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Above- and belowground community linkages in boreal peatlands and climate warming implications

Caitlyn Lyons, *The University of Western Ontario*

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

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Abstract

Aboveground plants provide resources to the belowground microbial community via plant litter and, in turn, the belowground microbial community provides nutrients for plant uptake, linking the two systems. My aim was to characterize and describe differences in plant community composition, plant litter quality and microbial community composition between two boreal peatlands in northern Ontario. These peatlands have contrasting plant and microbial communities, the *Sphagnum* moss-dominated peatland harboring a higher fungi to bacteria ratio compared to the *Carex* sedge-dominated peatland. Clear open top chambers were installed at both sites to simulate warming. Higher temperatures decreased *Sphagnum* moss in the *Sphagnum*-dominated peatland, increased aboveground biomass in the *Carex* sedge dominated peatland, and increased the heterogeneity in plant community composition at both sites. Shifts in aboveground plant community and subsequent plant litter quality inputs to the microbial community has potential implications for peatland carbon storage.

Keywords

Boreal peatlands, community composition, *Carex* sedges, *Sphagnum* moss, climate warming, plant-microbial interactions, litter quality, Fungi:Bacteria, Phospholipid fatty acids

Summary for Lay Audience

Dead plant material that enters the soil system is an important source of nutrients for soil microorganisms who, in turn, recycle nutrients and make them available for plant uptake. Peatlands are a type of wetland with a large organic soil layer composed of partially decomposed plant material called peat. Peat is rich in carbon, making peatlands an important global carbon store. Plants and microorganisms can be described along a spectrum of fast growing with high nutrient demands to slow growing with low nutrient demands, and plants are thought to be paired with microorganisms with similar traits. My thesis describes both the aboveground plant community and the belowground microbial community in two contrasting boreal peatlands located in northern Ontario. The two peatland sites I have characterized are: 1) a *Sphagnum* moss-dominated peatland with nutrient poor plants that is dominated by fungi, a slow nutrient cycler; and 2) a *Carex* sedge-dominated peatland with nutrient rich plants, dominated by bacteria, a fast nutrient cycler. The contrasting plant and soil microorganism communities have implications on carbon storage, with the Sphagnum-dominated peatland having the potential to store more carbon. I also explored the impacts of warming on the aboveground plant communities at both of these peatland sites using clear open top chambers that act as a greenhouse, warming the air. At both sites, under higher temperatures, plant community composition was more variable: in the *Sphagnum*-dominated peatland I saw a decrease in moss abundance, and in the *Carex*-dominated peatland I saw an increase in aboveground biomass. *Sphagnum* is important in maintaining the carbon sequestration ability of peatlands, so a reduction in *Sphagnum* moss could reduce the amount of carbon stored in boreal peatlands. Greater aboveground biomass in the *Carex*-dominated peatland under warming increases the amount of nutrient rich plant litter. This could increase the activity and also the amount of carbon cycled by the soil microorganisms, again reducing the carbon storage potential of boreal peatlands.

Co-Authorship Statement

Chapters contained within this thesis are planned manuscripts for submission to peer-reviewed journals. Chapter 2 was envisioned by both Dr. Zoë Lindo and Caitlyn Lyons; Lyons collected and analyzed the data, a subset of data from this chapter will be developed for publication by Lyons and Lindo. Chapter 3, experiment conceived and initiated by Lindo and Dr. Brian Branfireun in collaboration with the Ontario Ministry of Natural Resources and Forestry (OMNRF); Lyons collected and analyzed the data, any manuscripts arising from this work will be developed by both Lyons and Lindo with collaboration by both Branfireun and the OMNRF.

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List of Abbreviations

ANOVA	Analysis of Variance
C	Carbon
CF	*Carex*-dominated Fen
CWM	Community Weighted Means
F:B	Fungi:Bacteria
LAI	Leaf Area Index
MANOVA	Multivariate Analysis of Variance
MVDisp	Multivariate Dispersion Index
N	Nitrogen
NMDS	Non-Metric Multidimensional Scaling Ordination
OTC	Open-top Chamber
PCA	Principal Components Analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
PLFA	Phospholipid Fatty Acid
SF	*Sphagnum*-dominated Fen
SIMPER	Similarity of Percent Analysis

Chapter 1

1 Introduction

1.1 Linking aboveground and belowground communities

The aboveground (plant) and belowground (soil microbial) communities in terrestrial systems do not function independently, rather there is a feedback between the two. This feedback exists through an exchange of resources between the above- and belowground communities (Wardle et al. 2004). Plants provide resources to the microbial community via litter (Hättenschwiler et al. 2005) and root exudates (Porazinska et al. 2003; Brzostek et al. 2013). The belowground system in turn cycles soil nutrients during the process of decomposition, making them available for plant uptake. The life history traits of both the aboveground plant species and the belowground microbial groups can influence both the rate and the quality of resource exchange between the two systems. It has been long established that species demonstrate trade-offs in growth, reproduction, and more generally resource allocation and acquisition that leads to differences in life history strategies (Grime 1977; Wright et al. 2004; Westoby and Wright 2006). Grime (1977) was the first to describe and formalize this paradigm in plant species traits where he described fast-growing, nutrient exploitative and slow-growing, nutrient conservative dichotomous plant trait strategies. In reality, plants and other organisms are constrained by ecological trade-offs, but life history traits exist along a continuum between the two extremes (Grime 1977; Reich 2014). In addition, at a food web and ecosystem level, these differences in life history traits translates into differences in the nutritional value (quality) of plants and microorganisms with implications on resource cycling between the above- and belowground communities.

Plants that have fast growth rates tend to be nutrient exploitative, creating nutrient rich inputs to the belowground system (Reich 2014). On the other end of the spectrum there are slow growing, nutrient conservative plants, which reabsorb nutrients before senescing plant material, thus providing nutrient poor inputs to the belowground system (Reich 2014). The aboveground plant inputs can be described as either low quality (recalcitrant) or high quality (labile) (Manzoni et al. 2010). One way to classify aboveground plant

inputs is by examining the Carbon (C) to Nitrogen (N) ratio (C:N). Nitrogen is often the limiting resource in terrestrial systems (Vitousek and Howarth 1991), constraining growth and productivity. Plants that are efficient at acquiring N, and have greater N in their tissues, produce litter inputs to the soil system that are higher in N, and are thus considered to be more labile and of higher quality for microbial growth. Plants such as mosses that depict 'slow' life history traits such as short stature, slow growth rates and high shade tolerance, tend to succeed in more nutrient poor environments, withstanding lower amounts of resources that might be limiting to other plant species (Grime et al. 1990). In contrast, plants that depict 'fast' life history traits, such as sedges, tend to populate environments that are more nutrient rich and therefore provide more nutrient rich resources to the belowground (Keddy et al. 1998). Sedges are associated with the 'fast' life history traits such as tall height and fast growth, enabling efficient capture and utilization of resources such as light, water, nutrients or space (Grime 1974).

Traits exist at the level of the individual, but are mostly derived by species-specific morphological, physiological and behavioural traits. At the community-level, the ecological community is a collection of species demonstrating various life history strategies. The biomass ratio hypothesis postulates that the most dominant species will have the greatest effect on ecosystem processes (Grime 1998). As such, to determine traits of the community as a whole, ecologists often use community-weighted means (CWM) to account for the relative abundance of different species in a community. This is important when considering inputs to the belowground system, as both the plant species present and the relative dominance of each will impact both the quantity and quality (%C, %N, and C:N) of resources available to the soil microorganisms.

Aboveground plant inputs are the basal resource for the soil food web. The belowground soil microorganisms decompose the plant inputs and recycle soil resources making them available for plant uptake. Decomposition is a multi-step process involving both physical and chemical processes (Coleman et al. 2004). During the initial stage any of the dissolvable compounds are leached into the water present in the soil. The second stage involves the physical fragmentations of plant material by soil invertebrates and the microbial community. The final stage is mineralization; fungi and bacteria (decomposers)

transform the smaller pieces into basic inorganic forms of nitrogen, phosphorus and carbon that plants can uptake (Van Der Heijden et al. 2008). The microbial community can also utilize the dissolvable compounds produced by leaching (Allison et al. 2010; Blagodatsky et al. 2010) and furthermore much of the microbially derived products are reused by other microorganisms and the rest of the soil food web (Kögel-Knaber 2002).

Similar to their aboveground counterparts, microorganisms can also demonstrate 'fast-slow' life history traits. In addition to 'fast-slow' life history traits, Grime (1977) also recognizes three possible survival strategies: 1) ruderal, indicating an ability to colonize under high disturbance and have low stress tolerance; 2) stress-tolerant, indicating an ability to colonize under low disturbance and high stress; and 3) competitive, indicating an ability to colonize under low disturbance and low stress. Along this continuum, it is generally held that bacteria are considered ruderal, fast growing and nutrient exploitative whereas fungi are more stress tolerant, slow growing and nutrient conservative (Wardle et al. 2004). Bacteria are considered to cycle nutrients faster than fungi, demonstrating greater decomposition and high heterotrophic respiration rates (Wardle et al. 2004). Soil systems dominated by bacterial communities have been demonstrated to store less carbon and subsequently release more CO_2 to the atmosphere (Strickland et al. 2009; Strickland and Rousk 2010; Malik et al. 2016). Fungi are considered to have slow nutrient cycling and lower rates of heterotrophic respiration resulting in more carbon stored in soils (Malik et al. 2016). Furthermore, fungi have the ability to use specialized enzymes to break down more recalcitrant plant litter that bacteria cannot, yet fungi are not limited to utilizing only recalcitrant low quality litter; they also utilize labile litter (Waldrop and Firestone 2004; Caruso et al. 2018). The C:N values of microbial biomass are indicative of 'fast' versus 'slow' processes where bacteria C:N is typically lower (greater proportional N values) than that of fungal biomass (Six et al. 2006; Strickland and Rousk 2010; Waring et al. 2013), and there appears to be a consistent link between litter C:N and Fungi:Bacteria ratio (F:B) across a variety of different soil types (Soares and Rousk 2019).

1.2 Boreal peatlands

Peatlands, wetlands with organic soils greater than 40 cm deep, cover ~13% of the Canadian landscape, and the majority (~97%) of Canadian peatlands are located in the boreal region (Tarnocai et al. 2011). Not only are peatlands a dominant feature on the Canadian landscape, they are also a unique ecosystem to study above- and belowground community linkages because the aboveground plants leave their legacy as partially decomposed organic matter or "peat". Decomposition is a slow process in boreal peatlands compared to other ecosystems because low temperatures, waterlogged and acidic conditions slow decomposition rates, allowing for the accumulation of peat (Moore et al. 2007). Plant productivity in peatlands is also generally low, but the even slower decomposition rate creates an accumulation of undecomposed plant material (peat) that is a C store and establishes peatlands as important global C sinks. This net gain of C to the soil system in peatlands means that peatlands store 1/3 of the world's terrestrial C despite only covering ~3% of the globe (Gorham 1991). As the plant litter is an important constituent of the peat, the aboveground plant community has a strong influence on the inputs to the belowground microbial community and the C storage potential of peatlands. At the same time, the microbial community (fungi and bacteria), as the primary decomposers of this plant material, are also important when considering the C sequestration ability of peatlands. Decomposition rate is the main determinant of net C storage potential for peatlands.

Boreal peatlands are not uniform in terms of aboveground plant community composition, hydrology, or nutrient content. Rather, they exist along a continuum from nutrient poor, hydrologically unconnected and *Sphagnum*-dominated bogs to relatively nutrient rich, hydrologically connected and vascular plant dominated fens (Rydin and Jeglum 2013). This continuum likely extends to the belowground microbial community as well. Several studies have examined the aboveground plant community composition in boreal peatlands (for example, Whitehouse and Bayley 2005; Locky and Bayley 2006; Palozzi and Lindo 2017), while other studies have examined the belowground microbial community composition in boreal peatlands (for example, Haynes et al. 2015; Asemaninejad et al. 2017a, 2019), but few studies have examined them jointly (but see

Borga et al. 1994). Both the above- and belowground community play roles in ecosystem functions such as C storage in boreal peatlands, and both should be studied in tandem especially when climate change is expected to impact both the plant (Weltzin et al. 2003; Jassey et al. 2013; Buttler et al. 2015; Dieleman et al. 2015) and microbial communities (Bragazza et al. 2013; Asemaninejad et al. 2017b, 2018).

1.3 Climate warming effects on ecological communities

Anthropogenic activities have altered the environment so intensively that many scientists agree we have entered a new geological epoch, the Anthropocene (Crutzen 2002). One aspect of this new epoch is the rise in atmospheric CO_2, associated with human activities; which is inducing climate warming across the globe. The ever-increasing atmospheric levels of CO_2 are unprecedented within the past 22,000 years and are 40% above pre-industrial levels (IPCC 2013). There is a linear relationship between CO_2 levels and temperature (Allen et al. 2009; Gillett et al. 2013) as CO_2 is a greenhouse gas. As humans continue to emit CO_2 through the burning of fossil fuels, global temperatures are predicted to continue to rise. A special report published by the IPCC indicates that global average temperatures have risen by 1ºC (likely between 0.8 and 1.2 ºC) in 2017 since pre-industrialization and are expected to rise by 0.2 ºC (0.1 and 0.3 ºC) with each passing decade (IPCC 2018). While there are other global change factors besides rising CO_2 concentrations, such as alterations in precipitation, increased NOx deposition and other global pollutants, and land use change / habitat loss that are affecting ecological communities (Sala et al. 2000), it is also important to quantify the direct consequences of climate warming on ecological communities and ecosystem-level processes.

Rising temperatures alters abiotic conditions, disrupting ecological communities. Community composition is a function of both species' interactions with the abiotic environment and interactions between species. Species' ranges encompass the possible habitable environments, and alterations in abiotic conditions can shift environments from habitable to uninhabitable for certain species while shifting from uninhabitable to habitable for others (Walther 2010). Climate warming tends to shift ranges of terrestrial organisms towards higher elevations and latitudes (Walther et al. 2002; Parmesan and Yohe 2003). Furthermore, shifts in the abiotic environment can also shift biotic

interactions, modifying the outcomes of competition, decoupling mutualistic partnerships, and altering predator-prey dynamics. Predicting the effects of climate warming on community composition is difficult to generalize as the responses tend to depend on species' life history traits although fast life history traits tend to win under warming (Parmesan 2007; Berg et al. 2010).

Across the globe, rising temperatures are altering community composition and the rates of key ecosystem processes they mediate. Yet, temperature increases are not uniform across the globe, with certain regions experiencing increases in temperature much higher than the global average, such as higher latitudes like the boreal zone. Warming effects in high latitude regions can result in snow, ice and permafrost melt, thereby decreasing the regional albedo and creating a positive feedback to further amplify warming in northern regions (Holland and Bitz 2003). Canada's Changing Climate Report 2019 indicates that Canada has seen an increase in temperature of 1.7ºC (likely between 1.1 and 2.3ºC) between 1948 and 2016 compared to the pre-industrial temperatures, whereas northern Canada has seen an increase of 2.3ºC (likely between 1.7 and 3ºC) (Zhang et al. 2019). Furthermore, all four of the predicted climate scenarios from the IPCC (2013) indicate that Canada's projected increase in temperature is twice the corresponding global temperature increase (Zhang et al. 2019). As such, it is clear that Canada's northern ecosystems are at an increased risk to rising temperatures.

1.4 Climate change and peatland plant communities

Several previous studies have examined the impacts of rising temperatures on boreal peatland plant communities. These studies have mainly focused on *Sphagnum*-dominated peatlands, with the generally consensus that there will be a shift in the 'fast-slow' spectrum, away from the slower growing *Sphagnum* spp. towards the faster growing vascular plant species (Weltzin et al. 2000; 2003; Fenner et al. 2007; Dieleman et al. 2015). Mechanistically this arises as warming shifts the competitive outcome in favour of the faster growing, nutrient exploitative species. The various studies have shown shifts towards different vascular plant types. For instance, Dieleman et al. (2015) and Fenner et al. (2007) in a mesocosm lab experiment noted a shift from *Sphagnum* spp. to graminoids, while Weltzin et al. (2000; 2003) (using a similar design) found an increase

in shrub dominance. Jassey et al. (2013) and Buttler et al. (2015), in a field study, found an increase in total vascular abundance using passive warming open-top chambers (OTC) and Bragazza et al. (2016) also found an increase in vascular plant abundance by transplanting peat cores with intact vegetation to a lower altitude with warmer temperatures. Finally, Bragazza et al. (2013), in an observational study, observed higher shrub biomass at lower altitudes with higher soil temperatures compared to peatlands at higher elevations with lower soil temperatures. Fewer studies have focused on graminoid dominated peatlands such as *Carex* spp.. Where studies have been done, Weltzin et al. (2000; 2003) using a mesocosm design, and Mäkiranta et al. (2018) using passive warming OTCs, no shifts in plant community composition under warming were found. However, Weltzin et al. (2000; 2003) did find an increase in annual net primary productivity of graminoids.

1.5 Site selection and description

Two boreal peatlands sites were selected for this thesis, they are located near White River, Ontario (48°21'N, 84°20'W); these sites have been monitored as long-term research sites by the Ontario Ministry of Natural Resources and Forestry for the past 15 years (see Webster and McLaughlin (2010) for full description). The two boreal peatland sites are fens; one fen has a nutrient poor status and is dominated by *Sphagnum* spp. mosses while the other fen has an intermediate nutrient status and is dominated by *Carex* spp. sedges. The fens will henceforth be referred as SF (*Sphagnum*-dominated fen) and CF (*Carex*-dominated fen), respectively. Both the SF (4.5 ha) and the CF (10.2 ha) are surrounded by mixed wood forests, while the SF has a small lake on the southeastern side, and the CF has two small stream tributaries on the northern and southwestern edges.

There is an understory of *Sphagnum* mosses (*S. magellanicum* Brid., *S. angustofolium* (C.E.P. Jensen ex Russow) C.E.O Jensen, *S. fuscum* (Schimp.) Klinggr., and *S. girgensohnii* (Russow)) in the SF. *Sphagnum* mosses have morphological traits such as distinct branching architecture, small leaf size and hyaline cells, enabling *Sphagnum* to thrive in waterlogged conditions and outcompete vascular plants (Turetsky et al. 2008). In addition to the *Sphagnum* mosses, the SF also has a moderate cover of ericaceous

shrubs such as Labrador tea (*Rhododendron groenlandicum* Oeder), leatherleaf (*Chamaedephne calyculata* L. Moench), Bog laurel (*Kalmia polifolia* Wagenh.), Bog rosemary (*Andromeda polifolia* L.), and lowbush blueberry (*Vaccinium angustifolium* Aiton). Ericaceous shrubs are evergreen, allowing plants to persist in nutrient poor environments through leaf longevity and reducing nutrient loss through leaf litter production. The SF is also sparsely treed by two coniferous species: black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch). Both species have adventitious roots that allow them to persist in waterlogged conditions.

Carex spp. predominate the CF; the main species include *C. stricta* Lam., *C. oligosperma* Michx., and *C. lasciocarpa*. The three *Carex* spp. tend to grow in small patches semi-isolated from one another, as *Carex* spp. spread laterally by rhizomatous growth to form clonal patches, rarely reproducing by seed. *Carex* spp. also have specialized tissue structures (aerenchyma) to retain oxygen enabling *Carex* spp.to persist in low oxygen environments, such as waterlogged peatlands. Leatherleaf and sweet gale (*Myrica gale* L.) are the most abundant shrubs found in the CF. Sweet gale is a deciduous shrub and is more prevalent than leatherleaf, indicative of the intermediate nutrient status at this peatland where sweet gale is able to allocate more resources to new leaf growth every year. *Sphagnum* mosses occupy sparse patches in the CF (see Palozzi and Lindo (2017) for previous plant community description).

1.6 Thesis objectives and rationale

In this thesis, I investigate plant and microbial community linkages in boreal peatlands located in northern Ontario, and examine changes in plant community composition for two peatland vegetation types under warming. One peatland is dominated by *Sphagnum* mosses (*Sphagnum* Fen (SF)) and the other dominated by *Carex* sedges (*Carex* Fen (CF)); these sites also differ in nutrient status, and hydrology. My specific objectives were to:

1) Link the aboveground plant community composition to the belowground microbial community composition by characterizing the aboveground plant

quality (%C, %N, and C:N) to the belowground peat quality at both the SF and CF in an observational study (Chapter 2).

2) Compare plant community composition under passive warming to control temperature plots in both the SF and CF using univariate community indices and multivariate analysis (Chapter 3).

I describe and compare the plant and microbial communities of the SF and the CF. The two vegetation types (*Sphagnum* and *Carex*) represent the dominant plants found in the majority of boreal peatlands. To characterize the plant community composition, I measured the aboveground biomass for each plant species, and to characterize the belowground microbial community, I used phospholipid fatty acid analysis. I then link the plant and microbial communities by describing the quality of the plant inputs and the peat environment by determining the %C, %N, and C:N of the fresh plant material, annual plant litter inputs, and the peat.

I then analyzed the effects of passive warming on plant community composition in those same two peatlands in a large-scale field warming experiment over two years. I used clear OTCs to simulate warming at both the SF and CF and compared the warming plant communities to un-warmed (control) plots. Field experiments can provide greater ecological validity compared to lab-based studies, as they can better simulate natural systems. The response of vascular peatlands under warming are understudied and yet are equally important to consider. In both chapters I considered the aboveground plant inputs and the ecosystem-level process of C storage in boreal peatlands.

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Chapter 2

2 Above- and belowground community linkages in boreal peatlands

2.1 Introduction

Traditionally, the aboveground (plant) and belowground (soil) communities have been studied in isolation from one another, yet a greater appreciation of the interconnectivity between the two has emerged over the last three decades (Schnitzer et al. 2011; Bardgett and van der Putten 2014). The plant community (i.e. producers) provides resources to the belowground consumers (i.e. decomposers), but decomposition processes also release important nutrients that are key resources to their aboveground counterparts, creating a flow of nutrients and energy between the two subsystems. Aboveground plants provide organic carbon to the belowground consumers via plant litter (Hättenschwiler et al. 2005), and belowground, plants provide important resources to root-associated organisms (i.e. the rhizosphere) (Porazinska et al. 2003; Brzostek et al. 2013). While belowground food webs are considered 'donor-controlled', suggesting limited or no ability of the soil community to regulate or feedback to aboveground plant communities (Van Der Heijden et al. 2008), plant communities are often associated with certain microbial communities. Recent perspectives suggest that above- and belowground communities are more tightly linked than previously thought (Porazinska et al. 2003; Eisenhauer 2012), and that both the above- and belowground community composition influence one another (Carlson et al. 2010; Shanmugam and Kingery 2018). However, the extent to which these above- and belowground pairings are causal (and bidirectional), or correlational (i.e. both plant and microbial communities are associated with resource gradients, independently) is under debate (Carlson et al. 2010; Orwin et al. 2010; Fan et al. 2015; Li et al. 2015).

There are various ways for plant species to acquire and allocate resources, presenting a long-standing trade-off paradigm in life history strategies (Grime 1977; Wright et al. 2004; Westoby and Wright 2006). Plant species are described to exist along a continuum of fast-growing, nutrient exploitative life history traits vs slow-growing, nutrient conservative life history traits that translate into differences in plant nutritional value (for

aboveground herbivores) and litter quality for belowground decomposers (Grime 1977; Reich 2014). Litter is thus often described as either ‘labile’ or ‘recalcitrant’, where faster growing plants produce labile litter that is more nutrient (mainly nitrogen (N)) rich, contains simpler carbon (C) compounds, and has lower C:N. Labile litter is considered to be high quality litter, facilitating faster decomposition and nutrient cycling (Manzoni et al. 2010) because the C compounds are easier to decompose, and N is often the main limiting nutrient in terrestrial systems (Vitousek and Howarth 1991). Plants that are slow growing, are typically conservative in their nutrient acquisition, are typically more heavily defended with structural compounds and secondary metabolites, and consequently produce more recalcitrant litter (low N, complex C compounds, higher C:N) and lower litter quality that leads to slower decomposition and nutrient cycling (Reich 2014). As soil microbial communities mineralize organic N from plant litter and make it bio-available for plant uptake, it can be hypothesized that microbial communities that have life history traits requiring more N will be paired with aboveground plant communities that have higher litter quality, more labile (low C:N), and vice versa.

Above- and belowground communities are particularly linked in peatlands because the whole soil profile is comprised of partially decomposed plant matter (peat) that largely dictates the nutrients available to the belowground microbial communities. Decomposition rates in peatlands are lower than the aboveground plant biomass production due to water saturation and often low temperatures (in boreal zones) such that aboveground plant C inputs are net sequestered in the soil as a build-up of peat. However, not all peatlands are equal in terms of decomposition rates, which depends on hydrological regimes, nutrient inputs from ground water, and aboveground plant community composition. Peatlands exist on a continuum of hydrological connectivity and nutrient inputs (e.g. bogs, nutrient poor fens to nutrient rich fens). This continuum is related to vegetation: bogs and nutrient-poor fens are typically dominated by *Sphagnum* spp. mosses while, intermediate nutrient or nutrient-rich fens are typically dominated by sedges (e.g. *Carex* spp.) (Rydin and Jeglum 2013). These two dominant plant functional types also represent the ‘fast-slow’ life history traits (Palozzi and Lindo 2017a) that are thought to affect the belowground microbial communities (Borga et al. 1994; Haynes et al. 2015) through different litter quality. *Sphagnum* spp. mosses have more recalcitrant

litter (low N, and high phenolics that mask cellulose and make tissue more resistant to microbial breakdown) compared to *Carex* spp. sedges, and therefore *Sphagnum* spp. peatlands are predicted to have slower nutrient cycling and differences in soil properties (Turetsky et al. 2008; Palozzi and Lindo 2017b).

Belowground, the microbial community also exists along a 'fast-slow' life history continuum. Peatland microbial communities contain high diversity of fungi (Asemaninejad et al. 2017) and bacteria, and less significantly archaea (Asemaninejad et al. 2019) where fungal and bacterial microorganisms are typically considered different functional groups because they differ in cell biomass and life history traits that leads to differences in decomposition dynamics. While both fungi and bacteria have the ability to use high quality, labile C substrates (Waldrop and Firestone 2004; de Vries and Caruso 2016), bacteria tend to outcompete fungi in this environment while the opposite is true under low quality, recalcitrant C, where fungi outcompete bacteria (Strickland et al. 2009b, a). As such, fungi are sometimes considered 'slow' C and nutrient cyclers that immobilize nutrients within long-lived biomass, while bacteria are considered 'fast' cyclers with nutrients turning over and being mineralized through bacterial cell metabolism and death (Joergensen and Wichern 2008; Strickland and Rousk 2010). Bacterial communities can be further classified as either Gram+ or Gram- bacteria and rather than differing across the 'fast-slow' dichotomy these groups differ in their preferred C source: Gram+ bacteria prefer soil organic matter derived C (i.e. microbially processed) and Gram- bacteria prefer plant derived C (Kramer and Gleixner 2008; Fanin et al. 2019). This 'fast-slow' dichotomy of both aboveground plants and belowground microbial communities has consequences for C sequestration and C release (dissolved organic C and CO_2) in peatland soils. Given predicted peatland plant shifts (Jassey et al. 2013; Dieleman et al. 2015; Bragazza et al. 2016) and increases in decomposition rates under climate change (Bond-Lamberty et al. 2018; Jenkinson et al. 1991), understanding plant-soil microbial interactions is of growing importance.

Whether differences in microbial communities that stem from differences in aboveground plant community properties (e.g. plant litter quality) feedback to affect the plant community, and on what spatio-temporal scales is currently unknown (Van Der Heijden

et al. 2008). Differences in the abundance of fungi and bacteria is thought to lead to different rates of C and nutrient cycling that can affect plant community composition. In this study, I characterize the aboveground plant community and the belowground microbial community in two boreal peatlands: an intermediate nutrient fen that is dominated by *Carex* spp. sedges and a nutrient-poor fen dominated by *Sphagnum* spp. mosses. I characterize the aboveground plant communities through species level morphological identification, and I identify microbial groups based on phospholipid fatty acids (PLFA) biomarkers extracted from the peat. My objective is to relate the above- and belowground communities by examining 1) the nutrient quality of the aboveground plant community, 2) the quality of the annual plant litter inputs to the belowground system, and 3) the quality of the peat in which the microbial communities reside. As *Sphagnum* has conservative nutrient-use strategies, in the *Sphagnum*-dominated fen, I predict lower litter quality and subsequently a smaller and more fungal dominated microbial community compared to the *Carex*-dominated fen with more nutrient exploitative traits that would produce higher litter quality and support a larger and more bacterial dominated microbial community.

2.2 Materials & Methods

2.2.1 Site description

The two fen sites chosen for this study are located near White River, Ontario (48°21'N, 84°20'W) and are a part of a larger boreal peatland complex that has been monitored as long-term research sites by the Ontario Ministry of Natural Resources and Forestry for the past 15 years. The mean annual precipitation is 980 mm and the mean annual temperature is 2.1°C for the region (see Webster and McLaughlin (2010) for full description). The two fens are approximately 2 km apart. One fen is dominated by *Sphagnum* spp. mosses and has a nutrient poor status while the other fen is dominated by *Carex* spp. sedges and has an intermediate nutrient status; the fens will henceforth be referred as SF (*Sphagnum*-dominated fen) and CF (*Carex*-dominated fen), respectively. The SF (4.5 ha) is sparsely forested and is bounded by mixed-wood forest and abuts a small lake, while the CF (10.2 ha) is mostly open and is surrounded by mixed-wood forests with two small stream tributaries on the northern and southwestern edges.

The SF, as the name suggests, has a blanket of *Sphagnum* mosses (*S. magellanicum* Brid., *S. angustofolium* (C.E.P. Jensen ex Russow) C.E.O Jensen, *S. fuscum* (Schimp.) Klinggr., and *S. girgensohnii* (Russow)), is moderately covered by shrubs including Labrador tea (*Rhododendron groenlandicum* Oeder), leatherleaf (*Chamaedephne calyculata* (L.) Moench), and lowbush blueberry (*Vaccinium angustifolium* Aiton), and is sparsely treed by black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch). *Carex* spp. predominate the CF vegetation where *C. stricta* Lam. grows in patches semi-isolated from *C. oligosperma* Michx., and *C. lasciocarpa*. Shrubs, leatherleaf and *Myrica gale* L. (sweet gale) in lesser amounts also inhabit the CF and *Sphagnum* mosses occur in sparse patches (See Palozzi and Lindo (2017a) for previous plant community description).

2.2.2 Aboveground plant sampling

The aboveground plant community was assessed in 0.25m^2 plots (n=12) from each fen during June, July, and August 2018, totaling 72 plots. Within each haphazardly chosen plot, all aboveground plant biomass was destructively sampled by clipping at the root-shoot interface, sorted by species using the keys of Newmaster et al. (1997), and were dried at 60°C for a minimum of 48 hrs. To determine *Sphagnum* spp. biomass, 5 cm^2 of *Sphagnum* carpet was collected and the photosynthetic shoots were retained as the sample, the biomass was then dried and multiplied by 25 to determine an estimate of *Sphagnum* biomass for each plot — the section collected was determined to be the best representation of the plot, in terms of species and density. I calculated plant richness, Shannon's diversity index (H'), and Pielou's evenness (J') based on the aboveground biomass calculated from each plot using the vegan package in R (Oksanen et al. 2018), where:

$$H' = -\sum_{i=1}^{k} p_i \ln(p_i)$$

$$J' = \frac{-\sum_{i=1}^{k} p_i \ln(p_i)}{\ln(S)}$$

In these equations, p_i is the proportional aboveground biomass based on destructive sampling of each plant species and S is species richness.

The aboveground plant quality (i.e. %C and %N content, C:N) was assessed by collecting leaves from each species (photosynthetic shoots for moss species, based on Bond-Lamberty and Gower (2007)) from three randomly selected plots across all time points (Appendix A). Leaves and shoots for each species were ground using a stainless steel blade grinder, and homogenized within each plot. Some rare species that had low biomass were therefore only sampled from one plot. Leaves were analyzed for %C, %N, and C:N using a combustion analyzer (vario MAX cube Elementar CNS analyzer) with birch leaf (*Betula papyrifera* Marsh.) as the quality control.

The community weighted mean (CWM) for each plant quality trait (i.e. %C, %N, C:N) was calculated for each of the 72 plots using the equation:

$$CWM_{trait} = \sum (p_i \times x_i)$$

where p_i is again the proportional aboveground biomass based on destructive sampling of each plant species, while x_i is the trait value for that particular species. The CWM takes into account both the quality (%C, %N, C:N) of each plant species and the biomass of each plant species to determine one quality (%C, %N, C:N) for the entire community.

2.2.3 Plant litter and peat sampling

Litter traps were deployed haphazardly at each fen to determine both quantity and quality of seasonal litter inputs to the soil system. Litter traps were constructed with a black mesh (1 mm) bottom, allowing moisture, but not plant litter to filter through. At each fen, five 0.25 m^2 litter traps were deployed in August 2017, with litter collection in October 2017 (end of growing season), June 2018 (winter), and October 2018 (growing season). The litter from each trap was dried at 60°C for a minimum of 48 hours to determine the total quantity of litter inputs. After drying and weighing the litter, the litter was ground and homogenized using a stainless steel blade grinder, and analyzed for %C, %N, and C:N using a combustion autoanalyzer (vario MAX cube Elementar C:N) as described above.

Five surficial peat samples (top 5-10 cm, approximately 100 g) were collected haphazardly from each fen in October 2017. A subsample of peat (15 g wet weight) was used to measure the moisture content gravimetrically. The peat was dried at 60°C for one week and re-weighed after drying. The soil moisture content was calculated using the formula:

$$\% \text{ Moisture} = ((\text{g wet weight} - \text{g dry weight}) / \text{g dry weight}) \times 100.$$

Heterotrophic basal respiration was used to estimate microbial activity and was measured using a Licor Infrared Gas Analyzer (IRGA LI-8100A) and Multiplexer unit (LI-8150). A 50 g wet weight subsample of peat was placed in 250 ml mason jars (n=5 from each peatland site) and aluminum foil was wrapped around each jar to ensure only heterotrophic basal respiration was measured. Respiration was measured over 12 hours at room temperature; measurements for each sample were averaged over 90 seconds for 30 minutes, with a 30 second purge of the headspace between measurements. Peat from each sample was ground and analyzed for %C, %N, and C:N using a combustion autoanalyzer (vario MAX cube Elementar C:N) as previously described, and all remaining subsamples of peat were frozen at -80°C and lyophilized for determination of the microbial community composition.

2.2.4 Phospholipid fatty acid analysis

The peat microbial community was characterized by PLFA analysis using methods modified from Quideau et al. (2016) and Buyer et al. (2010). All glassware used was rinsed with acetone and hexane, all reagents were ACS grade, and only glass was used for all reagents. A 0.3 g subsample from each lyophilized peat sample was ground using a mortar and pestle for the CF and a stainless steel blade grinder for the SF. The PLFAs were then extracted using the Bligh and Dyer method, which consists of a 2:1:0.8 ratio of methanol:chloroform:0.15M citrate buffer (Bligh and Dyer 1959). As peat samples are highly organic, 0.9 mL of chloroform was used for the CF and 2.1 mL of chloroform was used for the SF, and the citrate buffer was added as suggested by Frostegård and Bååth (1996) to extract more PLFAs when working with highly organic soils. The internal standard 19:0 PC (1,2-dinonadecanoyl-sn-glyvero-3-phosphocholine) was added to each

sample prior to PLFA extraction and subsequently used to calculate extraction efficacy. Samples were subsequently vortexed for 30 s, shaken for 2 h, and centrifuged for 1 h at 2500 rpm. The supernatant was removed and the Bligh and Dyer extractant procedure was repeated again on the peat samples to ensure thorough PLFA extraction. Chloroform (i.e. 1.8 ml for CF and 4.2 ml for SF) and citrate buffer (i.e. 0.72 ml for CF and 1.68 ml for SF) was added to the supernatant, and the samples were left for 12 h to separate.

Following separation, the upper aqueous layer was disposed of, and the lower organic phase was evaporated under N_2 gas in a hot water bath to accelerate evaporation and prevent oxidation. Samples were re-dissolved in 2 ml chloroform and PLFAs were separated from other fatty acids using a solid phase extraction column (50 mg silica gel SPE 96-well plate). Columns were conditioned with 1 ml methanol and 1 ml chloroform and the phospholipids were eluded with 0.5 ml of 5:5:1 methanol:chloroform:deionized water. The samples were again evaporated under N_2.

Methyl-esters were added to the PLFAs using 0.5:0.5:1 methanol:chloroform:methanolic potassium hydroxide. Samples were incubated for 15 minutes at 37°C, cooled to room temperature, and 0.6 ml of hexane and 0.2 ml of chloroform were added to each sample. Samples were neutralized with 0.5 ml 1M acetic acid, 0.8 ml deionized water was added, and samples were vortexed prior to being centrifuged at 2000 rpm for 5 minutes. The upper hexane layer was removed, and the extraction process was repeated with the lower layer (0.6 ml of hexane and 0.2 ml of chloroform). The upper hexane layer from the second extraction was added to the first and the organic phases were evaporated under N_2. All samples were subsequently re-dissolved in hexane and the fatty acid methyl esters were detected by gas chromatography (Agilent HP 6890 GC with an Agilent Ultra 2 column: 5% Phenyl Methyl Siloxane, Model: 19091B – 102, Length: 25.0m, Diameter: 200.00 micrometers, Thickness: 0.33) using flame ionization detector. The Sherlock software® (MIDI Inc.) was used to assign specific PLFAs into microbial groups, calculate total and microbial group biomass, and calculate percent biomass of the PLFA assigned to each microbial group. PLFAs biomarkers and their associated microbial groups are listed in Appendix B. I calculated PLFA richness (total number of PLFAs), Shannon's diversity index, and Pielou's evenness based on the proportional PLFAs.

2.2.5 Statistical analysis

Plant species richness, Shannon's diversity and Pielou's evenness were analyzed using a two-way ANOVA implemented in R (version 3.4.3) using the vegan package (Oksanen et al. 2018) — because each plot was destructively sampled, all plots are considered independent, so I used fen and month as the main effects. Aboveground plant quality was analyzed using two-way MANOVA implemented in R to determine differences between the CWM of %C, %N, and C:N for the SF and CF aboveground biomass, with fen and month as the main effects. Litter quantity was analyzed using a two-way repeated measures ANOVA and litter quality (%C, %N, and C:N) was analyzed using two-way repeated measures MANOVA in Statistica (version 7.0) with fen and time period (i.e. end of growing season, winter, and growing season) as the main effects (StatSoft. Inc., 2004). To determine if each individual dependent litter quality variable (%C, %N, and C:N) varied between sites, separate two-way repeated measures ANOVA were run. A one-way MANOVA was used to analyze peat quality (%C, %N, and C:N) with fen type as the main effect.

The MIDI software separated the PLFA microbial biomass into six microbial groups: arbuscular mycorrhiza fungi (AM fungi), fungi (all other fungi besides AM fungi), anaerobic bacteria, gram positive bacteria (Gram+), gram negative bacteria (Gram-), and actinomycetes. Actinomycetes, was not included in the analysis as the duplicate demonstrated >70% variation. The total biomass and biomass of each microbial group was analyzed using a one-way MANOVA with fen type as the main effect (version 3.4.3; R Development Core Team). I also calculated the overall fungal:bacterial (F:B) ratio and Gram+:Gram- ratio for each sample, and these were also included in the one-way MANOVA. I analyzed PLFA richness, diversity and evenness using a one-way ANOVA with fen as the main effect.

To determine whether there were significant differences between either the aboveground plant community composition or the belowground microbial community, permutational multivariate ANOVA (PERMANOVA) based on Bray-Curtis dissimilarity was used, and results were visualized using a Non-metric multidimensional scaling (NMDS) ordination. The Bray-Curtis matrix consists of pairwise distances between each community (i.e.

community dissimilarity), and the communities are plotted as points in non-metric multidimensional space with more dissimilar communities plotted farther away from one another in ordination space. Dissimilarities in composition between communities were examined for statistically significant differences between fen sites by comparing the distribution of dissimilarities using 1000 permutations. For the belowground microbial community any PLFA that contributed to less than 1% of the biomass across the five replicates was not included in the analysis. The adonis function in the vegan package in R (Oksanen et al. 2018) was used for the PERMANOVA and NMDS visualization. Finally, a Principal Components Analysis (PCA) using vegan was performed on the belowground microbial community composition based on PLFA percentages (Oksanen et al. 2018). Site scores from the PCA were extracted for the 2 main axes and linear regressions that included all environmental variables (soil moisture, basal respiration, %C, %N, C:N of the peat) were used as explanatory variables to determine which environmental variables were associated with particular PLFAs.

2.3 Results

2.3.1 Aboveground plants and litter

The SF demonstrated nearly 2× greater aboveground plant richness than the CF ($F_{(1,70)}$=0.257.2, P<0.001) (Fig. 2.1), and also had significantly greater Shannon's diversity index but lower Pielou's evenness (Table 2.1). There were no significant differences among monthly sampling times for plant survey data (richness: $F_{(2,70)}$=0.065, P=0.938, diversity: $F_{(2,70)}$=0.485, P=0.618, evenness: $F_{(2,70)}$=0.549, P=0.580), and any difference between fen types was not affected by sampling time (i.e. interactive effects) (richness: $F_{(2,70)}$=2.775, P=0.069, diversity: $F_{(2,70)}$=0.944, P=0.394, evenness: $F_{(2,70)}$=0.051, P=0.950) although plant species richness was lowest during July in the SF and highest during July in the CF. The differences in plant richness during July in the SF was driven by early seasonal small herbs such as *Maianthemum trifolium* (L.) Sloboda that decrease in abundance after June and *Carex* species such as *C. disperma* Dewey that increased in abundance during August (Fig. 2.1).

Table 2.1 Plant variables measured at two peatland sites in northern Ontario, Canada. Values are means ± standard error (n=12). F & P values correspond to the main effect of fen corresponding to two-way ANOVAs for Shannon's diversity and Pielou's evenness and two-way MANOVAs for %C, %N, and C:N.

	Sphagnum-dominated fen	*Carex*-dominated fen	$F_{(1,70)}$	P
Plant Shannon's diversity	1.46 ± 0.04	1.22 ± 0.04	17.07	**<0.001**
Plant Pielou's evenness	0.63 ± 0.02	0.73 ± 0.02	15.46	**<0.001**
Plant CWM C content (%)	47.89 ± 0.19	49.34 ± 0.21	27.78	**<0.001**
Plant CWM N content (%)	1.18 ± 0.02	1.60 ± 0.04	109.94	**<0.001**
Plant CWM C:N content	42.80 ± 0.51	33.83 ± 0.62	118.93	**<0.001**

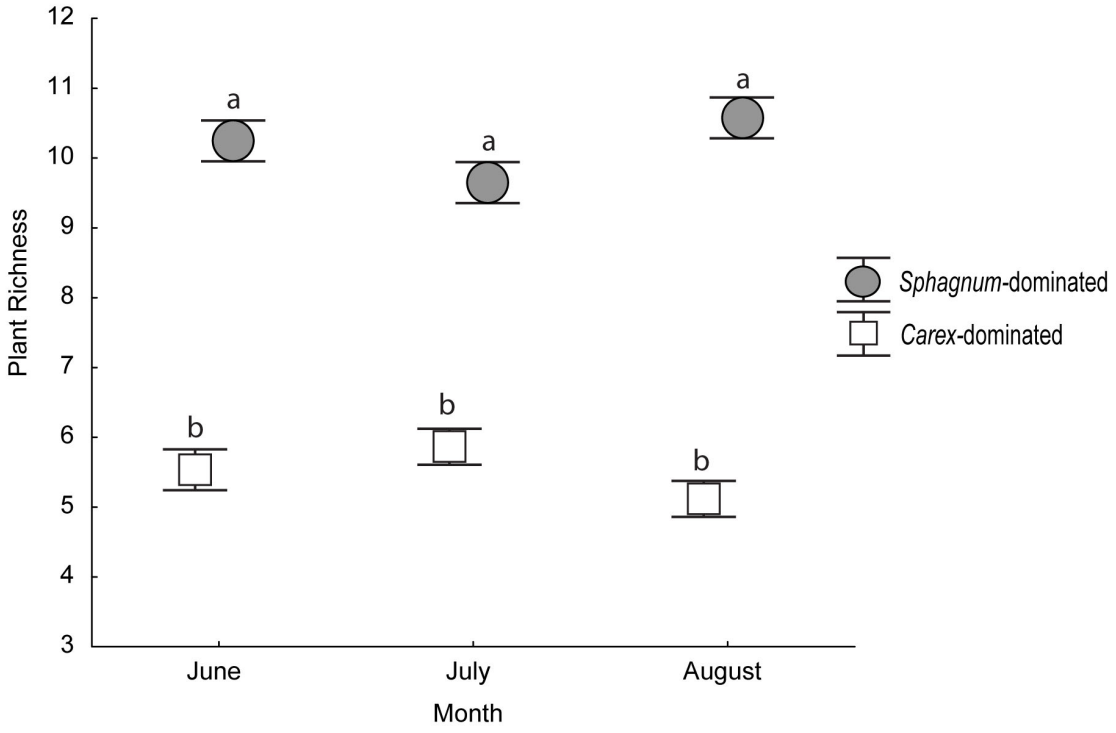

Figure 2.1 Mean plant richness at both the *Sphagnum*-dominated and *Carex*-dominated fen across three sampling time points (June, July and August) during 2018. Letters denote significant differences using Tukey HSD post-hoc comparisons and error bars are standard error.

When considering the aboveground plant community, I found significant differences between the two fens (PERMANOVA: $F_{(1,71)}$=47.945, P=<0.001) (Fig. 2.2), as well as shifts in the aboveground plant community across the three sampling times ($F_{(2,71)}$=2.773, P=0.005). This shift in plant community during the growing season was more pronounced in the CF, leading also to a significant fen by month interaction effect ($F_{(1,71)}$=3.293, P=0.004) (Fig. 2.3). The CWM for %C and %N of fresh plant material was significantly greater in the CF compared to the SF, however the fresh plant quality did not change across the three sampling months (Table 2.1), leading to a C:N in the SF compared to the CF (Table 2.1). The mosses including *Sphagnum* species and *Pleurozium schreberi* (Brid.) Mitt. had low %N, driving the high C:N ratio in SF, while the abundant *Myrica gale* and lesser abundant *Salix pedicellaris* Pursh. had relatively high %N, driving the low C:N in the CF (See Appendix A for full list of species and their C and N fresh litter values).

There was no difference in litter biomass between the two fens (fen main effect: $F_{(1,16)}$=0.297, P=0.601), however there was variation in litter biomass across the three sampling periods (time main effect: $F_{(2,16)}$=4.79, P=0.023) which was mainly driven by the CF where the highest litter biomass was collected after the growing season and the lowest biomass collected after the winter (Fig. 2.4) (fen × time interaction: $F_{(2,16)}$=6.548, P=0.008). The overall repeated measures MANOVA model was significant for litter quality (%C, %N, C:N) across fens ($F_{(1,16)}$=427.7, P<0.001) and time ($F_{(2,16)}$=6.6, P=0.024), while there was also a fen × time interaction ($F_{(2,16)}$=16.3, P=0.002). Litter quality (i.e. C:N) was lowest in SF litter collected at the end of the first growing season where C:N values were the highest of all litter collected (fen × time interaction: $F_{(2,16)}$=13.12, P<0.001), yet the SF litter had consistently higher C:N values compared to the CF (fen main effect: $F_{(1,8)}$=379.60, P<0.001) (Fig. 2.4). The C:N values of the litter were related to changes in both %C and %N across sampling times (%C time × fen interaction: $F_{(2,16)}$=19.10, P<0.001, %N time × fen interaction: $F_{(2,16)}$=18.43, P<0.001). For instance, the high C:N values of litter at the SF during the end of the growing season (August-October) was not due to high %C but rather dramatically lower %N (Fig. 2.4). In the CF, high %N values were observed in the growing season accumulated litter (June –

Oct) (Fig. 2.4), and low values of %C were observed during the winter accumulated litter (Oct – June) in the CF (Fig. 2.4). Litter %C was consistently greater (%C fen main effect: $F_{(1,8)}$=49.13, P<0.001, %C time main effect: $F_{(2,16)}$=54.69, P<0.001) and %N consistently lower (%N fen main effect: $F_{(1,8)}$=308.37, P<0.001, %N time main effect: $F_{(2,16)}$=29.19, P<0.001) at the SF compared to the CF (Fig. 2.4).

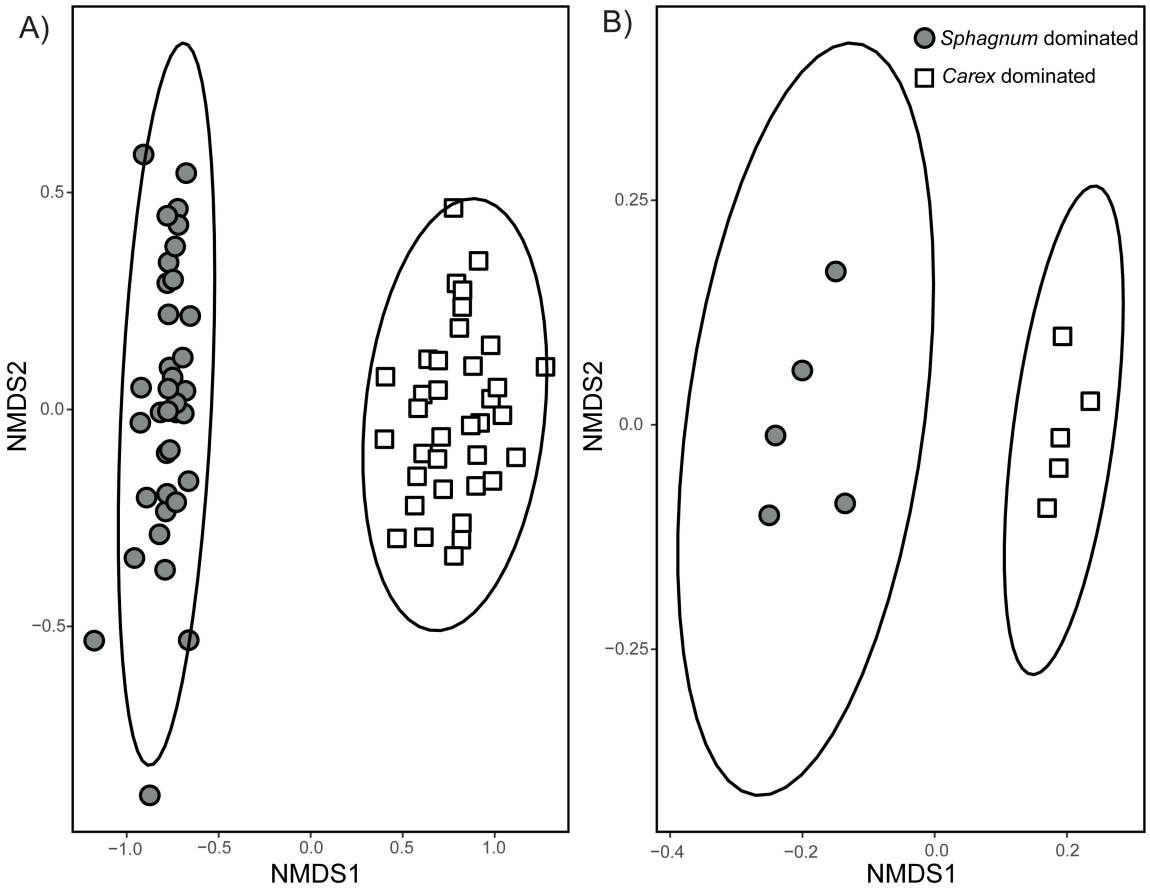

Figure 2.2 Compositional similarities of A) aboveground plant communities (n=36) and B) belowground microbial communities (n=5). Aboveground plant communities are based on aboveground biomass of individual plant species from 0.25m^2 plots. Belowground microbial communities are based on PLFAs extracted from the top 5-10cm of peat. Stress is 0.1 with k=2 (number of dimensions) for the aboveground plant communities and 0.05 with k=2 for the belowground microbial communities. The ellipses indicate 95% confidence intervals.

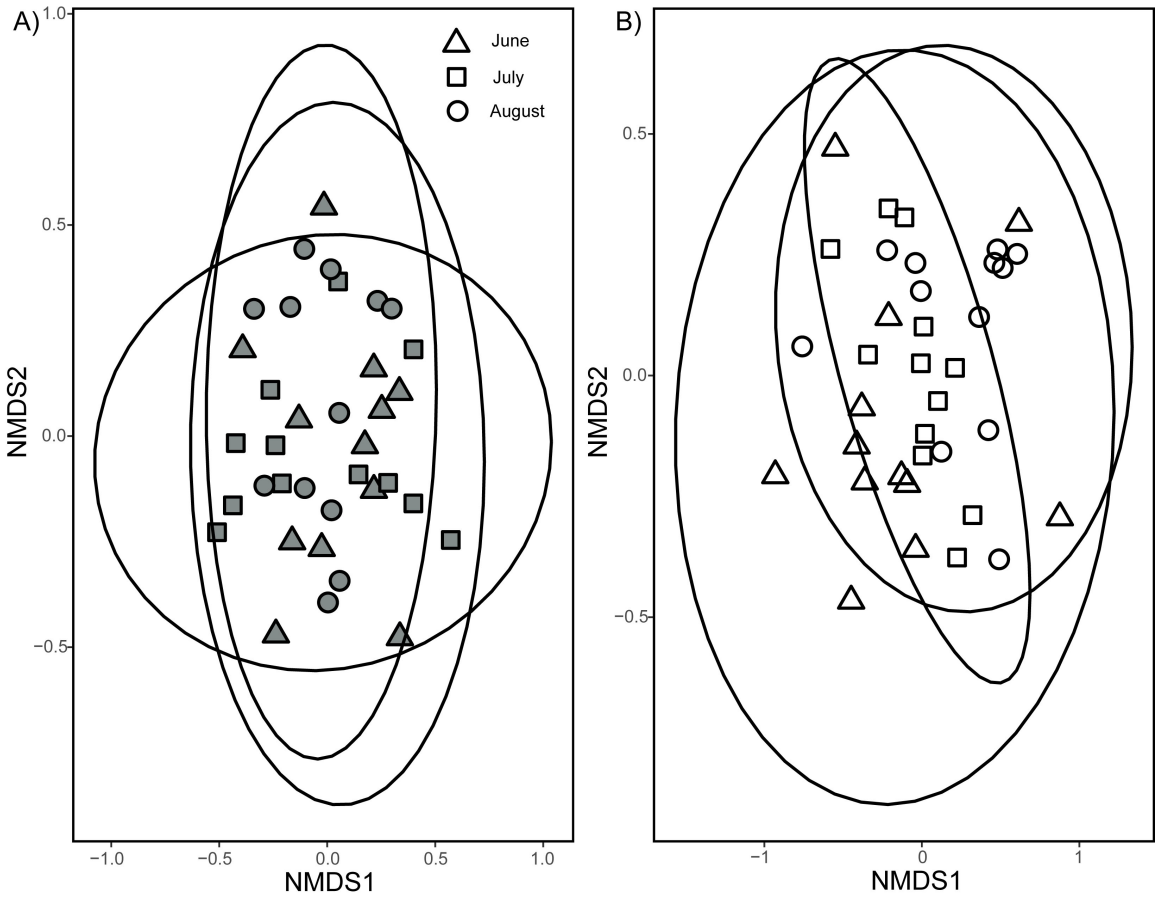

Figure 2.3 Compositional similarities of A) aboveground plant communities in the *Sphagnum*-dominated fen (n=36) and B) aboveground plant communities in the *Carex*-dominated fen (n=36) across three sampling periods in 2018: June, July, and August. Aboveground plant communities are based on aboveground biomass of individual plant species from 0.25m^2 plots. Stress is 0.24 with k=2 (number of dimensions) for the SF and 0.16 with k=2 for the CF. The ellipses indicate 95% confidence intervals.

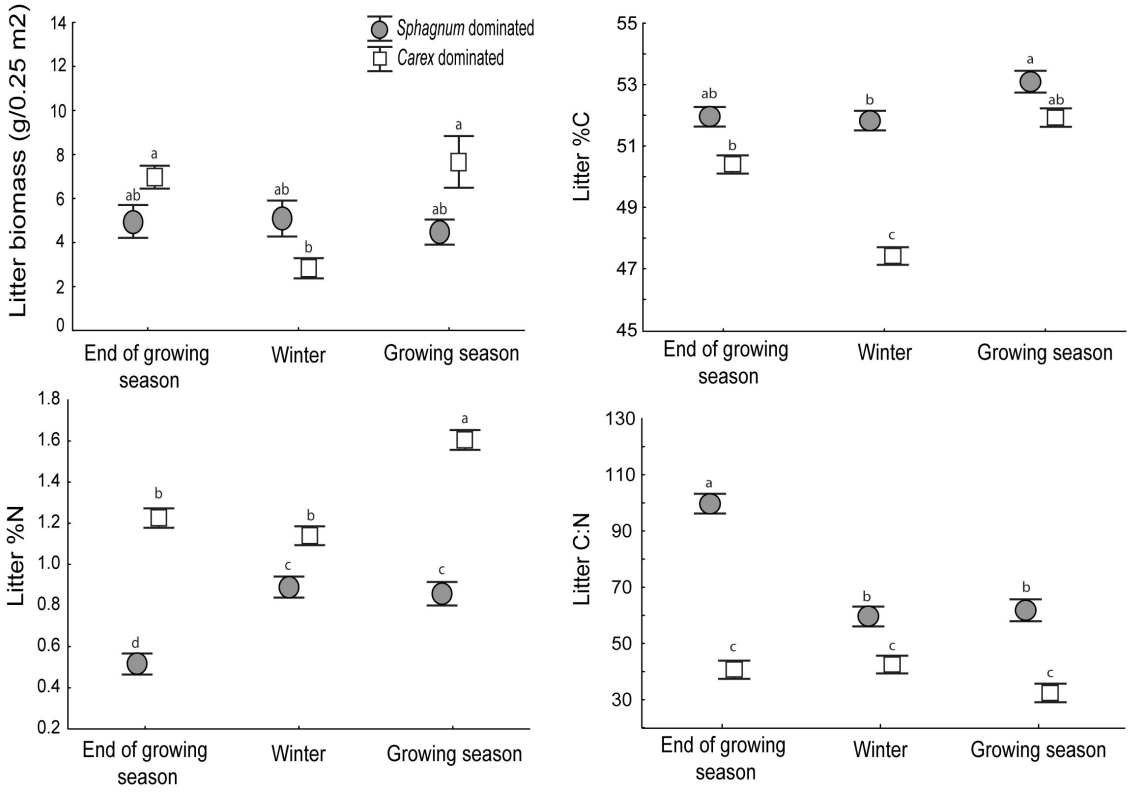

Figure 2.4 Mean litter biomass (g/0.25 m^2), %C, %N, and C:N at both the *Sphagnum*-dominated and *Carex*-dominated fen across three sampling times: end of growing season, winter, and growing season (n=5). Letters denote significant differences after Tukey HSD post hoc comparisons and error bars are standard error.

2.3.2 Peat quality and belowground microbial community

Belowground, the quality (i.e. %C, %N, C:N) of the peat mirrored the trends in the aboveground plant litter inputs from the litter traps and CWMs of the aboveground plant communities, where I found significantly greater %C, significantly lower %N, and significantly greater C:N (Table 2.2) in the SF compared to the CF. The peat moisture content was significantly lower in the SF compared to the CF, while basal respiration was 2× greater (Table 2.2). There was no significant difference in PLFA richness or PLFA Shannon's diversity between the fens, however, the SF had greater Pielou's evenness of PLFAs compared to the CF (Table 2.2).

Overall fungal to bacterial ratios (F:B) were significantly greater in the SF compared to the CF ($F_{(1,8)}$=164.93, P=<0.001)(Fig. 2.5), and all microbial groups (fungi and bacteria) also demonstrated biomass differences between fens (Fig. 2.5). While the SF had a greater fungal biomass, this was due to fungal groups such as saprophytic fungi ($F_{(1,8)}$=47.10, P<0.001), rather than arbuscular mycorrhizal (AM) fungi, which were more abundant in the CF ($F_{(1,8)}$=51.55, P<0.001). The SF also had significantly less overall PLFA biomass ($F_{(1,8)}$=91.81, P<0.001), and less anaerobic bacteria ($F_{(1,8)}$=7.28, P=0.027), Gram+ bacteria ($F_{(1,8)}$=51.62, P<0.001), and Gram- bacteria ($F_{(1,8)}$=138.5, P<0.001) biomass than the CF. However, the SF had a greater Gram+ bacteria:Gram- bacteria ratio ($F_{(1,8)}$=61.91, P<0.001) compared to the CF (Fig. 2.5). Correspondingly, the belowground microbial community was highly dissimilar between the two fens (PERMANOVA: $F_{(1,9)}$=23.90, P=0.007) (Fig. 2.2).

Table 2.2 Peat variables measured at two peatland sites in northern Ontario, Canada (n=5). Values are means ± standard error, and statistical F & P values correspond to main effect of fen. Peat %C, %N, and C:N results are based on one-way MANOVA. Peat moisture content and basal respiration results are based on one-way ANOVA. PLFA univariate community indices results correspond to one-way ANOVA.

	Sphagnum-dominated fen	*Carex*-dominated fen	$F_{(1,8)}$	P
Peat C content (%)	44.67 ± 0.22	40.56 ± 0.95	17.68	**0.003**
Peat N content (%)	0.844 ± 0.13	2.158 ± 0.05	92.43	**<0.001**
Peat C:N content	57.25 ± 7.30	18.81 ± 0.26	22.73	**<0.001**
Peat moisture content (%)	1117.28 ± 129.16	699.31 ± 46.55	9.27	**0.016**
Basal respiration ($gCO_2/m^2/h$)	0.040 ± 0.004	0.088 ± 0.015	8.74	**0.018**
PLFA richness	38.4 ± 1.5	41.4 ± 1.08	2.63	0.143
PLFA Shannon's diversity	2.84 ± 0.03	2.75 ± 0.03	3.89	0.084
PLFA Pielou's evenness	0.78 ± 0.004	0.74 ± 0.005	30.16	**0.001**

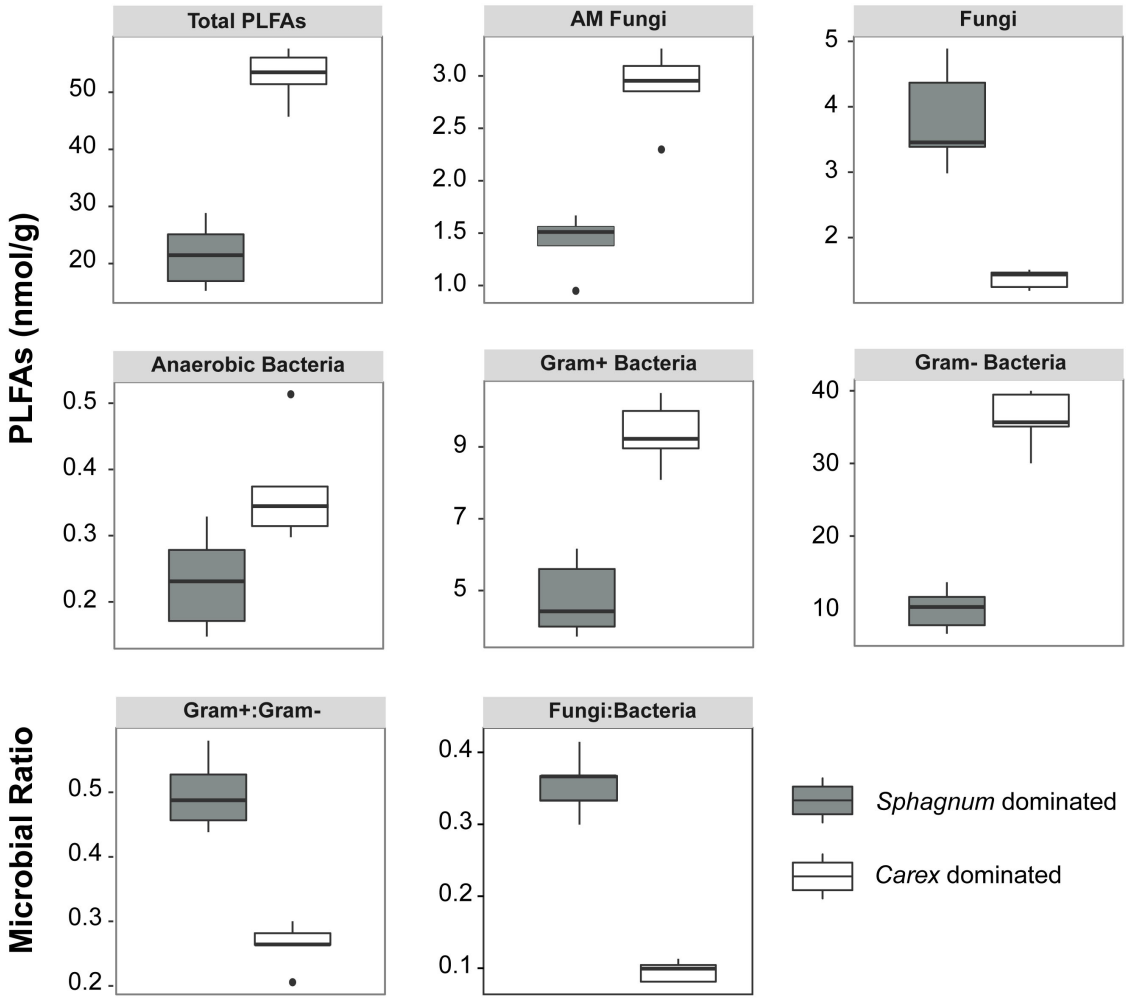

Figure 2.5 Boxplots of the total amount of PLFAs in the peat, the different microbial groups, the Gram+ to Gram- ratio, and the fungi to bacteria ratio (n=5). All means are significantly different between the SF and CF based on a one-way MANOVA

The relationship of specific PLFAs with peat %C and peat %N was revealed in the PCA, where the first PC axis (PC1) explained 45.93% of the total variance in PLFAs, and site scores were significantly related to peat %C (R^2=0.983, P=0.046) and peat %N (R^2=0.983, P=0.008) (Fig. 2.6). The positive PC1 values are associated with low %C values and high %N, while negative PC1 values are associated with high %C and low %N. The second PC axis (PC2) explained an additional 31.21% of the PLFA variance (first two PCA components combined explained 77.14% of the variance), but PC2 was not significantly related to any of the variables. The high %C and low %N peat from the SF was related to PLFA 16:0 (-0.39) (Gram+ bacteria) and 18:2ω6c (-0.45) (saprophytic fungi). The low %C and high %N peat from the CF was characterized by PLFA 18:1ω7c (0.66) (Gram- bacteria). The 18:3ω6c (general fungi) and 10Me16:0 (actinomycetes) were found in highest abundance in a single SF sample; this sample also had higher moisture and higher N compared to the other four samples from the SF.

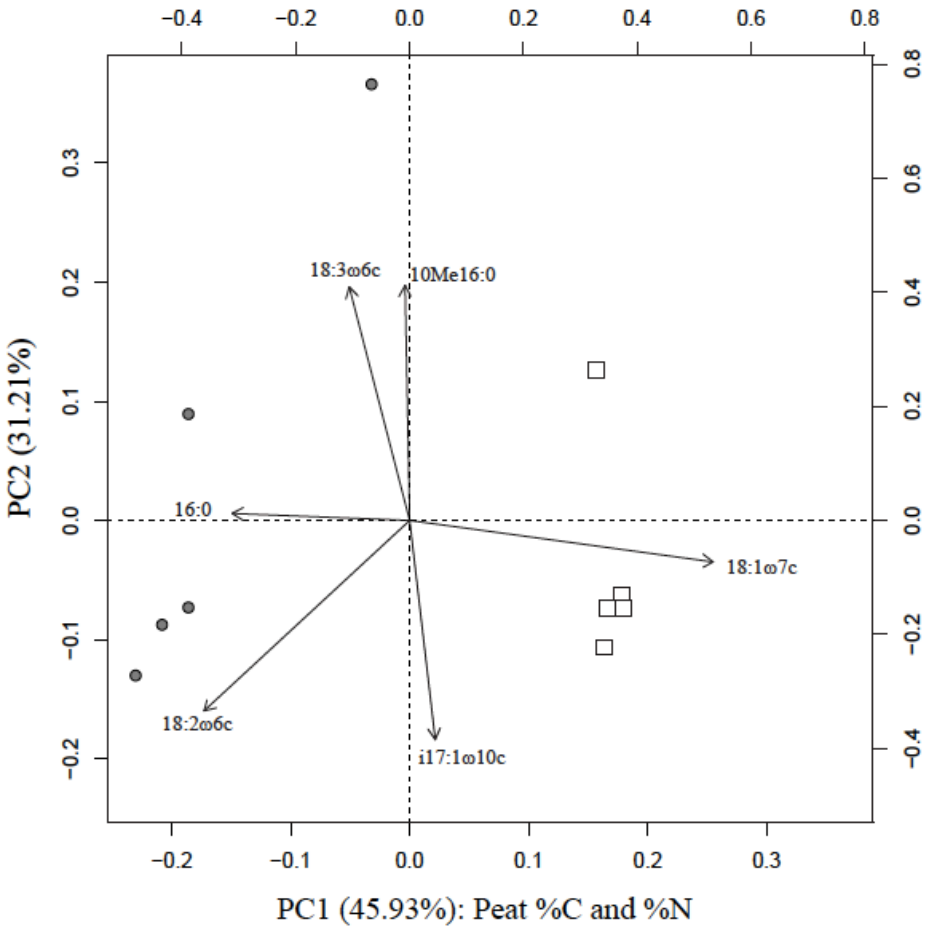

Figure 2.6 Principal Components Analysis biplot for the belowground microbial communities based on the PLFAs (n= 5); only PLFAs with scores greater than 0.2 are shown. Positive PC1 values correspond to low %C and high %N and negative PC1 values correspond to high %C and low %N. Positive PC2 values did not correspond to any of the measured environmental variables. 16:00 is a fatty acid associated with Gram+ bacteria, 18:3ω6c and 18:2ω6c corresponds with general fungi, 10Me16:0 corresponds with actinomycetes, 18:1ω7c corresponds with Gram- bacteria, i17:1ω10c corresponds to Gram- bacteria. The SF is indicated by gray circles and the CF is indicated by white squares.

2.4 Discussion

The connection between the above- and belowground systems in boreal peatlands is innate, as the peat in which the belowground community resides is composed of the partially decomposed aboveground plant community. This study demonstrates that the belowground microbial community in peatlands is distinct across two dissimilar aboveground plant communities. The belowground microbial community relies on resource inputs from the aboveground system. Rhizodeposits (i.e. root exudates) contribute important labile C (Jones et al. 2009), and peatlands (fens) that are hydrological connectivity to ground water also receive important nutrients through water transport (Rydin and Jeglum 2013). Many peatlands are dominated by *Sphagnum* moss (bogs and nutrient poor fens), and can be hydrologically decoupled (bogs), making litter inputs integral resource inputs to microbial communities in *Sphagnum*-dominated peatlands. Even in vascular plant dominated and hydrologically connected peatlands (intermediate to nutrient rich fens), litter inputs play a key role in providing basal resources to the belowground communities. Litter inputs are dictated by the plant community composition (i.e. species richness, diversity and evenness, as well as specific plant species identities). For instance, the quality of the more dominant plant species will contribute more to the litter quality than the quality of a lesser dominant plant species. I found that litter inputs across the SF and CF fens had similar %C, %N, and C:N values to the CWM values based on the individual fresh plant litters. Even though litter values may not have been driven by the dominant vegetation types, i.e. *Sphagnum* and *Carex* in the SF and CF, respectively because *Sphagnum* doesn't 'litter', the litter quality was still significantly higher (low C:N) in the CF compared to the SF. Ericaceous shrubs such as *Chamaedaphne calyculata* and *Andromeda polifolia* (L.) contribute significantly to litter inputs in the SF and similarly to *Sphagnum* also have low litter quality. Del Giudice and Lindo (2017) also found similar C:N values for *Sphagnum* (~40), but did however find higher C:N for *Carex magellanica* (~55) than was found in this study.

While this 'legacy' of the plants was further found in the peat (i.e. the CF had greater %N and lower C:N) and absolute values of %N were even greater belowground in the CF peat. Similarly, Palozzi and Lindo (2017a) also found more biologically available N

(NO_3^- and NH_4^+) in the CF peat compared to the SF peat, which may be related to greater hydrological connectivity to ground water in the CF (Rydin and Jeglum 2013), rather than litter %N inputs. *Carex* spp. sedges are able to efficiently capture resources such as nutrients, light and space due to their tall height and fast growth (Keddy et al. 1998). In the SF this was evident as the *Carex* spp. had higher %N than the *Sphagnum* spp., this however was not quite as evident in the CF where the *Carex* and *Sphagnum* spp. had more similar %N. The low C:N in the CF appear to be driven by the shrub species *Myrica gale* and *Salix pedicellaris.* Traits such as short stature, low relative growth rates and longer life spans are more typical of *Sphagnum* spp., making them more conservative in their nutrient requirements (Grime 1974; Grime et al. 1990) as evident by their high C:N in this study and others (Aerts et al. 2001; Turetsky 2003). *Sphagnum* C:N was not consistent between the two sites, suggesting that the lower C:N in the CF could be indicative of the higher N availability in the peat.

The SF and CF differed greatly in terms of aboveground species richness, diversity and evenness, but these diversity trends were not as evident in the belowground community. For instance, while the SF has a much more heterogeneous plant community with greater species richness, diversity and lower evenness, the microbial community had similar PLFA richness across both sites. While the SF did have greater PLFA evenness and marginally greater PLFA diversity, it appears that greater aboveground plant diversity does not lead to greater belowground diversity. Rather, differences in the overall quality of plant litter inputs could be a more important predictor of microbial diversity (Wardle et al. 2004) than plant diversity *per se*, and lead to the distinct microbial communities between these two sites (Wardle et al. 1999). For instance, greater nutrient availability in the CF likely explains the greater microbial biomass and marginally greater PLFA richness. Similarly, *Sphagnum* litter, in addition to being nutrient poor, has high phenolic content that is generally resistant to microbial breakdown (Turetsky 2003) and has high cation exchange abilities (Clymo 1963), leading to a more acidic and less favourable environment for microbes.

Fungi in general were more dominant in the SF than the CF, including the ectomycorrhiza, ericoid mycorrhiza, and saprophytic fungi, but not the arbuscular

mycorrhiza. While *Sphagnum* spp. mosses do not have roots and therefore cannot make root associations with mycorrhiza, the SF also contained several ericaceous shrubs such as *Vaccinium angustifolium*, *Chamaedaphne calyculata*, *Kalmia polifolia* Wagenh., *Rhododendron groenlandicum*, and *Andromeda polifolia* that are known to form root associations with ericoid mycorrhiza, while *Picea mariana* and *Larix laricina* also found in the SF, are known to form associations with ectomycorrhizal fungi (Thormann et al. 1999). Ectomycorrhizal and ericoid mycorrhizal fungi also produce N-degrading enzymes that allow them greater access to N sources compared to arbuscular mycorrhiza fungi (Averill et al. 2014), which could also correlate with the lower N availability observed by Palozzi and Lindo (2017a) in the SF (i.e. immobilized as fungal biomass).

Averill et al. (2014) suggest that there could be more C stored in ecto- and ericoid mycorrhizal fungi-dominated soil compared to soils dominated by arbuscular mycorrhizae. Fungi in general demonstrate slower C processing compared to bacteria, and high F:B soils have been shown to contain greater amounts of soil organic matter and respire less, which suggests a greater C sequestration potential (i.e. more C in soils and less lost as CO_2) (Malik et al. 2016). Saprophytic fungi also play a key role in C sequestration / C loss through respiration because they breakdown more recalcitrant organic matter that contain compounds such as phenolics, lignin, and tannins using extracellular enzymes (Strickland and Rousk 2010). The SF is dominated by *Sphagnum* spp. mosses and although *Sphagnum* does not produce lignin, the polyphenolic compounds produce by *Sphagnum* mimics the compound structure of lignin and tannins (Verhoeven and Liefveld 1997) explaining why the SF has more PLFA biomarkers associated with fungal groups such as saprophytic. Other plants present in the SF also have recalcitrant tissues such as *Picea mariana* and ericaceous evergreen shrubs (*Andromeda polifolia, Chameadaphne calyculata,* and *Kalmia polifolia)* that make long-lived tissues, including woody stems and roots and leaves covered with thick epicuticular waxes (Jacquemart 1998; Eckstein et al. 1999; Wright et al. 2004), and are more associated with saprophytic fungi decomposition.

The high C:N of *Sphagnum* in the SF pairs well with the high C:N of fungal biomass, and is suggestive of fungi having lower nutrient demands compared to bacteria (Strickland

and Rousk 2010; Waring et al. 2013). Similarly, at the CF site, greater bacterial dominance can be attributed to the lower C:N aboveground plant community providing a more N rich environment that pairs with the low C:N commonly associated with bacterial biomass (Strickland and Rousk 2010; Waring et al. 2013). While fungi are able to use both labile and recalcitrant resources (Waldrop and Firestone 2004; de Vries and Caruso 2016) the CF has greater %N litter inputs, especially during the growing season, helping to support the larger bacterial-dominated belowground community. Anaerobic bacteria were particularly more abundant at the CF compared to the SF. While I found the SF had greater moisture content, which could suggest less oxygen, the SF has a lower water table compared to the CF (Webster and McLaughlin 2010), and *Sphagnum* growth (via epical capitulum with senescence 5-10 cm below) leads to larger pore spaces allowing greater aeration (Ingram 1978), while water is contained within specialized hyaline cells (Kostka et al. 2016). At greater peat depths and closer proximity to the water table, we would expect a greater concentration of anaerobic bacteria in the SF (Asemaninejad et al. 2019) whereas in the CF, the higher water table suggests presence of anaerobic bacteria near the surface.

That said, one microbial index that is thought to relate directly to the aboveground plant composition is the Gram+ and Gram- bacteria, and the Gram+:Gram- ratio (Waldrop and Firestone 2004; Kramer and Gleixner 2008). It has been proposed that Gram+ use soil organic matter derived C (i.e. microbially processed) while Gram- use plant derived C which is considered to be a more labile source (Kramer and Gleixner 2008; Fanin et al. 2019). My study supports this as the plant inputs in the CF were more labile (i.e. lower C:N and greater %N) than the plant inputs from the SF, and lower Gram+:Gram- in the CF. While both Gram+ and Gram- bacteria had greater biomass in the CF, I found that the Gram+ PLFA marker 16:00 was associated with high peat %C and low peat %N, and the Gram- PLFA marker 18:1ω7c was associated with low peat %C and high peat %N in my PCA ordination. Borga et al. (1994) also found a larger Gram+:Gram- in *Sphagnum*-dominated peatlands compared to *Carex*-dominated. Previous literature also supports that *Carex* spp. sedges and other vascular plants (main plant input in the CF) produce more labile C compounds (i.e. simpler C compounds and less aromatic rings) than the main plant input in the SF (i.e. *Sphagnum* spp. mosses) (Del Giudice and Lindo 2017; Palozzi

and Lindo 2017a; Mastný et al. 2018). Higher Gram+:Gram- ratios have also been linked to lower soil respiration rates suggesting slower C cycling and subsequently greater C storage in soils (Whitaker et al. 2014), leading to my conclusion that the SF is potentially a greater C sink than the CF.

Finally, greater arbuscular mycorrhizal biomass in the CF may be explained also by the aboveground plant community, as well as differences in hydrology at the two sites. Arbuscular mycorrhiza require plants with roots but also ideal hydrological conditions. Mentzer et al. (2006) using wet prairie soil determined that a higher percentage of arbuscular mycorrhiza fungi was related to intermittent flooding conditions, and the CF has two small streams along both the southern and northern boundaries, the CF also has a higher water table that is often at or above the soil surface (Webster and McLaughlin 2010). While there is discrepancy in the literature as to whether or not *Carex* spp. sedges are able to form association with arbuscular mycorrhiza (Muthukumar et al. 2004), it appears that some *Carex* spp. sedges may form associations with arbuscular mycorrhiza (Miller et al. 1999; Cornwell et al. 2001). Similarly, while the shrub *Myrica gale*, which is also abundant in the CF, is known to form associations with ectomycorrhiza and there has also been sparse evidence that *Myrica gale* can form associations with arbuscular mycorrhiza (Skene et al. 2000). Mycorrhizal associations are poorly known and we are increasingly finding less specificity than previously thought where, depending on habitat, even the same host species can show varying mycorrhizal associations (Guillermo Bueno et al. 2019; Sun et al. 2019; Tedersoo et al. 2019). This study further suggests that mycorrhizal associations may not be specific and might vary across habitat types where plant species such as *Carex* spp. sedges and shrubs such as *Myrica gale* may form associations with arbuscular mycorrhiza.

The hydrological and nutritional continuum that peatlands demonstrate provide a unique opportunity to understand the above- and belowground communities that are present as these systems are predicted to shift under climate warming. Various above- and belowground communities also have different ecosystem functions, specifically in terms of C cycling, which has large implications for climate change as peatlands are important terrestrial C stores. I demonstrate how the microbial community is linked to litter nutrient

inputs, which are dictated by the plant community, but are not dictated by the diversity of the plant community. That said, whether nutrient availability both in peat and plant litter (C:N) nutrient values is a direct feedback between the microbial community and the plant community is still not entirely clear. What is clear is that changes in plant communities that shift the nutrient content of litter inputs will alter the microbial community (Jassey et al. 2013; Bragazza et al. 2015). I found that the high quality plants and litter present in the CF are associated with high quality peat, supporting a larger but also more active microbial community, this is particularly relevant in terms of climate change as warming and elevated CO_2 has been shown to alter peatland plant communities, specifically shifting *Sphagnum* spp. dominated peatlands towards more vascular plant dominated communities (Jassey et al. 2013; Dieleman et al. 2015; Bragazza et al. 2016). Peatlands and in particular boreal peatlands, harbour slow decomposition rates making peatlands the largest terrestrial C store, storing 1/3 of the world's terrestrial C (Gorham 1991). Subsequent shifts in litter quality (increased nutrient-rich litter) may lead to larger, more active and more bacterial dominated peat communities as suggested here, which are thought to be less efficient at storing C than fungal dominated communities.

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Chapter 3

3 Climate warming and plant community shifts in boreal peatlands

3.1 Introduction

Boreal peatlands provide important ecosystem services such as carbon storage. It is estimated that northern peatlands store 310 Gt of carbon, corresponding to 40% of the carbon held in the atmosphere (762 Gt) (IPCC 2007 (Fig. 7.3); Rydin and Jeglum 2013). The accumulation of peat (partially decomposed plant matter) is due to slow decomposition rates enabling carbon storage. Peatlands have a high-water table, acidic conditions, and boreal peatlands also have low temperatures contributing to slow decomposition rates. The aboveground plant communities are important predictors of carbon storage (Hollingsworth et al. 2008; Larmola et al. 2013; Bragazza et al. 2016) as they are the main constituent of peat and as such variations in plant communities could contribute to different carbon storage potentials of peatlands.

Peatlands exist on a continuum of not only plant community composition (i.e. *Sphagnum* mosses to vascular plants), but also hydrology and nutrient content. There are two main classification of peatlands: bogs (hydrologically isolated from ground water) and fens (hydrologically connected to ground water), and within fens there is also a gradient of nutrient status from rich to poor which also harbor different plant communities. *Carex* (sedge)-dominated fens are typically more nutrient rich with low plant community species richness, while *Sphagnum*-dominated fens tend to be nutrient poor with a carpet of *Sphagnum* mosses and an overstory of ericaceous shrubs. *Carex* species are more easily decomposed due to their labile litter (Del Giudice and Lindo 2017; Mastný et al. 2018) and therefore promote faster carbon cycling and potentially less carbon storage (Bragazza et al. 2013; Suseela et al. 2013; Walker et al. 2016; Lopatin et al. 2019). *Sphagnum* mosses are key to carbon storage in boreal peatlands as *Sphagnum* mosses are the dominant peat forming vegetation (Kuhry and Nicholson 1992) and have antimicrobial properties inhibiting decomposition (Clymo 1963; Spearing 1972). *Sphagnum* is considered an ecosystem engineer because the accumulation of *Sphagnum*

peat alters the local hydrology and pore water biogeochemistry, creating more advantageous environmental conditions for *Sphagnum* (van Breemen 1995; Turetsky 2003). It is suggested that any changes to plant community composition in boreal peatlands could impact their carbon storage potential.

The IPCC 2018 special report looking at the impacts of global warming states that human-induced warming reached approximately 1ºC above pre-industrial levels in 2017 and will continue to rise by 0.2 ºC each decade (IPCC 2018). Ecosystems including boreal peatlands, are experiencing these rising temperatures. In a lab experiment Dieleman et al. (2015) found that under higher temperatures graminoid species outcompeted the previously dominant *Sphagnum* species. Similarly, Jassey et al. (2013) found greater vascular plant abundance and lesser *Sphagnum* coverage under warming; several other studies have found similar patterns (Weltzin et al. 2000, 2003; Breeuwer et al. 2010; Buttler et al. 2015; Bragazza et al. 2016). An increase in vascular plant abundance in peatlands at the expense of *Sphagnum* also changes environmental conditions such as increasing nutrient content through the addition of more labile carbon inputs through litter (Del Giudice and Lindo 2017; Palozzi and Lindo 2017) and root exudates (Jones et al. 2009; Bragazza et al. 2013; Robroek et al. 2016; Dieleman et al. 2017), altering the local hydrology, and increasing pH (van Breemen 1995; Mastný et al. 2018) all reinforcing the further expansion of vascular plants. This can have implications on the ecosystem function of peatlands where we could see an increase in decomposition rates, reducing the carbon storage potential of boreal peatlands.

The shift from *Sphagnum* mosses to vascular plants in *Sphagnum*-dominated peatlands under warming is fairly well studied, but what is less understood is plant community shifts under warming in peatlands currently dominated by vascular plants such as *Carex* sedges and other graminoids. Weltzin et al. (2000, 2003), using a mesocosm experiment, found an increase in graminoid annual net primary productivity under warming, but graminoid cover only responded to water table treatments and not warming treatments. Similarly, Mäkiranta et al. (2018), in a field experiment at two sites, found no effect of warming or water table treatments on graminoid aboveground biomass. More field-based studies are needed to understand the response of *Carex*-dominated peatlands to climate

warming.

The objectives of this experimental field study were to quantify plant community changes under warming in two peatlands differing in aboveground plant community composition, a *Sphagnum* spp. dominated fen (SF) and a *Carex* spp. dominated fen (CF). To simulate warming, I used clear open top chambers (OTCs), which act as a greenhouse to passively warm the air within the OTC, and they also mirror the degree of human-induced warming (~1ºC). I used univariate community indices such as richness, Shannon's diversity, and Pielou's evenness, and multivariate community techniques to explore plant community differences between the warming and control treatments. Furthermore, aboveground biomass was quantified using leaf area index (LAI) to monitor plant growth within warming and control treatments. I predicted a decrease in *Sphagnum* abundance and a corresponding increase in vascular plant abundance in the SF, while in the CF I predicted an increase in biomass (as measured by LAI) without a change in community composition.

3.2 Materials & Methods

3.2.1 Site description

The study sites were the same sites described in Chapter 2, located in a northern boreal peatland complex near White River, Ontario (48°21'N, 84°20'W) that receive a mean annual precipitation of 980 mm and have a mean annual temperature of 2.1ºC (see Webster and McLaughlin, 2010 for full description). The study was performed over two growing seasons (June – August) during 2017 and 2018. The two sites chosen for this study are a *Sphagnum*-dominated fen (SF) and a *Carex*-dominated fen (CF) located ~2 km apart that are part of the Ontario Ministry of Natural Resources and Forestry long-term research monitoring sites. As the names suggest, these two sites differ by their aboveground vegetation, where the SF has a full ground covering moss layer composed of *Sphagnum* spp. while the CF is densely populated with *Carex* spp. The SF covers 4.5 ha in area, is sparsely treed and is surrounded by mixed-wood deciduous and coniferous boreal forest; it is bound on the southern edge by a narrow lake. The CF, on the other hand, covers 10.2 ha in area, is open without tree cover, and is bordered by two small

streams running along the northern and southern edges flowing into a main stream southeast of the site, and mixed-wood deciduous coniferous boreal forest on the surrounding upslopes.

The dominant vegetation at both sites was initially surveyed by Palozzi and Lindo (2017) and is further described here. All vegetation was identified using *Wetland Plants of Ontario* by Newmaster et al. (1997). The *Sphagnum* spp. at the SF includes *S. magellanicum* Brid., *S. angustifolium* (C.E.P. Jensen ex Russow) C.E.O. Jensen, and *S. fuscum* (Schimp.) Klinggr., with *S. girgensohnii* (Russow) in lesser amounts. The SF topography, on the microscale, consists of hummocks formed by *S. fuscum* while *S. girgensohnii* is more present in hollows. Other low-lying species include stiff clubmoss (*Lycopodium annotinum* L.), small cranberry (*Vaccinium oxycoccos* L.), creeping snowberry (*Gaultheria hispidula* (L.) Muhl. ex Bigelow) and low densities of *Carex disperma* Dewey and *Carex pauciflora* Lightf. Shrubs in the SF include Labrador tea (*Rhododendron groenlandicum* Oeder), leatherleaf (*Chamaedephne calyculata* (L.) Moench), and lowbush blueberry (*Vaccinium angustifolium* Aiton); sweet gale (*Myrica gale* L.) and bog laurel (*Kalmia polifolia* Wagenh.) are present in lower abundances. The tree species in the SF include black spruce (*Picea mariana* (Mill.) B.S.P) and tamarack (*Larix laricina* (Du Roi) K. Koch). The CF is dominated by *C. stricta* Lamb., *C. oligosperma* Michx., and *C. lasiocarpa* Ehrh in varying amounts where *C. stricta* tends to grow in patches semi-isolated from patches of *C. oligosperma* and *C. lasiocarpa*. Other than *Carex* spp., the CF has shrubs that include sweet gale, leatherleaf, and sparse patches of *Sphagnum* spp. The CF doesn't have the same hummock-hollow structure as the SF, where we see less variability on small spatial scales, but the *Carex* spp. and shrub spp. tend to form more predictable patches on the larger scale. Hummock structures of *S. angustifolium* are also sparsely present in the CF.

3.2.2 Sampling design

Both the SF and CF research sites are implemented with 16 experimental plots delineated by cylindrical PVC collars approximately 40 cm deep (30 cm belowground; 10 cm aboveground) and 1 m in diameter. At each site, eight plots have OTCs 1.2 m tall that rest within the collars, anticipated to passively warm the air ~1-2°C above ambient

temperature (Jassey et al. 2013; Buttler et al. 2015; Mäkiranta et al. 2018); OTCs were established for the first time in June 2017 and were retained for the length of the growing season, but removed during the winter, and re-established in June 2018. The experiment follows a block design, where at each site the 16 experimental plots were equally divided into four different blocks based on location; two plots were assigned to warming and two assigned to non-warming treatments to account for any spatial factors inherent to the site (Appendix C).

3.2.3 Environmental properties

A weather station was installed and maintained at both sites by the Ontario Ministry of Natural Resources and Forestry to record air temperature, total rainfall, peat moisture, and peat temperature across both the 2017 and 2018 growing season and are presented as site descriptors (Table 3.1). At the plot level, air temperature was measured both inside the OTC and outside the OTC a couple of times a week (n=28 in the SF & n=21 in the CF) from June to August 2017 using a thermometer (Thermocouple Traceable Fisher Scientific).

In 2017, peat temperature at 5 cm depth and peat moisture at 10 cm depth was measured ~once a week (n=8 in the SF & CF) and was averaged across three points within each chamber to account for any topographical variability. Peat temperature was measured using a thermometer, while moisture was measured in the field using a soil moisture meter (HH2 Delta-T Devices). Peat moisture at 10 cm depth was also measured from June to August 2018 (n=5 in the SF & CF), while peat surface temperature was recorded using HOBO data loggers (U23 Pro v2, MA, USA). The HOBOs were deployed in June 2018 in two control and two warming treatments at both sites.

Table 3.1 Environmental variables for the two experimental peatland sites near White River, Ontario. Values are based on weather station data collected every 15 seconds, and are means (± standard deviation) over the growing season (May – August). Total rainfall is rainfall over the growing season.

	Sphagnum-dominated fen		*Carex*-dominated Fen	
	2017	2018	2017	2018
Air temperature (°C)	12.62 ± 6.77	14.72 ± 7.25	12.53 ± 6.39	14.62 ± 6.85
Total rainfall (mm)	385.5	259.1	377.8	301.3
Peat temperature at 5 cm (°C)	13.78 ± 3.74	13.09 ± 5.88	12.01 ± 3.44	13.18 ± 4.08
Peat moisture at 10 cm (%)	26.04 ± 0.61	29.03 ± 4.23	42.01 ± 0.14	41.29 ± 1.47

3.2.4 Vegetation surveys

Plant community composition was determined for all experimental plots (N=32) in June 2017 and June 2018 prior to OTC deployment for that growing season. In June 2017, the experimental plots had not been subject to the OTCs previously (baseline prior to experiment initiation); in 2018, the experimental plots had been previously warmed over the 2017 growing season (baseline prior to year two warming). Plant community composition was subsequently determined for all chambers in mid-July and late August in both 2017 and 2018. Experimental chambers were sampled using the point-intercept method (Bråthen and Hagberg 2004), which is a non-destructive sampling method where plant identifications are made systematically across 100 intersecting points within a 1 m^2 square grid, and the plant nearest to each intersection is identified. Using this method allowed the generation of both total plant species richness and the relative abundance of each plant species. Because the experimental plots were circular, plant identifications were not made for point intersections outside of the experimental chambers. To account for any differences in total number of intersections among experimental plots, I standardized the data to 1 m^2 (i.e. number of individuals/m^2).

Due to the dominance of *Sphagnum* as ground cover at the SF, I made two plant identifications for each intersection; the nearest moss spp. and nearest non-moss spp. to ensure that species other than *Sphagnum* spp. were enumerated. As such in the SF, ~200 (minus any points outside the plots) plant identifications were determined, while ~100 plants were identified per plot in the CF. If there was no living plant within approximately 3 cm of the grid intersection, the point was considered a 'non-detect' indicating either bare soil or a dead plant. At the SF, a full non-detect was considered when neither a vascular nor a moss was within 3 cm of the point intersect (both 'non-detect moss', and 'non-detect vascular' data was recorded). Plants were identified using Newmaster et al. (1997), however, due to difficulties differentiating between certain species in the field, *S. magellanicum*, *S. fallax* (Klinggr.) Klinggr., and *S. rubellum* Wills. were grouped together at the SF (listed as S. *magellanicum* in Appendix A), while in the CF site *C. oligosperma* and *C. lasiocarpa* were not distinguishable unless they possessed seed heads (listed as Cala.Caol).

Due to the ongoing nature of the experiment, destructive biomass sampling was not possible, so the leaf area index (LAI) was measured within all experimental chambers as a proxy for total biomass using a LAI wand (ACCUPAR-LP-80) held just above the peat surface. The LAI wand measures all incoming photosynthetically active radiation and calculates total leaf area as a function of canopy light interception. Functionally, the LAI wand is only able to make measurements for vegetation that is above the ground surface and as such cannot be used to predict *Sphagnum* spp. biomass. As the SF has a more heterogeneous vegetation landscape with larger amounts of ground cover, I performed ten LAI measurements for each experimental plot to obtain an average value, while I made five measurements for an accurate LAI measurement in the CF.

3.2.5 Statistical analysis

I compared the temperature inside and outside the warming (OTC) treatment during the 2017 growing season using a repeated measures ANOVA for each site separately (treatment and block as the main effects and time as the repeated measure). Block as a main effect or interaction was insignificant for species richness in the SF and CF, Shannon's diversity in the SF, and Pielou's evenness in the CF and so it was not retained as a factor in the repeated measures ANOVA, but it was included as a factor for all others analyses. Peat moisture at 10 cm and peat temperature at 5 cm in 2017, and peat moisture at 10 cm in 2018 were analyzed using a repeated measures ANOVA in Statistica (version 7.0) (StatSoft, Inc., 2004), where the sites were analyzed separately, and treatment and block were used as main effects with time as the repeated measure.

For the vegetation data, the two peatlands (SF and CF) were analyzed separately as differences in SF and CF with respect to the vegetation community (richness, abundance and composition) were previously established (see Chapter 2 and Palozzi and Lindo (2017)). I analyzed the effects of warming on plant species richness, Shannon's diversity index (*H'*), Pielou's evenness (*J'*), the number of non-detects (from moss and vascular plants in the SF and total non-detects in the CF), and LAI using two-way repeated measures ANOVA separately for both the SF and CF and with the four sampling time points as the repeated measure in Statistica (version 7.0) (StatSoft, Inc. 2004). I used the vegan package in R to calculate both Shannon's diversity index and Pielou's evenness

(Oksanen et al. 2018). Tukey HSD post hoc tests were performed to determine differences between time points for Pielou's evenness, moss non-detects and vascular non-detects in the SF and CF. Fisher's LSD post hoc tests were performed to determine LAI differences across time, as the Tukey HSD post hoc is less conservative, finding more differences, that appeared to have biologically irrelevant results.

Individual plant species standardized abundances (number of individuals/m^2) at both sites were used to assess overall community composition among the temperature treatments. Plant community compositional dissimilarity among plots was compared using a Bray-Curtis dissimilarity matrix on Hellinger transformed data in base R (version 3.4.3m R Development Core Team) and using the vegan package (Oksanen et al. 2018). In community data sets, often each species is not present in all plots creating many zeros which can heavily skew the dissimilarity matrix. The Hellinger transformation accounts for this. Each site was analyzed separately, and the dissimilarity based on experimental treatment (warming vs control), month (July and August), experimental block, and year (2017 & 2018) was assessed for significance using the adonis function for Permutational ANOVA (PERMANOVA) in the vegan package in R (Oksanen et al. 2018). Community compositional differences between warming treatments were visualised using non-metric multidimentional scaling (NMDS) ordination biplots. A multivariate dispersion index (MVDisp), as a measure of community variability, indicating community dissimilarity within both the warming and control communities at both sites was calculated using the MVDisp program in Primer 5 (Primer-E Ltd. 2001).

Based on the output of the NMDS visualization, I tested whether the control plant communities were a nested subset of the warming plant communities using the nestedtemp function in the bipartite package in R (Dormann et al. 2009). This package calculates a nestedness 'temperature' (T) based on a binary presence-absence matrix. I used the following parameter specifications: PopSize = 30, n.ind =7, and n.gen=2000 based on recommendations from the literature (Rodríquez-Grionés and Santamaría 2006). In this analysis, a T of 0 represents complete nestedness where one community contains a perfect subset of another more diverse community, while a T value of 100 suggests complete randomness of species distributions among sites. The significance of the

calculated T is determined by testing it against the mean T of 10 000 randomly drawn matrices, and the probability of detecting a nested community pattern is subsequently compared to a null model. The bipartite package generates three null models, but I present only the output of null model 3 because it is considered to be the most conservative and reliable, with low probability of both type I and type II errors (Rodríquez-Grionés and Santamaría 2006).

To further examine the percent similarity of plant communities within control treatments and within warming treatments, as well as the overall dissimilarity between control and warming treatments, I used Similarity of percent analysis (SIMPER) using the SIMPER package in Primer 5 (Primer-E Ltd. 2001). Finally, to examine individual plant species response to warming, Principal Components Analysis (PCA) was performed on the standardized and Hellinger transformed data plant community composition data using the vegan package (Oksanen et al. 2018). To help explain PCA ordination axes, site scores from the first two axes of the analysis were used in a one-way ANOVA with block, month, and treatment as separate main effect independent variables. Significant relationships between site scores and independent variables were used to interpret the overall PCA biplot.

3.3 Results

3.3.1 Environmental conditions

I found that OTCs increased the air temperature by 1-2°C across the 2017 growing season (Table 3.2). The peat was significantly warmer at 5 cm depth in 2017 in the SF in the OTC warming treatments compared to the control treatments, but there was no difference in peat temperature observed in the CF (Table 3.3), although the peat in the OTC plots were approximately 0.5°C warmer than the control plots. There were no significant differences in peat moisture at 10 cm depth between the warming and control treatments in either site in 2017 or 2018 (Table 3.3). The surface air temperature as recorded by HOBO dataloggers in 2018 was only measured at two warming and two control plots at each site, and one HOBO in a control plot at the SF malfunctioned. As such, the data were not statistically analyzed, however, the warming treatments appear to

be between 0.5 and 1°C higher than the controls (Table 3.3). The large standard deviations in surface temperature are due to the natural large fluctuations in temperature that occur between day and night.

3.3.2 Univariate community measures

All univariate community measures (species richness, Shannon's diversity index, Pielou's evenness index) were similar between warming and control treatments at both the SF and CF demonstrating no significant main effect of treatment or time by treatment interaction (Table 3.4). Although Shannon's diversity and Pielou's evenness did not show a main effect of treatment nor a interaction effect (time × treatment) there was a main effect of time in the SF where diversity in July 2017 and July 2018 was higher than August 2017, and in July 2017 evenness was significantly higher than both August 2017 and August 2018 evenness (Table 3.4) (diversity: $F_{(3,24)}$=4.52, P=0.008, evenness: $F_{(3,24)}$=7.433, P=0.001). This is likely due to the rare and small herbaceous plants such as *Geocaulon lividum* (Richardson) Fern. and *Maianthemum trifolium* (L.) Sloboda that tend to peak in July creating a more diverse and even plant community and dwindle in August. The warming treatment did, however, have an effect on moss non-detects in the SF, where over time there was greater abundance of moss non-detects in the warming treatments compared to the control treatments. Warming generated an immediate response and was most apparent after the first sampling time point (July 2017) where the number of moss non-detects in the warming treatments continue to be greater than the controls for the duration of the sampling time points (Table 3.4). In the CF there was no difference between the warming and control treatments in terms of the number of non-detects.

Table 3.2 Air temperature inside and outside of warming treatment plots at the two experimental fen sites measured on average twice a week from June to August 2017. Values are means ± standard deviation. Letters denote significant differences.

	Air temperature in 2017 (°C)	
	***Sphagnum*-dominated fen**	***Carex*-dominated fen**
Inside the chamber	23.46 ± 1.34^{a}	23.36 ± 1.17^{a}
Outside the chamber	22.56 ± 1.22^{b}	21.46 ± 1.04^{b}
Statistical result	$F_{(1,14)}= 70.0$ **P<0.001**	$F_{(1,14)}= 92.50$ **P<0.001**

Table 3.3 Peat environmental variables (means± standard deviation) within both the control and warming treatments at both sites. Statistical results indicate significant differences between main effect of treatment using a two-way repeated measures ANOVA (treatment and blocks as main effects, time as repeated measure).

	Peat temperature (°C) at 5 cm (2017)	**Peat moisture (%) at 10 cm (2017)**	**Peat moisture (%) at 10 cm (2018)**
		Sphagnum-dominated fen	
Warming	17.97[a] ± 3.72	29.09 ± 11.12	19.88 ± 6.52
Control	17.09[b] ± 3.81	30.37 ± 10.71	20.39 ± 7.30
Statistical result	$F_{(1,8)}$=9.55 **P=0.015**	$F_{(1,5)}$=1.42 P=0.287	$F_{(1,7)}$=1.03, P=0.344
		Carex-dominated fen	
Warming	15.21 ± 4.31	53.93 ± 16.06	39.61 ± 12.65
Control	14.76 ± 2.44	57.09 ± 13.42	42.75 ± 13.04
Statistical result	$F_{(1,8)}$=1.01 P=0.344	$F_{(1,5)}$=1.94 P=0.222	$F_{(1,7)}$=0.55, P=0.482

	June peat surface temperature (°C)	**July peat surface temperature (°C)**	**August peat surface temperature (°C)**
		Sphagnum-dominated fen	
Warming	18.21 ± 9.51	19.21 ± 7.30	16.98 ± 6.84
Control	17.41 ± 10.00	18.79 ± 8.26	16.81 ± 8.02
		Carex-dominated fen	
Warming	17.26 ± 6.87	18.73 ± 6.19	16.96 ± 6.32
Control	17.08 ± 7.92	18.48 ± 6.94	16.47 ± 7.01

Table 3.4 Plant species richness, diversity and evenness (based on unstandardized data) for the *Sphagnum* and *Carex*-dominated fens. Non-detects in the SF are presented as separate mean number of measurements with no moss ground cover or vascular plant, while non-detects in the CF represent absolute (moss or vascular) non-detects as observed during plant-intercept surveys in the field. Values are means ± standard error. Statistical F and P values correspond to treatment by time interactions using a repeated measures ANOVA. Letters denote significant differences based on Tukey HSD post hoc test for time by treatment interaction.

***Sphagnum*-dominated fen**							
		July 2017	**August 2017**	**July 2018**	**August 2018**	**$F_{(3,24)}$**	**P**
Species Richness	Warming	13.88 ± 0.30	14.00 ± 0.50	14.25 ± 0.62	14.50 ± 0.53	0.31	0.585
	Control	13.88 ± 0.46	13.25 ± 0.73	14.63 ± 0.38	14.13 ± 0.55		
Shannon's diversity Index	Warming	2.24 ± 0.04	2.19 ± 0.05	2.23 ± 0.05	2.21 ± 0.05	1.00	0.403
	Control	2.28 ± 0.04	2.16 ± 0.05	2.29 ± 0.04	2.23 ± 0.05		
Pielou's evenness Index	Warming	0.85 ± 0.01	0.83 ± 0.01	0.84 ± 0.01	0.83 ± 0.02	0.70	0.564
	Control	0.88 ± 0.01	0.84 ± 0.01	0.85 ± 0.01	0.84 ± 0.01		
Moss non-detects	Warming	9.75 ± 2.79[a]	7.75 ± 3.45[b]	11.69 ± 5.35[b]	7.94 ± 3.95[b]	4.60	**0.011**
	Control	12.75 ± 2.74[a]	6.13 ± 1.25[b]	7.63 ± 2.36[b]	3.94 ± 1.26[b]		
Vascular non-detects	Warming	4.13 ± 0.99	5.00 ± 1.48	4.69 ± 1.48	6.19 ± 1.86	1.24	0.322
	Control	4.00 ± 1.38	4.50 ± 1.42	3.75 ± 1.71	6.94 ± 1.89		

***Carex*-dominated fen**							
		July 2017	**August 2017**	**July 2018**	**August 2018**	**$F_{(3,24)}$**	**P**
Species Richness	Warming	6.65 ± 0.42	6.50 ± 0.50	6.00 ± 0.57	5.63 ±0.46	1.51	0.226
	Control	6.13 ± 0.30	6.38 ± 0.26	6.25 ± 0.31	6.13 ± 0.23		
Shannon's diversity Index	Warming	1.46 ± 0.10	1.40 ± 0.08	1.33 ± 0.07	1.29 ± 0.09	1.15	0.348
	Control	1.51 ± 0.06	1.47 ± 0.06	1.47 ± 0.04	1.50 ± 0.05		
Pielou's evenness Index	Warming	0.78 ± 0.05	0.76 ± 0.03	0.77 ± 0.04	0.76 ± 0.05	0.27	0.845
	Control	0.83 ± 0.02	0.80 ± 0.02	0.81 ± 0.01	0.83 ± 0.02		
Total Non-detects	Warming	8.13 ± 1.19	9.38 ± 2.15	2.88 ± 0.44	7.63 ± 1.85	1.72	0.190
	Control	6.50 ± 1.22	7.00 ± 1.56	4.00 ± 1.22	4.13 ± 1.68		

The LAI was similar in the warming and control treatments in the SF ($F_{(1,24)}$=3.13, P=0.115) (Fig. 3.1A). The SF did have a significant time effect where August 2017 warming and control and July 2017 warming treatments have significantly lower LAI than August 2018 warming and control chambers (Fig. 3.1A). However, the CF's warming treatments had higher LAI compared to the control chambers ($F_{(1,24)}$=5.10, P=0.054) with a significant time by treatment interaction where we can see that the warming effect is greatest in July 2017 and begins to diminish overtime ($F_{(3,24)}$=4.20, P=0.016) (Fig. 3.1B). The LAI was nearly 2× greater in the CF compared to the SF.

3.3.3 Community measures

Plant species community composition was dissimilar between warming and control treatments at both sites (SF: $F_{(1,57)}$=2.30, P=0.023, CF: $F_{(1,57)}$=6.95, P=0.003) (Fig. 3.2). The NMDS for both sites demonstrate how the warming treatments are more heterogeneous (larger dissimilarity indicated by larger spread in ordination space) compared to the control treatments, and the warming communities seem to not only be dissimilar from the control treatments but also dissimilar from each other. The MVDisp index also demonstrated more tightly clustered plant communities under the control conditions compared to the warming treatments, where the warming plant communities were more dissimilar from one another compared to the control plant communities (SF: control=0.857; warming=1.143 CF: control=0.826; warming=1.174). Yet, both sites only demonstrate a somewhat weak, albeit significant, nestedness pattern of control plant communities nested within the warming plant communities (SF: T=30.51, null T=46.86, variance=5.05, P=<0.001; CF: T=21.9, null T=38.37, variance=11.02, P=<0.001).

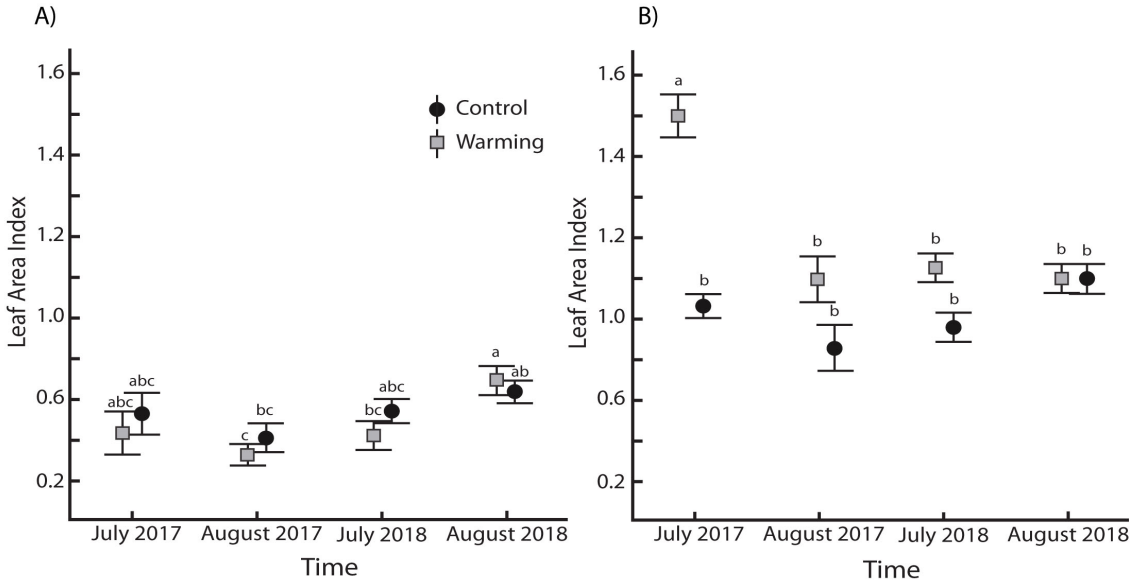

Figure 3.1 Mean Leaf Area Index as a proxy for plant biomass (excluding mosses and other ground cover) for both control and warming chambers across two growing seasons (2017 & 2018) for the A) *Sphagnum*-dominated fen (SF) and B) the *Carex*-dominated fen (CF). Error bars represent standard error.

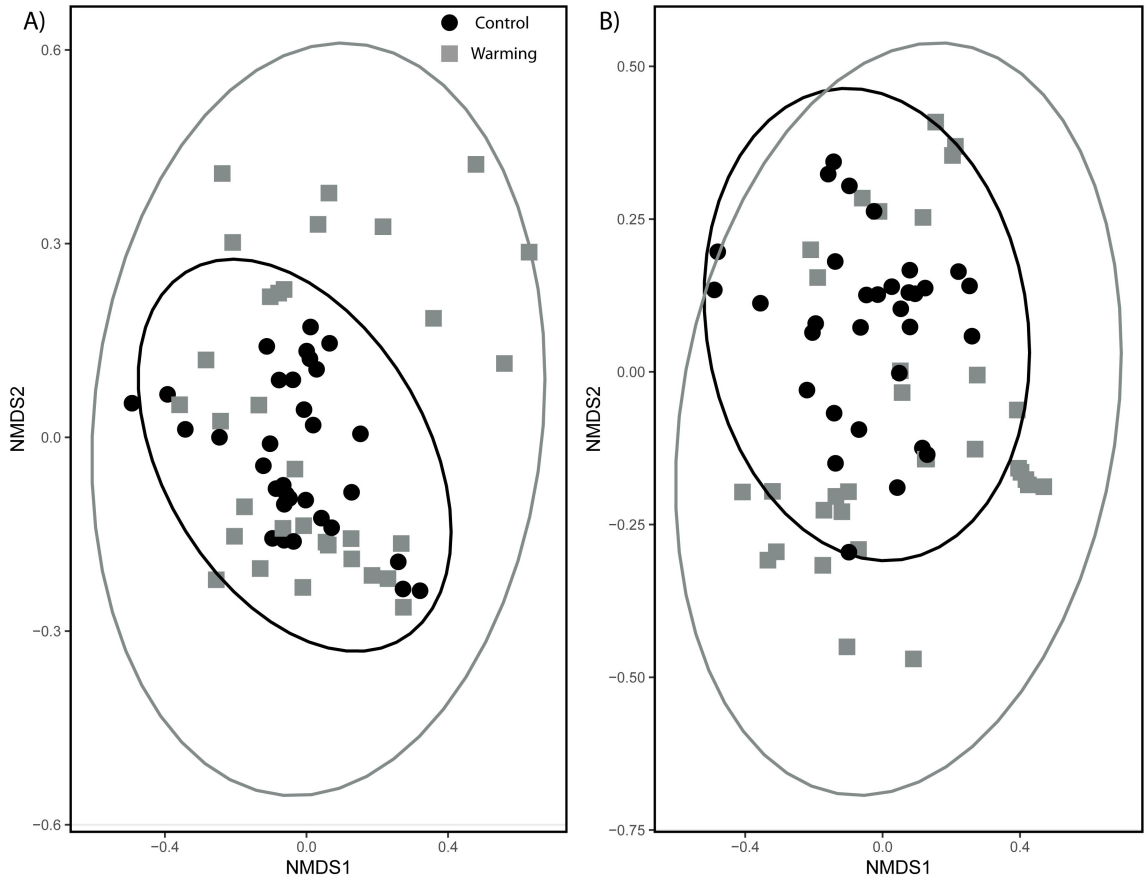

Figure 3.2 Compositional similarities of plant communities across two growing seasons under control and warming treatments in the *Sphagnum*-dominated fen (SF) (A) and the *Carex*-dominated fen (CF) (B). Ordination stress as a measure of ease to plot the communities in space is 0.17 for SF with three axes and stress is 0.13 for CF with three axes. The ellipses represent 95% confidence intervals.

In the SF the SIMPER analysis demonstrated that the plant communities within the warming treatments were 60.56% similar compared to the control treatments that demonstrated more similarity at 66.66%. The pattern was similar at the CF where the SIMPER analysis demonstrated 64.35% similarity within the warming plant communities but 72.38% similarity for the control treatments. The SIMPER analysis for the SF also demonstrated that the warming and control plant communities were 37.27% dissimilar where *S. magellanicum*, *S. fuscum,* and non-detects explain 36.91% of the dissimilarity between the warming and control treatments. In the CF the SIMPER analysis demonstrated that control and warming plant communities were 33.92% dissimilar and *C. lasiocarpa*, *C. oligosperma*, *S. angustifolia*, and *C. stricta* explain 64.24% of the dissimilarity between control and warming plant communities. Both sites demonstrate greater similarity within the control treatments compared to the warming treatments, yet the similarity between treatments is similar (SF: 62.73% and CF: 66.08%) to within treatments.

There was not a significant year effect on plant community composition in the SF ($F_{1,57}$=2.04, P=0.064), however there were significant month effects where July and August plant community composition was significantly dissimilar ($F_{1,57}$=2.25, P=0.031). The small herbs (*Maianthemum trifolium* and *Geocaulon lividum*) species are more prevalent earlier in the growing season and become less prevalent closer to the end, likely contributing to this difference. Both the SF and CF demonstrated significant block effects when considering plant community composition (SF: $F_{3,57}$=4.67, P=0.001, CF: $F_{1,57}$=2.04, P=0.064), demonstrating the heterogeneous nature of both sites. There were also significant year effects in the CF, where 2017 was significantly dissimilar from 2018 ($F_{1,30}$=3.29, P=0.016). In 2017 & 2018 there were large differences in both temperature and precipitation, and this had an effect on the CF but not the SF. Unlike the SF, the CF plant community composition did not change between months ($F_{1,30}$=0.59, P=0.631).

The first two PCA components explained 42.17% of the variance, PC 1 explained 23.29% and PC 2 explained 18.88% in the SF. The site scores for both PC 1 ($F_{3,57}$=12.53, P<0.001) and PC 2 ($F_{3,57}$=3.38, P=0.024) are both primarily related to the aforementioned block effects (Fig. 3.3). Block 2 (positive PCA axis 1) and Block 1 (negative PCA axis

1), and then Block 4 (positive PC 2 values) and Block 1 and Block 3 (negative PC 2 values) differentiate the SF plant communities in ordination space (Fig. 3.3A). Warming treatment was not a significant factor in plant community composition based on the PCA axis scores. Although, visually non-detects seem to be driving a number of warming plots (Fig. 3.3A). In the CF, the principal component analysis results demonstrate that the first two components explain 62.07% of the variance. In the CF, however, the first principal component is correlated with treatment ($F_{1,57}$=29.71, P<0.001) as well as having a block effect ($F_{3,57}$=15.07, P<0.001) (Fig. 3.3B). In this case, *Sphagnum angustifolium* is driving the positive axis of PC 1 (0.94), and is associated with control treatments. The second principal component is further correlated with block effects ($F_{3,57}$=9.33, P<0.001), whereby *C. stricta* (0.62) and *C. oligosperma*/*C. lasciocarpa* (-0.68) drove the positive and negative axis scores of PC 2 (Fig. 3.3B), respectively. I also found that *C. stricta* was associated with mainly with Block 1 and *C. oligosperma*/*C. lasciocarpa* were associated with Blocks 2 & 3.

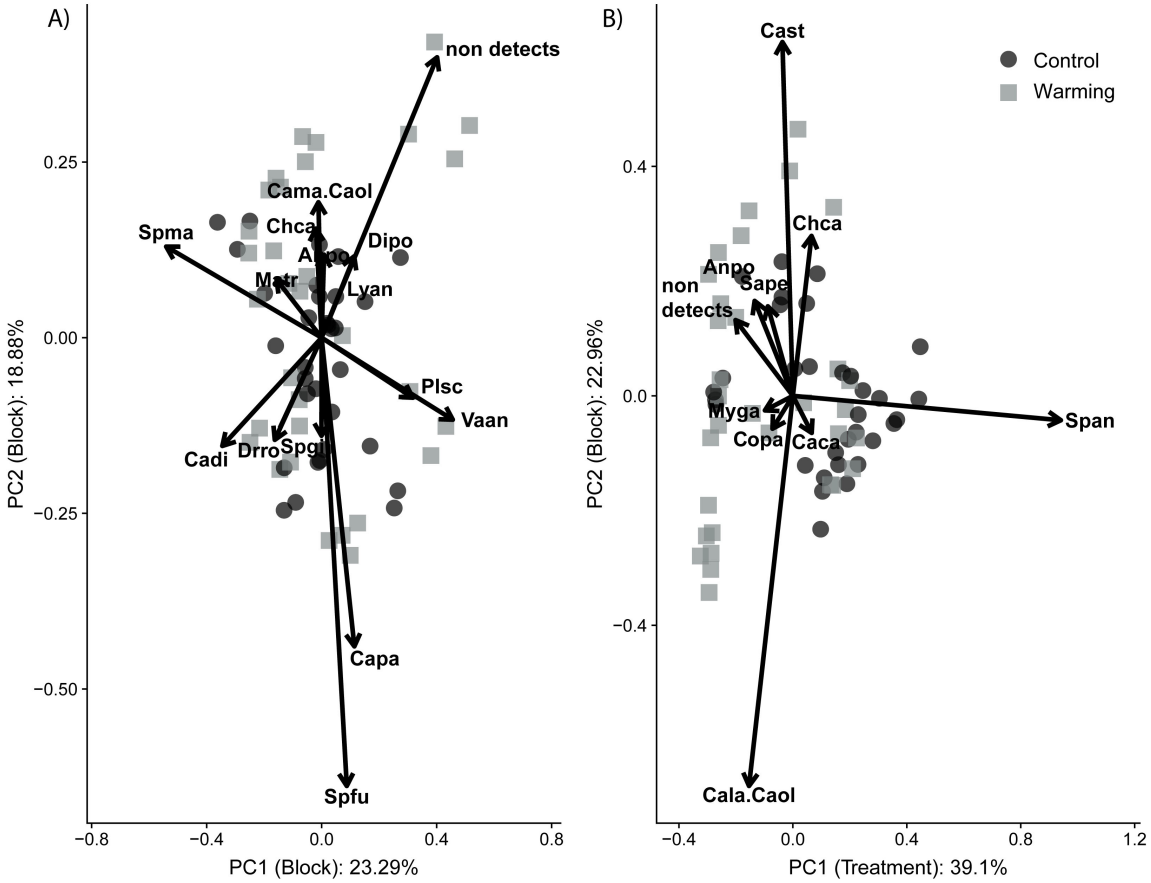

Figure 3.3 Principal component analysis for the SF (A) and the CF (B) across two growing seasons under both control and warming conditions. Block 2 is associated with positive axis 1 values, block 1 is associated with negative axis 1 values, block 4 is associated with positive axis 2 values and blocks 1 and 3 are associated with negative axis 2 values in the SF. In the CF, positive axis 1 values are driven by control treatment species, positive axis 2 values are driven by species associated with block 1, and positive axis 2 values are driven by species in blocks 2 & 3. Species names can be found in Appendix D.

3.4 Discussion

In many ways, the warming induced similar patterns on plant community composition at both sites where I observed increased random heterogeneity. However, warming had divergent effects on the dominant vegetation of *Sphagnum* mosses and vascular plants at the sites. At the SF, warming had a large negative effect on *Sphagnum* that manifested in an increase in the number of moss non-detects but without any effect on vascular plants, as was observed by the similar LAI under both warming and control treatments. On the other hand, warming increased LAI at the CF under warming, demonstrating an increase in biomass due to warming on vascular plants.

Contrary to my predictions and contrary to previous studies such as Dieleman et al. (2015) who attributed *Sphagnum* decline under warming to the increase of vascular plants, specifically a low-growing *Carex* species (*C. disperma*), I did not detect an increase in vascular plant abundance in the SF under warming. In that study, which was a controlled mesocosm study, the loss of *Sphagnum* was attributed to increased nutrient availability giving *C. disperma* a competitive advantage over *Sphagnum* (Dieleman et al. 2015). Other studies have also shown how vascular plants outcompete *Sphagnum* mosses under higher temperatures (Weltzin et al. 2000; Breeuwer et al. 2010; Jassey et al. 2013; Buttler et al. 2015; Dieleman et al. 2015; Bragazza et al. 2016), where increased nutrient mineralization under higher temperatures is thought to benefit fast growing vascular plants over slower growing plants with conservative nutrient-use strategies such as *Sphagnum* (Turetsky et al. 2012). The vascular plants are then able to further outcompete *Sphagnum* for light by shading and further reducing *Sphagnum* fitness (Van Der Wal et al. 2005). While I suspect that after additional growing seasons of warming in the SF, the vascular plants will begin to respond to warming with increase productivity at the further expense of *Sphagnum*, here I demonstrate a decline in *Sphagnum* abundance under warmer temperatures prior to vascular plant biomass increases.

Sphagnum productivity and survival is determined by moisture (Thompson and Waddington 2008), temperature (Hobbie et al. 1999), and the presence of other plants, therefore *Sphagnum* productivity may be more susceptible to indirect effects of higher temperatures such as shifts in peat moisture as well as shifts in vascular plant

abundances. *Sphagnum* mosses are well-cited to 'engineer' their environment, especially with respect to moisture conditions (van Breemen 1995). To do this, *Sphagnum* employ two strategies; first *Sphagnum* have hyaline cells that allow them to retain moisture, and second the densely packed growth form, using capillary wicking, moves moisture from lower soil levels to the surface, maintaining high moisture levels in peatlands (Kostka et al. 2016). While *Sphagnum* can withstand high levels of desiccation, and can become physiologically dormant during extreme desiccation, it is possible that the decline in *Sphagnum* I observed was due to both the direct effects of warming combined with increased desiccation (Robroek et al. 2016). Studies outside of peatlands, have generally found higher temperatures to have a positive relationship with *Sphagnum* when moisture availability is sufficient (Harley et al. 1989; Gunnarsson 2005). This is corroborated by Lang et al. (2012) when using a natural climatic gradient, but when using OTCs, they noted a decline in *Sphagnum* which they conclude is due to an experimental artefact — the OTCs provide protection from rain and dewfall, altering moisture availability.

During July 2017, the number of moss non-detects was higher in the controls compared to the warming treatments in the SF, which may indicate an initial increase in *Sphagnum* productivity following short-term (1 month) warming. Some studies have also found increased *Sphagnum* productivity under warming, where higher temperatures increased microbial activity, allowing more nutrient release and faster decomposition, and promoting *Sphagnum* growth (Sonesson et al. 2002; Dorrepaal et al. 2003; Gunnarsson 2005; Breeuwer et al. 2008). However, after July 2017, this trend was reversed and became stronger over time with a higher number of moss non-detects in the warming treatments compared to the controls. In 2018, which was a significantly warmer and drier year compared to 2017, the small decrease in moisture content in the warming treatments could have exacerbated moss desiccation to increase the number of moss non-detects compared to the control treatments. Previous studies also highlight the important indirect and interactive effects of warming (Turetsky et al. 2012; Dieleman et al. 2015). While other studies have found no response of *Sphagnum* to warming (Weltzin et al. 2000; Walker et al. 2015), or decreases in *Sphagnum* productivity or cover under warming

(Jassey et al. 2013; Dieleman et al. 2015), several studies also suggest *Sphagnum* response may be species dependant (Breeuwer et al. 2010).

The overall response of the plant community in the CF was closer to my prediction that overall biomass would increase under warming. As *Carex* species exhibit fast growing strategies, the observed higher LAI in the CF is indicative of an increase in *Carex* productivity in the warming treatments. However, while this was apparent during the first growing season, LAI was more similar between warming and control treatments during the second growing season. This decreased response over time may be due to differences in the 2017 and 2018 growing season. For instance, Weltzin et al. (2000; 2003) highlighted the importance of both water table and temperature for graminoid productivity, where under higher temperatures and higher water table graminoid productivity increased but only under higher water table did graminoid cover increase. During the growing season of 2017 it was both cooler and wetter (greater amounts of precipitation) compared to the growing season of 2018, which saw warmer temperatures and less precipitation. This could explain why the effect of warming on LAI was diminished in 2018; a lower water table in 2018 counteracted the benefits of warming. This is in contrast to Mäkiranta et al. (2018) that found no effect of warming and water table on graminoid cover but did note an increase in shrubs under higher temperatures, suggesting that the high water table associated with sedge dominated fens may mitigate the effects of warming. Another hypothesis is that warming only had a short-term effect on growth and productivity, as has been shown for CO_2 enrichment (Leakey et al. 2009). These effects of warming on sedge dominated peatlands is still unclear, but continued warming at this site could elucidate mechanisms in future years.

In this study, I also show that warming led to random heterogeneous plant communities in both SF and CF sites, rather than shifting the plant community in predictable ways such as a shift towards vascular plants in the SF. This can be attributed to an increase in rare plant species such as true mosses (*Dicranum polysetum* Swartz) in some SF warming treatments, *Carex* species such as *C. oligosperma* and *C. magellanica* Lam. in others, and even *Malampyrm lineare* Desr. (Narrowleaf cow wheat) and *Alnus incana* (L.) Moench. (Speckled alder) in some warming plots. In the CF warming treatments, some of the rarer

plant species that increased in abundance included *Calamagrostis canadensis* (Michx.) P. Beauv. (Bluejoint reedgrass) in some, *Comarum palustre* L. (Marsh cinquefoil) in others, and a decrease in *S. angustifolia*.

There are two ecological processes that are thought to determine community composition: deterministic processes and stochastic processes (Hutchinson 1957; Pacala and Tilman 1994; Hubbell 2001; Bell 2001; Harpole and Tilman 2006; 2007). In a deterministic approach, the re-structuring of peatland plant communities under climate change, for example as found by Dieleman et al. (2015), is predictive in that higher temperatures lead to graminoid species outcompeting the previously dominant *Sphagnum* species. Several other studies (e.g. Weltzin et al. 2000; Breeuwer et al. 2010; Buttler et al. 2015; Bragazza et al. 2016) also found greater vascular plant abundance and lesser *Sphagnum* coverage under warming. And yet while these studies suggest that deterministic processes are key in structuring peatland plant communities under climate change conditions, Måren et al. (2018) suggest that earlier in community structuring after a disturbance (in that case fire), stochastic processes may be more important in structuring plant communities in the short term (vs deterministic processes that play out over longer time spans). I suspect that stochastic effects were more important in influencing the patterns in plant community composition describe in this study, where two years of passive warming led to plant communities being more heterogeneous, and where at both sites there was a random increase in rarer plant species. The plant community composition under warming can be described as random as each warming plot developed a somewhat unique plant community composition compared to other warming plots. Zhang et al. (2016) in a grassland ecosystem also demonstrated that stochastic processes have greater effects on rare species while more deterministic processes are linked to changing patterns in dominant species. Again, with future years of warming at these sites, I predict to see more deterministic processes (i.e. conforming to predictions based on a mechanistic understanding) structuring plant community assembly and this to be more evident with the more dominant plant species.

Finally, peatlands provide varying degrees of ecosystem services such as carbon sequestration that are linked to the aboveground vegetation communities. *Sphagnum*

mosses are integral to the carbon storage abilities of peatlands, as they are recalcitrant and have antimicrobial properties, slowing down the rate of decomposition (Turetsky et al. 2012), and therefore, a decrease in *Sphagnum* cover will have implications for carbon storage. An increase in vascular plant biomass in an already vascular dominated fen, may also affect carbon storage in belowground systems as vascular plant root exudates and litter inputs will introduce more labile carbon to the belowground system, potentially increasing decomposition rates (van Breemen 1995; Larmola et al. 2013; Bragazza et al. 2016). In addition to the direct effects of climate warming on boreal peatlands there will also be indirect effects such as changes in peat moisture, and changes in aboveground plant community. This study demonstrates how plant community shifts in two boreal peatland types might not be quite as deterministic as once thought, and the impact of climate warming during the beginning stages may be more unpredictable than the literature suggests.

3.5 References

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Chapter 4

4 Discussion

4.1 Aboveground – belowground community linkages

The aboveground plant community and the belowground microbial community are connected in a bi-directional flow of resources of carbon and nutrients (e.g. N) (Wardle et al. 2004). The aboveground plants provide carbon to the belowground microorganisms through litter inputs, where plants uptake CO_2 into their tissues and as senescence occurs, leaves are dropped and become a resource for soil microorganisms. Plants also release labile carbon through root exudates to entice associations with microorganisms (Jones et al. 2009). Belowground, the soil system mineralizes organic nutrients through decomposition to in turn, provide resources to the aboveground plant community via root uptake. However, whether aboveground and belowground systems influence each other in terms of diversity and function is still unclear. In this thesis, I demonstrate that two peatland sites that differ in aboveground vegetation have belowground systems that functionally match their vegetation counterparts (Chapter 2), and that changes in plant communities under experimental warming (Chapter 3) depend on the dominant vegetation functional type, specifically along the 'fast-slow' spectrum (Reich 2014).

4.2 Plant communities along the 'fast-slow' spectrum

Plant life history traits described along a continuum from nutrient conservative and slow growing to nutrient exploitative and fast growing (Grime 1977; Reich 2014), were epitomized in the *Sphagnum* / *Carex* dichotomy of my two peatland sites, and translated into differences in Carbon:Nitrogen ratio (C:N) in the fresh litter, the litter collected in litter traps, as well as the peat itself, all which has implications on the resource input to the belowground microbial community. The community weighted mean (CWM) values of C:N from fresh litter collected from species at the *Sphagnum*-dominated fen (SF) was over 20% greater than the C:N of the *Carex*-dominated fen (CF), indicating lower quality litter. The difference in aboveground resource inputs was further pronounce in the litter produced by both sites where once again the fast-growing, nutrient exploitative traits of

the dominant vegetation in the CF produced richer, more labile litter (lower C:N) compared to the SF. As the peat is composed of partially decomposed plant matter, the CF peat also had almost three times lower C:N compared to the SF.

The fast-slow spectrum of plant traits may also have played a role in the changes I observed in my two peatland plant communities under two years of passive warming. The CF responded quickly with increased biomass under warming in the first year, while the SF saw a slower decline in moss biomass. Numerous studies have demonstrated similar shifts in peatland plant communities under warming, but usually within a single peatland. For instance, in mesocosm designs both Dieleman et al. (2015) and Fenner et al. (2007) noted an increase in graminoid cover under higher temperatures at the expense of *Sphagnum* cover in a *Sphagnum*-dominated fen. In the field, Jassey et al. (2013) and Buttler et al. (2015) using open top chambers (OTC) generally found an increase in total vascular abundance in the chambers compared to outside the chambers that had greater moss abundance. Others have found increases in shrub biomass under warming; Bragazza et al. (2013) observed higher shrub biomass at lower altitudes and higher soil temperatures, and when Bragazza et al. (2016) transplanted peat cores with intact vegetation to a lower altitude they found an increase in vascular plant frequency. While Weltzin et al. (2000; 2003) also found an increase in shrub dominance in a mesocosm design using infrared loading to initiate warming.

However, inconsistent with the literature, the decline in *Sphagnum* abundance in the SF was not at the expense of an increase in vascular plant abundance, suggesting that *Sphagnum* decline was due to physiological tolerances rather than vascular plants outcompeting *Sphagnum* in warmer environments. *Sphagnum* spp. have an optimum temperature of below 15ºC for maximum productivity and efficient photosynthetic processes, while vascular vegetation tend to have higher optimum temperatures, above 15ºC (Hobbie et al. 1999). *Sphagnum* spp., as ecosystem engineers (van Breemen 1995), alter their environment to reinforce *Sphagnum* development by maintaining a high-water table, and cool and acidic conditions that inhibits vascular plant growth. As such, the decline in *Sphagnum* under warming at the SF may lead to expansion of vascular plants in the near future.

There have been remarkably fewer studies (only two) focusing on the effects of warming in *Carex*-dominated peatlands, but document similar results. Weltzin et al. (2000; 2003) used a mesocosm design with infrared heat lamps to increase soil temperature between 1.6-4.1ºC, whereas Mäkiranta et al. (2018) performed a field study using OTCs, similar to my study, that warmed the soil surface ~1.5ºC. Weltzin et al. (2000; 2003) found an increase in annual net primary productivity of graminoids, but graminoid cover did not change, while Mäkiranta et al. (2018) also found no effect of warming on plant community composition, net primary production or biomass. Although warming seemed to not be a large driver in sedge dominated peatlands according to these studies, both studies showed that water table did; with a higher water table increasing graminoid cover (Weltzin et al. 2000; 2003) and a decrease in water table depth increasing shrub cover (Mäkiranta et al. 2018). While I found greater LAI in the CF under warming, the increase in LAI was measured at the plot level and is therefore not possible to connect to any individual plant species. The LAI trend was most obvious during the 2017 growing season (higher precipitation year) which supports the findings of Weltzin et al. (2000; 2003) where graminoids benefit from a higher water table. The 2018 growing season (lower precipitation year) demonstrated much closer LAI between the warming and control treatments suggesting either no annual response to warming or rapid adaptation to warming treatments. Both Weltzin et al. (2000; 2003) and Mäkiranta et al. (2018) found similar results to this study, warming did not invoke shifts in plant community composition in a sedge dominated peatland.

4.3 Microbial communities along the ‘fast-slow’ spectrum

Trade-offs in the fast-slow plant spectrum (Reich 2014) were mirrored in the decomposition dynamics of the microbial functional groups. Similar to plants, microbial communities demonstrate different life history strategies, with bacteria considered as fast growing and nutrient exploitative and fungi as slow growing and nutrient conservative (Wardle et al. 2004). While many saprotrophic fungi possess specialized enzymes to decompose complex carbon compounds (i.e. recalcitrant carbon substrates), there is also evidence of fungi communities using both labile and recalcitrant carbon inputs (deVries and Caruso 2016) whereas bacteria typically only use more labile carbon substrates

(Waldrop and Firestone 2004). Further, the C:N value of bacteria biomass is typically lower than that of fungi biomass (Six et al. 2006; Strickland and Rousk 2010; Waring et al. 2013), and I show that the CF with lower C:N plant litter and peat, also harbored not only a larger microbial community in terms of biomass as depicted by phospholipid fatty acid (PLFA) analysis, but also a more bacterial dominated microbial community. There appears a consistent link between litter C:N and Fungi:Bacteria ratio (F:B) across a variety of different soil types (Soares and Rousk 2019), and my study corroborates these findings; the SF with higher C:N harbors a higher F:B compared to the CF.

Another important index to consider is the Gram+ bacteria:Gram- bacteria ratio (Gram+:Gram-), because it is thought that Gram+ use soil organic matter derived carbon (dissolved organic carbon and microbially-derived detritus), whereas Gram- use plant derived carbon, such as carbon from root exudates and plant litter, which is typically more labile carbon (Waldrop and Firestone 2004; Kramer and Gleixner 2008; Fanin et al. 2019). A very similar study to this one, Borga et al. (1994), used PLFAs to describe the microbial community in both a *Sphagnum*-dominated and a *Carex*-dominated peatland and also found a larger Gram+:Gram- in the *Sphagnum*-dominated peatland. This is consistent and may be explained by *Sphagnum* mosses lacking roots, whereas the CF is mainly vascular plants providing labile carbon through root exudates to the microbial community.

4.4 Warming induced heterogeneity in plant communities

My predictions for the SF plant community under warming were for decreased *Sphagnum* alongside increased *Carex*, and I predicted greater overall biomass at the CF. While both these predictions were somewhat met, both sites demonstrated increased heterogeneity under warming. This heterogeneity appeared due to random shifts in a variety of plant species but no consistent increase or decrease in any particular plant species. Generally, warming increased some of the rarer plant species, but again, not any particular species.

Community ecologists have long been interested in studying the diversity, abundance, and community composition and the processes that underlie these patterns (Hutchinson 1959; Chesson 2000). There are two ecological theories associated with species

distributions: niche theory (Hutchinson 1957) and neutral theory (Hubbell 2001). Niche theory focuses on species interactions with their biotic and abiotic environment and suggests that species occupy different niches because they are constrained by different resources (Pacala and Tilman 1994; Harpole and Tilman 2006; 2007); species abundances are associated with their fitness and therefore determines community composition. Alternatively, Hubbell (2001) and others have proposed that neutral processes structure ecological communities, i.e. that community composition is a function of random (stochastic) events of ecological drift, migration and speciation, and not fitness or trait variation among species. These theories are no longer considered to be mutually exclusive but rather operating in tandem, and the relative importance of deterministic (niche) and stochastic (neutral) processes are ecosystem and timescale dependent (Cadotte 2007; Dumbrell et al. 2010; Zhang et al. 2011; Måren et al. 2018). That said, stochastic processes are thought to influence rare species, while deterministic processes are linked with dominant species (Zhang et al. 2016). Thus, my findings align more with stochastic processes and neutral theory.

Both stochastic and deterministic processes can play a role in structuring plant communities (Gravel et al. 2006; Chu et al. 2007; Zaplata et al. 2013; Måren et al. 2018), but may be timescale dependant. For instance, during the first two years after burning in heathlands in Northern Europe, Måren et al. (2018) found that stochastic processes played a larger role in structuring plant communities and in later years, deterministic processes were more important. Similarly, other studies have shown that deterministic processes become more important during longer time scales (Gravel et al. 2006; Chu et al. 2007; Zaplata et al. 2013). So, while *Sphagnum* was unable to persist under the higher temperatures, random vascular species filled these gaps, suggesting stochastic processes structured the SF community. However, I predict that more deterministic processes will structure the SF plant communities under future years of warming, specifically, increased abundance of both shrubs and graminoid species as shown for other studies (Weltzin et al. 2000; 2003; Fenner et al. 2007; Bragazza et al. 2013; 2015; Jassey et al. 2013; Buttler et al. 2015; Dieleman et al. 2015).

4.5 The role of plant and microbial communities in carbon cycling

Sphagnum is essential to the carbon storage potential of peatlands, as it has recalcitrant, low quality litter (Turetsky 2003; Del Giudice and Lindo 2017; Palozzi and Lindo 2017), and high cation exchange capacity inhibiting microbial activity and slowing decomposition rates (Clymo 1963; Spearing 1972). A reduction in *Sphagnum* under climate warming could reduce the carbon storage potential of boreal peatlands. Yet, in a *Carex*-dominated peatland an increase in vascular plant aboveground biomass could increase carbon storage if this increase is in woody shrub tissue and growth. However, increased vascular plant growth increases the amount of labile litter available to the belowground system and would also correspond to increases in root biomass and therefore labile carbon root exudates. More labile carbon inputs could increase decomposition rates (De Graaff et al. 2010), and 'prime' the microbial decomposition of long-term stored carbon (Kuzyakov et al. 2000; Brant et al. 2006). The extent and importance of microbial priming is unknown, but it is thought to reduce the carbon storage potential of boreal peatlands (Walker et al. 2016).

In accordance with the growth strategies of both the plants and the microorganisms, a more bacterial dominated soil community is thought to be less efficient at nutrient cycling and carbon accumulation (Wardle et al. 2004). Consistent with other studies (Blagodatskaya and Anderson 1998; Malik et al. 2016; Zhou et al. 2018), I show greater soil respiration (i.e. microbial activity) at the CF site where the microbial community was bacterial-dominated. Similarly, Whitaker et al. (2014) found that higher Gram+:Gram- microbial communities had lower respiration rates than lower Gram+:Gram- microbial communities. A change in aboveground plant communities under climate warming will indirectly affect the belowground microbial communities, but there are also direct consequences of warming to the microbial community. Decomposition performed by the microbial community is the main control on how much carbon is returned to the atmosphere (i.e. via heterotrophic soil respiration), which is primarily determined by abiotic processes such as temperature and soil moisture. Higher temperatures increase microbial activity, decomposition rates, and soil respiration (Aerts 2006; Bardgett et al.

2008). There is a potential under climate warming for higher decomposition rates to increase efflux of CO_2 to the atmosphere and create a positive feedback on climate warming.

4.6 Study limitations and future directions

Peatlands exist in a continuum from nutrient rich fens heavily dominated by *Carex* spp. and receiving nutrients from mineral rich groundwater sources, to ombrotrophic bogs, hydrologically isolated from ground water inputs and dominated by *Sphagnum* mosses; between the two extremes there are numerous peatland types. In this thesis, I examine only two peatland types on this continuum (nutrient poor and intermediate nutrient fens) and discuss plant litter inputs and corresponding microbial communities. A better understanding of aboveground-belowground linkages may arise if future studies include more peatland types, or even expand the continuum to other habitat types (e.g. forests, marshes etc.). For instance, Haynes et al. (2015) who examined the microbial communities at the same sites that I examined here but using DNA extractions also found highly dissimilar microbial communities, as well as at a nutrient rich fen site nearby. Unfortunately, that site (nutrient rich fen) no longer exists and a full vegetation survey was not performed, so we cannot draw any further conclusions about the aboveground-belowground community linkages.

One major challenge in studying *Sphagnum*-dominated plant communities is that *Sphagnum* litter does not "fall" to the soil surface, but rather *Sphagnum* senescence occurs along the main stem. As such, it is difficult to determine where the 'aboveground' and 'belowground' subsystems transition, and *Sphagnum* litter was not considered in the evaluation of the plant litter inputs at either site. Regardless, the C:N values of the litter and the peat clearly differentiate the SF and CF in the directions that the CWM plant values suggest. That said, *Sphagnum* growth and changes in abundance, density, or composition is also more challenging to observe than for vascular plants. As such, my observations of moss decline may be underestimates, especially in the CF where *Sphagnum* patches were more sporadic. If physiological tolerances are responsible for the observed number of 'non-detects' that I attribute to moss decline, using a growth

measuring tool such as the crank-wire method may provide a first indication of physiological stress to *Sphagnum*.

Similarly, a full analysis of carbon compounds in addition to the total C, total N, and C:N values I present here could better characterize the plant litter quality. There are various types of carbon compounds that contribute to plant litter quality such as carbohydrates, amino acids, waxes, lipids, tannins, and lignins (Lorenz et al. 2007; Suseela et al. 2013). The carbon chemical structure (e.g. aromaticity) affects not only decomposition of plant litter but also governs the microbial group responsible for decomposition. Fungi are efficient decomposers of recalcitrant compounds (e.g. lignin) through the use of extracellular enzymes and secondary metabolites, while bacteria can competitively exclude slower growing fungi in a labile compound (e.g. sugars and amino acids) dominated environment (Waldrop and Firestone 2004; Brant et al. 2006). A technique such as Fourier transformed infrared spectroscopy (FTIR) could better resolve the chemical composition of the plant litter and provide greater insight into microbial carbon use.

Further to this, the examination of microbial carbon use efficiency (CUE), the ratio between carbon assimilated into microbial biomass and carbon respired as CO_2 or decomposer metabolism (Manzoni et al. 2012), has recently been proposed as an indicator of carbon storage potential. High CUE signifies efficient microbial growth and carbon storage, while low CUE represents inefficient growth, and release of carbon to the atmosphere (Manzoni et al. 2012). Temperature, substrate quality, the microbial biochemical pathways, and nutrient availability all effect CUE (Keiblinger et al. 2010). Temperature increases metabolic costs and more recalcitrant substrates require more enzymatic steps to be degraded, both postulating an increase in energy demands and a decrease in efficiency (Ågren and Bosatta 1987; Dijkstra et al. 2011). Frey et al. (2013) demonstrated that the temperature response of CUE in grassland soils is substrate dependent where highly recalcitrant and highly labile substrates demonstrate no response although substrates with intermediate lability have lower CUE at higher temperatures. Dissimilarly, Sihi et al. (2017) in a temperate peatland found a decrease in CUE with increasing temperature when using only one labile substrate, glucose. Carbon use

efficiency has yet to be measured in boreal peatlands but is an important factor to consider under changing temperatures and plant litter inputs to predict carbon storage potential under future climatic scenarios.

Finally, my warming experiment using OTCs produced warming scenarios below IPCC predictions for boreal systems, and plant communities were only examined across two growing seasons. A stronger warming treatment could have elicited a stronger plant community response, but I anticipate that changes in plant communities will continue to emerge even with these moderate temperature increases. Lastly, while in Chapter 2 I documented paired plant-microbe communities, I did not examine shifts belowground under warming in Chapter 3. Bragazza et al. (2013) found a strong relationship between temperature, plant litter C:N, and F:B in peatlands using a natural gradient, where higher temperatures lead to low C:N and low F:B. Jassey et al. (2013) used OTCs to initiate warming and found predictable differences in aboveground plant communities (shifting from *Sphagnum* to shrub dominance) but only found differences in higher trophic levels of the belowground food webs and no differences in microbial groups. As Chapter 2 establishes a strong connection between the above- and belowground communities in peatlands, and Chapter 3 suggests shifts in plant communities under warming, I suggest that future studies include PLFA analysis to determine the effects of warming concurrently on plant and microbial communities.

4.7 Conclusions and significance

Peatlands are important terrestrial carbon stores, making the above- and belowground relationship important to understand in the context of current and future climate change. Above- and belowground communities both influence and are influenced by their abiotic and biotic environments, and this study highlights the conceptual link between aboveground plant communities and belowground microbial communities in boreal peatlands. The more nutrient rich *Carex* spp. dominated plant community harbours a microbial community dominated by fast growing, nutrient exploitative bacteria, that may be less efficient in carbon storage, whereas the nutrient poor *Sphagnum* spp. dominated plant community is associative with slower growing, nutrient conservative fungi. Climate warming is predicting a shift towards faster growing, nutrient exploitative traits in

peatland plants (Weltzin et al. 2000; 2003; Fenner et al. 2007; Bragazza et al. 2013; 2016; Jassey et al. 2013; Buttler et al. 2015; Dieleman et al. 2015). I corroborate these predictions, albeit at a slower rate than previously observed, towards an increase in vascular plant dominance and a decrease in *Sphagnum* spp. abundance. These shifts towards vascular plants with higher nutrient quality plant inputs are expected to have corresponding shifts in belowground microbial communities that process plant-derived carbon inputs. The direction and magnitude of these belowground shifts could increase decomposition rates, increase carbon emissions, and decrease peat accumulation rates, with consequences on the carbon storage potential of boreal peatlands (van Breemen 1995; Larmola et al. 2013; Bragazza et al. 2016).

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Appendices

Appendix A: The %C, %N, and C:N values for fresh plant material collected from each species observed at two peatland sites in northern Ontario. Values are means ± standard error for three replicate plants where possible.

***Sphagnum*-dominated fen**			
Plant	%C	%N	C:N
Andromeda polifolia L.*	52.22 ± 0.49	1.18 ± 0.19	45.12 ± 6.30
Carex disperma Dewey	44.13 ± 0.49	1.58 ± 0.15	28.14 ± 2.48
Carex magellanica Lam./*Carex oligosperma* Michx.	44.00 ± 0.15	1.40 ± 0.08	31.43 ± 1.80
Chamaedaphne calyculata (L.) Moench	52.38 ± 0.09	1.24 ± 0.14	42.79 ± 4.90
Gaultheria hispidula (L.) Muhl. Ex Bigelow	45.74 ± 0.58	0.8 ± 0.08	57.68 ± 5.81
Geocaulon lividum (Richardson) Fern. (Santalaceae)	46.58	2.02	23.01
Kalmia polifolia Wagenh.	51.03 ± 0.39	1.54 ± 0.22	33.43 ± 4.77
Larix laricina (Du Roi) K. Koch	47.64	0.80	59.76
Lycopodium annotinum L.	46.25 ± 0.05	0.76 ± 0.11	61.54 ± 8.98
Maianthemum trifolium (L.) Sloboda	44.34 ± 0.12	5.97 ± 0.61	7.47 ± 0.71
Picea mariana (Mill.) B.S.P	43.92	0.60	73.03
Pleurozium schreberi (Brid.) Mitt.	43.89	0.78	56.30
Rhododendron groenlandicum Oeder	51.25 ± 0.27	1.11 ± 0.10	46.67 ± 4.38
Sphagnum angustifolium (C.E.P. Jensen ex Russow)	44.57 ± 0.38	0.98 ± 0.03	45.41 ± 1.51
Sphagnum fuscum (Schimp.) Klinggr.	44.91 ± 0.75	0.91 ± 0.10	49.57 ± 6.31
Sphagnum mangellanicum Brid.	44.33 ± 0.75	0.97 ± 0.11	46.21 ± 5.02
Vaccinium angustifolium Aiton	47.66 ± 0.14	1.39 ± 0.14	34.5 ± 3.64
Vaccinium oxycoccos L.	49.16 ± 0.48	1.25 ± 0.13	39.51 ± 4.02
***Carex*-dominated fen**			
Carex lasiocarpa Ehrh /*Carex oligosperma* Michx.	44.49 ± 0.41	1.12 ± 0.12	40.05 ± 4.12
Carex stricta Lamb.	45.90 ± 0.10	1.02 ± 0.04	44.91 ± 1.81
Chamaedaphne calyculata (L.) Moench	51.45 ± 0.38	1.42 ± 0.04	36.25 ± 0.64
Myrica gale L.	50.69 ± 0.33	2.22 ± 0.13	22.89 ± 1.35
Salix pedicellaris Pursh.	48.07 ± 0.55	2.21 ± 0.30	21.98 ± 3.01
Sphagnum angustifolium (C.E.P. Jensen ex Russow)	42.68 ± 1.40	1.28 ± 0.11	33.41 ± 3.83

**Andromeda polifolia* fresh litter was only collected from the SF, %C, %N, and C:N measured values were also used in the CF

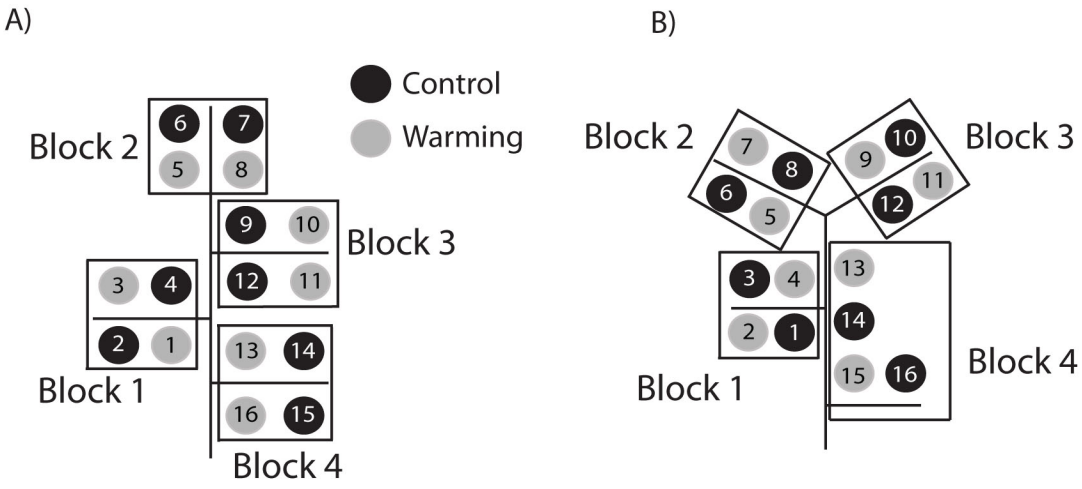
Appendix B: Specific PLFA biomarkers associated with various microbial groups

PLFA biomarkers	PLFA group	Specific PLFA markers
Bacteria	Multiple groups	i15:0, a15:0, i16:0, i17:0, a17:0, cy17:0, cy19:0, 16:1ω7, 18:1ω7, 17:1ω9
Gram + bacteria	Branched PLFAs	i15:0, a15:0, i16:0, i17:0, a17:0
Gram - bacteria	Cyclopropyl and monounsaturated PLFAs	cy17:0, 16:1ω7, 18:1ω7, 17:1ω9
Actinomycetes	10Me PLFAs	10Me16:0, 10Me17:0, 10Me18:0
Fungi	Polyunsaturated PLFAs	18:2ω6,9, 18:3ω 6,9,12*
Arbuscular mycorrhiza fungi	Monounsaturated PLFAs	16:1ω5
Saprophytic fungi	Unsaturated PLFAs	18:1ω9, 18:2ω6,9
Ectomycorrhiza fungi	Unsaturated PLFAs	16:1ω9, 18:2ω6,9
Anaerobic bacteria	Cyclopropyl PLFAs	cy17:0, cy19:0

References: (Vestal and White 1989; Frostegård and Bååth 1996; Olsson 1999; Högberg et al. 2007; Moore-Kucera and Dick 2008; Pratt et al. 2012; Willers et al. 2015; Quideau et al. 2016)

* 18:3ω6 is also found in eukaryotic organisms such as plants and algae but is typically not found in bacteria

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



Appendix D: Plant Species list for both the *Sphagnum*-dominated fen and *Carex*-dominated fen.

Plant species in the *Sphagnum*-dominated fen			
Trees	Lala	*Larix laricina* (Du Roi) K. Koch	Tamarack
	Pima	*Picea mariana* (Mill.) B.S.P	Black spruce
Shrubs	Alin	*Alnus incana* (L.) Moench (Betulaceae)	Speckled alder
	Anpo	*Andromeda polifolia* L. (Ericaceae)	Bog rosemary
	Chca	*Chamaedaphne calyculata* (L.) Moench	Leatherleaf
	Gahi	*Gaultheria hispidula* (L.) Muhl. Ex Bigelow	Creeping snowberry
	Kapo	*Kalmia polifolia* Wagenh.	Bog laurel
	Rhgr	*Rhododendron groenlandicum* Oeder	Bog labrador tea
	Vaan	*Vaccinium angustifolium* Aiton	Lowbush blueberry
	Vaox	*Vaccinium oxycoccos* L.	Bog cranberry
Sedges	Cadi	*Carex disperma* Dewey	Two-seed sedge
	Cama/Caol	*Carex magellanica* Lam./*Carex oligosperma* Michx.	Boreal bog sedge/Fewseed sedge
	Capa	*Carex pauciflora* Lightf.	Few-flowered sedge
Herbs	Drro	*Drosera rotundifolia* L. (Droseraceae)	Round-leaved sundew
	Geli	*Geocaulon lividum* (Richardson) Fern.	False toadflax
	Matr	*Maianthemum trifolium* (L.) Sloboda	Threeleaf false lily of the valley
	Meli	*Malampyrm lineare* Desr.	Narrowleaf cow wheat
	Sapu	*Sarracenia purpurea* L.	Purple pitcher plant
Mosses	Dipo	*Dicranum polysetum* Sw.	Dicranum moss
	Lyan	*Lycopodium annotinum* L.	Stiff clubmoss
	Plsc	*Pleurozium schreberi* (Michx.) Trevis	Feather moss
	Span	*Sphagnum angustifolium* (C.E.P. Jensen ex Russow)	Fine bogmoss
	Spfu	*Sphagnum fuscum* (Schimp.) Klinggr.	Rusty bogmoss
	Spgi	*Sphagnum girgensohnii* Russ.	Girgensohn's bogmoss
	Spma	*Sphagnum mangellanicum* Brid.	Mangellan's moss

Plant species in the *Carex*-dominated fen			
Trees	Lala	*Larix laricina* (Du Roi) K. Koch	Tamarack
Shrubs	Anpo	*Andromeda polifolia* L.	Bog rosemary
	Chca	*Chamaedaphne calyculata* L. Moench	Leatherleaf
	Myga	*Myrica gale* L.	Sweetgale
	Sape	*Salix pedicellaris* Pursh.	Bog willow
Sedges	Cala.Caol	*Carex lasiocarpa* Ehrh/*Carex oligosperma* Michx.	Woollyfruit /Fewseed sedge
	Cast	*Carex stricta* Lamb.	Tussock sedge
Grasses	Caca	*Calamagrostis canadensis* (Michx.) P.Beauv.	Bluejoint reedgrass
Herbs	Frvi	*Fragaria virginiana* Duchesne	Wild strawberry
	Copa	*Comarum palustre* L.	Marsh Cinquefoil
	Trfr	*Triadenum fraseri* (Spach) Glea.	Bog St. John's wort
Mosses	Span	*Sphagnum angustifolium* (C.E.P. Jensen ex Russow)	Fine bogmoss

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Curriculum Vitae

Caitlyn Lyons

Academic History

MSc	*In Progress*	Biology	University of Western Ontario
	In Progress	Environment & Sustainability	University of Western Ontario
BSc	2016	Environmental Science, Co-op	University of Guelph

Awards & Distinctions

2019 Biology Travel Award, $250
University of Western Ontario, London, Ontario, Canada

2019 Environment & Sustainability Travel Award, $650
University of Western Ontario, London, Ontario, Canada

2019 Environment & Sustainability Excellence Award, $1,000
University of Western Ontario, London, Ontario, Canada

2019-2018 Ontario Graduate Scholarship (OGS QEII), $15,000
University of Western Ontario, London, Ontario, Canada

2018 Environment & Sustainability Excellence Award, $1,000
University of Western Ontario, London, Ontario, Canada

2018 Ruth Horner Arnold Fellowship, $1,500
University of Western Ontario, London, Ontario, Canada

2016 Leslie Way Scholarship, $500
University of Guelph, Guelph, Ontario, Canada

Teaching Experience

2018 - 2017 Teaching Assistant, Department of Biology, Ecosystem Ecology, Population Ecology, Community Ecology, and Statistics for Science
University of Western Ontario, London, Ontario, Canada

Professional & Academic Service

2018 Chairperson, 9th Annual Biology Graduate Research Forum
University of Western Ontario, London, Ontario, Canada

2019 - 2018 Outreach and logistics committee member and finance committee, EnviroCon 2018 & EnviroCon 2019
University of Western Ontario, London, Ontario, Canada

Outreach & Volunteer Activities

2019 - 2018 Board member for the Thames Region Ecological Association
London, Ontario, Canada

2019 - 2018 Thames Region Ecological Association representative on the Advisory Committee on the Environment for the City of London, Ontario, Canada

2019 Developed a climate change experiment for a grade 6 class
M. F. McHugh Education Centre, Ottawa, Ontario, Canada

2018 - 2009 Girl Guide leader
82nd London Guides, 45th Burlington Guides, 1st Meadowbrook Guides
Girl Guides of Canada

2018 Organizer, Soil ecology day at University of Western Ontario
University of Western Ontario, London, Ontario, Canada

Peer Reviewed Contributions

May, W., Dawson, M.P., Lyons, C.L. (2018). Response of sunflowers (*Helianthus annuus* L.) to varying seeding rates and nitrogen fertilizer rates in a no-till cropping system in Saskatchewan. Canadian Journal of Plant Science 98(6):1331–1341.

Conference Contributions

Lyons, C.L. (2019). "Is climate warming harmful to peatland plants?" Retiring with strong minds, Kiwanis senior centre, London, Ontario, Canada [12 minute presentation to the general public]

Lyons, C.L., Meehan, M.L. (2019). "Peatland dwellers: The hidden world." Pint of Science 2019, London, Ontario, Canada. [45 minute presentation to the general public]

Lyons, C.L., Lindo, Z. (2019). "Boreal peatlands: Characterized in terms of both above and belowground components and the impacts of climate warming on plant communities." EnviroCon 2019, London, Ontario, Canada. [Standard talk]

Lyons, C.L., Lindo, Z. (2018). "Plant community shifts in Boreal peatlands after two years of passive warming." Biology Graduate Research Forum (BGRF), London, Ontario, Canada. [Standard talk]

Lyons, C.L., Lindo, Z. (2018). "Climate warming and plant community shifts in Boreal peatlands." Ontario Ecology, Ethology, and Evolution Colloquium (OE3C), London, Ontario, Canada. [Lightning talk]

Work Experiences

2017 - 2016 Assistant Forestry Technician
Ministry of Natural Resources and Forestry
Ontario Forest Research Institute, Sault Ste. Marie, Ontario, Canada

2016 - 2013 Eco-House Programme Facilitator & Environmental Science Cluster Leader, University of Guelph Residence Life, Guelph, Ontario, Canada

2015	Summer Research Assistant Agriculture and Agri-Food Canada Indian Head Research Farm, Indian Head, Saskatchewan, Canada
2014	Environmental Research Assistant Environment and Climate Change Canada Canada Centre for Inland Waters, Burlington, Ontario, Canada
2014	Assistant Global Atmospheric Watch Lab Operator Environment and Climate Change Canada Global Atmospheric Watch observatory, Alert, Nunavut, Canada