
Brachychthonius sp.
Camisia segnis
Ceratozetes nr. parvulus
Cultroribula divergens
Limnozetes onondaga
Liochthonius sp.
Naiazetes n. sp.
Nothrus borussicus
Podoribates longipes
Suctobelbella nr. sarekensis
Trhypochthoniellus setosus canadensis
B)
NMDS 2
1.0
0.5
0.0
−0.5
−1.0
NMDS 1
−1.0
−0.5
0.0
0.5
1.0
1.5
stress = 0.176
Peatland type
Sphagnum-dominated fen
Carex-dominated fen

Figure 2.2 A) Venn diagram showing the overlap between species extracted from peat soil samples collected in a *Sphagnum*-dominated fen (SF) and a *Carex*-dominated fen (CF) between 2015–2020 near White River Ontario, Canada. Shared species that were dominant (i.e., >10× more abundant) in either fen have different colours. B) Non-metric multidimensional scaling (NMDS) plot depicting community assembly of oribatid mites in a *Sphagnum*-dominated (brown) and a *Carex*-dominated (green) fen. NMDS is based on Bray-Curtis percent similarity of standardised species abundances for each species in 174 samples. Oribatida community composition was different between sites (PERMANOVA: $F_{1,172} = 105.50$, $P = 0.001$).

2.5 Discussion

Extensive sampling over five years at two peatland sites collected 80 species of oribatid mites, of which 69 occurred in the *Sphagnum*-dominated fen and 51 occurred in the *Carex*-dominated fen. This sampling, along with the updated checklist of oribatid mites in Canada (Behan-Pelletier and Lindo, 2019) brings the total known peatland oribatid mite fauna to 186 species, of which 45 species are newly recorded in peatlands in Canada. Among species previously recorded and collected at both my sampling sites, several have also been found in abundance in Europe such as *Hypochthonius rufulus* C.L. Koch, 1836, *A. ardua*, *T. maior*, and *O. nova* (Seniczak et al., 2019). Several of these are cosmopolitan species found in a variety of habitats, thus not strict peatland species. For instance, *O. nova* is a species found around the world, and possibly the most common and widespread arthropod in terrestrial environments (Norton and Palmer, 1991), which indicates that the oribatid mite fauna of peatlands also comprises non-peatland specialised species. Donaldson (1996) similarly suggest that there are only a few highly specialised species that occur in very high abundances in natural peatlands. Specifically, Donaldson (1996) found high abundance of the genus *Limnozetes* Hull, 1916, and particularly *L. palmerae* Behan-Pelletier, 1989, which they attributed to a semi-aquatic habitat association, preference for acidic environments, and its small size.

The SF in particular had a greater number of generalist (i.e., non-peatland specialist) species. For example, among the 29 species unique to the SF, *Gozmanyina majestus* (Marshall and Reeves, 1971) was highly abundant, although only previously recorded primarily in acidic forest soil (Cianciolo and Norton, 2006), which might suggest that habitat associations are driven by pH (Kaneko and Kofuji, 2000) as the SF also has low pH. Alternatively, the presence of non-peatland specialist species at the SF could be explained by wind dispersal of oribatid mites from the adjacent forest, a phenomenon seen for other oribatid mites (Behan-Pelletier and Winchester, 1998). Similarly, I recorded several species previously not documented for peatlands including members of the families Cepheidae Berlese, 1896 (*Cepheus* n. sp., *Eupterotegaeus ornatissimus* (Berlese, 1908)) and Gymnodamaeidae Grandjean, 1954 (*Pleodamaeus* n. sp.) that are typically found in drier environments. As a result, the SF had higher species richness and diversity compared to the CF because of these unique species and species that appear to be peatland specialists, such as *E. mahunkai*, *M. badius*, and *L. guyi* that were also present. While I noted that several mesophilous peatland species were found at the SF, some species were more commonly (e.g., *T. maior*, *L. guyi*) or solely (*T. setosus canadensis*, *L. onondaga* Behan-Pelletier, 1989) collected at the wetter CF that were typically semi-aquatic species. In addition to differences in water table that help explain the distributions of aquatic species, the SF site has greater vascular plant and moss species richness (Lyons et al., 2020), leading to heterogeneous microhabitats such as hummock/hollow topography (see Chapter 3), greater saprophytic fungal biomass (Lyons and Lindo, 2020), and diverse fungal (Asemaninejad et al., 2017) and bacterial (Asemaninejad et al., 2019) communities that provide food resources for many oribatid mites species (Lehmitz and Maraun, 2016; Schneider and Maraun, 2005).

Peatland records for the entirely parthenogenetic family Brachychthoniidae Thor, 1934 were considerably expanded, with nine new species records added to the checklist. As important was the update on Suctobelbidae Jacot, 1938, whose members are also predominantly asexually reproducing species. Until Behan-Pelletier and Lindo (2019), only four named species of Suctobelbidae were listed for peatlands in Canada; here I added records of eleven more species in two genera (*Allosuctobelba* Moritz, 1970 and *Suctobelbella* Jacot, 1937), although with relatively lower taxonomic resolution as I was not able to confirm all species identities. While there are 12 described species of *Suctobelbella* in Canada (Behan-Pelletier and Lindo, 2019), there are many undescribed species. For instance, Beaulieu et al. (2019) estimate 48 undescribed or unrecorded *Suctobelbella* species but note that based on molecular barcode information this number may be an underestimate. *Suctobelbella* are a parthenogenetic genus that shows cryptic diversity, which must be reconciled with the species concept.

It has been noted that both the number of parthenogenetic species as well as their individual abundances are higher in peat bogs than other habitats (e.g., forest floor soils) (Maraun et al., 2019); while this was not overly evident for species richness in the SF (39 parthenogenetic vs. 30 sexual species), more than 2/3 of the species in the CF were parthenogenetic (36 parthenogenetic vs. 15 sexual species). Overall, the abundance of individuals of parthenogenetic species, however, was about 10-fold greater than that of sexual species at both fens. One possible explanation for higher richness of parthenogenetic species in the CF might be related to a lower efficacy of free-standing spermatophores produced by males in wet habitats such as peatlands (Norton and Palmer, 1991), resulting in taxonomic groups like Brachychthoniidae and Eniochthoniidae Grandjean, 1947 within the Enarthronota being preadapted to these wet habitats (Behan-Pelletier and Bissett, 1994).

Notably missing from the peatland fauna in Canada compared to other boreal systems (Behan-Pelletier, 1999) are species in the predominantly sexually reproducing

Punctoribatidae Thor, 1937, many of which are found in dry microhabitats. However, while the family is present in all ecozones of Canada (Beaulieu et al., 2019), different genera exhibit different habitat preferences. For example, two of the five described *Punctoribates* Berlese, 1908 in Canada (*P. palustris* (Banks, 1895) and *P. punctum* (C.L. Koch, 1839)) are reported from *Sphagnum* in peat bog and wet *Sphagnum* habitats, respectively, while only two of the 17 described *Mycobates* Hull, 1916 (*M. incurvatus* Hammer, 1952 and *M. yukonensis* Behan-Pelletier, 1994) are recorded from bog tundra or peat habitats (Behan-Pelletier and Lindo, 2019). That said, while there are 35 described species in Punctoribatidae, there are an estimate of 30 additional unrecorded or undescribed species in Canada (Beaulieu et al., 2019).

Among the 45 species as new records for Canadian peatlands, at least five species are confirmed as undescribed (*Pleodamaeus* n. sp., *Cepheus* n. sp., *Propelops* n. sp., *Trichoribates* n. sp., *Naiazetes* n. sp.), suggesting great potential for more species to yet be described, and clearly more taxonomic studies are needed on peatlands in North America. For example, despite *Protoribates haughlandae* Walter and Latonas, 2013 being widely distributed across the province of Alberta (Walter and Latonas, 2013), this species has only recently been collected by the systematic sampling of peatland sites. Even though the oribatid mite fauna in Europe is considerably more studied than in Canada, many studies still list species as morphospecies, which could also potentially translate to new species or new records for peatlands worldwide (e.g., Markkula, 2014; Seniczak et al., 2020; Sidorchuk, 2008).

Embedded in the expanded checklist of Canadian peatland oribatid mites are geographical as well as habitat factors that dictate the presence and distribution of these mites. Prior to 1994, the vast majority of peatland records were for eastern Canada and within the boreal ecozone, as were mine. The addition of records from western Canada and the subarctic will continue to increase the number of known peatland species, as does extensive and repeated sampling at single locations. Thus, I suggest that future studies focus more on these sites with repeated sampling and/or more consideration of habitat specific associations. For instance, Donaldson (1996) found significantly different oribatid mite species assemblages across three different *Sphagnum* moss habitats within a single location, while at the same time, the abundance and dominance of particular species changed over one growing season. Taken together, this work highlights that, despite the importance of peatlands as soil reservoirs for carbon and biodiversity, peatlands and other wetland systems remain understudied with respect to oribatid mite fauna in Canada compared to other habitat types.

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Chapter 3

3 Drivers of decomposer communities and decomposition differ across a hummock-hollow microtopology in boreal peatlands

3.1 Introduction

In northern boreal peatland ecosystems, decomposition is naturally slow due to the combination of low seasonal temperatures, anaerobic and acidic conditions caused by high level of water table and the resistant and low carbon quality nature of *Sphagnum* mosses as the dominant vegetation (Hogg, 1993; Lindsay, 2010). Fens represent one type of peatland with a typically high-water table maintained by groundwater sources (Lindsay, 2010; McLaughlin and Webster, 2013), and where there is a notable presence of hummock-hollow microtopological systems (Belyea and Clymo, 2001; Nungesser, 2003). Hummocks are dry raised areas above the water table with lower pH where the dominant vegetation is often *Sphagnum magellanicum* Brid., and S. *fuscum* (Schimp.) Klinggr. with greater amounts of shrubs, while hollows are wet depressions with higher pH that have *S. fallax* (Klinggr.) Klinggr. and *S. angustifolium* (C. Jens. ex Russ.) C. Jens.) as prevalent species (Andrus et al., 1983; Johnson et al., 2015).

Hummock-hollow microtopology in boreal peatlands have previously shown to differ in vegetation (Vitt and Slack, 1984; Weston et al., 2017), fungal (Asemaninejad et al., 2017) and bacterial (Asemaninejad et al., 2019) communities, but studies examining peatland microarthropods in this system are lacking, although studies have previously characterised more general microarthropod fauna in peatlands (e.g., Chapter 2; Krab et al., 2014; Lindo, 2015; Minor et al., 2016; Mumladze et al., 2013). Several unexpected terrestrial oribatid mite species have been found in the SF (Chapter 2) and although it is still unclear what the drivers of microarthropods are in *Sphagnum*-dominated peatlands, plants and microflora may be important factors given they both differ across these peatlands' topography. At the same time, fauna may be associated with moisture (wet-dry gradient (Minor et al., 2019)), or plant litter material (Gergócs et al., 2015), either because of the physical habitat it provides, and/or the microflora communities that act as primary decomposers and serve as food resource for microarthropods (Maraun et al., 2011; Siepel and de Reuiter-Dijkman, 1993; van der Heijden et al., 2008). Also, the role microarthropods play in decomposition is poorly quantified (García-Palacios et al., 2013), which could be important for C flux (but see Chapter 5).

Decomposition, the process through which dead organic matter is broken down and carbon is either immobilized or mineralized to the atmosphere, is controlled largely through three main factors: climate (including microclimate), plant litter quality (e.g., nutrient status), and the biotic decomposer community, including microbes and microarthropods (Bradford et al., 2016; Coûteaux et al., 1995; Keiser and Bradford, 2017; Peña-Peña and Irmler, 2016; Wall et al., 2008). The relative contribution of these factors, however, differs depending on the spatial and temporal scale of observation. For instance, decomposition rates across large spatial scales are primarily dictated by climate factors such as temperature and soil moisture conditions (Aerts, 1997; Coûteaux et al., 1995; Wall et al., 2008), while at very small scales the activity of the decomposer community, including both primary (i.e., fungi and bacteria) and secondary (e.g., microarthropods) decomposers, can influence rates of decomposition (Yang and Chen, 2009; Zhang et al., 2001). That said, Cornwell et al. (2008) concluded that plant functional traits that indicate or dictate plant litter quality are the predominant factor on rates of decomposition across biomes after accounting for differences in climate. The intensity and interaction of climate factors and litter quality, however, vary according to the ecosystem and ultimately modulate the effects of soil microarthropods on litter decomposition (García-Palacios et al., 2013; Wall et al., 2008)

In this study, I examined the oribatid mite communities that colonise plant litter of three prevalent peatland plant functional types (*Sphagnum* moss, *Carex* sedge, and *Chamaedaphne* shrub) in hummock and hollow microtopological systems in a *Sphagnum*-dominated nutrient poor fen. I also explored rates of litter decomposition for these three litter types. Then, I looked for a correlation between oribatid mite species composition and litter mass loss. In doing so, I asked whether plant type or microtopology drives oribatid mite community and decomposition rates in a boreal peatland hummock-hollow system in northern Canada. I predicted oribatid mite communities to be more diverse in hollows than on hummocks due to the higher moisture levels of this microhabitat and that *Sphagnum* mosses would have the lowest decomposition rates due to their lowest carbon quality.

3.2 Materials & Methods

3.2.1 Experimental design

The study was conducted in the *Sphagnum*-dominated fen near White River, ON described in Chapter 2. At this site, the presence of hummock and hollow topologies is evident, alongside flat ‘lawn’ areas. Chapter 2 provides a full description of the site including vegetation and a complete list of oribatid mite species collected over repeated sampling events. In this study, I used a total of 30 litterbags (10 cm × 7 cm with 1 mm mesh) filled with 0.54–0.62 g dry weight of *Sphagnum* moss, *Carex* sedge, or

Chamaedaphne shrub leaves and placed in the field for one year to examine oribatid mite fauna colonization and decomposition rates. The choice of plants represents different litter quality levels from common species at the site (Appendix B). More than one species of each genus may have been present in *Sphagnum* and *Carex* plant type litter (*Sphagnum* litterbags could have included *S. magellanicum* but was mostly *S. angustifolium; Carex* litterbags were either *C. magellanica* or *C. oligosperma*, which are only differentiable during seed set). All plant litter was collected from the site in the previous year, and air dried in the lab. Subsamples of litter were oven dried at 60°C for 48 hours to allow for determination of the remaining moisture content of the air-dried samples. The mesh size of the litterbags was designed to allow entry and colonization by microfauna and most mesofauna, specifically oribatid mites (Acari: Oribatida), the dominant microarthropods in peatlands. Absolute dry weights of litter were recorded, and one litterbag of each plant type was deployed to five hummocks and five hollow microhabitats in June of 2015. Hummocks and hollows were chosen as pairs in relative proximity to one another (approx. 2 m apart on average). Litterbags were placed on the surface and held in place with pin flags. A single Hobo® datalogger was placed in a representative hummock and hollow to track surface temperature and relative humidity every half an hour for the year.

Litterbags were collected after one year, placed in separate plastic bags and kept cool until return to the laboratory. Any debris or litter deposited on the surface of, or vegetation grown through the litterbags, was removed. Within 72 hours of collection, samples were extracted from the litterbags using Tullgren funnels over three days into 75% EtOH using a low wattage (25W) bulb. Litterbags were further oven dried at 60°C for 48 hours and the contents reweighed. Decomposition rate of litter from each litterbag was measured as mass loss using the following equation:

$$Mass\ loss\ = \frac{initial\ dry\ weight\ (g) - final\ dry\ weight\ (g)}{initial\ dry\ weight\ (g)} \times 100$$

I also used mass loss to estimate the decomposition constant (k) using the exponential model created by Olson (1963):

$$L_t\ =\ L_0\ \times\ e^{-kt}$$

where L_0 = mass at time zero, L_t = mass at time t, t = time of incubation in years and k = the decomposition constant. The inverse of k gives an estimate of the mean residence time (i.e., time required for the litter to decompose, in years) of the plant litter.

Following extraction, all invertebrates were morphotyped to order/family level under a stereomicroscope (Nikon SMZ 745T). As the dominant group in my samples (53.60% of all microarthropods), oribatid mites had representative individuals slide mounted in Hoyer's and identified to the family and genus level under a compound microscope (Nikon Eclipse Ni) using keys in Norton and Behan-Pelletier (2009) and literature provided by The Ohio State University Summer Acarology course. Final Oribatida species level identifications were made using primary literature and confirmed where possible against reference material. Data on invertebrates other than oribatid mites is presented in Appendix C.

For each sample I determined oribatid mite species abundance (# of indiv. of adults and immature / g dwt), adult oribatid mite species richness (# of species / g dwt), and the proportional richness and abundance of oribatid mites in relation to all microarthropods considered together (in percentage). I also calculated two diversity indices for adult oribatid mites as follows: Shannon's diversity index (H'):

$$H' = -\sum Pi \times lnPi$$

Where P_i is the proportional abundance of the *i*th species.

Pielou's Evenness (J):

$$J = \frac{H'}{ln(S)}$$

Where *H'* is Shannon's diversity, and *S* is species richness.

3.2.2 Statistical analysis

Decomposition as measured by mass loss was analysed for differences between hummock and hollow microtopology, plant litter type, and the interaction between microtopology and plant type using a full-factorial Analysis of Variance (ANOVA) with a Tukey HSD *post hoc* test. I did not statistically analyse the decomposition constant (*k*) or the mean residence time, as they are directly derived from mass loss rates and would show the same statistical trends.

Oribatid mite abundance, species richness, proportional richness and abundance, Shannon's diversity (H') and Pielou's evenness (J) were analysed by ANOVA under a full-factorial design with microtopology and plant litter type as factors. I used Tukey HSD as *post hoc* to determine differences between and within treatment levels (microtopology and plant litter type) using the "emmeans" package (Lenth, 2020) and the function {cld} in "multcomp" (Hothorn et al., 2008) in R statistical program (R Core Team, 2020). Oribatid community composition was further assessed by a two-way permutation multivariate ANOVA (PERMANOVA) based on Bray-Curtis dissimilarity using the function {adonis} in the "vegan" package (Oksanen et al., 2019) to compare community structure among plant litter type and microtopologies. Results were visualized using a non-metric multidimensional scaling (NMDS) ordination (Clarke, 1993), where communities (i.e., samples) that are more similar to one another are plotted closely together. In addition, I performed nestedness analysis to interpret community structure by identifying whether smaller assemblages were subsets of larger oribatid mite species assemblages. For the nestedness analysis, I used "bipartite" package (Dormann et al., 2009) and the functions {nestedtemp}, and {oecosimu} with {C.score} as parameters in R. Finally, Spearman's correlations were performed to examine whether the abundance and richness of oribatid mites correlated with decomposition rates of plant litter type. All analyses used an alpha of 0.05, and final plots were created in R with "ggplot2" package (Wickham, 2016).

3.3 Results

3.3.1.1 Oribatid mite diversity in litterbags

I identified 17 species from 506 specimens of oribatid mites colonising litterbags after one year; ten species were unique to the hollow litterbags, while three species (*Trhypochthonius tectorum* (Berlese, 1896) s.l., *Mainothrus badius* (Berlese, 1905), and *Lepidozetes singularis* Berlese, 1910) were found solely in the hummock litterbags; four species of oribatid mites were found in both hollow and hummock microhabitats, although these were not necessarily the most abundant species (Appendix D). Oribatid mite richness was greater in hollow microtopologies compared to hummocks ($F_{1,24}$ = 25.633, P < 0.001), but did not differ significantly between plant litter types ($F_{2,24}$ = 0.04, P = 0.957). In addition, there was no significant interaction between microtopology and plant litter type for oribatid mite species richness ($F_{2,24}$ = 0.451, P = 0.641).

Oribatid mite abundance colonizing litterbags was low; yet they were the most abundant group present in the litterbags (53.6%), and their abundance also showed the opposite pattern to mass loss following results for species richness; abundance did not significantly vary across plant litter types ($F_{2,24} = 1.401$, $P = 0.265$), instead, microtopology was the main driver of abundance with hollows having significantly greater abundance than hummocks ($F_{1,24} = 7.359$, $P = 0.012$) (Table 3.1). There was no significant interaction between plant litter type and microtopology for oribatid mite abundance ($F_{2,24} = 1.09$, $P = 0.350$).

Shannon's diversity based on adult oribatid mites exhibited similar trends as species richness, and was significantly higher in hollows compared to hummocks ($F_{1,24} = 26.177$, $P < 0.001$) (Table 3.1), but did not differ between plant litter types ($F_{2,24} = 1.320$, $P = 0.285$). There was no significant interaction between microtopology and plant litter type ($F_{2,24} = 0.569$, $P = 0.573$). Pielou's evenness values were also significantly higher in hollows compared to hummocks ($F_{1,19} = 11.644$, $P = 0.002$), but not different between plant litter types ($F_{2,19} = 1.929$, $P = 0.172$). There was no significant interaction between microtopology and plant litter type for Pielou's evenness either ($F_{2,19} = 1.664$, $P = 0.215$) (Table 3.1).

Table 3.1 Oribatid mite richness, abundance, adult abundance, immature abundance, Shannon's diversity (H') and species evenness (J) for litterbags composed of three different peatland plant litter functional types placed in hollow and on hummock microtopologies of a *Sphagnum*-dominated fen.

Values are means ± standard error. Values followed by different letters are significantly different based on Tukey HSD *post hoc* analysis.

	Peat moss: *Sphagnum*		Shrub: *Chamaedaphne*		Sedge: *Carex*	
	Hummock	Hollow	Hummock	Hollow	Hummock*	Hollow
Richness (# species / g dwt)	2.45 ± 0.76^{ab}	8.27 ± 1.83^{ab}	1.39 ± 0.94^{b}	10.21 ± 1.62^{a}	0.72 ± 0.72^{b}	9.82 ± 3.73^{a}
Abundance (# indiv. / g dwt)	7.40 ± 3.48^{a}	130.69 + 70.83^{b}	2.73 ± 0.86^{a}	37.00 ± 12.90^{b}	0.72 ± 0.72^{a}	53.74 ± 29.09^{b}
Shannon's diversity (H')	0.26 ± 0.16^{bc}	0.93 ± 0.22^{ab}	0.13 ± 0.13^{bc}	1.20 ± 0.19^{a}	-	0.72 ± 0.31^{abc}
Pielou's evenness (J)	0.62 ± 0.31^{ab}	0.69 ± 0.10^{ab}	0.25 ± 0.25^{ab}	0.85 ± 0.06^{a}	-	0.60 ± 0.20^{ab}

* Only one species present: *Malaconothrus mollisetosus* Hammer, 1952

The proportional contribution of oribatid mite species richness to the total richness of the samples was significantly lower in *Carex* litterbags ($F_{2,20} = 11.784$, $P < 0.001$) compared to *Sphagnum* (Tukey HSD, $P = 0.002$) and *Chamaedaphne* (Tukey HSD, $P = 0.001$) litterbags. The proportional richness also displayed a significant plant litter type-by-microtopology interaction ($F_{2,20} = 4.449$, $P = 0.002$), where it was similar in hollow samples across all plant types and in hummock *Sphagnum* litterbags (~ 61%), but was significantly greater in hummock litterbags composed of *Chamaedaphne* (100%) and near zero (~4%) in hummock *Carex* litterbags. However, the proportional richness did not differ between hummocks and hollows when all plant litter types were considered together (main effect of microtopology: $F_{1,20} = 1.559$, $P = 0.226$). Results for the proportional abundance of oribatid mites to all microarthropods were similar to trends in richness with all hollow litterbags and *Sphagnum* litterbags from hummocks having similar values (~ 67%) (plant litter type: $F_{2,23} = 8.822$, $P = 0.001$; plant litter type × microtopology interaction: $F_{2,23} = 7.663$, $P = 0.002$) while hummock litterbags of *Chamaedaphne* (100%) and *Carex* (~3%) were dichotomous in whether oribatid mites were the dominant fauna (Figure 3.1).

Community composition of the oribatid community as analysed by PERMANOVA was significantly different between the hummock and hollow microtopologies ($F_{1,23} = 2.39$, $P = 0.001$). The NMDS plot demonstrates that hollow litterbags clustered more closely together (i.e., had greater similarity in composition) than hummock litterbag samples (Figure 3.2A), suggesting that communities in hollows are more homogeneous than in hummocks, and a possible nested subset. However, the nestedness analysis showed the opposite result and suggests that the oribatid mite communities in hummocks are composed of different sets of species from those present in hollows (C.score = 0.63, nestedness temperature = 14.82) (Figure 3.2B). In other words, the majority of species was found in hollow litterbag samples and individuals in hummocks appear to be found at random.

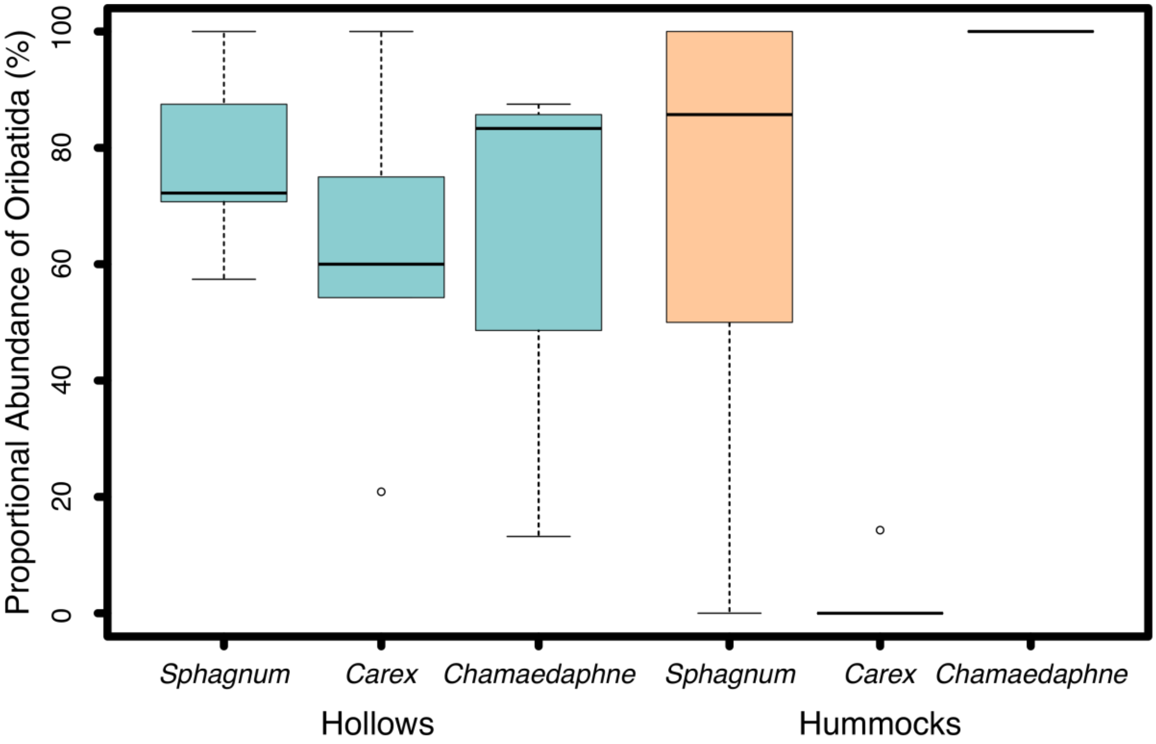

Figure 3.1 Proportional abundance of Oribatida in litterbags composed of three peatland plant litter functional types placed for one year in hummock and hollow microtopologies.

Bars are box and whisker plots denoting median value (solid thick line), upper and lower quartile values (box delineation), maximum and minimum values (whiskers) and outliers (circles).

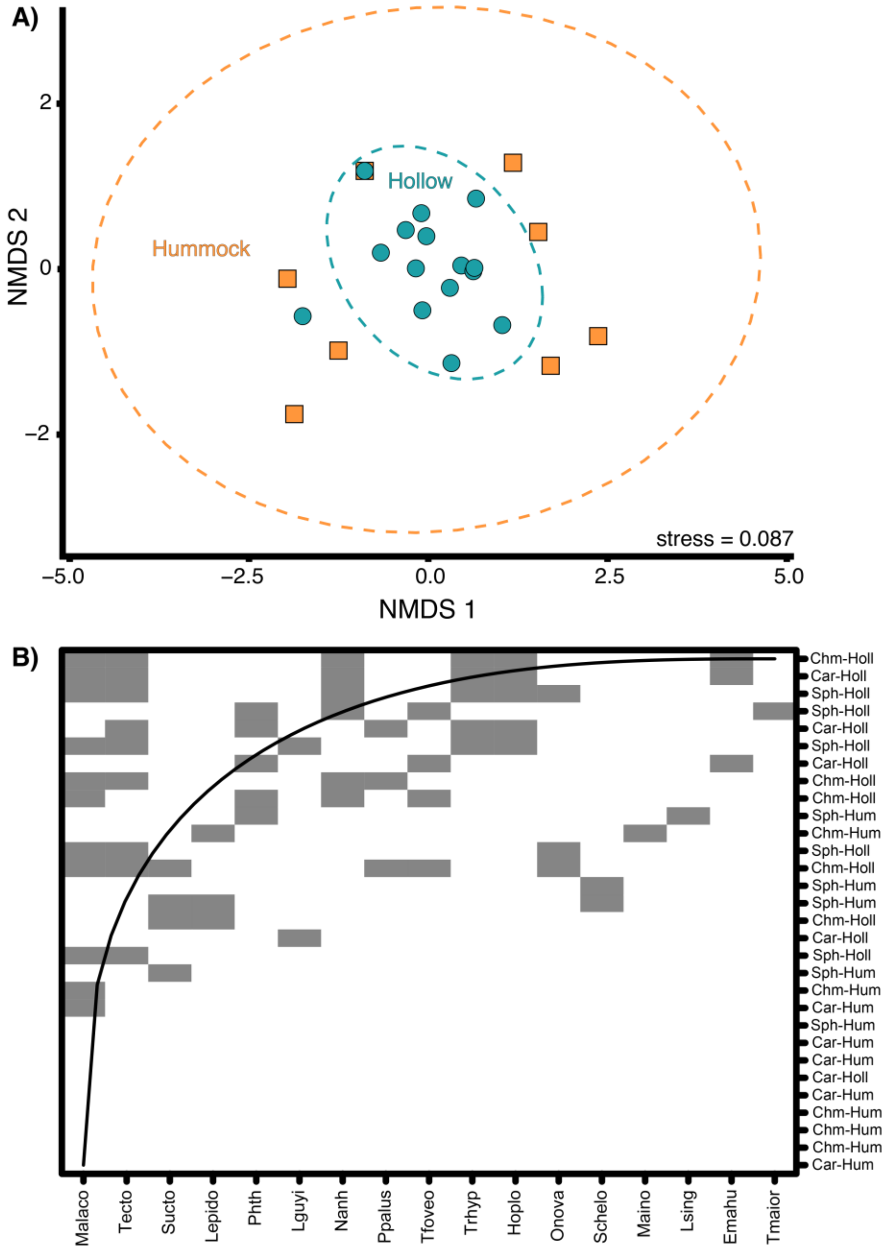

Figure 3.2 A) Non-metric multidimensional scaling (NMDS) plot depicting community assembly of oribatid mites in a hummock-hollow system in a nutrient-poor fen B) Matrix of oribatid mite species occurrence in hummock-hollow system. NMDS is based on Bray-Curtis percent similarity of species standardised abundances (n° individuals per g dry weight litter) for each species in 21 samples. Each column in B) represents an oribatid mite species and each row represents one litterbag sample. Black squares indicate species presence, and white spaces indicate species absence. See Appendix D for full species list.

3.3.1.2 Decomposition dynamics

Mass loss was not significantly correlated with total oribatid mite abundance (R = -0.168, P = 0.372), or oribatid mite richness (R = 0.134, P = 0.479). Plant litter type had a significant effect on the rate of decomposition as measured by mass loss of the three different litter types ($F_{2,24} = 48.884$, $P < 0.001$), with the highest mass loss observed for *Carex* followed by *Chamaedaphne* and then *Sphagnum* (Tukey HSD, $P < 0.001$) (Table 3.2). Neither microtopology ($F_{1,24} = 0.330$, $P = 0.571$) nor its interaction with plant type ($F_{2,24} = 1.032$, $P = 0.371$) showed significant effect on decomposition rate. In a similar way, because decomposition constant (*k*) and mean residence time are measures derived from mass loss data, *Sphagnum* litter had the lowest decomposition constant and the highest mean residence time (Table 3.2), indicating that a longer period would be required for litter of this plant functional type to be decomposed in boreal peatlands.

Table 3.2 Decomposition rates and dynamics (decomposition constant (*k*) and mean residence time) for three peatland plant functional type litters after one year litterbag placement in dry hummocks and moist hollow microtopologies. Values are means ± standard error. Values followed by different letters are significantly different based on Tukey HSD *post hoc* analysis.

	Moss: *Sphagnum*	Shrub: *Chamaedaphne*	Sedge: *Carex*
	Mass Loss Decomposition (%)		
Hummock	21.64 ± 1.81^{cd}	28.87 ± 1.62^{bc}	41.23 ± 2.42^{ab}
Hollow	18.99 ± 4.01^{d}	32.15 ± 0.98^{b}	43.75 ± 1.16^{a}
	Decomposition constant (*k*)		
Hummock	0.24 ± 0.02	0.34 ± 0.02	0.54 ± 0.04
Hollow	0.22 ± 0.05	0.39 ± 0.01	0.58 ± 0.02
	Mean residence time (year)		
Hummock	2.05 ± 0.10	1.72 ± 0.05	1.38 ± 0.05
Hollow	2.31 ± 0.22	1.61 ± 0.03	1.32 ± 0.02

3.4 Discussion

Aboveground and belowground systems are intricately linked by the entry of plant litter and other detritus to the soil system where they undergo decomposition. Controls on decomposition are often largely driven by abiotic factors such as temperature and moisture, the ecostoichiometric and chemical composition of the plant litter, as well as the composition of the detrital community (Bradford et al., 2016; Keiser and Bradford, 2017; Wall et al., 2008). Here, using litterbags of three different peatland plant litter functional types (moss, sedge, shrub) placed at two different micro-environmental sites (hummock and hollow), I showed that abiotic environmental conditions are the main drivers of community structure for detrital invertebrates, while plant litter quality is a more important determinant of decomposition dynamics in boreal peatlands.

The differences in micro-climate conditions between hummocks and hollows were only measured at a single hummock-hollow site, while litterbags were placed across five hummock-hollow microtopologies, thus generalisation of hummock and hollow micro-climates is limited. However, my data for temperature and relative humidity suggested that hummocks are drier, warmer and more variable than hollows (see Appendix E), but that the magnitude of those differences is potentially minor. Yet, significant differences were seen in the richness and abundance of microarthropods associated with hummock and hollow microtopologies. Microarthropods are sensitive to moisture regimes and humidity of microhabitats, with low moisture conditions limiting species richness, abundance, and diversity (Lindberg, 2003; Lindo and Winchester, 2007; Materna, 2000; Minor et al., 2019; Pflug and Wolters, 2001; Siepel, 1996) in many ecosystems. Similarly, desiccation (drainage) in a *Sphagnum* bog has been shown to decrease oribatid mite species richness (Lehmitz, 2014), as I found in hummocks compared to hollows. Minor et al. (2019) also found lower abundance of oribatid mites in hummocks vs. wetter areas of a Russian *Sphagnum* peatland. Oribatid mites as the dominant and representative microarthropod group in peatland systems (Laiho et al., 2001; Lindo, 2015; Silvan et al., 2000) showed similar results to Collembola (a decrease in richness and abundance in drier conditions; Appendix C), suggesting many microarthropod groups are similarly responding to microclimate conditions or latent differences in resource availability. Richness and abundance trends between hummocks and hollows may be related to abiotic conditions either in microclimate as suggested above, or through physical or chemical aspects associated with different *Sphagnum* species (Belyea and Clymo, 2001), such as greater nutrient availability, higher pH (Clymo, 1987), and a more diverse fungal (Asemaninejad et al., 2017) and bacterial (Asemaninejad et al., 2019) community in hollows when compared to hummocks.

Greater richness and abundance of oribatid mites in hollows led to more homogeneous community composition with most hummock species also being found in hollows, although three oribatid mite species were unique to the hummock microtopology. A recent study of the fungal communities of hummock and hollow peat at the same location revealed statistically distinct fungal community composition between hollows and hummocks, with the hollows containing a more diverse fungal community than hummocks (Asemaninejad et al., 2017). In this chapter, the community composition of the hummock samples appeared to be composed of random individuals, rather than a nested subset of the hollow species. However, upon closer examination of oribatid mites, I found plant litter type helped structure the hummock communities (but not in the hollows). *Carex* litter placed on hummocks had nearly zero oribatid mites colonise the litterbags, whereas only oribatid mites colonised the *Chamaedaphne* litterbags on hummocks. I cannot fully explain this result, although the presence and spatial distribution of *Chamaedaphne calyculata* has been shown to determine fungal turnover and play a key role in the structure of microbial communities by releasing dissolved organic carbon (DOC) (Lin et al., 2014). It may be that microbial (fungal) resources were more readily available in *Chamaedaphne* versus *Carex* litterbags on hummocks, or alternatively the small, tough leaves of *Chamaedaphne* may have created more favourable physical conditions for oribatid mites, possibly through the retention of moisture.

Litterbags in this chapter yielded lower species richness than other peatland studies that have sampled the peat-soil directly (e.g., Chapter 2; Lindo, 2015), although *Trhypochthonius tectorum* (Berlese, 1896) s.l. and *Lepidozetes* sp. were found in the litterbags, but not in Chapter 2 or Lindo (2015). While I found on average 23.55 oribatid mite species/peat soil sample in the SF in Chapter 2, the average oribatid mite richness was only 4 species/litterbag in hollows and 1.42 on hummocks. Total oribatid species richness was also higher in Chapter 2, where I found 59 species in the SF compared to only 17 species found in the litterbags. Nonetheless, asexually reproducing oribatid mite species (parthenogenetic) also dominated the litterbags (64% of all species, 64% of the species in hollows and 71% of the species on hummocks), exceeding the trend seen for the full assemblage (56% of all species were asexual in the SF (Chapter 2)). In addition, most oribatid species found in the litterbags exhibit some level of sclerotization/ mineralization that might indicate desiccation tolerance (76% of all species, 61% of the species in hollows and 80% on hummocks), which was higher than that in the full oribatid mite assemblage (59% of all species in SF – Chapter 2). On average, litterbags also had less individuals of oribatid mites compared to the average found in Chapter 2 (38.72 ind. / g dwt litter compared to 86.43 ind. / g dwt peat soil, respectively). Besides being represented by more parthenogenetic oribatid species, more individuals of parthenogenetic species than sexual species were also found in litterbags (~7.5-fold greater), although this was lower than the proportion found for the full oribatid assemblage in the SF in Chapter 2 (10-fold greater). Also different was the proportion of sclerotized/mineralized individuals, where I found almost twice as many individuals (std abundance) in litterbags compared to the full assemblage (sclerotized/mineralized individuals represented 62% of all individuals in litterbags and 34% of all individuals in the SF). Both richness and abundance proportions seemed to indicate higher desiccation tolerance in the species found in litterbags than in Chapter 2.

The litterbag technique is widely used to study decomposition (Moore et al., 2017; Prescott, 2005; Yavitt et al., 2019), and can also be used to address questions of soil fauna litter associations and colonisation processes (Peña-Peña and Irmler, 2016; Soong et al., 2016). Linking the two (soil fauna composition and decomposition rates) has proved elusive and advocated to be included in decomposition models (García-Palacios et al., 2013; Wall et al., 2008) — here, patterns in fauna diversity (richness, abundance) were not correlated with mass loss rates, which is understandable as previous studies suggest contributions of fauna to decomposition are mostly indirect through the microbial communities, and therefore hard to measure (Cárcamo et al., 2001; de Resende et al., 2013; Faber and Verhoef, 1991; Joo et al., 2006; Moore et al., 1988; Seastedt, 1984; Zhang et al., 2001; but see Section 5.3.2.). Nonetheless, Höfer et al. (2001) found a strong positive correlation between decay rates and macroarthropod biomass in a litterbag study in Amazonian ecosystems, González and Seastedt (2001) found significant effects of soil fauna on litter decomposition in tropical wet, dry, and subalpine forests using fauna exclusion experiments, and Peña-Peña and Irmler (2016) also found that soil fauna contributed to the litter breakdown with 13–57% in an exclusion experiment in the Brazilian Cerrado. Oribatid mites are generally regarded as fungivorous, however can span a wide range of feeding functional groups (Schneider et al., 2004; Schneider and Maraun, 2005). For instance, feeding modes of oribatid mites based on digestive (carbohydrase) enzyme activity (Berg et al., 2004; Siepel and de Ruiter-Dijkman, 1993), and natural abundance stable isotopes (Heidemann et al., 2014; Schneider et al., 2004) distinguished four major (but overlapping) feeding guilds: herbivorous grazers, fungivorous grazers, omnivorous herbo-fungivorous grazers, and omnivorous opportunistic scavengers. These feeding groups are consistent for peatland oribatid mites (Behan-Pelletier and Hill, 1983). More recently Lehmitz and Maraun (2016) demonstrated that the detrital food web in *Sphagnum* dominated peatlands was derived from *Sphagnum* mosses, but posit that direct feeding on intact *Sphagnum* was unlikely considering its low quality (e.g., higher C:N ratio; see Appendix B), and Lehmitz and Maraun (2016) suggest that the majority of oribatid mite species were secondary decomposers feeding on microbial groups (fungi, bacteria, microfauna) in close association with *Sphagnum* mosses (Jassey et al., 2013). In this chapter, oribatid mite communities were not significantly different between plant litter types or correlated with decomposition rates, possibly because they were not directly feeding on them. Therefore, and considering oribatid mite feeding preferences, changes in the diversity and/or biomass of microbial groups caused by different levels of soil moisture are likely another indirect but important factor here in addition to soil moisture acting as a direct driver of oribatid mite communities in my microhabitat sites.

Differences in environmental conditions (moisture and temperature) at the small spatial scale of hummock and hollow microtopology did not contribute to differences in litterbag mass loss, rather decomposition rates were driven by functional plant litter type. Differences among plant litter quality (i.e., litter chemistry, carbon lability, or ecostoichiometric ratios) likely underpin this result as has been seen in peatlands (Del Giudice and Lindo, 2017; Moore et al., 2007, 2005), and other ecosystems (Cornwell et al., 2008; Makkonen et al., 2012; Zhang et al., 2008). For instance, carbon-to-nitrogen (C:N) values are often inversely correlated with decomposition rates (Enriquez et al., 1993; Limpens and Berendse, 2003), and a previous study of *Sphagnum* and *Carex* litter collected from the same peatland reported C:N values of ~45 and ~30, respectively, with the ratio difference being driven by greater %N content in *Carex* (Lyons and Lindo, 2020). In that study, mass loss rates for *Sphagnum* and *Carex* litter over one year were comparable to the values reported here (~20% and ~55% mass loss, respectively). Carbon lability may also explain mass loss rates for these three plant functional groups. For instance, during a short-term leaching experiment, mass loss of these three species corresponded to the total dissolved organic carbon released, and it was shown to be greater and composed of more labile carbon compounds in the vascular species (sedges and shrubs) compared to *Sphagnum* mosses (Del Giudice and Lindo, 2017). That said, the absolute values of mass loss did not account for any mass loss due to handling and not accounting for this step means the total mass loss is likely to be a slight overestimate of the decompositional mass loss.

Decomposition rates measured over one year reflect short-term decomposition dynamics, and may not represent longer-term decomposition rates (Moore et al., 2017), or predict litter contributions to the stable organic carbon (SOC) pool (Cotrufo et al., 2015; Moore et al., 2007). In boreal peatlands, SOC stocks play an important role in models of carbon stores and fluxes, and knowledge of decomposition processes can improve these models (Wieder et al., 2013). My results suggest that potentially impending shifts in the aboveground plant communities of boreal peatlands (Buttler et al., 2015; Dieleman et al., 2015; Lyons et al., 2020) from *Sphagnum* mosses to vascular plants (both sedges and shrubs) under climate warming will have cascading effects on belowground processes. Further enhanced decomposition of more labile vascular plant litter may accelerate the decomposition of more recalcitrant SOC through potential priming effects (Wang et al., 2015) and reduce the carbon sequestration potential of boreal peatlands. Taken together, changes in the diversity and/or biomass of microbial groups (e.g., fungal vs. bacterial dominance), inputs of litter with different quality (e.g., lower in *Sphagnum* mosses vs. higher *Carex* sedges), and abiotic factors (e.g., soil moisture, temperature) in peatlands can cause bottom-up effects affecting the topology of the detrital food web, and may ultimately translate into altered carbon fluxes, with ecosystem-level consequences (see Chapter 5).

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Chapter 4

4 Responses of oribatid mites to warming in boreal peatlands depend on fen type

4.1 Introduction

Boreal peatlands are ecosystems important for carbon cycling (Beaulne et al., 2021; Harenda et al., 2018). Peatland soils store about 1/3 of the world's terrestrial carbon (Limpens et al., 2008) yet only cover ~3% of the globe (Gorham, 1991), which makes them a key component of potential mitigation strategies in response to global climate warming. Nonetheless, climate warming is predicted to increase soil temperature between 2.27°C ± 0.97°C and 4.36°C ± 1.69°C (models for RCP 4.5 and 8.5, respectively) for boreal ecosystems by the end of the 21st century (Soong et al., 2020), which is predicted to decrease soil carbon through changes in both aboveground and belowground biodiversity.

Warming experiments specific to northern peatlands have shown significant decreases in *Sphagnum* moss cover, alongside increased vascular plant biomass (Dieleman et al., 2015; Fenner et al., 2007), increased heterogeneity in plant communities (Lyons et al., 2020) and increased CO_2 (Bragazza et al., 2013; Dieleman et al., 2016a; Tian, 2019; Tian et al., 2020) and CH_4 emissions (Tian, 2019). Correspondingly, peatland vegetation has been shown to shift from low-nutrient mosses to more degradable vascular plant litter inputs (Buttler et al., 2015; Dieleman et al., 2015; Fenner et al., 2007; Jassey et al., 2013), coinciding with more labile carbon availability (Dieleman et al., 2017, 2016b) in the peat soils. This is also correlated with increases in phenolics associated with sedge root growth (James, 2020), greater microbial activity (Asemaninejad et al., 2017), shifts in fungal composition favouring recalcitrant compound decomposers (Asemaninejad et al., 2018), and faster organic matter decomposition (Dieleman et al., 2016b). These warming-induced shifts in plants will likely cascade and affect soil microarthropod communities with poorly documented ecosystem-level consequences, as above- and belowground communities in boreal peatlands have been shown to be linked (Lyons and Lindo, 2020).

Oribatid mites (Acari: Oribatida) are commonly the dominant group of arthropods in terrestrial soils (Norton and Behan-Pelletier, 2009) and are well represented in terms of diversity in wetlands such as boreal peatlands (Behan-Pelletier and Bissett, 1994; Chapter 2; Lindo, 2015). Oribatid mites are a major component of detrital food webs, being responsible for secondary decomposition of organic matter (Hubert, 2001; McBrayer et al., 1977) and playing an important role in carbon transformation in boreal peatlands. Carbon transformation by oribatid mites in peatlands is also potentially under threat with climate change, but despite their importance, oribatid mites in peatlands have not been extensively investigated under climate change scenarios. In the few studies to date, peatland warming has been shown to impact and alter oribatid communities, with the primary driver of compositional shifts being increases in abundance of small-bodied species and immatures in an 18-month mesocosm experiment (Lindo, 2015), while Markkula et al. (2019) found that year-round warming did not affect oribatid abundance, but it decreased their richness in a 16-year field experiment in a sub-Arctic peat bog in Sweden.

Responses of oribatid mites to warming are, however, more commonly investigated in other ecosystems such as boreal forests (Meehan et al., 2020), temperate heathlands (Holmstrup et al., 2017), alpine heathland (Hågvar and Klanderud, 2009), and tundra ecosystems (Alatalo et al., 2017). Negative, neutral, or even positive warming-induced changes have been recorded for oribatid abundance, richness, and community composition, but the majority have found negative effects on soil microarthropods (Blankinship et al., 2011). Nonetheless, responses to warming have being previously suggested to be functional group- or taxon-specific (Bokhorst et al., 2008; Briones et al., 2009; Wu et al., 2014).

The effects of warming on oribatid mite communities can be indirect through associated changes in soil moisture levels (Blankinship et al., 2011; Holmstrup et al., 2017; Wu et al., 2014), as water content has been shown to structure oribatid mite communities in *Sphagnum* peatlands (Minor et al., 2019, 2016), as well as in other ecosystems (Lindo et al., 2012; Taylor and Wolters, 2005; Vestergård et al., 2015). In fact, during experimental warming manipulations in the field, warming-induced reductions in soil moisture have been suggested to be a more significant driver of oribatid communities than higher temperatures alone (Bokhorst et al., 2008; Kardol et al., 2011).

The mechanisms through which warming directly affects soil invertebrate communities involve accelerated metabolic rates, including growth, reproduction, respiration, and mortality (Brose et al., 2012; Brown et al., 2004), as well as enhanced consumption rates by predators, leading to trophic cascades (Lang et al., 2014), as for other ectothermic taxonomic groups (Ehnes et al., 2011; Gillooly et al., 2011). The indirect effects of warming on soil invertebrate communities involve bottom-up cascades due to changes in the quality of their basal resources (detritus input) (A'Bear et al., 2013; Chapter 3; Walter, 1985) caused by shifts in vegetation (e.g., Lyons et al., 2020) and shifts in microbial community composition (e.g., Asemaninejad et al., 2018), besides warming-induced changes in the physical aspects of soils. Specifically, warming can cause soil moisture content to decrease (Blankinship et al., 2011; Lang et al., 2014; Schwarz et al., 2017; Wu et al., 2014), which can benefit some terrestrial invertebrate species if it enhances habitable soil pore space (Turnbull and Lindo, 2015), but lower soil moisture content in peatlands may be detrimental to semi-aquatic species (Minor et al., 2019). Thus, the effects of warming on soil oribatid mites are likely both direct and indirect at the same time.

Here I examined responses in oribatid mite communities across two contrasting peatland types under experimental warming over four years. I hypothesised that the direct effects of warming on metabolic process would accelerate developmental rates. Therefore, I predicted that warming would increase the proportion of immatures in the community, and total abundance, especially of parthenogenetic species (as seen by Lindo (2015)). I hypothesised that the indirect effects of warming, specifically warming-induced drying of peat soils, would increase habitable soil pore space. Therefore, I predicted increases in terrestrial species, but potentially decreases in semi-aquatic species under warming, leading to no net change in species richness, but significantly altered community composition.

4.2 Materials & Methods

4.2.1 Experimental design

To examine the effects of warming on oribatid mite communities and other microarthropods, 16 experimental plots were established at each of the two fen sites near White River, ON in June 2016. A full description of the two sites is presented in Chapter

2, but briefly, the two sites differ in dominant vegetation, water table (soil moisture), and nutrient availability. One fen is dominated by *Sphagnum* mosses (SF) with a lower water table and low nutrient availability, while the second fen is dominated by *Carex* sedges (CF) with a higher water table and intermediate levels of nutrient availability. The experiment follows a block design; at each fen, the 16 experimental plots were equally divided into four blocks to account for any spatial factors inherent to the site, and within each block, two plots were assigned to warming and two plots were control (i.e., ambient temperature) (Figure 4.1). Plots were circular and delineated by cylindrical PVC collars (1 m diameter) inserted 30 cm into the peat substrate with an additional 10 cm extending above-ground. All plots were located roughly within a 25 m^2 area within each site and accessed by boardwalks to lessen disturbance of the surrounding environment. At the time of plot establishment, plots assigned to warming treatments had six evenly spaced vertical heating rods (60W Watlow FireRod® immersion heaters) installed to a depth of 50 cm below the peat surface in preparation for active ground warming (Figure 4.2B). Plots were left to recover for one year prior to the experiment commencing.

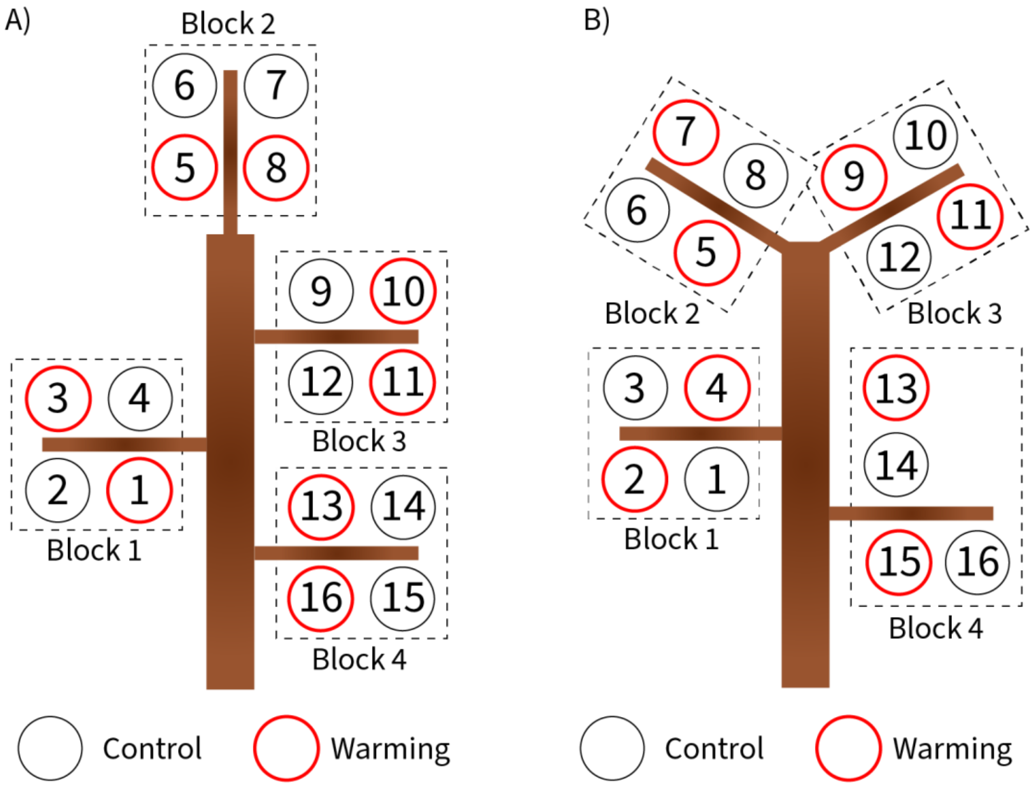

Figure 4.1 A schematic map of the experimental set-up for the two peatland sites. A) the *Sphagnum*-dominated fen (SF) and B) the *Carex*-dominated fen (CF). At both sites, the experiment included four blocks with four plots each to account for spatial heterogeneity in plant community composition and microtopologies. Within each block, two plots were assigned to warming and two plots were control (ambient).

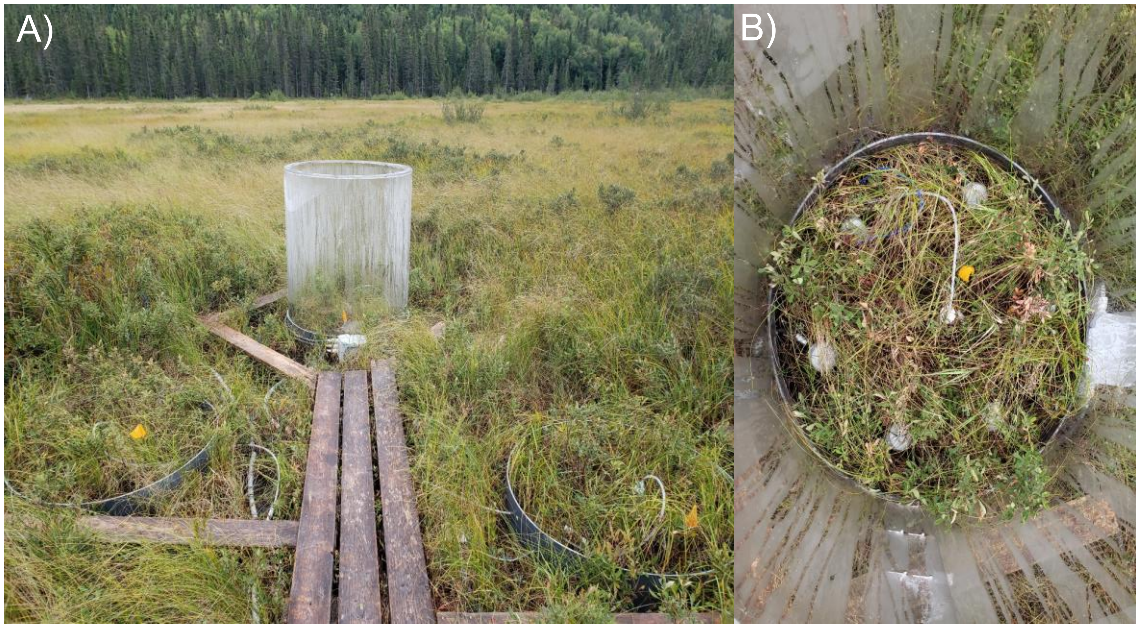

Figure 4.2 A) Lateral and B) top-down view of an open-top chamber (OTC) in the CF.
Figure A) also shows two plots without chambers as control plots (foreground), and B) depicts the caps of the six heating rods (white circles) used for active belowground warming. Note that the chamber walls look opaque due to early morning precipitation/condensation.

In June 2017 half of the plots (8 plots) at each site were implemented with clear open top chambers (OTCs – 1.2 m tall, 1 m diameter) that rested within the PVC collars (Figure 4.2A). The OTCs were constructed based on ITEX chambers (but with straight sides), and passively warmed the daytime air temperature by 0.95°C ± 1.2°C and 1.8°C ± 1.4°C in the SF and CF, respectively, as seen in other OTC experiments (Alatalo et al., 2017; Buttler et al., 2015; Jassey et al., 2013; Mäkiranta et al., 2018). The OTCs also passively warmed the soil temperature at 5 cm by 0.53°C ± 0.16°C and 0.24°C ± 0.02°C in the SF and CF, respectively. The OTCs were retained for the length of the growing season of each year between 2017–2020, being deployed in June and removed in October. In 2019, active heating was established via the installed heating rods in addition to passive warming by the OTCs. Heating rods were programmed through Watlow EZ-ZONE® Configurator software to gradually warm the peat to a target temperature of +4ºC above ambient peat temperatures over the summer. For each warming treatment plot, a temperature sensor was placed inside the plot and coupled to a reference sensor placed ~10 m outside the experimental area to regulate the warming treatment and maintain a +4ºC offset; both thermocouples were installed at a depth of 25 cm. Effects of the heating rods combined with the OTCs warmed the soil temperature at 5 cm by 3.77°C ± 0.03°C and 2.29°C ± 0.05°C in the SF and CF, respectively in 2019.

Air temperature and total rainfall were recorded during the time of this study by a weather station installed and maintained by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry. The average 24-hour air temperature at 2 m was 14.05°C ± 0.39°C in June 2017, 14.39°C ± 0.66°C in June 2018, 13.39°C ± 0.65°C in June 2019 and 14.27°C ± 0.44°C August 2019. Total rainfall (rainfall over the month sampling occurred) was 117 mm in June 2017, 58.3 mm in June 2018, 40.5 mm in June 2019 and 84.8 mm in August 2019. Soil moisture content (Delta-T HH2 Moisture Meter) and soil temperature (Thermocouple Traceable Fisher Scientific) were measured at 5 cm depth in three different locations within each plot around the time of sampling during the course of the experiment. Information on vegetation (Lyons et al., 2020), gas flux (James, 2020; Tian, 2019) and porewater chemistry (Sun, 2021) are also available under the same experiment.

4.2.2 Soil sampling and processing

To assess the long-term effects of warming on microarthropods, soil sampling was performed in early June of each year between 2017–2020. In 2019, as active warming was induced, an extra sampling event occurred at the end of August to investigate the short terms effects of warming. In every sampling event, one peat soil sample (8.13g ± 0.25g SE dwt) was collected from the surface moss (i.e., the bryosphere, *sensu* Lindo and Gonzalez, 2010) of each plot in each fen, totalling 160 samples. Soil samples were placed in plastic bags and kept cool until return to the laboratory.

Within 72 hours of collection, samples were weighed and extracted using Tullgren funnels over three days into 75% EtOH. Following microarthropod extraction, samples were weighed a second time to standardise fauna counts (richness and abundance) on a per dry weight basis, and also to calculate soil moisture content from the samples as it follows:

$$Moisture\ content = \frac{wet\ weight\ (g) - dry\ weight\ (g)}{dry\ weight\ (g)} \times 100$$

All microarthropods were sorted into major taxonomic groups and counted under a stereomicroscope (Nikon SMZ 745T). All adult oribatid mites (Acari: Oribatida) as the dominant group (71.59% of all microarthropods) were identified to the species level under a compound microscope (Nikon Eclipse Ni) using keys in Norton and Behan-Pelletier (2009) and literature provided by The Ohio State University Summer Acarology course. Representative oribatid mite specimens were slide mounted using Hoyer’s medium for the identification process. Final species level identifications were made using keys and species descriptions from the primary literature and confirmed where possible against reference material. Immature: adult ratios were calculated, which because developmental times of oribatid mites are known to be slow, is suggested as a better indication of population dynamics compared to abundance because immature: adult ratio reflects metabolic or reproduction constraints (Norton, 1994) whereas abundance is affected by many variables. Information on microarthropods (biomass) other than oribatid mites collected in this study is presented in Chapter 5.

4.2.3 Statistical analyses

Five univariate measures of oribatid mite communities were computed using the R statistical program (R Core Team, 2020) with functions from the base and "vegan" package (Oksanen et al., 2019) for each sample collected: oribatid mite species richness, abundance (immatures and adults included), immature: adult ratio, Shannon's diversity (H') of adults, and Pielou's evenness (J) of adults. I compared and analysed these five univariate measures across time (2018–2020) using a Linear Mixed-Effects model (LMM) with warming and time as fixed effects. I included experimental plots nested within experimental blocks as a random effect to account for the repeated sampling at the plot level and to account for any inherent spatial (i.e., block) effects; as block was often a statistically significant source of variation, I retain the block parameter in all subsequent parametric analyses. I used the function {lmer} within the "lme4" package (Bates et al., 2015) to fit the models, the function {anova} in "lmerTest" package (Kuznetsova et al., 2017) to test for differences in the aforementioned measures in response to warming and over time (Type III ANOVA), and I used Tukey HSD as *post hoc* to determine differences between and within treatment levels (warming) and sampling events (time) using "emmeans" package (Lenth, 2020) and the function {cld} in "multcomp" (Hothorn et al., 2008). I used the function {ranova} in "lmerTest" to determine the significance of random effects (chamber nested within block, and block) with an LRT test (Likelihood ratio test statistic) with a Chi-squared p-value. The two sites (SF vs CF) were analysed separately because these two sites differ significantly in the richness, abundance, diversity, evenness, and community composition of oribatid mites (see Chapter 2).

Three actively heated plots in the SF were removed from the univariate analyses in August 2019 due to a technical malfunction in the warming treatment (i.e., they did not warm; plots 1, 3 and 5). Also, samples collected in June 2017 were not included in my LMM models because they were collected just prior to the OTCs being established for the first time (i.e., pre-warming conditions). Preliminary analysis of these five variables for the 2017 samples using an Anova show no significant pre-warming differences between plots designated as warming vs control (Table 4.1), and no pre-warming differences were found at the community level either (SF: PerManova: $F_{1,15} = 1.309$, $P = 0.239$, Nmds stress = 0.205, CF: Permanova: $F_{1,15} = 0.579$, $P = 0.762$, Nmds stress = 0.116).

To examine overall adult oribatid mite community composition (i.e., multivariate analyses that include species identifications), I performed a two-way permutation multivariate Anova (PerManova) based on Bray-Curtis dissimilarity of composition among samples to determine how warming and time affected communities across all sampling events (2017–2020, with June 2017 plots all considered control). This test was performed in R using the {adonis} function. I subsequently performed an additional PerManova to test for warming effects for each sampling time individually. The oribatid mite community analysed through these PerManova tests was further assessed visually using non-metric multidimensional scaling (Nmds). In addition, when communities appeared nested in NMDS plots, I performed nestedness analysis to interpret community structure by identifying whether reduced species assemblages were subsets of larger assemblages. For the nestedness analysis, I used the “bipartite” package (Dormann et al., 2009) and the functions {nestedtemp}, which generates a nestedness temperature value between 0–100, with lower values indicative of nestedness, and {oecosimu} with {C.score} as parameter, where the C.score ranges between 0 (no checkerboards = absence of species in a sample) and 1 (only checkerboards = presence of a species in a sample).

While the PERMANOVA tested for the effects of warming and time on oribatid mite communities, I implemented distance-based redundancy analyses (DBRDA) also based on Bray-Curtis dissimilarity of composition among samples (communities) to include environmental variables and test their relationship with specific species, rather than all species considered together as one entity at the community level. In other words, I tested whether warming, time, plot and sample moisture content help explain the variance of the data (accounting for species abundance) of the top 50% of species that had the highest axis loadings using data from 2017–2020 (Appendix F). Axis loadings reflect how much of the variance in the data of each individual species is explained by each axis. To do this examination for the adult oribatid mite communities, I performed a preliminary DBRDA on all species collected between 2017–2020 for each fen separately using the function {capscale} in the “vegan” package in R statistical program, which provides a Pseudo-F value (i.e., the measure of the significance of the overall analysis). I used the sum of the absolute value of the axis loadings for each species from the first two (i.e., dominant) axes (CAP1, CAP2) to determine this top 50% that led to including 34 species for the SF and 24 species for the CF. I repeated the analysis with these species for all data collected between 2017–2020, and I used these species in subsequent DBRDA analysis for each individual sampling event (except 2017) with warming and moisture content as explanatory variables. Some species were excluded in years when they were absent from all samples (# of species examined in SF: June 2018 n = 33, June 2019 n = 31, August 2019 = 33, June 2020 = 32; # of species examined in CF: June 2018 n = 22, June 2019 = 22, August 2019 n = 23, June 2020 n = 22). For clarity, the factor 'plot' is not shown in the DBRDA plots for all data collected between 2017–2020. All analyses used an alpha of 0.05, and final plots were created in R with the packages "ggplot2" (Wichkam, 2016) and "ggrepel" (Slowikowski et al., 2021).

Finally, I used the function {ggscatter} in the package "ggpubr" (Kassambra, 2020) to run Pearson's correlations between average soil temperature and average soil moisture content for both fens using data from 2018–2020, as well as data for each year individually. Increases in temperature tended to correlate with reductions soil moisture content in the SF, although this was not always statistically significant (2018–2020: R = -0.24, P = 0.064; June 2018: R = -0.42, P =0.1; June 2019: R = -0.14, P = 0.62; August 2019: R = -0.61, P = 0.027; June 2020: R = -0.13, P = 0.63). Higher temperatures still correlated with lower soil moisture content in the CF, although effects were weaker (2018–2020: R = -0.074, P = 0.56; June 2018: R = -0.077, P = 0.78; June 2019: R = -0.005, P = 0.98; August 2019: R = -0.49, P = 0.057; June 2020: R = -0.28; P = 0.3). In both fens, correlations were stronger for higher soil temperatures induced by active warming in August 2019.

4.3 Results

4.3.1 Warming effects at the *Sphagnum*-dominated fen

Warming as a main effect did not affect richness (# of species / g dwt) significantly when all sampling events were analysed together ($F_{1,11.65}$ = 0.045, P = 0.511) (Table 4.1); passively warmed plots were not significantly different from control plots (Tukey HSD, June 2018: P = 0.746; June 2019: P = 0.976; June 2020: P = 0.920), but active warming in August 2019 marginally increased richness (Tukey HSD, P = 0.072; Figure 4.3A). Resultingly, oribatid species richness significantly changed over time (main effect of time: $F_{3,40.39}$ = 4.739, P = 0.006), driven by sampling in August 2019 (Tukey HSD between June and August 2019: P = 0.007) when the lowest values were found under ambient conditions (Table 4.1). Richness in the subsequent sampling event (June 2020), though, was statistically similar to that of all other events (Tukey HSD of time: August 2019: P = 0.237; June 2018, P = 0.587; June 2019, P = 0.367). There was no significant interaction of warming × time ($F_{3,40.39}$ = 1.204, P = 0.320) (Table 4.1). However, richness was also significantly lower in the control plots in August 2019 compared to control plots of the other periods (Tukey HSD between control plots: June 2018: P = 0.003; June 2019: P = 0.002; June 2020: P = 0.050). Lastly, neither plot nested within block (LRT = 1.064, P = 0.302) nor block as a main effect (LRT = 0.105, P = 0.745) showed significant random effects on oribatid species richness, demonstrating the homogenous nature of plots and blocks for the number of oribatid species present.

Table 4.1 Oribatida species richness, abundance, immature: adult ratio, Shannon's diversity (H') and species evenness (J) for samples collected over four years in the *Sphagnum*-dominated fen.

Values are calculated using standardised values based on per gram dry weight as means ± standard error. Values followed by different letters are significantly different based on Tukey HSD post hoc analysis for time × warming interaction. June 2017 pre-warming values are shown for comparison but were not included in the LLM models.

		***Sphagnum*-dominated fen**				
		Jun-17*	**Jun-18**	**Jun-19**	**Aug-19**	**Jun-20**
Richness (# species / g dwt)	Control	3.74 ± 0.39	4.50 ± 0.43^{a}	4.56 ± 0.47^{a}	2.59 ± 0.21^{b}	3.97 ± 0.49^{ab}
	Warming	4.09 ± 0.47	4.32 ± 0.43^{ab}	4.54 ± 0.34^{a}	3.81 ± 0.48^{ab}	3.92 ± 0.34^{ab}
Abundance (# indiv. / g dwt)	Control	75.94 ± 13.99	79.31 ± 8.81	99.29 ± 22.80	120.73 ± 29.36	93.35 ± 12.49
	Warming	76.12 ± 12.14	79.39 ± 12.04	85.69 ± 12.92	109.92 ± 16.97	76.22 ± 12.20
Immature: adult ratio	Control	0.65 ± 0.10	1.09 ± 0.34^{b}	1.05 ± 0.16^{b}	2.69 ± 0.55^{a}	1.28 ± 0.11^{b}
	Warming	0.63 ± 0.08	0.97 ± 0.22^{b}	1.04 ± 0.18^{b}	1.39 ± 0.11^{ab}	1.00 ± 0.16^{b}
Diversity (H')	Control	2.48 ± 0.07	2.49 ± 0.08	2.55 ± 0.06	2.33 ± 0.09	2.39 ± 0.12
	Warming	2.55 ± 0.05	2.46 ± 0.09	2.48 ± 0.06	2.47 ± 0.10	2.66 ± 0.03
Evenness (J)	Control	0.77 ± 0.02	0.78 ± 0.01	0.79 ± 0.01	0.78 ± 0.01	0.75 ± 0.02
	Warming	0.78 ± 0.01	0.79 ± 0.01	0.79 ± 0.01	0.76 ± 0.01	0.82 ± 0.01

* pre-warming conditions (i.e., control and warming treatments were not yet enacted)

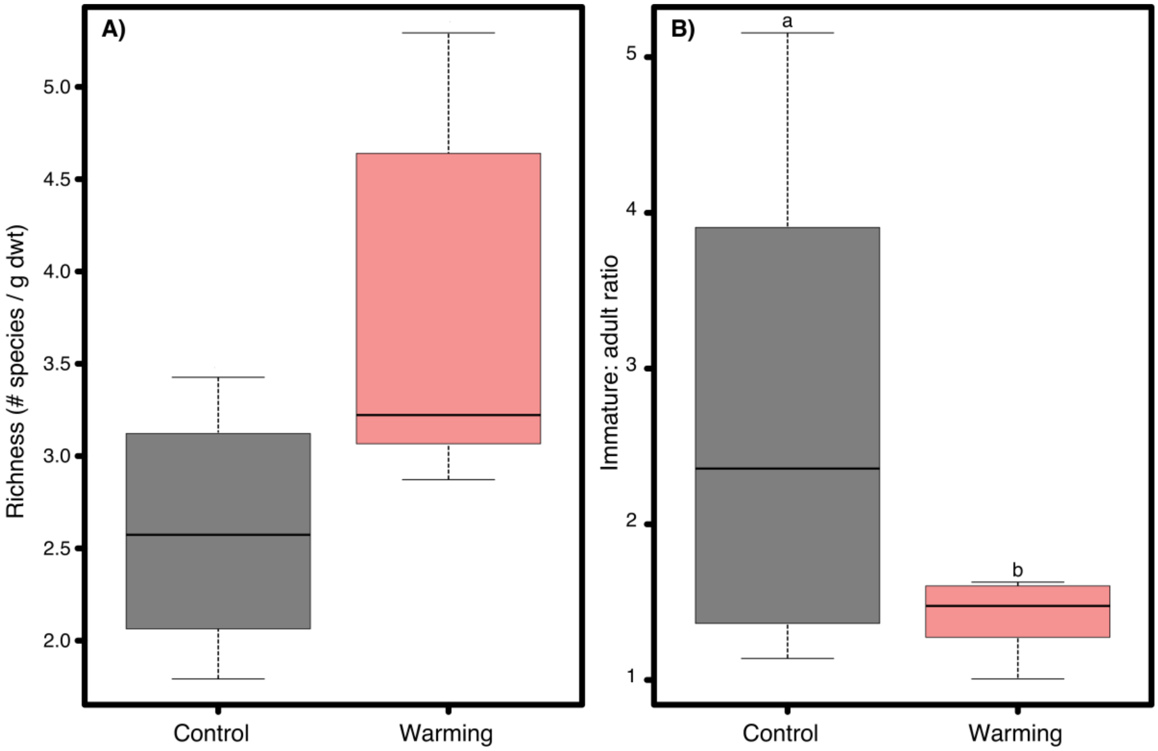

Figure 4.3 Effects following active warming on oribatid mite richness and immature: adult ratio in the SF in August 2019.

A) Oribatid mite species richness and B) Immature: adult ratio of oribatid mites from peat soils collected in the *Sphagnum*-dominated fen in August 2019. Letters denote significant differences after Tukey HSD *post hoc* comparisons. In the boxplot: lower and upper box boundaries represent 25% and 75$^{\%}$ percentiles, respectively; the line inside the box represents the median; lower and upper error lines are 10% and 90% percentiles, respectively.

The abundance of oribatid mites (# of indiv. of adults and immatures / g dwt) did not change under warming when all sampling events were analysed together ($F_{1,14.59}$ = 0.361, P = 0.556) (Table 4.1), nor when tested separately (Tukey HSD June 2018: P =0.997; June 2019: P = 0.572; August 2019: P = 0.673; June 2020: P = 0.478). Changes in abundance over time followed the opposite pattern of changes in richness; abundance only marginally (but not significantly) changed over time (main effect of time: $F_{3,39.51}$ = 2.198, P = 0.103) (Table 4.1), but not until August 2019, when the highest values were found (as opposed to the lowest richness values in the same period). There was no significant interaction of warming × time for abundance ($F_{3,39.51}$ = 0.151, P = 0.927). The random effects of plots nested within blocks were statistically significant for abundance, demonstrating that the plots were highly heterogeneous in terms of the number of individuals repeatedly sampled in each plot (LRT = 8.259, P = 0.004). The random effects of block alone were not statistically significant (main effect of block: LRT = 0.000, P = 1.000).

The immature: adult ratio of oribatid mites significantly decreased under warming when all sampling events were analysed together ($F_{1,53}$ = 4.396, P = 0.040) (Table 4.1), but this decrease was only significant under active warming in August 2019 (Tukey HSD: P = 0.006, Figure 4.3B) (i.e., active warming drove the main effects of warming); passive warming did not affect the immature: adult ratio (Tukey HSD of time: June 2018: P = 0.763; June 2019: P = 0.963; June 2020: 0.487). Active warming decreased the ratio in August 2019 by reducing the abundance of immatures by ~28%, and of adults by ~9%. Changes in the immature: adult ratio mirrored changes in abundance over time, and the ratio in August 2019 was significantly higher than that in all June sampling (Tukey HSD:

June 2018: $P = 0.009$; June 2019: $P = 0.010$; June 2020: $P = 0.002$), which led to a significant main effect of time ($F_{3,53} = 5.009$, $P = 0.003$) (Table 4.1). Specifically, changes in the ratio over time were driven by differences in control plots in August 2019 that had the highest ratios compared to all June sampling regardless of treatment (Tukey HSD of control plots: June 2018: $P = 0.001$; June 2019: $P < 0.001$; June 2020: $P = 0.004$; Tukey HSD of warmed plots: June 2018: $P = 0.001$; June 2019: $P = 0.002$; June 2020: $P = 0.002$). Correspondingly, both control and warmed plots in August 2019 had a higher proportion of immatures than June sampling times, and these effects were driven by increases in immatures, rather than a change in the abundance of adult oribatid mites. Even though both warming and time were significant as main effects, their interaction was not significant ($F_{3,53} = 1.848$, $P = 0.149$) (Table 4.1). Immature: adult ratio had no significant random effects of plot within block, or block (both: LRT = 0.000, $P = 1.000$).

The Shannon’s diversity (H’) of adult oribatid mites did not change significantly under warming when all sampling events were analysed together ($F_{1,14.64} = 0.901$, $P = 0.357$) (Table 4.1), but significantly increased in June 2020 under passive warming (Tukey HSD: $P = 0.026$, Figure 4.4A); no significant changes in diversity were seen under warming in the other periods. Diversity did not significantly change over time either ($F_{3,40.17} = 1.142$, $P = 0.343$) (Table 4.1). Yet, there was a marginal interaction of warming × time ($F_{3,40.17} = 2.218$, $P = 0.100$) (Table 4.1), also caused by the increase in diversity by passive warming in June 2020. Lastly, plot nested within block (LRT = 3.603, $P = 0.057$) had a marginal random effect, whereas block as a main effect (LRT = 0.000, $P = 1.000$) showed no significant random effects on oribatid species diversity, demonstrating the heterogenous nature of plots, but homogeneous nature of blocks for the diversity of oribatid mite species.

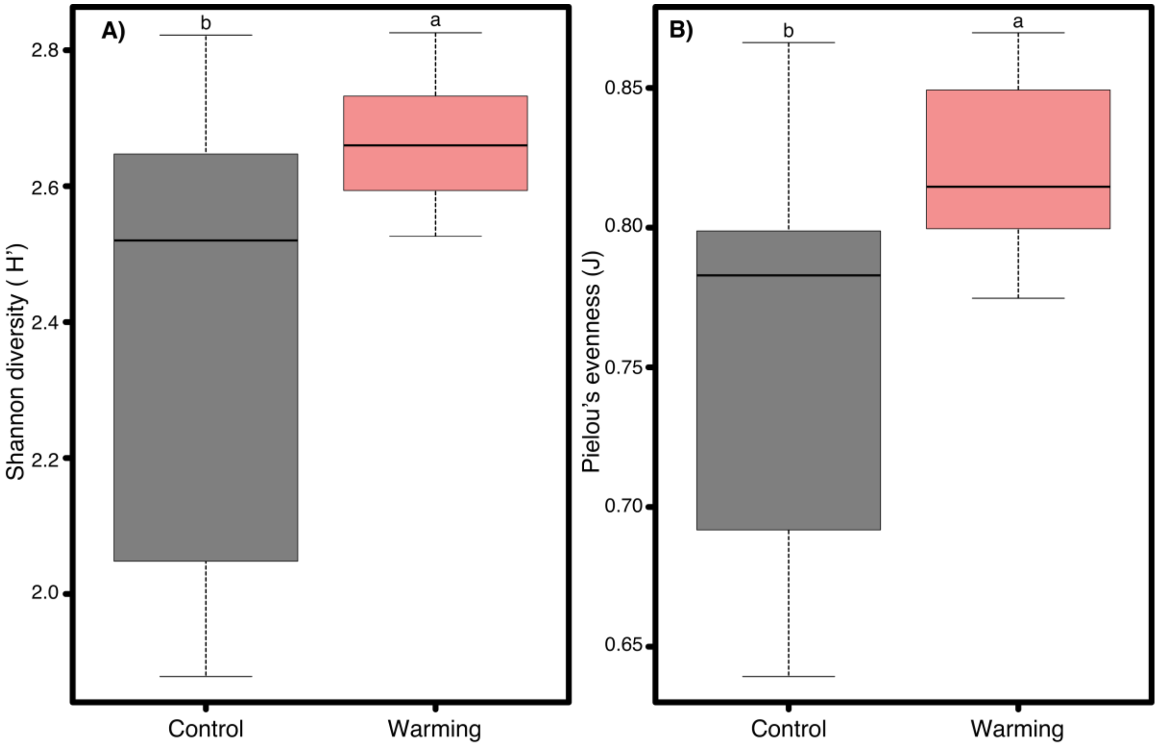

Figure 4.4 Effects following passive warming on oribatid mite diversity and evenness in the SF in June 2020.

A) Oribatid mite Shannon's diversity index and B) Oribatid mite Pielou's evenness from peat soils collected in the *Sphagnum*-dominated fen in June 2020. Letters denote significant differences after Tukey HSD *post hoc* comparisons. In the boxplot: lower and upper box boundaries represent 25% and 75$^{\%}$ percentiles, respectively; the line inside the box represents the median; lower and upper error lines are 10% and 90% percentiles, respectively.

Following a similar pattern to diversity, the evenness (J) of adult oribatid mites also did not significantly change under warming ($F_{1,12.08}$ = 1.206, P = 0.293) (Table 4.1), but it significantly increased in June 2020 under passive warming (Tukey HSD: P = 0.020, Figure 4.4B); no changes in diversity were seen under warming in the other periods. Evenness did not significantly change over time either ($F_{3,40.92}$ = 0.368, P = 0.775) (Table 4.1), and there was not a significant interaction of warming × time for evenness ($F_{3,40.92}$ = 1.517, P = 0.224) (Table 4.1). The increase in evenness in June 2020 can be translated as a more equal distribution of individuals among the species sampled under warming. Lastly, neither plot nested within block (LRT = 0.021, P = 0.884) nor block as a main effect (LRT = 0.520, P = 0.819) showed significant random effects on evenness, demonstrating the homogenous nature of plots and blocks in regard to the evenness of samples collected between 2018–2020.

4.3.2 Oribatid mite community measures at the *Sphagnum*-dominated fen

At the community compositional (i.e., multivariate) level, warming did not significant affect the composition of oribatid mite communities from 2017–2020 in the SF (PERMANOVA: $F_{1,75}$ = 1.206, P = 0.286) (Figure 4.5A), rather oribatid communities significantly changed over time (PERMANOVA: $F_{4,72}$ = 2.030, P = 0.001) (Figure 4.5B). Specifically, dissimilarity (i.e., variability in community composition) in oribatid communities was highly variable among years, leading to differences between warming and control treatments in certain sampling times. Dissimilarity is demonstrated as the distance between samples and the size of the 95% confidence ellipse in the NMDS plots.

When comparing oribatid community composition over time, dissimilarity (heterogeneity) was low in June 2017, 2019, and 2020, higher in June 2018, and the highest in August 2019, although this was the only sampling performed in the month of August across the years. The high variability in community composition between control and warmed August 2019 communities was mainly due to high variability in the composition of control communities. In other words, dissimilarity between communities in June 2018 and August 2019 was higher than all periods considered, and both had greater dissimilarity compared to the other sampling events.

When analysing the 34 species with highest axis scores in the preliminary DBRDA analysis, time (Pseudo-$F_{4,55}$ = 1.917, P = 0.001), plot (Pseudo-$F_{15,55}$ = 1.872, P = 0.001) and moisture content (Pseudo-$F_{1,55}$ = 2.358, P = 0.001) were significant factors explaining the variance of oribatid mite communities, while warming was only marginally so (Pseudo-$F_{1,55}$ = 1.397, P = 0.073) (Figure 4.6, and Appendix G for individual species responses to warming). Together, the axes CAP1 and CAP2 significantly explained 13.75% of the variance (Pseudo-$F_{1,55}$ = 7.221, P = 0.001 and Pseudo-$F_{1,55}$ = 5.787, P = 0.001, respectively), but, although not shown in the plot, the third and fourth axes (CAP3 and CAP4) also significantly explained an additional 9.03% the variance in oribatid mite communities.

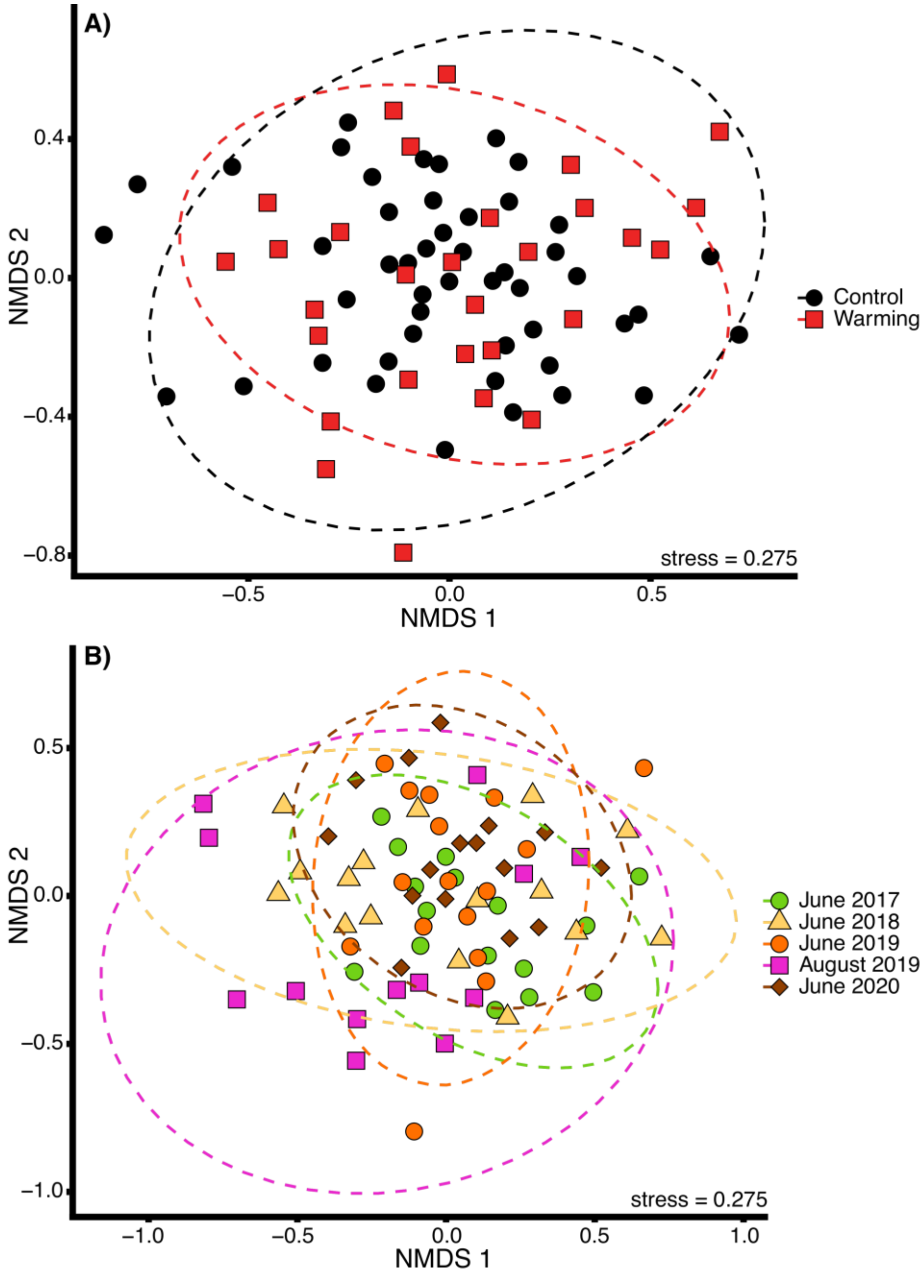

Figure 4.5 Compositional similarities of oribatid mite communities under warming in the *Sphagnum*-dominated fen sampled across four years.

Seventy-seven samples were collected in June 2017, June 2018, June 2019, August 2019 and June 2020. A) Communities are plotted by warming treatment and B) Communities are plotted by sampling event. Oribatid mite communities are based on standardised abundance of individual species from each plot. Stress = 0.275, number of dimensions (k) = 2. The ellipses indicate 95% confidence intervals.

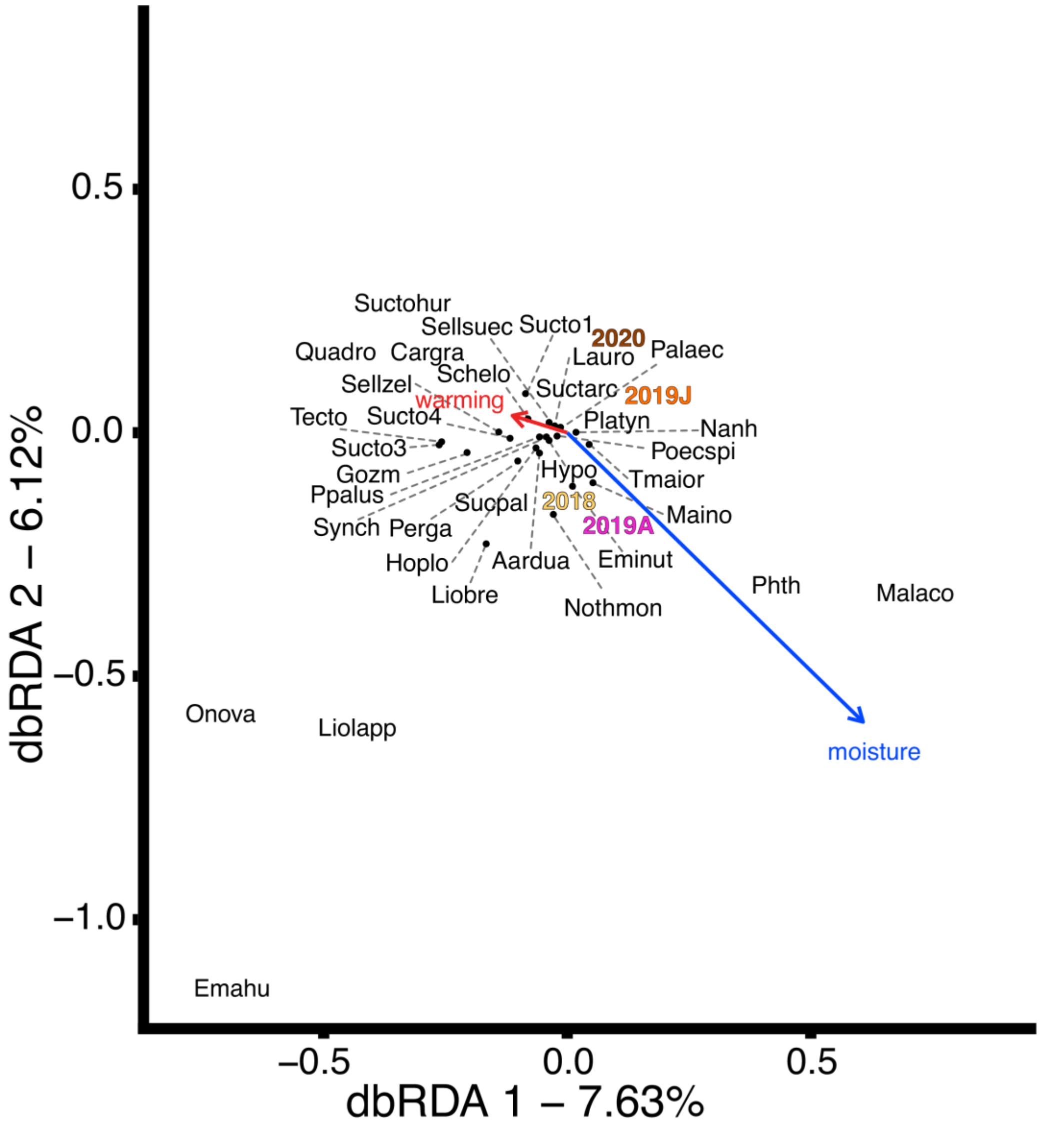

Figure 4.6 Abiotic factors driving *Sphagnum*-dominated fen oribatid mite community composition (2017–2020) in peat soil samples analysed by DBRDA. The top 50% species with the highest axis loadings are plotted and related to moisture content, warming, year (sampling event) and plot. Arrows indicate how the explaining variables are related to ordination space, and black dots at the end of gray dashed lines represent the actual location of species in this multidimensional space. See Appendix F for full species list and Appendix G for individual species responses to warming. For clear visualization, chambers are not plotted.

Examining the warming effects at individual sampling times, oribatid mite communities did not significantly change under warming (PERMANOVA June 2018: $F_{1,14} = 0.407$, $P = 0.952$; PERMANOVA June 2019: $F_{1,14} = 0.195$, $P = 0.999$; PERMANOVA August 2019: $F_{1,12} = 1.478$, $P = 0.165$; PERMANOVA June 2020: $F_{1,14} = 1.695$, $P = 0.104$) (Figure 4.7A–D). However, the NMDS plot for June 2019 shows higher variability in the composition of warmed communities, and control communities appear to be nested within communities from warmed plots (Figure 4.7B). Results of the nestedness tests suggest that the oribatid communities under control plots are, to a certain degree, subsets of species from the communities present in warmed plots (C.score = 0.46, nestedness temperature = 33.22); in other words, although ~70% of the species occurred in both control and warmed plots in June 2019, ~10% only occurred in control plots and ~20% only occurred under warming.

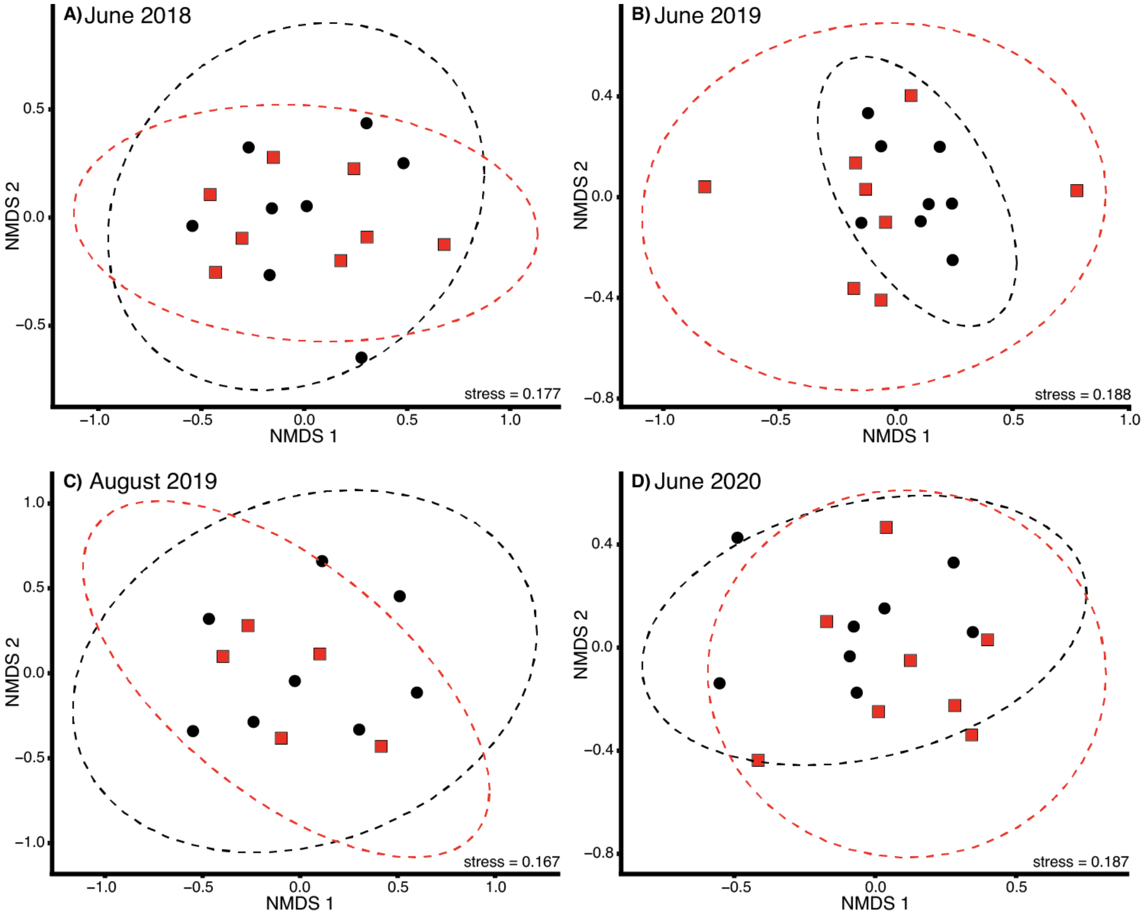

Figure 4.7 Compositional similarities of oribatid mite communities under warming in the *Sphagnum*-dominated fen within each sampling event.

Oribatid communities in A) June 2018 (passive warming; n = 16), B) June 2019 (passive warming; n = 16), C) August 2019 (active warming; n = 13), and D) June 2020 (passive warming; n = 16). Black dots represent control plots and red squares represent warmed plots. In all plots: number of dimensions (k) = 2. The ellipses indicate 95% confidence intervals.

For the dbRDA analysis in June 2018, the first axis CAP1 significantly explained 19.41% of the variance (Pseudo-$F_{1,13}$ = 3.270, P = 0.004), while the second axis CAP2 was not significant (Pseudo-$F_{1,13}$ = 0.573, P = 0.891), and moisture content was a significant factor explaining the variance in oribatid communities (Pseudo-$F_{1,13}$ = 3.260, P = 0.002), while warming was not (Pseudo-$F_{1,13}$ = 0.583, P = 0.879) (Figure 4.8A). In June 2019 moisture content was again a significant factor explaining the variance of oribatid communities (Pseudo-$F_{1,13}$ = 1.865, P = 0.012), while warming was not (Pseudo-$F_{1,13}$ = 0.317, P = 0.995) (Figure 4.8B). Here, the first axis CAP1 significantly explained 12.3% of the variance (Pseudo-$F_{1,13}$ = 1.868, P = 0.044), while the second axis CAP2 was not significant (Pseudo-$F_{1,13}$ = 0.314, P = 0.998). Similar DBRDA analysis results were observed for August 2019 and June 2020, where moisture content was a significant factor explaining the variance of oribatid communities (August 2019: Pseudo-$F_{1,10}$ = 1.833, P = 0.044; June 2020: Pseudo-$F_{1,13}$ = 1.953, P = 0.028), and warming was not a significant factor although it was nearly significant in June 2020 (Pseudo-$F_{1,13}$ = 1.713, P = 0.057) and had some, albeit non-significant explanatory power in August 2019 (Pseudo-$F_{1,10}$ = 1.549, P = 0.105) (Figure 4.8C–D). In August 2019, the first axis CAP1 marginally explained 14.03% of the variance (Pseudo-$F_{1,10}$ = 1.878, P = 0.125), while the second axis CAP2 also only marginally explained an additional 11.24% of the variance (Pseudo-$F_{1,10}$ = 1.504, P = 0.124). In June 2020, the first axis CAP1 significantly explained 17.5% of the variance (Pseudo-$F_{1,13}$ = 2.917, P = 0.005), while CAP2 was not a significant axis (Pseudo-$F_{1,13}$ = 0.750, P = 0.697).

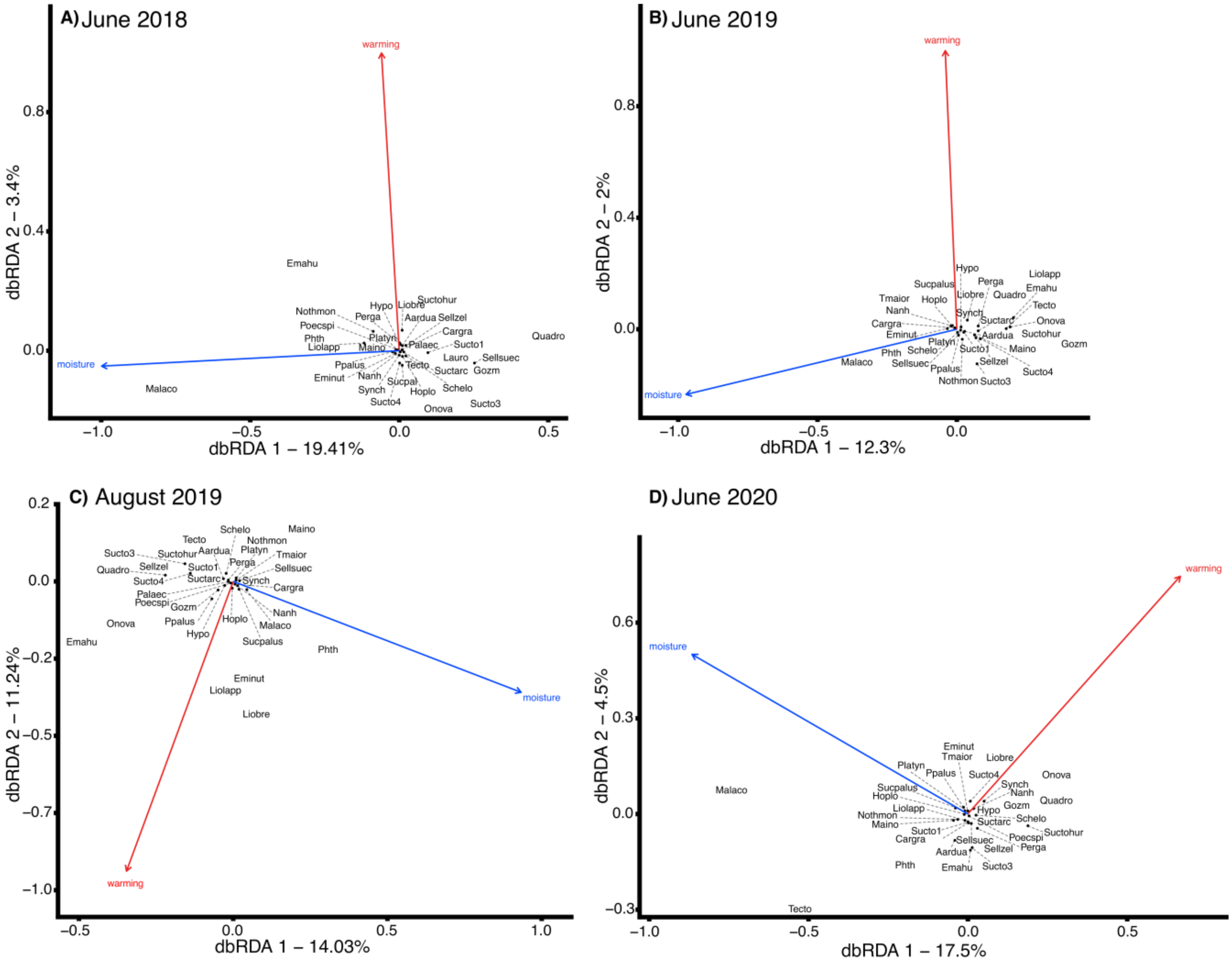

Figure 4.8 Abiotic factors driving *Sphagnum*-dominated fen oribatid mite community composition within each sampling event in peat soil samples analysed by dbRDA.

The top 50% species with the highest axis loadings are plotted and related to moisture content and warming. Arrows indicate how the explaining variables are related to ordination space, and black dots at the end of gray dashed lines represent the actual location of species in this multidimensional space. See Appendix F for full species list.

4.3.3 Warming effects at the *Carex*-dominated fen

Warming as a main effect did not significantly affect richness (# of species / g dwt) in the CF when all sampling events were analysed together ($F_{1,11}$ = 1.287, P = 0.280) (Table 4.2). Active warming in August 2019 significantly decreased richness (Tukey HSD, P = 0.010; Figure 4.9A) compared to other sampling times in June, where passive warming did not significantly affect richness (Tukey HSD June 2018: P = 0.818; June 2019: P = 0.971; June 2020: 0.848). Oribatid species richness also significantly changed over time (main effect of time: $F_{3,42}$ = 7.731, P < 0.001) (Table 4.2), being either significantly or only marginally higher in June 2019 compared to the other sampling events (Tukey HSD of time: June 2018: P = 0.001; August 2019: P = 0.001; June 2020: P = 0.060); however, there was no significant interaction of warming × time ($F_{3,42}$ = 2.083, P = 0.116) (Table 4.2). Thus, overall, richness was significantly lower in the actively warmed plots in August 2019 compared to the passively warmed plots of June 2019 and 2020 (Tukey HSD between warmed plots: P < 0.001 and P = 0.015, respectively), but not different from the richness in warmed plots in June 2018 (Tukey HSD between warmed plots: P = 0.364). Lastly, plot nested within block did not (LRT = 0.717, P = 0.397) show significant random effects on oribatid species richness, but the main effects of block (LRT = 4.115, P = 0.042) did, demonstrating the heterogeneous nature of blocks in terms of the number of oribatid species present in each of the four blocks in the CF.

Table 4.2 Oribatida species richness, abundance, immature: adult ratio, Shannon's diversity (H') and species evenness (J) for samples collected over four years in the *Carex*-dominated fen.

Values are calculated using standardised values based on per gram dry weight as means ± standard error. Values followed by different letters are significantly different based on Tukey HSD post hoc analysis for time × warming interaction. June 2017 pre-warming values are shown for comparison but were not included in the LLM models.

		***Carex*-dominated fen**				
		Jun-17*	**Jun-18**	**Jun-19**	**Aug-19**	**Jun-20**
Richness (# species / g dwt)	Control	1.38 ± 0.23	0.99 ± 0.19^{ab}	1.59 ± 0.26^{a}	1.29 ± 0.19^{ab}	1.40 ± 0.13^{a}
	Warming	1.54 ±0.16	1.04 ± 0.17^{ab}	1.59 ± 0.20^{a}	0.70 ± 0.08^{ab}	1.35 ± 0.09^{ab}
Abundance (# indiv. / g dwt)	Control	18.31 ± 3.93	13.85 ± 2.37	25.78 ± 4.06	22.88 ± 5.20	30.08 ± 10.91
	Warming	17.23 ± 2.30	13.96 ± 3.60	24.12 ± 4.68	12.25 ± 1.58	26.71 ± 3.37
Immature: adult ratio	Control	0.79 ± 0.08	1.36 ± 0.25^{b}	1.07 ± 0.13^{b}	1.49 ± 0.15^{b}	1.04 ± 0.07^{b}
	Warming	1.03 ± 0.19	1.35 ± 0.20^{b}	0.96 ± 0.10^{b}	2.45 ± 0.33^{a}	0.95 ± 0.12^{b}
Diversity (H')	Control	1.72 ± 0.13	1.58 ± 0.17	1.61 ± 0.11	1.97 ± 0.12	1.69 ± 0.13
	Warming	1.98 ± 0.18	1.58 ± 0.15	1.62 ± 0.10	1.67 ± 0.13	1.57 ± 0.06
Evenness (J)	Control	0.71 ± 0.04	0.71 ± 0.03	0.69 ± 0.03	0.75 ± 0.03	0.68 ± 0.03
	Warming	0.76 ± 0.05	0.69 ± 0.04	0.69 ± 0.04	0.76 ± 0.02	0.64 ± 0.01

* pre-warming conditions (i.e., warming plots were not yet under experimental treatment)

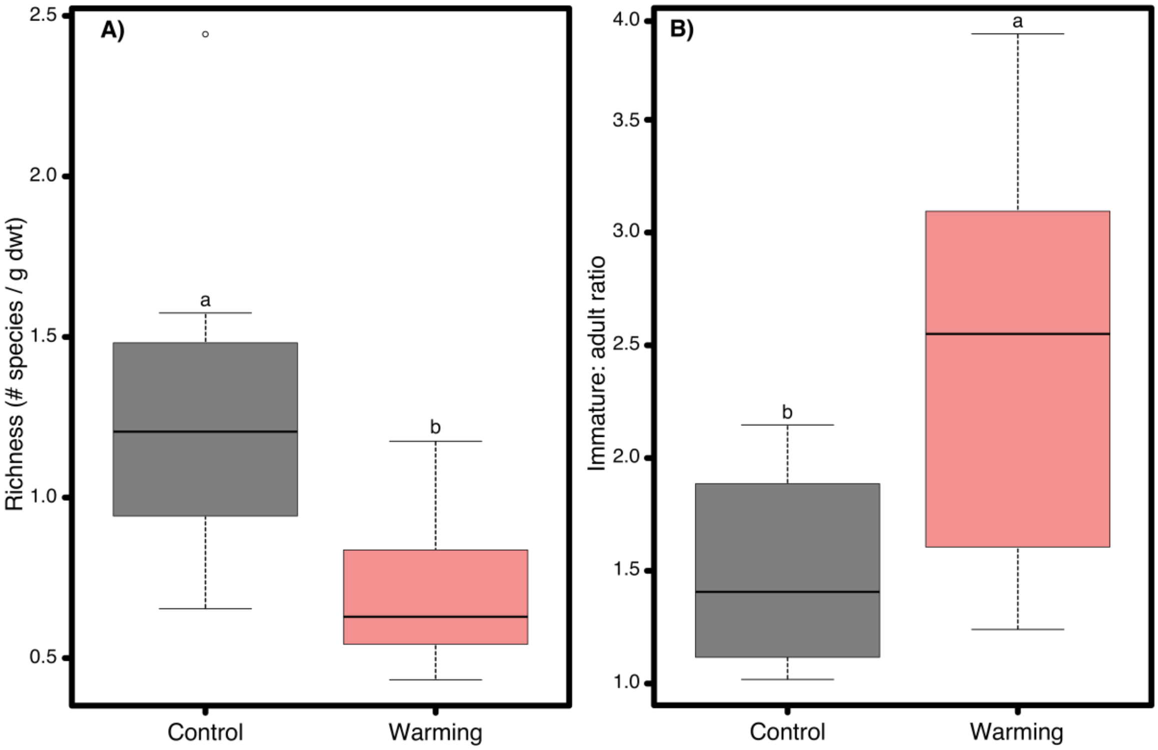

Figure 4.9 Effects following active warming on oribatid mite richness and immature: adult ratio in the CF in August 2019.

A) Oribatid mite species richness and B) Immature: adult ratio of oribatid mites from peat soils collected in the *Carex*-dominated fen in August 2019. Letters denote significant differences after Tukey HSD *post hoc* comparisons. In the boxplot: lower and upper box boundaries represent 25% and 75$^{\%}$ percentiles, respectively; the line inside the box represents the median; lower and upper error lines are 10% and 90% percentiles, respectively; the circle represents data falling outside 10% and 90% percentiles.

The abundance of oribatid mites (# of indiv. of adults and immatures / g dwt) did not change under warming when all sampling events were analysed together ($F_{1,11}$ = 0.946 P = 0.351) (Table 4.2), nor when tested separately (Tukey HSD June 2018: P = 0.986; June 2019: P = 0.81; August 2019: P = 0.129; June 2020: P = 0.627). Nonetheless, abundance in plots under active warming in August 2019 was on average half of that of the same period for control plots. Abundance significantly changed over time ($F_{3,42}$ = 4.188, P = 0.011) (Table 4.2), marginally increasing from June 2018 to June 2019 (Tukey HSD for time: P = 0.091), not changing significantly in August 2019 (Tukey HSD for time: P = 0.384), then marginally increasing from August 2019 to June 2020 (Tukey HSD for time: P = 0.100). There was no significant interaction of warming × time for abundance ($F_{3,42}$ = 0.528, P = 0.665) (Table 4.2), and neither the random effects of plots nested within blocks (LRT = 0.819, P = 0.365) nor main effects of block (LRT = 1.664, P = 0.197) were statistically significant for abundance, demonstrating that plots are homogeneous in terms of the number of individuals repeatedly sampled from each plot within each block.

The immature: adult ratio of oribatid mites did not significantly change under warming when all sampling events were analysed together ($F_{1,56}$ = 1.895, P = 0.174) (Table 4.2), but when tested separately, warming significantly increased the ratio in August 2019 under active warming (Tukey HSD: P < 0.001) (Figure 4.9B), although passive warming did not change the immature: adult ratio (Tukey HSD June 2018: P = 0.979; June 2019: P = 0.690; June 2020: P = 0.743). The increase in the ratio caused by active warming in August 2019 plots were due to a combined decrease of ~37% in the abundance of immatures and an even more pronounced decrease in the abundance of adults (~46%). The immature: adult ratio also significantly changed over time ($F_{3,56}$ = 11.185, P < 0.001) (Table 4.2) being significantly higher in August 2019 compared to other sampling events due to a decrease in the abundance of adults, but not immatures (Tukey HSD for time: June 2018: P = 0.014; June 2019: P < 0.001; June 2020: P < 0.001). Specifically, the immature: adult ratio was significantly higher (in fact the highest) in warmed plots in August 2019 compared to all other treatment levels of all periods, leading to a significant interaction of warming × time ($F_{3,56}$ = 3.559, P = 0.019) (Table 4.2). The random effects of plot nested within block, and main effects of block were not significant for the immature: adult ratios (both: LRT = 0.000, P = 1.000).

The Shannon's diversity (H') of adult oribatid mites did not change significantly under warming when all sampling events were analysed together ($F_{1,11}$ = 0.764, P = 0.400) (Table 4.2), but it marginally decreased under active warming in August 2019 (Tukey HSD: P = 0.093); no significant changes in diversity were seen under passive warming in the other periods. Diversity only marginally changed over time ($F_{3,42}$ = 2.123, P = 0.111) (Table 4.2), and this trend was only driven by slightly higher diversity levels in August 2019 compared to June 2018 (Tukey HSD for time: P = 0.115). There was no significant interaction of warming × time ($F_{3,42}$ = 0.945, P = 0.427) (Table 4.2), although diversity was the highest in control plots in August 2019. Lastly, plot nested within block (LRT = 4.302, P = 0.038) had significant random effects, but block as a main effect (LRT = 0.474, P = 0.491) showed no significant random effects on oribatid species diversity, demonstrating the heterogeneous nature of plots sampled over time, but homogeneous nature of blocks in regard to the diversity of oribatid mite species.

Following a pattern similar to diversity, the evenness (J) of adult oribatid mites also did not significantly change under warming when all sampling events were analysed together ($F_{1,11}$ = 0.158, P = 0.697) (Table 4.2), nor when tested separately (Tukey HSD June 2018: P = 0.702; June 2019: P = 0.964; August 2019: P = 0.883; June 2020: P = 0.458). However, evenness significantly changed over time ($F_{3,42}$ = 2.908, P = 0.045) (Table 4.2), and this was driven by a decrease in evenness from August 2019 to June 2020 (Tukey HSD of time: P = 0.030), although evenness in June 2020 was no different than in June 2018 and June 2019. A decrease in evenness can be translated as a more unequal distribution of individuals among the species sampled in June 2020 (i.e., some species having more individuals than others). There was no significant interaction of warming × time for evenness ($F_{3,42}$ = 0.195, P = 0.898) (Table 4.2). Lastly, neither plot nested within block (LRT = 1.039, P = 0.307) nor block as a main effect (LRT = 0.093, P = 0.760) showed significant random effects for evenness, demonstrating the homogenous nature of plots and blocks in regard to the overall evenness of samples collected between 2018–2020.

4.3.4 Oribatid mite community measures at the *Carex*-dominated fen

At the community compositional (i.e., multivariate) level, warming showed marginal effect on the composition of oribatid mite communities from 2017–2020 in the CF (PERMANOVA: $F_{1,78}$ = 1.823, P = 0.061; Figure 4.10); warmed plots were slightly more similar to one another compared to control plots, suggesting lower variability in the composition of communities under warming. In addition, the composition of oribatid communities significantly changed over time (PERMANOVA: $F_{4,75}$ = 4.788, P = 0.001)

(Figure 4.10); specifically, dissimilarity in oribatid community composition slightly increased from June 2017 to June 2018 (i.e., communities became more variable in their composition), then returned back to being more similar in June and August 2019 until June 2020, when communities showed the highest similarity. The degree of dissimilarity between communities can be seen by the distance between their points on the plot in the graphical NMDS plots, and by the size of the 95% confidence ellipse; both were lower and smaller, respectively, in June 2020.

When analysing the 24 species with highest axis scores in a DBRDA analysis, time (Pseudo-$F_{4,58}$ = 2.746, P = 0.001), plot (Pseudo-$F_{15,58}$ = 1.373, P = 0.001), warming (Pseudo-$F_{1,58}$ = 1.641, P = 0.024) and moisture content (Pseudo-$F_{1,55}$ = 1.463, P = 0.045) were significant factors explaining the variance in oribatid communities (Figure 4.11, and Appendix G for individual species responses to warming). Together, the axes CAP1 and CAP2 significantly explained 15.36% of the variance (Pseudo-$F_{1,58}$ = 7.578, P = 0.001 and Pseudo-$F_{1,58}$ = 6.669, P = 0.001, respectively). The third axis (CAP3) also significantly explained additional 3.48% the variance in oribatid communities (Pseudo-$F_{1,58}$ = 3.229, P = 0.011).

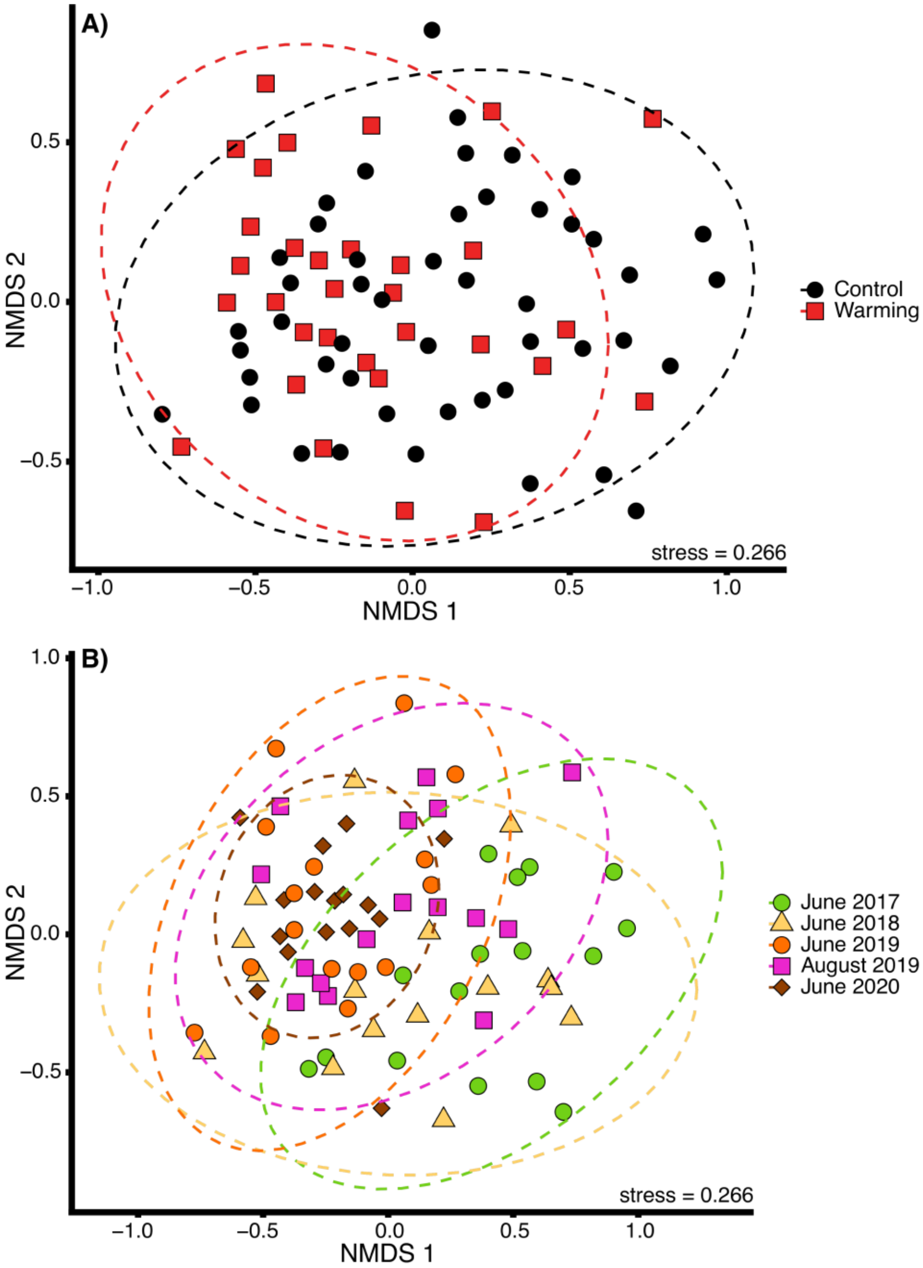

Figure 4.10 Compositional similarities of oribatid mite communities under warming in the *Carex*-dominated fen sampled across four years.

Eighty samples were collected in June 2017, June 2018, June 2019, August 2019 and June 2020. A) Communities are plotted by warming treatment and B) Communities are plotted by sampling event. Oribatid mite communities are based on standardised abundance of individual species from each plot. Stress = 0.266; number of dimensions (k) = 2. The ellipses indicate 95% confidence intervals.

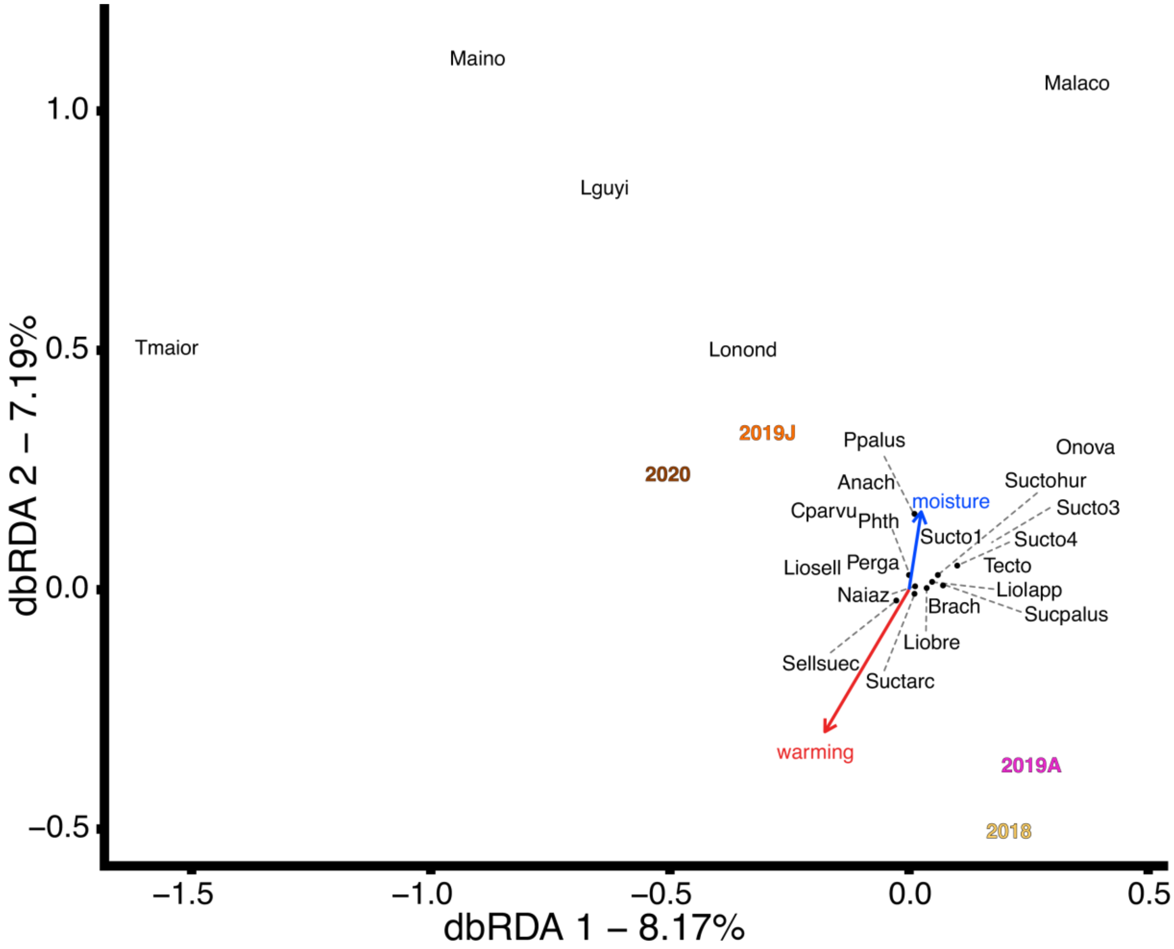

Figure 4.11 Abiotic factors driving *Carex*-dominated fen oribatid mite community composition (2017–2020) in peat soil samples analysed by DBRDA.

The top 50% species with the highest axis loadings are plotted and related to moisture content, warming, year (sampling event) and plot. Arrows indicate how the explaining variables are related to ordination space, and black dots at the end of gray dashed lines represent the actual location of species in this multidimensional space. See Appendix F for full species list and Appendix G for individual species responses to warming. For clear visualization, chambers are not plotted.

Examining the warming effects at individual sampling times, oribatid mite communities did not significantly change under passive warming (PERMANOVA June 2018: $F_{1,14}$ = 0.469, P = 0.965; PERMANOVA June 2019: $F_{1,14}$ = 0.195, P = 0.999; PERMANOVA June 2020: $F_{1,14}$ = 0.562, P = 0.755) (Figure 4.12A–D). However, active warming marginally increased the similarity in oribatid communities (PERMANOVA August 2019: $F_{1,14}$ = 1.710, P = 0.098), that in other words became more homogeneous in terms of the species present and their abundance. The outlier warmed point (outside the ellipse) in August 2019 (Figure 4.12C) is a warmed plot whose peat soil sample was overly dry (~57% drier than average dwt of other samples from warmed plots); removing it from the NMDS increased the significance of the analysis (PERMANOVA August 2019: $F_{1,14}$ = 2.498, P = 0.034), and warmed plots then nest within control plots (C.score = 0.41, nestedness temperature = 25.87). In other words, with the exception of one species (*Phthiracarus* sp.), all species in the warmed plots were also present in control plots, demonstrating that warmed communities were a subset of communities in control plots; control plots had eight additional species that were not present in the warmed plots. However, the opposite pattern is seen in the NMDS plot for June 2019 (Figure 4.12B) where there is higher variability in the composition of warmed communities, but nestedness analysis suggests that the oribatid communities under control plots are only moderately a subset of species from the communities present in warmed plots (C.score = 0.49, nestedness temperature = 23.66). In this case ~67% of the species sampled occurred in both control and warmed plots in June 2019, with ~13% of species unique in control plots and ~20% of species only occurred in warmed plots. As such, even though the NMDS results show control communities plotted within warmed communities, the presence of unique species in control plots do not confer a complete nested configuration to this treatment in June 2019. Specifically, semi-aquatic species like *Naiazetes* n. sp. did not persist in warmed plots and were only found in the control plots.

For the DBRDA analysis in June 2018, neither the first axis CAP1 (Pseudo-$F_{1,13}$ = 1.282, P = 0.487) nor the second axis CAP2 (Pseudo-$F_{1,13}$ = 0.570, P = 0.902) significantly explained the variance. In addition, neither moisture content (Pseudo-$F_{1,13}$ = 1.282, P = 0.213) nor warming (Pseudo-$F_{1,13}$ = 0.571, P = 0.939) were significant factors explaining the variance of oribatid communities, which suggests factors not measured in this study were the drivers of those communities (Figure 4.13A). Similar dbRDA analysis results were observed in June 2019, where the variance in oribatid communities is not significantly explained by moisture content (Pseudo-$F_{1,13}$ = 1.025, P = 0.362) or warming (Pseudo-$F_{1,13}$ = 0.300, P = 0.988) in neither of the two axes (CAP1: Pseudo-$F_{1,13}$ = 1.028, P = 0.705; CAP2: Pseudo-$F_{1,13}$ = 0.297, P = 0.979) (Figure 4.13B). In August 2019, however, the variance in oribatid communities was marginally explained by warming (Pseudo-$F_{1,13}$ = 1.647, P = 0.093), whereas moisture content was not a significant factor (Pseudo-$F_{1,13}$ = 1.307, P = 0.210); the first axis CAP1 marginally explained 13.64% of the variance in oribatid communities (Pseudo-$F_{1,13}$ = 2.175, P = 0.086), but the second axis CAP2 was not significant (Pseudo-$F_{1,13}$ = 0.778, P = 0.615) (Figure 4.13C).

When excluding the same outlier previously removed for the NMDS in August 2019, I found that warming became a significant factor (Pseudo-$F_{1,12}$ = 2.411, P = 0.022), and moisture content became a factor marginally explaining the variance in oribatid communities (Pseudo-$F_{1,12}$ = 1.532, P = 0.123); in this case the first axis CAP1 significantly explained 21.25% of the variance (Pseudo-$F_{1,12}$ = 3.883, P = 0.011), and

CAP2 was not significant Pseudo-$F_{1,12}$ = 0.554, P = 0.866). In June 2020, on the other hand, moisture content was the factor significantly explaining the variance in oribatid communities (Pseudo-$F_{1,13}$ = 2.109, P = 0.029), but warming was not (Pseudo-$F_{1,13}$ = 0.744, P = 0.683) (Figure 4.13D). The first axis CAP1 marginally explained 13.35% of the variance (Pseudo-$F_{1,13}$ = 2.116, P = 0.099), but the second axis CAP2 was not significant (Pseudo-$F_{1,13}$ = 0.737, P = 0.685).

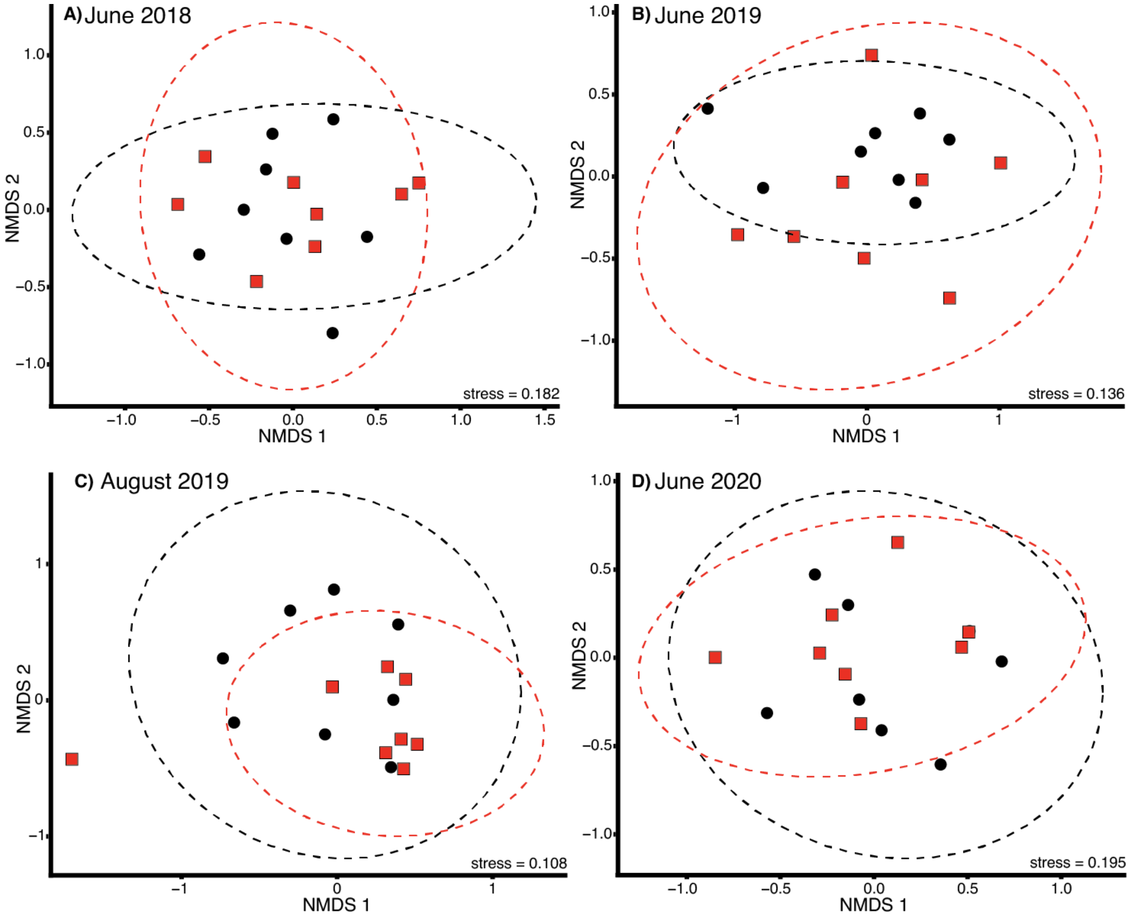

Figure 4.12 Compositional similarities of oribatid mite communities under warming in the *Carex*-dominated fen within each sampling event.

Oribatid communities in A) June 2018 (passive warming; n = 16), B) June 2019 (passive warming; n = 16), C) August 2019 (active warming; n = 16), and D) June 2020 (passive warming; n = 16). Black dots represent control plots and red squares represent warmed plots. In all plots: number of dimensions (k) = 2. The ellipses indicate 95% confidence intervals.

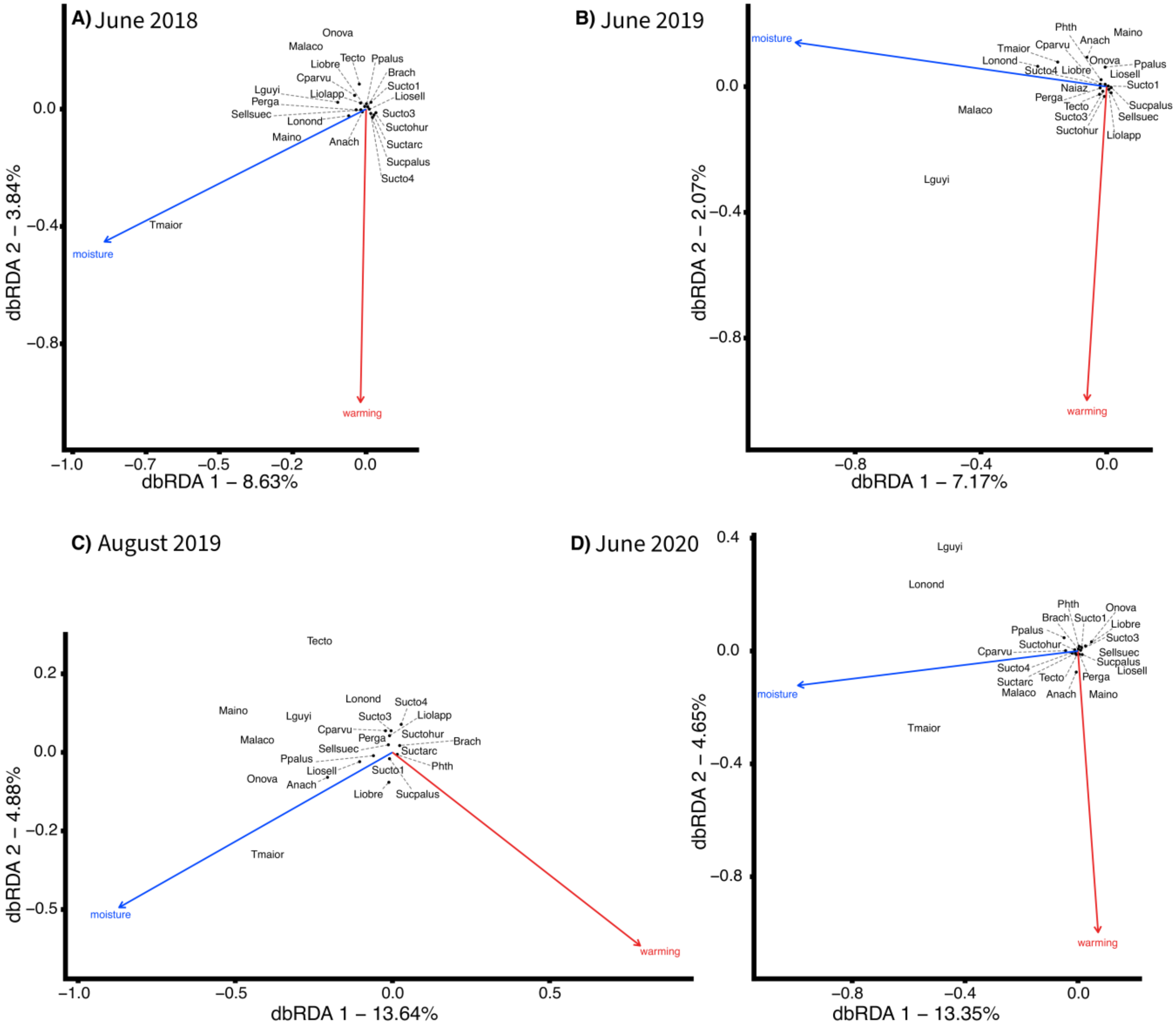

Figure 4.13 Abiotic factors driving *Carex*-dominated fen oribatid mite community composition within each sampling event in peat soil samples analysed by DBRDA. The top 50% species with the highest axis loadings are plotted and related to moisture content and warming. Arrows indicate how the explaining variables are related to ordination space, and black dots at the end of gray dashed lines represent the actual location of species in this multidimensional space. See Appendix F for full species list.

4.4 Discussion

In many ways, warming produced contrasting patterns of oribatid mite community responses at each site, where, contrary to my predictions, I observed an increase in richness and a decrease in immature abundance at the SF, but a decrease in richness and an increase in immature: adult ratio at the CF. However, both responses likely result from the same mechanism, namely warming-induced reductions in soil moisture. For instance, at the CF, the species lost under warming were semi-aquatic species (e.g., *Naiazetes* n. sp.) and/or known peatland specialist species (e.g., *Eniochthonius mahunkai*, *E. minutissimus*), which correlated with soil moisture in the ordination plots (e.g., *Mainothrus badius, Malaconothrus mollisetosus, Limnozetes onondaga, L. guyi*). At the SF, moisture was also likely a main factor driving community composition, because as warmed plots became drier, they facilitated more terrestrial species often not found in peatland environments (e.g., *Eupterotegaeus ornatissimus, Discoppia* sp., and *Pilogalumna* sp.; see Appendix G). Overall, these shifts led to increased heterogeneity at the SF, and a somewhat nested community at the CF. However, the majority of these results were only observed or statistically significant under active warming treatments.

Responses of oribatid mites to warming in peatlands have not been investigated in full, with only two studies to date where species were identified to the species level. Lindo (2015) found no significant effect of warming (+4ºC, +8ºC) on species richness after an 18-month long mesocosm experiment using intact 25 kg peat monoliths from the SF site. However, warming significantly increased abundance that was driven by greater numbers of immatures (32% immatures at the start of the experiment to 59% under +8ºC) and small-bodied, parthenogenetic species. On the other hand, Markkula et al. (2019) found a reduction in species richness after year-round passive warming in a 16-year field experiment in a tundra bog, but reductions in richness were not significant when plots covered with OTCs were only deployed during the summer. While reductions in richness were observed for the CF in my experiment, it is possible that an increase in richness at the SF was due to more habitable conditions (e.g., soil pore space) that supported new species. Specifically, it is possible that species dispersed from nearby forested areas, as some species found in warmed plots were unexpected and normally associated with drier habitats (e.g., forests). The SF is surrounded by mixed-wood forest, and while oribatid mites are poor active dispersers (Norton, 1980), they can be passively wind dispersed (Behan-Pelletier and Winchester, 1998) across substantial distances, as inferred by Lindo et al. (2008) and Lindo (2010).

Warming, especially active warming in 2019, dried the peat compared to control plots at the SF, which may have created more favourable environmental conditions for forest species to survive. Warming may have increased pore space and aerobic conditions indirectly through drying effects (Turnbull and Lindo, 2015), increasing habitat availability (Nielsen et al., 2008) as most oribatid mites are not big enough to move soil particles like macroinvertebrates can (e.g., beetles, earthworms). In this case, community composition in the SF may follow a species sorting metacommunity paradigm (Wilson, 1992), which considers that all species have dispersal rates sufficient enough to reach new habitats but will only persist in favourable habitats. In other words, I posit that species were dispersed from the forest but filtered by the peat environmental conditions, and specifically in this case, by peat moisture levels.

In contrast, in naturally wetter peatlands like the CF, where water table levels are often close to the peat surface (compared to ~30 cm below it in the SF), warming the plots caused the loss of peatland-specific and/or semi-aquatic species like *Eniochthonius mahunkai*, *E. minutissimus*, and *Naiazetes* n. sp. in all warmed plots in the CF (Appendix G). In the CF, my results are more similar to Markkula et al. (2019), who also inferred reductions in species richness to the interactive effects of warming and moisture content. Supporting this are the results of Minor et al. (2019), who examined oribatid mite communities along a nutrient-water table gradient in Russia and found similar species to my CF site associated with more saturated conditions that were not present under drier conditions in the same bog. Namely, these were semi-aquatic species in the genus *Limnozetes*, and *Tyrphonothrus maior*; both of which I observed correlated with higher moisture conditions in multivariate ordinations at the CF.

Contrary to my prediction that oribatid mites would increase in abundance in response to warming, specifically due to increases in the abundance of immatures as seen in Lindo (2015), the abundance of oribatid mites did not change under warming in either of my fen sites, in line with Markkula et al. (2019). Yet responses of oribatid abundance to warming in non-peatland systems have been mixed (even in studies within the same ecosystem), and most studies have found no significant changes of total oribatid abundance to warming (Alatalo et al., 2017; Bokhorst et al., 2008; Coulson et al., 1996; Hågvar and Klanderud, 2009; Kardol et al., 2011; Meehan et al., 2020; Roos et al., 2020; Sjursen et al., 2005, Wu et al., 2014), while a few studies found warming to decrease oribatid abundance (Blankinship et al., 2011; Harte et al., 1996; Vestergård et al., 2015).

However, the two previous studies that detail the response of peatland oribatid mites at the species level found that warming significantly increased the abundance of small-bodied, non-sexually (parthenogenetic) reproducing species in the families Brachychthoniidae and Suctobelbidae (Lindo, 2015; Markkula et al., 2019). In my study, the average and total abundance of Brachychthoniidae and Suctobelbidae were higher under warming, albeit not significantly so. Specifically, five species within Brachychthoniidae, *Brachychthonius bimaculatus, Liochthonius brevis, L. lapponicus* and *Poecilochthonius spiciger* (SF), and *Sellnickochthonius suecicus* and *P. spiciger* (CF) increased in abundance under warming. But it was the decreases in the abundance of other species, especially semi-aquatic species such as *Malaconothrus mollisetosus* (Malaconothridae), *Limnozetes guyi* (Limnozetidae) and *Mainothrus badius* (Trhypochthoniidae) at both fen sites (Appendix G) that led to no significant differences in abundance between treatments.

Developmental times of oribatid mites are known to be slow, and the immature: adult ratio has been suggested as a better indication of population dynamics compared to abundance because abundance can fluctuate whereas immature: adult ratio reflects metabolic or reproduction constraints (Norton, 1994). Although no changes in overall abundance in response to warming were found in either fen, the immature: adult ratio responded in opposite ways in each fen: decreasing in the SF and increasing in the CF. In the SF, the decrease in immature: adult ratio under active warming was caused by decreases in immatures combined with increases in adult oribatid mites. Specifically, the abundance of adults increased in two ways; some forest species increased in abundance such as *G. majestus* (~100% under active warming), while others only occurred under warming conditions like for instance, *Carabodes polyporetes*, a typical boreal forest species. On the other hand, the increase in immature: adult ratio under warming in the CF was caused by decreases in both immatures and adult oribatid mites, but adults decreased more than immatures. Again, the warming-induced loss of semi-aquatic species drove this trend.

Decreases in the abundance of immature oribatid mites under warming were reported by Alatalo et al. (2017) in a tundra ecosystem warmed for 20 years, which they attributed to warming-induced lower moisture conditions that potentially were unfavourable for immatures but not adult oribatid mites, considering the former may have higher susceptibility to desiccation by lack of sclerotization. Alternatively, Alatalo et al. (2017) suggest that reductions in juvenile stages may have been due to faster reproduction and development, that was mis-matched with sampling time. In laboratory experiments using *Trhypochthoniellus setosus* (Willmann 1928) and *Ameronothrus lineatus* (Thorell, 1871) (Kuriki, 1993; Søvik and Leinaas, 2003, respectively), faster reproduction rates were observed under warmer conditions leading to a greater proportion of immatures in the population. Similarly, faster reproduction rates were suggested to explain the increased immature abundance observed by Lindo (2015). It is possible that timing of sampling may have influenced immature: adult abundances in my study. For instance, Anderson (1975) studied a time series of abundances for adult and juvenile oribatid mites using litterbags in a beech/chestnut forest in England and found that juveniles had several seasonal peaks in abundance, namely May, August, and December. Examining two specific cosmopolitan species (*Tectocepheus velatus* and *Oppiella nova*) also present in my study, Reeves (1969) found similar results with all juvenile stages of

O. nova peaking in August (increasing from July−Sept.), and a second peak for later stage juveniles in November, while *T. velatus* also had peak abundance in larva and protonymphs in August and peak abundance in deutonymphs and tritonymphs in November, December, and again in April.

4.4.1 Oribatid mite diversity and community composition

Overall, oribatid mite diversity (H’) and evenness (J) did not significantly change under warming in either fen, in line with other peatland warming field experiments (Markkula et al., 2019) as well as in other ecosystems (Bokhorst et al., 2008; Holmstrup et al., 2017; Meehan et al., 2020). However, significant increases in diversity and evenness were observed in the SF in June 2020 under warming. Furthermore, several species were only present in warmed plots in 2020, such as *Pilogalumna* sp. and *Liebstadia* cf. *humerata*, for example. Another example is *Gozmanyina majestus*, a species that occurred in considerably higher abundance and more frequently in 2020 warmed plots; this species was unique to the SF and previously recorded primarily in acidic forest soil (Cianciolo and Norton, 2006), supporting, again, the hypothesis that species are being wind dispersed from the surrounding forest into the SF.

At the multidimensional level, warming did not significantly change communities in the SF. However, the stress value for the NMDS plots of oribatid mite communities in both fens was high, suggesting interpretation is to be done with caution (Clarke, 1993). When analysing data within sampling periods, I found increased heterogeneity in warmed plots in June 2019 at the SF site reflecting unique species present that are potentially dispersing in from the surrounding forest. This is in contrast to Lindo (2015), who found communities from the same SF had reduced variability under warming following 18 months, which was driven by increased abundances of parthenogenetic species in the families Brachychthoniidae, Suctobelbidae, and *O. nova*. In that study, however, dispersal of new species into the system was not possible because oribatid mite communities were contained within a laboratory mesocosm experiment of intact peat monoliths. In the CF, I did find a pattern of increased homogeneity, especially under active warming in August 2019. However, reduced variability under warming was driven by species loss of the semi-aquatics as previously mentioned to create a somewhat nested community structure, rather than increased abundance of small-bodied species as observed by Lindo (2015).

4.4.2 Drivers of oribatid mite communities

Considering oribatid mites have a low active dispersal capacity (Norton, 1980), they are thus vulnerable to environmental changes at the microhabitat scale. I observed that most of the individual species' responses to direct warming and/or indirect warming-induced soil moisture loss appear somewhat independent and differed between the fen sites (Appendix G). Although using a coarser taxonomic scale, Koltz et al. (2018) also found responses of arthropods to natural increases in temperature to be taxon- and habitat-specific, and these differential responses to be responsible for altering the structure of arctic communities in wet fen, mesic heath and arid heath habitats sampled over 18 years in Greenland. However, Koltz et al. (2018) found that changes in community composition in response to warming were weaker in wetter habitats, suggesting warming and moisture interact to dictate species-specific responses, and may explain the weak correlations of oribatid species with single environment factors at the multidimensional level.

That said, peat moisture content and warming were the significant drivers explaining the variance in the species I examined using DBRDA which corroborates that semi-aquatic or known peatland-specific species (e.g., *E. mahunkai*, *M. badius*, *E. minutissimus, M. mollisetosus, T. maior*, *L. guyi*, *L. onondaga*) are correlated with high moisture levels. Warming, on the other hand, was mostly associated with small-bodied and parthenogenetic species like *Suctobelbella* spp., *Quadroppia quadricarinata*, *O. nova*, and *Sellnickochthonius zelawaiensis*, but primarily only observed in the SF. But some species members of Suctobelbidae and Brachychthoniidae were also more closely related to warming in the CF as well. Increases in these groups parallel results by both Markkula et al. (2019) and Lindo (2015).

Nonetheless, other factors not measured here likely also contributed to oribatid mite community structure in my study. Specifically, plant diversity (Minor et al., 2019, 2016), fungal diversity (Bokhorst and Wardle, 2014; Koukol et al., 2009; Schneider et al., 2005), and bacterial diversity (Crotty et al., 2011; Pollierer et al., 2012) have been shown to structure oribatid mite communities in other systems. Oribatid mites are an important component of detrital food webs, being responsible for secondary decomposition of organic matter (Soong et al., 2016) and nutrient cycling (Wang and Ruan, 2011) by consuming fungi and bacteria (but see Lehmitz and Maraun, 2016; Schneider and Maraun, 2005 for other feeding preferences). Therefore, changes in biomass, abundance and/or richness in microbial abundance or functional group (i.e., fungi vs bacteria) can affect oribatid mite communities (Sjursen et al., 2005), consistent with bottom-up control in soil food webs. Oribatid mites are also believed to live in a relatively predator-free environment (Peschel et al., 2006) due to their morphological defences, which reduces top-down control on their populations by predatory mites. While not examined here, changes in fungal (Asemaninejad et al., 2018) and plant communities (Dieleman et al., 2015; Lyons et al., 2020) have been observed under warming at the SF site, or when SF soils are incubated in the lab. Given that changes in peatland plant communities can enhance root exudates and increase the amount of high-quality litter (Dieleman et al., 2017, 2016b; Fenner et al., 2007), it is possible that changes in oribatid communities under warming may be mostly indirect through changes in food resources (i.e., bottom-up effects).

Finally, both interannual differences in weather, seasonality, and the use of OTCs themselves may have influenced my results. Meehan et al. (2020) found warming-induced responses in microarthropod communities using OTCs in a boreal forest were enhanced in wetter years. Further, Markkula et al. (2019) argued that climate warming in northern peatlands may manifest itself differently in different seasons of the year. Taken together, while August 2019 had the highest precipitation levels, and the strongest warming-induced results, I could not disentangle the active warming effect nor a potential seasonality effect. Open-top chambers (OTCs) have been long used in climate change studies to warm the vegetation and soil (Marion et al., 1997), and significant effects on both plant (Buttler et al., 2015; Jassey et al., 2013; Lyons et al., 2020) and microarthropod communities (Markkula et al., 2019; Meehan et al., 2020) have been observed despite often low levels of warming. Warming by OTCs is maximized (up to +5.2°C) when soil is dry and bare (Marion et al., 1997), the opposite of peatland habitats. Nonetheless, I found passive warming of both air and soils consistent with other studies in peatlands (Buttler et al., 2015; Jassey et al., 2013).

Ultimately, despite low levels of warming for most of my study, I was able to observe changes in oribatid communities likely caused by concomitant peat drying and possibly due to changes in their food resources (Asemaninejad et al., 2018; Lyons et al., 2020). It has been suggested that multiple global change factors drive soil functions and diversity (Rillig et al., 2019), thus further examining multiple environmental drivers of peatland oribatid mite communities, like moisture and pH, is warranted (Chapter 3). Moreover, as oribatid mite communities are responsive to multiple environmental changes, and play important mid-trophic level roles in soil food webs, changes in oribatid mite community composition may have consequences for carbon flux in soil systems (Chapter 5).

4.5 References

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Chapter 5

5 Modelling detrital food webs

5.1 Introduction

Food web models represent feeding relationships and can be used to trace the flow of energy, nutrients and mass between species or functional groups across different trophic levels (Garvey and Whiles, 2017; Moore and de Ruiter, 2012; Paine, 1980). Yet, even though soils play crucial roles in carbon and nutrient cycling (Adhikari and Hartemink, 2016; Bardgett and van der Putten, 2014), and 90% of the primary production in terrestrial ecosystems enters the belowground system as the basal resource for the soil food (i.e., as detritus) (Gessner et al., 2010), soils are understudied from a food web perspective (Coleman et al., 2011). One possible explanation could be the high species richness and complexity of detrital food webs (Anderson, 2009), with most previously modelled food webs poorly resolved with respect to functional or trophic groups (de Ruiter et al., 1993; de Ruiter et al., 1994; Hunt et al., 1987), and generally only depicting presence/absence of trophic relationships (i.e., connectedness food webs) rather than quantifying interaction strength or energy flow (but see Gauzens et al., 2019; Jochum et al., 2021; Koltz et al., 2018).

Food web models that quantify energy (i.e., carbon) and nutrient (i.e., nitrogen) flow using a mass balance approach (i.e., energetic models) are considered the best approach (Ghedini et al., 2020), as they can reveal the fate of carbon stocks and help estimate carbon and nitrogen balance in soil systems (i.e., release or sequestration) (Moore and de Ruiter, 2012). These ‘energetic’ food web models (*sensu* Moore and de Ruiter, 2012) assume that energy and matter is conserved, thus consumed biomass can be quantified into assimilated and unassimilated fractions (O’Neill, 1969). Assimilated biomass is carbon used for growth, repair, reproduction, and metabolic activities of organisms, while unassimilated carbon is returned to the environment as feces, contributing to the detritus pool (Moore and de Ruiter, 2012) (Figure 5.1). Only a handful of energetic soil food web models exist, mostly for grassland and agricultural systems (de Ruiter et al., 1993; de Ruiter et al., 1994; Hunt et al., 1987), but these are not well-resolved for species diversity (but see Koltz et al. (2018)), neither do they estimate the contribution of individual food web nodes (i.e., trophic groups) to the energy flux (but see Holtkamp et al. (2011)). Food web structure and dynamics govern flows of energy and nutrients in ecosystems; however, how food webs will respond to global change factors is also not yet well understood, nor what the outcomes of altered food web structure will be on ecosystem-level processes like carbon and nitrogen mineralization. Well-resolved food webs can increase our understanding of ecosystem functioning (Barnes et al., 2018), processes that influence species diversity (Guerrero-Ramírez and Eisenhauer, 2017; Rooney and McCann, 2012), ecosystem productivity (Sackett et al., 2010; van der Heijden et al., 2008), stability (Moore et al., 2005; Rooney et al., 2006), as well as nutrient cycling (Coleman et al., 1983; Kitchel et al., 1979).

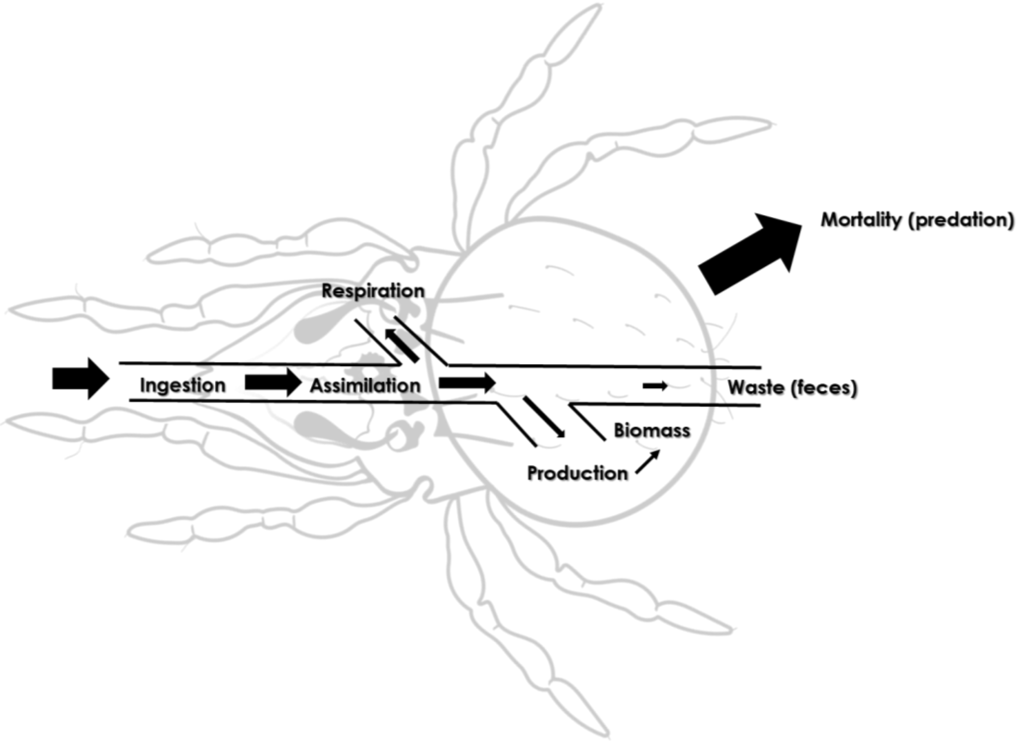


Figure 5.1 Carbon/nitrogen flow diagram of an individual oribatid mite (*Suctobelbella* sp.) as an example for all food web nodes.

The mass ingested is assimilated or released as feces; assimilated energy is used for metabolic processes (mineralization; e.g., respiration) or transformed into body mass, which is then available for predation by the next trophic level. Assimilated mass is transferred when the mite is consumed. Arrow size roughly represents the energy allocation of each process.

Warming can affect terrestrial food webs through different mechanisms including increase in predation rates (Davidson et al., 2021; Ramachandran et al., 2021; Thakur et al., 2017), increase in attack rates and decrease in handling times of macrofaunal decomposers (Ott et al., 2012), indirect changes in body size distributions towards small-bodied species (Brose et al., 2012; Lindo, 2015), and increases in food web connectedness associated with more predatory species and decrease in stability (Sentis et al., 2020). The effects of warming can cascade and affect lower trophic levels (Barton et al., 2009; Lang et al., 2014), and ultimately alter energy fluxes (Pries et al., 2017; Schwarz et al., 2017).

No one has characterised a soil food web for a high carbon storage ecosystem such as boreal peatlands, nor quantified the contribution of oribatid mites (as the dominant microarthropods; Chapter 2; Chapter 4) to energy fluxes using an energetic food web model. Given the role of peatlands in carbon storage worldwide, understanding how energy fluxes at the scale of the soil food web deems essential to complement the information available on the balance of carbon sequestration and release from peatlands. For example, to date, empirical data on gas flux (CO_2 and CH_4 emissions) have been recorded at my research sites (James, 2020; Tian, 2019) alongside available long-term predictions derived from process-based models, specifically the Wetland-DNDC (DeNitrification-DeComposition) (Zhang et al., 2002) model by Webster et al. (2013). However, the DNDC model relies solely on carbon and nitrogen biogeochemistry (accounting for hydrology, temperature, plant and carbon dynamics), and does not include biological processes and feedbacks, particularly in soils, such as the role of microarthropods in carbon and nitrogen cycling, nor their responses to warming.

As such, the objective of my last thesis data chapter was to create energy-flux food web models for the peat-soil system for both the *Sphagnum*-dominated fen (SF) and the *Carex*-dominated fen (CF) sites to: 1) characterise the change in carbon and nitrogen flux under ambient, passive and active warming treatments, 2) compare carbon and nitrogen flux dynamics between the two sites, and 3) quantify the contribution, both direct and indirect, of oribatid mites to C and N mineralization (respiration) values. My initial model was a connectedness food web outlined by Hunt et al. (1987), and I used the established energetic methods of Moore and de Ruiter (2012) and Buchkowski and Lindo (2021). Given the differences in nutrient status and water table level (Webster and McLaughlin, 2010), plant community composition (Lyons et al., 2020) and oribatid mite community (Chapter 2; Chapter 4) between these two peatland sites, I predicted that carbon and nitrogen fluxes would be dramatically different between the two sites, as would the effects of warming and the contributions of oribatid mites to these flux values. The goal of this chapter was to thus provide a template for which further empirical data can be established, and trends can be validated with empirical data, however, that is beyond the scope of this chapter. Energetic models have been shown to accurately model systems dynamics, and thus this work should provide prediction for larger ecosystem changes, such as carbon dynamics caused by climate warming.

5.2 Materials & Methods

5.2.1 Soil food web parameterization

This study was performed using empirical data, where possible, from the *Sphagnum*-dominated fen (SF) and the *Carex*-dominated fen (CF) sites as presented in Chapter 2. Recall that the two sites differ in dominant vegetation, water table, and nutrient availability. Briefly, the SF is dominated by *Sphagnum* mosses with a lower water table and low nutrient availability and has a notable presence of hummock-hollow microtopologies on its landscape, while the CF is dominated by *Carex* sedges, has a higher water table and a moderate level of nutrients. The SF also has greater abundance and richness of oribatid mites compared to the CF (Chapter 2).

To parameterize the soil food web at the SF and CF sites, I used and synthesized microarthropod samples collected to characterise the microarthropods from pre-experimental (August 2015 (five samples/fen), during passive (June 2017 (16 samples/fen), June 2018 (18 samples/fen), June 2019 (16 samples/fen)) and after active August 2019 (16 samples/fen) and June 2020 (16 samples/fen)) warming treatments. In total the microarthropod data were derived from 174 samples that are categorized into ambient (pre-treatment and control plots), passive (warmed plots in 2018, 2019, 2020), and active (2019) warming treatments. From these samples, all soil invertebrates were enumerated at the order or family level corresponding to the nodes (function / trophic groups) in my soil food webs (see Chapter 2 for full details of sampling). This created nine arthropod trophic groups in my conceptualized soil food web.

Other data for trophic groups (i.e., food web nodes) that I used to parameterize my food webs were mostly sampled in the same SF and CF sites, but not performed by me, including for nematodes (Kamath, 2018), litter inputs (Lindo, unpublished data; Lyons and Lindo, 2020), plant litter quality (Lyons and Lindo, 2020), soil organic carbon (Webster et al., 2013), and phospholipid fatty acid analysis (PLFA) of microbial communities (Lyons and Lindo, 2020). I estimated protist biomass values using data from Jassey et al. (2015), who performed a similar passive warming climate change experiment in a *Sphagnum*-dominated fen site in France, as this data was not available for my sites.

At the base of each soil food web are the detrital inputs. Five litter traps (0.25 m^2) were deployed at each fen site in June 2017, and collected annually until 2019 to determine the quantity (biomass) and the quality (nutrient status) of plant litter inputs to the soil system (Lindo, unpublished data; Lyons and Lindo, 2020) as basal detrital inputs. Litter from each trap was oven dried at 60°C to determine total litter inputs and %C, %N and C:N were assessed using a combustion autoanalyzer (Lyons and Lindo, 2020). All litter inputs that had C:N values >30 were considered as part of the 'recalcitrant' detritus node, and C:N values <30 were considered as part of the 'labile' detritus node. Adding to both the recalcitrant and the labile detrital node was also resident soil organic carbon, estimated for both fens using data in Webster et al. (2013), based on the combination of carbon density measurements over the depth of the peat profile for the organic horizons. Root exudates were not explicitly included in my food web models as a separate node, but were included in the labile carbon node.

For the microbial data, five peat soil samples (0.3g dwt) were collected outside of experimental plots in 2018 at each fen, and fungal and bacterial communities were characterised by PLFA analysis (Lyons and Lindo, 2020) using methods modified from Quideau et al. (2016) and Buyer et al. (2010). Microbial biomass was estimated for the microbial community as the following identified groups: fungi (including arbuscular mycorrhiza fungi (AMF), and saprotrophic fungi) and bacteria (including anaerobic bacteria, gram+ bacteria, gram- bacteria and actinomycete bacteria) (Lyons and Lindo, 2020). For bacteria and fungi, I converted PLFA concentrations (nmol/g) to biomass using the following factors based on Williams et al. (2014): bacteria: 363.6 nmol = 1 mg C, fungi: 11.8 nmol = 1 mg C, and AMF: 1.047 nmol = 1 mg C.

Protists were not collected from the sites. Rather, I used data from Jassey et al. (2015). In that study, Jassey and colleagues collected and identified protozoans to the species level where possible from a similar climate change experiment between 2008–2013 using open-top chambers (OTCs) at the Forbonnet peatland located in France (46°49’25”N, 6°10’20”E), which is roughly in the same latitude as my peatland sites. In total, 48 samples were collected (6 samples / treatment (warming vs control) × 4 sampling events = 48 samples). I estimated protist biomass using the body mass of protists estimated in Jassey et al. (2015) following Jassey et al. (2011) conversion factors based on Weisse et al. (1990). Jassey et al. (2011) assumed geometrical shapes of protists and converted to body mass using the formula:

$$1\mu m^3 \ = \ 1.1 \times \ 10^{-7} \mu g \ C$$

For nematodes (Nematoda), data were compiled from five peat soil samples (ave. 5g dwt) collected from the top 10 cm of the peat soil from each site in October 2017 (Kamath, 2018); these samples were from the area surrounding, but not inside the experimental plots described in Chapter 4. Nematodes were extracted in water using the Baermann funnel technique (Forge and Kimpisnki, 2008), fixed with 8% dilute formalin solution, and had Rose Bengal stain added for visualization. Nematodes were assigned to feeding groups based on mouthpart characteristics outlined in Bongers (1994) and Tarjan et al. (1977), and measured for body size that allowed me to estimate nematode biomass at the functional (trophic) level. Nematode body mass (wet weight) was estimated from nematode body size following Andrássey (1956):

$$W = \frac{(L \times D^2)}{1.6 \times 10^6}$$

where W is the mass (µg) per individual nematode, L is the nematode length (µm), and D is the greatest body diameter (µm). Biomass is the product of body mass times abundance for each nematode functional group.

5.2.2 Biomass estimates

With the exception of litter from the litter traps, that was weighed with a scale in g of dwt, different indirect methods were used to estimate the biomasses of food web nodes for which weighing was not feasible. At each site, detritus was calculated as the sum of soil organic carbon with litter input divided equally (i.e., in half) into biomass for the high-quality detritus and for the low-quality detritus pools. For that, litter inputs were averaged across three sampling events (October 2017, 2018, 2019), to match the unit outputs of the fluxes (i.e., g C / m^2 / year).

For microarthropods, specifically, I used established allometric equations based on body size (length or diameter; width, and height) for the microarthropods and soil-dwelling macroarthropods sampled. Measurements of body size were taken from pictures of specimens captured with a microscope Nikon Eclipse Ni, and with the image analysis program NIS Elements. Representative individuals of mites, springtails, spiders and pseudoscorpions were measured.

For the oribatid, prostigmatid (Acari: Prostigmata) and astigmatid (Acari: Astigmata) mites, body masses (wet weight) were estimated using Lebrun (1971)'s equation for individuals:

$$\log M = 1.53 \times \log L + 1.53 \times \log W - 6.67$$

where *M* is the body mass in µg, *L* is the average length (µm), and *W* is the average width (µm) for each species. Mesostigmatid mite (Acari: Mesostigmata) body mass (wet weight) was estimated using Persson and Lohm (1977)'s equation:

$$M = 0.85 \times (L^{2.09} \times W^{0.84} \times 10^{-6.44})$$

where *M* is the body mass in µg, *L* is the average length (µm), and *W* is the average width (µm) for each species. Springtail (Hexapoda: Collembola) body mass (wet weight) was calculated using allometric length–weight relationships from Edwards (1967):

$$M = (b \times L)^3$$

where *M* is body mass in µg, *L* is the average length (mm), and *b* is a coefficient for the relationship between body length and body weight that is family specific. Values for *b* used in this chapter were: 2.81 for Hypogastruridae, 2.22 for Onychiuridae, 3.06 for Isotomidae, 2.46 for Entomobryidae and 3.8 for Sminthuridae.

For spiders (Arachnida: Araneae), I used the equation in Pennel et al. (2018) to estimate body masses (dry weight):

$$M = \exp\,(a + b \times \ln L)$$

where *M* is body mass in mg, *L* is length (mm), and *a* and *b* are coefficients for ground spiders (*a* = -1.86873, *b* = 2.80107). For pseudoscorpions (Arachnida: Pseudoscorpiones) I used the equation by Höfer and Ott (2009) to estimate body masses (wet weight):

$$\ln M = a + b \times \ln L$$

where *M* is body mass in mg, *L* is length (mm), and *a* and *b* are coefficients (*a* = -1.892, *b* = 2.515).

All biomass calculations used in the models were converted to g C / m^2 for all nodes, which was a two-step process, depending on the group. First I converted any biomass that was estimated in g wet weight (wwt) to g dry weight (dwt) using conversion factors available in the literature: pseudoscorpions (dwt = 0.38 × wwt; Höfer et al. (2009)), mesostigmatid (dwt = 0.4 × wwt), oribatid (dwt = 0.41 × wwt), prostigmatid (dwt = 0.48 × wwt) and astigmatid mites (dwt = 0.4 × wwt; all mites followed Newton and Proctor (2013)), springtails (dwt = 0.3 × wwt; Petersen (1975)), and nematodes (dwt = 0.25 × wwt; Wieser (1960)). Next, I assumed that the biomass of C was 50% of the dry weight of all nodes following Esterner and Elser (2002).

Biomasses were calculated for each peatland site (SF, CF) under three scenarios: ambient (control) temperature conditions, passive warming conditions, and active warming (see Section 5.2.6).

5.2.3 Functional group assignment and food web structure

All nodes of my food web models were based on trophic groups rather than taxonomic identifications (Appendix H). From top-down on the food web I grouped arthropod-feeding mites belonging to Mesostigmata and Prostigmata into the node “predatory mites” and the nematode-feeding mites (Zerconidae) into the “Zerco” node. All spiders were grouped into one node of predatory ground spiders, while all pseudoscorpions comprised their own node as well. Nematodes were separated into four trophic groups (predatory, omnivorous, fungivorous, and bacterivorous) based on their mouthpart morphology that indicates feeding preference. Oribatid mite species were grouped into two nodes: non-edible, where members are phylogenetically more-derived species with high levels of sclerotization and protection (considered inhabitants of enemy-free space by Peschel et al. (2006)), or edible, where species are non- or weakly sclerotized, unprotected, and small-bodied. Non-predatory prostigmatid mites, astigmatid mites, springtails, protists, fungi, and bacteria had each their own individual node. Both “low quality” (resistant) and “high quality” (easily degradable) detritus had equal biomass of soil organic carbon and detritus included in their nodes.

For all my models I used a food web consisting of these 18 nodes representing functional (trophic) groups (Table 5.1). Feeding interactions (i.e., consumer – resource interactions) were derived from Hunt et al. (1987), Koltz et al. (2018) and Moore and de Ruiter (2012) and weighted feeding preferences where required were derived from Hunt et al. (1987) and de Vries and Caruso (2016). Trophic interactions are presented as a matrix with consumers as rows and resources as columns. Values indicate the absence of a feeding interaction (0), the presence of a feeding interaction (1) where there is no weighted feeding preference, and the presence of a feeding interaction with weighted preferences (0.3; 0.7), where values represent the percentages (i.e., 30% and 70%, respectively) of which consumers feed on resources when these are not a limiting factor. Specifically, in my models the bacteria consume roughly twice as much labile litter/detritus than recalcitrant litter/detritus, while fungi show the opposite preference pattern.

Table 5.1 Matrix depicting the feeding interactions (i.e., consumer – resource links) for the 18 trophic groups used in the food web models.

Each row and column represent one node of the food web models. The value 1 represents the presence and 0 the absence of a feeding interaction between a row node (consumer) and the column node (resource). The value 1 also implies no feeding preference (i.e., a consumer feeds entirely on the resource when available), whereas 0.3 and 0.7 means that nodes show 30% and 70% of preference, respectively, over a specific food resource.

	Predmite	Zerco	Spiders	Pseudo	FunPros	Astig	OribEdi	OribNEdi	Coll	NemPre	NemBac	NemFun	NemOmn	Protis	Bacteria	Fung	LowDet	HighDet
Predmite	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0
Zerco	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
Spiders	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0
Pseudo	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0
FunPros	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Astig	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
OribEdi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
OribNEdi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Coll	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NemPre	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
NemBac	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
NemFun	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NemOmn	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Protis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.7
Fung	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0.3
LowDet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HighDet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Predmite: Predatory mites; Zerco: Nematode-feeding mites; Spiders: Spiders; Pseudo: Pseudoscorpions; FunPros: Fungivorous prostigmatid mites; Astig: Astigmatid mites; OribEdi: Edible oribatid mites; OribNEdi: Non-edible oribatid mites; Coll: Springtails; NemPre: Predatory nematodes; NemBac: Bacterivorous nematodes; NemFun: Fungivorous nematodes; NemOmn: Omnivorous nematodes; Protis: Protists; Bacteria: Bacteria; Fung: Fungi; LowDet: Low quality litter and detritus; HighDet: High quality litter and detritus.

5.2.4 Model parameterization

For each node, I designated the following parameters: biomass, death rate (i.e., turnover rate), feeding assimilation efficiency, biomass production efficiency and body C:N ratio — all parameters except biomass were derived from de Ruiter et al. (1993), Hunt et al. (1987), Koltz et al. (2018) and Moore and de Ruiter (2012). See Table 5.2 for the parameters (except biomass) used in all the models.

Death rates represent death not related to consumption and are expressed as the inverse of the organism's life span (Moore and de Ruiter, 2012). The death rate values I used are available in the literature (de Ruiter et al., 1993; Hunt et al., 1987; Koltz et al., 2018). During a trophic interaction (i.e., feeding), only a proportion of consumed resource biomass is assimilated by the consumer, and the remainder that is unassimilated (e.g., feces) (Figure 5.1) returns to the high-quality ('labile') detritus node. Assimilated biomass is then either mineralized as a result of metabolic processes (e.g., respiration, excretion), or is used for production of biomass (e.g., growth and reproduction) (Figure 5.1) that is dictated by specific production efficiencies(Moore and de Ruiter, 2012) (Table 5.2).

Table 5.2 Parameters used to run the food web models.

Included are death rate, assimilation rate, production efficiency, and C:N ratio for each node of all models.

Node	Death rate (g/g yr-1)	Assimilation efficiency (%)	Production efficiency (%)	C:N
Predmite	1.84	60	35	8
Zerco	1.84	90	35	8
Spiders	0.5	60	35	4
Pseudo	0.5	60	35	4
FunPros	4	50	35	8
Astig	4	50	35	8
OribEdi	1.2	50	35	8
OribNEdi	1.2	50	35	8
Coll	4	50	35	8
NemPre	6	50	37	10
NemBac	5	60	37	10
NemFun	4	38	37	10
NemOmn	8	60	37	10
Protis	6	95	40	7
Bacteria	1.2	100	30	4
Fung	1.2	100	30	10
LowDet	0	100	100	57.25
HighDet	0	100	100	18.81

From de Ruiter et al. (1993), Hunt et al. (1987), Koltz et al. (2018) and Moore and de Ruiter (2012)

Due to these inefficiencies in trophic interactions (i.e., losses to feces (assimilation efficiency) and metabolic processes (production efficiency)) (Figure 5.1), the amount of biomass transferred between nodes decreases with each successive trophic level, such that less energy is available for predators relative to lower trophic levels. As such, the calculations for carbon and nitrogen fluxes in my models start from the top predator down the food web, assuming that 1) matter is conserved, 2) detritus is not a limiting resource, 3) predators (i.e., spiders, predatory mites, nematode-feeding mites and pseudoscorpions) are not fed upon by any other fauna in the scale I used (but their loss to predation is included in their death rate), and that 4) the mass flowing through the food web is enough to support the top predators.

Node biomass was derived from field-based measurements of abundance, and calculations of individual body mass (see section 5.2.2). For a list of the groups included in each node, see Appendix H.

Table 5.3 Biomass (g dry weight C / m^2) used for each food web model.

Node	Biomass (g C / m^2)					
	Sphagnum-dominated fen (SF)			*Carex*-dominated fen (CF)		
	Control temperature	Passive warming	Active warming	Control temperature	Passive warming	Active warming
Predmite	0.00233	0.00179	0.00342	0.00107	0.00060	0.00059
Zerco	0.00021	0.00020	0.00032	-	-	-
Spiders	0.51504	0.20179	0.58263	0.15608	0.05952	0.01238
Pseudo	0.00368	0.00457	-	0.00333	0.00186	0.00291
FunPros	0.00158	0.00100	0.00410	0.00019	0.00009	0.00013
Astig	0.00001	0.00001	0.00003	0.00001	0.00001	0.00001
OribEdi	0.01695	0.01154	0.01865	0.00348	0.00274	0.00200
OribNEdi	0.01857	0.01256	0.01729	0.00741	0.00719	0.00243
Coll	0.00085	0.00017	0.00015	0.00036	0.00019	0.00015
NemPre	0.00002	0.00002	0.00001	0.00002	0.00002	0.00001
NemBac	0.00001	0.00001	0.00001	0.00015	0.00013	0.00011
NemFun	0.00005	0.00004	0.00003	0.00217	0.00187	0.00156
NemOmn	0.00001	0.00001	0.00001	0.00033	0.00028	0.00023
Protis	2.58550	1.60163	0.62052	2.58550	1.60301	0.62052
Bacteria	10.94	11.10	11.27	33.10	33.60	34.09
Fung	81.21	68.01	54.81	29.68	24.86	20.03
LowDet	135,707	135,707	135,707	43,730	43,730	43,730
HighDet	135,707	135,707	135,707	43,730	43,730	43,730

5.2.5 Carbon and nitrogen cycling in the models

I used the energetic model R code in Buchkowski and Lindo (2021) to calculate carbon and nitrogen fluxes at each fen site under natural and warmed conditions (fluxes in grams C or N / m^2 / year). All food web models assumed that the system is at equilibrium (i.e., steady state). Carbon fluxes were calculated as the sum of fluxes for the whole matrix (i.e., for all individual nodes) including C mineralization (respiration) and C retained in the nodes (assimilated carbon that goes into biomass). Nitrogen fluxes were calculated using the carbon fluxes and the C:N ratios of all nodes (Buchkowski and Lindo, 2021: Equation 1) as the consumption rate divided by the prey C:N ratio. The C:N ratios for each node in the food web model were taken from the literature (de Ruiter et al., 1993; Hunt et al., 1987; Koltz et al., 2018), except for the detritus pools, for which ratios were specifically determined for both sites in Lyons and Lindo (2020).

5.2.6 Food web models

To assess C and N mineralization rates and the contribution of oribatid mites in these fluxes for boreal peatland systems, I created 12 food web model scenarios that include each fen site described in Chapter 2, three warming scenarios (control, passive, active warming) observed in Chapter 4, and these same models with oribatid mites (edible and non-edible) nodes removed from the food webs. For all model scenarios, I used the same parameters listed in Table 5.2, except for the node biomass values that were calculated for each model scenario based on field available data (see Table 5.3). Soil organic carbon stock and litter inputs were assumed to be always in excess, and I therefore used the same values across all models. The first model scenario represented the *Sphagnum*-dominated fen under ambient (control) temperature conditions ($SF_{ambient}$), where node arthropod biomasses were derived from samples collected in 2015 (prior to the climate change experiment initiated), data from the experimental plots without OTCs (control, never warmed plots) including all experimental plots sampled in June 2017 (pre-warming conditions), and also data from ambient plots collected between 2015-2020; biomasses were averaged across all sampling events. Nematode, microbial groups, detritus and litter values were derived from the SF but from outside the experimental plots, while protist data were obtained from control plots of the climate change experiment in Jassey et al. (2015). A similar model was created for the CF under ambient / control conditions ($CF_{ambient}$).

The next set of model scenarios were for the SF and CF under passive warming ($SF_{passive}$, $CF_{passive}$ respectively). Arthropod data were collected from experimental plots with OTCs between 2018-2020, and biomasses were averaged across sampling events as well. Protist data were obtained from experimental plots with OTCs in Jassey et al. (2015), who also provided nematode biomass responses to passive warming; protist and nematode biomass decreased by 38% and 14%, respectively under passive warming based on Jassey et al. (2015). I assumed changes in the biomass of fungi and bacteria from an 18-month warming greenhouse experiment that used peat-soil from the SF in 2013 which saw a 16.5% and 32.25% decrease of fungi and an increase of 1.5% and 3% of bacteria under passive and active warming, respectively.

For the SF and CF subjected to active warming scenarios (SF_{active}, CF_{active} respectively), I used arthropod data collected in August 2019 from the experimental plots warmed with OTCs and heating rods (Chapter 4); nematode and protist biomasses were estimated to decrease by 28% and 76%, respectively, as I assumed the active warming effects to be two-fold that of passive warming seen in Jassey et al. (2015).

Finally, in addition to these six model scenarios, I subsequently removed oribatid mite biomasses (both edible and non-edible nodes together) from the food webs and recalculated flux values in order to determine their specific effects on carbon and nitrogen mineralization. For that, I first calculated C and N mineralization for each individual node in all 12 food webs, except litter/detritus, as those are not living organisms. Then, to determine the contribution of oribatid mites (the two oribatid mite nodes considered together) to C and N mineralization, I used the formulas presented in Holtkamp et al. (2011) to calculate their direct and indirect effects:

$$Direct\ effects = \frac{mineralization\ of\ a\ node}{total\ mineralization}$$

$$Indirect\ effects = \frac{total\ mineralization\ with - without\ the\ node\ present}{total\ mineralization\ with\ the\ node\ present}$$

Both direct and indirect effects of oribatid mites on the mineralization of C and N were multiplied by 100 and are thus presented as the percentage of total C and N mineralization, respectively, or as actual contribution in (g / m^2 / year) for all food web models.

5.3 Results

The biomass for the invertebrates, and for all living organisms together (microbes included) are presented in Appendix I for all food webs. The biomass of all living organisms under ambient conditions (i.e., litter/detritus excluded) was nearly 1.5 times higher in the SF (95.30 g C / m^2) compared to the CF (65.55 g C / m^2), and was predominantly within the primary microbial consumer groups of bacteria and fungi

(99.41% and 99.73%, respectively for the SF and CF). The biomass of invertebrates under ambient conditions was more than 3 times higher in the SF (0.56 g C / m^2) compared to the CF (0.17 g C / m^2). Increases in soil temperature (Chapter 4) decreased the overall biomass of living organisms (invertebrates, protists and microbes included) by 8.25% under passive and 16.43% under active warming, and that of invertebrates only by 57.34% under passive and 87.10% under active warming in the CF. The biomass of microbes (fungi and bacteria considered together) decreased by 6.89% under passive warming and by 13.78% under active warming in the CF. The biomass of living organisms also decreased under warming in the SF (by 15.05% under passive and 29.34% under active warming), which was mainly driven by decreases in microbial biomass (by 14.14% under passive and 28.29% under active warming). However, although the biomass of invertebrates decreased by 58.21% under passive warming, it increased by 12.04% compared to ambient conditions under active warming, due to increased abundance and therefore biomass of predatory mites, spiders, fungivorous prostigmatid mites, astigmatid mites, and edible oribatid mites. On average, the biomass of oribatid mites accounted for 7.12% of the invertebrate biomass across all food web models. Even though oribatid mites were the most abundant group of invertebrates in both sites (Chapter 2; Chapter 4), the body mass of individual spiders was considerably higher as they are bigger, which translated into them accounting for 90.10% of the invertebrate biomass on average across all food web models (Table 5.3). Protists in both sites decreased in biomass by 38.00% under passive and 76.00% under active warming.

5.3.1 Food web carbon and nitrogen cycling

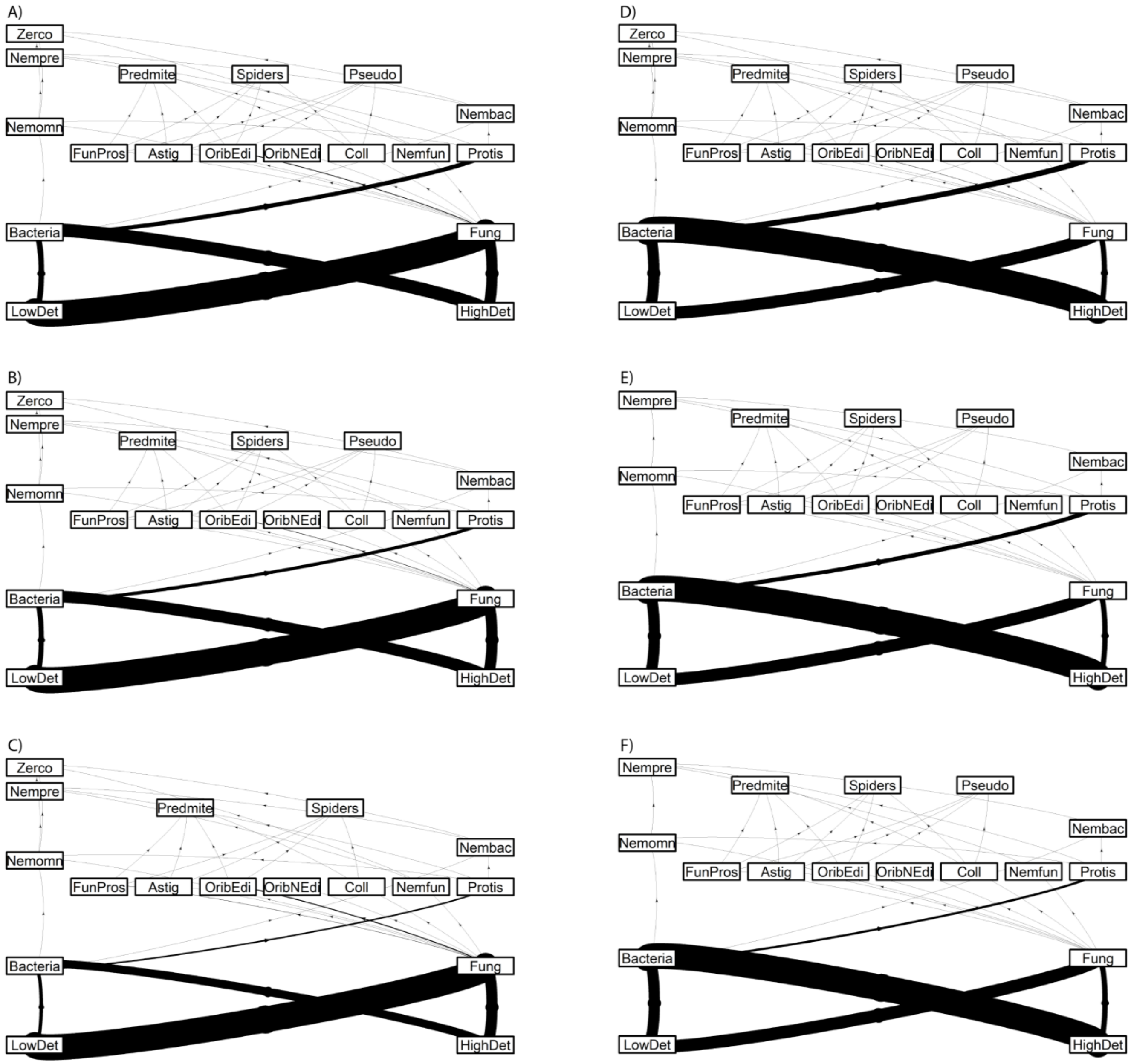
The soil food web in the SF had a calculated flux of 579.23 g C / m^2 / year under ambient conditions, and under warming the fluxes decreased to 440.03 g C / m^2 / year (passive) and 344.90 g C / m^2 / year (active) (Table 5.4). In other words, passive warming decreased the C flux through the soil food web by 24.03%, and active warming did so by 40.45% in the SF. Similar trends were seen for the CF, where carbon fluxes were not as high, being 438.81 g C / m^2 / year under ambient conditions, but also decreased under warming to 348.05 g C / m^2 / year under passive warming and 260.47 g C / m^2 / year under active warming (Table 5.4), which translates into decreases of 20.68% (passive warming) and 40.64% (active warming) in the C flux in the CF. The same pattern was also found for C mineralization (respiration) and C retained in the food webs (Table 5.4).

Similar to carbon dynamics, total N fluxes decreased with warming in both SF and CF, and total N fluxes were slightly higher in the SF (ambient conditions: 28.60 g N / m^2 / year; passive warming: 20.11 g N / m^2 / year; active warming: 13.74 g N / m^2 / year) compared to the CF (ambient conditions: 25.46 g N / m^2 / year; passive warming: 18.63 g N / m^2 / year; active warming: 11.95 g N / m^2 / year) (Table 5.4).Warming reduced net nitrogen mineralization at both sites (Table 5.4). The CF immobilized nitrogen under ambient conditions (i.e., negative mineralization), so warming only increased the rate of nitrogen sequestration. The SF mineralized nitrogen under ambient conditions. Passive warming only reduced nitrogen mineralization rate, while active warming flipped the system from net mineralization to net immobilization (Table 5.4).

Table 5.4 Calculated C and N flux values (g / m^2 / year) for soil food webs from a *Sphagnum*-dominated fen (SF) and a *Carex*-dominated fen (CF) under ambient (field control conditions) and passive and active warming scenarios.

In the total N mineralization column, positive values indicate N mineralization (respiration, release from food web) and negative values indicate N immobilization (retention in the food web).

	Total C flux	Total C mineralization	Total C retained	Total N flux	Total N mineralization	Total N retained
$SF_{ambient}$	579.23	396.96	182.27	28.60	1.22	27.37
$SF_{passive}$	440.03	303.41	136.61	20.11	0.02	20.09
SF_{active}	344.90	236.54	108.35	13.74	-0.91	14.66
$CF_{ambient}$	438.81	300.84	137.97	25.46	-1.41	26.87
$CF_{passive}$	348.05	239.91	108.13	18.63	-2.63	21.27
CF_{active}	260.47	180.92	79.55	11.95	-3.84	15.80


A)
Zerco
Nempre
Predmite
Spiders
Pseudo
Nembac
Nemomn
FunPros
Astig
OribEdi
OribNEdi
Coll
Nemfun
Protis
Bacteria
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Spiders
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Zerco
Nempre
Predmite
Spiders
Nembac
Nemomn
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Nembac
Nemomn
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Protis
Bacteria
Fung
LowDet
HighDet

Figure 5.2 Visualization of the carbon flux food web model of the invertebrate community in a *Sphagnum*-dominated and a *Carex*-dominated fen in Northern Ontario, Canada.

Boxes represent nodes that are connected by links representing the feeding relationships. The width of the arrows is proportional to the amount of C transferred (g C / m^2 / year). Oribatid mites are included in all models: A) food web depicting the SF under ambient conditions; B) SF under passive warming; C) SF under active warming; D) CF under ambient conditions; E) CF under passive warming; F) CF under active warming. The fungal channel is dominant in the SF (left plots A-C), whereas the bacterial is the dominant in the CF (right plots D-F). In both fens, the amount of C transferred from bacteria to protists decreased under warming, as seen by the line becoming thinner under warming compared to under ambient conditions. Predmite: Predatory mites; Zerco: Nematode-feeding mites; Spiders: Spiders; Pseudo: Pseudoscorpions; FunPros: Fungivorous prostigmatid mites; Astig: Astigmatid mites; OribEdi: Edible oribatid mites; OribNEdi: Non-edible oribatid mites; Coll: Springtails; NemPre: Predatory nematodes; NemBac: Bacterivorous nematodes; NemFun: Fungivorous nematodes; NemOmn: Omnivorous nematodes; Protis: Protists; Bacteria: Bacteria; Fung: Fungi; LowDet: Low quality litter and detritus; HighDet: High quality litter and detritus.

5.3.2 Contributions by oribatid mites to C and N mineralization

Trends for total C and N mineralization follow total C and N flux values, so here I present the results for calculated contributions to C and N mineralization. While the majority of C and N mineralization was performed by microbes in all food web models, the oribatid mites were the largest contributors to C and N processes of all the invertebrate groups, yet they still only directly contributed <1% to C and N mineralization in both sites.

Oribatid mites contributed more to C mineralization in the SF (ave. 0.59% relative direct contribution to total C mineralization; ave. 1.74 g / m^2 / year) than in the CF (ave. 0.12% relative direct contribution to total C mineralization; ave. 0.33 g / m^2 / year) considering their direct effects. The direct contributions of oribatid mites to C mineralization were different under warming scenarios, being the highest under active warming (2.22 g / m^2 / year) and the lowest under passive warming in the SF (0.90 g / m^2 / year), with intermediate values found under ambient conditions (2.11 g / m^2 / year). In the CF, though, the oribatid mite direct contributions to C mineralization were reduced with warming (ambient: 0.64 g / m^2 / year; passive: 0.27 g / m^2 / year; active warming: 0.07 g / m^2 / year).

In a similar way, the direct contributions to N mineralization by oribatid mites were also higher in the SF (ave. 1.97% relative direct contribution to total N mineralization; ave. 0.15 g / m^2 / year) than in the CF (ave. 0.20% relative direct contribution to total N mineralization; ave. 0.02 g / m^2 / year). The direct contributions of oribatid mites to N mineralization under warming followed the same trend seen for C, where it was the highest under active waring (0.19 g / m^2 / year), the lowest under passive warming (0.07 g / m^2 / year), and intermediate values were found at current conditions

(0.18 g / m^2 / year). Direct contributions to N mineralization by oribatid mites decreased with warming in the CF, again following the trends for C mineralization (ambient: 0.05 g / m^2 / year; passive: 0.02 g / m^2 / year; active warming: 0.006 g / m^2 / year).

Oribatid mites indirectly contributed <0.5% to C and N mineralization in both sites under all warming scenarios. The indirect contributions of oribatid mites to C flux were higher in the SF (ave. 0.19% relative indirect contribution to total C mineralization; ave. 0.001 g / m^2 / year) than in the CF (ave. 0.06% relative indirect contribution to total C mineralization; ave. 0.0006 g / m^2 / year), following their aforementioned direct contributions. The effects of warming on the indirect contributions of oribatid mites to C mineralization followed same trend of their direct contributions, being the highest under active warming (0.002 g / m^2 / year) and lower under passive warming and ambient conditions (both: 0.001 g / m^2 / year) in the SF. In the CF, the indirect contributions to C mineralization did not follow trends seen for the direct contributions. Instead, I found the highest indirect contributions to C mineralization under passive warming (0.0007 g / m^2 / year), the lowest under active warming (0.0004 g / m^2 / year), and intermediate values under ambient conditions (0.006 g / m^2 / year).

The indirect contributions to N mineralization by oribatid mites were higher in the CF (ave. 1.27 g / m^2 / year) than in the SF (ave. 1.03 g / m^2 / year). The indirect contributions of oribatid mites to N mineralization under warming followed a different trend seen for C in both fens; in the CF, it was the highest under active warming (1.51 g / m^2 / year), followed by passive warming (1.22 g / m^2 / year) and ambient conditions (1.08 g / m^2 / year). Similarly, indirect contributions to N mineralization by oribatid mites increased with warming in the SF (ambient: 0.91 g / m^2 / year; passive warming: 0.99 g / m^2 / year; active warming: 1.18 g / m^2 / year).

5.4 Discussion

Oribatid mites comprised large amounts of the invertebrate biomass at both peatland sites corresponding to their general abundance at both sites compared to other invertebrate groups. At the same time, the vast majority of biomass, and therefore flux of both C and N, was attributed to the fungal and bacterial groups, which show opposite patterns of dominance at the two fen sites; biomass was greater for the fungi in the SF, and greater for the bacteria in the CF (Lyons and Lindo, 2020). In general, all flux values (total flux, mineralization rates) were dictated by overall and individual node biomass estimates. As such, when biomass values changed under warming, particularly for the microbial consumer (primary decomposer) groups, flux values were affected. Besides the natural differences in biomass of living organisms and corresponding fluxes between sites, I showed that warming would likely decrease both C and N flux at the SF and CF, a result that is strongly linked to decreases in overall microbial biomass, as well as changes in fungal:bacterial ratios under warming. Consistent with biomass responses to warming, while C mineralization by fungi decreased, that of bacteria increased under warming at both sites. A less evident response is seen for N mineralization by fungi and bacteria that both slightly decreased under warming possibly due to greater N availability to microbial communities through higher-quality plant litter inputs under warming (Lyons and Lindo, 2020; Lyons et al., 2020). Greater soil N availability is suggested to increase microbial N through immobilization (i.e., opposite of mineralization) (Yin et al., 2012; Zhong et al., 2019), although non-significant changes in microbial N immobilization under warming also seem to be common (Bai et al., 2013).

The calculated C flux values for the SF and CF under ambient conditions were lower than measured values for these peatlands. For example, Tian et al. (2020) measured net ecosystem exchange (total C flux) in a greenhouse experiment using mesocosms from the CF (19 L mesocosms of soil and vegetation), and found ecosystem respiration values to be ~930 g C / m^2 / year, although these values included the respiration of living vegetation. In a similar greenhouse experiment using mesocosms (also 19 L mesocosms of soil and vegetation) from the SF, Dieleman et al. (2016) measured ~606 g C / m^2 / year, again, these values also included respiration of living vegetation. James (2020) found no differences in ER between sites during the growing season in the field, but that average gross ecosystem productivity (GEP; difference between net ecosystem exchange and ecosystem respiration values = gross photosynthesis) was 17% higher at the SF fen than the CF under ambient conditions. My calculated values (~580 g C / m^2 / year and ~440 g C / m^2 / year for total fluxes in the SF and CF, respectively) also account for C and N being retained as well as mineralized (respired) from the food webs. One explanation is that flux values roughly followed biomass values for different trophic groups, and I did not include vegetation production or respiration that would contribute to GEP and ER under field conditions; I estimate that vegetation biomass was 5-36 times greater than my microbial biomass (all groups combined). This would also explain why I found higher total and respiration (mineralization) flux values in the SF whereas lab mesocosm studies have found greater GEP/ER in the CF (see Tian et al. (2020) vs Dieleman et al. (2016)). The plants in the CF are predominantly vascular plants with higher photosynthetic rates than the moss-dominant SF (Lyons et al., 2020), leading to consequently higher gas exchange (Syed et al., 2006), and respiration values measured in the field for the CF.

At the same time, my calculated C mineralization (respiration) values under warming decreased, whereas empirical measurements of respiration rates by all aforementioned studies increased under warming; Dieleman et al. (2016) found a 48% increase in response to warming for the SF mesocosms, Tian et al. (2020) found 43% (+4°C) and 97% (+8°C) increases for the CF mesocosms, and James (2020) found active warming in 2019 increased ER by an average of 21.8% at the CF and only marginally increased it at the SF. That said, warming-induced reductions in C flux were observed by Schwarz et al. (2017), who empirically showed an overall decrease in energy flux by 12% in disturbed and undisturbed forest stands under warming (+1.7°C, +3.4°C) that they attributed to warming-induced decreases in soil moisture that impacted soil microbial communities. While the contribution of vegetation to ecosystem respiration, as well as the response of plants to warming are important components in overall ecosystem-level C flux values (Dusenge et al., 2021), the main discrepancy in C flux trends under warming between my models and empirical measurements was likely due to a lack of metabolic scaling in my models.

The metabolic theory of ecology (Brown et al., 2004) provides a framework that links changes in temperature to metabolic rate of individuals, which then allows predictions of warming at the individual/population level, that can be extrapolated to the ecosystem level. Increases in temperature are known to increase metabolic losses (Gillooly et al., 2001) from microbial (Allison et al., 2010) and invertebrate (Thakur et al., 2018) organisms. Even though this metabolic scaling was not part of my models, the results provided here do suggest that changes in microbial biomass under warming will significantly alter C flux rates, and therefore should be incorporated into C budget models for climate change predictions. To date, the vast majority of C models are based on broad scale geochemical models (e.g., DNDC, McGill wetland model, DAYCENT, etc.) and do not consider the ecological responses of soil communities.

While there has been a lack of energetic soil food web models in general, and to date this study is the first to model boreal peatlands, the flux values calculated at my two sites were high compared to other energetic soil food web models. For instance, Koltz et al. (2018) found C flux to be as low as 60 g / m^2 / year for a tundra system in the Arctic, while Schwarz et al. (2017) found an average C flux of 79 g C / m^2 / year in 40–60-year-old mixed aspen–birch–fir forests. My C flux values (~580 and ~440 g C / m^2 / year in SF and CF, respectively) were nearly an order of magnitude greater than these two studies. That said, the energy flux results of Potapov et al. (2019) for tropical systems in Indonesia are 2× higher than my calculated values (1035-1673 g wwt / m^2 / year), despite the authors only including five trophic groups (omnivores, predators, large decomposers, small decomposers and herbivores) and not including microbes, which were the main contributors of flux in my models. The large flux values by Potapov et al. (2019) are likely due to the direct and exclusive feeding of large-biomass detritivores on detritus, besides their models using mass on a fresh weight basis instead of C mass basis like in mine. Roughly converting wet weight to dry weight (dwt = 0.4 × wwt), and then to mass of C (biomass of C = 0.5 × dwt; Sterner and Elser (2002)), the values of Potapov et al. (2019) become lower (~155-250 g C / m^2 / year) than those for my peatland sites.

In all the aforementioned studies, the grouping and/or inclusion of trophic groups differed from my models, suggesting that food web conceptualization and parameterization are important for obtaining realistic and/or comparable flux values. Yet, biomass estimates also underlie some of the discrepancies in flux values between my sites and the literature. While Koltz et al. (2018) presented a more comprehensive food web that included several nodes not in my models (roots, enchytraeids, flying insects, diatoms, pollen, mammal blood and aboveground plant tissue), their invertebrate, and most importantly, their microbial biomasses, were considerably lower than mine, which resulted in a C flux that was 5-10× lower (invertebrate biomass was >50× higher at the SF and CF, and microbial biomass was 5.2× higher at the SF and 3.8× higher at the CF compared to Koltz et al. (2018)).

Previous studies suggest contributions of fauna to decomposition are mostly indirect through the microbial communities, and therefore hard to measure (e.g., Cárcamo et al., 2001; Chapter 3; Joo et al., 2006; Moore et al., 1988). Recent advances in food web modeling, such as the models employed here, have allowed estimates of their contributions (Holtkamp et al., 2011; Schwarz et al., 2017), which substantiate a small relative contribution (<1%) to overall fluxes, and the vast majority of C and N mineralization and transformations are performed by the fungi and bacteria (Bloem et al., 1994; de Ruiter et al., 1994; Koltz et al., 2018). Previous PLFA (Lyons and Lindo, 2020) and genomic data (Asemaninejad et al., 2017, 2018, 2019) showed that my sites house diverse and abundant microbial communities, that, together with oribatid mite communities (Chapter 2), are essential players in C fluxes. The high biomass of microbial groups (fungal, bacterial) alongside their respective ratios (i.e., fungal:bacterial) are important determinants of C flux in peatlands (Bragazza et al., 2013) that are largely responsible for decompositional processes that maintain high C storage capacity of boreal peatlands (Beaulne et al., 2021; Frolking et al., 2011; Hugelius et al., 2020). Fungal and bacterial groups are also purported to form contrasting energy channels (Hunt et al., 1987; Moore et al., 2004) that confer stability of soil systems (Moore and Hunt, 1988; Rooney and McCann, 2012), although the exclusivity of these channels has recently been debated (de Vries and Caruso, 2016). However, these two energy channels likely enhance overall diversity of the invertebrates because each channel supports a somewhat non-overlapping group of trophic nodes. Considerably higher biomasses of microbes compared to faunal biomass appear to drive the fluxes and obscure the fauna contributions to C and N mineralization. Adding to this, microbes also tend to have greater assimilation efficiencies (e.g., higher C mineralization) (Moore and de Ruiter, 2012), which also helps to explain their higher contribution to flux values in energetic models.

That said, despite oribatid mites being numerically dominant among the invertebrate groups and therefore having relatively high biomass, oribatid mites present some interesting considerations within food web models. First, oribatid mites are generally well protected from predators through mechanical (e.g., box mites (Schmelzle et al., 2015; Schmelzle and Blüthgen, 2019)), chemical (e.g., gland reservoirs (Brückner and Heethoff, 2017, 2018)) and/or morphological defences (e.g., cuticular hardening (Brückner et al., 2016; Norton and Behan-Pelletier, 1991), and thus are believed to live in a ‘predator-free’ space (Peschel et al., 2006). Using knowledge of oribatid mite taxonomy and ecology, I split oribatid mites into two groups based on their defence as a proxy for edibility. Following Schwarzmüller et al. (2015), I considered the non-edible oribatid mite node as “trophic whales” where energy from basal resources (here the fungal channel) terminates at the non-edible oribatid mite node and does not reach the top predators. As such, non-edible oribatid mites might act as biotic buffers (*sensu* Schwarzmüller et al. (2015)) under warming because they can immobilize C and N and divert increased energy from enhanced growth of the microbial groups, thereby retaining it within the detrital food web.

Similarly, Staddon et al. (2010) observed that when predators were lost due to habitat fragmentation, small edible oribatid mites increased in abundance (due to prey release) and N immobilization rates (as they are poor assimilators), thereby also retaining N in their biomass. The slow growth rates and long-life spans of many oribatid mites in boreal systems (Hansen, 2000; Norton, 1994; Tilrem, 1994) may also help immobilize energy flux in peatlands under warming. Besides the direct contributions to C and N mineralization, oribatid mites also contribute to ecosystem processes by influencing the turnover rate at other levels (i.e., indirect contributions); however, these indirect effects appear to be an order of magnitude lower than direct effects. In fact, until now, and due to the lack of determination of the contribution of specific taxa to C and N fluxes, we used to state that indirect effects were important to consider; my results showed that the indirect effects of oribatid mites to C and N mineralization are practically null, although my models were static and population-level dynamics are not considered. Nonetheless, indirect effects of oribatid mites have been observed on microbial growth through grazing-stimulation (Kaneko et al., 1998), preventing senescence (Lussenhop, 1992), and dispersal of propagules (Renker et al., 2005).

5.4.1 Food web assumptions

As with all models, certain assumptions were made in the models I used to calculate flux. First, I assumed that all dead biomasses (i.e., C and N not lost to respiration or predation) re-entered the food web as part of the high-quality litter/detritus pool. While my C:N values of the high-quality detritus pool were lower than the low quality (recalcitrant) detrital pool, the average C:N of most organisms was still lower (i.e., higher quality; ave. 7.8) than that of the high-quality pool itself (18.8), which has some important implications for both C and N cycling. As the model employs an ecostoichiometric approach, N flux values were calculated based on C flux values and the C:N ratios of the nodes. All food webs in this chapter mineralized C and generally immobilized N in order to maintain their C:N ratios, given the high quality of dead animal biomass. An alternative to my approach could be thus to remove dead animal biomass from the high-quality pool and create a separate a pool for them ("necromass" *sensu* Buckeridge et al. (2020)), where the C:N ratios are lower than 18.8. However, whether this would improve the food web models is not clear. Necromass is a difficult pool to measure in field conditions, which would make validation of calculated values an unlikely task.

Even though I did not include plant biomass in my soil food webs, Koltz et al. (2018) showed that less than 1% of the energy in their food web came from live plant biomass (i.e., aboveground plant tissue and roots) in a tundra system. Nonetheless, changes in plant community composition affect the input of litter through both quantity and quality, and can alter the amount of energy available. Warming-induced sedge expansion and moss reduction have been shown for my sites (Dieleman et al., 2015; Lyons et al., 2020), which will potentially alter the C:N ratio of the litter as the basal resource inputs to the soil food webs, and thus may cascade and affect the amount of energy fluxed with further consequences to carbon storage.

While I chose to implement biomass changes to trophic groups under warming based on available empirical data, food web topology can change in both node biomass as well as node linkages under warming. For instance, feeding preferences may change under warming (Bestion et al., 2019, Frances and McCauley, 2018) as species seek to minimize prey handling time and/or maximize energy gains to offset metabolic costs. In my food webs I used uniform feeding preferences for all soil fauna and protists, which may have resulted in an overestimation of feeding on less preferred groups. Additionally, I did not account for any direct metabolic costs of warming at the individual level. Ongoing modelling projects within my lab group that use a new R package called *fluxweb* (Gauzens et al., 2019) provide functions that account for metabolic scaling of metabolism based on warming using the Boltzmann equation (Ehnes et al., 2011) that is based on individual body size of each species; however, the *fluxweb* package does not use an ecostoichiometric approach, and therefore cannot estimate N cycling flux values.

Alongside this is the consideration that individual and community level decreases in body size for invertebrates are predicted under warming scenarios. For instance, Sheridan and Bickford (2011) proposed the idea of community downsizing, where losses in large-bodied organisms alongside increases in small-bodied organisms will lead to a reduction in the average body size of an individual within the community (i.e., the community weighted mean of body size). Indeed, community downsizing has been observed in soil systems under warming (Lindo, 2015), and I observed small, but non-significant increases in some small-bodied oribatid mites under warming (Chapter 4). While I did not model body sizes, Lindo (2015) suggested that community downsizing may be linked to lower trophic transfer efficiency with consequences to energy dynamics, and will affect flux values in models where metabolic scaling is linked to organismal body size (e.g., *fluxweb*). Lastly, the assimilation and production efficiencies I used were based on laboratory studies under controlled conditions, and although they are expected to change under warming, the directionality or magnitude of those changes are yet to be determined.

Understanding how soil communities are structured is important to predict how they may respond to warming (Chapter 4). However, to predict the ecosystem-level consequences of warming on soil communities, a food web approach that tracks energy and nutrients provides more comprehensive results. I showed that the microbial-invertebrate food web models in two peatland sites in northern Ontario produce realistic trends in energy flux responses to warming, and the flux values derived from these models need to be more closely compared to empirical measurements. That said, I showed that overall fluxes and their response to warming are fen dependant, consistent with emerging empirical data. Oribatid mites as the majority of the invertebrate abundance did not reflect biomass trends (i.e., large bodies, low abundant spiders, and small bodied, highly abundant microbes), yet still were important invertebrate contributors of energy and nutrient flux, albeit less important than protists, fungi, and bacteria. One important take-home is that this work demonstrates how warming-induced changes in biomasses are drivers of fluxes, although metabolic costs to warming are also expected to be important parameters in predicting flux values. As previously mentioned, current models used to predict the effects of climate change on these key carbon storage ecosystems fail to include the ecological processes of the soil biodiversity. While preliminary, the approach and results presented here provide a way forward in understanding soil community trophic interactions to carbon and nitrogen dynamics in boreal peatlands under warming.

5.5 References

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Chapter 6

6 General Discussion

Oribatid mites are the dominant microarthropods in peatlands (e.g., Belanger, 1976; Lindo, 2015; Silvan et al., 2000), demonstrating high species richness (Chapter 2), abundance (Chapter 4) and biomass (Chapter 5) compared to other soil invertebrate groups. However, they are relatively understudied in these systems compared to in other ecosystems in Canada such as boreal and deciduous forests (Beaulieu et al., 2019; Behan-Pelletier and Bissett, 1994; Behan-Pelletier and Lindo, 2019). As such, the drivers of oribatid mite communities in peatlands are less well known. In this thesis, I demonstrated that a) differences in peatland type, specifically plant composition, water table, nutrient levels and pH housed unique oribatid mite communities (Chapter 2), b) soil moisture was a key abiotic variable for oribatid mite communities even within a single site, and more important than litter quality (Chapter 3), c) temperature-induced changes in soil moisture (Chapter 4) can drive both species losses and species gains, and d) changes in oribatid mite communities, and the soil food web more broadly, affected the flux of carbon and nitrogen in boreal peatlands (Chapter 5).

Soil moisture is a known driver of oribatid mite communities across a variety of terrestrial ecosystem types (Elo et al., 2018; Jakšová et al., 2020; Tsiafouli et al., 2005) with the vast majority of studies showing a positive relationship of richness and abundance with soil moisture. However, this relationship is actually unimodal (not linear, positive) as saturated soils decrease habitable pore space that can reduce richness and abundance. As such, peatlands, with their high-water table compared to other terrestrial systems, exist closer to this ‘threshold’ of soil moisture; fully saturated peatlands like the

CF have lower species richness than peatlands like the SF. Previous studies have shown that lowered levels of moisture have overall negative effects on peatland oribatid mite richness (Lehmitz, 2014) and proportional abundance (Silvan et al., 2000), but I show that this result depends on the initial soil moisture conditions and saturation levels, and thus the response depends on peatland type and microhabitats (microtopology) within a peatland. Communities of semi-aquatic oribatid mite species that favour from a high-water table and more ‘terrestrial’ species that dominate in drier areas of the peatland (Minor et al., 2016, 2019) respond differently to changes in moisture leading to drying-induced losses in species richness at wet sites, and increased species richness at drier peatland sites.

Plant community composition, and more specifically plant litter inputs to the soil system, is also a main driver of oribatid mite communities. For example, oribatid richness and abundance have been shown to be higher in conifer systems than in deciduous systems in forest floor samples from Alberta (Lindo and Visser, 2004) and litter samples from Quebec (Sylvain and Buddle, 2010), which seems to be related to heterogeneous microhabitats created by the persistence of coniferous litter in different stages of decomposition over years (Hansen and Coleman, 1998). Similarly, litter originated from a diverse plant community (i.e., mixed litter) have greater variety of microhabitats housing higher diversity of oribatid mites (Hansen, 2000; Hansen and Coleman, 1998). Additionally, litter quality has also been shown to drive oribatid mite communities (Gergócs and Hufnagel, 2016; Gergócs et al., 2015), and here I demonstrated that litter type helped structure communities on hummocks, with *Carex* spp. (sedge) litterbags housing barely any oribatid mites, but *Chamaedaphne calyculata* (shrub) litterbags being colonised solely by them. Furthermore, plant communities also have strong effects on soil chemistry and physics including soil moisture, pH, bulk density, carbon and nitrogen content (Waring et al., 2015), which further influence oribatid mite communities. As such, the two peatland sites I examined that differed in water table (soil moisture) and plant community composition as major drivers of oribatid mite communities correspondingly housed significantly different oribatid mite communities.

Plants also form the basal resource of soil food webs and affect microbial communities. The composition and dynamics of oribatid mite communities are known to be influenced by both microbial communities, their main resource (Norton and Behan-Pelletier, 2009), and the plant communities, which fuel the belowground system with litter of different qualities (Gergócs et al., 2015). Oribatid mites are mostly considered secondary decomposers (e.g., Hubert, 2001; McBrayer et al., 1977), feeding mainly on fungi (Schneider and Maraun, 2005), and in less proportions on detritus, which they reduce and fragment through a process called comminution (García-Palacios et al., 2013; Siepel and de Ruiter-Dijkman, 1993), ultimately facilitating the decomposition process and nutrient cycling (carbon and nitrogen) by microbial communities in soil systems (Broadbent, 2021; Crossley, 1977). However, I demonstrated that the contribution (direct or indirect) of oribatid mites to decomposition and carbon or nitrogen flux is lower than previously thought. That said, interactions of oribatid mites with the peatland microbial community are likely still important in structuring oribatid mite communities.

Microbial communities also change in composition across the different peatland types (Lyons and Lindo, 2020). Microbial communities in peatlands are diverse in fungi (Asemaninejad et al., 2017), and in lower proportions bacteria and archaea

(Asemaninejad et al., 2019). Higher fungal-to-bacterial (F:B) ratios found in poor fens (e.g., the SF site) where litter is more resistant are related to slow carbon and nutrient cycling rates predominantly performed by fungi (Strickland et al., 2009), while the opposite is true on the other end of this spectrum (e.g., the CF site), where bacteria outcompete fungi for labile carbon originated in vascular plants. This ‘fast-slow’ spectrum has implications for both oribatid mite community structure as well as carbon and nutrient cycling (Joergensen and Wichern 2008; Strickland and Rousk, 2010). That said, we still lack population-level studies of oribatid mite – microbial interactions.

6.1 Warming-induced responses on peatland oribatid mite communities and potential consequences for carbon and nitrogen fluxes

Climate warming is suggested as the main driver of community change in the future (after habitat loss; Sala et al., 2000), and northern systems like boreal peatlands will experience greater changes in temperature than lower latitude systems (IPCC, 2018). Temperature has direct (i.e., metabolic) and indirect effects on soil communities. While I anticipated warming to accelerate developmental rates through enhanced metabolic processes leading to increased abundance of oribatid mite immatures and small bodied-species, I observed limited evidence of this response. I also expected that the indirect effects of warming, specifically warming-induced changes in moisture, would cause no net change in species richness as increases in terrestrial oribatid mite species and decreases in semi-aquatic species balanced out. Instead, I found that warming had contrasting effects on the oribatid mite community at both peatland sites, and depended on the peatland type where increases in terrestrial oribatid mite species were likely via dispersal from surrounding forests at the SF, and reduction in species richness through losses of semi-aquatic species only occurred at the CF.

Ultimately, climate warming will alter ecological communities (Guo et al., 2018; Nelson et al., 2017; Pelini et al., 2014; Zhu et al., 2020), and this will occur in both aboveground as well as belowground for terrestrial systems. Previous warming experiments at these sites suggest shifts in plants from mosses to vascular plants (Dieleman et al., 2015; Lyons et al., 2020), with anticipated belowground effects through the processing of detritus by the soil food web. At the food web level, I observed that warming generally decreased the biomasses of invertebrates and microbial groups with consequent decreased C and N fluxes in both sites, as biomass appears to be the most important driver of fluxes (Chapter 5). Specifically, warming increased the biomass of bacteria, but decreased that of fungi so that faster C and N cycling performed by bacteria (faster energy channel; Moore and Hunt (1988)) could be a potential future consequence of climate warming. Also important are changes in plant communities under warming (Lyons et al., 2020) shown to favour higher litter quality (vascular plants over mosses), which ultimately reinforces the prediction that warming may switch peatlands from carbon sinks to carbon sources (Bragazza et al., 2016; Dieleman et al., 2015; Jassey et al., 2013; Lyons et al., 2020), or in the context of my thesis, from *Sphagnum*-dominated to *Carex*-dominated, with further changes in oribatid mite communities.

Warming-induced changes in the soil food web will alter the flux of carbon and nitrogen in boreal peatlands. The soil food web models created here are well-resolved and supported by empirical data and ecological knowledge of the response of peatland systems to experimental warming. This is novel because previous published soil food webs are limited to mostly agricultural systems (but see Koltz et al., 2018 and Potapov et al., 2019), and generally do not account for ecological changes (but see Holtkamp et al. (2011) for secondary succession on ex-arable land). In addition, given the importance of peatlands for carbon cycling (Harenda et al., 2018), I estimated the contribution of each food web node to C and N fluxes (i.e., mineralization) and I concluded that the role of invertebrates in detrital food webs is minimal, although oribatid mites were still the most important microarthropod players of C and N cycling at both SF and CF under all scenarios. However, because of their high biomass and contributions to cycling, monitoring microbial diversity may be more effective under a conservation perspective in peatlands considering bacteria and fungi were responsible for >99% of C and N mineralization in all scenarios of both fen sites. Nonetheless, oribatid mite C and N mineralization response to warming followed that of bacteria and fungi in both sites (all decreased), oribatid mites could potentially be an alternative indicator group in monitoring programs given microbes and microarthropods show the same trends, and microarthropods are relatively easy to sample. Oribatid mites have been shown as good soil quality indicators (Gergócs and Hufnagel, 2009; Lehmitz et al., 2020), although no studies have looked at them under a C and N cycling perspective in peatlands.

6.2 Study limitations and future directions

Although my peatland oribatid mite data are of high taxonomic resolution (i.e., species-level identifications) and possibly the best resolved for Canadian peatlands that is currently available, they are still local data from only two peatland sites and may not reflect the oribatid mite fauna of the entire country, although extrapolation is difficult given a lack of similar studies. Prior to Behan-Pelletier and Bissett (1994), the vast majority of peatland records were for eastern Canada and within the boreal ecozone, as are mine. The addition of records from western and Atlantic Canada and the subarctic will continue to increase the number of known peatland species, as does extensive and repeated sampling at single locations.

Sampling time is a consideration that could have affected my observed results, as seasonality affects oribatid mite species richness, abundance and community composition (Anderson, 1975; Berg, 1991; Cepeda-Pizarro et al., 1996; Haarløv, 1960; Harding, 1971). Most of the samples I collected were from late spring (June), with only one year of data examining late summer (August) communities. June samples were typically wetter (following snow melt) and preceded annual experimental treatments, thus experimental effects were ‘carry-overs’ from the previous year, potentially limiting the magnitude of response, but also perhaps mitigating treatment effects through enhanced moisture contents in June. Generally lower oribatid mite abundances are observed in late summer (Wehner et al., 2018) related to both typically dry soil conditions, but also related to their reproductive ecology. Oribatid mites are known to have overlapping generations with multiple reproductive events throughout the year, often with peak adult abundance in spring and fall (Reeves, 1969; Seniczak et al., 2019). While I only sampled once in August and am therefore not able to disentangle any seasonal effects in this sampling period, I found the strongest treatment effects in my August samples. This is likely because of the magnitude of the warming (active warming) and that I was able to sample immediately following four months of warming treatment (as opposed to beginning of next summer). That said, although my 2019 June sampling event did not demonstrate statistically significant effects, this sampling event as well as ongoing sampling (June

2020, Sept. 2020, June 2021; pers. comm. Z. Lindo) suggest changes due to warming are persistent. Future research thus should include sampling prior to and at the end of experimental warming so to distinguish short- from long-term effects on oribatid mite communities. In addition, although not always logistically feasible, sampling on a monthly basis and accounting for the plant composition at the sample level (or lack thereof, i.e., bare soil) as well as crossing oribatid mite community data with environmental information obtained at the time of sampling (e.g., soil moisture, soil temperature) will help disentangle seasonal effects from experimental effects.

The contributions of oribatid mites and other microarthropods to decomposition and nutrient cycling in soil systems are difficult to quantify. The use of energetic food web models provides a tool to quantify these contributions, but it is not without its own limitations. For instance, we lack data for key model parameters such as C:N ratio, assimilation and production rates, and death rate, especially at the species level. I used literature values for a few representative groups (e.g., de Ruiter et al., 1993; de Ruiter et al., 1994; Hunt et al., 1987) and extrapolated these physiological parameters to coarser taxonomic levels, which likely affected the calculation of carbon and nitrogen fluxes. These parameters are near impossible to measure *in situ*, and likely differ depending on the ecosystem, the time after feeding measurements are taken, and intraspecific variation (de Ruiter et al., 1993, 1994; Martinson et al., 2008; Moore and de Ruiter, 2002; Moorhead and Sinsabaugh, 2006). Determining accurate carbon use efficiencies at more refined taxonomic levels (not necessarily species-level, but accounting for important species-level traits) will enhance the resolution of soil food webs, and our understanding for carbon cycling (Frey et al., 2013).

Similarly, accurate parameterization of the soil food web is an ongoing endeavor and several recent studies have focused on soil food webs to understand carbon storage (Schmitz et al., 2017), nutrient cycling (Thoresen et al., 2021), and soil organism interactions (DeAngelis, 2016). Challenges include obtaining accurate biomass estimates for small-bodied and often cryptic species, and taxonomic resolution for taxa that span all domains of life. Biomass in this thesis, and elsewhere, was often determined with different techniques, as soil organisms span several orders of magnitude in body size. While soil organic matter (including plant litter) can be measured directly, estimating the biomass of microbes and invertebrates is performed indirectly through assays (e.g., PLFAs) or linear regression equations based on representative species-level body size. Inaccurate biomass measurements or estimates can lead to under or over estimation of C and N fluxes, as my work suggests biomass is a driving variable in energetic food web models of flux. However, food web models available in the literature share similar methodologies and thus limitations (e.g., de Ruiter et al., 1994; Holtkamp et al., 2011; Hunt et al., 1987; Koltz et al., 2018), and consequently can at least be compared across different studies.

There is currently no published soil food web resolved at the species level, which has implications for overall food web topology that may affect flux calculations. Recently, Buchkowski and Lindo (2021) using the same ecostoichiometric food web model as Chapter 5, showed that ‘lumping’ together species at the base of the food webs (e.g., fungi and bacteria) caused higher deviations in the calculation of C and N mineralization than higher trophic levels, as lower levels commonly differ in C:N ratios. Lumping species within a trophic node also ignores species-level physiological parameters such as efficiencies. Thus, greater taxonomic and autecological knowledge at the species level will help create a more accurate representation of the fate of C and N fluxes at the soil food web scale, where fewer assumptions need to be made based on the literature. Also, food webs resolved at the species level will likely depict the complexity found in soil systems better, given, for example, that non-feeding species interactions have been largely excluded from food web theory (Kéfi et al., 2012), including in this thesis.

6.3 Conclusions and significance

Peatlands are ecosystems important for carbon storage worldwide, and their conservation can be used as a nature-based climate change mitigation tool. Oribatid mites are intrinsically associated with peatlands, where they are the dominant microarthropod fauna. Oribatid mite communities in peatlands were shown to be diverse and abundant, and this thesis highlights the drivers of those communities, namely soil moisture (water table), and dominant vegetation type. Climate warming is anticipated to affect both of these drivers as peat soils become drier and vascular plants outcompete mosses. My study of two peatland sites — a nutrient-poor, *Sphagnum*-dominated fen with a lower water table and an intermediate nutrient level, *Carex*-dominated fen with a high-water table might be considered as two ends of a gradient for peatland types (National Wetlands Working Group, 1997). In most cases, climate warming showed negative effects on oribatid mites (Blankinship et al., 2011), mostly indirectly through changes in soil moisture content and/or bottom-up cascades due to changes in resource quality. I also provide support to that as peatland oribatid mite community composition was driven by interactions between temperature and moisture, but dependant on peatland type. Future climate warming, and the reduced moisture and increased vascular plant inputs, will shift oribatid mite communities into a configuration that reflects more terrestrial conditions or along the gradient of peatland types, and into systems that have higher carbon fluxes (Chapter 5).

Ultimately, individual physiologies such as metabolism, population dynamics and interactions among members of ecological communities will all be affected by climate warming with cascading consequences for carbon, energy, and nutrients cycle through ecosystems. Taking a food web approach that incorporates eco-stoichiometry, feeding efficiencies, and species interactions provides a way forward to linking these ecological levels. My food web models for two peatland sites allowed me to calculate soil C and N fluxes for future climate warming scenarios. While I was not able to incorporate temperature-metabolic relationships that are certainly important in calculations of energetic flux, my work has demonstrated that organismal biomasses dictate flux values.

The relationship between biodiversity and ecosystem functions (BEF) (Harrison et al., 2014; Hooper et al., 2005; Loreau et al., 2001) has been debated since the 1980s, with losses of biodiversity as the starting point. Local scale biodiversity dictates overall ecosystem function and corresponding ecosystem services (Thompson et al., 2018) like climate regulation. Thus, ongoing losses in biodiversity due to climate warming alongside other ecological stressors such as habitat loss, pollution, and eutrophication (Sala et al., 2000) will impact peatland carbon storage capacity. Although oribatid mites are small and their individual contributions low, their diversity and abundance allow us to use them as models for understanding BEF relationships.

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Appendices

Appendix A Updated checklist of Oribatida of Canadian peatlands.

	Previously recorded[1]	SF	CF
Family Palaeacaridae Grandjean, 1932			
Palaeacarus hystricinus Trägårdh, 1932	+	+	+
Family Brachychthoniidae Thor, 1934			
Brachychthonius bimaculatus Willmann, 1936		+	
Brachychthonius sp.			+
Eobrachychthonius latior (Berlese, 1910)		+	
Liochthonius brevis (Michael, 1888)		+	+
Liochthonius forsslundi (Hammer, 1952)	†		
Liochthonius lapponicus (Trägårdh, 1910)		+	+
Liochthonius sellnicki (Thor, 1930)		+	+
Liochthonius sp.	+		+
Poecilochthonius spiciger (Berlese, 1910)		+	+
Sellnickochthonius lydiae (Jacot, 1938)	+		
Sellnickochthonius suecicus (Forsslund, 1942)		+	+
Sellnickochthonius zelawaiensis (Berlese, 1910)		+	+
Synchthonius crenulatus (Jacot, 1938)	+	+	
Family Eniochthoniidae Grandjean, 1947			
Eniochthonius mahunkai Norton and Behan-Pelletier, 2007	†	+	+
Eniochthonius minutissimus (Berlese, 1903)	+	+	+
Family Hypochthoniidae Berlese, 1910			
Hypochthonius rufulus C.L. Koch, 1835	+	+	+
Family Trichthoniidae Lee, 1982			
Gozmanyina majestus (Marshall and Reeves, 1971)		+	
Family Gehypochthoniidae Strenzke, 1963			
Gehypochthonius rhadamanthus Jacot, 1936	†		
Family Parhypochthoniidae Grandjean, 1932			
Parhypochthonius aphidinus Berlese, 1904	+		
Family Eulohmanniidae Grandjean, 1931			
Eulohmannia ribagai (Berlese, 1910)	†		
Family Euphthiracaridae Jacot, 1930			
Acrotritia ardua (C.L. Koch, 1841)	+	+	+
Microtritia minima (Berlese, 1904)		+	
Microtritia simplex (Jacot, 1930)	†		
Family Phthiracaridae Perty, 1841			

Atropacarus striculus (C.L. Koch, 1835)	†		
Hoplophorella thoreaui (Jacot, 1930)		+	+
Hoplophthiracarus illinoisensis (Ewing, 1909)[2]	+		
Phthiracarus boresetosus Jacot, 1930		+	+
Phthiracarus globosus (C.L. Koch, 1841)	†		
Phthiracarus longulus (C.L. Koch, 1841)	†		
Phthiracarus sp.		+	+
Family Perlohmanniidae Grandjean, 1954			
Perlohmannia sp nr. *coiffaiti* Grandjean, 1961	†		
Family Crotoniidae Thorell, 1876 (incl. Camisiidae auct.)			
Camisia biurus (C.L. Koch, 1839)	+		
Camisia foveolata Hammer, 1955	†		
Camisia lapponica (Trägårdh, 1910)	†		
Camisia segnis (Hermann, 1804)	+		+
Camisia spinifer (C.L. Koch, 1835)	+		
Heminothrus longisetosus Willmann, 1925		+	
Platynothrus capillatus (Berlese, 1914)	†		
Platynothrus peltifer (CL Koch, 1839)	+		
Platynothrus punctatus (L. Koch, 1879)	†	+	
Platynothrus thori (Berlese, 1904)[3]	+		
Family Malaconothridae Berlese, 1916			
Malaconothrus mollisetosus Hammer, 1952		+	+
Tyrphonothrus foveolatus (Willmann, 1931)	†	+	
Tyrphonothrus maior (Berlese, 1910)[4]	+	+	+
Tyrphonothrus sp.	+		
Family Nanhermanniidae Sellnick, 1928			
Nanhermannia dorsalis (Banks, 1896)[5]	+	+	
Nanhermannia n. sp.	+		
Nanhermannia sp.	+		
Family Nothridae Berlese, 1896			
Nothrus anauniensis Canestrini and Fanzago, 1876	+		
Nothrus borussicus Sellnick, 1928			+
Nothrus monodactylus (Berlese, 1910)		+	+
Nothrus palustris C.L. Koch, 1839	+		
Nothrus pratensis Sellnick, 1928	†		
Nothrus silvestris Nicolet, 1855	†		
Nothrus truncatus Banks, 1895	†		
Nothrus sp.	+		
Family Trhypochthoniidae Willmann, 1931			
Mainothrus badius (Berlese, 1905)	+	+	+

Trhypochthoniellus longisetus (Berlese, 1904)	†		
Trhypochthoniellus setosus canadensis Hammer, 1952	+		+
Trhypochthonius cladonicola (Willmann, 1919)	†		
Trhypochthonius tectorum (Berlese, 1896) s.l.	+		
Trhypothchonius sp.	+		
Family Hermanniellidae Grandjean, 1934			
Hermanniella robusta Ewing, 1918	+		
Family Neoliodidae Sellnick, 1928			
Platyliodes scaliger (C.L. Koch, 1839)	+		
Family Gymnodamaeidae Grandjean, 1954			
Pleodamaeus n. sp.		+	+
Family Damaeidae Berlese, 1896			
Epidamaeus arcticolus (Hammer, 1952)	†		
Epidamaeus bakeri (Hammer, 1952)	†		
Epidamaeus gibbofemoratus (Hammer, 1955)	†		
Epidamaeus kodiakensis Hammer, 1967	†		
Family Liacaridae Sellnick, 1928			
Dorycranosus parallelus (Hammer, 1967)	†		
Family Cepheidae Berlese, 1896			
Cepheus n. sp.		+	
Eupterotegaeus ornatissimus (Berlese, 1908)		+	
Family Astegistidae Balogh, 1961			
Cultroribula divergens Jacot, 1939	†		+
Cultroribula sp.	+		
Family Peloppiidae Balogh, 1943			
Ceratoppia bipilis (Hermann, 1804)	+	+	+
Ceratoppia quadridentata (Haller, 1882)	†		
Ceratoppia quadridentata arctica Hammer, 1955	+	+	
Ceratoppia sexpilosa Willmann, 1938	†		
Family Carabodidae C.L. Koch, 1837			
Carabodes granulatus Banks, 1895	†	+	+
Carabodes labyrinthicus (Michael, 1879)	†		
Carabodes polyporetes Reeves, 1991	†	+	
Carabodes radiatus Berlese, 1916	†		
Family Oppiidae Grandjean, 1951			
Discoppia sp.		+	
Lasiobelba (*Antennoppia*) *rigida* (Ewing, 1909)	†		
Lauroppia maritima (Willmann, 1929)[6]	†		
nr. *Lauroppia* sp.		+	
Moritzoppia nr. *clavigera* (Hammer, 1952)		+	

Oppiella nova (Oudemans, 1902)	+	+	+
Oppiella (*Moritzoppia*) *translamellata* (Willmann, 1923)[7]	†		
Subiasella (*Lalmoppia*) *maculata* (Hammer, 1952)	†		
Family Quadroppiidae Balogh, 1983			
Quadroppia quadricarinata (Michael, 1885)	+	+	+
Quadroppia skookumchucki Jacot, 1939	†		
Family Thyrisomidae Grandjean, 1954			
Pantelozetes sp.[8]	†		
Pantelozetes alpestris (Willmann, 1929)	†		
Family Suctobelbidae Jacot, 1938			
Allosuctobelba sp. 1		+	
Allosuctobelba sp. 2		+	
Suctobelbella (*S.*) *arcana* Moritz, 1970	†	+	+
Suctobelbella hammerae (Krivolutsky, 1965)	†		
Suctobelbella hurshi Jacot, 1937		+	+
Suctobelbella laxtoni Jacot, 1937		+	+
Suctobelbella nr. *longirostris* (Forsslund, 1941)	†	+	
Suctobelbella palustris (Forsslund, 1953)		+	+
Suctobelbella nr. *palustris* (Forsslund, 1953)	†		
Suctobelbella nr. *sarekensis* (Forsslund, 1941)			+
Suctobelbella sp. 1		+	+
Suctobelbella sp. 2		+	+
Suctobelbella sp. 3		+	+
Suctobelbella sp. 4		+	+
Suctobelbella sp. 5		+	
Suctobelbella spp.	+		
Family Tectocepheidae Grandjean, 1954			
Tectocepheus sarekensis Trägårdh, 1910	†		
Tectocepheus velatus Trägårdh, 1905	+	+	+
Family Caleremaeidae Grandjean, 1965			
Veloppia pulchra Hammer, 1955	†		
Family Hydrozetidae Grandjean, 1954			
Hydrozetes lacustris (Michael, 1882)	†		
Hydrozetes octosetosus Willmann, 1931	†		
Hydrozetes sp.	+		
Family Limnozetidae Grandjean, 1954			
Limnozetes atmetos Behan-Pelletier, 1989	+		
Limnozetes borealis Behan-Pelletier, 1989	+		
Limnozetes canadensis Hammer, 1952	+		
Limnozetes ciliatus (Schrank, 1803)	+		

Limnozetes guyi Behan-Pelletier, 1989	+	+	+
Limnozetes latilamellatus Behan-Pelletier, 1989	+		
Limnozetes lustrum Behan-Pelletier, 1989	+		
Limnozetes onondaga Behan-Pelletier, 1989			+
Limnozetes palmerae Behan-Pelletier, 1989	+		
Limnozetes sp.	+		
Family Ameronothridae Vitzthum, 1943			
Ameronothrus sp.	+		
Family Tegeocranellidae Balogh and Balogh, 1988			
Tegeocranellus muscorum Behan-Pelletier, 1997	†		
Family Cymbaeremaeidae Sellnick, 1928			
Scapheremaeus palustris (Sellnick, 1924)	+		
Family Phenopelopidae Petrunkevich, 1955			
Eupelops septentrionalis (Trägårdh, 1910)	+	+	
Propelops n. sp.		+	+
Family Unduloribatidae Kunst, 1971			
Unduloribates dianae Behan-Pelletier and Walter, 2009		+	
Family Achipteriidae Thor, 1929			
Achipteria coleoptrata (Linnaeus, 1758)	+	+	
Anachipteria sp.		+	+
Parachipteria nivalis (Hammer, 1952)	+		
Parachipteria travei Nevin, 1976	†		
Family Tegoribatidae Grandjean, 1954			
Tectoribates borealis Behan-Pelletier and Walter, 2013	†		
Tegoribates americanus Hammer, 1958	+		
Family Haplozetidae Grandjean, 1936			
Peloribates canadensis Hammer, 1952	†		
Peloribates pilosus Hammer, 1952	+		
Protoribates capucinus Berlese, 1908	†		
Protoribates haughlandae Walter and Latonas, 2013	†		
Protoribates lophotrichus (Berlese, 1904)		+	+
Protoribates sp.[9]	+		
Rostrozetes ovulum (Berlese 1908)[10]	+		
Family Mochlozetidae Grandjean, 1960			
Podoribates longipes (Berlese, 1887)	+		+
Family Oribatulidae Thor, 1929			
Lucoppia nr. *apletosa* (Higgins and Woolley, 1975)		+	+
Oribatula tibialis (Nicolet, 1855)	+	+	
Phauloppia boletorum (Ewing, 1913)	+	+	
Zygoribatula bulanovae Kulijew, 1961	+		

Family Parakalummidae Grandjean, 1936			
Neoribates aurantiacus (Oudemans, 1914)	+		
Family Scheloribatidae Grandjean, 1933			
Dometorina plantivaga (Berlese, 1895)	+		
Liebstadia humerata Sellnick, 1928		+	
Liebstadia similis Michael, (1888)	†		
Scheloribates laevigatus (C.L. Koch, 1835)	+		
Scheloribates pallidulus (C.L. Koch, 1841)	+	+	
Scheloribates sp.	†		
Family Ceratozetidae Jacot, 1925			
Ceratozetes parvulus Sellnick, 1922	+		+
Dentizetes ledensis Behan-Pelletier, 2000	†		
Diapterobates humeralis (Hermann, 1804)	+		
Diapterobates notatus (Thörell, 1871)	+		
Fuscozetes bidentatus Banks 1895	+		
Fuscozetes fuscipes (C.L. Koch, 1844)	+		
Ghilarovizetes longisetosus (Hammer, 1952)	†		
Lepidozetes singularis Berlese, 1910	+	+	
Melanozetes tanana Behan-Pelletier, 1986	†		
Neogymnobates luteus (Hammer, 1955)	†		
Svalbardia paludicola Thor, 1930	†		
Trichoribates copperminensis Hammer, 1952	†		
Trichoribates polaris Hammer, 1953	†		
Trichoribates n. sp.		+	
Trichoribates sp.	+		
Family Punctoribatidae Thor, 1937			
Mycobates incurvatus Hammer, 1952	†		
Mycobates yukonensis Behan-Pelletier, 1994	†		
Punctoribates palustris (Banks, 1895)	†	+	+
Family Zetomimidae Shaldybina, 1966			
Heterozetes aquaticus (Banks, 1895)	†		
Heterozetes minnesotensis (Ewing, 1913)	†		
Naiazetes n. sp.			+
Zetomimus cooki Behan-Pelletier and Eamer, 2003	†		
Zetomimus francisi (Habeeb, 1974)	†		
Zetomimus setosus (Banks, 1895)	†		
Family Galumnidae Jacot, 1925			
Pergalumna emarginata (Banks, 1895)	+	+	+
Pilogalumna sp.		+	+

[1] Original record by Behan-Pelletier and Bissett (1994) denoted by + with updates from Behan-Pelletier and Lindo (2019) denoted by †

[2] as *Hoplophthiracarus paludis* Jacot, 1938

[3] as *Heminothrus thori* (Berlese, 1904)

[4] as *Trimalaconothrus novus* (Sellnick, 1921)

[5] probably *Nanhermannia coronata* Berlese, 1913

[6] as *Oppiella maritima* (Willmann, 1929)

[7] as *Oppiella translamellata* (Willmann, 1923)

[8] as *Gemmazetes* sp.

[9] as *Xylobates* sp.

[10] as *Rostrozetes foveolatus* Sellnick, 1925

Appendix B The %C, %N, and C:N values for fresh plant material collected from each species observed at the *Sphagnum*-dominated peatland in northern Ontario, Canada.

Values are means ± standard error for three replicate plants. Values for *Carex* spp. are averaged over *Carex disperma* Dewey and *Carex magellanica* Lam./*Carex oligosperma* Michx, whereas values for *Sphagnum* spp. are averaged over *S. angustifolium* (C.E.P. Jensen ex Russow), *S. fuscum* (Schimp.) Klinggr. and *S. magellanicum* Brid. Adapted from Lyons (2020).

Plant	%C	%N	C:N
Carex spp.	44.06 ± 0.09	1.48 ± 0.05	29.78 ± 1.08
Chamaedaphne calyculata (L.) Moench	52.07 ± 0.04	1.23 ± 0.07	42.79 ± 2.44
Sphagnum spp.	44.60 ± 0.20	0.95 ± 0.02	47.06 ± 1.50

Appendix C List of invertebrates other than oribatid mites and their average abundance sampled from hummock-hollow systems.

Abundance values are averages (# indiv. per g dry weight litter) (± SE) for hummocks and hollows.

Group	Morphospecies	Hummock	Hollow
Acari	Prostigmata	0.80 ± 0.55	1.97 ± 0.60
Acari	Mesostigmata	0.77 ± 0.53	3.33 ± 1.51
Acari	Astigmata	0	0.50 ± 0.34
Collembola	Onychiuridae sp. 1	0.25 ± 0.25	24.38 ± 7.73
Collembola	Onychiuridae sp. 2	0	26.56 ± 11.94
Collembola	Hypogastruridae sp. 1	0.69 ± 0.49	19.17 ± 9.58
Collembola	Poduromorpha sp. 1	0.40 ± 0.40	0.64 ± 0.35
Collembola	Sminthuridae sp. 1	0	0.14 ± 0.14
Collembola	Tomoceridae sp. 1	0	0.18 ± 0.18
Collembola	Poduromorpha sp. 2	0.77 ± 0.53	0.38 ± 0.27
Arthropoda	Other microarthropods*	2.07 ± 0.95	4.46 ± 2.01

* Includes small spiders and insect larvae of the orders Coleoptera and Diptera (mostly chironomids)

Appendix D List of oribatid mite species (Acari: Oribatida) and their average abundance sampled from hummock-hollow systems.

Species are listed in taxonomic order. Abundance values are averages (# indiv. per g dry weight litter) (± SE) for hummocks and hollows.

Code	Species	Hummock	Hollow
Emahu	*Eniochthonius mahunkai*	0	0.59 ± 0.32
Phth	*Phthiracarus* sp.	0	0.61 ± 0.33
Hoplo	*Hoplophorella thoreaui**	0	2.24 ± 1.15
Malaco	*Malaconothrus mollisetosus*	0.38 ± 0.27	8.79 ± 3.94
Tmaior	*Tyrphonothrus maior*	0	0.38 ± 0.38
Tfoveo	*Tyrphonothrus foveolatus*	0	3.73 ± 2.61
Trhyp	*Trhypochthonius tectorum*	0.14 ± 0.14	0
Maino	*Mainothrus badius*	0.15 ± 0.15	0
Nanh	*Nanhermannia dorsalis*	0	2.39 ± 1.23
Tecto	*Tectocepheus velatus*	0	5.46 ± 1.56
Onova	*Oppiella nova*	0	6.40 ± 3.58
Sucto	*Suctobelbella* spp.	0.40 ± 0.29	0.80 ± 0.55
Lguyi	*Limnozetes guyi*	0.13 ± 0.13	22.76 ± 20.26
Lsing	*Lepidozetes singularis*	0.26 ± 0.26	0
Lepido	*Lepidozetes* sp.	0.57 ± 0.43	2.49 ± 2.49
Schelo	*Scheloribates pallidulus*	0	0.28 ± 0.19
Ppalus	*Punctoribates palustris*	0	0.55 ± 0.30

* The genus *Hoplophorella* needs major taxonomic revision, and it is possible than more than one species was identified as *Hoplophorella thoreaui*.

Appendix E Temperature regimes in hummock-hollow system in a *Sphagnum*-dominated peatland over 12-month litterbag study.

Monthly minimum, average and maximum temperatures are shown in Celsius. Relative humidity was expressed as percentage of the amount of water vapor present needed for saturation. A single Hobo datalogger was placed in a representative hummock and hollow to track surface temperature and relative humidity every half an hour for the year.

Hummock						
	Temperature			**Relative Humidity**		
	min	**average**	**max**	**min**	**average**	**max**
15-Aug	-0.3	14.7	29.9	61.1	95.1	100
15-Sep	-3.2	12.9	29.8	61	97.3	100
15-Oct	-6.4	2.7	22	88	99.4	100
15-Nov	-3.2	1.8	12.3	87.3	98.1	100
15-Dec	-5.5	-1.1	2.5	75.6	97.1	100
16-Jan	-4.1	-1.5	-0.1	100	100	100
16-Feb	-3.4	-1.6	-0.6	100	100	100
16-Mar	-2.8	-0.8	0	100	100	100
16-Apr	-8.3	1.1	17	83	99.7	100
16-May	-5	9.8	27.9	82.6	99.1	100
16-Jun	0.5	15	33.8	59.9	97.9	100
16-Jul	3	17.5	31.6	1	65.4	100
16-Aug	4.5	18	30.2	1	61.1	96.633

Hollow						
	Temperature			**Relative Humidity**		
	min	**average**	**max**	**min**	**average**	**max**
15-Aug	-0.1	14.2	27.2	73.1	97.1	100
15-Sep	-4.9	11.9	27.2	54.3	96.8	100
15-Oct	-7.9	2.1	16.5	80.6	99.1	100
15-Nov	-4	1.8	11.9	88.4	99.9	100
15-Dec	-2.5	0	1.6	100	100	100
16-Jan	-1	-0.1	0.2	100	100	100
16-Feb	-0.2	0	0.1	100	100	100
16-Mar	-0.1	0	0.1	100	100	100
16-Apr	-8.6	0.6	18	52.2	97.7	100
16-May	-6.6	8.9	28.9	43.5	91.6	100
16-Jun	-0.6	13.6	34.3	56.6	96.2	100
16-Jul	2	15.8	30.2	63.8	98	100
16-Aug	3.6	16.4	28.9	55.6	90.8	100

Appendix F Oribatid mite species sampled from the SF and CF and included in dbRDA analysis based on their axis loadings.

These represent 50% of the species in each fen (SF: n = 34; CF: n = 24). Species are listed in decreasing order of by the sum of their absolute total scores for axes CAP1 and CAP2.

***Sphagnum*-dominated fen**		***Carex*-dominated fen**	
Emahu	*Eniochthonius mahunkai*	Tmaior	*Tyrphonothrus maior*
Onova	*Oppiella nova*	Maino	*Mainothrus badius*
Malaco	*Malaconothrus mollisetosus*	Malaco	*Malaconothrus mollisetosus*
Liolapp	*Liochthonius lapponicus*	Lguyi	*Limnozetes guyi*
Phth	*Phthiracarus* sp.	Lonond	*Limnozetes onondaga*
Suctohur	*Suctobelbella hurshi*	Onova	*Oppiella nova*
Quadro	*Quadroppia quadricarinata*	Sucto3	*Suctobelbella* sp. 3
Tecto	*Tectocepheus velatus*	Liosell	*Liochthonius sellnicki*
Liobre	*Liochthonius brevis*	Anach	*Anachipteria* sp.
Sucto3	*Suctobelbella* sp. 3	Cparvu	*Ceratozetes parvulus*
Gozm	*Gozmanyina majestus*	Sucto1	*Suctobelbella* sp. 1
Sucpalus	*Suctobelbella palustris*	Tecto	*Tectocepheus velatus*
Nothmon	*Nothrus monodactylus*	Ppalus	*Punctoribates palustris*
Perga	*Pergalumna emarginata*	Sucto4	*Suctobelbella* sp. 4
Sucto1	*Suctobelbella* sp. 1	Sucpalus	*Suctobelbella palustris*
Sellzel	*Sellnickochthonius zelawaiensis*	Suctohur	*Suctobelbella hurshi*
Sucto4	*Suctobelbella* sp. 4	Liolapp	*Liochthonius lapponicus*
Maino	*Mainothrus badius*	Perga	*Pergalumna emarginata*
Eminut	*Eniochthonius minutissimus*	Liobre	*Liochthonius brevis*
Sellsuec	*Sellnickochthonius suecicus*	Sellsuec	*Sellnickochthonius suecicus*
Aardua	*Acrotritia ardua*	Brach	*Brachychthonius* sp.
Suctarc	*Suctobelbella* (*S.*) *arcana*	Phth	*Phthiracarus* sp.
Hoplo	*Hoplophorella thoreaui*	Suctarc	*Suctobelbella* (*S.*) *arcana*
Tmaior	*Tyrphonothrus maior*	Naiaz	*Naiazetes* n. sp.
Ppalus	*Punctoribates palustris*		
Hypo	*Hypochthonius rufulus*		
Synch	*Synchthonius crenulatus*		
Schelo	*Scheloribates pallidulus*		
Lauro	nr. *Lauroppia* sp.		
Cargra	*Carabodes granulatus*		
Palaec	*Palaeacarus hystricinus*		
Poecspi	*Poecilochthonius spiciger*		
Nanh	*Nanhermannia dorsalis*		
Platyn	*Platynothrus punctatus*		

Appendix G List of oribatid mite species (Acari: Oribatida) and their average abundance sampled from control and warmed plots in both fens.

Species are listed in taxonomic order. Abundance values are averages (# indiv. per g dry weight peat) (± SE) for treatment levels in each site.

	Sphagnum-dominated fen		*Carex*-dominated fen	
Species	Control	Warming	Control	Warming
Family Palaeacaridae				
Palaeacarus hystricinus	0.016 ± 0.011	0.032 ± 0.020	0.006 ± 0.006	0.010 ± 0.010
Family Brachychthoniidae				
Brachychthonius bimaculatus	0.005 ± 0.005	0.036 ± 0.018	0	0
Brachychthonius sp.	0	0	0.006 ± 0.004	0.007 ± 0.007
Eobrachychthonius latior	0	0.009 ± 0.009	0	0
Liochthonius brevis	0.984 ± 0.145	2.157 ± 0.383	0.043 ± 0.020	0.026 ± 0.014
Liochthonius lapponicus	3.924 ± 0.643	5.412 ± 1.019	0.033 ± 0.017	0.008 ± 0.005
Liochthonius sellnicki	0.038 ± 0.017	0.032 ± 0.20	0.378 ± 0.094	0.385 ± 0.099
Liochthonius sp.	0	0	0	0.003 ± 0.003
Poecilochthonius spiciger	0.018 ± 0.010	0.029 ± 0.016	0.007 ± 0.005	0.061 ± 0.007
Sellnickochthonius suecicus	0.279 ± 0.161	0.114 ± 0.050	0.050 ± 0.027	0.115 ± 0.063
Sellnickochthonius zelawaiensis	0.496 ± 0.194	0.413 ± 0.117	0.004 ± 0.004	0
Synchthonius crenulatus	0.291 ± 0.087	0.368 ± 0.096	0	0
Family Eniochthoniidae				
Eniochthonius mahunkai	3.867 ± 0.653	5.064 ± 1.119	0.003 ± 0.003	0
Eniochthonius minutissimus	0.432 ± 0.125	0.993 ± 0.271	0.002 ± 0.002	0
Family Hypochthoniidae				
Hypochthonius rufulus	0.071 ± 0.023	0.170 ± 0.046	0.004 ± 0.004	0.004 ± 0.004
Family Trichthoniidae				
Gozmanyina majestus	1.187 ± 0.416	1.078 ± 0.264	0	0
Family Euphthiracaridae				
Acrotritia ardua	0.440 ± 0.053	0.345 ± 0.067	0	0
Microtritia minima	0.020 ± 0.010	0.027 ± 0.010	0	0
Family Phthiracaridae				
*Hoplophorella thoreaui**	0.275 ± 0.072	0.271 ± 0.076	0	0
Phthiracarus boresetosus	0.024 ± 0.015	0.024 ± 0.012	0.006 ± 0.006	0
Phthiracarus sp.	2.098 ± 0.329	1.730 ± 0.413	0.034 ± 0.020	0.014 ± 0.007
Family Crotoniidae				
Camisia segnis	0	0	0.004 ± 0.004	0
Heminothrus longisetosus	0.004 ± 0.004	0.004 ± 0.004	0	0
Platynothrus punctatus	0.092 ± 0.028	0.094 ± 0.027	0	0
Family Malaconothridae				
Malaconothrus mollisetosus	4.776 ± 0.644	3.816 ± 0.553	1.036 ± 0.419	0.905 ± 0.501
Tyrphonothrus foveolatus	0	0.052 ± 0.052	0	0
Tyrphonothrus maior	0.005 ± 0.005	0.308 ± 0.284	2.915 ± 0.339	3.162 ± 0.479
Family Nanhermanniidae				
Nanhermannia dorsalis	0.063 ± 0.027	0.104 ± 0.047	0	0

Family Nothridae				
Nothrus borussicus	0	0	0	0.004 ± 0.004
Nothrus monodactylus	1.021 ± 0.268	0.711 ± 0.173	0	0
Family Trhypochthoniidae				
Mainothrus badius	1.471 ± 0.320	0.752 ± 0.155	2.004 ± 0.543	1.771 ± 0.424
Trhypochthoniellus setosus canadensis	0	0	0	0.004 ± 0.004
Family Gymnodamaeidae				
Pleodamaeus n. sp.	0.005 ± 0.005	0	0	0
Family Cepheidae				
Eupterotegaeus ornatissimus	0	0.004 ± 0.004	0	0
Family Astegistidae				
Cultroribula divergens	0	0	0	0.006 ± 0.006
Family Peloppiidae				
Ceratoppia bipilis	0.004 ± 0.004	0.007 ± 0.007	0.011 ± 0.005	0.011 ± 0.005
Ceratoppia quadridentata	0	0.010 ± 0.010	0	0
Family Carabodidae				
Carabodes granulatus	0.029 ± 0.017	0.049 ± 0.017	0	0
Carabodes polyporetes	0	0.012 ± 0.009	0	0
Family Oppiidae				
Discoppia sp.	0	0.008 ± 0.008	0	0
nr. *Lauroppia* sp.	0.099 ± 0.099	0.006 ± 0.006	0	0
Moritzoppia nr. *clavigera*	0.005 ± 0.005	0	0	0
Oppiella nova	3.380 ± 0.724	3.897 ± 0.505	0.626 ± 0.180	0.146 ± 0.040
Family Quadroppiidae				
Quadroppia quadricarinata	0.791 ± 0.293	1.480 ± 0.336	0.007 ± 0.005	0.016 ± 0.007
Family Suctobelbidae				
Allosuctobelba sp.1	0.021 ± 0.012	0.055 ± 0.032	0	0
Suctobelbella (S.) *arcana*	0.198 ± 0.058	0.192 ± 0.071	0.003 ± 0.003	0.020 ± 0.012
Suctobelbella hurshi	1.615 ± 0.333	1.921 ± 0.311	0.036 ± 0.011	0.048 ± 0.015
Suctobelbella laxtoni	0.027 ± 0.014	0.006 ± 0.006	0.008 ± 0.006	0.020 ± 0.017
Suctobelbella nr. *longirostris*	0.029 ± 0.018	0.055 ± 0.032	0	0
Suctobelbella palustris	0.586 ± 0.142	0.672 ± 0.126	0.151 ± 0.044	0.169 ± 0.045
Suctobelbella nr. *sarekensis*	0	0	0.010 ± 0.007	0.006 ± 0.006
Suctobelbella sp. 1	0.378 ± 0.073	0.311 ± 0.073	0.096 ± 0.030	0.060 ± 0.017
Suctobelbella sp. 2	0	0.007 ± 0.007	0	0.007 ± 0.005
Suctobelbella sp. 3	2.435 ± 0.358	1.714 ± 0.272	0.121 ± 0.028	0.148 ± 0.048
Suctobelbella sp. 4	1.291 ± 0.179	1.263 ± 0.142	0.066 ± 0.019	0.066 ± 0.023
Suctobelbella sp. 5	0.057 ± 0.020	0.058 ± 0.025	0	0
Family Tectocepheidae				
Tectocepheus velatus	5.577 ± 0.756	4.594 ± 0.606	0.303 ± 0.130	0.095 ± 0.026
Family Limnozetidae				
Limnozetes guyi	0.022 ± 0.017	0	1.082 ± 0.381	0.827 ± 0.372
Limnozetes onondaga	0	0	0.639 ± 0.344	0.229 ± 0.102
Family Phenopelopidae				
Eupelops septentrionalis	0.004 ± 0.004	0	0	0

Propelops n. sp.	0	0.009 ± 0.009	0	0
Family Unduloribatidae				
Unduloribates dianae	0.005 ± 0.005	0	0	0
Family Achipteriidae				
Achipteria coleoptrata	0	0.004 ± 0.004	0	0
Anachipteria sp.	0.009 ± 0.009	0.004 ± 0.004	0.450 ± 0.094	0.373 ± 0.058
Family Haplozetidae				
Protoribates lophotrichus	0.339 ± 0.082	0.307 ± 0.079	0.004 ± 0.004	0
Family Mochlozetidae				
Podoribates longipes	0	0	0.005 ± 0.005	0
Family Oribatulidae				
Lucoppia nr. *apletosa*	0	0.013 ± 0.008	0	0
Phauloppia boletorum	0	0.004 ± 0.004	0	0
Family Scheloribatidae				
Liebstadia humerata	0.027 ± 0.012	0.025 ± 0.018	0	0
Scheloribates pallidulus	0.171 ± 0.042	0.093 ± 0.034	0	0
Family Ceratozetidae				
Ceratozetes parvulus	0	0	0.274 ± 0.075	0.162 ± 0.043
Lepidozetes singularis	0.010 ± 0.007	0.026 ± 0.013	0	0
Trichoribates n. sp.	0.006 ± 0.006	0.031 ± 0.031	0	0
Family Punctoribatidae				
Punctoribates palustris	0.407 ± 0.084	0.505 ± 0.126	0.318 ± 0.085	0.175 ± 0.041
Family Zetomimidae				
Naiazetes n. sp.	0	0	0.020 ± 0.012	0
Family Galumnidae				
Pergalumna emarginata	0.279 ± 0.073	0.358 ± 0.106	0.021 ± 0.011	0.022 ± 0.011
Pilogalumna sp.	0	0.010 ± 0.007	0	0.003 ± 0.003
Immatures	58.471 ± 8.592	43.642 ± 4.575	11.041 ± 1.767	9.226 ± 0.941
Adults	39.705 ± 2.700	41.882 ± 2.918	10.786 ± 1.573	9.087 ± 1.144

* The genus *Hoplophorella* needs major taxonomic revision, and it is possible that more than one species was identified as *Hoplophorella thoreaui*.

Appendix H Taxonomic groups included in nodes of food web models for a *Sphagnum*-dominated fen and a *Carex*-dominated fen in Northern Ontario.

Food web node	Taxonomic groups included
Predatory mites	e.g., Bdellidae, Cunaxidae, Rhagidiidae, Trombidiidae, Ascidae, Zerconidae, Laelapidae, Parholaspididae, Blattisociidae and Ologamasidae
Nematode-feeding mites	Zerconidae
Spiders	all species
Pseudoscorpions	all species
Fungivorous prostigmatid mites	e.g., Tydeidae, Heterostigmatina, Eupodidae, Tarsonemidae
Astigmatid mites	all species
Edible oribatid mites	*Palaeacarus hystricinus* Trägårdh, 1932 *Brachychthonius bimaculatus* *Brachychthonius* sp. *Eobrachychthonius latior* *Liochthonius brevis* (Michael, 1888) *Liochthonius lapponicus* (Trägårdh, 1910) *Liochthonius sellnicki* (Thor, 1930) *Liochthonius* sp. *Poecilochthonius spiciger* (Berlese, 1910) *Sellnickochthonius suecicus* (Forsslund, 1942) *Sellnickochthonius zelawaiensis* (Berlese, 1910) *Synchthonius crenulatus* (Jacot, 1938) *Gozmanyina majestus* (Marshall and Reeves, 1971) *Malaconothrus mollisetosus Hammer, 1952* *Discoppia sp.* nr. *Lauroppia* sp. *Moritzoppia* nr. *clavigera* (Hammer, 1952) *Oppiella nova* (Oudemans, 1902) *Quadroppia quadricarinata* (Michael, 1885) *Suctobelbella (S.) arcana* Moritz, 1970 *Suctobelbella hurshi* Jacot *Suctobelbella laxtoni* Jacot, 1937

	Suctobelbella nr. *longirostris* (Forsslund, 1941)
	Suctobelbella palustris (Forsslund, 1953)
	Suctobelbella nr. *sarekensis* (Forsslund, 1941)
	Suctobelbella sp.1
	Suctobelbella sp.2
	Suctobelbella sp.3
	Suctobelbella sp.4
	Suctobelbella sp.5
	Tectocepheus velatus Trägårdh, 1905
Non-edible oribatid mites	*Eniochthonius mahunkai* Norton and Behan-Pelletier, 2007
	Eniochthonius minutissimus (Berlese, 1903)
	Hypochthonius rufulus C.L. Koch, 1835
	Acrotritia ardua (C.L. Koch, 1841)
	Microtritia minima (Berlese, 1904)
	Hoplophorella thoreaui
	Phthiracarus boresetosus Jacot, 1930
	Phthiracarus sp.
	Camisia segnis (Hermann, 1804)
	Heminothrus longisetosus Willmann, 1925
	Platynothrus punctatus (L. Koch, 1879)
	Tyrphonothrus foveolatus (Willmann, 1931)
	Tyrphonothrus maior (Berlese, 1910)
	Nanhermannia dorsalis (Banks, 1896)
	Nothrus borussicus Sellnick, 1928
	Nothrus monodactylus (Berlese, 1910)
	Mainothrus badius (Berlese, 1905)
	Trhypochthoniellus setosus canadensis Hammer, 1952
	Pleodamaeus n. sp.
	Cepheus n. sp.
	Eupterotegaeus ornatissimus (Berlese, 1908)
	Cultroribula divergens Jacot, 1939
	Ceratoppia bipilis (Hermann, 1804)
	Ceratoppia quadridentata arctica Hammer, 1955
	Carabodes granulatus Banks, 1895
	Carabodes polyporetes Reeves, 1991
	Allosuctobelba sp.1
	Allosuctobelba sp.2
	Limnozetes guyi Behan-Pelletier, 1989
	Limnozetes onondaga Behan-Pelletier, 1989
	Eupelops septentrionalis (Trägårdh, 1910)

	Propelops n. sp.
	Unduloribates dianae Behan-Pelletier and Walter, 2009
	Achipteria coleoptrata (Linnaeus, 1758)
	Anachipteria sp.
	Protoribates lophotrichus (Berlese, 1904)
	Podoribates longipes (Berlese, 1887)
	Lucoppia nr. *apletosa* (Higgins and Woolley, 1975)
	Oribatula tibialis (Nicolet, 1855)
	Phauloppia boletorum (Ewing, 1913)
	Liebstadia cf. *humerata* Sellnick, 1928
	Scheloribates pallidulus (C.L. Koch, 1841)
	Ceratozetes parvulus Sellnick, 1922
	Lepidozetes singularis Berlese, 1910
	Trichoribates n. sp.
	Punctoribates palustris (Banks, 1895)
	Naiazetes n. sp.
	Pergalumna emarginata (Banks, 1895)
	Pilogalumna sp.
Springtails	Hypogastruridae (four spp.)
	Isotomidae (six spp.)
	Sminthuridae (eight spp.)
	Onychiuridae (five spp.)
	Entomobryidae (five spp.)
	Tomoceridae (two spp.)
Predatory nematodes	all species
Bacterivorous nematodes	all species
Fungivorous nematodes	all species
Omnivorous nematodes	all species
Protists	Ciliates (three spp.)
	Rotifers (five spp.)
	Testate Amoebae (14 spp.)
Bacteria	Anaerobic Bacteria
	Gram+ Bacteria
	Gram- Bacteria

	Actinomycete Bacteria
Fungi	AM Fungi Fungi
Low quality litter	Low quality litter Soil organic carbon
High quality litter	High quality litter Soil organic carbon

Appendix I Summarized biomasses of the 12 food web models.

	Invertebrate biomass ($g\ C / m^2$)	**Living organisms' biomass ($g\ C / m^2$)**
$SF_{ambient}$	0.559	95.302
$SF_{ambient}$ - no oribatid mites	0.524	95.267
$SF_{passive}$	0.234	80.959
$SF_{passive}$ - no oribatid mites	0.210	80.935
SF_{active}	0.627	67.338
SF_{active} - no oribatid mites	0.591	67.302
$CF_{ambient}$	0.175	65.551
$CF_{ambient}$ - no oribatid mites	0.164	65.541
$CF_{passive}$	0.074	60.141
$CF_{passive}$ - no oribatid mites	0.065	60.131
CF_{active}	0.023	54.779
CF_{active} - no oribatid mites	0.018	54.775

Curriculum Vitae

Carlos Barreto

Post-secondary Education

08/2016 – 10/2021	**Ph.D. Biology** University of Western Ontario
08/2008 – 12/2012	**B.Sc. Biological Sciences** Federal University of Ouro Preto

Honours and Awards

2021	CSEE Excellence in PhD Research (Runner-up)
2021	CSEE BIPOC Foundational Research Microgrant
2021	Robert and Ruth Lumsden Graduate Fellowship in Science, Faculty of Science, Western University
2021	Travel Subsidy, Society of Graduate Students, Western University
2020	J.D. Detwiler Award, Biology Department, Western University
2020	Outstanding Student Presentation, First Place, Acarological Society of America Meeting
2020	Danks Scholarship, Entomological Society of Canada
2020	Travel Subsidy, Society of Graduate Students, Western University
2020	CSEE BIPOC Spotlight Library Microgrant
2020	Mitacs Research Training Award
2020	Western Summer 2020 Student Internship
2020	Abstract Award, Acarological Society of America
2020	Entomological Society of Canada International Congress of Entomology (ICE) Travel Award, Entomological Society of Canada
2019	Travel Subsidy, Society of Graduate Students, Western University
2019	Dr. Lloyd M. Dosdall Memorial Scholarship, Entomological Society of Canada
2019	Science International Engagement Fund Award, Faculty of Science and Science International at Western University
2019	Mitacs Globalink Research Award
2019	Faculty of Science Graduate Teaching Award, Masters of Environmental Science Program, Western University
2019	Travel Subsidy, Society of Graduate Students, Western University
2018	Dr. Rene R. Roth Memorial Award, Biology Department, Western University

2018	Harry Hoogstraal Memorial Fellowship for the Acarology Summer Program, Ohio State University
2018	Graduate Student Travel Award, Biology Department , Western University
2018	Travel Student Award Grant, Acarological Society of America
2017	Travel Subsidy, Public Service Alliance of Canada Local 610, Western University
2017	Travel Subsidy, Society of Graduate Students, Western University
2017	Graduate Student Travel Award, Biology Department, Western University

Publications

Barreto, C., Branfireun, B.A., McLaughlin, J.W., Lindo, Z. 2021. Responses of oribatid mites to warming in boreal peatlands depend on fen type. Pedobiologia 89:150772, DOI: 10.1016/j.pedobi.2021.150772

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Meehan, M.L., **Barreto**, C., Turnbull, M.S., Bradley, R.L., Bellenger, J-P., Darnajoux, R., Lindo, Z. 2020. Response of soil fauna to simulated global change factors depends on ambient climate conditions. Pedobiologia 83:150672, DOI: 10.1016/j.pedobi.2020.150672

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Barreto, L., **Barreto**, C. (*under review*). Perceptions of primary and middle school students on caves and possibilities for Environmental Education. Holos.

Editorial and reviewer activities

Editorial Board Member of Pedobiologia — Journal of Soil Ecology

Guest Editor for a Special Issue on Response of Soil Biodiversity to Global Change in Pedobiologia — Journal of Soil Ecology

Reviewer for Ecology, Écoscience, Ecosystems, Experimental and Applied Acarology, Insect Conservation and Diversity, PeerJ, Soil & Tillage Research, Soil Organisms

Conference presentations

*indicates primary speaker/presenter

37. **Barreto***, C., Branfireun, B.A., McLaughlin, J.W., Lindo, Z. 2021. Responses of oribatid mites to warming in boreal peatlands depend on fen type. Entomological Society of Canada meeting. Online oral presentation.

36. **Barreto***, C., Fabiano-da-Silva, W. 2021. Arachnological studies presented at the Brazilian Ecological Society meetings between 2003–2019. XV Congresso de Ecologia do Brasil. Online oral presentation.

35. Barroso*, G., **Barreto**, C. 2021. Exploring the use of predatory mites for the control of *Raoiella indica* Hirst (Acari: Prostigmata: Tenuipalpidae) in Southern Brazil. XV Congresso de Ecologia do Brasil. Online oral presentation.

34. **Barreto***, C., Branfireun, B.A., McLaughlin, J. Lindo, Z. 2021. Responses of oribatid mites to warming in boreal peatlands depend on fen type. Canadian Society for Ecology and Evolution Annual Meeting 2021. Online oral presentation.

33. Pettit*, T., **Barreto**, C., Buchkowski, R., Branfireun, B., Lindo, Z. 2021. Modeling soil carbon cycling in boreal peatlands under future climate warming scenarios. Ontario Ecology, Ethology and Evolution Colloquium. Guelph, ON. Online oral presentation.

32. Dehens*, S., **Barreto**, C., Lindo, Z. 2021. Comparing vegetation survey methods on boreal peatland plant communities under climate warming. EnviroCon. London, ON. Online oral presentation.

31. Pettit*, T., **Barreto**, C., Buchkowski, R., Branfireun, B., Lindo, Z. 2021. Modeling soil carbon cycling in boreal peatlands under future climate warming scenarios. Ontario Biology Day. Hamilton, ON. Online oral presentation.

30. Meehan, M.L., **Barreto***, C., Turnbull, M.S., Bradley, R.L., Bellenger, J., Darnajoux, R., Lindo, Z. 2020. Response of soil fauna to simulated global change factors depends on ambient climate conditions. Festival of Ecology - British Ecological Society. Online poster presentation.

29. **Barreto***, C., de Paula, A.S. 2020. Distribuição potencial atual e futura de *Nysius simulans* (Hemiptera: Lygaeidae) em plantações de soja na América do Sul. V Mostra da Pós-Graduação da UFOP, Encontro de Saberes 2020, Ouro Preto, Brazil. Online oral presentation.

28. **Barreto***, C., de Paula, A.S. 2020. Potential distribution of *Nysius simulans* (Stål) (Hemiptera: Lygaeidae) in soybean crops in South America under current and future climate. Entomological Society of America Meeting, Orlando, FL. Online poster presentation.

27. **Barreto***, C., Rillig, M.C., Lindo, Z. 2020. Addition of polypropylene and polyester

in soil affects decomposition rates but not microarthropod communities. Acarological Society of America’s symposium Current Advances in Acarology in the Entomological Society of America Meeting, Orlando, FL. Invited speaker. Online oral presentation.

26. **Barreto***, C., Lindo, Z. 2020. Weak effects of warming and CO2 on soil microarthropod communities. SPRUCE All-Hands meeting, Oak Ridge, TN. Online oral presentation.

25. **Barreto***, C., Lindo, Z. 2019. Climate change field experiment shows weak effects of warming and neutral effects of CO2 on soil microarthropod communities. Joint Meeting of the Acadian Entomological Society, the Entomological Society of Canada and the Canadian Society for Ecology and Evolution, Fredericton, NB. Oral presentation.

24. **Barreto***, C., Lindo, Z. 2019. Warming has different effects on top-down and bottom-up trophic cascades in a soil acarine predator-prey system. Building Bridges: Micro-, Meso- and Macrofauna processes across systems, Göttingen, Germany. Oral presentation.

23. Lindo, Z., Ramirez, I., McNeil, J.N., **Barreto***, C. 2019. Are soil mesofauna at the monarch overwintering sites affected by secondary plant compounds sequestered by monarch butterflies? Building Bridges: Micro-, Meso- and Macrofauna processes across systems, Göttingen, Germany. Poster presentation.

22. de Paula*, A. S., **Barreto**, C. 2018. Species distribution modeling to evaluate the impact of climate change on the distribution of *Nysius simulans* (Stål) (Heteroptera: Lygaeoidea: Orsillinae). 6th Quadrennial Meeting of The International Heteropterists' Society, La Plata, Argentina. Poster presentation.

21. Meehan*, M., **Barreto**, C., Kustec, J., Turnbull, M. S., Bradley, R., Bellenger, J., Lindo, Z. 2018. The impact of warming on two trophic levels in microarthropod communities. ESA, ESC and ESBC Joint Annual Meeting, Invited speaker at the Soil Mites: Minute Arthropods with a Monumental Role Symposium, Vancouver, British Columbia. Oral presentation.

20. **Barreto***, C., Lindo, Z. 2018. Does warming alter top-down and bottom-up trophic cascades in a soil acarine predator-prey system? ESA, ESC and ESBC Joint Annual Meeting, Invited speaker at the Soil Mites: Minute Arthropods with a Monumental Role Symposium, Vancouver, British Columbia. Oral presentation.

19. Meehan*, M., **Barreto**, C., Kustec, J., Turnbull, M. S., Bradley, R., Bellenger, J.,

Lindo, Z. 2018.Warming rewires trophic linkages in belowground forest communities. 9th Annual Biology Graduate Research Forum, Western University, London, Ontario. Oral presentation.

18. **Barreto***, C., Lindo, Z. 2018. Warming alters top-down and bottom-up trophic cascades in a soil acarine predator-prey system. 48th Ontario Ecology, Ethology and Evolution Colloquium, London, Ontario. Oral presentation.

17. Kustec*, J., **Barreto**, C., Lindo, Z. 2018. Shifts in Collembola communities under top-down and bottom-up effects are mediated by warming. 48th Ontario Ecology, Ethology and Evolution Colloquium, London, Ontario. Oral presentation.

16. **Barreto***, C., Barreto, L. 2018. Perceptions of primary and middle school students from Brazil on caves and possibilities for Environmental Education. EnviroCon 2018, London, Ontario. Oral presentation.

15. **Barreto***, C., Kustec, J., Lindo, Z. 2018. Predator and Prey Enrichment Response in Soil. NSERC Strategic Project annual meeting - Predicting Annual Allowable Cut. Ministère des Forêts, de la Faune et des Parcs, Québec, Québec. Oral presentation.

14. **Barreto***, C., Lindo, Z. 2017. Do decomposer and decomposition dynamics across a hummock-hollow topology differ in boreal peatlands? 2017 Joint Meeting of the Entomological Societies of Canada and Manitoba. Winnipeg, Manitoba. Oral presentation.

13. **Barreto***, C., Lindo, Z. 2017. Factors affecting decomposers and decomposition dynamics differ in boreal peatlands. 2017 Ontario Ecology, Ethology and Evolution Colloquium. Kingston, Ontario. Oral presentation.

12. **Barreto***, C., Lindo, Z. 2017. Factors affecting decomposers and decomposition dynamics differ in boreal peatlands. Canadian Society for Ecology and Evolution Annual Meeting 2017. Victoria, British Columbia. Oral presentation.

11. **Barreto***, C. Lindo, Z. 2017. Oribatid mites in hummock-hollow microtopology in a Boreal peatland in White River, Ontario. NSERC Strategic Project annual meeting - Northern Peatland Ecosystem Responses to Climate Change, Ministry of the Environment, Toronto, Ontario. Oral presentation.

10. **Barreto***, C.R.A., Paula, A.S. 2016. Phylogenetic analysis of the Rhodniini tribe (Heteroptera: Reduviidae). 7th Annual Biology Graduate Research Forum, Western

University, London, Ontario. Oral presentation.

9. **Barreto***, C.R.A., Nepomucena, T.C., Horta, A.L., Paula, A.S. 2012. Do temperature and moon luminosity interfere in Heteroptera (Insecta: Hemiptera) survey from Itacolomi State Park? XX Honour Thesis Seminar, Ouro Preto, Brazil. Oral presentation.

8. **Barreto***, C.R.A., Paula, A.S. 2011. Phylogenetic analysis of Rhodniini (Insecta: Hemiptera: Heteroptera: Reduviidae: Triatominae) using morphological, morphometric, and molecular characters. XIX Honour Thesis Seminar, Ouro Preto, Brazil. Oral presentation.

7. **Barreto***, C.R.A., Nepomucena, T.C., Paula, A.S. 2011. Morphological, morphometric, and molecular characters in cladistic analysis of Rhodniini Tribe (Insecta: Hemiptera: Heteroptera: Reduviidae: Triatominae). X Congresso de Ecologia do Brasil, São Lourenço, Brazil. Poster presentation.

6. Raimundo*, R.L.S., **Barreto**, C.R.A., Paula, A.S. 2010. Cladistic analysis of Rhodniini Tribe (Hemiptera: Reduviidae). XVIII Honour Thesis Seminar, Ouro Preto, Brazil. Poster presentation.

5. **Barreto***, C.R.A., Paula, A.S. 2010. Cladistic and Biogeographical analysis of Rhodniini Tribe (Hemiptera: Heteroptera: Reduviidae: Triatominae) and areas of endemism of associated Neotropical palm trees. XVIII Honour Thesis Seminar, Ouro Preto, Brazil. Poster presentation.

4. **Barreto***, C.R.A., Paula, A.S. 2010. How do bioclimatic variables explain potential distribution of Rhodniini (Heteroptera: Reduviidae: Triatominae) species in Neotropical region on current and Last Glacial Maximum periods? II Simpósio de Entomologia UFV, Viçosa, Brazil. Poster presentation.

3. Machado*, N.A.M., Ribeiro, P.S., **Barreto**, C.R.A., Martins, I.S., Leite, M.G.P., Kozovits, A.R. 2010. *Eremanthus erythropappus* (DC.) MacLeish (Asteraceae) seedlings development in substrates from mining abandoned areas. 61º Congresso Nacional de Botânica, Manaus, Brazil. Oral presentation.

2. **Barreto***, C.R.A., Raimundo, R.L.S., Galvão, C., Paula, A.S. 2010. Bioclimatic variables participation in the potential distribution of Rhodniini species (Heteroptera: Reduviidae: Triatominae) on Neotropical region on current, future, and Last Glacial Maximum periods. SIMBIO 2010 - I Simpósio de Biodiversidade, Rio Paranaíba, Brazil. Poster presentation.

1. Machado*, N.A.M., Ribeiro, P.S.C., **Barreto,** C.R.A., Leite, M.G.P., Kozovits, A.R. 2009. Low-cost methods for rehabilitation of areas degraded by Bauxite mining at Quadrilátero Ferrifero, MG. Congresso Iberoamericano e do Caribe sobre Restauração Ecológica, Curitiba, Brazil. Poster presentation.

Professional Experience

08/2021 – present	**Soils and Water Research Biologist** at the Ontario Forest Research Institute, MNDMNRF, Sault Ste. Marie, Canada
09/2016 – 10/2021	**Teaching Assistant** and **Research Assistant** at the University of Western Ontario
09/2018 – 08/2021	**Greenhouse Technical/Research Support I** at the University of Western Ontario
08/2020 – 11/2020	**Mitacs Research Intern** at the University of Western Ontario
01/2020 – 04/2020	**Course content Marker** for the Ecosystem Ecology class at the University of Western Ontario
09/2019 – 12/2020	**Lecturer/Course Coordinator** of the Community Ecology class at the University of Western Ontario
05/2019 – 08/2019	**Visiting Graduate Researcher** at the Institut für Biologie, Freie Universität Berlin, Germany
02/2016 – 08/2016	**Biology Laboratory Coordinator** at Carste Ciência e Meio Ambiente, Brazil
04/2014 – 04/2016	**External Research Consultant** at Instituto do Carste, Brazil
02/2013 – 02/2016	**Junior Biologist** at Carste Ciência e Meio Ambiente, Brazil
01/2010 – 08/2012	**Undergraduate Teaching Assistant** at Federal University of Ouro Preto, Brazil

09/2009 – 08/2012	**Undergraduate Student Researcher** at Federal University of Ouro Preto, Brazil

Mentoring

09/2020 – 04/2021	Graduate Advisor, the University of Western Ontario Project: Vegetation Data Survey Methods: An Analysis of Point-Intercept and Visual Estimation Data on Boreal Peatland Plant Communities Student: Shae-Lynn Dehens
09/2020 – 04/2021	Graduate Advisor, the University of Western Ontario Project: Quantifying carbon and nitrogen mineralization in a peatland soil food web Student: Trevor Pettit
09/2019 – 04/2020	Graduate Advisor, the University of Western Ontario Project: Songs at stopover: Do species differ in their temporal aggregation? Student: Christian Buchanan-Fraser

Personal Experience

2021 – current	Acarological Society of America (Social Media Manager)
2021	PSAC Local 610 Elections – Chief Returning Officer
2021	Career-day panelist, the University of Western Ontario
2021	Earth Science Career Info Session panelist, the University of Western Ontario
2020 – 2021	Steward at PSAC Local 610
2020 – 2021	Reach the World Expedition
2020	National Scholarships ranking
2020	Current Advances in Acarology symposium panelist, Acarological Society of America meeting
2019 – 2021	Food Support Committee at PSAC Local 610
2017 – 2021	Canadian Society of Ecology and Evolution Student representative at the University of Western Ontario