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## Peatland Plant-soil Feedbacks Dictate Ecosystem Properties and Processes

Julia E. Palozzi, *The University of Western Ontario*

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

A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology

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## Abstract

Interactions between plants and soil are increasingly recognised as drivers of ecosystems through dictating ecosystem properties and processes. My thesis explores the linkage between aboveground and belowground in Boreal peatlands, where soil (i.e., peat) is partially decomposed plant material, thus presenting opportunity for strong plant-soil relationships to arise. In an observational study, I show feedbacks between chemical plant traits (e.g., leaf N) of the dominant ecosystem engineer (*Sphagnum* moss or *Carex* sedge) and peat environment drive slow or fast cycles to regulate aboveground plant growth and belowground peat properties such as pH, moisture and nutrients, in two contrasting peatland types. In a field experiment, I show pure and mixed litters of dominant peatland plants (*Sphagnum* and *Carex*) decompose more quickly in their site of origin, consistent with a home-field advantage. Peatland plant-soil feedbacks shape ecosystem properties and decompositional processes, collectively dictating ecosystem function, such as nutrient cycling and carbon storage.

## Keywords

Boreal peatlands, *Carex* sedge, ecosystem engineering, home-field advantage, litter quality, plant ecological strategy, plant functional traits, plant-soil interaction, *Sphagnum* moss

## Co-Authorship Statement

The role of plant-soil feedbacks in shaping ecosystem properties (e.g. plant community, soil environment) and processes (e.g. decomposition rates) in boreal peatlands were studied by Julia Palozzi under the supervision of Dr. Zoë Lindo. Manuscripts arising from this work were prepared (synthesis and writing) by both Julia Palozzi and Dr. Zoë Lindo, and two manuscripts corresponding to Chapters 2 and 3, respectively have been submitted:

Palozzi, J.E. and Lindo, Z. Boreal peat properties link to plant functional traits of ecosystem engineers. In revision for *Plant and Soil*. (PLSO-S-16-02110)

Palozzi, J.E. and Lindo, Z. Pure and mixed litters of *Sphagnum* and *Carex* exhibit a home-field advantage in Boreal peatlands. Submitted to *Soil Biology and Biochemistry*. (SBB-2017-103)

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## Chapter 1

### 1 Introduction

#### 1.1 Plant-soil interactions

Plant-soil interactions influence ecosystem properties and processes, collectively driving ecosystem functioning. Plants can shape biotic and abiotic soil properties through exerting physical, chemical and biological influences on the belowground (soil) environment. For instance, approximately 90% of all terrestrial aboveground carbon finds its way to the belowground system (Meier & Bowman, 2008) mostly through leaf litter inputs, such that the chemical composition of leaf litters are a major driver of soil organic matter properties. Differences in the chemical and nutrient status of leaf litter (litter quality) can affect soil pH (Finzi *et al.*, 1998) and nutrient availability (Aert *et al.*, 1999), which in turn can affect microbial community composition (Wardle *et al.*, 2004; Bezemer *et al.*, 2006). Belowground, the structure and activity of the microbial and other soil communities ultimately control rates of decomposition and nutrient cycling (Bardgett & van der Putten, 2014; Van Nuland *et al.*, 2016). Thus, plant-induced changes to soil systems can, in turn, indirectly influence aboveground plant performance (van der Putten *et al.*, 2013; 2016); these plant-soil feedbacks can be either positive, creating beneficial conditions for certain plant species, or negative, with adverse effects on certain species. Most plant-soil feedbacks are reported as negative among different species (van der Putten *et al.*, 2013) promoting species co-existence (Bever, 2003). Less prevalent, positive feedbacks can promote species dominance (Klironomos, 2002), which is particularly evident in plants considered to be ecosystem engineers—dominant organisms that create and modify their habitats (*sensu* Jones *et al.*, 1994).

There is growing consensus that plant-soil feedbacks are key in shaping ecosystem properties (Bardgett *et al.*, 2005; Kardol *et al.*, 2013) such as plant community composition (De Deyn *et al.*, 2004; Reinhart *et al.*, 2012), microbial community structure (de Vries *et al.*, 2012), and soil properties such as moisture and pH (Ehrenfeld *et al.*, 2005). Changes in ecosystem properties due to plant-soil feedbacks can have cascading

effects on the rates of ecosystem process (Bardgett *et al.*, 2005) such as decomposition (Wardle *et al.*, 2012; van der Putten, 2013; Van Nuland *et al.*, 2016), nutrient cycling (Jassey *et al.*, 2013), productivity, and succession (De Deyn *et al.*, 2003). However, even though a large body of literature points to plant-soil feedbacks as drivers of ecosystem properties, a mechanistic understanding of how plant communities affect belowground systems is lacking.

## 1.2 A trait-based approach to linking plant and soil

While plant-soil feedbacks present a conceptual framework in which plant-soil interactions can be evaluated (van der Putten *et al.*, 2013), linkages between plant and soil have been quantified and investigated mechanistically using a plant functional trait approach (Baxendale *et al.*, 2014; Kardol *et al.*, 2015). Plant functional traits are heritable characteristics that influence plant growth, reproduction or survival (*sensu* Garnier *et al.*, 2016) and are increasingly being used as tools to help understand plant community structure (Dolédec *et al.*, 1996) and ecosystem functioning at various levels of spatial and biological organization (Shipley *et al.*, 2016). Plant functional traits have been linked to both soil properties and plant growth, providing a solid platform for studying plant-soil feedbacks at a general level (Baxendale *et al.*, 2014).

Plant traits are typically measured at the individual plant level, but are often realised at the community-level. For instance, plant-specific leaf traits may dictate physiological processes of nutrient and energy acquisition, which in turn may govern how fast that leaf decomposes (Orwin *et al.*, 2010). However, community-weighted means (CWM) of plant traits such as leaf nitrogen (N), relative growth rate, or leaf dry matter content can explain ecosystem-level variation in processes such as rates of litter decomposition (Garnier *et al.*, 2004) and patterns in soil microbial communities (de Vries *et al.*, 2012). Community-weighted means account for the relative abundance of different species in a community and their trait value (Garnier *et al.*, 2004) as suggested by the biomass ratio hypothesis (Grime, 1998), which postulates that the most dominant species proportionally have the greatest effect on ecosystem function.

### 1.3 Plant life history strategies relate to ecosystem-level processes

Variations in plant functional traits reflect adaptations to their physical environment, which often include trade-offs among different plant functions and life history strategies (Westoby & Wright, 2006; Lavorel *et al.*, 2007; Bardgett *et al.*, 2014; Garnier *et al.*, 2016). Plant strategy typically represents plant functional characteristics that perform well in some environments and poorly in others, but exist roughly along a spectrum of competitive, reproductive or resource-management (survival) traits (Grime, 1974; 1977). Thus plant strategy exists along a continuum of fast-growing, nutrient-demanding, but stress-intolerant species versus slow-growing, nutrient-conserving and stress-tolerant species. For instance, competitive ability of plants, such as sedges, have been correlated with tall height and fast growth (Keddy *et al.*, 1998) enabling efficient capture and utilisation of resources such as light, water, nutrients or space, although these traits are not well suited for stressful or disturbed habitats (Grime, 1974). Conversely, plants that have traits such as being short in stature, low relative growth rates, and typically long-lived (Wright *et al.*, 2004), can endure stress such as nutrient limitations, shading and drought (Grime, 1974). Mosses are an example of stress-tolerant species that often inhabit nutrient-poor environments (Grime, 1990).

At the individual plant level, differences in traits among species often relate to plant strategy. Perhaps most notable are the trade-offs between growth potential and leaf construction costs (investment) (Díaz *et al.*, 2016) that relate to a strategy of resource acquisition or conservation (Reich, 2014), and dictate carbon (C), nutrient and water management of stems, roots and leaves. Resource-acquisitive plant species are typically short-lived, tall, fast-growing and possess resource-rich (C, N, P) leaves that are easily decomposable (labile) for soil microbes. At the other end of the spectrum resource-conservers are typically shorter, slower-growing, and long-lived with nutrient-poor tissues (Wright *et al.*, 2004; Reich, 2014), creating litter that is hard to decompose or break down (recalcitrant) by soil microbes. Species ecological strategy has been consistently correlated with litter decomposability, providing insights to plant-soil

feedbacks that drive carbon cycling (Cornwell *et al.*, 2008). For instance, de Vries *et al.* (2012) found resource-conservative traits associated with slow growing species to be linked to soil fungal-based energy channels reflective of slow nutrient cycling, and resource-acquisitive traits aimed at fast growth were linked with bacterial-based energy channels and faster nutrient cycling. Therefore, plant strategy can play an important role in ecosystem processes.

## 1.4 Plant traits and decomposition processes

Plant leaf and functional trait combinations relating to the resource economics spectrum (e.g., growth rates, leaf N, height) are widely used as indicators of litter quality, that dictate how readily decomposable plant litter is by soil microbes. Absolute litter quality is quantified using physical (e.g., leaf toughness) and chemical (e.g., secondary metabolites) traits (Pérez-Harguindeguy *et al.*, 2000), but is also related to plant growth and leaf construction that can be governed by environmental nutrient status.

Traditionally, litter decomposition is regulated by climate (temperature and moisture), quality and quantity of plant litter, and type and abundance of the microbial community (Couteaux *et al.*, 1995), although the importance of each factor varies with spatial scale (García-Palacios *et al.*, 2016). The notions that litter quality (Cornwell *et al.*, 2008) and soil microbes (van der Heijden *et al.*, 2008) independently control decomposition rates at local scales are challenged by a relatively recent ecological theory called the home-field advantage, which posits that plants are more efficiently decomposed (broken down) in their native versus a foreign environment due to specific decomposer-litter relationships (Hunt *et al.*, 1988; Gholz *et al.*, 2000; Keiser *et al.*, 2014). Microbial adaptation to the most prevalent plant litter is a hypothesis proposed to explain decomposition results in a number of home-field advantage studies (Vivanco & Austin, 2008; Ayres *et al.*, 2009) but fails to corroborate results of others (St. John *et al.*, 2011; Veen *et al.*, 2015), highlighting the need for a more comprehensive understanding of decomposition dynamics at local scales.

## 1.5 Boreal peatlands as a relevant system

Growing evidence points to plant-soil linkages as drivers of ecosystem functioning (e.g., nutrient cycling) in many systems, yet none other would be more apparent than in Boreal peatlands, where plants leave a legacy in partially decomposed plant material as peat. Partial decomposition of plant material is due to cool temperatures and waterlogged, anoxic and acidic soil conditions compounded by nutrient-poor plant material (Moore *et al.*, 2007). Due to the slow decomposition of plants, Boreal peatlands are key players in global carbon dynamics storing one-third of the world's soil C in only 2 to 3% of Earth's land surface (Gorham, 1991). Peatland types (e.g. nutrient-rich, intermediate and poor fens to bogs) are classified by gradients of moisture, nutrients and pH, and characteristic aboveground and belowground dominant species (Rydin & Jeglum, 2013), making Boreal peatlands an ideal system to compare ecosystem states and identify potential mechanisms generating and/or explaining ecosystem properties and processes. Moreover, Boreal peatland plant communities are expected to shift under climate change conditions (Buttler *et al.*, 2015; Dieleman *et al.*, 2015, 2016) underscoring the need for a deeper understanding of peatland plant community dynamics and their role in driving plant-soil feedbacks. Although a significant research effort has been put forth to study the importance of plant community composition for ecosystem processes in peatlands (Ward *et al.*, 2009; Buttler *et al.*, 2015; Dieleman *et al.*, 2015; Potvin *et al.*, 2015; Robroek *et al.*, 2015; Ward *et al.*, 2015), studying plant-soil interactions and feedbacks from a functional trait perspective has not been extensively done, providing a novel opportunity.

## 1.6 Thesis rationale and objectives

To investigate the role of plant-soil feedbacks in driving peatland properties, I studied plant communities, plant functional traits, and soil properties across two fen peatlands differing in nutrient content, hydrology, and dominant plant functional type to link peat properties to plant functional traits in the context of ecosystem engineering (Chapter 2). Following, I performed a reciprocal transplant litter decomposition experiment to examine how plant-soil feedbacks control ecosystem processes such as decomposition in the context of the home-field advantage (Chapter 3). In both chapters I consider the plant

strategy framework, specifically the ‘fast-slow’ spectrum indicating litter quality, to study plant-soil linkages and gain a mechanistic understanding of plant responses and effects on ecosystem-level processes. My specific objectives were to:

- 1) Quantify the relationships between peatland plant species abundance, plant functional traits and peat variables at two contrasting peatland (fen) sites using multivariate ordination techniques in an observational study.
- 2) Test for the home-field advantage using two dominant peatland plants (*Sphagnum* moss and *Carex* sedge) in two peatland types differing in nutrient status in a field experiment.

In the observational study (Chapter 2), I investigated how plant traits are related to belowground peat properties in two peatland types differing in nutrient status. I assessed aboveground plant community composition (richness and abundance), collected and analysed leaves for aboveground plant traits, and collected peat to quantify peat environments. I used spectroscopy techniques to identify organochemical compounds in the peat, and multivariate ordinations to quantify relationships among species-traits-environment and to compare compositional similarity. I used plant strategy (litter quality and chemistry) to mechanistically explain the engineering of peat conditions by the ecosystem engineers: *Sphagnum* and *Carex*. In the field experiment (Chapter 3), I measured the decomposition rates (mass loss) of two dominant peatland plants to test for specific plant-soil relationships known as the home-field advantage. This field experiment was performed using pure and mixed plant litters of *Sphagnum*-moss and *Carex*-sedge. I also measured aboveground (temperature and relative humidity) and belowground (pH, moisture, available N, microbial biomass) environmental conditions pertinent to decomposition. I used a set of equations that quantifies the home-field advantage, allowing me to separate differences in mass loss attributed to litter or site quality. I discussed mechanisms to explain the home-field advantage results of pure and mixed litters. In Chapter 4, I discussed how results from my studies provided evidence for plant-soil feedbacks in dictating peatland properties (fen conditions) and processes (decomposition dynamics). I also discussed potential caveats of my work, and concluded



by suggesting avenues of further research that would enhance our understanding of plant-soil feedbacks based on my results.

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## Chapter 2

# 2 Boreal peat properties link to plant functional traits of ecosystem engineers

## 2.1 Introduction

Understanding the structure and composition of plant communities (Cornwell & Ackerly, 2009), and identifying mechanisms affecting variation in species distribution (Klironomos, 2002), are major goals in community ecology (McGill *et al.*, 2006). Plant community composition results from a series of abiotic and biotic filters (Garnier *et al.*, 2016), where plant strategy (*sensu* Grime, 1977) is put into a context of physiological tolerances and ecological trade-offs (Westoby & Wright, 2006). However, an often overlooked mechanism of community structure is the presence of certain organisms exerting a strong influence on the distribution of other species and the environment through ecosystem engineering. Ecosystem engineers are organisms that directly or indirectly influence the flow of resources for other species, and in doing so, modify, create and maintain habitats (*sensu* Jones *et al.*, 1994). While all organisms to some degree engineer their environment (Wright & Jones, 2006), some species strongly affect community organization and species abundance through environmental feedbacks that facilitate their own dominance and govern local scale patterns of species richness (Jones *et al.*, 1997).

Plant ecosystem engineers generally modify their ecosystem by altering local abiotic factors, creating strong feedbacks between the aboveground plant community and the belowground soil environment that favour their own expansion. In doing so these ecosystem engineers can modify many core ecosystem properties, including soil moisture and pH, as well as nutrient availability. For instance, fast growing plants with high nutrient demands tend to produce nutrient-rich, labile litter that facilitates faster decomposition, and increases soil nutrient availability, while slow growing plants with low nutrient demands tend to produce nutrient-poor, recalcitrant, litter that facilitates

slower nutrient cycling and reduces soil nutrient availability (Reich, 2014). These life history trade-offs have more recently been placed within a trait-based approach to examining ecosystem engineering (Bouma *et al.*, 2012; Emery & Rudgers, 2014). Plant functional traits are any heritable physiological, morphological or phenological characteristic that influence fitness through plant growth, reproduction, or survival (*sensu* Garnier *et al.*, 2016). Plant functional traits can be used to understand plant community structure (Dolédéc *et al.*, 1996), and can predict ecosystem functioning for a wide range of environments at various levels of spatial and biological organization (Shipley *et al.*, 2016). Investigating plant functional traits is seen as a robust method to determine how plant composition, and the associated diversity among traits, can reveal underlying ecosystem-level processes attributed to ecosystem engineers (Petchey & Gaston, 2002).

Understanding the role of plant functional traits, and the relationship between aboveground vegetation and belowground soil variables, is especially important in Boreal peatlands, where *Sphagnum* moss has long been thought of as an ecosystem engineer (van Breeman, 1995). *Sphagnum* is a key peat-forming bryophyte in Boreal ecosystems. Slow growing and producing nutrient-poor litter, *Sphagnum* mosses facilitate large accumulations of peat that are important carbon sinks (van Breemen, 1995). However, recent field (Buttler *et al.*, 2015) and laboratory (Dieleman *et al.*, 2015) experiments have demonstrated that *Sphagnum*-dominated peatlands can shift towards sedge-dominated communities under future climate change conditions. Graminoid species (including sedges of the genus *Carex*) have not traditionally been considered ecosystem engineers (but see Crain & Bertness, 2005); however, the distributions of both *Sphagnum* and *Carex* species are related to resource gradients (e.g. soil moisture, soil pH, nutrient availability) that largely affect the peat accumulation of the dominant peatland plant functional type (Rydin & Jeglum, 2013). Thus, both *Sphagnum*-moss spp. and *Carex*-sedge spp. may be considered ecosystem engineers as they are both linked to abiotic changes related to the chemical composition of living and dead plant material (Belyea & Clymo, 2001; Crain & Bertness, 2005).

Despite the growing popularity of utilizing plant functional traits in deciphering ecosystem engineering, the trait-based approach has not addressed engineering in Boreal



peatlands where *Sphagnum* and *Carex* traits drive a tug-of-war over peatland moisture, pH and nutrients levels that ultimately dictate peat accumulation and therefore carbon storage. In a mechanistically-based observational study I quantified vegetation community composition, plant functional traits, and peat-soil variables to elucidate engineering mechanisms driving plant community structure and carbon storage in two contrasting peatland sites differing in resource status and dominant plant growth form. Specifically, I use peat spectral organochemical properties and a series of statistical ordination techniques to explore the link between plant traits and peat quality, and explain how different plants can be linked to ecosystem level processes, such as decomposition and nutrient cycling.

## 2.2 Materials & Methods

### 2.2.1 Study site

The study was performed in a Boreal peatland complex approximately 40 km southwest of White River, Ontario, Canada (48°21'N, 84°20'W) in August 2015. The study sites are a nutrient-poor and an intermediate nutrient fen, located 2 km apart, which are a part of a long-term research-monitoring project established by the Ontario Ministry of Natural Resources and Forestry. For brevity these sites will be hence referred to as the 'poor fen' and the 'intermediate fen', respectively. Maps of the site can be found in Appendix A. The region experiences a mean annual temperature of 2.1°C and a mean annual precipitation of 980 mm (see McLaughlin & Webster (2010) for a full site description). The intermediate fen (10.2 ha) is mostly open, delineated by coniferous forest with two main tributaries running along the northern and southwestern edges. The poor fen (4.5 ha) contains forested and partially treed areas, and is bounded by boreal forest and a lentic lake.

Prior to this study a full vegetation survey had not been performed. However, as established here, the intermediate fen area is dominated by *Carex* sedges (*C. oligosperma* Michx., *C. stricta* Lam.) and ericaceous shrubs such as sweet gale (*Myrica gale* L.), and leatherleaf (*Chamaedaphne calyculata* (L.) Moench) with sporadic patches of *Sphagnum*

moss as the main type of bryophyte. The dominant vegetation of the poor fen includes *Sphagnum* moss (*S. magellanicum* Brid., *S. angustifolium* (C.E.O. Jensen ex Russow) C.E.O. Jensen, and *S. fuscum* (Schimp.) Klinggr., with lesser amounts of *S. centrale* C.E.O. Jensen, and *S. fallax* (Klinggr.) Klinggr.). Trees and shrubs at the poor fen include black spruce (*Picea mariana* (Mill.) B.S.P.), tamarack (*Larix laricina* (Du Roi) K. Koch), leatherleaf, and bog Labrador tea (*Rhododendron groenlandicum* Oeder), with low densities of lowbush blueberry (*Vaccinium angustifolium* Aiton), Canadian blueberry (*Vaccinium myrtilloides* Michx) and sweet gale. Ground cover other than *Sphagnum* includes stiff clubmoss (*Lycopodium annotinum* L.), small cranberry (*Vaccinium oxycoccos* L.), creeping snowberry (*Gaultheria hispidula* (L.) Muhl. ex Bigelow), and low densities of *C. disperma* Dewey.

## 2.2.2 Sampling design

Five 1×1 m plots were randomly selected from representative 25×25 m areas in both the poor and intermediate fens. Within each site, the minimum distance between plots was 1 m, and the maximum distance between plots was 20 m. Vegetation surveys were performed in each 1×1 m plot to assess species richness as well as each species' percent cover. Plant species were identified in the field using Legasy (1995) and Newmaster *et al.* (1997). Species percent cover was measured using an adapted Braun-Blanquet scale by a single observer as recommended by Rochefort *et al.* (2013). Alongside plant species composition, ten aboveground functional trait measurements were made using material collected from each species in every 1×1 m plot in accordance with Pérez-Harguindeguy *et al.* (2013). Surface peat samples (20×20×25 cm) were collected alongside plant community and trait data from the north-facing side of each plot to assess 19 environmental variables.

To quantify functional traits three upper, photosynthetically active leaves were collected from each vascular species, while whole moss shoots were collected from *Sphagnum* mosses. Total plant height was also determined in the field at the time of leaf collection. The collected leaf and moss samples were then stored in plastic bags and kept cool and moist until further processing. In the lab, specific leaf area (SLA), wet and dry leaf

weight, leaf thickness index, leaf area, leaf mass per area, as well as leaf C and N content were determined. Specific leaf area is defined as the one-sided leaf area (cm<sup>2</sup>) divided by dry weight (g) and was determined by a digitally scanning the three leaves collected from each species at each plot and calculating area using the Image J program (v1.49; Rasband, 2016). In the cases of mosses, photosynthetically active whole shoots were used as the functional analogue of a leaf as done by Bond-Lamberty & Gower (2007). Wet leaf weights were obtained before scanning and leaves were subsequently dried for 48 hours at 60°C to calculate the leaf dry matter content (LDMC), which represents the dry weight (mg) divided by the wet weight (g). Leaf thickness index was calculated as the inverse of  $SLA \times LDMC$  (Vile *et al.*, 2005). Leaf area and leaf mass were obtained as plant traits after calculating SLA, and leaf mass per area (LMA) was calculated as the inverse of SLA (Wright *et al.*, 2002).

Total C and N leaf concentrations were measured for 14 species using a combustion autoanalyser (vario MAX CN, Elementar) with glutamic acid as calibrant and birch leaf as the quality control. The same dried leaf samples that were used to determine SLA were ground using an electric grinder prior to analysis; however, species were pooled by site to obtain the minimum 0.2 g material required for analysis. Carbon-to-nitrogen ratios (C:N) were calculated using the total C and N values and treated as a separate plant functional trait.

Intact peat monolith samples were collected manually using a key-hole saw, wrapped in aluminum foil and kept in a 4 °C fridge until processed. Litter biomass was determined by collecting senesced vegetation from the surface of each peat monolith and weighing it after drying (48 h at 60 °C). A 5×5×5 cm subsample of peat was extracted from the centre of each peat monolith for coarse root biomass (>2 mm diameter); roots were washed from surrounding peat matrix and oven dried at 60 °C for 48 h. Gravimetric moisture content was determined from another 5×5×5 cm of subsampled peat dried at 60 °C for 72 h using the formula:

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

The same peat samples were further dried at 105°C for 24 h before determining organic matter (carbon) content via loss-on-ignition (LOI) at 550°C for 8 h (Chambers *et al.*, 2011) using the equation:

$$\text{Organic matter content (\%)} = (\text{dry weight}_{105^\circ\text{C}} - \text{dry weight}_{550^\circ\text{C}}) \times 100.$$

The pH of peat samples was determined using 2 g dry weight equivalent of fresh peat in 11 mL of distilled water using a calibrated glass probe, after stirring occasionally for one hour. The filtrate of the pH sample was used to determine electrical conductance (EC) following vacuum filtration using Whatman #42 filters, and measured using a glass electrode. Available nutrients ( $\text{PO}_4^{-3}$ ,  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) were extracted from each peat sample by shaking 5 g dry weight equivalent of peat in 40 mL of 2 N potassium chloride (KCl) to liberate nitrate and ammonium, or 40 mL Bray's Solution (dilute  $\text{NH}_4\text{F}$  in HCl) for 1 hour to liberate phosphate, followed by filtration through Whatman GF/A filter paper. Available  $\text{PO}_4^{-3}$  was analysed using the fluoride colourimetric method, while available  $\text{NH}_4^+$  was measured by the indophenol-blue method and  $\text{NO}_3^-$  was measured by the hydrazine method using a Technicon AA3 autoanalyzer.

Heterotrophic (basal) respiration was determined for 35 g wet weight subsample of peat with a Licor multiplexer Infrared Gas Autoanalyzer (IRGA LI-8100A and Multiplexer unit LI-8150) in 250 ml Mason jars with approximately 2 cm headspace. The quantified  $\text{CO}_2$  flux values are expressed as mL  $\text{CO}_2$  / g dry weight / h. Following basal respiration measurements, substrate-induced respiration was performed in order to calculate microbial biomass. Samples were amended with 10 mg glucose and respiration was measured for an additional 12 hours. Microbial biomass (mg  $\text{CO}_2\text{-C}$  / g dwt) was calculated according to Anderson and Domsch (1978) based on the lowest respiration rate (flux- $\text{CO}_2$ ) prior to the commencement of microbial growth:

$$\text{Microbial biomass C} = 40.4 \times \text{flux-}\text{CO}_2 + 0.37.$$

Metabolic quotient ( $q\text{CO}_2$ ) was calculated as the basal respiration-to-biomass ratio. In doing so I quantified the amount of  $\text{CO}_2$  produced per unit microbial biomass C as a measure of microbial carbon resource use efficiency.

To determine decomposition rates of *Carex* and *Sphagnum* litters between poor and intermediate fen sites, mass loss was measured in the field over one year. *Sphagnum* and *Carex* litters were collected from both poor and intermediate fen sites and treated as separate litter types (2 plant types  $\times$  2 sites). Senesced plant material was air dried for two weeks, and used to create 40 litterbags containing 1 g dry weight equivalent litter in a 9 $\times$ 10 cm litterbag with a mesh size of 1 mm. Eight litter bags of each plant type were placed on the peat surface of the 1 $\times$ 1 m sample plot (2 subsamples at each corner) (2 plant types  $\times$  2 sites  $\times$  5 plots  $\times$  8 litterbags = 80 litterbags). Total mass loss (%) was calculated after one year.

Lastly, Fourier transform infrared spectroscopy (FTIR) was performed on a 5 g dry weight equivalent subsample of the surface peat to characterise the organic chemical functional groups present in the peat. Fourier transform infrared spectroscopy identifies chemical compounds in peat through the use of the vibrational characteristics of structural chemical bonds (Artz *et al.*, 2008), and can distinguish between carbohydrates, lignins, cellulose, fats, lipids and waxes. Generally, it is used as an indicator of organic matter quality or decompositional processes and the development of peat organic materials (Artz *et al.*, 2008; Broder *et al.*, 2012). Each subsample was extracted from an undisturbed section of the sampled peat monolith. Subsamples were freeze-dried and ground with an electric grinder prior to analysis. The FTIR spectra of 0.5 g homogenised peat sample were recorded using a Tensor 27 series (Bruker Optics Ltd, Milton, Ontario) equipped with a Golden Gate ATR sample loading system (Specac Inc., NJ, USA). Spectra were acquired by taking the average of 200 scans at 4 cm<sup>-1</sup> resolution over the wavenumber range of 500-4000 cm<sup>-1</sup> (Table 2.1). To compare FTIR spectral differences in poor and intermediate fen peat, means and 95% confidence intervals of the absorption intensities were calculated for all wavenumbers. To compare decomposability of the different peats, humification indices were calculated from FTIR spectral data using ratios of absorption intensities of aromatic, aliphatic, carboxylic acid and phenolic moieties to polysaccharides, which reflect source plant material and decomposability through the relative proportions of complex substances to easily degradable compounds (Broder *et al.*, 2012). Each ratio was calculated at the plot level first, and then averaged to obtain a site-level humification index.

**Table 2.1 Organochemical spectral properties of poor and intermediate fen peat.**

Mean ( $\pm$  SE) absorbance intensities and assigned absorbance bands for organochemical compounds in poor and intermediate fen peat identified using Fourier transform infrared spectroscopy. One-way ANOVA was used to test for differences between site means.

Wave Number (cm <sup>-1</sup> )	Chemical	Intermediate Fen Average ( $\pm$ SE)	Poor Fen Average ( $\pm$ SE)	$F_{(1,8)}$	$P$
720	Long chain alkanes	0.001 (0.0002)	0.0050 (0.0027)	12.2	<b>0.008</b>
835	Lignin	0.004 (0.0005)	0.0050 (0.0029)	0.651	0.443
1030	Polysaccharides	0.092 (0.0022)	0.089 (0.0068)	0.639	0.447
1265	Lignin	0.027 (0.0029)	0.028 (0.0025)	0.122	0.736
1371	Phenolic (lignin) and aliphatics	0.027 (0.0036)	0.029 (0.0020)	0.351	0.570
1426	Humic acids (caryboxylate/carboxylic structures)	0.027 (0.0034)	0.024 (0.0020)	0.511	0.495
1450	Phenolic (lignin) and aliphatics	0.027 (0.0031)	0.020 (0.0019)	3.91	0.083
1475	Wax	0.020 (0.0024)	0.011 (0.0017)	12.6	<b>0.007</b>
1515	Lignin-like/phenolic structures	0.033 (0.0034)	0.017 (0.0022)	20.1	<b>0.002</b>
1550	Proteinaceous compounds	0.033 (0.0041)	0.015 (0.0024)	19.1	<b>0.002</b>
1650	Aromatics	0.046 (0.0046)	0.029 (0.0029)	14.0	<b>0.006</b>
1708	Free organic acids	0.022 (0.0021)	0.027 (0.0020)	4.31	0.068
1720	Carboxylic acids, aromatic esters	0.021 (0.0021)	0.028 (0.0019)	10.8	<b>0.011</b>
2850	Fats, wax, lipids	0.035 (0.0023)	0.041 (0.0022)	7.27	<b>0.027</b>
2920	Fats, wax, lipids	0.041 (0.0023)	0.050 (0.0033)	9.53	<b>0.015</b>
3340	Cellulose	0.054 (0.0019)	0.083 (0.0041)	125.5	<b>&lt;0.000</b>
<b>Humification indices</b>					
1515/1030	Phenolic index	0.36 (0.045)	0.19 (0.008)	14.74	<b>0.005</b>
1650/1030	Aromatic index	0.55 (0.066)	0.36 (0.016)	7.82	<b>0.023</b>
1720/1030	Carboxylic acid index	0.23 (0.026)	0.32 (0.004)	11.47	<b>0.010</b>
2920/1030	Lipid index	0.46 (0.035)	0.57 (0.028)	5.56	<b>0.046</b>

Note: significant p-values ( $p \leq 0.05$ ) are bolded; N=5.

Absorption peaks indicative of structural units in organic matter were used as indicators of peat organic matter quality and identified according to Niemeyer *et al.* (1992).

### 2.2.3 Data analyses

Plant community data were assessed for species richness (S), percent cover as sample abundances ( $N_0$ ), Shannon's entropy (H), Shannon's diversity index ( $N_1$ ) and Pielou's evenness (J) for each plot using the vegan package in R (version 3.1.2; R Development Core Team). Plant trait data were used to calculate functional diversity indices (i.e. functional richness, evenness, divergence, dispersion, Rao's quadratic entropy) using the dbFD command in the FD package (Laliberté & Legendre, 2010), to characterise the diversity of species traits among sampled plots. See Garnier *et al.* (2016) for full a description of indices used. Community weighted means (CWM) for each trait were also calculated for each plot using:

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

Where  $CWM_{\text{trait}}$  is the CWM for trait  $x$ ,  $p_i$  is the percent cover of species  $i$  in the community, and  $x_i$  is the trait value for the species  $i$ . One-way analysis of variance (ANOVA) was used to characterise and quantify the difference in mean values of plant, trait and peat-soil variables between these two specific fen sites. For the decomposition litterbags, I used a two-way ANOVA to examine the main and interactive effects of decomposition rate between poor and intermediate fens sites, as well as between *Sphagnum* and *Carex* plant litters. These statistical analyses of variables were used to quantify the comparisons between the two sites studied.

To examine how poor and intermediate fen sites were structured with respect to plant composition, and the composition of species traits, and peat soil conditions, separate Bray-Curtis percent similarity matrices were constructed for plant community composition (27 species total), peat-soil variables, and plant species functional trait composition using the vegdist function in the vegan package of R. Dissimilarities were visualised using the metaMDS function to compute non-metric multidimensional scaling

(NMDS) ordination plots, and quantified using the `adonis` function to perform PERMANOVA. Simper analyses were also used to determine the contribution of individual species, peat variables or traits to the respective overall Bray-Curtis dissimilarity using the `sim` command in the `vegan` package (Clarke, 1993). The standard use of NMDS is to create a two-dimensional representation of species composition, where each data point represents the composition of species at a certain sampling location (i.e. plot). Data points that group close together on the NMDS represent plots that are more similar in species composition than data points that are further apart. For our peat-soil and CWM trait values, the NMDS plots were similar, in that each data point represented the composition (environmental or trait, respectively) of each plot. However, in addition to these ordinations, I performed NMDS with PERMANOVA as described above using a trait  $\times$  species matrix. In this ordination, trait composition uses species rather than sites, and the output presented becomes a representation of trait composition for each species. Thus data points that cluster close together represent species that have similar trait compositions, while data points that are further apart, represent species that differ in trait composition. Prior to analysis, species were assigned dominance to fen type (binary poor or intermediate fen) based on the total abundance of that species at each site, with the criteria of at least 51% overall abundance in one site or another.

Lastly, I used the co-inertia analysis RLQ (R-mode Linked to Q-mode) to relate characteristics of plant traits to the characteristics of the environment (Dolédec *et al.*, 1996); using three data matrices: species  $\times$  plot (L), plant trait  $\times$  species (Q), and environmental variables  $\times$  plot (R). Relative percent cover of the species and their associated traits used in RLQ analysis can be found in Appendices B and C, respectively. Initial correspondence analysis (CA) was performed on the species  $\times$  plot data, while principle components analysis (PCA) was performed on the plant trait  $\times$  species, and environmental variables  $\times$  plot data. Subsequently both environmental (R matrix) and trait (Q matrix) ordinations were constrained with species (L matrix) scores for the RLQ analysis using the `dudi.pca` command, and RLQ analysis was carried out with the `rlq` command in `ade4`, a support package for `vegan` (Dray & Dufour, 2007).

RLQ is thus performed via a double inertia analysis of two arrays (R and Q) with a link



expressed by the contingency table (L), where the rows of L (sites) corresponded to the rows of R (sites) and the columns of L (species) corresponded to the rows of Q (species) (Dray & Dufour, 2007). Permutation tests (Monte Carlo,  $n=999$ ) were performed to test whether sites (model 2), species (model 4), and sites and species (model 5) scores could be explained by trait-environment relationships using the `randtest` function. The final RLQ product is presented as a three-way plot in which species-trait-environment relationships are interpreted by correlating the spatial location of objects in the co-created plots. Subsequent fourth-corner analysis was performed to test the strength of the pairwise relationships between environmental conditions and plant traits using Dray & Legendre's (2008) two-step approach which combines results of 1000 permutations of model 2 and 4 to obtain significance (Sterk *et al.*, 2013). All calculations were completed using the `ade4` package (Dray & Dufour, 2007).

## 2.3 Results

### 2.3.1 Comparison of site characteristics

The average species richness ( $\pm$  SE) was 2.5 times greater in the nutrient poor fen ( $15.2 \pm 1.2$  species/m<sup>2</sup>) compared to the intermediate nutrient fen site ( $6.0 \pm 1.1$  species/m<sup>2</sup>) ( $F_{1,8} = 36.2$ ,  $P < 0.001$ ). The sum of percent cover of vegetation for all species at a plot was not different between sites (poor =  $218.4 \pm 18.5\%$ ; intermediate =  $182.3 \pm 20.7\%$ ) ( $F_{1,8} = 1.69$ ,  $P = 0.23$ ). See Appendix D for a summary of plant community diversity descriptors. Several peat-soil properties differed between the poor and intermediate fen sites (Table 2.2); the intermediate fen had characteristically higher pH, root biomass, metabolic quotient, and total available N than the poor fen, while the poor fen site had greater vegetative biomass, moisture, and organic matter. Electrical conductivity, available phosphate, and microbial biomass did not differ between the sites (Table 2.2).

**Table 2.2 Plot and peat-soil variables of the poor and intermediate fen.**

Summary of peat-soil environmental (plot) conditions (average  $\pm$  SE) of the nutrient-poor and intermediate nutrient fen sites located near White River, Ontario. One-way ANOVA was used to test for differences between site means.

Variable	Intermediate Fen Average ( $\pm$ SE)	Poor Fen Average ( $\pm$ SE)	$F_{(1,8)}$	$P$
Vegetation biomass (g)	0.5 (0.2)	5.0 (1.6)	8.18	<b>0.021</b>
Litter biomass (g)	3.7 (1.8)	2.1 (0.7)	0.72	0.420
Root biomass (g/cm <sup>3</sup> )	7.4 (1.6)	2.6 (0.5)	8.96	<b>0.017</b>
pH (in dH <sub>2</sub> O)	5.4 (0.0)	4.8 (0.1)	64.27	<b>&lt;0.001</b>
EC (dS/m)	73.2 (6.2)	80.5 (2.9)	1.12	0.320
Moisture content (%)	87.8 (0.4)	90.1 (0.9)	6.37	<b>0.036</b>
Organic matter (%)	83.7 (3.6)	97.8 (0.3)	15.00	<b>0.005</b>
Basal respiration (mL CO <sub>2</sub> /g dry weight/h)	0.1 (0.0)	0.1 (0.0)	1.99	0.196
Microbial biomass (mg CO <sub>2</sub> -C/g dry weight)	3.2 (0.4)	5.0 (0.7)	4.67	0.063
Metabolic quotient	0.02 (0.0)	0.01 (0.0)	22.40	<b>0.002</b>
PO <sub>4</sub> <sup>-3</sup> (mg/L)	1.2 (0.5)	4.4 (1.9)	2.76	0.136
NO <sub>3</sub> <sup>-</sup> (mg/L)	0.2 (0.1)	0.1 (0.0)	11.00	<b>0.011</b>
NH <sub>4</sub> <sup>+</sup> (mg/L)	0.1 (0.1)	0.00 (0.0)	1.69	0.230

Note: significant p-values ( $p \leq 0.05$ ) are bolded; N=5.

In terms of decomposability of litters and decomposition rates at each site, I found both significant and interactive effects of plant litter type and fen site, where *Carex* litter lost roughly 2.75 times greater mass over one year than *Sphagnum* litter ( $F_{1,36} = 620$ ,  $P < 0.001$ ), and the intermediate fen had significantly faster decomposition rates than the poor fen ( $F_{1,36} = 10.25$ ,  $P = 0.003$ ), but the site trend was significant only for *Carex* litter ( $F_{1,36} = 27.804$ ,  $P < 0.001$ ). Average mass loss for the different litters was as follows: poor fen *Sphagnum* = 24.0% ( $\pm 1.3$ ); intermediate fen *Sphagnum* = 20.6% ( $\pm 1.5$ ); poor fen *Carex* = 55.5% ( $\pm 2.1$ ); intermediate fen *Carex* = 69.1% ( $\pm 1.4$ ).

In terms of plant functional trait CWMs, the intermediate fen had 3-fold greater height, and 1.5-fold greater leaf dry matter content (LDMC) than the poor fen (Table 2.3). The poor fen trended towards having greater specific leaf area (SLA), leaf mass per area (LMA), leaf C and C:N content, and had 2-fold greater leaf thickness than the intermediate fen (Table 2.3). Considering the functional diversity indices, the intermediate fen had significantly greater functional richness and evenness, while the poor fen had significantly greater functional divergence and Rao's quadratic entropy, and trended towards having higher functional dispersion (Table 2.4).

The FTIR spectra varied between the two fen types, but both fens displayed absorption bands typical of humic substances (Fig. 2.1, Table 2.1). Peat from the poor fen had a significantly greater proportion of cellulose (wave number  $3340\text{ cm}^{-1}$ ), aliphatic structures ( $2920\text{ cm}^{-1}$  and  $2850\text{ cm}^{-1}$ ), carboxylic acids ( $1720\text{ cm}^{-1}$ ), and long chain alkanes of aromatic structures ( $720\text{ cm}^{-1}$ ). The intermediate fen peat scored higher for aromatics ( $1650\text{ cm}^{-1}$ ), lignin-like and phenolic structures ( $1515\text{ cm}^{-1}$ ) and alkyl groups at  $1475\text{ cm}^{-1}$  representing plant wax. Both polysaccharides ( $1030\text{ cm}^{-1}$ ) and humic acids ( $1426\text{ cm}^{-1}$ ), enhancers of decomposition rates and indicators of humification, respectively, did not differ between the fens. For the humification indices, the poor fen had greater aliphatic lipids and carboxylic acid moieties than the intermediate fen, while the intermediate fen had greater aromatic and phenolic index values (Table 2.1).

**Table 2.3 Plant functional traits of the poor and intermediate fen.**

Community weighted means (average  $\pm$  SE) of plant functional traits collected from vegetation surveys performed at poor and intermediate nutrient fen sites near White River Ontario, Canada. One-way ANOVA was used to test for differences between site means.

Trait	Intermediate Fen Average ( $\pm$ SE)	Poor Fen Average ( $\pm$ SE)	$F_{(1,8)}$	$P$
Height (cm)	72.0 (0.79)	21.5 (4.2)	141.30	<b>&lt;0.001</b>
Leaf area (cm)	10.1 (0.95)	6.7 (1.2)	4.79	0.060
Leaf mass (g)	0.0890 (0.006)	0.046 (0.002)	39.67	<b>&lt;0.001</b>
SLA (cm <sup>2</sup> /g)	128.2 (1.24)	135.8 (19.5)	0.15	0.710
LMA (g/cm <sup>2</sup> )	0.008 (0.000)	0.010 (0.001)	2.76	0.135
LDMC (mg/g)	530.4 (43.0)	331.6 (51.1)	8.85	<b>0.018</b>
Leaf thickness index	1.56e <sup>-5</sup> (1.5e <sup>-6</sup> )	3.56e <sup>-5</sup> (2.4e <sup>-6</sup> )	48.67	<b>&lt;0.001</b>
Leaf C (%)	47.9 (0.51)	49.4 (0.89)	2.09	0.186
Leaf N (%)	1.53 (0.02)	1.45 (0.04)	2.79	0.133
Leaf C:N	32.7 (0.42)	37.4 (2.3)	4.00	0.080

SLA= specific leaf area, LDMC= leaf dry matter content, LMA= leaf mass per area.  
Note: significant p-values ( $p \leq 0.05$ ) are bolded.

**Table 2.4 Functional diversity indices of plant functional traits.**

Mean ( $\pm$  SE) functional diversity indices of plant functional traits measured during vegetation surveys of a nutrient poor and intermediate nutrient fen sites in central Ontario, Canada. One-way ANOVA was used to test for differences between site means.

Functional Diversity Index	Intermediate Fen Average ( $\pm$ SE)	Poor Fen Average ( $\pm$ SE)	$F_{(1,8)}$	$P$
Richness (FRic)	9.4 (1.7)	3.7 (0.8)	8.64	<b>0.019</b>
Evenness (FEve)	0.9 (0.0)	0.5 (0.1)	24.10	<b>0.001</b>
Divergence (FDiv)	0.6 (0.1)	0.9 (0.0)	9.23	<b>0.016</b>
Dispersion (FDis)	1.7 (0.2)	2.4 (0.2)	4.09	0.779
Rao's quadratic entropy (Q)	3.7 (0.5)	6.5 (0.9)	7.69	<b>0.024</b>

FRic = volume of functional space occupied by species in the community

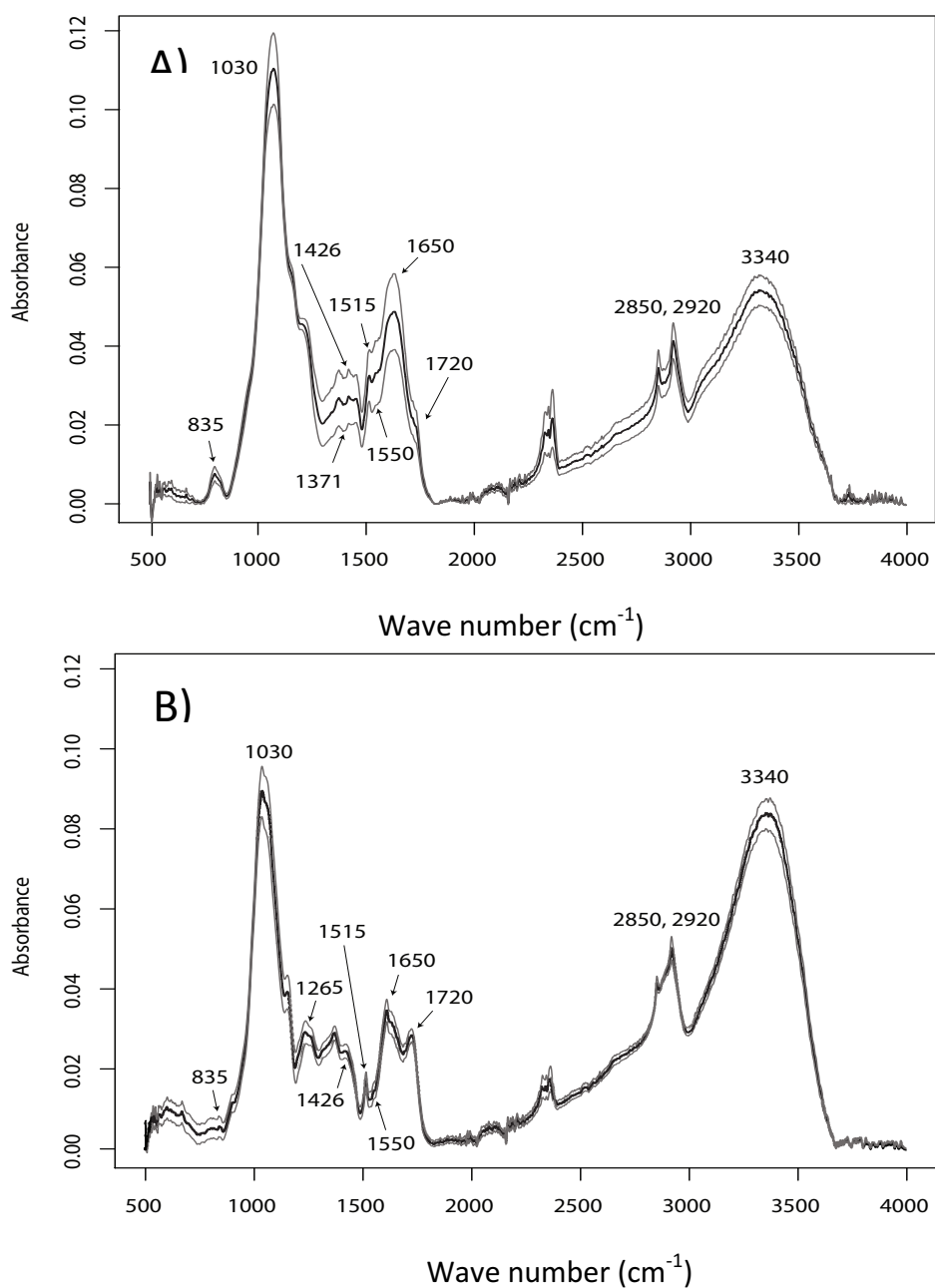
FEve = regularity of the distribution of trait abundances within functional space

FDiv = spread of distribution of trait abundances within functional space

FDis = mean distance of each species and the centroid of all species in the community in multidimensional trait space

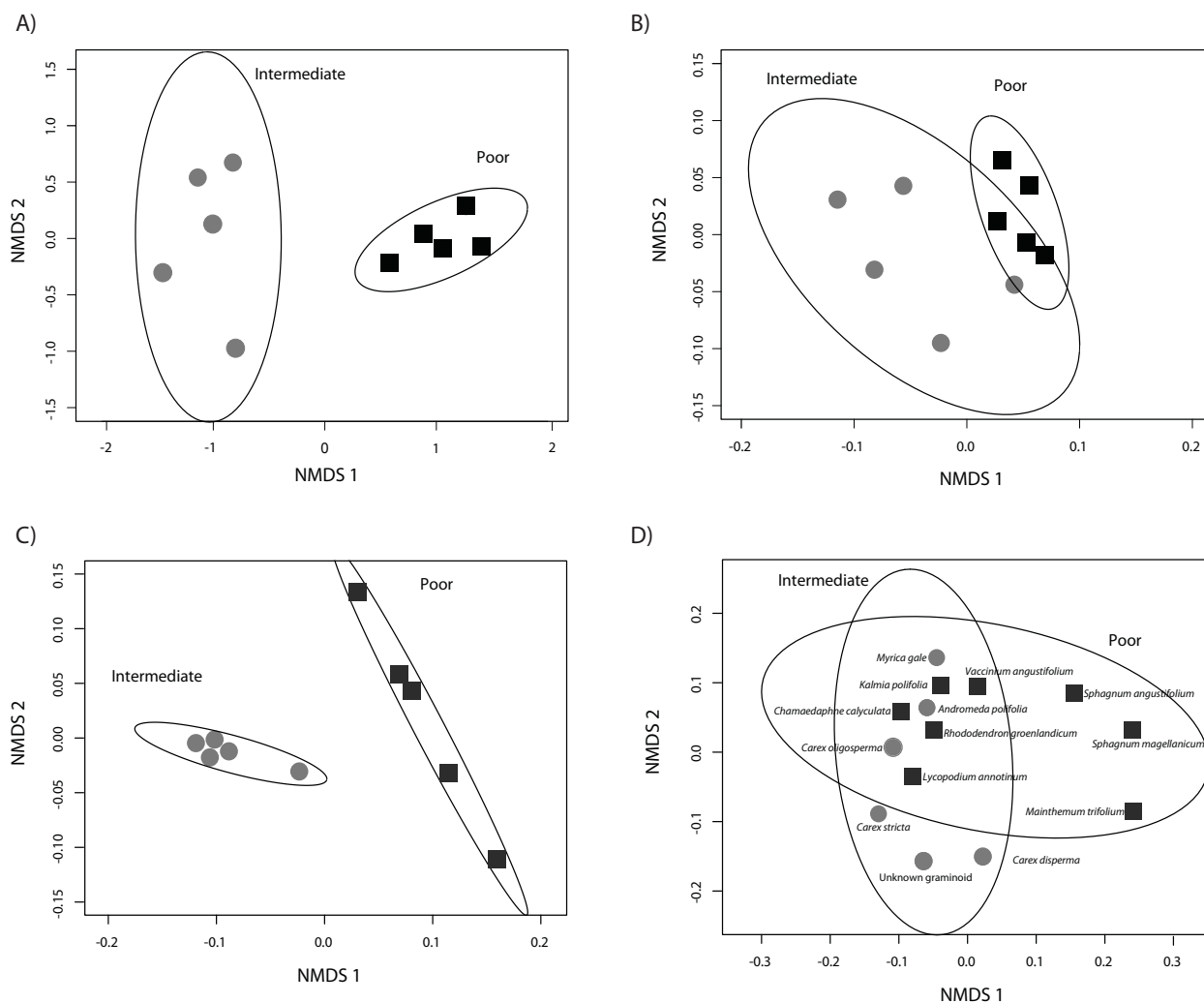
Q = sum of distances between species weighted by relative abundance

Note: significant p-values ( $p \leq 0.05$ ) are bolded.



**Figure 2.1** Organochemical spectral properties of poor and intermediate fen peat.

Organochemical spectral properties ( $\pm 95\%$  confidence intervals) produced by Fourier transform infrared (FTIR) spectroscopy of A) intermediate nutrient fen (N=5) and B) nutrient-poor fen peat (N=5) collected near White River, Ontario, Canada.



**Figure 2.2 Compositional similarities of plant communities, peat properties, plot-level functional traits and species-level functional traits.**

Nonmetric multi-dimensional scaling (NMDS) plots showing compositional similarity of A) plant species composition (N=27) B) environmental (peat-soil) variables (N= 19) C) community-weighted means (N=10) and D) species functional traits (N=14). The poor fen is represented by black squares, the intermediate fen by gray circles, and 95% confidence intervals by the ellipses.

### 2.3.2 Compositional similarity of site characteristics

Plant species community composition was highly dissimilar between poor and intermediate fen sites ( $F_{1,8} = 9.88$ ,  $P = 0.001$ ,  $R^2 = 0.553$ ) (Fig. 2.2a). Simper analysis identified *C. stricta*, *M. gale*, and *C. oligosperma* as predominant species at the intermediate fen, and *Sphagnum magellanicum* and *S. fuscum* at the poor fen generating 67% of the dissimilarity between the two fen plant communities. The peat variables were also different between fen sites ( $F_{1,8} = 5.99$ ,  $P = 0.009$ ,  $R^2 = 0.428$ ), although relatively more similar than the plant community composition (Fig. 2.2b). The Simper analysis determined that 75% of the dissimilarity between the belowground peat conditions was cumulatively explained by organic matter content and electrical conductance.

Examining the functional trait compositions of sampled plots, I also found high dissimilarity and a significant difference between fen types ( $F_{1,8} = 6.29$ ,  $P = 0.008$ ,  $R^2 = 0.440$ ) (Fig. 2.2c). Here, differences in functional trait composition were mainly driven by LDMC and plant height (86% dissimilarity explained). However, when considering functional trait composition of the species, high similarity of trait composition exists for many species found at both fen locations (Fig. 2.2d). For example, the ericoid mycorrhizal shrub *C. calyculata* found in high abundance at the poor fen site and the arbuscular mycorrhizal shrub *M. gale* found in high densities at the intermediate fen are grouped closely together (Fig. 2.2d). This high overlap of many species found at both locations resulted in no significant difference in overall trait composition of plant species between fen sites ( $F_{1,12} = 3.09$ ,  $P = 0.105$ ,  $R^2 = 0.205$ ). However, the species with greatest dissimilarity in trait composition were *Sphagnum* spp. dominating at the poor fen and *Carex* spp. dominating at the intermediate fen site.

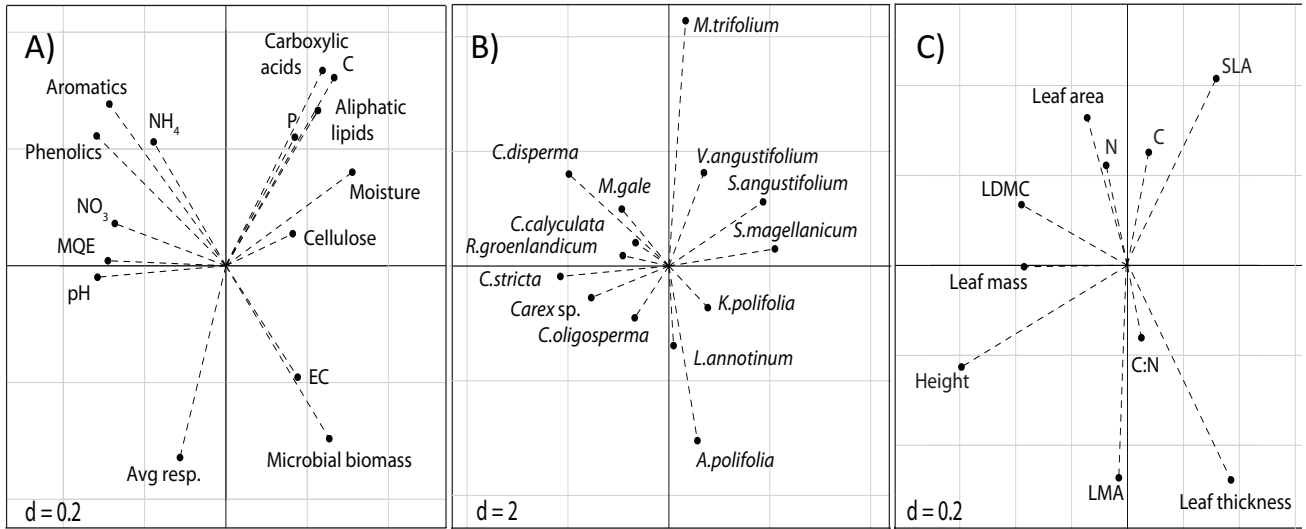
### 2.3.3 Species-trait-environment relationships

The first axes of the RLQ analysis explained 95.8% of the cross-matrix of species traits and environmental variables, separating peat-soil, plant species, and associated plant traits of the two fen types (total inertia = 14.39) (Fig. 2.3). The environmental data (R) axis 1 explained 46% of the variation and axis 2 explained 21% with pH and moisture,



and four organochemical peat properties (aromatics and phenolics vs. carboxylic acids and aliphatic lipids) as main drivers separating the intermediate and poor fens (Fig. 2.3a). The species data (L) was explained with cumulative 74% variation (axis 1: 46%, axis 2: 28%), with axis 1 being driven by *Carex* vs. *Sphagnum* spp. (Fig. 2.3b). For the results of the trait data (Q), axis 1 explained 90% of the trait variation, where height of the dominant vegetation was the main driver (Fig. 2.3c).

Subsequent fourth-corner analysis did not reveal significant pairwise relationships between any particular trait and peat-soil property, likely due to large Bonferroni correction adjusted p-values to account for multiple comparisons (ter Braak *et al.*, 2012). Yet, the Monte Carlo permutations of the variances explained by the RLQ analysis found that differences between sites were explained by trait-environmental relationships ( $P = 0.007$ ). The model in which both species and sites were combined was also explained by trait-environment relationships ( $P = 0.002$ ), but considering species alone, this model was not significant ( $P = 0.141$ ).



**Figure 2.3 Species-trait-environment linkages.**

RLQ triplot showing relationships among A) peat-soil conditions, B) plant species, and C) plant traits. Links can be made between peat variables, plant traits and species by correlating the spatial location of the objects between the plots.

## 2.4 Discussion

In boreal peatlands, plants leave a legacy in partially decomposed plant material as peat. I show that plant traits of two different dominant plant functional types significantly explain much of the peat-soil environment, particularly numerous organochemicals that are indicators of decomposition dynamics. Using FTIR spectra, a dichotomy in peat constituents was observed between the *Sphagnum*-dominated nutrient poor and the *Carex*-dominated intermediate nutrient fen sites, where the intermediate fen had a larger amount of ‘decomposition products’ (e.g., polysaccharides, phenolics) while there was a larger proportion of ‘undecomposed materials’ (e.g. wax, cellulose) in the nutrient-poor fen site. That said, while differences between the two sites were explained by the RLQ relationship between plant traits and peat-soil variables, this trait-mediated environment did not explain overall plant species composition at these sites. This suggests that while the dominant plant species traits exert influence on their environment, feedbacks from the peat environment to plant composition are weak, based off the peat variables I quantified in this study.

Chemical composition of plant litter is important for the rate of litter decomposition and nutrient cycling. Chemical traits of leaves, mainly different nutrients (e.g. N) and carbon compounds (e.g. polysaccharides, phenolics, carboxyl groups) interact directly or indirectly with the biotic and abiotic environment to modulate pH and nutrient levels and drive ecosystem engineering in peatlands. Specifically, I found differences in pH, organic matter and several organochemical properties of the peat that can be directly related to mechanisms underlying peat accumulation (or its inverse, decomposition). It is generally agreed that *Carex* litter decomposes more rapidly than *Sphagnum* litter due to more labile, water-soluble carbon compounds of the respective plant litter (Del Giudice & Lindo, 2017). The mass loss data corroborates faster-decomposing *Carex*, pointing to enhanced nutrient cycling and availability as is consistent with higher available nitrogen in the intermediate fen peat. However, I observed not just faster decomposition rates in the *Carex*-dominated intermediate fen, but also greater utilization of organic materials within the belowground peat system observed through greater microbial carbon use efficiency. Recently, it has also been suggested that faster decomposition in *Carex*-

dominated peatlands may be stimulated through priming effects of low molecular weight phenolics associated with root exudation (Fenner *et al.*, 2007; Dieleman *et al.*, 2016). The high amount of phenolic compounds in peat observed at the intermediate fen site is consistent with high root biomass in the peat, in addition to laboratory studies that correlated high phenolic compound concentrations with vascular plant expansion under experimental climate change scenarios in Boreal peatlands (Robroek *et al.*, 2015; Dieleman *et al.*, 2016). Similarly, Scheffer *et al.* (2001) also observed peatland soluble phenolics ( $\text{mg g}^{-1}$ ) to be 2–12 times greater in litter of *Carex* species than that of *Sphagnum*. The observation of high phenolics coincided with high LDMC as a functional trait in the RLQ analysis, and as LDMC is considered an indicator of leaf ‘toughness’ is likely also linked to the presence of ericaceous shrubs such as sweet gale at the intermediate nutrient fen site. At the same time, LDMC is a trait that can be protective against wind, which is advantageous for *Carex*’s relatively tall height.

While *Sphagnum* litter is typically nutrient poor (Hoorens *et al.* 2002), and litter C:N ratios are thought to be a predictor of long-term decomposition rates for peatland plants (Limpen & Berendse, 2003), only minor differences between community-weighted mean C:N ratios were observed in this study. Rather the poor fen site scored higher in peat constituents for aliphatic lipids, and carboxylic acid groups that can be attributed to the presence of *Sphagnum*. *Sphagnum* cells have a strong lipid coating associated with their cell walls (van Breemen, 1995) and are composed of polysaccharides possessing carboxylic acid groups, which are largely responsible for their acidic nature that facilitates an engineering of acidic environments (Eppinga *et al.*, 2009). Compounds such as sphagnum acid (p-hydroxy-beta-(carboxymethyl)-cinnamic acid) and other phenolics can have a pathogenic effect on bacteria (Hájek *et al.*, 2011) and anti-microbial properties (Verhoeven & Liefveld, 1997), leading to reduced decomposition rates (Verhoeven & Toth, 1995). However, the observed aliphatic lipids, fats and waxes may not be entirely resulting from the dominant *Sphagnum*. Ericaceous shrubs such as leatherleaf, bog rosemary, and bog laurel that were observed at the poor fen site have leaves that are covered with thick epicuticular waxes (Jacquemart, 1998), and may contain a considerable amount of lipids (Pancost *et al.* 2002). The high abundance of pH-lowering

chemical traits of *Sphagnum*, coupled with high proportions of cellulose in the FTIR spectra, point to relatively slower rates of decomposition at the poor fen, slower nutrient cycling, and enhanced C storage.

Spectroscopic techniques are increasingly being used to not only characterise constituents of peat (soil organic matter), but also infer peat forming process and decomposition at the micro-scale (Heller *et al.*, 2015). Belowground, the relative abundances of the chemical compounds identified by FTIR spectroscopy serve as a strong mechanistic link between plant traits (e.g. leaf chemical properties) and ecosystem level processes (e.g. decomposition). Through linking organic chemical properties of peat to plant traits that derive them, I demonstrate how these species drive ecosystem-level rates of decomposition and nutrient cycling. However, it is probable that some ecosystem engineering of the different belowground peat environments is generated through functional traits of the dominant species not measured in this study. For instance, it has long been known that *Sphagnum* possesses physical (morphological, structural and anatomical) traits that contribute to the engineering of wetness, acidic and nutrient levels in peatlands. *Sphagnum* branch and stem morphology mediate water transport upward by wicking water through the spaces between leaves, and branches and stem in the upper *Sphagnum* canopy (acrotelm) (Rydin & Jeglum, 2013), but decrease water flow in subsurface peat when the finely porous tissue of lower *Sphagnum* canopy (catotelm) collapses leading to decreased hydraulic conductivity, anoxic environments and decreased decomposition rates (Belyea & Clymo, 2001). *Sphagnum* has long been purported to acidify peat-soil conditions through acidic polysaccharides within *Sphagnum* cell walls (e.g. uronic acids) (Painter, 1983), which gives *Sphagnum* its high cation exchange capacity and facilitates acidification (Clymo, 1963). Similarly, physical and structural traits of *Carex* are shown to mitigate negative effects of anoxia through litter accumulations that reduces water-logging (Crain & Bertness, 2005) and increases pH (Eppinga *et al.*, 2009), while forming peat of a different nature.

Significant differences in overall peat-soil environments, plant species composition, and plant functional traits, were driven by the dominant plant species, *Sphagnum* spp. and *Carex* spp. Despite low similarity of species composition at poor and intermediate fen

sites there was significant overlap of trait distribution among species, indicating that the same sets of traits are being represented at both fen sites, suggesting that the majority of non-dominant species share similar functional trait values between sites. Yet, impacts of both *Sphagnum* and *Carex* as ecosystem engineers on the plant community become apparent when the fen sites are interpreted from functional perspectives, where both taxonomically and functionally different plant communities dominated by *Carex* spp. or *Sphagnum* spp. were associated with differences in peat environments.

## 2.5 Conclusion

Feedbacks in aboveground-belowground systems are increasingly being recognised as drivers of ecosystem processes (Wardle *et al.*, 2004; Jasse *et al.*, 2013). In both peatland types, aboveground plant traits of the key ecosystem engineer drove properties of the belowground peat environment. Understanding *Sphagnum* and *Carex* as ecosystem engineers of boreal peatlands will enhance our understanding of mechanisms underpinning peatland plant community dynamics. As shifts in peatland plant communities under future climate change conditions are expected, specifically from moss- to sedge-dominated plant communities (Dieleman *et al.*, 2015, 2016), research should focus on the mechanistic link between plant traits (e.g. leaf chemical properties) and ecosystem level processes (e.g. carbon storage) that govern plant-soil feedbacks, as change at the ecosystem level will largely be mediated by key species, such as these ecosystem engineers. Belowground peat organochemical constituents between the *Sphagnum*-dominated nutrient poor and the *Carex*-dominated intermediate nutrient fen sites helped reveal differences in decomposition rates, and thus the potential for carbon storage.

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## Chapter 3

### 3 Home-field decomposition dynamics of *Carex* and *Sphagnum* pure and mixed litters

#### 3.1 Introduction

Decomposition is a key ecosystem process driving carbon (C) and nutrient cycling, with leaf litter providing a main source of C to the belowground system (Hättenschwiler *et al.*, 2005; Meier & Bowman, 2008). Decomposition processes are regulated by the interaction among climate, type and abundance of microbial community, and quality and quantity of plant litter (Coûteaux *et al.*, 1995; García-Palacios *et al.*, 2016). Each regulator is of different importance at various scales; climate is thought to be the predominant regulator at global and ecosystem scales (Aerts, 1997; Zhou *et al.*, 2008), while plant litter quality is thought to control decomposition at regional scales (Cornelissen *et al.*, 1999; Cornwell *et al.*, 2008; García-Palacios *et al.*, 2016). At local scales, there is growing recognition of an intimate interaction between plant litter and decomposer communities regulating decomposition known as the home-field advantage (HFA) (Hunt *et al.*, 1988; Gholz *et al.*, 2000). The home-field advantage theory of decomposition suggests that decomposer communities may be adapted to the plant litter they encounter most often, resulting in plant litter decomposing more quickly in its place of origin (home) versus an alternative location (away), and invoking a positive plant-soil feedback (van der Putten *et al.*, 2013).

The simplicity of the home-field advantage question has prompted many investigations yielding inconsistent results (e.g., Ayres *et al.*, 2009; St. John *et al.*, 2011; Perez *et al.*, 2013), lending to a more complex interaction at play. Several hypotheses have been proposed to explain results of home-field advantage experiments. The traditional litter quality hypothesis sufficiently explains the results of a number of home-field advantage studies (Makkonen *et al.*, 2012; Fanin *et al.*, 2016), while a more conditional hypothesis was put forth by Veen *et al.* (2015) who proposed that home-field advantage is stronger

for recalcitrant litter types or in colder biomes. The home-field advantage has also been linked to the functional breadth hypothesis (Keiser *et al.*, 2011, 2014) to suggest that microbial communities are constrained by the quality of historical resource inputs. As such, microbial communities from recalcitrant litter environments have a wider functional capacity and can degrade a wider variety of litter qualities than microbial communities from labile litter environments that are functionally narrow in their capacity (Strickland *et al.*, 2009a, 2009b). At the root of the functional breadth hypothesis is local adaptation of microbial communities, where variations in the local environment act as selective pressures conferring differential success of species in their ‘home’ versus ‘away’ environment (Rúa *et al.*, 2016), resulting in the most common litter decomposing more quickly at home. While these different hypotheses can explain idiosyncrasies of home-field advantage experiments, a generalised mechanism driving a home-field advantage remains to be determined.

Recent investigations have explored the role of non-additive effects of litter mixtures in decomposition in the context of a home-field advantage (Davidson Jewell *et al.*, 2015; Chomel *et al.*, 2015; Gao *et al.*, 2016). Litter-mixing effects commonly display non-additive interactions (Gartner & Cardon, 2004), where synergistic effects are attributed to nutrient transfer or improved microclimate, while less common inhibiting effects of mixed litter are more enigmatic. Within a home-field advantage context, some studies have found evidence for a home-field advantage in mixed litters (Chomel *et al.*, 2015), while others have found no home-field advantage (Davidson Jewell *et al.*, 2015) or mixed home-field advantage results (Gao *et al.*, 2016), highlighting the need for further research in both mixed litter decomposition dynamics and home-field advantage.

Despite its popularity, the home-field advantage has not been extensively tested in boreal peatlands, where the relationships between aboveground and belowground systems drive ecosystem function such as C storage and nutrient cycling (Jassey *et al.*, 2013). Boreal peatlands are ecosystems where plant growth exceeds decomposition, resulting in plant material accumulating as peat, sequestering vast amounts of carbon (Belyea & Clymo, 2001). Slow decomposition is due to cool and waterlogged soils, and generally poor quality plant litter. Boreal peatlands are typically characterised as being moss- or sedge-

dominated, and distributions of these plant types are related to gradients of peat moisture (Jeglum, 1971), pH (Clymo, 1963) and nutrients (Vitt & Chee, 1990), all factors that also dictate decomposition processes. Recent field (Buttler *et al.*, 2015) and laboratory (Dieleman *et al.*, 2015, 2016) studies have shown that the dominant plant community can switch from moss- to sedge-dominated under climate change conditions, yet the implications of this for ecosystem functioning, such as C storage, are unclear. As sedges are generally more readily decomposed (Scheffer *et al.*, 2001), a plant community switch may accelerate decomposition and potentially affect carbon storage. Taken together, there is a need to understand factors contributing to decomposition in Boreal peatlands, specifically by detecting any specific relationships between plant and decomposers governing the rate of decomposition, such as the home-field advantage.

I performed reciprocal transplant experiments to test for the presence of the home-field advantage using two dominant peatland plant types (*Sphagnum* moss and *Carex* sedge) across two peatlands differing in nutrient status (poor and intermediate fen) for both pure and mixed species litterbags. Aboveground (temperature and relative humidity) and belowground (microbial biomass, available nitrogen, pH, moisture) environmental characteristics pertinent to litter decomposition were measured alongside mass loss of litter. I predicted that decomposition patterns would be a function of site and litter quality as opposed to a home-field advantage, because higher quality *Carex* plant litter is expected to decompose faster than *Sphagnum* litter regardless of location, and that decomposition would also occur more quickly at the site of higher nutrient availability (intermediate fen).

## 3.2 Materials & Methods

### 3.2.1 Site description

The litterbag reciprocal transplants were performed in two boreal peatland sites differing in nutrient status located 40 km southwest of White River, Ontario, Canada (48°21'N, 84°20'W). The nutrient-poor and intermediate-nutrient fens (henceforth 'poor fen' and 'intermediate fen', respectively) are located approximately 2 km apart, and are a part of a

larger peatland complex that comprises a long-term research monitoring project established by the Ontario Ministry of Natural Resources and Forestry (see Appendix A for site maps). A description of site and plant community composition can be found in section 2.2.1.

In August 2015, intact peat monolith samples were collected manually to 35 cm depth for each of five 1×1 m randomly selected plots in both the poor and intermediate fens; monoliths were wrapped in aluminum foil and kept in a 4°C fridge until processed for the following peat-soil variables: organic matter (carbon) content via loss-on-ignition, pH, and available N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) and available P ( $\text{PO}_4^{3-}$ ). Microbial activity, biomass and carbon use efficiency (metabolic quotient ( $\text{qCO}_2$ )) were also assessed via heterotrophic respiration ( $\text{mL CO}_2 / \text{g dry weight} / \text{h}$ ), substrate induced respiration (SIR) ( $\text{mg CO}_2\text{-C} / \text{g dwt}$ ), and as the basal respiration-to-biomass ratio, respectively.

### 3.2.2 Litter decomposition experiment

To test for the home-field advantage of litter decomposition, mass loss was measured in the field after one year using *Sphagnum* and *Carex* litters collected from both poor and intermediate fen sites. Approximately 500 g (wet weight) of *Sphagnum* dominated by *S. magellanicum* and *Carex* dominated by *C. stricta* plant material was collected haphazardly across a broad area in both fens in June 2015. Vegetation was air dried in separate plastic bins (for each plant and fen type) for two weeks, chopped to smaller pieces with scissors and homogenized by hand mixing within the bins once dried. Remaining moisture content (%) was calculated gravimetrically for each plant type from each site by drying three aliquots at 60°C for 48 hours. Moisture content was calculated as:

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

Initial litter quality for each plant type from both sites was assessed for total carbon (TC), total nitrogen (TN) and total sulphur (TS) using 0.2 g ground plant material for TC and TN, and 0.3 g ground plant material for TS. Total C and N were determined in ceramic crucibles loaded into a VarioMax CN analyser (Elementar Americas Inc., NJ, USA),

while TS was analysed using CS-800 autosampler (Eltra Helios, Haan, Germany). Three blanks and five calibrants (arginine) were analysed at the start of each run to ensure the analytes were within detectable limits, and birch leaf was used at the quality control every 20<sup>th</sup> sample. Subsequent measures of C:N, C:S, and N:S ratios as indicators of plant litter quality were calculated from TC, TN, and TS values.

Air-dried litter was used to create six types of litterbags: poor fen *Sphagnum*, intermediate fen *Sphagnum*, poor fen *Carex*, intermediate fen *Carex*, and mixed *Sphagnum* and *Carex* litter from each fen site. I used 1 g dry weight equivalent plant litter (0.5 g each plant type in the mixed litterbags) to construct 120 litterbags (9×10 cm with 1 mm mesh). Each litterbag received a unique aluminum tag identifier to recognise individual litterbags upon retrieval. In August 2015, five 1×1 m plots were randomly selected from a representative 25×25 m section in both the poor and intermediate fens. Each plot received two litterbags of each: *Sphagnum* and *Carex* litterbags from their home site, *Sphagnum* and *Carex* litterbags from the ‘away’ site, and mixed litter (*Sphagnum* and *Carex*) litterbags from both home and away. Litterbags were placed in sets of three on the surface at the four corners of each 1×1 m plot. Environmental plot conditions (temperature and relative humidity) were tracked throughout the year (August 2015 to August 2016) with a HOBO data logger (U23 Pro v2, MA, USA). Each of the ten plots received one data logger. Data loggers were protected with a weather-proof polyethylene cap and placed on the surface in the centre of each plot and measurements were tracked every 30 min. Once the data were downloaded, pivot tables were used to calculate the average: daily temperature, maximum temperature, minimum temperature and relative humidity for each plot. Then, measurements were grouped by month, and site means were obtained and plotted to detect monthly average cycles. It should be noted that a data logger in the intermediate fen failed to track measurements, thus for the poor fen N=5 and intermediate fen N=4.

Litterbags were collected after one year in August 2016. Any green vegetation that had grown through the mesh was picked out at time of collection, and each litterbag was kept in a lightly closed paper bag while travelling back to the laboratory. Upon return, litter from litterbags was carefully removed with forceps and dried at 60°C for 48 hours. Once



dried, litter was weighed, and mass loss was calculated using the equation:

$$\text{Mass loss (\%)} = \frac{\text{weight of litter added (g)} - \text{weight of litter post collection (g)}}{\text{weight of litter added (g)}} \times 100.$$

After drying, litters from mixed litterbags were revisited to determine individual contribution of *Sphagnum* and *Carex* litters to overall mass loss for each mixed litterbag. *Sphagnum* and *Carex* litters were separated and weighed, and species-specific mass loss was calculated to determine the individual mass loss of each species.

### 3.2.3 Statistical analyses

Initial plant litter nutrient content (TC, TN, TS) and litter quality (C:N, N:S, C:S) were evaluated for differences between species, and between collection sites using a factorial MANOVA with plant and site as factors in Statistica (version 7.0) (Statistica, 2004). Significant differences were evaluated for overall MANOVA effects as well as univariate results for each plant litter value. Peat-soil variables were compared using ANOVA. Separate full-factorial ANOVA were performed for mass loss of the pure and mixed litters using a three-way (plant, site, home/away) and two-way (site, home/away) ANOVA, respectively. Individual mass loss of *Sphagnum* and *Carex* litters from the mixed litterbags was analysed with two-way RM-ANOVA with decomposition location (home/away) and fen site as main factors, and plant litter type as a non-independent (spatial) repeating factor. Monthly average of temperature and relative humidity were calculated for each fen site and analysed by one-way RM-ANOVA with site as main factor and monthly average as the repeating factor. Tukey's post-hoc test was performed on all significant results to reveal differences among treatments.

The home-field advantage was calculated separately for each pure litter type, as well as for species-specific litters within mixed litterbags. To quantify the home-field advantage, I used a set of calculations provided by Ayers *et al.* (2009) and used by Veen *et al.* (2015):

$$\text{ADH}_i = \text{HDD}_i - \text{ADD}_i - H$$

$$\text{HDD}_i = \sum (D_{iI} - D_{jI})$$

$$\text{ADD}_i = \sum (D_{iJ} - D_{jJ})$$

$$H = \sum \text{HDD}_i / (n - 1)$$

Where  $\text{ADH}_i$  (additional decomposition at home of species  $i$ ) is the percent mass loss of species  $i$  in its home (environment  $I$ ) relative to away environments;  $\text{HDD}_i$  (home decomposition difference of species  $i$ ) represents mass loss ( $D$ ) of litter type  $i$  at home (environment  $I$ ) relative to other litter types (e.g.  $j$  originating from environment  $J$ ) in away environment  $I$ ;  $\text{ADD}_i$  (away decomposition difference of litter type  $i$ ) represents the difference between mass loss of litter type  $i$  in the away environment  $J$  and mass loss of litter type  $j$  in its home environment  $J$ ;  $D_{iI}$  is the mass loss of litter  $i$  in environment  $I$ ,  $D_{jI}$  is the mass loss of litter  $j$  in environment  $I$ ,  $D_{iJ}$  is mass loss of litter  $i$  in environment  $J$  and  $D_{jJ}$  is mass loss of litter  $j$  in environment  $J$ ;  $H$  is the sum of all  $\text{HDD}_i$ , and  $n$  is the total number of litter types. These equations account for differences in litter and site quality that may lead to absolute differences in mass loss and spurious home-field advantage.

### 3.3 Results

#### 3.3.1 Environmental plot conditions

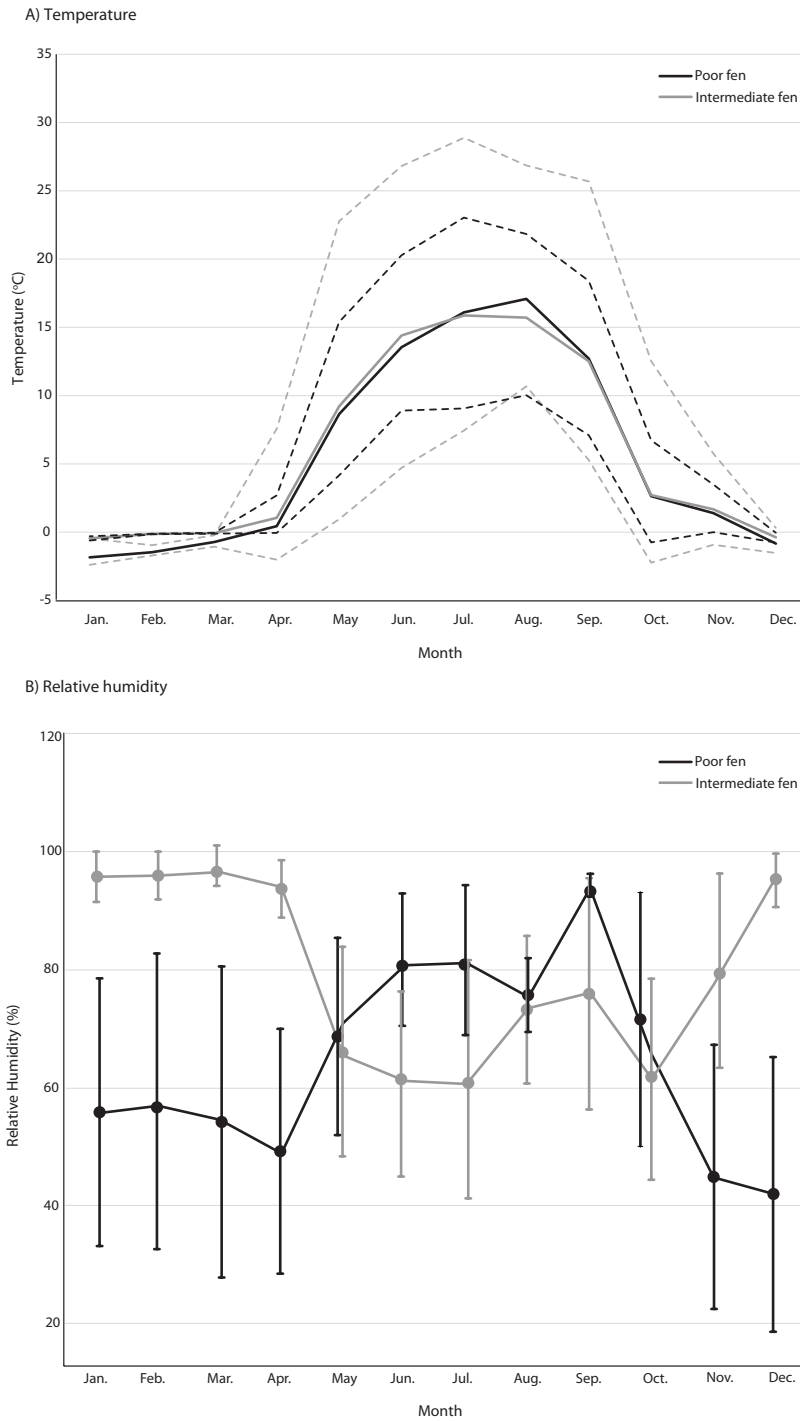
The average daily temperature ( $\pm$  SE) of the growing season (May to August) was similar between the intermediate fen site ( $13.8 \pm 1.6$  °C) and the poor fen ( $13.8 \pm 1.9$  °C) (Fig. 3.1). Both sites experienced similar temperatures throughout the year, although the poor fen site had greater temperature extremes than the intermediate fen, being colder in winter and warmer in summer, resulting in a marginally insignificant site by time interaction ( $F_{11,77} = 1.90$ ,  $P = 0.051$ ). Relative humidity of both sites was similar during the growing season with average ( $\pm$  SE) relative humidity of 77.1% (2.4) in the intermediate and 65.3% (2.9) in the poor fen (Fig. 3.1). Statistically, sites did not differ in relative humidity; however, during the winter (snow-cover) season relative humidity was almost twice as high at the intermediate fen site compared to the poor fen. However, due

to the margin of error associated with plot-level and data logger variability, temperature and relative humidity results are ultimately inconclusive.

In the peat-soil environment, the intermediate fen had higher pH ( $F_{1,8} = 64.27$ ,  $P < 0.001$ ; intermediate =  $5.4 (\pm 0.0 \text{ SE})$ ; poor =  $4.8 (\pm 0.1)$ ), and 2 times higher total available N as  $\text{NO}_3^-$  ( $F_{1,8} = 11.00$ ,  $P = 0.011$ ; intermediate =  $0.2 (\pm 0.1) \text{ mg/l}$ ; poor =  $0.1 (\pm 0.0) \text{ mg/l}$ ) than the poor fen, while the poor fen site had 1.2 times greater organic matter ( $F_{1,8} = 15.00$ ,  $P = 0.005$ ; intermediate =  $83.7 (\pm 3.6) \%$ ; poor =  $97.8\% (\pm 0.3\%)$ ). Microbial carbon use efficiency measured as the metabolic quotient ( $q\text{CO}_2$ ) as an indicator of the amount of  $\text{CO}_2$  produced per unit microbial biomass C, was low at both sites, but 2-fold greater in the intermediate fen (0.02) compared to the poor fen (0.01) ( $F_{1,8} = 22.40$ ,  $P = 0.002$ ).

### 3.3.2 Plant litter quality

Overall chemical composition of litters was significantly different between sites (Wilks = 0.036,  $F_{6,3} = 13.3$ ,  $P = 0.029$ ), plant types (Wilks = 0.001,  $F_{6,3} = 597$ ,  $P < 0.001$ ), and had a significant site-by-plant type interaction (Wilks = 0.014,  $F_{6,3} = 35.2$ ,  $P = 0.007$ ). Based on the univariate results, all plant litters had TC values ranging between 45-47% (Table 3.1), with TC values being 1-fold greater in the poor fen sites ( $P < 0.001$ ) (Table 3.2). However, this difference was significant only for *Sphagnum* (interaction  $P = 0.005$ ). *Carex* had 2-fold greater TN compared to *Sphagnum* litter ( $P < 0.001$ ), and both plant litters had greater TN at the intermediate fen site ( $P < 0.001$ ). Total S was also 2-fold greater in *Carex* litters compared to *Sphagnum* ( $P < 0.001$ ), and was greater at the intermediate fen site ( $P < 0.001$ ), but this difference was only significant for *Carex* (interaction  $P = 0.013$ ). For plant litter quality indices, most were significantly different between plant types and sites; C:N values were 2 to 3 times greater for *Sphagnum* than *Carex* litters ( $P < 0.001$ ), and *Sphagnum* had 1.5 times greater C:N values at the poor fen versus intermediate fen site (site  $P < 0.001$ , interaction  $P < 0.001$ ) but *Carex* did not differ between the sites.



**Figure 3.1 Temperature and relative humidity of the poor and intermediate fen.**

Average A) temperature and B) relative humidity ( $\pm$  SE) of the intermediate nutrient fen (N=4) and nutrient-poor fen plots (N=5) near White River, Ontario. Dashed lines represent maximum and minimum daily average temperatures.

**Table 3.1 Nutrient concentrations (%) of *Sphagnum* and *Carex* plant litters.**

Average ( $\pm$  SE) % nutrient contents of *Sphagnum* and *Carex* litters of the nutrient-poor and intermediate nutrient fen sites located near White River, Ontario.

Nutrient	<i>Sphagnum</i>		<i>Carex</i>	
	Poor	Intermediate	Poor	Intermediate
Total C %	46.4 (0.13) <b>a</b>	45.2 (0.18) <b>c</b>	46.0 (0.03) <b>ab</b>	45.7 (0.07) <b>b</b>
Total N %	0.60 (0.02) <b>d</b>	0.88 (0.03) <b>c</b>	1.60 (0.02) <b>b</b>	1.85 (0.04) <b>a</b>
Total S %	0.07 (0.004) <b>c</b>	0.08 (0.002) <b>c</b>	0.14 (0.001) <b>b</b>	0.16 (0.003) <b>a</b>
C:N	76.9 (2.14) <b>a</b>	51.5 (2.09) <b>b</b>	28.8 (0.45) <b>c</b>	24.6 (0.53) <b>c</b>
C:S	689 (38.1) <b>a</b>	593 (18.7) <b>a</b>	332 (2.8) <b>b</b>	278 (5.5) <b>b</b>
N:S	9.0 (0.62) <b>c</b>	11.5 (0.12) <b>a</b>	11.6 (0.21) <b>a</b>	11.3 (0.20) <b>b</b>

**Note:** Lowercase letters denote Tukey's significance ( $p \leq 0.05$ ) where values followed by same letter are not significantly different; N=3.

**Table 3.2 Plant litter nutrient content MANOVA results.**

Univariate results from the MANOVA test of nutrient contents of *Sphagnum* and *Carex* litters of the nutrient-poor and intermediate nutrient fen sites located near White River, Ontario.

Nutrient Variable	Site		Plant		Site × Plant	
	$F_{1,8}$	$P$	$F_{1,8}$	$P$	$F_{1,8}$	$P$
Total C	43.1	< <b>0.001</b>	0.086	0.777	14.3	<b>0.005</b>
Total N	75.4	< <b>0.001</b>	1039	< <b>0.001</b>	0.101	0.759
Total S	40.3	< <b>0.001</b>	859	< <b>0.001</b>	10.1	<b>0.013</b>
C:N	91.9	< <b>0.001</b>	595	< <b>0.001</b>	47.6	< <b>0.001</b>
C:S	12.2	<b>0.008</b>	244	< <b>0.001</b>	0.965	0.355
N:S	10.7	<b>0.011</b>	11.5	<b>0.010</b>	15.9	<b>0.004</b>

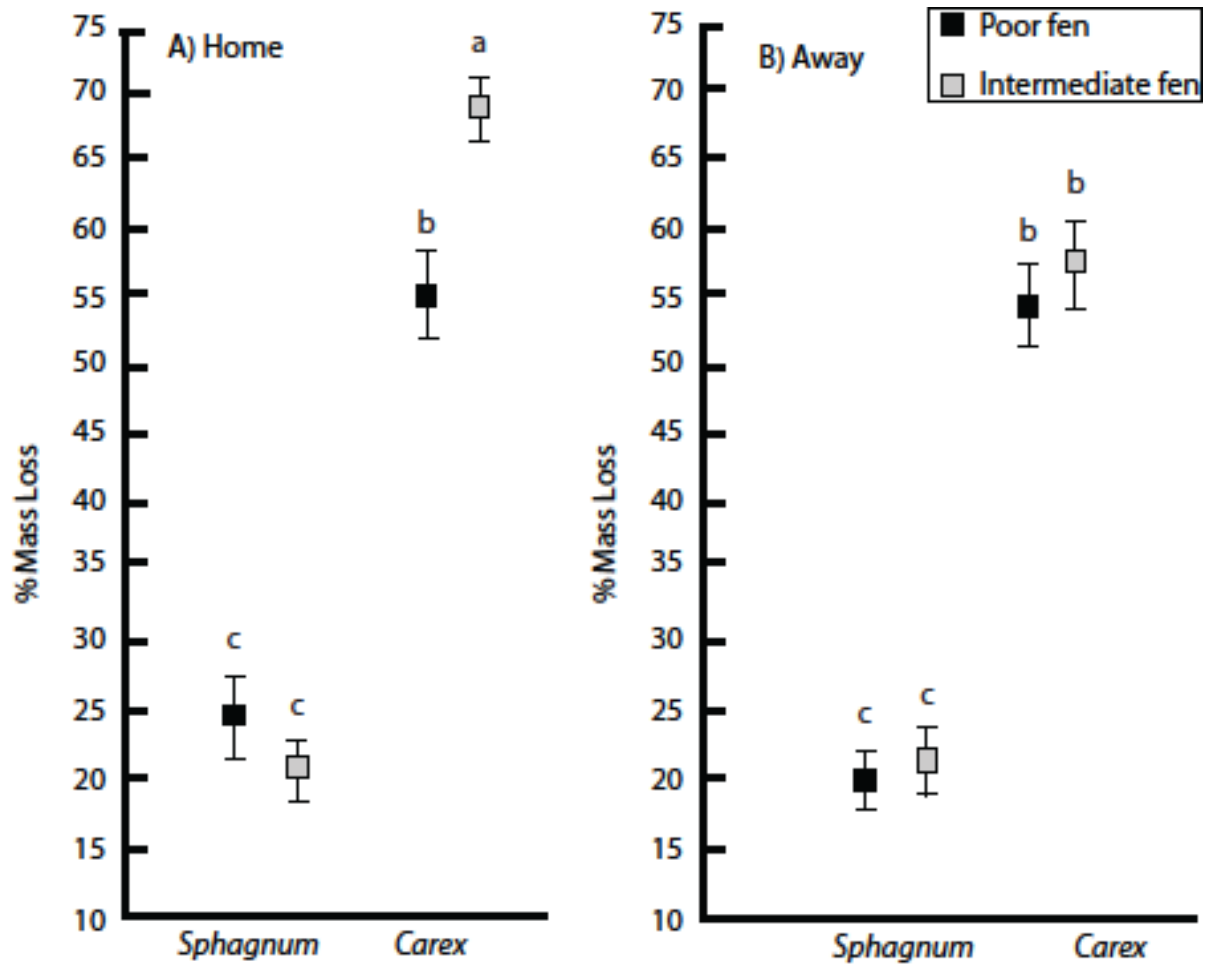
**Note:** Bold values indicate significance ( $p \leq 0.05$ ).

The C:S values were 2-fold greater for *Sphagnum* compared to *Carex* ( $P < 0.001$ ) and 1.2 times greater at the poor fen site for both litter types ( $P = 0.008$ ). Lastly, for N:S values, *Sphagnum* at the poor fen site had the lowest value (interaction  $P = 0.004$ ), driving a significant plant type effect ( $P = 0.010$ ) and site effect ( $P = 0.011$ ).

### 3.3.3 Litter decomposition and the home-field advantage

*Carex* litters lost more mass on average than *Sphagnum* in both the pure (ANOVA  $F_{1,71} = 1253$ ,  $P < 0.001$ ) and mixed litter (RM-ANOVA  $F_{1,36} = 201.2$ ,  $P < 0.001$ ) experiments regardless of litter origin and destination (Fig. 3.2, Fig. 3.3). In the pure litter experiment, *Sphagnum* had no difference in mass loss whether at home or away at either fen site, while *Carex* decomposed more quickly at home in the intermediate fen than at home in the poor fen or away at either site (Fig. 3.2), leading to a significant main effects of decomposition location ( $F_{1,71} = 15.5$ ,  $P < 0.001$ ) and site ( $F_{1,71} = 12.2$ ,  $P < 0.001$ ), and a significant three way interaction between decomposition location, plant litter type and site effect ( $F_{1,71} = 12.6$ ,  $P < 0.001$ ) (Table 3.3).

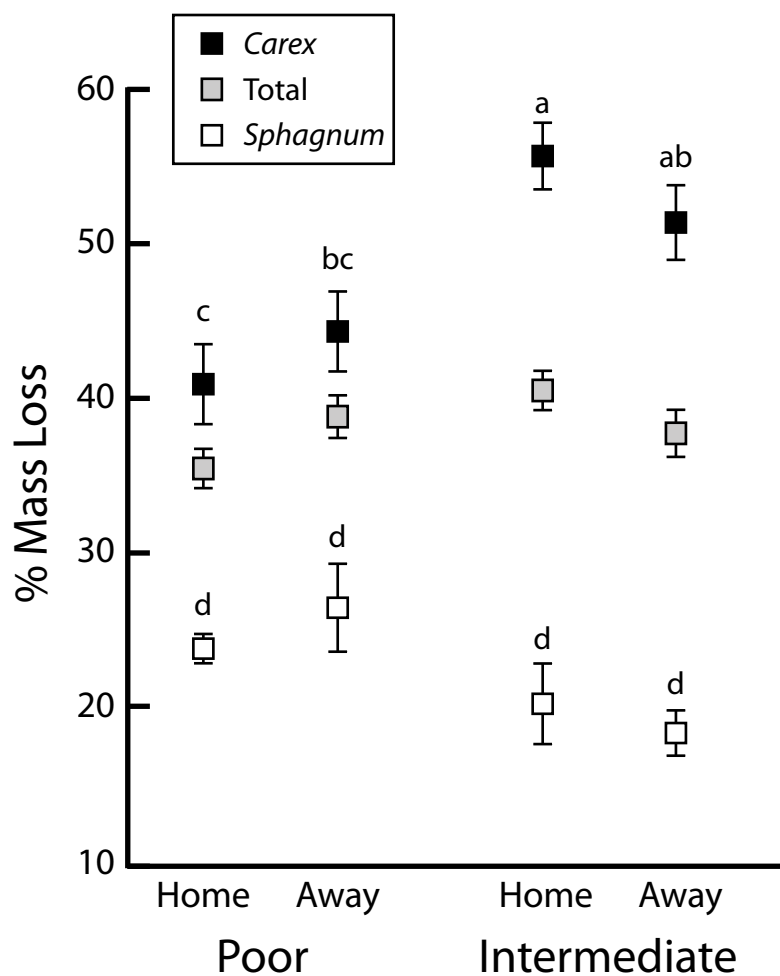
For mixed litters, overall mass loss revealed an interaction between decomposition location and site ( $F_{1,36} = 5.43$ ,  $P = 0.026$ ) (Fig. 3.3), where litters had greater mass loss at home in the intermediate fen, but marginally greater mass loss when placed away at the poor fen. When the *Sphagnum* and *Carex* litters were analysed for their individual mass loss contributions, a similar overall location by site interaction was observed paralleling the total decomposition trends ( $F_{1,36} = 5.16$ ,  $P = 0.029$ ), as well as the differences in mass loss between *Sphagnum* and *Carex* as previously mentioned ( $F_{1,36} = 201.2$ ,  $P < 0.001$ ). However, individual *Sphagnum* and *Carex* litters also demonstrated a plant-by-site interaction where *Sphagnum* had greater mass loss at the poor fen site, while *Carex* had greater mass loss at the intermediate fen site ( $F_{1,36} = 21.2$ ,  $P < 0.0001$ ), such that the overall trend in the mixed litterbags demonstrated that both poor and intermediate fen litters decomposed faster at the intermediate fen site (Fig. 3.3).



**Figure 3.2** Mass loss (%) of *Sphagnum* and *Carex* pure litters.

Mass loss (%) of pure *Sphagnum* and *Carex* litters placed in A) home and B) away locations. Black and grey symbols indicate litters placed at a nutrient-poor fen or nutrient intermediate fen, respectively, near White River, Ontario, Canada. Tukey's post-hoc analysis indicated by lowercase letters, and error bars are standard error, N=10.





**Figure 3.3 Mass loss (%) of *Sphagnum* and *Carex* mixed litters.**

Mass loss (%) of individual *Sphagnum* and *Carex* litters from destructively sampled mixed litterbags. Black symbols indicate litters placed at a home, and grey symbols away, in a peatland complex near White River, Ontario, Canada. Tukey's post-hoc analysis indicated by lowercase letters after performing repeated measures ANOVA, N=10.

**Table 3.3 Summary of main and interactive effects for mass loss of pure litters.**

Summary of interactive effects of the ANOVA results from mass loss rates of *Sphagnum* and *Carex* litter in a home-field advantage decomposition experiment performed in a peatland complex near White River, Ontario.

Interactive Effects	<i>F</i>	<i>P</i>
Decomposition location × Plant × Site	12.6	<b>0.001</b>
Decomposition location × Plant	4.90	<b>0.030</b>
Decomposition location × Site	1.80	0.184
Plant × Site	19.5	<b>&lt;0.000</b>

To calculate the home-field advantage, a series of equations are used to consider and compare the decomposition rate of each plant litter in its home site against all other plant litters at the home site of the litter of interest, and with other plant litter respective home sites (Ayers *et al.*, 2009). The final calculation produces either a positive value suggesting a home-field advantage, or a negative value suggesting greater decomposition at away sites. Both the intermediate *Carex* and the poor fen *Sphagnum* demonstrated strong (positive) home-field advantage in pure and mixed litters (Table 3.4). The poor fen *Carex* and intermediate fen *Sphagnum* had home-field advantage values relatively close to zero in pure litter mixtures, but strongly negative home-field advantage values when present in mixed litterbags (Table 3.4). Mixing of litters increased the positive home-field advantage for poor fen *Sphagnum*, dramatically decreased the home-field advantage for poor fen *Carex* and intermediate fen *Sphagnum*, and had no effect on the intermediate fen *Carex*.

### 3.4 Discussion

Decomposition of plant litter is dictated by three main interacting factors: climate (temperature and moisture), substrate (litter) quality, and biological components of the detrital food web. Consistent with my predictions, *Carex* with higher quality litter (lower C:N) decomposed more quickly than *Sphagnum* across all sites and situations; however, greater mass loss was observed only for *Carex* litters at the site of higher nutrients (intermediate fen). In contrast to my predictions, patterns of decomposition followed a home-field advantage framework. For pure litters, a strong positive home-field advantage for *Carex* at the intermediate fen site was observed, and moderately positive home-field advantage for *Sphagnum* at the poor fen site. This was supported in the absolute mass loss rates, but elucidated, particularly for *Sphagnum*, in the set of home-field advantage equations provided by Ayres *et al.* (2009), which helps account for differences in litter quality and site. Similar results were observed for mixed litters, yet the positive home-field advantage was observed only for the dominant plant species of a particular site (i.e. *Sphagnum* from the poor fen and *Carex* from the intermediate fen).

**Table 3.4 Home-field advantage of pure and mixed plant litters.**

Home-field advantage (HFA) quantified as additional decomposition at home (ADH) of the pure and mixed litter types of *Sphagnum* and *Carex* litters of the nutrient-poor and intermediate nutrient fen sites located near White River, Ontario.

<b>Home litter type</b>	<b>Pure</b>	<b>Mixed</b>	<b>Interaction</b>
Poor fen <i>Sphagnum</i>	12.6	21.19	synergistic
Poor fen <i>Carex</i>	4.08	-26.18	antagonistic
Intermediate fen <i>Sphagnum</i>	-7.2	-23.41	antagonistic
Intermediate fen <i>Carex</i>	29.58	28.62	additive

Interaction summarises the effect of mixed litters on the home-field advantage of a species, where synergistic indicates greater home-field advantage when mixed, while antagonistic indicates less home-field advantage when mixed and additive means no effect.

In mixed litters, the positive home-field advantage for *Carex* from the intermediate fen did not benefit from having *Sphagnum* in the same litterbag, while *Sphagnum* from the poor fen did benefit from having *Carex* in the same litterbag, as seen by an increase in the positive home-field advantage value. In the case where *Sphagnum* and *Carex* were not the dominant vegetation, no home-field advantage was observed for pure litters, while both species displayed strong negative home-field advantage results when in mixed litterbags, indicating an antagonistic mixed litter effect.

The home-field advantage theory invokes plant litters being more readily decomposed by the microbial members of the home environment; thus, a home-field advantage occurs when there is greater mass loss at home. Home-field advantage experiments have revealed that more recalcitrant litter types show stronger home-field advantage (Wallenstein *et al.*, 2013; Gergócs & Hufnagel, 2016) consistent with functional breadth hypothesis (Keiser *et al.*, 2014; Fanin *et al.*, 2016), while other studies have found litter quality to have no effect on the home-field advantage (Veen *et al.*, 2015). While plant traits, such as chemistry and toughness (Pérez-Harguindeguy *et al.*, 2000) that dictate litter quality are recognised as a main controls of decomposition rates at various spatial scales (Cornwell *et al.*, 2008; De Deyn *et al.*, 2008) and may explain up to two-thirds of decomposition rates (Cleveland *et al.*, 2014; Fanin *et al.*, 2016), I observed a home-field advantage regardless of litter quality for the dominant plant species of its respective site.

Carbon-to-nitrogen (C:N) ratios are thought to be a predictor of decomposition rates where a high C:N ratio has been correlated with low decomposition and vice versa (Limpens & Berendse, 2003). Indeed, *Carex* has a lower C:N ratio and higher overall nutrient content than *Sphagnum*, corroborating the high mass loss rates seen in my and other experiments (Scheffer *et al.*, 2001; Del Giudice & Lindo, 2017). In addition, plants grown in more nutrient-rich environments tend to have relatively greater mass loss rates than their nutrient-poor counterparts, suggesting that peat differences between the sites play a role in determining rates of decomposition. Yet this intermediate vs. poor fen dichotomy does not explain differences in the home-field advantage, even considering differences in microclimate (temperature and relative humidity) that also suggested that the intermediate fen should support higher decomposition rates. Taken together, the

positive home-field advantage results for the dominant plant species at each site implies a microbial component to the story.

Microbial studies performed previously at the same White River Experimental Peatland complex found distinct bacterial communities, but less-different fungal communities that had no preferential substrate utilization, which generally discounts the home-field advantage theory for this site (Haynes *et al.*, 2015). However, Haynes *et al.* (2015) also show that peatland decomposition dynamics vary temporally with the highest rates of decomposition for all plant types (sedge and *Sphagnum*) occurring at the beginning of the growing season, coinciding with high rates of microbial activity. These results alongside my field experiment suggest that the functional breadth hypothesis may help explain home-field advantage results, and how *Sphagnum* can decompose more quickly in the lower nutrient site, a trend also observed in another peatland decomposition experiment (Bragazza *et al.*, 2007). They performed a similar litterbag reciprocal transplant study of minerotrophic (high nutrient, groundwater-fed) versus ombrotrophic (nutrient poor, precipitation-fed) sites, and found *Sphagnum* to decompose more quickly at the ‘home’ ombrotrophic peatland and graminoids to decompose more quickly at the ‘home’ minerotrophic peatland, also suggesting microbial adaptability to habitat-specific *Sphagnum* and graminoid litter chemistry.

Current distributions of microorganisms are the result of historical factors, including dispersal and adaptations to local conditions that change over space and time (Fuhrman, 2009). Local adaptation is the differential success of species or genotypes in their native versus foreign environment arising from selective pressures imposed by biotic or abiotic aspects of the local environment (*sensu* Rúa *et al.*, 2016), and is a potential mechanism explaining theories like the home-field advantage. In decomposition studies, Strickland *et al.* (2009a) found that a particular microbial community’s ability to degrade litter was a function of resource use history. Similarly, de Vries *et al.* (2012) has linked resource-conservation plant traits, such as slow growth and low-nutrient litter, and resource-acquisition plant traits like fast growth and high-nutrient litter, to fungal versus bacterial-based energy channels, respectively. This local adaptation and feedback system of ‘slow’ versus ‘fast’ microbial communities in poor and intermediate fen sites, respectively, may

explain the home-field advantage seen for both pure *Carex* and *Sphagnum* litters. However, while resource use history (Strickland *et al.*, 2009a) and functional breadth (Keiser *et al.*, 2011) of peatland microbial communities (Bragazza *et al.*, 2007) correspond to the home-field advantage results of pure litters, it does not tell the whole story when considering litter mixtures.

Mixed litters exhibited strong home-field advantage effects only for dominant plants of the home site (i.e. poor fen *Sphagnum* and intermediate fen *Carex*), similar to the pure litters treatments. Yet, while poor fen *Sphagnum* benefitted from having *Carex* in the same bag, the intermediate fen *Carex* was unaffected by the presence of *Sphagnum*. Further to this, as mentioned above, both litters were negatively affected in mixture when placed in their subdominant ‘home’ environment. These patterns can be explained by considering the nutrient quality of each litter type. *Carex* can lose a significant amount of its original mass purely from leaching (Del Giudice & Lindo, 2017), providing labile sources in dissolved organic carbon for microbes (Scheffer *et al.*, 2001) to fuel decomposition of the more recalcitrant *Sphagnum* (Verhoeven & Toth, 1995) at the nutrient poor fen site increasing the home-field advantage phenomenon. Synergistic interactions such as these observed for nutrient-poor plants in peatlands (Orwin & Ostle, 2012) commonly arise from litter mixing (Chapman *et al.*, 2013) and are accelerated by litter components with higher N contents (Gartner & Cordon, 2004). However, at the same time, *Carex* from the intermediate home site was unaffected by the addition of nutrient poor *Sphagnum* litter.

Conversely, negative home-field advantage effects emerged for species considered rare or subdominant at home (i.e. *Sphagnum* at the intermediate fen and *Carex* at the poor fen) supporting the idea that different litter responses can occur for the same plant types in different environments (Chomel *et al.*, 2015). *Sphagnum* litter is notorious for inhibiting decomposition through secondary compounds (Verhoeven & Livfield, 1997; Bragazza *et al.*, 2007) that may explain antagonistic effects on *Carex* at the poor fen site, while avoidance of *Sphagnum* in the presence of *Carex* at the intermediate fen site might explain the antagonistic effects of litter mixtures for intermediate fen *Sphagnum*. On the whole, these results align with the trend that decomposition of recalcitrant litter types is

accelerated in litter mixtures, while decomposition rates of more rapidly decomposing litters are unaffected (Hättenschwiler *et al.*, 2005). Yet, these results highlight the differential decomposition patterns of mixed litters and show how conventional single-litter decomposition hypotheses, such as functional breadth and litter quality, may not be applicable to litter mixtures.

### 3.5 Conclusion

While local adaptation of the microbial communities to litter quality, and its ramifications (e.g. resulting in greater functional breadth) are a mechanism explaining the home-field advantage of pure litters, litter quality does not adequately explain the home-field advantage results of the mixed litter, highlighting the need for more home-field advantage studies focusing on litter mixtures and to analyse litter types separately. Although the decomposer communities at each site were not quantified, this home-field advantage experiment provides a mechanistic example of how local litter responds to decomposer communities and may act as an important selective force. Accounting for absolute mass loss and detangling mass loss data from the home-field advantage sheds light on aboveground-belowground linkages, permitting a more mechanistic explanation of the home-field advantage. This study is novel because I have two plant types at both sites in differing densities, versus a plant type per each environment, and I show that the dominant plant type loses more mass on average at home versus an away location. If peatland plant communities are to transition to *Carex*-dominated from *Sphagnum*-dominated, I would predict accelerated decomposition rates. However, whether alterations in plant communities and decomposition processes will lead to overall alterations in carbon cycling will likely be dependent on the nature of the aboveground-belowground linkage.

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## Chapter 4

### 4 Discussion

#### 4.1 Traits, litter quality, and decomposition

Physical (e.g. leaf thickness) and chemical (i.e. leaf nutrient concentrations) traits of plant material determine litter quality, a key regulator of decomposition rates at local scales (Cornwell *et al.*, 2008) affecting carbon storage and sequestration (De Deyn *et al.*, 2008). In this thesis I demonstrate how functional traits, in particular chemical attributes, of *Carex* and *Sphagnum* interact with and shape the peat environment (Chapter 2) and drive decomposition rates of their litters (Chapter 3). Specifically, higher nutrient content of litters is known to correlate with faster decomposition rates (Xu *et al.*, 2017). Litter chemistry analysis revealed that *Carex* litter is richer in nutrients (greater N and S) than *Sphagnum* litter, resulting in significantly lower C:N ratios, which typically translate to better quality litter and thus faster decomposition rates (Limpens & Berendse, 2003). Collectively, these results help explain how *Carex* decomposed more quickly than *Sphagnum* regardless of litter origin or destination, with an average mass loss of 55-70% in one year.

Height and leaf dry matter content, both positively correlated with *Carex* spp., were identified as the main traits driving variation in my RLQ analysis that linked plant communities to belowground peat environment variables. While not a direct link to decomposition rates, tall height is indicative of a nutrient-acquisitive strategy aimed at fast-growth and rapid nutrient uptake, in synchronisation with faster decomposition rates. High leaf dry matter content, a measure of toughness, could be a by-product of high nitrogen metabolism, typical for sedges in acidic environments (Choo *et al.*, 2002), or indicate allocation of resources for structural integrity to protect against wind (Pérez-Harguindeguy *et al.*, 2013). In contrast to *Carex*, *Sphagnum* is short, slow-growing, non-vascular and has nutrient-poor tissues, which help explain the low mass loss of 20-24% observed in the field experiment. However, many of *Sphagnum*'s unique traits that facilitate slow decomposition are difficult to measure, yet are well documented in the

literature. For instance, *Sphagnum*'s thin cell walls, with higher proportions of carboxylic acid groups (Painter 1983), facilitates rapid cation exchange (Rydin & Jeglum, 2013) to acidify the environment and slow decomposition (Stalheim *et al.*, 2009). Similarly, recalcitrant tissue with higher polyphenolic content (Verhoeven & Toth, 1995) and to a lesser extent lipids (van Breemen, 1995), also make *Sphagnum* tissue notoriously difficult to decompose. While I did not directly measure these physiochemical properties of *Sphagnum*, these traits became apparent when I examined the peat environment, observing specifically low pH and high carboxylic acid and lipid components in peats that were correlated with *Sphagnum* in the RLQ plots. Other antibiotic properties of *Sphagnum* litter include the release of inhibitory compounds that retard microbial activity (Verhoeven & Livfield, 1997) such as sphagnan, a pectin-like polymer that binds to ammonia rendering it unavailable for microorganisms (Rydin & Jeglum, 2013), which could help explain the slowed decomposition of *Carex* when mixed with *Sphagnum* in the mixed litterbags.

## 4.2 Traits, life history strategy and ecosystem-level feedbacks

A common thread between my two data chapters is the link between plant growth strategy (nutrient acquisition or conservation) and decomposition rates that can feedback to dictate the aboveground plant community and belowground peat properties. Nutrient-acquisitive or conservative strategies manifest as trait combinations indicative of fast growth/decomposition and slow growth/decomposition, respectively (Reich, 2014). *Sphagnum*'s high leaf thickness, short stature and higher C:N ratios (Appendix C) are consistent with a nutrient-conservative ecological strategy for plants that are slow-growing with low nutrient demands, facilitating slow decomposition. Slow decomposition and mineralisation of poor quality plant litter is a feedback that acts to maintain dominance of nutrient-poor species by effectively reducing the competitive ability of nutrient-demanding, fast-growing plants such as *Carex* (Berendse, 1994; Aerts, 1999; Dorrepaal *et al.*, 2007). Conversely, the tall height and higher nutrient litter quality of *Carex* is suggestive of a nutrient-acquisitive ecological strategy characteristic of wetland sedges, driving fast decomposition to release nutrients and support its own fast

growth (Keddy *et al.*, 1998); factors creating a positive feedback to nutrient-availability (Dorrepaal *et al.*, 2007).

Taken together, *Carex* and *Sphagnum* occupy different ends of the ‘fast-slow’ plant economics spectrum (Reich, 2014), resulting in different nutrient dynamics that feedback to ecosystem-level process rates. This aboveground-belowground linkage is apparent in the dichotomy of species, traits and peat variables between poor and intermediate fen sites as demonstrated in the RLQ analyses of Chapter 2. The intermediate fen site possesses ‘fast’ species, traits, and peat environment, indicated by the correlation amongst *Carex*, height and peat properties of higher pH, available N and root biomass. Faster decomposition at the intermediate fen is also supported by the greater proportion of ‘decomposition products’ in the peat identified by FTIR spectroscopy, such as polysaccharides and low molecular weight phenolics, as well as the higher efficiency in utilising C by soil microbes (i.e. microbial metabolic quotient) and faster decomposition of *Carex* at the intermediate fen. At the same time, similar plant-soil linkages can also be made in the poor fen with *Sphagnum* mosses as the dominant plant functional group. *Sphagnum* decomposed slowly in both peat environments reflective of slow nutrient cycling, and demonstrated correlations with low pH, higher peat moisture and organic matter, and the ‘undecomposed materials’ of carboxylic acids, aliphatic lipids, fats and wax, and cellulose, which collectively point to slow decomposition rates at the poor fen site (Brown *et al.*, 1988).

### 4.3 ‘Fast-slow’ cycling and the home-field advantage

The home-field advantage posits that plants are decomposed more efficiently in their home environment. A home-field advantage was observed for the dominant plant at each site (i.e. *Sphagnum* in poor fen, *Carex* in intermediate fen) for both the pure and mixed litters, which has not been documented before. While differences in litter quality and peat environments explain absolute mass loss (decomposition rates), they did not fully explain the observed home-field advantage, suggesting a microbial decomposer component. Unfortunately, a full description of the microbial communities at each site was beyond the scope of this thesis. Previous research on the microbial communities at this same White River peatland complex and similar peatlands from the Hudson’s Bay lowlands



have found similar rates of microbial activity (CO<sub>2</sub> production) across a rich to poor fen gradient (Myers *et al.*, 2012), although a follow-up study by Godin *et al.* (2012) found microbial activity was highly variable seasonally across peatland types when comparing spring and fall. Preston *et al.* (2012) found environmental factors to dictate microbial activity and community structure, while Haynes *et al.* (2015) found substrate quality to be most important to decomposition rate. Taken together, these results suggest more research is needed to connect microbes to decomposition, as it remains hard to gauge controls on microbial decomposition and activity given the mixed results of these studies.

Microbial community structure has been linked to biotic (plant traits) and abiotic (pH, organic matter, C, nutrients) factors (e.g. Orwin *et al.*, 2010; de Vries *et al.*, 2012; Legay *et al.*, 2016) that fit within a ‘fast-slow’ plant ecological strategy framework. Nutrient-conservative plant traits leading to low pH and nutrients, and high organic matter accumulation have been correlated with fungal-dominated communities and slow nutrient cycling, while nutrient-acquisition plant traits leading to high nutrient mineralisation rates have been correlated with bacterial-dominated communities (Orwin *et al.*, 2010; de Vries *et al.*, 2012). Consistent with this is the increasing importance (Haynes *et al.*, 2015), abundance (Orwin *et al.*, 2010) and dominance (Rousk *et al.*, 2010) of fungi in more nutrient-poor, acidic peatland types. These results collectively suggest that the ‘fast-slow’ spectrum may be a general ecosystem (aboveground species and traits, and belowground conditions and communities) property versus just a property of plants.

While the fast-slow spectrum has been linked to process rates in previous studies (e.g. de Vries *et al.*, 2012), it has yet to be fully considered in a home-field advantage context. The home-field advantage is suggested to be a result of specialised decomposer-litter relationships (Wardle *et al.*, 2004) generated by historical resource inputs (Strickland *et al.*, 2009), which over time (Keiser *et al.*, 2011) shape a microbial community’s ability to degrade a certain quality of litter (Keiser *et al.*, 2014). Local adaptation of soil microbes to dominant plant litter could explain why the dominant plants were decomposed more efficiently in their native versus transplanted environments. Through successive rounds of growth and decomposition, decomposer communities may be selected for by the most prevalent plant litter resulting in corresponding ‘slow’ and ‘fast’ soil microbial

communities. Fungi are better suited to decompose more recalcitrant substrates, such as *Sphagnum*, whereas bacteria that dominate in more nutrient-rich peatland types (Myers *et al.*, 2012; Haynes *et al.*, 2015) are more competitive for the higher-nutrient, more labile substrates such as *Carex*. The rate at which plant litters are decomposed correspond to the respective nutrient demands of *Sphagnum* and *Carex*, propagating the plant growth-decomposition feedback. Although my data cannot determine causal links between drivers, microbial adaptation to litter chemistry of most prevalent plant litter has been a mechanism explaining similar reciprocal transplant results in other peatland studies (e.g., Bragazza *et al.*, 2007).

#### 4.4 Boreal peatlands as models for ecosystem feedbacks

Plant litter decomposition is a key ecosystem process controlling nutrient cycling and availability, regulating plant growth. This feedback between plant decomposition and production is especially important in systems with low nutrient input, low plant productivity, and even lower decomposition rates, such as peatlands (Dorrepaal *et al.*, 2007). Boreal peatlands are ideal systems for studying plant-soil feedbacks because the soil is literally the aboveground plant material in a partially decomposed state, presenting opportunity for strong plant-soil relationships to arise. At the same time, recent field (Buttler *et al.*, 2015) and laboratory (Dieleman *et al.*, 2015) studies of warming and elevated CO<sub>2</sub> conditions suggest a rapid shift in Boreal peatland plant community composition. Thus changes in the aboveground plant community are expected to have cascading effects on belowground communities and processes. Previous studies have shown that plant-environment interactions can drive peatland plant community stability (Pedrotti *et al.*, 2014; Dieleman *et al.*, 2015), peat properties (Jassey *et al.*, 2014) and processes related to peat accumulation (Belyea & Clymo, 2001) and decomposition (Bragazza *et al.*, 2015). Here, I have provided evidence that demonstrates the important role of litter quality in plant-soil feedbacks that shape peatland properties (Chapter 2) and processes (Chapter 3) for Boreal peatlands through ecosystem engineering and litter decomposition, respectively. Other peatland studies (e.g. Malmer *et al.*, 1994; Dorrepaal *et al.*, 2007) have found similar positive feedbacks of litter quality that reinforce

differences in nutrient availability enhancing conditions for its own growth, especially with *Sphagnum* and the production of nutrient-poor litter. Plant-soil feedbacks are critical for maintaining the carbon sequestering function of peatland ecosystems (Jassey *et al.*, 2013). Although most plant-soil feedbacks are reported as negative (van der Putten *et al.*, 2013), both ecosystem engineering and the home-field advantage are positive, suggesting that Boreal peatland ecosystems are more unique than initially thought.

## 4.5 Caveats, limitations and future directions

In peatlands, strong conceptual links can be made between species traits and environmental factors, although quantitative links may be more spurious due to problematic measurement of functional traits of contrasting growth forms (graminoid vs. bryophyte). For instance, high specific leaf area (SLA = one sided area/dry mass) is reflective of nutrient-rich habitats yet were taken from *Sphagnum* species, mainly due to its low density (large aboveground shoots and lightweight material). While analysing SLA of *Sphagnum* in this way is suggested (e.g. Bond-Lamberty & Gower, 2007), it poses problems for comparing trait values between highly disparate growth forms. The high SLA values of *Sphagnum* detract from the other traits, statistically masking potentially important trait-species-environment relationships. This highlights the need for plant growth form specific trait analyses, as moss shoots do not necessarily function like leaves of vascular plants (Rice *et al.*, 2008).

Similarly, while my RLQ trait analysis presented a clear dichotomy between the fen species, traits and environments suggestive of ecosystem engineering, the fourth-corner analysis revealed the trait-environment relationships to be insignificant. Some of this may be statistical, as a significant ‘solution’ is generally easier to reach when more species, and fewer traits, are included in RLQ trait analysis (ter Braak *et al.*, 2012). In my analysis, the number of species used in RLQ trait analysis was constrained by the number of species with leaf C and N data, as these were seen as important plant traits (Chapin, 2003). The standardised trait protocols provided by Pérez-Harguindeguy *et al.* (2013) indicate that three, photosynthetically active leaves should be collected for each trait measured. While this was not a problem for most trait measurements, there was often not enough dry material (i.e. 0.3 g dry weight) present for small-leaved plants (e.g.

snowberry, low-bush blueberry), needled species (e.g. black spruce and tamarack), or mosses (e.g. *Sphagnum fuscum*) to be included in the C and N analysis. However, while including these species might have diversified results of the RLQ analysis, they were not necessarily abundant and may not have qualitatively influenced my results.

While I provide insight into how some functional traits are involved in ecosystem engineering and litter decomposition, not all relevant traits of *Sphagnum* and *Carex* were measurable. For instance, ecosystem engineering is attributable to both physical presence (e.g. leaf shadow) and physical activity (e.g. smothering vines) of organisms (Jones *et al.*, 1994). In my system, *Carex*'s ability to build tussocks (Crain & Bertness, 2005) and *Sphagnum*'s capacity to build hummocks are likely also primary mechanisms by which these plants physically engineer their environment. While it might be difficult to assess the capacity of these plants to build structures, the presence or absence of hummocks or tussocks within the plots could be used a metric of activity-based ecosystem engineering if the study were to be repeated. Another caveat is that while aboveground traits are accounted for in my study, belowground traits are under-represented. Root exudates of sedge species including low-weight molecular phenolics are a potential priming mechanism enhancing decomposition in peatlands (Robroek *et al.*, 2015; Dieleman *et al.*, 2016), and would have been strong evidence for *Carex* stimulating faster decomposition in the intermediate fen. My analyses of vegetation and root biomass illustrate the trend of resource allocation aboveground in the poor fen and belowground in the intermediate fen are consistent with other studies (Myers *et al.*, 2012). However, root exudation of peatland vascular plants has also been found to have negligible effects on decomposition rates in the same White River peatland complex (Basiliko *et al.*, 2012), suggesting more explicit tests of root exudates as a priming effect on decomposition are needed.

A significant limitation for Chapter 3 and my assertion of home-field advantage decomposition dynamics is the lack of microbial compositional data and analyses. I did not find significant differences in microbial biomass or activity between the sites, consistent with other studies performed at this peatland complex (Myers *et al.*, 2012; Haynes *et al.*, 2015), yet the microbially-adapted home-field advantage mechanism does not necessitate these differences. Determining differences in microbial communities can

be performed through relatively simple metrics (e.g. phospholipid fatty acids that determine fungal:bacterial ratios) or highly intensive methods (e.g. next generation sequencing of species-level identification), neither of which were available for this study, and neither of which would prove local adaptation. As such, while I provide evidence for a home-field decomposition advantage, mechanisms generating the home-field advantage remain somewhat unclear. Measuring local adaptation is typically performed through reciprocal transplants (Blanquart *et al.*, 2013) as I have done here, although quantifying the microbial community structure of the peat monoliths would have provided more solidity to my claims of fungal-based energy channels dominating in the poor fen, and bacteria in the intermediate fen, that contribute to driving the slow or fast feedbacks of the respective site. Lastly, although poor and intermediate fen *Sphagnum* had significantly different nutrient concentrations, this was not reflected in significantly different mass loss rates suggesting that more time might be needed for the effects to be realised. However, studies of *Sphagnum* decomposition have found comparable mass loss rates after seven years (Moore & Basiliko, 2006), and different mass loss rates between the two *Sphagnum* types would not necessarily have changed interpretations of the home-field advantage.

Overall, I provide evidence for how ecosystem properties of a nutrient poor and intermediate nutrient peatland are generated and maintained by key plant ecosystem engineers, namely *Sphagnum* and *Carex* species that correspondingly drive litter-environment feedbacks. Given that plant-soil feedbacks grow stronger over time (Dorrepaal *et al.*, 2007), future directions should investigate the conditions that could destabilise these litter-environment feedbacks to cause a shift between peatland types, and which plant traits are most important in facilitating this change. My litter mixture results lend support to a synergistic litter dynamic between poor fen *Carex* and *Sphagnum*, enhancing *Sphagnum* decomposition (but not vice versa). With changes in climate (warming and elevated atmospheric CO<sub>2</sub>) that induce changes in plant community structure from mosses to vascular plants, the presences of more labile litter combined with root exudates might 'prime' deep peat for accelerated microbial decomposition (Robroek *et al.*, 2015; Dieleman *et al.*, 2016) presenting another avenue for further research.

## 4.6 Conclusions and significance

There have been several studies that investigate the role of peatland plant community composition under climate change scenarios (e.g. Ward *et al.*, 2009; Potvin *et al.*, 2015; Dieleman *et al.*, 2015), yet relatively few provide insight into contemporary peatland plant community dynamics. Further, the functional attributes of peatland plants are understudied compared to other ecosystems such as grasslands or forests (Garnier *et al.*, 2004; Conti & Diaz, 2013). Data provided from my research will help fill a knowledge gap in the functional attributes of peatland plants. I found that both *Sphagnum* and *Carex* species are potential ecosystem engineers, generating different peat environments that feed back to different rates of decomposition, providing potential insights to carbon storage of these two ecosystems. The ability of these peatland plants to transform environments through their traits makes the trait-environment linkage in peatlands very strong (Rydin & Jeglum, 2013). The expected shift in plant community from moss- to sedge-dominated (Dieleman *et al.*, 2015; Robroek *et al.*, 2015) implies changing litter inputs to a more labile material, and an associated feedback to enhanced growing conditions and nutrient cycling rates (Dorrepaal *et al.*, 2007). As my results show that the home-field advantage does not alter absolute mass loss of plant litter, studies should focus on whether the shift in belowground microbial community will occur before, after, or alongside the shift in dominant plant litter. On that same note, whether a low nutrient environment or nutrient-conservative plant type came first (or high nutrient and nutrient-acquisitive) is a chicken-and-egg relationship requiring further investigation.

## 4.7 References

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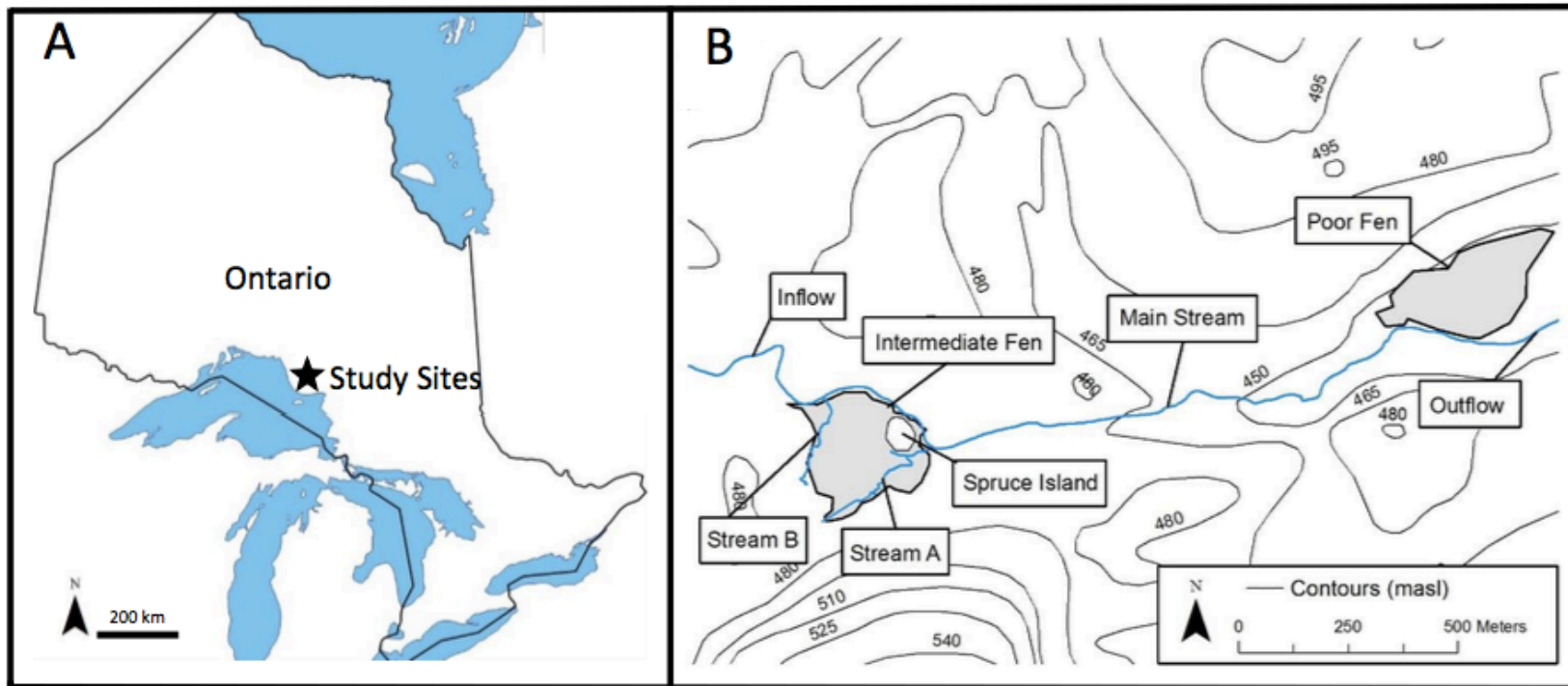
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## Appendices

**Appendix A:** Maps of Boreal peatland complex near White River, ON.

Map of A) White River, ON (48°21'N, 84°20'W) and B) relative locations of the intermediate and poor fen.



Maps created by M. Mack, UWO.

**Appendix B:** Summary of relative percent cover (%) of Boreal peatland plant species used in RLQ trait analysis.

	<b>Intermediate fen</b>					<b>Poor fen</b>				
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
<i>Andromeda polifolia</i>	0	0	0	0	0	0	25	9	19	50
<i>Carex disperma</i>	0	0	0	0	0	0.5	0	0.5	0.5	0.5
<i>Carex oligosperma</i>	0	75	0	0	100	10	0	0	0	0
<i>Carex stricta</i>	100	75	100	90	0	0	0	0	0	0
<i>Chamaedaphne calyculata</i>	1	1	25	29	5	55	5	25	5	40
<i>Kalmia polifolia</i>	0	0	0	0	0	2	5	15	13	10
<i>Rhododendron groenlandicum</i>	0	0	0	0	0	9	25	8	24	3
<i>Lycopodium annotinum</i>	0	0	0	0	0	0.5	25	10	16	10
<i>Mainthemum trifolium</i>	0	0	0	0	0	1	3	0.5	0.5	3
<i>Myrica gale</i>	51	51	75	37	10	0	0	0	0	0
<i>Sphagnum angustifolium</i>	0	0	0	0	0	55	24	36	0.5	40
<i>Sphagnum magellanicum</i>	0	0	0	0	0	45	26	50	1	40
Carex sp.	0.5	0.5	0	0.5	0	0	0	0	0	0
<i>Vaccinium angustifolium</i>	0	0	0	0	0	0.5	2	18	27	0

**Appendix C:** Summary of species' traits used in RLQ trait analysis.

Species	Height (cm)	Leaf Area (cm)	Leaf Mass (g)	LDMC ( $\mu\text{g/g}$ )	SLA ( $\text{cm}^2/\text{g}$ )	LMA ( $\text{g}/\text{cm}^2$ )	Leaf Thickness Index	C (%)	N (%)	C:N
<i>Andromeda polifolia</i>	43.0	1.634	0.029	470.33	56.59	0.018	0.000038	53.1	1.35	39.4
<i>Carex disperma</i>	65.0	34.407	0.157	322.46	228.32	0.004	0.000014	44.5	1.50	29.6
<i>Carex oligosperma</i>	73.0	7.217	0.070	336.97	132.93	0.008	0.000022	45.4	1.41	32.2
<i>Carex stricta</i>	75.3	17.099	0.134	569.41	129.41	0.008	0.000014	46.4	1.22	38.1
<i>Chamaedaphne calyculata</i>	56.2	5.040	0.028	436.70	180.45	0.006	0.000013	53.2	1.74	30.7
<i>Kalmia polifolia</i>	34.2	1.418	0.017	473.33	87.95	0.011	0.000024	51.7	2.05	25.2
<i>Ledum groenlandicum</i>	45.0	7.163	0.044	605.84	154.88	0.007	0.000013	53.2	1.50	35.4
<i>Lycopodium annotinum</i>	17.5	7.609	0.068	429.38	125.93	0.010	0.000022	48.9	0.91	57.3
<i>Mainthemum trifolium</i>	13.9	35.378	0.069	154.06	482.50	0.003	0.000016	48.3	2.93	16.5
<i>Myrica gale</i>	87.5	6.384	0.043	500.17	188.45	0.006	0.000012	50.9	2.57	20.5
<i>Sphagnum angustifolium</i>	4.5	10.870	0.028	130.58	397.88	0.003	0.000019	44.0	1.55	28.5
<i>Sphagnum magellanicum</i>	4.3	16.404	0.049	86.82	362.25	0.003	0.000036	45.0	1.58	28.6
<i>Carex</i> sp.	51.0	23.176	0.224	393.20	115.45	0.009	0.000022	44.4	0.84	52.7
<i>Vaccinium angustifolium</i>	31.0	5.994	0.018	336.87	335.11	0.003	0.000009	49.0	1.94	25.3

Note: Leaf thickness index was calculated using the equation  $LT = (\text{SLA} \times \text{LDMC})^{-1}$  from Vile *et al.*, (2005).

**Appendix D:** Summary of plant community diversity descriptors for poor and intermediate fen plant communities.

Values are mean ( $\pm$ SE). One-way ANOVA was used to test for differences between site means.

Community Descriptor	Intermediate fen	Poor fen	$F_{1,8}$	$P$
Richness (spp./m <sup>2</sup> )	6.0 (1.1)	15.2 (1.2)	36.2	<b>&lt; 0.001</b>
Percent cover (%)	182.3 (20.7)	218.4 (18.5)	1.69	0.230
Shannon Diversity ( $H$ )	1.04 (0.11)	1.96 (0.07)	49.5	<b>&lt; 0.001</b>
Simpson Diversity ( $N_i$ )	0.57 (0.05)	0.82 (0.01)	22.1	<b>0.001</b>
Pielou's Evenness ( $J$ )	0.61 (0.08)	0.72 (0.03)	1.83	0.213

## Curriculum Vitae

- Name:** Julia E. Palozzi
- Post-secondary Education and Degrees:** Western University, MSc  
London, Ontario Canada  
2015–present
- University of Toronto, BSc Hons  
Toronto, Ontario, Canada  
2010–2014
- Honours and Awards:** William G. Dean Scholarship in Geography Field Research  
2014
- Related Work Experience**
- Teaching Assistant (Ecosystem Ecology; BIO4405)  
The University of Western Ontario  
2016–2017
- Teaching Assistant (Community Ecology; BIO3445)  
2015-2016
- Project Biologist (Peatland & Climate Change Research)  
Ontario Ministry of Natural Resources  
2015
- Resource Technician (Peatland & Climate Change Research)  
Ontario Ministry of Natural Resources  
2014–2015
- Research Assistant (peat core analysis)  
University of Toronto  
2013–2014
- Publications:**
- Palozzi, J.E. and Lindo, Z. Boreal peat properties link to plant functional traits of ecosystem engineers. In revision for *Plant and Soil*. (PLSO-S-16-02110)
- Palozzi, J.E. and Lindo, Z. Pure and mixed litters of *Sphagnum* and *Carex* exhibit a home-field advantage in Boreal peatlands. Submitted to *Soil Biology and Biochemistry*. (SBB-2017-103)