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# Effects of experimental warming and reduced moisture on oribatid mite communities in boreal peatlands

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Supervisor: Zoë Lindo, *The University of Western Ontario* A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology © Emelie Obi 2025

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### Abstract

Temperature and moisture are two key factors that are expected to change under current and future climate projections, with significant impacts on ecosystems and biological communities. In northern latitudes, boreal peatlands, known as major carbon stores, are particularly vulnerable to these changes. Changes in temperature and moisture levels are predicted to shift boreal peatlands from carbon sinks to carbon sources by altering decomposition dynamics, primarily through effects on below-ground communities such as microarthropods, as well as effects on below-ground processes such as decomposition and nutrient cycling. Oribatid mites are one of the most dominant microarthropod communities in boreal peatlands as well as other terrestrial systems; they contribute to carbon flux and soil nutrient cycling by feeding on decomposing organic matter and regulating microbial communities. Here, I used both field and controlled lab experiments to study the effects of experimental warming and moisture reduction on oribatid mite communities. I observed significant changes in oribatid mite community composition under warmer temperatures, driven by a decline in diversity and evenness due to an increase in smaller ( $< 300 \mu m$ ) oribatid mites. This compositional shift towards smaller oribatid mites also led to a decline in average community body size. Overall, my results show that temperature was a strong driver of shifts in oribatid mite communities in boreal peatlands.

# Keywords

Soil biodiversity, climate change, microarthropods, Oribatida, mites, body size, peatlands, community downsizing, temperature, drying, community weighted mean

# Summary for Lay Audience

The organisms that live in soils are estimated to make up more than half (59%) of all species on Earth. These organisms play important roles, such as breaking down organic debris, cycling soil nutrients, and helping soils store carbon; these processes are essential for the proper functioning of many ecosystems. Recent climate predictions suggest that climate change will impact soil ecosystems, affecting the abundance, richness, diversity, and functions of soil organisms. The effects of climate change on soil organisms will arise through several factors, particularly increases in soil temperature and reductions in soil moisture. Changes in these factors are especially important in wetland systems like boreal peatlands, which are characterised by low temperatures and high moisture conditions. Low temperatures and high moisture slow down decomposition in boreal peatlands; combined with the presence of unique soil organisms, this allows boreal peatlands to hold more carbon than other terrestrial systems, making them significant carbon stores. Climate change is expected to increase temperature and reduce moisture in boreal peatlands, affecting soil organisms in ways that could shift boreal peatlands from carbon stores to carbon sources. To understand how soil organisms in boreal peatlands will respond to climate change, I conducted a field and a lab experiment to mimic future climate conditions, particularly changes in soil temperature and moisture. I focused on oribatid mites, one of the most dominant groups of soil organisms. My results show that temperature was a strong factor affecting oribatid mite communities in boreal peatlands. More specifically, I found that warmer temperatures changed community structure by increasing the abundance of smaller oribatid mites, which in turn reduced overall diversity. This increase in smaller oribatid mites led to a reduction in the average body size of the oribatid mite communities. As one of the dominant groups in soils, changes in oribatid mite communities may alter decomposition and nutrient cycling processes in peatland, ultimately impacting the ability of peatlands to function as long-term carbon storage.

# **Co-Authorship Statement**

Sampling for both Chapter 2 and 3 was carried out at the BRACE (Biological Response to Changing Environment) experimental sites. The BRACE project is a collaboration between the University of Western Ontario (Zoë Lindo and Brian Branfireun) and the Ontario Ministry of Natural Resources, Ontario Forest Research Institute (OMNR-OFRI) (Jim McLaughlin and Carlos Barreto).

The research idea for Chapter 2 was conceived by Emelie Obi and Zoë Lindo. Emelie Obi and Zoë Lindo contributed to sampling. Sample processing and data analysis were performed by Emelie Obi. A research manuscript from this Chapter has been prepared by both Emelie Obi and Zoë Lindo for submission to the Journal of Applied Soil Ecology.

The research idea for Chapter 3 was conceived by Zoë Lindo. Experimental design, sampling and set-up were performed by Emelie Obi and Zoë Lindo. Emelie Obi maintained the experiment, processed the samples, and analysed the data. A research manuscript from this Chapter may be developed in future by Emelie Obi and Zoë Lindo.

## Acknowledgments

Graduate study is never easy, but with the right supervision, it can be a smoother journey, especially for a student still learning how to conduct research. The Lindo Lab has been an incredible environment for learning and growth, and I will always be grateful for the opportunity to work under Dr. Zoë Lindo's supervision. Zoë has an exceptional understanding of what each of their supervisees need to succeed and provides the necessary support. Their research and supervisory skills are outstanding, matched only by their ability to make excellent hot sauces! :)

I also extend my gratitude to the members of the Lindo Lab whom I met at the beginning and/or end of my MSc programme: Trevor, Holly, Sam, Cristina, Pedro, Emily, and Martin, for their contributions, comments, and feedback on my research. Sincere thanks to my advisors, Dr. Erik Emilson (whom I never got the opportunity to physically meet) and Dr. Vera Tai (who also agreed to be my thesis reader). Special thanks to Dr. Carlos Barreto, whose initial work on Oribatida at the BRACE sites was invaluable to me. I am also grateful to the other collaborators on the BRACE experiment, especially Dr. Brian Branfireun. During my programme, I had the privilege of meeting fellow graduate students who became friends: Thank you, Mika, for your help with statistics; thank you, Maedeh (and your mom), for the wonderful conversations and your delicious Persian meals; Arani, I appreciate you for always reminding us to take a break and have fun.

I am overly grateful to my parents, George and Rita Obi, for ensuring I received more education than they were able to. To my brothers, Franklyn and Bonaventure, thank you for your constant support and encouragement; I would not have been able to travel to Canada without your financial assistance. To my sisters, Theresa and Zita, thank you for making me laugh and reminding me that I have only two choices: to succeed or to SUCCEED (haha). I also appreciate my friends in Nigeria, especially Kelechi, Rona, and Caleb, for checking on me and making me smile with hilarious conversations. Also, thanks to Dr. Aline Noutcha at the University of Port Harcourt Nigeria, for always checking up on me and asking about my research. Finally, my heartfelt gratitude goes to Chibuzo and Frank for coming into my life at the perfect time. I do not think that I would have been able to complete this MSc. program without the support of all these wonderful people. Thank you all so much! *Dàálų nų, rìnne*!

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# Chapter 1

## 1 General Introduction

#### 1.1 Climate change and its effects on ecosystems

Climate change refers to long-term changes in average global weather conditions such as temperature and precipitation. Anthropogenic activities, especially industrialisation, which often involves fossil fuel burning and land-use changes, have led to the ongoing release of CO<sub>2</sub>, methane, and other greenhouse gases (GHGs) into the atmosphere that is causing increases in atmospheric  $CO_2$  levels and concomitant global warming. The Intergovernmental Panel on Climate Change (IPCC) forecasts that continuous GHG emissions will continue to increase global temperatures with a current prediction under the SSP-5 forecast scenario (a mid-line prediction) that average global temperature may rise by +4°C in 50 to 100 years (IPCC, 2023). Increase in global temperatures will also lead to increases in extreme weather events such as heatwaves, alongside rising sea levels, and changes in precipitation (Balting et al., 2021; IPCC, 2023). While changes in temperature and other climate factors will differ from region to region, northern latitudes are predicted to experience a greater degree of warming and more severe weather conditions. For example, under the IPCC prediction scenario of +4°C, the northern latitudes may experience warming twice that at about +8°C (IPCC, 2023). Similarly, while some regions may face higher rainfall and flooding events, others may experience drought. Overall, shifts in temperature levels, precipitation patterns and altered moisture levels, and occurrence of extreme weather events are all expected to happen under climate change.

Although the effects of climate change may vary from region to region, all ecosystems and biological communities will be affected regardless of their location on the globe. Climate change effects on biological communities will either be direct and/or indirect. The direct effects will arise through shifts in metabolic and reproductive rates (Dillon et al., 2010; Seebacher et al., 2015), shifts in physiology and phenology (Gardner et al., 2011; Numata et al., 2022) as well as changes in species interactions (see Fontúrbel et al., 2021) and distributions (Pecl et al., 2017). Other effects of climate change on biological communities will occur indirectly through changes in resource availability and/or changes in ecosystems. For example, some ecosystems will experience more extreme weather events such as wildfires, heatwaves, droughts or flooding (IPCC, 2023). In aquatic systems, such as oceans, climate change will impact biodiversity through deoxygenation, acidification, and coral reef bleaching (see review by Doney et al., 2012). Depending on their location, some terrestrial ecosystems will be affected by flooding due to rising sea levels caused by permafrost thawing, while others (such as forests and wetlands) may dry out, due to increasing temperatures and evaporation, and become dominated by new species (Hogg and Hurdle, 1995). These shifts in biodiversity and ecosystems will alter their functions, and some critical systems such as soils that are currently known to store significant amounts of carbon (Hiederer and Köchy, 2011; Scharlemann et al., 2014) may become carbon sources. The soil system, in addition to storing high amounts of carbon, supports a significant amount of biodiversity (Anthony et al., 2023). At the same time, soil systems are vulnerable, as climate change, via rising temperatures and altered moisture levels, will elevate decomposition rates (Kirschbaum, 1995), releasing large amounts of stored carbon into the atmosphere further contributing to climate change. Therefore, understanding how climate change will alter abiotic conditions, such as temperature and moisture, as well as biological communities in soils and other important terrestrial systems, is essential for predicting changes in ecosystem health and functions.

# 1.2 Boreal peatlands under climate change

The boreal forest is an ecological system that dominates the boreal ecozone, which is found between 50°N and 65°N of the equator (Hayes et al., 2022). Although the boreal forest serves purposes such as forestry, it also known for its ability to store significant amounts of carbon in its vegetation and soils (Kurz et al., 2013), especially in its wetlands (peatlands) (Bradshaw and Warkentin, 2015). Broadly, peatlands are terrestrial wetland ecosystems in which saturated conditions (high water table) prevent plant inputs from decomposing fully, leading to the accumulation of partially decomposed organic matter called peat. Accumulated organic material in peatlands exceeds 40 cm in depth. Boreal

peatlands (wetlands found in the northern latitudes) cover ~30% of the boreal region, globally (Wieder and Vitt, 2006). These peatlands, which account for 80% of peatlands in the world, are characterised by their hydrology i.e., high moisture (water-table) conditions which causes anoxia prevents plant material from decomposing fully. But they are also known to have low temperatures which further slows down microbial activity and decomposition, further supporting the formation of peat. However, boreal peatlands can be characterised by other factors such as their chemistry (whether nutrient-poor or rich) and their vegetation type, which are also dependent on their hydrology.

At least 550 gigatons of carbon is stored in peatlands, more than other ecosystems globally (Xu et al., 2018; Hugelius et al., 2020) making them significant global carbon stores, despite occupying only 3% of the earth's land surface. In Canada, boreal peatlands cover  $\sim 13\%$  of the land area and are estimated to store 147 gigatons of carbon (Tarnocai, 2009); this amounts to 59% of Canada's total soil organic carbon (Tarnocai, 1996). Boreal peatlands support unique above-ground communities such as mosses (*Sphagnum*) and sedges (*Carex*) (Wieder and Vitt, 2006), and below-ground communities such as microbes (Mitchell et al., 2003) and invertebrates (Batzer et al., 2016; Barreto and Lindo, 2021). These communities play important roles in carbon flux in the peatland systems. Above-ground communities (vegetation) serve as sources for organic matter inputs, while below-ground communities contribute to decomposition of organic litter and nutrient cycling. Given their location and importance, boreal peatlands are one of the ecosystems that are expected to be significantly affected by climate change because future temperatures in the boreal region are predicted to be twice the average global predicted levels in 50 to 100 years. Changes in temperature and moisture, two factors shaping boreal peatlands, will alter decomposition and carbon dynamics, ultimately affecting their ability to store carbon (Juan-Ovejero et al., 2020).

# 1.3 Soil biodiversity

Soil biodiversity is a collection of various organisms living within the soil (or a similar) system. Recent estimates place soil biodiversity at 59% of all biodiversity on Earth (Anthony et al., 2023); an update from a past estimate, 17 years prior, that placed soil biodiversity at 25% (Decaëns et al., 2006). Soils are highly heterogeneous even within a

small area, thereby supporting a significant number of species. Soil organisms are also small (many are microscopic) and this allows them to exist in significant numbers even within a small volume of soil (Giller, 1996; Bardgett, 2005). Soil systems are comprised of organisms that can be roughly categorised based on body size: microorganisms(e.g., fungi, bacteria and protozoa), microfauna (e.g., nematodes with body size less than 100 µm), mesofauna (mites and Collembola with body size between 100 µm to 2000 µm), and macrofauna (e.g., earthworms and termites with body size above 2000 µm) (Bardgett, 2005) all of which perform different ecosystem roles. Although there are some roles that overlap between different sizes, the different sizes allow soil organisms to occupy different ecological niches within the soil system, forming the very complex soil food web (Digel et al., 2014; Wolkovich, 2016; Potapov, 2022). Soil microorganisms, dominated by fungi and bacteria, are primarily responsible for the bulk of primary decomposition, breaking down complex organic compounds (Bardgett, 2005) and making nutrients like nitrogen available.

The soil mesofauna form an important part of the soil food web encompassing different functional groups (e.g., herbivores, omnivores, predators and detritivores), and are often dominated by microarthropods including mites (Oribatida, Prostigmata, Astigmata, Mesostigmata) and Collembola. Mesofauna grazing on microbes (Bardgett et al., 1993a) and dispersing their propagules (Visser et al., 1985), regulate microbial populations (Bray et al., 2019), but they can also feed directly on decomposing organic litter (detritus) like decaying leaves and logs. Through feeding on detritus, they can break down organic litter into smaller particles for microbes, supporting decomposition and microbial activity. At the same time, their movement through the soil system enables them to transport organic matter as well as soil nutrients from one location in the soil to another. However, their movement through the soil system can be influenced by soil pore space, as they, like other mesofauna, are too small to create their own habitable spaces, unlike macrofauna. Nonetheless, their actions on litter as well as their movement through the soil system make them important contributors to soil structure and functions.

Microarthropods occur in many terrestrial ecosystems where they perform roles in decomposition, nutrient cycling, and in regulation of microbial communities, and are

highly abundant and species rich in systems with high organic matter such as forests, grasslands, peatlands, as well as agricultural soils. For instance, in a review, Petersen and Luxton (1982) reported microarthropod densities to range between 100 m<sup>-2</sup> in a Californian desert to 792,000 m<sup>-2</sup> in a pine forest, while Bardgett et al. (1993b) reported densities of microarthropods in an agricultural grassland to be over 50,000 m<sup>-2</sup>. Microarthropod communities are regulated by several abiotic factors (e.g., pH, soil pore space), and can be highly responsive to changes in their environment such as changes in temperature and soil moisture conditions, making them ideal bioindicators of environmental change (Behan-Pelletier, 1999; Kay et al., 1999; Menta et al., 2018; Meehan et al., 2019). As ectotherms, microarthropods respond to increases in temperature by elevating metabolic and reproductive rates (Gillooly et al., 2001; Brown et al., 2004), which can increase microarthropod abundance, but temperatures above 35 -40°C are typically lethal (Madge, 1965; Hodkinson et al., 1995). Microarthropod relationship with soil moisture is typically positive (i.e., greater soil moisture has greater abundance and richness) while lower soil moisture levels can induce stress or mortality. However, this relationship is unimodal as very high soil moisture can occlude/reduce airfilled pore space and decrease microarthropod abundance.

#### 1.4 Oribatid mites

Oribatid mites (Acari: Oribatida) are microscopic arachnids ranging in size between 150  $-1,100 \mu$ m. With densities averaging around 100,000 m<sup>-2</sup> in most soil systems (Norton and Behan-Pelletier, 2009), oribatid mites are one of the most abundant and diverse soil microarthropod communities found in terrestrial systems. Oribatid mites tend to be the dominant microarthropod group in forest systems (Petersen and Luxton, 1982; Lindo and Winchester, 2006), but they can also be present in arboreal (Behan-Pelletier and Winchester, 1998), littoral (Bayartogtokh and Chatterjee, 2010), and semi-aquatic habitats (e.g., peatlands) (Behan-Pelletier and Bissett, 1994; Lehmitz, 2014; Barreto and Lindo, 2021). Over 11,000 species have been described globally, representing 172 families (Schatz and Behan-Pelletier, 2008; but see also Behan-Pelletier and Lindo, 2023). In Canada, over 580 species have been described so far with many more still to be described (Behan-Pelletier and Lindo, 2023). Most oribatid mites are fungivores while

others feed on decaying organic matter (Norton and Behan-Pelletier, 2009), playing both direct and indirect roles in the soil food web and carbon dynamics via organic matter fragmentation and decomposition. Oribatid mite density has been reported to be positively correlated with organic matter quantity (Battigelli et al., 2004), but can also be influenced by litter (Hansen and Coleman, 1998) or habitat type (Maraun and Scheu, 2000).

As with most microarthropods, temperature and moisture are also factors that drive oribatid mite abundance, richness, and composition. Warming generally increases metabolic and reproductive rates (Ermilov et al., 2004; Ermilov and Łochyńska, 2008) leading to faster developmental growth rates and faster population turnover rates. In studies of warming at the community level, smaller ( $\leq 300 \ \mu m$ ) oribatid mites have been found to increase in abundance, specifically oribatid mites from the families Brachychthoniidae and Suctobelbidae (Lindo, 2015; Markkula et al., 2019; Barreto et al., 2021), which are also parthenogenetic (asexual). Soil moisture significantly influences oribatid mite populations, with higher moisture generally leading to greater abundance and diversity (Lindo et al., 2012; Siebert et al., 2019; Feketeová et al., 2021), though specific effects can vary depending on the season and other factors. However, at saturated (high soil moisture) levels, air-filled soil pore space and oxygen levels may be reduced, limiting oribatid mite populations. Therefore, in high soil moisture environments such as peatlands, a reduction in moisture has been shown to increase oribatid mite abundance (Barreto et al., 2021). There also appears to be a relationship between oribatid mite body size and soil moisture; for example, Xu et al. (2012) reported that under drought conditions in a field experiment, smaller oribatid mites increased in abundance possibly due to the ability of the mites to avoid desiccation by moving through tiny soil pore spaces into deeper soils.

Under climate change, changing temperature and moisture conditions are key factors that will affect soil communities (Blankinship et al., 2011; Goncharov et al., 2023) including oribatid mites. For example, while soil microarthropods may increase in abundance under warming due to elevated reproduction, the concomitant reduction in moisture may lead to physiological stress, desiccation and death, reducing abundance; this trend (of reduced

microarthropod abundance) has already been reported in both field (Alatalo et al., 2017; Xu et al., 2012) and laboratory experiments (Aupic-Samain et al., 2021). However, these studies were carried out on forest soils which generally have lower moisture levels than peatlands. Reports on the response of soil microarthropods to temperature and moisture in peatland systems are generally few when compared to reports from forest systems, but the existing studies show divergent trends (Markkula et al., 2019; Barreto et al., 2021; Pettit et al., 2023). Understanding how oribatid mites respond to climate change in peatlands may provide insights into the potential consequences of climate-driven changes in peatland food web and nutrient dynamics, and (by extension) carbon cycling.

# 1.5 Objectives and rationale

In my thesis, I examined how boreal peatland oribatid mite communities respond to experimental climate change conditions using both field and controlled laboratory experiments. The specific objectives of my study were to:

a) Observe the effect of experimental warming on moisture levels and oribatid mite communities in a field experiment and determine whether experimental warming leads to a reduction in community body size (Chapter 2).

b) Examine whether changes in oribatid mite communities in peatlands are driven by the main or interactive effects of temperature and moisture (Chapter 3).

For the first objective, I hypothesised that warming would increase oribatid mite metabolic rates and reproduction, and I predicted that this would increase the total abundance of oribatid mites as well as the proportion of oribatid juveniles. I also hypothesised that warming would induce soil moisture reduction (as observed by Barreto et al., 2021) which will create more habitable pore space and encourage immigration of new species, increasing oribatid mite diversity and evenness. Further, I hypothesised that the effect of warmer temperatures on metabolic rates and reproduction would be relatively higher for the smaller asexual oribatid mites, such as the Brachychthoniidae and Suctobelbidae families, as observed by Lindo (2015), Markkula et al. (2019), and Barreto et al. (2021). I predicted that the increase in these smaller asexual oribatid mite

families would increase the proportion of asexual oribatid mite individuals and that this compositional shift towards smaller oribatid mites would cause a reduction in the average community body size.

To address the second objective, I used a mesocosm experiment maintained for 4 months under controlled temperature and moisture conditions to determine whether temperature or moisture was the main driver of shifts in oribatid mite communities or whether the two factors had an interactive effect. I hypothesised that warmer temperatures would increase reproduction and lower moisture levels may create more habitable pore space leading to an overall shift in oribatid mite communities. I predicted increased oribatid mite abundance under elevated temperatures, but also predicted that the combined effect of increased temperature and reduced moisture would lead to greater number of individuals from smaller oribatid mite species and thus a reduction in the average community body size of the oribatid mite communities.

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# Chapter 2

# 2 Experimental climate warming in boreal peatlands alters oribatid mite communities through peat drying

# 2.1 Introduction

Global air temperatures have increased by about  $1.5^{\circ}$ C in the last century due to climate change, with a future global projection of +4°C in the next 50 – 100 years based on the Shared Socio-economic Pathway-5 (SSP-5) – one of the modelled scenarios for exploring future GHG emissions (Balting et al., 2021; IPCC, 2023). Concomitantly, climate change is predicted to alter precipitation patterns (Trenberth, 2011), and warming may also indirectly affect moisture availability, especially in soils (Zare et al., 2022; Qin et al., 2023). Although future projections forecast an average global temperature increase of ~+4°C in the next 100 years, ~+8°C is projected for the northern latitudes (IPCC, 2023), including areas of the arctic, subarctic, and boreal regions of Canada.

Boreal peatlands are terrestrial wetland environments found in the northern latitudes and cover ~30% of the boreal region (Wieder and Vitt, 2006) globally. They are characterised by low soil temperatures and high moisture (water-table) conditions which prevent plant material from fully decaying, resulting in the formation of partially decayed plant matter called peat (Wieder and Vitt, 2006). Globally, peatlands are estimated to store over 500 gigatonnes of carbon as peat, more than other ecosystems (Pan et al., 2011; Hugelius et al., 2020) making them significant global carbon stores. In Canada, boreal peatlands cover approximately 13% of the land area and are estimated to store 147 gigatons of carbon, which accounts for approximately 59% of Canada's total soil organic carbon (Tarnocai and Lacelle, 1996; Tarnocai, 2009). At the same time, boreal peatlands have unique below-ground communities, such as invertebrates (microarthropods) (Littlewood et al., 2010; Batzer et al., 2016) that are well adapted to the peatland system and contribute to nutrient and carbon flux. Microarthropods contribute to nutrient and carbon flux by transforming and translocating organic matter and regulating microbial communities. Global warming in boreal peatlands may accelerate decomposition rates

(Tarnocai, 2009; Helbig et al., 2020) and reduce soil moisture through increased evapotranspiration rates (Ofiti et al., 2022). Consequently, local changes in abiotic conditions (temperature and moisture) may affect the abundance, richness and composition of peatland communities (Markkula et al., 2019; Barreto et al., 2021). Combined, shifts in both abiotic conditions and biotic communities under climate change may affect the way peatlands sequester carbon (Juan-Ovejero et al., 2020).

Oribatid mites (Acari: Oribatida) are one of the most dominant microarthropod communities in terrestrial and semi-aquatic habitats. They are microscopic arachnids that range in body size from 150 to over 1000  $\mu$ m. Most oribatid mites reproduce sexually but ~10% of the species are asexual (Norton and Palmer, 1991) especially among the smaller (~150 – 300  $\mu$ m) species. Although the estimated direct impact of oribatid mites on carbon sequestration in peatlands is low, as the dominant soil microarthropod, they actively contribute to the breakdown of organic matter through consumption of litter and debris and regulation of microbial communities (see Behan-Pelletier and Lindo, 2023). Temperature and moisture are abiotic factors that drive the abundance, richness, and community composition of microarthropods (Siepel, 1996; Lindo et al., 2012), having a positive effect if temperatures remain below the lethal threshold of ~40°C (Madge, 1965) and moisture is not limiting soil pore space (Nielsen et al., 2008).

As with many ectotherms, the effect of warmer temperatures on microarthropods (including oribatid mites) often starts with accelerated metabolic rates at the individual level which leads to elevated reproduction at the population level. At the community level, this can manifest as increased abundance (Coulson et al., 1996; Kardol et al., 2011; Guo et al., 2022), alongside shifts in community composition. Based on established theories such as the temperature size rule (TSR) (Atkinson, 1994; Gillooly et al., 2001) and the metabolic theory of ecology (Brown et al., 2004), the effect of warmer temperatures is relatively higher for smaller individuals/species as they are known to have relatively higher metabolic rates than their larger counterparts. So, under warmer temperatures, smaller species may reproduce faster than larger species, thereby dominating their communities; this can lead to 'community downsizing', a term which has been used to describe the reduction in average community body size (Sheridan and Bickford, 2011; Lindo, 2015) due to compositional shifts (but see Olhberger, 2013). However, the response of soil microarthropod communities (including oribatid mites) to warming is often dependent on moisture conditions (Tsiafouli et al., 2005), particularly since warmer temperatures often correspond to lower moisture levels arising from increased evaporation and/or transpiration. While warmer temperatures may favour oribatid mites, reduced moisture levels (drying) can lead to desiccation and mortality. Studies on forest and grassland soils have shown that warming-induced drying typically affects oribatid mites negatively (Kardol et al., 2011; Alatalo et al., 2017). However, recent research suggests that warming-induced drying in wetlands such as peatlands may create more habitable soil pore spaces, potentially increasing oribatid mite abundance and richness (Barreto et al., 2021).

I investigated the response of oribatid mite communities following seven years of experimental warming at two boreal peatland systems that differ in water table and moisture conditions. I hypothesised that warming may increase oribatid mite metabolic rates and reproduction and predicted that this will increase juvenile proportion, total abundance and richness at the community level. Additionally, I hypothesised that warmer temperatures would favour the smaller asexual oribatid families, such as Brachychthoniidae and Suctobelbidae, as observed by Lindo (2015), Markkula et al. (2019), and Barreto et al. (2021), due to elevated metabolism under warming. I predicted that this would lead to an increase in the proportion of asexual oribatid species and that this compositional shift would cause a reduction in average community body size.

## 2.2 Materials and methods

#### 2.2.1 Study area

The study area is situated in the southern boreal ecozone, near White River, Ontario, Canada (48°21′ N, 84°20′ W). This area experiences a continental climate, heavily influenced by its proximity to Lake Superior. Historical data from Environment Canada (2023) shows that temperature can go below –40°C in winter to above 30°C in summer, but mean annual temperature is around 2.1°C (McLaughlin, 2009). Approximately 980 mm of precipitation is received annually, with about 40% falling as snow; growing season is between 70 to 100 days (Webster and McLaughlin, 2010). There are two fen peatlands at the study area that differ in various aspects such as nutrient status, water table and moisture levels (Webster and McLaughlin, 2010), above-ground vegetation (Palozzi and Lindo, 2017; Lyons et al., 2020; Hopkins, 2024), and below-ground mesofauna communities (Barreto and Lindo, 2021). Both sites are situated within 2 km of each other in the same watershed but are separated by a logging road and a patch of mixed deciduous and coniferous trees. The sites are part of the long-term BRACE (Biological Response to A Changing Environment) project initiated in 2012 and are long-term monitoring sites with the Ontario Ministry of Natural Resources and Forestry (MNRF).

The first site (Figure 2.1) is called the *Sphagnum*-dominated fen (SF). It is a 4.5 ha peatland characterised by a total peat depth of  $\sim 116$  cm, poor level of nutrients and a pH  $\sim$  4.1, and lower moisture conditions resulting from a water-table  $\sim$  30 cm below the peat surface (Webster and McLaughlin, 2010). Above-ground vegetation at this site is dominated by mosses like Sphagnum angustifolium (C.E.P. Jensen ex Russow), Sphagnum fuscum (Schimp.) Klinggr., and Sphagnum divinum (Flatberg ex Hassel), with lesser amounts of Dicranum polysetum Sw., and Pleurozium schreberi (Michx.) Trevis). The site also contains sedges (*Carex disperma* Dewey, *Carex magellanica* Lam., and Carex pauciflora Lightf.), and ericaceous hrubs like leatherleaf (Chamaedaphne calyculata (L.) Moench), Labrador tea (Rhododendron groenlandicum Oeder), bogrosemary (Andromeda polifolia L., and bog laurel (Kalmia polifolia Wagenh.). The site is sparsely treed with tamarack (Larix laricina (Du Roi) K. Koch), black spruce (Picea mariana (Mill.) B.S.P.), and some speckled alder (Alnus incana (L.) Moench); other vascular plants include herbs such as round-leaved sundew (Drosera rotundifolia L.), and threeleaf false lily of the valley (Maianthemum trifolium (L.) Sloboda), and small ground cover plants such as the creeping snowberry (Gaultheria hispidula (L.) Muhl. ex Bigelow), lowbush blueberry (Vaccinium angustifolium Aiton), and bog cranberry (Vaccinium oxycoccos L.) (Palozzi and Lindo, 2017; Lyons et al., 2020; Hopkins, 2024). Surrounding this site is a mixed wood forest and a small lake.



Figure 2.1: Diagram showing the *Sphagnum*- and *Carex*-dominated fens. Schematic representations of the experimental layout are presented below each fen site photograph. Blue and red circles represent warmed and ambient plots, respectively. Brown lines represent board walks. Not all boardwalks are shown.

The below-ground microbial communities at this site are dominated by fungi (Lyons and Lindo, 2020). The site also shows a higher abundance, richness, and diversity of mesofauna (Barreto and Lindo, 2021), featuring a community dominated by oribatid mite species such as *Eniochthonius mahunkai* Norton and Behan-Pelletier, 2007, a typical peatland species (Behan-Pelletier and Lindo, 2023).

The second site is called the *Carex*-dominated fen. It is a 10.2 ha peatland characterised by a total peat depth of  $\sim 60$  cm, intermediate level of nutrients and a pH  $\sim 5.4$ . High moisture conditions result from a higher water table close to the peat surface for most of the year (Webster and McLaughlin, 2010). Above-ground vegetation is dominated by sedge species (Carex lasiocarpa Ehrh, Carex oligosperma Michx., Carex stricta Lamb.), with shrubs such as sweetgale (Myrica gale L.) and bog rosemary (Andromeda polifolia L.) in lesser amounts. Other less dominant vegetation include leatherleaf (Chamaedaphne calyculata L. Moench), bog willow (Salix pedicellaris Pursh), Sphagnum sp., bluejoint reedgrass (Calamagrostis canadensis (Michx.) P.Beauv.), marsh cinquefoil (Comarum palustre L.) and St. John's wort (Triadenum fraseri (Spach) Glea.) (Palozzi and Lindo, 2017; Lyons et al., 2020; Hopkins, 2024). Surrounding the edges of the fen is a mixed wood forest and two small streams. The below-ground microbial community at this site is dominated by bacteria (Lyons and Lindo, 2020). Mesofauna abundance, richness and diversity at this site is lower compared to the Sphagnum-dominated fen, but it is also dominated by oribatid mites - particularly semi-aquatic species such as Limnozetes spp. and Tyrphonothrus maior (Berlese, 1910) (Barreto and Lindo, 2021).

#### 2.2.2 Experimental design

At each site, there are 16 (sixteen) 1-meter diameter plots; eight of these plots are ambient temperature (control) plots and eight are experimentally warmed plots. All plots (control and warmed) are delineated by a PVC collar inserted 30 cm into the peat and extending 10 cm above the peat surface. All plots are within a 25 m  $\times$  25 m relatively homogeneous 'lawn-like' area, avoiding distinct areas of hummocks and hollows. Plots are arranged in a randomized block design with four plots (2 warmed, 2 ambient) in each block for a total of 16 blocks and 32 experimental plots across both sites. For each of the warmed plots, a translucent open-top polycarbonate chamber (OTC) (1 m tall) is used to passively increase the air temperature by  $+2^{\circ}$ C. Passive warming has been ongoing during the growing season (June – October) since 2017. Also, in each of the warmed plots, there are six 50 cm heating rods (60W Watlow FireRod® immersion heaters) inserted vertically into the peat, which actively increases the ground temperature by  $+4^{\circ}$ C. Active warming was deployed in the growing season of 2019 and 2022. Warmed plots are drier than control plots by 15 - 20% depending on annual weather conditions (unpublished data), and moisture has also been shown to be about 21% lower (Sun et al., 2023) and negatively correlated with temperature (Barreto et al., 2021) under active warming. The observed moisture loss in the warmed plots is close to projected climateinduced moisture loss (27%) in the next 60 – 70 years for the west and central parts of Canada's southern boreal forest (He and Pomeroy, 2023), where my study sites are located.

#### 2.2.3 Field Sampling and data collection

In June and September 2023, I measured surface peat temperature (°C) at 5 cm, and surface peat moisture content at 5 cm (V/V %) in all plots using a Wet-2 sensor (Delta-T Devices Limited). As peat temperature at 5 cm is highly variable, I also measured temperature at 30 cm using a long stem thermometer. I collected a single peat soil sample (5 cm diameter  $\times$  5 cm depth) for microarthropod extraction from each plot (N=32  $\times$  2 times = 64). Samples were placed into plastic bags and kept cool in the field (with ice packs), and kept in a 4°C fridge until they were brought back to the Soil Biodiversity and Ecosystem Lab at Western University. Peat samples were placed on extractors within 48 hours of collection. Each peat sample was weighed prior to fauna extraction to obtain the wet weight. Extraction was done with a Berlese-Tullgren funnel over a 3-day period with fauna deposited into labelled vials containing 70% ethanol. After extraction, each peat sample was re-weighed to obtain the dry weight. Estimate of sample moisture was then calculated based on gravimetric mass loss of moisture using the formula:

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

For each sample, I identified and enumerated all microarthropods at the suborder level (i.e., Oribatida, Mesostigmata, Prostigmata, Astigmata, and Collembola). Further, I identified and enumerated all adult oribatid mites (Acari: Oribatida) to the species or
family (Brachychthoniidae and Suctobelbidae) level under a stereomicroscope (Nikon SMZ 745T) or compound microscope (Nikon Eclipse Ni) using taxonomic keys provided by Behan-Pelletier and Lindo (2023). To account for variations in samples, I standardised total oribatid abundance (adults and juveniles combined), and adult oribatid species richness by dry weight of peat samples. Abundance counts were then expressed as number of total individuals (adults or juveniles) per gram dry weight (# indiv./g dwt) while richness was expressed as number of species per gram dry weight (# species/g dwt) of peat soil. Mesostigmata, Prostigmata, Astigmata, and Collembola abundance were also standardised by dry weight (dwt) values of the peat samples and expressed as # indiv./g dwt. I calculated the Shannon-Weiner's (H') diversity index, Simpson's (D) diversity index, and Pielou's (J) evenness for the adult oribatid mite assemblage with the following equations, respectively:

$$H' = -\sum p_i \times ln \times p_i$$
$$D = 1/\sum p_i^2$$
$$J = H' / \ln(S)$$

Where  $p_i$  is the proportional abundance of each species based on adult identifications and S is species richness. The diversity indices (H' and J) were calculated in R using the {diversity} function from the 'vegan' package (Oksanen et al., 2022), while D was calculated using a syntax that matches the formula above. Finally, the average body length of each oribatid mite species was used to calculate the Community Weighted Mean (CWM) body size for each sample using the formula:

$$CWM = \sum p_i x_i$$

Where  $p_i$  is the proportional abundance of each species based on adult identification and  $x_i$  is the average body size (length) value for that species. Body lengths were determined from Behan-Pelletier and Lindo (2023) or measurements of individuals from the two sites.

### 2.2.4 Statistical analysis

For all statistical analysis, which were performed in R version 4.3.0 (R Core Team, 2023), I examined the two fen sites separately as they have previously been shown to differ significantly in mesofauna abundance, richness, diversity and composition (Barreto and Lindo, 2021). To first examine whether my sampling effort was satisfactory, I performed a species accumulation curve for the two sampling events combined, and rarefied the curve with 1000 permutations of the samples in random order using the {specaccum} function in the 'vegan' package (Oksanen et al., 2022). I also estimated species richness for both sampling events combined using Chao, Jackknife 1, Jackknife 2, and Bootstrap estimators with the function {specpool} also in the 'vegan' package. Richness estimation can only be performed with integers, so this was done using raw species richness values instead of standardised values.

I used a linear mixed-effects model (LMM) to test whether experimental warming treatment or time significantly affected my abiotic variables (surface peat temperature and moisture at 5 cm, peat temperature (30 cm), and sample moisture. In the models, treatment and time (month) were treated as main factors while plots nested within blocks were treated as random factors to control for spatial heterogeneity at the block level and account for repeated sampling at the plot level (like a repeated measures ANOVA). These models were built as:

#### *Variable of interest* ~ *Treatment* \* *Month, random* = $\sim 1|Block/Plots$

Model fitting was done using the {lme} function in the 'nlme' package (Pinheiro and Bates, 2023), and the {anova} function from the base package in R. The {nlme} function was used to fit the models while the {anova} function specified with a 'marginal' argument performed a type III ANOVA. Type III ANOVA tests main effects in the model while accounting for all other terms in the model. Plots nested within blocks were retained as random factors in all subsequent analysis with LMMs. Since I had two treatments and sampling times, I performed a 'pairwise' multiple comparison test on the LMM results while adjusting for significance with 'Bonferroni'. This was done using the {emmeans} function from the 'emmeans' package (Lenth, 2024) and the {cld} function

from the 'multcomp' package (Hothorn et al., 2008). The Bonferroni adjustment was applied to prevent a type 1 error due to multiple pairwise comparisons between warmed and ambient treatments across the two sampling times; it is a conservative approach that prevents overestimation of significance.

Similar LMMs were used to test the effect of experimental warming on the standardised abundance of microarthropods at the suborder level (Oribatida, Mesostigmata, Prostigmata, Astigmata, and Collembola), adult oribatid mite richness and diversity indices (H', D, J), the proportion of juveniles, proportion of asexual individuals, number of asexual species and CWM body size. The same LMMs were also used to test whether the standardised abundance of the small and asexual families Suctobelbidae and Brachychthoniidae, were significantly affected by warming treatment and time. While as with other analyses, these were performed separately for each study site; however, I also used an LMM to compare the proportion of asexual individuals, number of asexual species and the CWM body size between the two study sites, as these had not been tested before. In these models, 'site' was treated as fixed variable while 'treatment' was specified as random.

For the multivariate data, all species counts were also standardised by the dry weight of their respective samples. To explore the whole oribatid mite community composition, I calculated the Bray-Curtis dissimilarity composition among samples based on standardised adult oribatid mite abundances. The Bray-Curtis dissimilarity is an ecological distance measure used to quantify dissimilarities between different sites or samples based on their species composition i.e. species identity and proportional abundance. The dissimilarity values typically range from 0 to 1, with 0 indicating identical species compositions and 1 indicating completely different compositions. I examined and visualised the community composition of adult oribatid mites using non-metric multidimensional scaling (NMDS) with the {metaMDS} function in the 'vegan' package in R. On the NMDS plot, samples (or communities) that are more similar are plotted close to each other. Using the Bray-Curtis dissimilarity matrix, I tested for significant community compositional differences between treatments and between sampling times using a permutational analysis of variance (PERMANOVA) with the

{adonis2} function in 'vegan' package. A limitation with the {adonis2} function is that it is not able to account for repeated sampling unless specified; so, I first specified a permutation scheme with plots nested within blocks using the {with} function from the 'permute' package (Simpson, 2022) and {how} function from R base package.

To identify patterns in species composition, I performed a principal component analysis (PCA) using the {prcomp} function also in the 'vegan' package, and compared the axis factor loadings to the main effects of warming treatment and time using an LMM. The PCA is an indirect gradient dimensionality reduction method used to identify variables responsible for significant patterns in species composition. I also used peat temperature (30 cm) and sample moisture as predictor variables to perform a multiple linear regression on each of the principal component axes (PC1 and PC2) to investigate if either variable was responsible for variation in species composition. I then applied both peat temperature (30 cm) and sample moisture to a distance-based Redundancy Analysis (dbRDA) on species composition. The dbRDA is a direct gradient analysis for performing constrained ordinations on species composition data using non-Euclidean distance measures such as the Bray-Curtis distance measure, and is used to explore and visualise the relationship between species composition and environmental variables. I performed the dbRDA with the Bray-Curtis dissimilarity as the distance measure using the {capscale} function in 'vegan'. From the dbRDA analysis, species scores were extracted; only those species whose cumulative absolute axes contributions were  $\geq 50\%$ of the total contribution to the CAP axes were displayed on the dbRDA plot. This resulted in 28 species from the Sphagnum-dominated fen and 19 species from Carexdominated fen (Appendix B).

# 2.3 Results

# 2.3.1 Microarthropod abundance and richness from the *Sphagnum-* and *Carex-*dominated fens

In total, 26650 microarthropods (23063 Oribatida, 232 Mesostigmata, 961 Prostigmata, 1179 Collembola, 114 Astigmata, and 1101 other microarthropods including spiders and larva of Diptera and Coleoptera) were collected in June and September 2023 across both

fens. Adult oribatid mite richness across both fens was 40 species from 28 families. In the *Sphagnum*-dominated fen, Oribatida made up ~89% of all microarthropods, with a total of 16159 oribatid individuals; of these, 6491 (~40%) were adult Oribatida belonging to 23 families and 30 species. Similarly, in the *Carex*-dominated fen, Oribatida was the most abundant microarthropod group, comprising ~82% of all individuals collected, with a total of 6904 oribatid individuals, of which 2055 (~30%) were adults representing 17 families and 21 species.

The species accumulation curves for both study sites showed that richness gradually increased as more samples were processed (Figure 2.2). The big jump in the *Carex*-dominated fen accumulation curve (Figure 2.2B) was driven by five species that were only recorded in September samples: *Hoplophthiracarus illinoisensis* (Ewing, 1909), *Ceratoppia bipilis* (Hermann, 1804), *Pergalumna emarginata* (Banks, 1895), *Pilogalumna* sp., and *Naiazetes* sp. (a singleton). Estimated total richness based on Chao, Jackknife and Bootstrap estimates were between 31.5 - 33.0 species for the *Sphagnum*-dominated fen, average oribatid abundance per sample was  $202.84 \pm 11.23$  SE while richness was  $15.34 \pm 0.32$  SE. At the *Carex*-dominated fen, average abundance and richness per sample was  $64.22 \pm 7.13$  SE and  $8.06 \pm 0.57$  SE, respectively.



Figure 2.2: Accumulated adult oribatid mite species richness at the A) *Sphagnum*-dominated fen and B) *Carex*-dominated fen.

Collector curves (in black) show number of samples processed (x-axis) and number of accumulated number of species (y-axis) discovered at two different time points (left to right on x-axis, June samples:1 – 16; September samples: 17 – 32). Rarefied accumulation curves are plotted from means (in grey) and standard deviation of 1000 permutations of samples (brown/green) in random order.

## 2.3.2 Effect of warming treatment at the *Sphagnum*-dominated fen

Surface peat temperature (5 cm) was not significantly different between treatments (F<sub>1,11</sub> = 0.05, p = 0.834) but was significantly higher in September (F<sub>1,14</sub> = 139.84, p <0.001). Surface peat moisture (5 cm) was lower in the warmed plots by ~20% in June and ~19% in September, did not differ significantly between treatments (F<sub>1,11</sub> = 2.94, p = 0.114), but was significantly lower in September (F<sub>1,14</sub> = 36.15, p < 0.001). Peat temperature (30 cm) was significantly higher in warmed plots (F<sub>1,11</sub> = 14.216, p = 0.003) and higher in September (F<sub>1,14</sub> = 358.37, p < 0.001); the overall treatment effect was driven by observed effects within each sampling period (June: p = 0.003, September: p = 0.093). Sample moisture was lower in warmed plots by ~16% in June and ~8% in September but did not differ significantly between treatments (F<sub>1,11</sub> = 2.33, p = 0.155) or time (F<sub>1,14</sub> = 1.56, p = 0.232) (Table 2.1).

		Surface peat temperature °C (5 cm)	Surface peat moisture V/V% (5 cm)	Peat temperature °C (30 cm)	Sample moisture (%)
June	Ambient	$12.86\pm0.58^{b}$	$26.45\pm4.02^{\text{a}}$	$10.72\pm0.14^{\text{c}}$	$861.00\pm43.64$
	Warmed	$12.99\pm0.45^{b}$	$21.08\pm2.2^{ab}$	$11.33\pm0.12^{b}$	$727.94\pm84.65$
September	Ambient	$20.23\pm0.27^{\rm a}$	$11.35\pm1.66^{bc}$	$13.59\pm0.25^{\rm a}$	$799.66\pm47.76$
	Warmed	$20.52\pm0.4^{\rm a}$	$9.32\pm0.94^{\text{c}}$	$13.88\pm0.11^{a}$	$735.87\pm 66.45$

Table 2.1: Environmental variables measured at the Sphagnum-dominated fen.Values are averages ± standard error. Letters indicate significant groups.

Total oribatid abundance (adult and juveniles) did not differ significantly between ambient and warmed treatments ( $F_{1,11} = 0.10$ , p = 0.764) or time (sampling months) ( $F_{1,14}$ = 2.54, p = 0.133) but was observed to be higher in September. Adult oribatid richness was not significantly different between ambient and warmed treatment ( $F_{1,11} = 0.07$ , p = 0.801), but significantly higher in September ( $F_{1,14} = 6.13$ , p = 0.037). Although richness did not change between treatments, Shannon's (H') and Simpson's (D) diversity indices were lower in warmed plots, albeit non-significantly (H':  $F_{1,11} = 0.85$ , p = 0.378; D:  $F_{1,11}$ = 0.99, p = 0.339) (Table 2.2). Similarly, species evenness was observed to be nonsignificantly lower in warmed plots (J:  $F_{1,11} = 1.50$ , p = 0.246). The proportion of oribatid juveniles did not differ significantly between ambient and warmed plots ( $F_{1,11} = 0.08$ , p = 0.784) but increased significantly over time ( $F_{1,14} = 6.04$ , p = 0.028) with higher number of juveniles in September. Neither treatment ( $F_{1,11} = 0.24$ , p = 0.879) nor time ( $F_{1,14} =$ 2.764, p = 0.119) significantly affected the proportion of asexual oribatid individuals. Again, neither treatment ( $F_{1,11} = 0.24$ , p = 0.879) nor time ( $F_{1,14} = 2.764$ , p = 0.119) significantly affected the proportion of asexual oribatid individuals; specifically, the proportion of oribatid individuals ranged between 0.92 to 0.94. The number of asexual species did not also differ significantly between treatments ( $F_{1,11} = 0.61$ , p = 0.451), but, as with oribatid abundance and richness, it was higher in September, albeit marginally  $(F_{1,14} = 3.42, p = 0.086)$  (Table 2.2).

		Total Oribatida abundance (# indiv. / g dwt)	Adult Oribatida richness (# species/ g dwt)	Shannon's diversity (H')	Simpson's diversity (D)	Pielou's evenness (J)	Proportion of oribatid juveniles	Number of asexual oribatid species (# species/ g dwt)
Juno	Ambient	$94.11\pm14.13$	$3.21\pm0.17$	$2.06\pm0.05$	$5.86 \pm 0.39$	$0.77\pm0.02$	$0.51\pm0.05$	$2.73\pm0.18$
June	Warmed	$85.83\pm9.07$	$3.13\pm0.24$	$1.98\pm0.05$	$5.09\pm0.53$	$0.72\pm0.03$	$0.53\pm0.04$	$2.48\pm0.24$
Sontombou	Ambient	$136.92 \pm 20.95$	$3.97\pm 0.30$	$2.11\pm0.06$	$6.04\pm0.62$	$0.77\pm0.03$	$0.65\pm0.03$	$3.33\pm0.31$
September	Warmed	$151.3\pm26.82$	$3.60\pm0.25$	$1.93\pm0.08$	$4.88\pm0.60$	$0.71\pm0.03$	$0.60\pm0.05$	$2.93\pm0.30$

Table 2.2: Oribatid mite univariate community measures at the Sphagnum-dominated fen.Values are averages ± standard error. Letters indicate significant groups.

Nonetheless, average community body size marginally reduced in the warmed treatment ( $F_{1,11} = 13.065 \text{ p} = 0.107$ ) but did not change with time ( $F_{1,14} = 2.19, \text{ p} = 0.160$ ). The overall treatment effect on body size was driven by effects observed within each sampling period. Specifically, body size was ~7% and ~13% lower in the warmed plots in June (p = 0.108) and September (p = 0.005) (Figure 2.3).





The smaller asexual families Brachychthoniidae and Suctobelbidae showed contrasting responses to warming treatment. Overall, Brachychthoniidae was higher in the warmed plots by ~14% in June and ~48% in September but was not significantly affected by treatment ( $F_{1,11} = 0.09$ , p = 0.768) or time ( $F_{1,14} = 0.46$ , p = 0.505). But response of Brachychthoniidae to treatment differed within each sampling period, being nonsignificant in June (p = 0.768) and approaching significance in September (p = 0.087). Contrastingly, Suctobelbidae abundance was significantly lower in the warmed plots ( $F_{1,11} = 8.01$ , p = 0.01) and significantly lower in September ( $F_{1,14} = 17.50$ , p = 0.009); overall treatment effect on Suctobelbidae abundance was driven by significance in early summer (June: p = 0.016, September: p = 0.684) (Table 2.3). The effect of treatment and time for other microarthropod groups at the *Sphagnum*-dominated fen is shown in Appendix C. A significant relationship between CWM body size and proportion of asexual oribatid individuals was observed at this fen ( $F_{1,15} = 15.36$ , p = 0.001). Specifically, CWM body size tended to reduce as the proportion of asexual oribatid individuals metabelies.

 

 Table 2.3: Brachychthoniidae and Suctobelbidae abundance at the Sphagnumdominated fen.

		Brachychthoniidae	Suctobelbidae
I	Ambient	$10.65 \pm 1.44$	$5.35\pm0.64^{\rm a}$
June	Warmed	$11.84\pm2.08$	$3.44\pm0.30^{ab}$
Santamban	Ambient	$7.95\pm2.71$	$2.53\pm0.65^{\text{b}}$
September	Warmed	$15.34\pm4.44$	$2.24\pm0.30^{\text{b}}$

Values are standardized abundances (# indiv./g dwt)  $\pm$  SE. Letters indicate significant groups.

# 2.3.3 Community composition at the *Sphagnum*-dominated fen The effect of treatment on adult oribatid community composition was near significance (PERMANOVA: $F_{1,30} = 1.57$ , p = 0.093) as warmed plots became dissimilar from ambient plots and from themselves. Dissimilarity is displayed on the NMDS plots as the distance between samples and the size of the 95% confidence ellipse. Samples plotted close together have similar species composition and relative abundance. Time ( $F_{1,30} =$ 3.10, p = 0.004), as well as the interaction between treatment and time ( $F_{3,28} = 1.80$ , p =0.011) were also a significant drivers of community composition. The (outlier) point farthest away from other points is a plot (June-PF-8) with very low moisture level (61% lower than average); this corresponded with the presence (albeit in low abundance) of two species, *Lucoppia* nr. *apletosa* (Higgins and Woolley, 1975) and *Oribatula tibialis* (Nicolet, 1855) that only appeared in that plot. In the principal component analysis, the first two axes explained ~25% variation in adult oribatid mite community composition (Figure 2.4).



Figure 2.4: Non-metric multidimensional scaling plot of adult oribatid mite community composition at the *Sphagnum*-dominated fen for the June and September 2023 sampling period.

Community is plotted by treatment and time. Ellipses indicate 95% confidence intervals.

In the principal component analysis, the first two axes explained ~25% variation in adult oribatid mite community composition. The PC1 (explaining ~15 % variation) was associated with treatment, albeit marginally ( $F_{1,11} = 4.159$ , p = 0.066) but was nonsignificant with time ( $F_{1,15} = 0.000$ , p = 0.988). The PC2 (explaining ~9% variation) was not significant with treatment ( $F_{1,11} = 0.007$ , p = 0.934) but was marginally significant with time ( $F_{1,15} = 3.150$ , p = 0.096) (Figure 2.5). The regression with peat temperature (30 cm) and sample moisture as predictor variables on the PC axes showed that only PC1 was significantly associated with a variable (peat moisture: t = 6.57, p < 0.001). The overall regression model was also significant ( $F_{2,29} = 21.59$ , p < 0.001) implying a possible interactive effect of both peat temperature and sample moisture on species composition.



Figure 2.5: Principal Component Analysis (PCA) biplot of adult oribatid mite composition at the *Sphagnum*-dominated fen for the June and September 2023 sampling period.

Species are plotted against temperature and time effects. For full species names, see Appendix A.

The dbRDA model (Pseudo- $F_{1,29} = 2.80$ , p = 0.001) showed that peat temperature (Pseudo- $F_{1,29} = 3.10$ , p = 0.003) and peat moisture (Pseudo- $F_{1,29} = 2.49$ , p = 0.009) were significant drivers of adult oribatid mite composition explaining ~18% of the total variation in community composition. The first constrained dbRDA axes (CAP1) explained ~62% variation while the second axes (CAP2) explained ~38% and both axes were also significant (CAP1: Pseudo- $F_{1,29} = 3.44$ , p = 0.002; CAP2: Pseudo- $F_{1,29} = 2.15$ , p = 0.014) (Figure 2.6).



Figure 2.6: A distance-based redundancy analysis (dbRDA) plot of adult Oribatida from the *Sphagnum*-dominated fen mesocosms.

Species are plotted against temperature and moisture variables. Smaller dashed lines connect points to species, while larger and longer dashed lines (with arrows) show direction and strength of environmental variables. Full species names are listed in Appendix A.

# 2.3.4 Effect of warming treatment at the *Carex*-dominated fen

Surface peat temperature (5 cm) was not affected by treatment ( $F_{1,11} = 1.70$ , p = 0.218) and no significant trends were observed between ambient and warmed plots, but higher temperatures were recorded in September ( $F_{1,14} = 21.89$ , p < 0.001). Surface peat moisture (5 cm) did not show significant trend in plots and did not differ significantly between treatments ( $F_{1,11} = 0.01$ , p = 0.913) nor between sampling times ( $F_{1,14} = 0.56$ , p =0.466). Peat temperature (30 cm) was marginally higher in warmed plots ( $F_{1,11} = 3.203$ , p = 0.090) and significantly higher in September ( $F_{1,14} = 125.79$ , p < 0.001). Although sample moisture was lower in warmed plots by ~ 4% in June and 12% in September, it did not differ between treatments ( $F_{1,11} = 0.19$ , p = 0.673), but was significantly higher in September ( $F_{1,14} = 10.64$ , p = 0.006) (Table 2.4).

		Surface peat temperature °C (5 cm)	Surface peat moisture V/V% (5 cm)	Peat temperature °C (30 cm)	Sample moisture (%)
June	Ambient	$18.74\pm0.46^{\text{b}}$	$52.63\pm2.37$	$11.63\pm0.13^{\text{a}}$	$644.87 \pm 43.51^{ab}$
	Warmed	$17.81\pm0.34^{\text{b}}$	$53.06\pm2.65$	$11.89\pm0.13^{a}$	$617.68 \pm 51.37^{b}$
Santambar	Ambient	$21.97\pm0.62^{\rm a}$	$55.15\pm3.22$	$13.16\pm0.09^{b}$	$803.54 \pm 46.17^{a}$
September	Warmed	$21.67\pm0.56^{\text{a}}$	$54.99 \pm 2.68$	$13.26\pm0.07^{b}$	$710.16 \pm 38.96^{ab}$

Table 2.4: Environmental variables measured at the Carex-dominated fen.Values are averages ± standard error. Letters indicate significant groups

Total oribatid abundance was 43% lower in the warmed plots; this was not significant between treatments ( $F_{1,11} = 0.41$ , p = 0.533), but time was a significant effect as total oribatids were higher in September ( $F_{1,11} = 13.56$ , p = 0.003). However, the effect of treatment on total oribatid abundance varied between sampling months, being nonsignificant in June (p = 0.533) and significant in September (p = 0.037). There was no significant effect of treatment on richness ( $F_{1,11} = 0.166$ , p = 0.692) but richness was significantly higher in September ( $F_{1,14} = 7.60$ , p = 0.015) (Table 2.5). Shannon's (H') and Simpson's (D) diversity indices were unaffected by treatment (H':  $F_{1,11} = 0.27$ , p = 0.612; D:  $F_{1,11} = 0.50$ , p = 0.492) or time (H':  $F_{1,14} = 2.71$ , p = 0.122; D:  $F_{1,14} = 0.70$ ;  $F_{$ 0.417), and no significant trends were observed between warmed and ambient treatments (Table 2.5). Resultingly, evenness was also not affected by treatment ( $F_{1,11} = 1.13$ , p = (0.312) or time (F<sub>1,14</sub> = 0.06, p = 0.809). The proportion of juveniles did not significantly change with treatment ( $F_{1,11} = 2.91$ , p = 0.116) but was significantly higher in September  $(F_{1,14} = 11.04, p = 0.005)$ . The proportion of asexual individuals did not change with treatment ( $F_{1,11} = 1.52$ , p = 0.243) or time ( $F_{1,14} = 1.54$ , p = 0.235) but ranged between 0.88 to 0.94. Although the number of asexual species did not also differ between treatments ( $F_{1,11} = 0.07$ , p = 0.796), it was marginally higher in September ( $F_{1,15} = 4.06$ , p = 0.063) (Table 2.5).

Table 2.5: Oribatid mite univariate community measures at the *Carex*-dominated fen.Values are averages ± standard error. Letters indicate significant groups.

		Total Oribatida abundance (# indiv./ g dwt)	Adult Oribatida richness (# species/ g dwt)	Shannon's diversity (H')	Simpson's diversity (D)	Pielou's evenness (J)	Proportion of oribatid juveniles	Number of asexual oribatid species (# species/ g dwt)
Juno	Ambient	$17.45\pm4.73^{\text{b}}$	$0.80\pm0.14$	$1.33\pm0.19$	$3.42\pm0.65$	$0.68\pm0.06$	$0.57\pm0.04^{\text{bc}}$	$0.62\pm0.10$
June	Warmed	$11.13\pm2.07^{b}$	$0.89\pm0.20$	$1.42\pm0.19$	$3.88\pm0.79$	$0.74\pm0.07$	$0.48\pm0.04^{b}$	$0.65\pm0.14$
Sontombor	Ambient	$51.11\pm12.7^{\mathrm{a}}$	$1.30\pm0.17$	$1.59\pm0.14$	$3.86\pm0.59$	$0.70\pm0.03$	$0.73\pm0.04^{a}$	$0.85\pm0.08$
September	Warmed	$27.85\pm5.64^{ab}$	$1.10\pm0.20$	$1.46\pm0.18$	$3.61\pm0.58$	$0.74\pm0.03$	$0.70\pm0.05^{ab}$	$0.78\pm0.13$

CWM body size was not affected by treatment ( $F_{1,11} = 0.06$ , p = 0.808) or time ( $F_{1,14} = 0.02$ , p = 0.898) (Figure 2.7). Brachychthoniidae abundance did not change significantly between warmed and ambient treatments ( $F_{1,11} = 0.76$ , = p = 0.402) nor between sampling months ( $F_{1,14} = 2.34$ , p = 0.148) but was always higher in the warmed plots. Suctobelbidae abundance was neither affected by treatment ( $F_{1,11} = 0.00$ , p = 0.927) nor time ( $F_{1,14} = 0.70$ , p = 0.416) but, on average, lower in the warmed plots (Table 2.6). Unlike what I observed at the *Sphagnum*-dominated fen, CWM body size tended to increase with the proportion of asexual individuals, but this was not significant ( $F_{1,15} = 1.45$ , p = 0.247). The effect of treatment and time for other microarthropod groups at the *Carex*-dominated fen are shown in Appendix D.





 Table 2.6: Brachychthoniidae and Suctobelbidae abundance at the Carex-dominated fen.

		Brachychthoniidae	Suctobelbidae
June	Ambient	$0.08\pm0.04$	$0.54\pm0.16$
	Warmed	$0.37\pm0.16$	$0.49\pm0.15$
September	Ambient	$0.43\pm0.16$	$0.93\pm0.63$
	Warmed	$0.82\pm0.41$	$0.31\pm0.20$

Values are standardized abundances (# indiv./g dwt)  $\pm$  SE. None of the comparisons where significant.

# 2.3.5 Community composition at the Carex-dominated fen

At the community level, treatment was a significant driver of adult oribatid mite composition (PERMANOVA:  $F_{1,30} = 2.31$ , p = 0.017). Although some samples contained slightly dissimilar communities in September, overall community composition did not change significantly with time (PERMANOVA:  $F_{1,30} = 1.18$ , p = 0.154). However, there was still a significant interactive effect of treatment and time on community composition ( $F_{3,28} = 1.43$ , p = 0.033) (Figure 2.8).



Figure 2.8: Non-metric dimensional scaling plot of adult oribatid mite community composition at the *Carex*-dominated fen for the June and September 2023 sampling period.

Community is plotted by treatment and time. Ellipses indicate 95% confidence intervals

In the principal component analysis, the first two axes explained ~44% of the variation in community composition. The first axes (PC1) explained ~23% of the variation and was not significantly associated with treatment ( $F_{1,11} = 0.12$ , p = 0.740) but was affected by time ( $F_{1,15} = 4.82$ , p = 0.044). The second axes (PC2) explained ~21% variation and was marginally associated with treatment ( $F_{1,11} = 3.67$ , p = 0.082) but time was non-significant ( $F_{1,15} = 1.35$ , p = 0.263) (Figure 2.9). In the regression models, none of the PC axes were associated with peat temperature (30 cm) and/or sample moisture or their interaction.



Figure 2.9: Principal component analysis (PCA) biplot adult oribatid mite composition at the *Carex*-dominated fen for the June and September 2023 sampling period.

Species are plotted against temperature and time effects. For full species names, see Appendix A The dbRDA model (Pseudo- $F_{1,29} = 1.02$ , p = 0.430) showed that neither peat temperature (Pseudo- $F_{1,29} = 0.81$ , p = 0.607) nor peat moisture (Pseudo- $F_{1,29} = 1.24$ , p = 0.261) significantly affected species composition at the *Carex*-dominated fen, although they both explained ~7% variation. The constrained axes were also insignificant (CAP1:  $F_{1,29} = 1.48$ , p = 0.397; CAP2:  $F_{1,29} = 0.57$ , 0.847), although CAP1 explained ~72% while CAP2 explained 28% (Figure 2.10).





Species are plotted against temperature and moisture variables. Smaller dashed lines connect points to species, while larger and longer dashed lines (with arrows) show direction and strength of environmental variables. Full species names are listed in Appendix A.

# 2.3.6 Asexual Oribatida and average community body size between fens

The proportion of asexual oribatid individuals was nearly significantly ( $F_{1,61} = 3.17$ , p = 0.080) between *Sphagnum*- and *Carex*-dominated fens. The number of asexual oribatid species was significantly higher ( $F_{1,61} = 210.46$ , p < 0.001) in the *Sphagnum*-dominated fen. Concomitantly, CWM body size was significantly lower ( $F_{1,61} = 167.65$ , p < 0.001) in the *Sphagnum*-dominated fen (Figure 2.11).



#### Figure 2.11: Asexual Oribatida and average community body size between fens.

Proportion of asexual oribatid individuals (A); Number of asexual oribatid species (B); Community weighted mean (CWM) body size (C). Upper boundaries represent 25<sup>th</sup> percentile while lower boundaries represent 75<sup>th</sup> percentile; the horizontal line inside the box is the median

# 2.4 Discussion

### 2.4.1 Warming effect on abiotic factors

Climate change is anticipated to increase both air and soil temperatures, but also affect soil moisture through changes in precipitation (Trenberth, 2011), increased plant transpiration rates (Kirschbaum, 2008), and increased evaporation rates (Konapala et al., 2020). Here, I observed that seven years of experimental warming of two boreal peatland sites resulted in peat drying. Both fen sites showed reduced soil moisture as measured with a soil moisture probe and gravimetrically from samples collected for fauna, and although this trend was more strongly seen at the drier Sphagnum-dominated fen, it persisted in both spring (early June) and late summer (September) sampling seasons. The mechanism for this warming-induced drying is not clear but presumed to be due to increased evapotranspiration rates. Losses in Sphagnum mosses which have been observed at my study site (Dieleman et al., 2015; Lyons et al., 2020; Hopkins, 2024) as well as other peatland sites (Norby et al., 2019) may also contribute to warming-induced drying in peatlands as mosses are known to have high moisture holding capabilities (Rice, 2009) which makes them important ecosystem engineers in boreal peatland systems. Soil surface temperatures (5 cm) were only modestly higher at the Sphagnumdominated fen and lower at the Carex-dominated fen under experimental warming, the latter effect is possibly a result of shading from increased *Carex* productivity as has also previously been shown (Dieleman et al., 2015, Lyons et al., 2020). However, regardless of the mechanism, warming-induced drying was an environmental effect that affected oribatid mites at both sites of my study.

#### 2.4.2 Warming effect on abundance and richness

The relationship between microarthropod abundance and richness with soil moisture is often observed to be positive and generally linear such that decreases in soil moisture (or water content) are correlated with decreased oribatid mite abundance, density and/or diversity. However, the majority of studies on this relationship are from forest soils (Lindberg et al., 2002; Tsiafouli et al., 2005; Junggebauer et al., 2024) and grasslands (O'Lear and Blair, 1999; Chikoski et al., 2006) where soil moisture is generally much
lower than peatlands. At high levels of soil moisture, air-filled soil pore spaces become filled with water, and soils become anoxic, resulting in reduced habitable pore space for microarthropods and, therefore, lower richness and abundance (Larsen et al., 2004, Turnbull and Lindo, 2015). However, Barreto et al. (2021) suggested that in peatlands, warming-induced drying can lead to the loss of some species (specifically semi-aquatic), but may also create habitable pore spaces for species associated with drier environments. Overall, I did not observe any significant difference in total abundance and richness between ambient and warmed plots at either fen site in my study. However, trends were slightly variable between the fen sites and sampling times. In the drier Sphagnumdominated fen, oribatid abundance was slightly higher under experimental warming in September but not in June, and this was mainly driven by the Brachychthoniidae and Tectocepheus velatus. This slight difference between the two sampling months may be due to the greater moisture difference between warmed and ambient plots in June (~16% in June vs. ~8% in September). The slight increase in oribatid abundance under experimental warming was accompanied by a decrease in richness, diversity and evenness, likely due to the increase in Brachychthoniidae and Tectocepheus velatus, while typical wet habitat species (such as Eniochthonius mahunkai and Malaconothrus mollisetosus) were observed to be lower under experimental warming. At the Carexdominated fen, however, a non-significant reduction in total oribatid mite abundance under experimental warming was consistent across the sampling periods, driven by the reduction of semi-aquatic species (e.g., Tyrphonothrus maior, Trhypochthoniellus setosus canadensis, Limnozetes guvi). However, this did not correspond with consistent trends (reduction/increase) in richness, diversity and evenness. Specifically, richness, diversity and evenness were only observed to be non-significantly lower under experimental warming in September when moisture levels were lower between ambient and warmed treatment (~4% in June vs.  $\sim$ 12% in September). Overall, warming at the Sphagnumdominated fen, which already had a lower moisture condition, seems to reduce richness and diversity. But at the Carex-dominated fen, where moisture levels are higher, this trend was only observed in September when moisture levels under experimental warming dropped by 12%. This implies that warming effects on oribatid mite communities in the peatlands are possibly dependent on initial moisture levels.

#### 2.4.3 Warming effect on oribatid juveniles

Warming may increase oribatid juvenile presence at the community level, as it does abundance, by enhancing reproductive turnover at the population level through increased metabolism at the individual level (Lindo, 2015). And since oribatid mites have developmental times that differ between species, measuring juveniles may provide insights into how the community may shift under climate change. Contrary to my prediction that juvenile proportion would increase under warming, due to elevated reproduction, the juvenile proportion did not change significantly under warming. But I observed it to be slightly lower under warming at the *Carex*-dominated fen, where semiaquatic species, such as Tyrphonothrus maior, dominated. As with many soil microarthropods, oribatid juveniles are weakly sclerotized, and therefore less tolerant of drier conditions that are often concomitant with warming. So, while warming may lead to increased juvenile presence, drying may cause stress and eventual death by desiccation. Alternatively, the drying effect on juveniles may be indirect through impacts on adult oribatid mite activity such as feeding, which may affect reproduction. Thakur et al. (2017) showed that detritivore feeding activity was reduced by ~14% under warming and drying in a temperate boreal region. However, the exact mechanism behind this observed trend in juvenile proportion in my study remains unclear. The decline in oribatid juveniles under warming conditions has been reported in peatlands (Barreto et al., 2021), as well as forest systems (Alatalo et al., 2017), and this response was assumed to be due to drying. Contrastingly, in situations where warming-induced drying is prevented experimentally, warming was shown to be beneficial for oribatid juveniles (Lindo, 2015; Pettit et al., 2021).

#### 2.4.4 Warming effect on asexual oribatid mites and body size

While most oribatid mites reproduce sexually, about 10% are estimated to be parthenogenetic (asexually-reproducing) (Norton and Palmer, 1991) most of which occupy wetlands (Behan-Pelletier and Bissett, 1994; Maraun et al., 2019; Maraun et al., 2022) and are often small. The presence of asexual oribatid species in wetlands such as peatlands is thought to be due to the abundance of resources (Bluhm et al., 2016; Maraun et al., 2019) and/or the challenges faced by sexual species in reproducing effectively in wet habitats. Due to the relationship between temperature and metabolism, I had predicted that warming would elevate reproduction in the smaller asexual species, leading to an increase in the proportion of asexual individuals, and the number of asexual species. However, I only observed a non-significant lower number of asexual species under warming, especially at the *Sphagnum*-dominated fen. Typical features of most asexual oribatid species are small body size and weak sclerotization. With a high surface-to-volume ratio, they lose water quickly, and their weaker cuticle offers little protection against desiccation. So, while my study showed that some asexual species benefited from warming (Appendix A), their small size and weak sclerotization may have made some of them vulnerable to warming-induced drying; this may have led to the insignificant result in the proportion of asexual oribatid individuals between treatments.

Despite no change in the proportion of asexual oribatid individuals, I still observed a reduction in community body size under experimental warming at the Sphagnumdominated fen. While this effect was only marginal in June, it was significant at the end of the growing season (September). This trend was consistent with a higher abundance of Brachychthoniidae individuals which was ~48% more under experimental warming in September and nearly significant. As one of the dominant families under experimental warming and the smallest size recorded in my study, it is evident that the increase in Brachychthoniidae may have altered the composition of the community at the Sphagnumdominated site such that it impacted the average community body size. At the Carexdominated fen where Brachychthoniidae was not as high under warming, community body size did not change. Brachychthoniidae is a non-peatland group (family); they are known to dominate grasslands and prairies (Clapperton et al., 2002; Osler et al., 2008) which generally have lower moisture than peatlands. This suggests that Brachychthoniidae may not only benefit from warming, as previously thought by Lindo (2015) and Barreto et al., (2021), but also from the associated drying, which may create more habitable soil pore space for them. Suctobelbidae abundance, on the other hand, consistently reduced under warming at both study sites, with significant decreases observed at the drier Sphagnum-dominated fen. These observations are supported by the

PCA and dbRDA plots, which show a similar trend for Brachychthoniidae and Suctobelbidae. Brachychthoniidae was consistently associated with warmed treatment and peat temperature in both PCA and dbRDA plots, respectively across the study sites. In contrast, Suctobelbidae was associated with ambient treatment in PCA plots at both sites. Further, the dbRDA plots show Suctobelbidae that correlated with sample moisture at the drier *Sphagnum*-dominated fen, and interestingly, occupies an intermediate position between sample moisture and temperature at the wetter *Carex*-dominated fen. The decline in Suctobelbidae was possibly due to long-term (7 years) warming-induced drying effect – an important part of my study. Overall, this suggests that while some oribatid species may benefit from warming, this response may change over time, highlighting the importance of long-term studies for understanding the dynamics of oribatid mite responses to climate change.

#### 2.4.5 Warming effect on community composition

Trends observed on oribatid mite measures were also evident at the community level where, on the NMDS, warmed (and drier) plots) differed from ambient plots, and each other. At the *Sphagnum*-dominated fen, heterogeneity in the warmed plots was possibly driven by the combined decline of peatland species and an increase in non-peatland species (due to increased habitable soil spore spaces under warming-induced drying), as discussed earlier. In contrast, at the *Carex*-dominated fen where higher moisture levels supported semi-aquatic species dominance, heterogeneity in the warmed plots resulted solely from the decline in the abundance of the semi-aquatic species. Time was also a significant variable that affected community composition as oribatid mite communities in September were significantly different from June at both fens, especially in terms of abundance and richness. The effect of time may have been due to seasonality, but may have also been driven by the moisture difference between the two sampling periods; this may also explain the interactive effect of warming treatment and time on oribatid mite community composition on the NMDS.

#### 2.4.6 Conclusion

While my study only focused on the impacts of warming (and associated drying) on oribatid mites, I recognize that other unmeasured factors, such as changes in resource availability, can also affect oribatid mite communities under climate change. However, since my study systems are boreal peatlands where temperature and moisture drive most ecological processes, changes in resource availability may also be driven by temperature and moisture. Given how below-ground diversity and/or functions may be affected by interactions between multiple global change factors (Rillig et al., 2019; Peng et al., 2022), it is pertinent to conduct experiments to investigate and disentangle (Chapter 3) the simultaneous impacts of these multiple factors on below-ground communities and functions.

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# Chapter 3

# 3 Disentangling the effects of temperature and moisture on oribatid mite communities in boreal peatlands

# 3.1 Introduction

Climate change is forecasted to cause a +4°C increase in global temperatures based on the Shared Socioeconomic Pathway-5 (SSP-5) (IPCC, 2023). However, the impact of climate change on boreal systems is expected to be even more pronounced, with temperatures projected to rise by as much as +8°C (IPCC, 2023). Boreal peatlands – wetland environments where the rate of organic matter inputs exceeds the rate of decomposition found in northern latitudes – might be particularly susceptible to warming climate as boreal peatlands are typified by high moisture and low temperatures. Climate warming will also be concomitant with soil moisture loss (Balting et al., 2021), especially in northern regions including areas where boreal peatlands are located (He and Pomeroy, 2023), mostly because of increased evaporation and transpiration (Tarnocai, 2009; Helbig et al., 2020). Combined, these changes in temperature may have direct effects on decomposition processes (Ofiti et al., 2022) or indirect effects by altering both aboveground (Dieleman et al., 2015) and below-ground communities (Barreto et al., 2021) and affecting carbon dynamics and storage in peatlands.

Boreal peatlands host unique ecological communities adapted to waterlogged, nutrientpoor, and acidic conditions, including *Sphagnum* mosses, carnivorous plants, and microbial communities (Wieder and Vitt, 2006). Oribatid mites (Acari: Oribatida) are among the most dominant below-ground communities in terrestrial soils including peatlands. Importantly, oribatid mite communities are sensitive to environmental changes in temperature and moisture, when these changes are within non-lethal levels (Madge, 1965; Siepel, 1996). Like other ectothermic organisms, warmer temperatures generally promote increased abundance by elevating metabolism and reproduction. But warmer temperatures have been shown to favour smaller oribatid mites (300 µm) that seem to dominate their communities under warming (Lindo, 2015). This phenomenon is supported by the metabolic theory of ecology (Brown et al., 2004) which implies that smaller species or individuals will reproduce more quickly (especially under warmer conditions) due to elevated metabolic rates. As a result, communities may experience a shift towards smaller body sizes (Sheridan and Bickford, 2011; Lindo, 2015).

Oribatid mite abundance, species richness and activity typically increase with increasing soil moisture (Lindo et al., 2012, Siebert et al., 2019), but this relationship is unimodal as high levels of soil moisture can decrease habitable soil pore space. Most of what is known about the response of oribatid mites to changing moisture conditions are from forest systems where warming-induced drying (moisture reduction) leads to negative responses in oribatid mites (Alatalo et al., 2017; Siebert et al., 2019). However, in situations where high water table (or moisture conditions) reduces soil pore space, such as in peatlands, drying may benefit oribatid mites (Barreto et al., 2021). There is some indication that smaller mites increase under dry conditions (Xu et al., 2012), as has been reported for other soil communities (see Lu et al., 2023). But moisture often seems to interact with temperature (Tsiafouli et al., 2005), making its effects non-linear and difficult to predict, and warming-induced drying effects seen during climate change further complicate our understanding of these two factors. Some studies on peatland oribatid mite communities have revealed a negative relationship between temperature and moisture (Barreto et al., 2021; Barreto et al., 2023), suggesting that their interaction may be a more significant driver of oribatid mite communities. However, despite these findings, the interactive effects of temperature and moisture on the communities of oribatid mites in boreal peatlands remain poorly understood and have yet to be disentangled.

In this study, I used a factorial mesocosm experiment to disentangle the main and interactive effects of temperature and moisture on oribatid mite communities in boreal peatlands. I hypothesised that warmer temperatures would increase reproduction and lower moisture levels may create more habitable pore space leading to an overall positive effect oribatid mite community. I therefore predicted that this would lead to increased oribatid mite abundance and richness. I also hypothesised that the combined effect of temperature and moisture would lead to a reduction in the average body size of the

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oribatid mites and communities under warmer, drier conditions would have greater number of individuals from the smaller species.

# 3.2 Materials and methods

#### 3.2.1 Study area

The study area for sampling is in the southern boreal ecozone, near White River, Ontario, Canada (48°21' N, 84°20' W). Two fen peatlands that differ in various aspects such as nutrient status, water table and moisture levels, above-ground vegetation, and belowground biotic communities (Webster and McLaughlin, 2010; Palozzi and Lindo, 2017; Lyons et al., 2020; Barreto and Lindo, 2021) were selected for sampling. For a comprehensive site description, see Chapter 2. Briefly, both study sites are situated within 2 km of each other in the same watershed and are part of the long-term BRACE (Biological Response to A Changing Environment) project initiated in 2012. They are also long-term monitoring sites with the Ontario Ministry of Natural Resources and Forestry (MNRF). The first site is a Sphagnum-dominated fen. It is a 4.5 ha peatland characterised by a total peat depth of ~116 cm, and lower moisture conditions resulting from a water-table  $\sim 30$  cm below the peat surface (Webster and McLaughlin, 2010). It is fungal-dominated and has a higher abundance and richness of plant and mesofauna communities (Palozzi and Lindo, 2017; Lyons et al., 2020; Barreto and Lindo, 2021). The second site is called the *Carex*-dominated fen. It is a 10.2 ha peatland characterised by a total peat depth of  $\sim 60$  cm, intermediate level of nutrients and a pH  $\sim 5.4$ . High moisture conditions result from a higher water table close to the peat surface for most of the year at this site (Webster and McLaughlin, 2010). The site is also bacterial-dominated and shows a lower mesofauna abundance and richness when compared to the other site (Barreto and Lindo, 2021).

### 3.2.2 Study design and sampling

In June 2024, I collected peat samples from each of the *Sphagnum*- and *Carex*-dominated fens for a 4-month mesocosm experiment — roughly corresponding to the average boreal forest growing season. Samples were collected from open lawn-like areas (avoiding hummocks and hollows) with equal representation of *Sphagnum divinum* (Flatberg ex

Hassel) and *Sphagnum angustifolium* (C.E.P. Jensen ex Russow) mosses at the (*Sphagnum*-dominated fen,) or sedges (*Carex strica* Lamb.) and *Sphagnum* mosses at the (*Carex*-dominated fen). Before sampling, I measured the peat moisture using a handheld Wet-2 sensor to ensure that samples had similar moisture conditions. Specifically, moisture range for the *Sphagnum*-dominated and *Carex*-dominated fen samples were between 30 - 35 and 60 - 65% (V/V), respectively. A total of 20 samples from each site (6 cm diameter × 6 cm depth) were collected using a serrated knife, placed into plastic bags, and kept cool in the field, and returned to Western University within 48 hrs. Mesocosm samples were weighed, placed into 500 ml jars, and assigned to temperature ('ambient' or 'warmed') and moisture ('field-moist' or 'dry') treatment groups. Extra samples (4 from each site) were also collected to estimate average moisture content of mesocosm samples. Each extra sample was weighed before and after a 3-day drying period at  $60^{\circ}$ C to calculate moisture proportion by wet weight using the formula:

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

To estimate 20% moisture loss for the 'dry' mesocosm samples, I followed a three-step process. First, I estimated the initial water weight of each 'dry' mesocosm sample by multiplying its total weight by the average moisture proportion calculated from extra samples of the same fen (~0.92%). Next, I multiplied the calculated initial water weight by 0.8 to obtain the new water weight at 80%. Finally, I subtracted the new 80% water weight from the original mesocosm sample weight to determine the sample's weight at 20% moisture loss. Reducing the 'dry' mesocosm samples to their respective 20% moisture loss weight was achieved using 10 g of non-toxic desiccants (Traceable 3150 Humidity Sponge Indicators). Desiccants were replaced daily until 'dry' samples were at their required estimated 20% moisture loss weight. During this pre-experimental (drying) stage, all mesocosms were held at 12°C and weighed daily; drying time was 5 and 7 days for the Sphagnum- and Carex-dominated fen mesocosm samples, respectively. Fieldmoist samples were maintained by addition of filtered rainwater twice during the drying stage. Once 'dry' mesocosms had achieved their respective 20% moisture loss, all mesocosms were then placed into their respective treatments: 12°C/dry, 12°C/field-moist, 20°C/dry, and 20°C/ field-moist. Each group was replicated five times for each peatland

site (N = 40). The 12°C temperature treatment represented average boreal forest growing temperature (Environment Canada, 2023) while the 20°C temperature was chosen to model future warming scenario of ~8°C increase for northern latitudes in the next 50 – 100 years (Balting et al., 2021; IPCC, 2023) based on IPCC SSP-5 scenario. 'Field-moist' represented the actual moisture content of the samples as collected from the field, while 'dry' is close to projected climate-induced moisture loss (27%) in the next 60 – 70 years for the west and central parts of Canada's southern boreal forest (He and Pomeroy, 2023) – where my study sites are located. Moisture levels for all mesocosms were maintained bi-weekly using filtered rainwater.

After 4 months (late June – early November 2024), the whole sample from each mesocosm jar was placed in the Berlese-Tullgren apparatus for microarthropod extraction, and absolute moisture content was measured gravimetrically as described earlier (expressed as percent). For each mesocosm, I identified and enumerated all major microarthropod groups (Oribatida, Mesostigmata, Prostigmata, Astigmata, and Collembola). Further, I enumerated and identified all oribatid mites (Acari: Oribatida) to the species level to determine species abundance and richness. These counts were standardised by the dry weight of their respective mesocosm samples and are expressed per gram dry weight (g/ dwt); thus, abundance was expressed as number of individuals per gram dry weight (# indiv./g dwt) and richness was number of species per gram dry weight (# indiv./g dwt) and richness was number of species per gram dry weight (# indiv./g dwt) and richness was number of asexual oribatid species, and proportion of oribatid juveniles, number of asexual oribatid species, and proportion of asexual individuals as described in Chapter 2 and using average body size of each species, I estimated the community weighted mean (CWM) body size for each mesocosm sample as also described in Chapter 2.

#### 3.2.3 Statistical analysis

Similar to the field experiment described in Chapter 2, I analysed the two peatland sites separately as they have previously been shown to differ significantly in their species richness, abundances and community composition for oribatid mites (Barreto and Lindo, 2021; Chapter 2). Following 4 months of incubation under two temperature treatments and maintaining moisture, the average absolute moisture of the *Sphagnum* and *Carex*-

mesocosms were not significantly different between the moisture treatments (dry and field-moist) based on 2-way ANOVA because of high sample variability (Table 3.1). Therefore, I proceeded to analyse the data with a General Linear Model (GLM) using temperature as a categorical predictor and absolute moisture as a continuous predictor variable (i.e., similar to ANCOVA) to examine the interactive effect of temperature and moisture on my response variables: total oribatid mite abundance, adult oribatid mite richness, diversity, evenness, proportion of juvenile abundance, number of asexual oribatid species, and proportion of asexual individuals, and CWM body size. I also used the same model to test the effects of temperature and moisture on total standardized abundance of Mesostigmata, Collembola, Prostigmata, Astigmata and other microarthropods. Fitting of the models was done using the {glm} function from (emmeans) package (Lenth, 2024) in R. Models were written as:

#### glm (variable of interest ~ Temperature \* Moisture)

In the models, the 'family = Gamma(link = "log")' was specified as the distribution since my response variables were made up of non-integers (due to standardisation by dry mesocosm sample weight). To show the direction (slope) of the effect of moisture on the response variables at each temperature level, I used the function {emtrends} from the 'emmeans' package; {emtrends} estimates the marginal slope of a continuous predictor while adjusting for other factor (s) in a GLM. It does this by computing the derivative of the response variable with respect to the continuous predictor at different levels of categorical factors; a negative value indicates a negative relationship between the response variable and the continuous predictor and vice versa. Further, I examined and visualised the community composition of adult oribatid mites using a non-metric multidimensional scaling (NMDS) with the {metaMDS} function in the 'vegan' package in R. On the NMDS plot, mesocosms (or communities) that are more similar are plotted close to each other. Using the Bray-Curtis dissimilarity matrix, I tested for significant community compositional differences between temperature and moisture treatments using a Permutational Analysis of Variance (PERMANOVA) with the {adonis2} function in 'vegan' package (Oksanen et al., 2024). To identify patterns in species composition, I used a distance-based Redundancy Analysis (dbRDA) to relate species composition to temperature and moisture.

Table 3.1: Average absolute moisture content of the Sphagnum and Carex-dominated fen mesocosms following 4 months of moisture maintenance at differenttemperature and moisture treatments.

Temperature	Moisture treatment (%)	Sphagnum-dominated fen	Carex-dominated fen	
12°C	$Dry \qquad \qquad 90.22\pm0.57^{b}$		$89.98\pm0.53^{b}$	
	Field-moist	$90.12\pm0.32^{b}$	$93.07\pm0.64^{\rm a}$	
20°C	Dry	$90.99\pm0.27^{ab}$	$90.96\pm0.46^{\text{b}}$	
	Field-moist	$92.20\pm0.56^{\rm a}$	$91.95\pm0.34^{ab}$	

# 3.3 Results

#### 3.3.1 Descriptive data of mesocosm samples

A total of 20759 microarthropods (15554 Oribatida, 401 Mesostigmata, 552 Prostigmata, 3607 Collembola, 277 Astigmata, and 368 other microarthropods) were extracted from the mesocosm samples of both fen sites. Total adult Oribatida richness from both the *Sphagnum*-dominated and *Carex*-dominated fen mesocosms was 36 (Appendix D). In the *Sphagnum*-dominated fen mesocosms, total Oribatida abundance (adults and juveniles) was 10111 (~73% of all microarthropods); adult Oribatida was 6296 (~62%), belonging to 20 families and 25 species. Average Oribatida abundance per *Sphagnum*-dominated fen mesocosm was 57.85  $\pm$  10.83 SE indiv./g dwt while richness was 2.52  $\pm$  0.20 SE species/ g dwt. In the *Carex*-dominated fen mesocosm, total Oribatida was 3152 (~58%) from 19 families and 25 species. Average Oribatida abundance per *Carex*-dominated fen mesocosm was 32.04  $\pm$  3.38 indiv./g dwt while richness was 1.36  $\pm$  0.07 SE species/ g dwt.

# 3.3.2 Temperature and moisture effects on Oribatida univariate measures from the *Sphagnum*-dominated fen mesocosms

Total oribatid mite abundance more than doubled under 20°C (temperature:  $F_{1,16} = 22.33$ , p < 0.001). Although oribatid mite abundance tended to decrease with increasing moisture at 12°C (slope: -0.079) and 20°C (slope: -0.009), this was very far from being significant ( $F_{1,16} = 0.13$ , p = 0.719). There was also no significant effect of combined temperature and moisture on total oribatid mite abundance ( $F_{1,16} = 0.144$ , p = 0.709) (Figure 3.1A). Similar trends were observed for richness as species richness was only affected by the main effect of temperature ( $F_{1,16} = 17.35$ , p < 0.001) being higher at 20°C. But there was no main or interactive effect of temperature and absolute moisture (moisture:  $F_{1,16} = 0.985$ , p = 0.335; interaction:  $F_{1,16} = 0.027$ , p = 0.872) even if moisture was negatively correlated with richness at 12°C (slope: -0.079) and 20°C (slope: -0.009) (Figure 3.1B).





The figure shows the relationship between absolute moisture and abundance/richness under different temperature treatments. Data points represent individual mesocosms. Regression lines illustrate trends within each temperature treatment. Abundance: slope at 12°C (-0.079) and 20°C (-0.009); Richness: slope at 12°C (-0.079) and 20°C (-0.079).

Shannon's and Simpson's diversity (H', D) and evenness (J) values were lower at 20°C compared to 12°C, and similar to abundance and richness, all diversity indices (H', D, J) tended to increase with moisture at 12°C, but decrease with higher moisture at 20°C. Although the main effect of moisture was not significant on diversity and evenness, moisture and diversity (or evenness) at 12°C were positively correlated; but at 20°C this was reversed implying an interaction between temperature and moisture. This interaction was significant for H' and marginal for D and J (Table 3.2).

The proportion of oribatid individuals was lower at 20°C but temperature was not significant as a main effect. Moisture was positively correlated with the proportion of oribatid mite individuals at 12°C and 20°C as indicated by the slope, but both the main effect of moisture and the interaction between temperature and moisture were not significant (Table 3.2). The proportion of asexual oribatid individuals was lower at 20°C and this was significant (Table 3.2). While moisture was not a main effect, it had an interactive effect with temperature as the proportion of asexual oribatid mite individuals tended to decrease with increase in moisture. Although the proportion of asexual oribatid individuals was significantly higher at 20°C; but moisture nor its interaction with temperature did not seem to affect the number of asexual oribatid individuals (Table 3.2).

 Table 3.2: Oribatid mite community univariate measures from the Sphagnum-dominated fen mesocosms following 4 months of temperature treatment and moisture maintenance.

	Shannon's	Simpson's	Pielous' evenness	Proportion of	Proportion of	Number of asexual
	diversity (H')	diversity (D)	(J)	oribatid juveniles	asexual individuals	oribatid species
12°C	$1.98\pm0.03$	$0.82\pm0.01$	$0.76\pm0.02$	$0.43\pm0.01$	$0.98\pm0.00$	$1.61 \pm 0.1$
20°C	$1.84\pm0.06$	$0.76\pm0.02$	$0.68\pm0.02$	$0.39\pm0.03$	$0.93\pm0.02$	$2.51\pm0.24$
Temperature (F <sub>1,16</sub> )	F= 6.48, p = 0.022	F = 2.93, p = 0.106	F = 4.07, p = 0.061	F = 2.25, p = 0.153	F = 5.19, p = 0.037	F = 12.22, p = 0.003
Moisture (F <sub>1,16</sub> )	F = 1.69, p = 0.212	F = 0.54, p = 0.475	F = 2.67, p = 0.122	F = 0.873, p = 0.364	F = 0.401, p = 0.536	F = 0.59, p = 0.452
Interaction (F <sub>1,16</sub> )	F = 6.56, p = 0.021	F = 3.02, p = 0.101	F = 4.20, p = 0.057	F = 0.138, p = 0.716	F = 5.22, p = 0.036	F = 0.05, p = 0.823
Slope with moisture at 12°C	0.034	0.014	0.050	0.025	-0.008	-0.061
Slope with moisture at 20°C	- 0.056	-0.032	-0.036	0.057	-0.047	-0.034

Values are averages $\pm$ standard errors. B	solded values indicate signific	ant (or marginally significant) values.

Community body size reduced by about 5% at 20°C compared to 12°C, and this was only marginally significant ( $F_{1,16} = 3.48$ , p = 0.080). Body size tended to increase with moisture at both temperatures (slope at 12°C: 0.035; slope at 20°C: 0.023) but neither moisture not its interaction with temperature was significant (moisture:  $F_{1,16} = 1.68$ , p = 0.212; interaction:  $F_{1,16} = 0.067$ , p = 0.800) (Figure 3.2). Brachychthoniidae abundance at 20°C was more than ten times greater than at 12°C indicating that temperature significantly increase the number of Brachychthoniidae individuals ( $F_{1.16} = 25.07$ , p < 0.001). Brachychthoniidae abundance tended to slightly decrease with moisture at 12°C (slope: -0.208) but increased with moisture at 20°C (slope: 0.049). But neither moisture nor its interaction with temperature was a significant factor on Brachychthoniidae abundance (moisture:  $F_{1,16} = 0.04$ , p = 0.839; interaction:  $F_{1,16} = 0.52$ , p = 0.487) (Figure 3.3A). Suctobelbidae abundance was similar to Brachychthoniidae abundance with significantly higher (~59%) Suctobelbidae abundance at 20°C ( $F_{1.16} = 7.38$ , p = 0.015) compared to 12°C, but Suctobelbidae abundance was negatively correlated with moisture at both temperatures (slope at 12°C: -0.249; slope at 20°C: -0.087), although moisture nor its interaction with temperature were not significant effects (moisture:  $F_{1,16} = 0.75$ , p = 0.400;  $F_{1,16} = 0.23$ , p = 0.635) (Figure 3.3B). Temperature and moisture effects for other microarthropod groups are shown in Appendix E.



Figure 3.2: Community weighted mean (CWM) body size of oribatid mite communities in the *Sphagnum*-dominated fen mesocosms after 4 months of temperature treatment and moisture maintenance.

The figure shows the relationship between absolute moisture and community body size (estimated by a community weighted mean of average species body size) under different temperature treatments. Data points represent individual mesocosms. Regression lines illustrate trends within each temperature treatment. CWM body size: slope at 12°C (0.035) and 20°C (0.023).





The figure shows the relationship between absolute soil moisture and Brachychthoniidae/Suctobelbidae abundance under different temperature treatments. Data points represent individual mesocosms. Regression lines illustrate trends within each temperature treatment. Brachychthoniidae: slope at 12°C (-0.208) and 20°C (0.049); Suctobelbidae: slope at 12°C (-0.249) and 20°C (-0.087)

# 3.3.3 Community composition of Oribatida in the *Sphagnum*dominated fen mesocosms

At the community level, temperature was a significant driver of community composition (Permanova:  $F_{1,18} = 7.92$ , p = 0.001) causing distinct clustering of mesocosms at 12°C and 20°C (Figure 3.2). The ellipse as well as the spread of mesocosms at 20°C is larger, indicating that mesocosms had greater dissimilar (heterogenous) communities at that temperature. Moisture was also a significant driver of community composition (Permanova:  $F_{1,18} = 3.572$ , p = 0.013) as the driest and wettest mesocosms were quite far from each other on the NMDS plot. The effect of temperature of community composition appears to be dependent on moisture level (Permanova:  $F_{1,18} = 3.29$ , p = 0.001) and this was more visible at 20°C where the mesocosms with the highest moisture were farthest from each other.

The overall dbRDA model significantly explained oribatid mite community composition ( $F_{3,16} = 3.21$ , p = 0.004) and showed that temperature, explaining 30% of the variance in the ordination, was a significant driver of species composition (Pseudo- $F_{1,16} = 7.59$ , p = 0.001); smaller (<300 µm) and asexual oribatid mites (e.g., Brachychthoniidae, Suctobelbidae, Eniochthoniidae) were associated with the 20°C temperature treatment (Figure 3.5). Moisture accounted for only 6% variation and was not a significant factor (Pseudo- $F_{1,16} = 1.56$ , p = 0.179), while moisture and its interaction with temperature only explained 2%, with no significant effect on species composition (Pseudo- $F_{1,16} = 0.47$ , p = 0.862). On the dbRDA plot, temperature and moisture interaction aligned with the 20°C treatment. Combined, the dbRDA axes cumulatively explained 98% in species composition, with the first axis (CAP1) significantly explaining 81% (Pseudo- $F_{1,16} = 7.76$ , p = 0.002). The second axis explained 17% variation, but this was not significant (Pseudo- $F_{1,16} = 1.64$ , 0.326).



Figure 3.4: The *Sphagnum*-dominated fen mesocosm Non-metric Multidimensional Scaling (NMDS) plot of community compositional similarity based on Bray-Curtis calculations of dissimilarity.

Points represent mesocosms, coloured by absolute moisture content (%) and shaped by temperature treatments (12°C and 20°C). Dashed ellipses represent 95% confidence and indicate grouping by temperature treatments.



Figure 3.5: The *Sphagnum*-dominated fen mesocosms distance-based Redundancy Analysis (dbRDA) plot of adult oribatid mite species, temperature treatment and absolute moisture content.

Length and direction of treatment/ environmental vectors indicate strength and relationship to species, respectively.

# 3.3.4 Temperature and moisture effects on Oribatida univariate measures from the *Carex*-dominated fen mesocosms

Total oribatid mite abundance was 37% higher at 20°C compared to 12°C ( $F_{1,16} = 7.39$ , p = 0.015). Although abundance tended to increase with moisture at 12°C (slope: 0.099) and decrease with moisture at 20°C (slope: -0.120), moisture did not affect total oribatid mite abundance ( $F_{1,16} = 0.92$ , p = 0.351) nor did it interact with temperature ( $F_{1,16} = 2.46$ , p = 0.136) (Figure 3.6A). Similarly, richness increased slightly at 20°C, but the effect of temperature was not significant ( $F_{1,16} = 1.24$ , p = 0.282), and similar to abundances, richness tended to increase with moisture at both 12°C (slope: 0.036), and 20°C (slope: 0.003), but moisture did not significantly affect species richness ( $F_{1,16} = 0.66$ , p = 0.430) nor did it interact with temperature ( $F_{1,16} = 0.13$ , p = 0.724) (Figure 3.6B).

Although diversity (H', D) and evenness (J) were observed to be slightly higher at 20°C, temperature was not a significant effect. At 12°C, diversity and evenness tended to increase with increasing temperature, but this was reversed at 20°C. Nonetheless, moisture was not a significant effect and did not interact with temperature (Table 3.3). The proportion of oribatid juveniles was significantly higher at 20°C by 20% compared to mesocosms at12°C. Similar to diversity and evenness, the proportion of oribatid individuals tended to increase with moisture at 12°C and reduce with moisture at 20°C; but moisture nor its interaction with temperature did not significantly affect the proportion of oribatid mite individuals (Table 3.3). The proportion of asexual oribatid individuals was slightly lower at 20°C but this was not significant. Moisture and its interaction with temperature did not also seem cause any effect on the proportion of asexual oribatid species was slightly higher at 20°C but was neither affect by the temperature, moisture or their interaction (Table 3.3).



Figure 3.6: Total standardised oribatid mite abundance (A) and richness (B) in the *Carex*-dominated fen mesocosms following 4 months of temperature treatment and moisture maintenance.

The figure shows the relationship between absolute moisture and abundance/richness under different temperature treatments. Data points represent individual mesocosms. Regression lines illustrate trends within each temperature treatment. Abundance: slope at 12°C (0.099) and 20°C (-0.120); Richness: slope at 12°C (0.036) and 20°C (0.003).

Table 3.3: Oribatid mite community univariate measures from the *Carex*-dominated fen mesocosms following 4 months of temperature treatment and moisture maintenance.

	Shannon's	Simpson's	Pielous' evenness	Proportion of	Proportion of	Number of asexual
	diversity (H')	diversity (D)	(J)	oribatid juveniles	asexual individuals	oribatid species
12°C	$1.91 \pm 1.11$	$0.80\pm0.01$	$0.78\pm0.02$	$0.35\pm0.02$	$0.91\pm0.02$	$1.02\pm0.06$
20°C	$1.93\pm0.9$	$0.82\pm0.01$	$0.79\pm0.02$	$0.44\pm0.03$	$0.90\pm0.01$	$1.09\pm0.08$
Temperature (F <sub>1,16</sub> )	F = 0.11, p = 0.749	F = 0.63, p = 0.438	F = 0.31, p = 0.587	F = 4.88, p = 0.042	F = 0.10, p = 0.759	F = 0.61, p = 0.447
Moisture (F <sub>1,16</sub> )	F = 0.04, p = 0.838	F = 0.02, p = 0.893	F = 0.03, p = 0.863	F = 0.16, p = 0.696	F = 0.03, p = 0.861	F = 0.69, p = 0.420
Interaction (F <sub>1,16</sub> )	F = 0.31, p = 0.588	F = 0.25, p = 0.624	F = 0.30, p = 0.592	F = 0.93, p = 0.348	F = 0.23, p = 0.639	F = 0.24, p = 0.632
Slope with moisture at 12°C	0.006	0.001	0.002	0.031	-0.004	0.034
Slope with moisture at 20°C	-0.011	-0.008	-0.013	-0.049	0.007	-0.005

Values are averages ± standard errors. Bolded values indicate significant (or marginally significant) values.

Community body size was greater at 20°C, but this was not significant ( $F_{1,16} = 1.43$ , p = 0.250). At 12°C, body size was positively correlated with moisture (slope: 0.001) but this was reversed at 20°C with a much steeper slope (-0.053); nonetheless, moisture ( $F_{1,16} = 0.64$ , p = 0.435) and the interaction with temperature ( $F_{1,16} = 2.30$ , p = 0.149) were not significant effects (Figure 3.7). Brachychthoniidae abundance was slightly lower at 20°C, but this was not significant ( $F_{1,16} = 0.05$ , p = 0.826). Although Brachychthoniidae abundance tended to increase with moisture at both temperatures (slope at 12°C: 0.139; slope at 20°C: 0.466), moisture as well as its interaction with temperature did not seem to affect Brachychthoniidae abundance (moisture: 0.33, p = 0.572; interaction: 1.58, p = 0.227) (Figure 3.8A). Suctobelbidae abundance was slightly higher at 20°C but was also not affected by temperature ( $F_{1,16} = 0.01$ , p = 0.907), moisture ( $F_{1,16} = 0.17$ , p = 0.690) or their interaction ( $F_{1,16} = 2.04$ , p = 0.173). But Suctobelbidae was positively correlated with moisture at 12°C (0.114) and negatively correlated with moisture at 20°C (-0.268) (Figure 3.8B). Temperature and moisture effects for other microarthropod groups collected from the *Carex*-dominated fen mesocosms are shown in Appendix F.





The figure shows the relationship between absolute moisture and community body size (estimated by a community weighted mean of average species body size) under different temperature treatments. Data points represent individual mesocosms. Regression lines illustrate trends within each temperature treatment. CWM body size: slope at 12°C (0.001) and 20°C (-0.053).





The figure shows the relationship between absolute soil moisture and Brachychthoniidae/Suctobelbidae abundance under different temperature treatments. Data points represent individual mesocosms. Regression lines illustrate trends within each temperature treatment. Brachychthoniidae: slope at 12°C (0.139) and 20°C (0.466); Suctobelbidae: slope at 12°C (0.114) and 20°C (-0.268);
## 3.3.5 Community composition of Oribatida in the *Carex*-dominated fen mesocosms

In the *Carex*-dominated fen mesocosms, temperature was also a significant driver of community composition (Permanova:  $F_{1,18} = 2.55$ , p = 0.029) (Figure 3.9). On the NMDS plot, distinct clustering is observed for mesocosms at 12°C and 20°C. More specifically, mesocosm at 12°C had larger distances between them and a larger ellipse (representing 95% confidence intervals), indicating much more variance in community composition than samples at 20°C. Moisture alone (Permanova:  $F_{1,18} = 1.14$ , p = 0.340) did not affect community composition but interacted with temperature (Permanova:  $F_{1,18} = 1.99$ , p = 0.021). On the NMDS, mesocosms with medium to high moisture seem to cluster close to each other (Figure 3.9).

The dbRDA model (Pseudo- $F_{1,16} = 1.92$ , p = 0.013) showed that temperature, explaining 18% variation was a significant driver of species composition (Pseudo- $F_{1,16} = 2.59$ , p = 0.022) (Figure 3.10). Moisture explained 5% of the total variation, and was not significant (Pseudo- $F_{1,16} = 1.35$ , p = 0.192). However, the temperature and moisture interaction was only marginally significant (Pseudo- $F_{1,16} = 1.81$ , p = 0.079) and explained only 2% of the variation. The first axis (CAP1) significantly explained 72 % variation (Pseudo- $F_{1,16} = 4.12$ , p = 0.006) while the second axis (CAP2) explained 19% variation; the second axis was not significant in explaining oribatid mite community composition (Pseudo- $F_{1,16} = 1.11$ , p = 0.706).





Points represent mesocosms, coloured by absolute moisture content (%) and shaped by temperature treatments (12°C and 20°C). Dashed ellipses represent 95% confidence and indicate grouping by temperature treatments.



Figure 3.10: The *Carex*-dominated fen mesocosms distance-based Redundancy Analysis (dbRDA) plot of adult oribatid mite species, temperature treatment and absolute moisture content.

Length and direction of treatment and environmental vectors indicate strength and relationship to species, respectively.

#### 3.4 Discussion

Climate change is expected to alter soil temperature and moisture levels, affecting belowground communities such as oribatid mite communities directly and indirectly. Despite dominating many terrestrial systems, studies on the response of oribatid mite communities to climate driven changes have mostly been on forest soils, with limited research on oribatid mite communities in peatlands (but see Markkula et al., 2019; Barreto et al., 2021; Barreto et al., 2023). Nonetheless, these studies show that oribatid mite communities in peatlands may be responding differently than what has been observed in forest soils. The work of Barreto et al. (2021) and Barreto et al. (2023) suggest that the effects of experimental warming on peatland oribatid mite communities in a field setting is often concomitant with decreased soil moisture (making it difficult to determine the individual drivers of oribatid mite community shifts in peatlands). Despite these findings, the interactive effects of temperature and moisture on oribatid mite communities in boreal peatlands remain poorly understood. My mesocosm experiment was an attempt to disentangle the interactive effect of temperature and moisture on oribatid mite communities in peatland. In this experiment, I observed that temperature exerted an overall stronger effect than moisture.

### 3.4.1 Temperature and moisture effect on abundance, richness, diversity and evenness

I observed oribatid mite abundance and richness to be greater at 20°C. Although the greater richness was not statistically significant in the *Carex*-dominated mesocosms, the increase in abundance in both fen mesocosms supports my hypothesis that warmer temperatures would increase metabolic rates and reproduction, aligning with other controlled experimental studies that have reported the same trends for oribatid mites (Lindo, 2015) as well other microarthropods (Santonja et al., 2018; Meehan et al., 2021). While richness is not particularly driven by temperature, higher abundance increases the likelihood of seeing species, especially rare species. Mechanistically, increases in abundance were driven by individuals of the Brachychthoniidae family, however as this family was abundant in the *Sphagnum*-dominated fen to begin with, diversity and

evenness was reduced at 20°C due to dominance of these and other oribatid mites (e.g., Suctobelbidae, *Oppiella nova*), while at the *Carex*-dominated fen, these increases were minor, and did not affect diversity and evenness indices. Increase in these smaller oribatid mites, especially individuals of the Brachychthoniidae family, have previously been observed under warmer temperatures (Lindo, 2015; Markkula et al., 2019; Barreto et al., 2021; Chapter 2). These mites also reproduce asexually, but no study has yet to explain whether their reproductive mode, body size, the combination of both, or some other trait confers on them some ability to benefit from warming. Lindo (2015) was the first to report an increase in these smaller oribatid mites under warming. They suggested that this pattern is due to higher metabolic rates, as explained by the metabolic theory of ecology (Brown et al., 2004). According to this theory, smaller organisms have relatively higher metabolic rates, which may allow them to dominate their communities in warmer conditions — a phenomenon known as community downsizing (Sheridan and Bickford; see also Turnbull et al., 2014).

Soil moisture alone was not a significant factor affecting abundance, richness or diversity of oribatid mite communities in my study. It is likely that soil moisture was not limiting, physiologically nor high enough to reduce soil pore space (Shackels and Murphy, 1969; Sheela and Haq, 1991; Tsiafouli et al., 2005; Alatalo et al., 2017). However, I also observed that, at 20°C, diversity and evenness tended to reduce with increase in moisture in both the *Sphagnum-* and *Carex-*dominated fen mesocosms. Although this was not significant, it lends support to the hypothesis and the suggestion of Barreto et al. (2021), that lower moisture in peatlands may benefit oribatid mites by creating habitable soil pore spaces. Interestingly, other microarthropod groups also showed a tendency to decline with increased habitable pore space and implying that this extends to other microarthropod groups.

### 3.4.2 Temperature and moisture effect on juvenile and asexual oribatid mites

I had expected that the proportion of oribatid juveniles would follow the same trend as abundance (and richness) due to elevated reproduction as has been previously observed for oribatid mites (Petitt et al., 2023), but it was neither affected by temperature nor moisture. However, I did observe that at 20°C the proportion of oribatid juveniles was lower in the Sphagnum-dominated fen mesocosms and higher in the Carex-dominated fen mesocosms. The trend in the Carex-dominated, although non-significant, aligns with (Petitt et al., 2023) that observed significant increases in oribatid mite juveniles under warmer temperatures, suggesting that this increase was due to elevated reproduction under warming. The trend of lower juvenile abundance in the Sphagnum-dominated fen could be driven by an increased activity of predators (Mesostigmata) that significantly increased at 20°C. Most adult oribatid mites are highly sclerotised and chemically defended, making it difficult for predators to prey on them (Peschel et al., 2006), while juvenile oribatid mites are usually weakly sclerotised and therefore more susceptible to predation. Since Mesostigmata have been shown to increase in activity/feeding (Ramachandran et al., 2021) and abundance (Meehan et al., 2021) under warmer temperatures, and was observed to increase in the Sphagnum-dominated fen mesocosms, juvenile abundance (and thus proportion) under warming may have been affected due to top-down control by Mesostigmata.

Oribatid mites have a high rate of asexual reproduction; at an estimated 10% of all known species, it is the highest in arthropods (Norton and Palmer, 1991). Most of the asexual oribatid mites are also smaller. Therefore, I had expected that the increase in some asexual species (such as the Brachychthoniidae and others) would be concomitant with an increase in the proportion of asexual individuals, but this was not observed. The proportion of asexual oribatid individuals and the number of asexual species showed similar trends under 20°C in both *Sphagnum-* and *Carex-*dominated fen mesocosms, with both being lower at 20°C. However, this trend was stronger in the *Sphagnum-*dominated fen mesocosms where some significant effects were observed. For example, the proportion of asexual individuals in the *Sphagnum-*dominated fen significantly decreased

at 20°C and also decreased with increase in moisture; the number of asexual oribatid species significantly increased at 20°C but was unaffected by moisture. Similar to oribatid mite juveniles, some asexual oribatid mites are also weakly sclerotised therefore it is possible that the weaker species were preyed up on by predators like Mesostigmata as discussed above. However, I also observed increase in some sexual species (e.g., *Phthiracarus boresetosus, Hoplophorella* sp. and *Liebstadia humerata*) at 20°C, which seems like a more plausible reason why the proportion of asexual oribatid individuals did not differ significantly.

#### 3.4.3 Temperature and moisture effect on community composition

At the community level, temperature as main effect altered composition in the Sphagnum-dominated and Carex-dominated fen mesocosms, but the shifts were driven by different mechanisms. In the Sphagnum-dominated fen mesocosms, the communities became more dissimilar at 20°C as certain oribatid mites (e.g., Brachychthoniidae, Suctobelbidae and Oppiella nova) dominated the community and reduced diversity and evenness; these oribatid mites were also associated with temperature on the dbRDA plot. But in the *Carex*-dominated fen mesocosms, the communities seem to become more homogenous at 20°C; this was possibly due to a relatively balanced abundance of different species that led diversity and evenness to increase only slightly, as discussed previously. A main effect of moisture was only observed at the Sphagnum-dominated fen; the mesocosm with the lowest diversity also had the highest moisture content and was distinctly dissimilar from the mesocosms with the lowest moisture content and highest diversity. However, in both the Sphagnum and Carex-dominated fen mesocosm, moisture interacted with temperature to affect community composition. At 20°C, the Sphagnum-dominated fen mesocosms with higher moisture content varied from each other, whereas the Carex-dominated fen mesocosms were more similar to each other under the same temperature. Laboratory studies on how oribatid mite communities in peatlands respond to climate change factors are scarce. However, one study (Lindo, 2015) found that oribatid mite communities became homogenised at a warmer temperature (+8°C). Here, I show that the effect of temperature on the composition of oribatid mites in peatlands can lead to either heterogeneity or homogeneity, depending on the initial soil moisture and/or initial composition of oribatid mites at the peatland fen site.

#### 3.4.4 Conclusion

Since boreal peatlands are expected to be significantly affected by climate change, understanding how the oribatid mite communities in these systems respond to changing climate factors could provide insight into how other below-ground communities may also be impacted. The results from my experimental study showed that temperature rather than moisture had a stronger effect on oribatid mite communities in peatlands, and that the response of the oribatid mite communities to temperature also differed between peatland systems even under similar experimental treatments. While I did not observe a significant effect of moisture on oribatid mite abundance or richness, moisture interacted with temperature to alter community composition. Also, the changes observed further support the fact that warmer temperatures will favour certain smaller oribatid mites, with impacts on community body size. However, the observed responses in my study could have been driven indirectly by other unmeasured factors (e.g., microbial biomass). Therefore, studies that simultaneously measure both the direct effects of temperature and moisture on peatland oribatid mite communities, as well as the indirect effects via resource availability, are necessary to fully understand how temperature and moisture structure oribatid mite communities in boreal peatlands.

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#### Chapter 4

#### 4 General discussion

#### 4.1 Overview of findings

Microarthropods, particularly oribatid mites, are one of the dominant soil communities in terrestrial ecosystems, including boreal peatlands, where they drive soil carbon dynamics through organic litter decomposition and nutrient cycling (Norton and Behan-Pelletier, 2009). But these microarthropod communities, as well as the roles they perform, are dependent on abiotic factors such as temperature and moisture - both of which are projected to shift under current and future climate scenarios (Balting et al., 2021). Boreal peatlands, which store significant amounts of carbon (Xu et al., 2018; Hugelius et al., 2020) and support a high diversity of oribatid mites (Behan-Pelletier and Bissett, 1994; Lehmitz, 2014; Barreto and Lindo, 2021), will also be affected by changes in temperature and moisture (Tarnocai, 2009; Allison and Treseder, 2008; Helbig et al., 2020). Research on forest soil systems suggests that both rising temperatures and moisture levels generally increase oribatid mite abundance (Tsiafouli et al., 2005; Lindo et al., 2012; Siebert et al., 2019). However, Barreto et al. (2021) suggests that in saturated soils (like in peatlands), reduced soil moisture levels (induced by warmer temperatures), may create habitable soil pore spaces favouring dispersal of new species into the environment, which will increase species richness. In my field experiment (Chapter 2), I observed that seven years of experimental warming reduced soil moisture levels, but I could not find strong evidence that warming-induced reduction in soil moisture benefits oribatid mite communities in boreal peatlands. Instead, I observed that temperature increased smaller oribatid mites with reduction in average community body size. In my lab experiment (Chapter 3), moisture interacted with temperature to reduce oribatid mite diversity and evenness. I also observed that temperature increased the abundance of smaller oribatid mites and reduced community body size, like in the field experiment. Overall, my thesis demonstrates that temperature is a strong factor driving oribatid mite communities in boreal peatlands.

# 4.2 Temperature and moisture in the *Sphagnum*- and *Carex*-dominated fens

Under climate change, the increase in temperature will be accompanied by a reduction in moisture (Trenberth, 2011; Balting et al., 2021) driven by increased evaporation and/or evapotranspiration rates. This is already being observed in many ecosystems (Nielsen et al., 2024), and models for the boreal forest (He and Pomeroy, 2023) predict a similar pattern. In my field study, seven years of experimental warming has led to lower moisture levels in the warmed plots, particularly at the *Sphagnum*-dominated fen, where moisture levels were lower under warmer temperatures than in the *Carex*-dominated fen. More specifically, I observed that moisture levels under warmed plots in the *Sphagnum*-dominated fen dropped by roughly 20%, closely matching the modelled ~27% moisture reduction in the southern boreal region (He and Pomeroy, 2023). In contrast, the warming effect on moisture was less pronounced in the *Carex*-dominated fen. These divergent trends in temperature and moisture between the two sites could be due to three reasons: a) initial moisture between the two sites driven by water table, b) moisture holding capacity of the vegetation at both sites, and c) warming effects on the vegetation at both sites.

The water table in the *Sphagnum*-dominated fen (~30 cm) is lower than in the *Carex*dominated fen (~60 cm) (Webster & McLaughlin, 2010), influencing peat moisture levels. As a result, moisture in the *Sphagnum*-dominated fen was generally lower than in the *Carex*-dominated fen. Although *Sphagnum* mosses have higher water-holding capacities (Rice, 2009) than graminoids like *Carex*, they are also more vulnerable to warming (Dieleman et al., 2015; Lyons et al., 2020). Warming-induced *Sphagnum* losses have been reported in the *Sphagnum*-dominated fen (Lyons et al., 2020; Hopkins, 2024). This reduced *Sphagnum* coverage at the *Sphagnum*-dominated fen may have exposed the warmed plots to greater evaporation induced by the warming treatment, significantly lowering moisture levels. In contrast, *Carex* tends to thrive under warming (Dieleman et al., 2015; Lyons et al., 2020), particularly in above-ground biomass, which may provide shade and help mitigate the effect of warming on evaporation, leading to no significant changes in moisture levels between ambient and warmed plots. These differences (especially in initial moisture levels) between my study sites seemingly played a role in the abundance and structure of the oribatid mite communities I found. For example, I found that the 'drier' *Sphagnum*-dominated fen had a higher abundance (and richness) of oribatid mites dominated by non-peatland (or non-semi-aquatic) species (e.g., Brachychthoniidae, *Tectocepheus velatus*, *Oppiella nova*). Oribatid mite abundance and richness in the 'wetter' *Carex*-dominated fen was comparatively lower, and dominated by semi-aquatic oribatid mite species (e.g., *Tyrphonothrus maior*, *Malaconothrus mollisetosus*, *Trhypochthoniellus setosus canadensis*). These trends are almost identical to previous reports from the same sites (see Barreto and Lindo, 2018; Barreto et al., 2021). I also observed that the difference in moisture levels between my study sites also seemed to influence how the oribatid mite communities responded to experimental treatments in both the field and lab experiments.

# 4.3 Temperature and moisture effects on oribatid mite communities

Like other ectotherms (Gillooly et al., 2001), oribatid mite communities are known to respond to warmer temperatures. When within their thermal optima  $(35 - 40^{\circ}C)$ : Madge, 1965; Hodkinson et al., 1995), oribatid mites generally benefit from warming. This often begins with increase in their metabolic and reproductive rates at the individual and population level (Ermilov et al., 2004; Ermilov and Łochyńska, 2008). When observed at the community level, warming is shown to cause an increase in oribatid mite abundance (Lindo et al., 2012; Siebert et al., 2019; Feketeová et al., 2021) as well as changes in community composition or structure. Again, similar to other ectotherms, and based on the metabolic theory of ecology (Brown et al., 2004), smaller oribatid mites generally have a relatively higher metabolic and reproductive rates than their larger counterparts. Therefore, under warmer temperatures, smaller oribatid mites may dominate their communities as metabolic and reproductive rates are further increased (Lindo, 2015; Markkula et al., 2019; Barreto et al., 2021). In my study, I found evidence that warmer temperatures will benefit oribatid mites through increased abundance (and richness). I also found evidence of smaller (and asexual) oribatid mites benefiting from warmer temperature (Appendix A and D), but this did not lead to an increase in the proportion of

asexual oribatid individuals. Nonetheless, it aligns with other field (Barreto et al., 2021; Markkula et al., 2019) and greenhouse (Lindo, 2015) experimental studies in peatlands, which showed increased small asexual oribatid mite individuals under warmer temperatures. Also important to note is that increases in smaller asexual individuals (or species) has been observed for other microarthropod communities like predatory mites in the suborder Mesostigmata (Meehan et al., 2021).

Temperature was a strong driver of community composition in both the field and lab experiments, with oribatid mites showing distinct assemblages under different temperature treatments. This effect was more pronounced in the lab experiment, suggesting that controlled moisture levels may amplify temperature-driven responses. In the *Sphagnum*-dominated fen, warming consistently led to heterogeneity (as displayed on the NMDS ordinations), driven by a reduction in diversity and evenness across both field and lab experiments. This suggests that the dominance of smaller oribatid mites was the main mechanism driving community shifts. In contrast, diversity and evenness in the *Carex*-dominated fen, where these smaller oribatid mites were not dominant was slightly higher under warmer conditions in both the field and mesocosm experiments, indicating a more balanced distribution of species abundances. However, the *Carex*-dominated fen ordinations (NMDS) revealed a subtle difference between experimental settings: in the field, warming increased heterogeneity among samples, whereas in the lab, communities became more homogeneous under warmer temperatures.

Body size is a trait that is predicted to shift under climate change. More specifically, warmer temperatures will reduce the body size of many ectotherms from the individual to the community level (Gardner et al., 2011; Sheridan and Bickford, 2011; Olhberger et al., 2013). At the individual and population levels, this reduction in body size is primarily driven by plastic responses, where increased growth rates under warmer conditions affects ontogeny, leading to smaller size-at-age/stage (Gardner et al., 2011; Sheridan and Bickford, 2011; Olhberger et al., 2013). At the community level, reductions in body size are driven by compositional shifts in species assemblages (Olhberger et al., 2013; Lindo, 2015; Martins et al., 2023). In my study, I observed body size at the community level and found evidence that body size is being reduced under warmer temperatures driven by

increased dominance of smaller oribatid mites, particularly individuals of the Brachychthoniidae family that were consistently higher under elevated temperature treatments in both the field and lab experiments. Although Brachychthoniidae was the most prominent smaller group (< 200  $\mu$ m) that had higher abundance under warmer temperatures, I also observed that other smaller (< 300  $\mu$ m) oribatid mites (e.g., Eniochthoniidae, *Tectocepheus velatus*, and *Oppiella nova*) increased at warmer temperatures in both the field and lab experiments. All these smaller families/species are also asexual, but whether asexual reproduction is a factor in increased abundances under warming, or whether the metabolic effects of warming are solely on body size is unknown.

# 4.4 Ecological implications of observed changes in oribatid mite communities

Low temperature and high moisture are two factors that characterise boreal peatlands leading to deep accumulations of partially decomposed vegetation (peat) which also provides substrate for unique groups of soil-dwelling mites (Behan-Pelletier and Bissett, 1994; Lehmitz, 2014; Barreto and Lindo, 2018). As the dominant microarthropod group in soil systems, oribatid mite communities play important roles in decomposition by feeding on microbes (e.g., fungi) as well as on organic litter. Previous studies on forest soils show that higher microarthropod abundance can lead to reduction in fungal biomass (Hanlon and Anderson, 1979; Siepel and Maaskamp, 1994) and increased soil respiration (Kaneko et al., 1998) by bacteria. Similarly, Henegan et al. (1999) reported a positive correlation between higher oribatid mite richness and increased mass loss of litter. While the field experiment showed inconsistent seasonal trends in abundance and richness, possibly due to high variability as expected in natural systems, I observed that warmer temperatures in the lab experiment led to higher abundance and richness, especially in the Sphagnum-dominated fen. Although the relationship between oribatid mite abundance/richness and decomposition rates in peatlands is yet to be quantified, I would expect increased oribatid mite abundance and richness under warmer temperatures to reduce fungal biomass (especially in the Sphagnum-dominated fen), elevating decomposition by bacteria. Combined, this increase in litter loss and reduction in fungal

biomass may accelerate decomposition rates. Increased decomposition rates, especially in boreal peatlands, are a major concern in carbon budget models, as such can reduce carbon storage and release  $CO_2$  into the atmosphere. More carbon being released from peatlands into the atmosphere will further exacerbate climate change as  $CO_2$  in the atmosphere will increase global warming, leading to further changes in boreal peatlands as well as a continuous feedback loop.

Community downsizing, the shift towards a smaller average body size within a community, can have significant consequences, particularly for larger ectotherms. Smaller ectothermic species have a relatively higher metabolic and reproductive rates and are generally more physically active than their larger counterparts (Brown et al., 2004). Under warmer temperatures, these advantages may allow them to outcompete larger species, as has been suggested to affect aquatic ectotherms (Dufresne et al., 2009: Ohlberger et al., 2011). Additionally, since larger species require more resources to sustain themselves, they reach energetic deficiencies (due to higher oxygen demand under warmer temperatures) (Verbeck and Atkinson, 2013) faster than smaller species, especially when resources become limited. As a result, larger species may be more vulnerable to extinction or extirpation. In my study, while a reduction in larger oribatid mite species under warming temperatures was not evident, they did not perform as well as the smaller species. This adds to increasing research suggesting that smaller species will outcompete the large species under global warming (Dufresne et al., 2009; Ohlberger et al., 2011; Sheridan and Bickford, 2011; Lindo, 2015; Martins et al., 2023) with a possibility of biodiversity losses.

Changes in oribatid mite communities under warmer temperatures may also affect their interactions with other communities in the soil system. Due to high levels of defence and protection (mostly sclerotization) (Peschel et al., 2006; Brückner et al., 2016), oribatid mites are thought to live in an 'enemy-free' space. However, this defensive ability is not uniform across all oribatid mite taxa or life stages. Smaller and less sclerotized oribatid mites (Schneider and Maraun, 2009) including oribatid juveniles (Brückner et al., 2016) are susceptible to top-down control by predation. An increase in smaller oribatid mites under warmer temperatures, as observed in my study, could alter predator-prey

interactions (Brose et al., 2012). Oribatid mites are known to have stable populations due to their long life and high defensive traits. Therefore, this shift towards the 'weaker' mites under warming may lead to stronger top-down control especially since soil predators have been shown to benefit under warmer temperatures (Meehan et al., 2021; Ramachandran et al., 2021). And this may affect oribatid mite populations in ways that may potentially disrupt their functional roles in decomposition and nutrient cycling.

#### 4.5 Caveats and limitations

Some of my findings align with previous research conducted at the same study sites. For example, I observed that experimental warming reduced soil moisture and increased the abundance of smaller oribatid mites, similar to the findings of Barreto et al. (2021). However, there are notable differences between our studies. Barreto et al. (2021) detected compositional shifts only under combined active and passive warming (using heating rods) in August 2019. By the time I conducted my sampling, active warming was not in place due to logistical constraints, and only passive warming with open-top chambers remained. Despite this, I still observed significant changes in community composition under experimental warming, suggesting that the community may still be undergoing shifts. It remains unclear whether the changes I observed were a result from a temporal effect specific to my sampling year or from the experimental warming itself. My study was short-term (one year), and while I accounted for repeated seasonal sampling within this period using a linear mixed model, longer-term data are needed to determine whether these changes persist across years.

The lab experiment was maintained for four months to simulate a full growing season, however sampling was in fall (autumn), so seasonal/phenological effects cannot be discounted. Developmental rates of oribatid mites, which is mostly dependent on temperature (Ermilov et al., 2004; Ermilov and Łochyńska, 2008), varies greatly from species to species, even in lab settings where they have been reared under similar conditions (Pfingstl and Shatz, 2021). Seasonal studies have also shown different oribatid mite species peaking at different seasons (Cordes et al., 2022; Chen et al., 2024) even in peatlands (Seniczak et al., 2019). As a result, it is possible that seasonal mismatches in reproduction and development, which I could not control for, may have affected the

outcomes of my lab experiment. Also, while the lab experiment allowed me to isolate the main effects of temperature and moisture, it did not fully mirror natural conditions. For example, in my lab experiment, the temperature and moisture treatments were maintained for four months, which does not realistically reflect temperature and moisture dynamics in natural environments. Temperatures in the field, like those at the BRACE site, can exceed 30°C in the summer, with concomitant fluctuations in moisture levels that were not captured in my lab experiment. Moreover, the nature of my lab experiment did not allow for dispersal (see Lehmitz et al., 2012; Cordes et al., 2022), such as migration or emigration, which is an important factor in how soil oribatid mites respond to environmental stress.

While I attempted to identify all oribatid mites to the species level, this was not possible for all families, nor did I identify the juveniles. Families Brachychthoniidae and Suctobelbidae posed a challenge to identify to species-level, so all individuals within those two families were only identified to family-level. All genera within Brachychthoniidae and Suctobelbidae are usually small (< 200 µm), and all known species are asexual (see Behan-Pelletier and Lindo, 2023). However, one genus within Suctobelbidae, Allosuctobella, can be larger (>350 µm), though I only found two individuals. As such, I do not think that restricting identification of the individuals at the family-level changed the outcome of my results. However, it remains possible that a specific species within these families contributed more strongly to the observed trends than others. Furthermore, juvenile oribatid mites are morphologically different from adult stages, and only 8% have been described so far (Norton and Ermilov, 2014). Thus, correlating juveniles reliably to adults was not possible. Juveniles are important in understanding reproductive dynamics but since I could not identify what species the juveniles were, I also could not determine what species benefitted the most under warmer temperatures. Linking the most abundant juveniles to their species, using techniques like DNA metabarcoding, could provide insights into future community body size shifts. Nonetheless, I would still expect a similar trend where the smaller mites would have higher juveniles due to increased metabolic and reproductive rates under warming (Gillooly et al., 2001; Brown et al., 2004)

#### 4.6 Future studies

While my study showed the direct effects of temperature and moisture, I could not account for indirect effects due to changes in resource availability. Oribatid mite communities contribute to soil processes through their feeding activity on soil microbes as well as organic litter. Both soil microbes (Classen et al., 2015), litter quantity/quality and decomposition rates (Aerts, 2006; García-Palacios at al., 2013) have been shown to be affected by climate change. Therefore, future climate warming experiments that simultaneously measure the response of oribatid mites to temperature and moisture, as well as other factors (e.g., microbial activity, mass loss of organic litter), may provide insights into how temperature and moisture would directly and indirectly structure oribatid mite communities under climate change. Already, scientists are calling for multiple factors to be integrated into soil biodiversity research (Rillig et al., 2019) as soil process and communities will be affected a multitude of drivers under climate change.

Another thing to consider is how these changes in oribatid mite communities will affect carbon dynamics in peatlands. Soil food web models (Hunt et al., 1987; Elliot et al., 1988; de Ruiter et al., 1993), including recent models in boreal peatland systems (Barreto et al., 2024) often look at biomass changes and overlook metabolic shifts that could affect decomposition rates. Smaller oribatid mites, have relatively higher metabolic rates that further increases with temperature. So, with warming under climate change, will oribatid mites contribute more to decomposition (releasing  $CO_2$  back into the atmosphere), or will they be inefficient in their functions as they get closer to their thermal limits? To investigate this, future studies should consider measuring oribatid mite metabolic responses (e.g., respiration) under different temperature levels that mirror future temperature forecasts (e.g.,  $+8^{\circ}C$ ).

Integrating stable isotope analysis with climate warming studies in peatlands could provide valuable insights. Stable carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) isotope signatures have been widely used to trace the feeding sources and trophic positions of soil microarthropods, including oribatid mites (Schneider et al., 2004; Chahartaghi et al., 2005; Maraun et al., 2011; Pollierer and Scheu, 2021). In a *Sphagnum* peatland system, Lehmitz and Maraun (2016) used  $\delta^{13}$ C and  $\delta^{15}$ N to investigate oribatid mite trophic ecology and found that different oribatid mite species occupy distinct niches, functioning as primary decomposers, secondary decomposers, or predators. Therefore, applying stable isotopes in climate warming experiments could help track carbon dynamics through the detrital systems to show how climate change will alter decomposition in boreal peatlands.

#### 4.7 Conclusion

Soil systems account for 59% of global biodiversity (Anthony et al., 2023) and play a crucial role in ecosystem processes such as decomposition, nutrient cycling, organic matter formation, and carbon storage. At the same time, soils and soil organisms/communities depend on abiotic factors like temperature and moisture, both of which are expected to shift under current and future climate projections. While research on soil community responses to climate factors has expanded over the past decade, studies focusing on soil communities in boreal peatlands (or peatlands in general) remain less common than those in forest ecosystems. In this research, I investigated how oribatid mite communities – one of the dominant soil groups in boreal peatlands – respond to warming and associated reductions in moisture. My findings indicate that while moisture had some effects, temperature is a strong driver of changes in oribatid mite communities in boreal peatlands. Temperature increased oribatid mite abundance, especially of the smaller oribatid mites, which led to reduction in community body size. An increase in smaller oribatid mites is likely to accelerate decomposition rates, leading to greater carbon release into the atmosphere, and altering the ability of peatlands to function as long-term carbon sinks.

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### Appendices

### Appendix A: Oribatid mite species, abundance and trait list from the *Sphagnum*-dominated and *Carex*-dominated fens. Abundance values (# indiv./g dwt) are averages ± standard error

				Sphagnum-dominated fen		Carex-dominated fen	
Species	Species ID	Average body size (length) <sup>1</sup>	Reproductive mode <sup>2</sup>	Ambient	Warmed	Ambient	Warmed
Family Palaeacaridae Grandjean, 1932							
Palaeacarus hystricinus Trägårdh, 1932	Palae	360	asexual	$0.05\pm0.05$	$0.15\pm0.11$	0	0
Family Eniochthoniidae Grandjean, 1947							
Eniochthonius mahunkai Norton and Behan-Pelletier, 2007	Enioch1	326	asexual	$4.09 \pm 1.19$	$3.68 \pm 1.33$	$0.01\pm0.01$	0
Eniochthonius minutissimus (Berlese, 1903)	Enioch2	370	asexual	$0.75\pm0.29$	$1.75\pm0.55$	0	0
Family Hypochthoniidae Berlese, 1910							
Hypochthonius rufulus C.L. Koch, 1835	Нурос	675	asexual	$0.28\pm0.10$	$0.24\pm0.08$	$0.04\pm0.02$	$0.25\pm0.20$
Brachychthoniidae Thor, 1934	Brach	185	asexual	$9.30 \pm 1.52$	$13.59\pm2.41$	$0.25\pm0.09$	$0.59\pm0.22$
Family Trichthoniidae Lee, 1982							
Gozmanyina majestus (Marshall and Reeves, 1971)	Gozma	245.3	asexual	$0.82\pm0.28$	$1.14\pm0.29$	0	0
Family Phthiracaridae Perty, 1841							
Phthiracarus boresetosus Jacot, 1930	Phthi	420	sexual	0	0	$0.17\pm0.10$	$0.24\pm0.14$
Hoplophthiracarus illinoisensis (Ewing, 1909)	Hopht	420	sexual	$2.39\pm0.51$	$1.85\pm0.48$	$0.01\pm0.01$	0
Hoplophorella sp.1	Hoplo1	847.53	sexual	$0.16\pm0.06$	$0.13\pm0.05$	0	0
Family Euphthiracaridae Jacot, 1930							
Acrotritia ardua (C.L. Koch, 1841)	Acrot	733.44	asexual	$0.45\pm0.09$	$0.29\pm0.07$	0	0
Microtritia minima (Berlese, 1904)	Micro	202	asexual	0	$0.02\pm0.01$	0	0
Family Nanhermanniidae Sellnick, 1928							
Nanhermannia dorsalis (Banks, 1896)	Nanhe	580	asexual	$0.08\pm0.04$	$0.14\pm0.07$	0	0

Family Nothridae Berlese, 1896							
Nothrus monodactylus (Berlese, 1910)	Nothr1	760	asexual	$1.76\pm0.36$	$0.82\pm0.33$	0	0
Family Crotoniidae Thorell, 1876							
Platynothrus punctatus (L. Koch, 1879)	Platy	864	asexual	$0.05\pm0.05$	0	0	0
Family Malaconothridae Berlese, 1916							
Malaconothrus mollisetosus Hammer, 1952	Malac	430	asexual	$5.76\pm0.80$	$4.50\pm1.03$	$0.84\pm0.40$	$0.97\pm0.46$
Tyrphonothrus foveolatus (Willmann, 1931)	Tyrph1	410	asexual	$0.16\pm0.16$	0	0	0
Tyrphonothrus maior (Berlese, 1910)	Tyrph2	595	asexual	0	0	$3.12\pm0.36$	$1.51\pm0.28$
Family Trhypochthoniidae Willmann, 1931							
Trhypochthoniellus setosus canadensis Hammer, 1952	Tseto	620	asexual	0	0	$1.75\pm0.41$	1.60.49
Mainothrus badius (Berlese, 1905)	Maino	545.13	asexual	$1.74\pm0.48$	$0.69\pm0.24$	0	0
Family Suctobelbidae Jacot, 1938	Sucto	245	asexual	$3.94 \pm 0.57$	$2.84\pm0.26$	$0.73\pm0.32$	0.40.12
Family Oppiidae Grandjean, 1951							
Oppiella nova (Oudemans, 1902)	Oppie	270	asexual	$3.09 \pm 1.60$	$4.71\pm2.18$	$0.23\pm0.09$	$0.17\pm0.10$
Family Quadroppiidae Balogh, 1983							
Quadroppia quadricarinata (Michael, 1885)	Quadr	210	asexual	$0.39\pm0.09$	$0.54\pm0.13$	$0.03\pm0.02$	$0.01\pm0.01$
Family Peloppiidae Balogh, 1943							
Ceratoppia bipilis (Hermann, 1804)	Ctopp1	850	sexual	0	0	$0.02\pm0.01$	$0.03\pm0.02$
Family Tectocepheidae Grandjean, 1954							
Tectocepheus velatus Trägårdh, 1905	Tecto	298.5	asexual	$6.83 \pm 1.53$	$9.14 \pm 1.46$	$0.23\pm0.18$	$0.37\pm0.22$
Family Carabodidae C.L. Koch, 1837							
Carabodes polyporetes Reeves, 1991	Carab1	542.5	sexual	$0.01\pm0.01$	$0.02\pm0.02$	0	0
Carabodes granulatus Banks, 1895	Carab2	400	sexual	$0.02\pm0.02$	$0.01\pm0.01$	0	0
Family Galumnidae Jacot, 1925							
Pergalumna emarginata (Banks, 1895)	Perga	695	sexual	$0.09\pm0.05$	$0.05\pm0.03$	$0.04\pm0.02$	$0.01\pm0.01$
Pilogalumna sp.	Pilog	610	sexual	0	0	$0.02\pm0.01$	$0.02\pm0.01$
Family Limnozetidae Grandjean, 1954							
Limnozetes guyi Behan-Pelletier, 1989	Limno1	350	asexual	0	0	$0.84\pm0.33$	$0.17\pm0.06$

Limnozetes onondaga Behan-Pelletier, 1989	Limno2	327	asexual	0	0	$0.23\pm0.11$	$0.07\pm0.03$
Family Achipteriidae Thor, 1929							
Anachipteria sp.	Anach	462.5	sexual	0	0	$0.17\pm0.06$	$0.32\pm0.11$
Family Haplozetidae Grandjean, 1936							
Protoribates lophotrichus (Berlese, 1904)	Proto	560	asexual	$0.85\pm0.20$	$0.58\pm0.15$	0	0
Family Scheloribatidae Grandjean, 1933							
Scheloribates pallidulus (C.L. Koch, 1841)	Schel	400	sexual	0	$0.12\pm0.07$	0	0
Liebstadia humerata (C.L. Koch, 1835)	Liebs	345	sexual	0	$0.04\pm0.02$	0	0
Family Oribatulidae Thor, 1929							
Lucoppia nr. apletosa (Higgins and Woolley, 1975)	Lucop	802.5	sexual	0	$0.01\pm0.01$	0	0
Oribatula tibialis (Nicolet, 1855)	Oriba	470	sexual	0	$0.04\pm0.03$	0	0
Family Punctoribatidae Thor, 1937							
Punctoribates palustris (Banks, 1895)	Punct	453.5	sexual	$0.31\pm0.11$	$0.55\pm0.13$	$0.06\pm0.02$	$0.06\pm0.03$
Family Ceratozetidae Jacot, 1925							
Ceratozetes cf. parvulus Sellnick, 1922	Ceracf	288	sexual	$0.03\pm0.02$	$0.02\pm0.02$	0	0
<i>Ceratozetes</i> nr. <i>parvulus</i>	Ceranr	288	sexual	0	0	$0.28\pm0.10$	$0.12\pm0.04$
Family Zetomimidae Shaldybina, 1966							
Naiazetes sp.	Naiaz	405	sexual	0	0	$0.01\pm0.01$	0

<sup>1</sup>Average body size values were obtained from Behan-Pelletier and Lindo (2023), and personal records of ZL and CB based on individuals measured at the BRACE sites.

<sup>2</sup>Reproductive modes follow Maraun et al. (2019) and Maraun et al. (2022)

Appendix B: Oribatid mite species included in the dbRDA analysis. Species contributing at least 50% to the total axes loadings based on the absolute sum of their CAP1 and CAP2 loadings were selected; here they are listed in decreasing order by the sum of their absolute axes scores. These species represent >90% of the species in each fen (*Sphagnum*-dominated: n = 28; *Carex*-dominated: n

= 19).

	Spaghnum-dominated fen		Carex-dominated fen
Sucto	Suctobelbidae	Tyrph2	Tyrphonothrus maior
Enioch2	Eniochthonius minutissimus	Tecto	Tectocepheus velatus
Tecto	Tectocepheus velatus	Brach	Brachychthoniidae
Hopht	Hoplophthiracarus illinoisensis	Limno1	Limnozetes guyi
Maino	Mainothrus badius	Sucto	Suctobelbidae
Gozma	Gozmanyina majestus	Нурос	Malaconothrus mollisetosus
Nothr1	Nothrus monodactylus	Anach	Anachipteria sp.
Malac	Malaconothrus mollisetosus	Phthi	Phthiracarus boresetosus
Quadr	Quadroppia quadricarinata	Limno2	Limnozetes onondaga
Palae	Palaeacarus hystricinus	Perga	Pergalumna emarginata
Punct	Punctoribates palustris	Ceranr	Ceratozetes nr. parvulus
Schel	Scheloribates pallidulus	Oppie	Oppiella nova
Acrot	Acrotritia ardua	Pilog	Pilogalumna sp.
Nanhe	Nanhermannia dorsalis	Punct	Punctoribates palustris
Brach	Brachychthoniidae	Quadr	Quadroppia quadricarinata
Proto	Protoribates lophotrichus	Ctopp1	Ceratoppia bipilis
Нурос	Hypochthonius rufulus	Naiaz	<i>Naiazetes</i> sp.
Liebs	Liebstadia cf. humerata	Enioch1	Eniochthonius mahunkai
Oriba	Oribatula tibialis	Hopht	Hoplophthiracarus illinoisensis
Tyrph1	Tyrphonothrus foveolatus		
Hoplo1	Hoplophorella sp.1		
Lucop	Lucoppia nr. apletosa		
Micro	Microtritia minima		
Carab1	Carabodes polyporetes		
Carab2	Carabodes granulatus		
Ceracf	Ceratozetes cf. parvulus		
Platy	Platynothrus punctatus		
Perga	Pergalumna emarginata		

Appendix C: Major microarthropod groups, other microarthropods and total microarthropods at the *Sphagnum*-dominated and *Carex*-dominated fens.

Abundance values (#indiv. /g dwt) are averages ± standard error. Letters indicate significant groups based on a Bonferroni adjustment.

		Sphagnum-dominated site						
		Mesostigmata	Prostigmata	Astigmata	Collembola	Other microarthropods	Total microarthropods	
	Ambient	$1.56\pm0.22$	$3.53\pm0.55$	$0.42\pm0.25$	$7.36 \pm 1.01$	$1.18\pm0.25$	$108.17 \pm 14.76$	
June	Warmed	$1.14\pm0.19$	$5.23 \pm 1.69$	$0.59\pm0.14$	$9.36\pm2.76$	$0.63\pm0.11$	$102.78 \pm 12.83$	
	Ambient	$1.11\pm0.3$	$7.35 \pm 1.03$	$0.28\pm0.08$	$3.22\pm0.6$	$0.88\pm0.43$	$149.77 \pm 22.21$	
September	Warmed	$1.26\pm0.41$	$7.59 \pm 1.99$	$0.66\pm0.34$	$4.39\pm0.62$	$0.83\pm0.27$	$166.01 \pm 26.44^{\rm a}$	
	Treatment (F <sub>1,11</sub> )	F = 0.41, p = 0.329	F = 0.72, p = 0.415	F = 0.32, p = 0.582	F = 0.85, p = 0.377	F = 1.74, p = 0.214	F = 0.03, p = 0.851	
	Time (F <sub>1,14</sub> )	F = 0.16, p = 0.299	F = 7.24, p = 0.018	F = 0.21, p = 0.650	F = 3.83, p = 0.070	F = 0.53, p = 0.480	F = 2.20, p = 0.160	
	Treatment $\times$ Time (F <sub>1,14</sub> )	F = 0.94, p = 0.349	F = 0.52, p = 0.480	F = 0.23, p = 0.640	F = 0.08, p = 0.785	F = 0.71, p = 0.413	F = 0.28, p = 0.594	
	-			Carex-don	ninated site			
	-	Mesostigmata	Prostigmata	Astigmata	Collembola	Other microarthropods	Total microarthropods	
T	Ambient	$0.22\pm0.1$	$0.22\pm0.07$	$0.08\pm0.03$	$0.91\pm0.23$	$1.88\pm0.65^{ab}$	$20.76\pm5.43^{b}$	
June	Warmed	$0.10\pm0.03$	$0.28\pm0.07$	$0.11\pm0.05$	$1.25\pm0.30$	$0.77\pm0.08^{\rm a}$	$13.65\pm2.11^{\text{b}}$	
<b>C</b> ( ]	Ambient	$0.14\pm0.05$	$0.98\pm0.27$	$0.16\pm0.07$	$0.64\pm0.26$	$8.3\pm2.41^{\circ}$	$61.34\pm12.56^{ab}$	
September	Warmed	$0.32\pm0.12$	$0.79\pm0.58$	$0.28\pm0.14$	$1.28\pm0.67$	$4.54\pm1.36^{bc}$	$35.07\pm6.81^{\text{a}}$	
	Treatment (F <sub>1,11</sub> )	F = 1.25, p = 0.287	F = 0.02, p = 0.905	F = 1.10, p = 0.747	F = 0.37, p = 0.554	F = 0.30, p = 0.590	F = 0.53, p = 0.484	
	Time $(F_{1,14})$	F = 0.63, p = 0.440	F = 2.93, p = 1.093	F = 0.58, p = 0.460	F = 0.30, p = 0.591	F = 12.17, p = 0.004	F = 19.70, p < 0.001	
	$\begin{array}{c} \text{Treatment} \times \text{Time} \\ (F_{1,14}) \end{array}$	F = 3.99, p = 0.065	F = 0.15, p = 0.709	F = 0.30, p = 0.593	F = 0.18, p = 0.674	F = 1.03, p = 0.326	F = 1.97, p = 0.182	

	Species ID	Average body size (length) <sup>1</sup>	Reproductive mode <sup>2</sup>	Sphagnum		Carex	
				12°C	20°C	12°C	20°C
Palaeacaridae							
Palaeacarus hystricinus Trägårdh, 1932	Palae	360	asexual	$0.19\pm0.06$	$0.65\pm0.29$	$0.01\pm0.01$	0
Eniochthoniidae							
Eniochthonius mahunkai Norton and Behan-Pelletier, 2007	Enioch1	326	asexual	$2.33\pm0.66$	$5.39 \pm 1.94$	$0.03\pm0.03$	$0.09 \pm 0.07$
Eniochthonius minutissimus (Berlese, 1903)	Enioch2	370	asexual	$0.09\pm0.04$	$0.27\pm0.18$	0	$0.03\pm0.02$
Hypochthoniidae							
Hypochthonius rufulus C.L. Koch, 1835	Нурос	675	asexual	$0.15\pm0.06$	$0.32\pm0.13$	$0.8\pm0.23$	$0.3\pm0.07$
Brachychthoniidae	Brach	185	asexual	$2.7\pm0.8$	$36.53\pm10.15$	$3.95 \pm 1.11$	$3.7\pm 0.9$
Trichthoniidae							
Gozmanyina majestus (Marshall and Reeves, 1971)	Gozma	245.3	asexual	$1.14\pm0.27$	$1.85\pm0.84$	$0.01\pm0.01$	0
Phthiracaridae							
Phthiracarus boresetosus Jacot, 1930	Phthi	420	sexual	$0.12\pm0.06$	$4.67\pm2.91$	0	0
Phthiracarus sp. 1	Phthi2	950	sexual	0	0	$0.05\pm0.02$	$0.08 \pm 0.05$
Hoplophthiracarus illinoisensis (Ewing, 1909)	Hopht	420	sexual	0	$0.08\pm0.06$	$0.69\pm0.35$	$0.08\pm0.08$
Hoplophorella sp.1	Hoplo1	847.53	sexual	$0.24\pm0.06$	$0.62\pm0.21$	0	0
Euphthiracaridae							
Acrotritia ardua (C.L. Koch, 1841)	Acrot	733.44	asexual	$0.1\pm0.05$	$0.67\pm0.18$	$0.02\pm0.02$	0
Nanhermanniidae							
Nanhermannia dorsalis (Banks, 1896)	Nanhe	580	asexual	$1.19\pm0.54$	$3.2\pm0.7$	0	0
Nothridae							
Nothrus monodactylus (Berlese, 1910)	Nothr1	760	asexual	$0.16\pm0.06$	$0.4\pm0.19$	0	0
Nothrus borussicus Sellnick, 1928	Nothr2	955	asexual	0	0	$0.02\pm0.02$	$0.01\pm0.01$
Crotoniidae							

Appendix D: Oribatid mite species, abundance and traits list from the *Sphagnum* and *Carex*-dominated fen mesocosms. Abundance values (# indiv./g dwt) are averages ± standard error.
Platynothrus peltifer (CL Koch, 1839)	Platy2	1012 5					
	•	1012.5	asexual	0	0	$0.08\pm0.03$	0
Platynothrus thori (Berlese, 1904)	Platy3	982	asexual	0	0	$0.02\pm0.01$	0
Malaconothridae							
Malaconothrus mollisetosus Hammer, 1952	Malac	430	asexual	$2.81\pm0.38$	$5.63 \pm 1.28$	$1.92\pm0.5$	$2.93\pm0.56$
Tyrphonothrus foveolatus (Willmann, 1931)	Tyrph1	410	asexual	0	$0.02\pm0.02$	0	0
Tyrphonothrus maior (Berlese, 1910)	Tyrph2	595	asexual	0	0	$3.22\pm0.54$	$4.06\pm0.66$
Trhypochthoniidae							
Trhypochthoniellus setosus canadensis Hammer, 1952	Tseto	620	asexual	0	0	$0.45\pm0.08$	$3.28 \pm 1.01$
Mainothrus badius (Berlese, 1905)	Maino	545.13	asexual	$0.01\pm0.01$	$0.17\pm0.06$	0	0
Suctobelbidae	Sucto	245	asexual	$3.48\pm0.56$	$8.61\pm2.44$	$2.08\pm0.37$	$2.11\pm0.53$
Oppiidae							
Oppiella nova (Oudemans, 1902)	Oppie	270	asexual	$6.78 \pm 1.04$	$11.34\pm2.92$	$1.11\pm0.23$	$1.58\pm0.52$
Quadroppiidae							
Quadroppia quadricarinata (Michael, 1885)	Quadr	210	asexual	$0.12\pm0.06$	$0.21\pm0.19$	$0.07\pm0.03$	$0.13\pm0.05$
Tectocepheidae							
Tectocepheus velatus Trägårdh, 1910	Tecto	298.5	asexual	$5.77\pm0.74$	$6.17 \pm 1.27$	$0.18\pm0.06$	$0.12\pm0.04$
Carabodidae							
Carabodes polyporetes Reeves, 1991	Carab1	542.5	sexual	$0.12\pm0.04$	$0.06\pm0.03$	0	0
Galumnidae							
Pergalumna emarginata (Banks, 1895)	Perga	695	sexual	$0.07\pm0.04$	$0.02\pm0.02$	$0.02\pm0.02$	$0.07\pm0.03$
Limnozetidae							
Limnozetes guyi Behan-Pelletier, 1989	Limno1	350	asexual	0	0	$0.23\pm0.14$	$0.53\pm0.29$
Limnozetes onondaga Behan-Pelletier, 1989	Limno2	327	asexual	0	0	$0.01\pm0.01$	$0.05\pm0.03$
Achipteriidae							
Anachipteria sp.	Anach	462.5	sexual	0	0	$0.19\pm0.07$	$0.43\pm0.12$
Haplozetidae							
Protoribates lophotrichus (Berlese, 1904)	Proto	560	asexual	$0.01\pm0.01$	$0.52\pm0.21$	0	0
Scheloribatidae							
Scheloribates pallidulus (C.L. Koch, 1841)	Schel	400	sexual	$0.02\pm0.02$	$0.02\pm0.02$	0	0

Liebstadia humerata Sellnick, 1928	Liebs	345	sexual	$0.05\pm0.02$	$0.39\pm0.31$	0	0
Punctoribatidae							
Punctoribates palustris (Banks, 1895)	Punct	453.5	sexual	0	0	0	$0.01\pm0.01$
Ceratozetidae							
Ceratozetes nr. parvulus	Ceranr	288	sexual	0	0	$0.62\pm0.25$	$1.43\pm0.22$

<sup>1</sup>Average body size values were obtained from Behan-Pelletier and Lindo (2023), and personal records of ZL and CB based on individuals measured at the BRACE sites.

<sup>2</sup>Reproductive modes follow Maraun et al. (2019) and Maraun et al. (2022)

Appendix E: Major microarthropod groups, other microarthropods and total microarthropods from the Sphagnum-

dominated fen mesocosms. Values (indiv. /g dwt) are averages ± standard error.

Values are averages ± standard errors. Bolded values indicate significant (or marginally significant) values.

Mosostigmata		Prostigmate	Collombolo	Astigmata	Other	Total
	mesosugmata r rosugmata		Conembola	Astiginata	microarthropods	microarthropods
12°C	$1.72\pm0.44$	$4.53\pm0.61$	$11.09\pm4.5$	$2.6\pm1.42$	$0.49\pm0.11$	$68.54\pm6.91$
20°C	$3.17 \pm 1.00$	$3.32\pm0.76$	$33.79 \pm 4.99$	$1.39\pm0.51$	$1.18\pm0.5$	$178.97\pm22.6$
Temperature (F <sub>1,16</sub> )	F = 4.34, p = 0.054	F = 0.12, p = 0.732	F = 4.21, p = 0.057	F = 0.19, p = 0.672	F = 4.79, p = 0.044	F = 23.83, p = 0.000
Moisture (F <sub>1,16</sub> )	F = 2.09, p = 0.167	F = 0.81, p = 0.383	F = 0.02, p = 0.889	F = 3.14, p = 0.096	F = 0.811, 0.381	F = 0.30, p = 0.591
Interaction (F <sub>1,16</sub> )	F = 0.05, p = 0.832	F = 0.13, p = 0.721	F = 1.26, p = 0.278	F = 0.13, p = 0.719	F = 1.87, p = 0.190	F = 0.04, p = 0.836
Slope with moisture at 12°C	-0.205	-0.190	0.557	-0.666	0.062	-0.070
Slope with moisture at 20°C	-0.294	-0.086	-0.127	-0.449	-0.530	-0.033

Appendix F: Major microarthropod groups, other microarthropods and total microarthropods from the *Carex*-dominated fen mesocosms. Values (indiv. /g dwt) are averages ± standard error.

	Mesostigmata	Prostigmata	Collembola	Astigmata	Other microarthropods	Total microarthropods
12°C	$0.26\pm0.14$	$0.13\pm0.05$	$1.17\pm0.37$	$0.09\pm0.03$	$1.4\pm0.31$	$27.82\pm3.35$
20°C	$1.16\pm0.39$	$0.43\pm0.16$	$11.14 \pm 6.13$	$0.38\pm0.17$	$1.71\pm0.55$	$54.07 \pm 11.51$
Temperature (F <sub>1,16</sub> )	F = 5.44, p = 0.033	F = 4.83, p = 0.043	F = 4.88, p = 0.042	F = 4.18, p = 0.058	F = 5.49, p = 0.032	F = 5.81, p = 0.028
Moisture (F <sub>1,16</sub> )	F = 8.02, p = 0.012	F = 0.48, p = 0.500	F = 1.37, p = 0.259	F = 0.32, p = 0.578	F =2.42, p = 0.140	F = 1.81, p = 0.198
Interaction (F <sub>1,16</sub> )	F = 5.19, p = 0.037	F = 0.15, p = 0.706	F = 4.62, p = 0.047	F = 0.89, p = 0.359	F = 5.43, p = 0.033	F = 5.59, p = 0.031
Slope with moisture at 12°C	0.548	0.145	-0.239	0.010	0.175	0.098
Slope with moisture at 20°C	-0.426	-0.003	-1.001	-0.475	-0.397	-0.277

Values are averages ± standard errors. Bolded values indicate significant (or marginally significant) values.

## Curriculum Vitae

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**\*Obi, E.** & Lindo, Z. Simulated climate warming in boreal peatlands alters belowground communities through peat drying. Annual Conference of the Entomological Society of Ontario, University of Toronto, Scarborough, Ontario. October 2024. [Standard presentation]

Gbarakoro, T.N, Abajue, M.C. & **\*Obi, J.C**. Impact of oil palm plantation on soil microarthropods. 51st Annual Conference of the Entomological Society of Nigeria, Uyo, Akwa-Ibom State. October 2021. [Standard presentation]