The structure and function of peatlands in the Hudson Bay Lowland: response to environmental change

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"Peat is very squishy."

Anon. Carved into a stone pathway on the edge of a bog in The Flow Country, Scotland.

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Abstract

The peatlands of the Hudson Bay Lowland (HBL) are the world's second largest expanse of northern peatland and are globally important carbon (C) stores. Within the bogs and fens covering this extensive landscape, small-scale variations in surface elevation (microtopography – hummocks and hollows) form distinct spatial patterns accentuated by different vegetation cover related to water table depth. These spatial differences in peatland structure and biogeochemical function enable peatlands to occupy alternate dry and wet stable states, therefore increasing peatland resilience to environmental change.

The objectives of this research were to examine mechanisms controlling peatland structure and function through analysis of field evidence from HBL peatlands. Relationships among vegetation, hydrology, and nutrients were examined for peatland microforms to test current hypotheses and conditions of peatland development models, and whether these models are applicable to HBL peatlands. My analysis shows the development of surface patterns of microforms within the HBL peatlands may be explained by small-scale structuring mechanisms that control peat accumulation at the microform scale, specifically, the peat accumulation and water ponding mechanisms. Vegetation type is an important control, with greater shrub cover on hummocks associated with larger production for hummocks than hollows. My results also suggest the occurrence of different spatial patterns depends on position within a peat landform, with these differences attributed to varying ecohydrological settings related to landscape-scale hydrology. In turn, the ecohydrological setting influences the strength and direction of feedback mechanisms controlling peat accumulation at the microform scale.

Mat-forming lichens cover a large area of the surface of HBL peatlands (up to 50 % in places) and are an important control for peat accumulation and microform development. My results demonstrate that where there are thick lichen mats, local peat accumulation ceases

through smaller productivity, faster lichen decay rates, and a loss of structural integrity in underlying peat. Lichens therefore represent a significant temporary limit to peat growth, likely constraining or reducing hummock height relative to adjacent hollows.

The potential effects of hydrological change (drier conditions and lower water tables caused by gradual short-term drainage) on these relationships, and on peatland structure and function, were also assessed. My results reveal changes in vegetation and biogeochemical processes are dependent on microform. A significant loss of vegetation and associated biogeochemical changes in dry pools indicate a shift in ecosystem state. Minor changes for hummocks and intermediate microforms however, demonstrate the resilience of HBL peatlands to hydrological change that may be analogous to future climate change scenarios.

This thesis contributes new knowledge on the current state of bogs and fens in the HBL for which there has been limited research, and provides insight into possible mechanisms controlling peatland structure and function. This understanding will be invaluable when considering the risks of climate change and increasing development for infrastructure and mining in these iconic peatlands.

Résumé

Les tourbières des basses terres de la Baie d'Hudson (HBL) constituent la deuxième plus grande étendue de tourbières nordiques au monde, et sont d'importantes réserves de carbone (C) à l'échelle globale. Dans les "bogs" et les "fens" qui couvrent ce paysage étendu, les variations à petite échelle de l'élévation de surface (microtopographie – "buttes" et "dépressions") forment des modèles spatiaux distincts, accentués par un couvert végétal varié lié à la profondeur de la nappe phréatique. Ces différences de structure de les tourbières et de fonction biogéochimique permettent aux tourbières d'occuper des états secs et humidesen alternance, ce qui augmente la résilience des tourbières aux changements environnementaux.

Les objectifs de cette recherche étaient d'examiner les mécanismes de contrôle des structure et fonction des tourbières des HBL par l'analyse des mésures prises sur le terrain. Les relations entre végétation, hydrologie et nutriments ont été examinées pour les microformes de tourbières afin de tester les hypothèses actuelles et les conditions des modèles de développement des tourbières, et de vérifier si ces modèles sont applicables aux tourbières des HBL. Mon analyse montre que le développement des modèles de surface des microformes dans les tourbières des HBL peut être expliqué par des mécanismes de structuration de petite échelle qui contrôlent l'accumulation de tourbe à l'échelle des microformes, en particulier les mécanismes d'accumulation de tourbe et d'accumulation eau en surface. Le type de végétation est un contrôle important, une plus grande couverture d'arbustes sur les buttes" étant associée à une production plus importante pour les buttes que pour les dépressions. Mes résultats suggèrent également que la présence de différents modèles spatiaux dépend de leur localisation dans la tourbière, ces différences étant attribuées à différents paramètres écohydrologiques liés à l'hydrologie du paysage. L'hydrologie influence à sont tour la force et la direction des mécanismes de rétroaction qui contrôlent l'accumulation de tourbe à l'échelle des microformes.

Les tapis de lichens couvrent une grande partie de la surface des tourbières des HBL (jusqu'à 50 % par endroits) et constituent un contrôle important pour l'accumulation de tourbe et le développement de microformes. Mes résultats démontrent que, là où il y a d'épais tapis de lichen, l'accumulation locale de tourbe cesse en raison d'une productivité plus faible, des taux plus rapides de décomposition du lichen et une perte d'intégrité structurelle de la tourbe sous-jacente. Ceci représente une limite significative à la croissance de la tourbe, ce qui est susceptible de contraindre ou de réduire la hauteur des buttes par rapport aux dépressions adjacentes.

Les effets potentiels d'un changement hydrologique (conditions plus sèches et niveaux de nappes phréatiques plus bas causés par un drainage progressif à court terme) sur ces relations et sur les structure et fonction des tourbières ont également été évalués. Mes résultats ont révélé que des changements dans la végétation et les processus biogéochimiques dépendent de la microforme. Une perte importante de végétation et les modifications biogéochimiques qui y sont associées dans les dépressions sèches indiquent un changement dans l'état de l'écosystème. Cependant, des changements mineurs pour les buttes et les microformes intermédiaires démontrent une résilience des tourbières des HBL aux changements hydrologiques qui peuvent être analogues aux scénarios de changement climatique à venir.

Cette thèse apporte de nouvelles connaissances sur l'état actuel des "bogs" et des "fens" dans les HBL qui n'ont été que peu étudiées, et donne un aperçu des mécanismes possibles qui contrôlent la structure et la fonction des tourbières. La comprehension de ces processus sera très précieuse pour l'analyse des risques liés aux changements climatiques, au développement croissant des infrastructures ainsi qu'à l'exploitation minière dans ces tourbières emblématiques.

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PREFACE

i. Thesis Structure

This thesis comprises three chapters as research manuscripts (Chapters 3 to 5) that are in preparation for submission to peer-reviewed scientific journals. The manuscripts address a set of research objectives that are outlined in Section 1.2 and based on a full review of the literature. Connecting statements revisit these research objectives and explain the context of each chapter within the thesis. An overarching summary relating conclusions from each of the chapters to the thesis research objectives, and including suggestions for future research, is provided. As the research for all three chapters was undertaken at the same location, there are similarities in the methods across all chapters. Tables and figures for each manuscript are found at the end of each chapter, as required by academic journal formatting guidelines. References for all chapters and manuscripts are included in a combined list at the end of the thesis.

ii. Contribution of Authors

For all three manuscripts (chapters 3 to 5), I developed the research questions and research design, collected the data, completed the analysis and interpretation of results, and wrote the manuscripts as lead author. All three chapters were co-authored by Dr. Nigel Roulet and Dr. Tim Moore, both of whom advised me on research plans, methodology, data analysis, and provided comments and a critique of the manuscripts. Financial support came primarily from Dr. Nigel Roulet. The contribution of other co-authors (Chapters 3 and 4 only) are as follows:

<u>Chapter 3.</u> "Small-scale structuring mechanisms for surface patterns in peatlands of the Hudson Bay Lowland" by Lorna I. Harris, Nigel T. Roulet, Tim R. Moore, and Elyn Humphreys (to be submitted). Elyn Humphreys provided data from the EC towers at the sites in the Hudson Bay Lowland (HBL), and assisted with data analysis techniques and interpretation of results. Elyn also contributed to the revision of the manuscript.

<u>Chapter 4.</u> "Lichens: a limit to peat growth?" by Lorna I. Harris, Tim R. Moore, Nigel T. Roulet, and Andrew J. Pinsonneault (in review, *Journal of Ecology*). The idea of leachates from lichen mats potentially altering enzyme activity in underlying peat in the HBL developed during discussions with Andrew Pinsonneault. He provided invaluable advice on the methods and lab analysis for leachates and enzyme activity, and assisted with the analysis in the lab and interpretation of the results. He also contributed to the revision of the manuscript.

iii. Statement of Originality

This thesis contributes to our understanding of mechanisms controlling peatland structure and function, and how these mechanisms may be altered by environmental change. In particular, my thesis and manuscripts add to the currently limited scientific literature available for the HBL peatlands. The HBL is the world's second largest continuous expanse of northern peatland but our understanding of this iconic and remote landscape, which is threatened by climate change and development (infrastructure and mining), is limited. My thesis integrates ecological, hydrological, and biogeochemical processes to allow a more complete analysis of peatland ecosystems in the HBL, and places this in the context of landscape development at various spatial scales (e.g. development of individual microforms to peat landforms). My research also provides information for multiple stakeholders including indigenous communities, government, conservation organisations, and industry, with an interest in the HBL peatlands.

CHAPTER 1 – Overview

1.1 Introduction

Over 4.5 million km² or 3 % of the global land area is covered by peatland ecosystems (Yu et al., 2010). Ranging from the tropics to the subarctic, these diverse ecosystems are characterised by waterlogged conditions that reduce decomposition of plant matter which slowly accumulates as 'peat'. Almost 87 % of peatlands are found in northern latitudes (> 40° N), where high precipitation and cool climate conditions provide the ideal conditions for peat accumulation. These northern peatlands are a globally significant longterm terrestrial carbon (C) store, containing approximately 500 Pg C, or 80 % of total peatland carbon stocks (Gorham, 1991; Yu, 2012). Canada contains a large portion of this global C total, with 1.1 million km² of peatland extending through the boreal and subarctic ecoclimate zones (Tarnocai, 2006). The peatlands of the Hudson Bay Lowland (HBL) in northern Ontario, and extending into Quebec and Manitoba, comprise the world's second largest continuous expanse of northern peatland, covering over 250,000 km² and containing approximately 6 % (~ 30 Pg C) of the northern peatland C pool (Riley, 2011; Packalen et al., 2014). Yet C cycling in within these vast peatlands is now at risk from anthropogenic-driven climate warming (Tarnocai, 2006; IPCC, 2014; Page and Baird, 2016). Changes to HBL peatlands could switch their status from an important C sink to a source, causing a further increase in atmospheric carbon dioxide (CO₂) and further exacerbating climate change (Frolking et al., 2006; Frolking et al., 2011; McLaughlin and Webster, 2014). Understanding C cycling in peatland ecosystems and potential feedbacks to global climate is therefore essential.

To understand processes controlling C accumulation and loss in peatlands, it is important to understand how peatlands form and develop over time, and how internal biogeochemical processes and feedbacks control peatland structure and function. This knowledge is crucial if we are to predict with confidence, the possible impacts of external forcing (such as climate change) on peatlands (Yu et al., 2011; Page and Baird, 2016). Peatlands have been described as 'self-regulating' ecosystems with feedbacks among vegetation, hydrology, and nutrients controlling peatland response to environmental change (Ivanov, 1981; Belyea and Clymo, 2001; Belyea and Malmer, 2004; Belyea and Baird, 2006; Belyea, 2009; Morris et al., 2011a; Morris et al., 2015). Various hypotheses and models describe how these feedbacks cause spatial differences in peat accumulation and thus, the development of microtopography in peatlands (Belyea and Clymo, 1998, Belyea and Clymo, 2001; Rietkerk et al., 2004b; Eppinga et al., 2009a). Microforms (typically hummocks and hollows) may be identified not only by surface elevation, but also by distinct differences in vegetation cover related to water table depth (Andrus et al., 1983; Belyea and Clymo, 1998). It is these differences in microform structure and biogeochemical function (peatlandatmosphere CO₂ and methane (CH₄) exchange), that enable peatlands to occupy alternate 'dry' and 'wet' stable states, therefore increasing resilience to environmental change (Hilbert et al., 2000; Belyea and Clymo, 2001; Belyea and Malmer, 2004; Eppinga et al., 2009b). In many peatlands, microforms may converge to form distinct and often visually striking spatial surface patterns, such as parallel ridges and pools or maze-patterns (e.g. Glaser et al., 1981; Foster et al., 1988a; Eppinga et al., 2009a). Surface patterns in the HBL peatlands are particularly notable owing to the large number of peat landforms (bogs and fens) spread across such a vast landscape (Sjörs, 1959; Sjörs, 1963; Riley, 2011).

Although the models describing mechanisms for the development of microforms and spatial patterns in peatlands are plausible, there is a surprising lack of empirical evidence to support model assumptions (e.g. Belyea and Malmer, 2004; Eppinga *et al.*, 2008; Eppinga *et al.*, 2008; Eppinga *et al.*, 2010). Given the importance of these mechanisms for controlling peatland structure and

function, and therefore resilience to environmental change, more research is required. The influence of feedbacks among vegetation and hydrology on peat accumulation remains elusive, particularly when considering complex ecohydrological relationships that may vary within a peatland and for different peatland types (Waddington *et al.*, 2015; Malhotra *et al.*, 2016). Vegetation is an important factor influencing biomass production and decomposition in peatlands, as it determines photosynthetic capacity and litter quality (Belyea, 1996; Moore *et al.*, 2002; Moore *et al.*, 2007). Peatland vegetation may be classified into plant functional types (PFTs), with variation in plant production and decomposition rates frequently attributed to different PFTs (Frolking *et al.*, 2010; Laine *et al.*, 2012; Wang and Moore, 2014; Robroek *et al.*, 2015). These relationships remain uncertain however, and some common northern PFTs such as lichens, are rarely considered (Malmer and Wallen, 1999; Riley, 2011; Korrensalo *et al.*, 2016).

Climate warming may push peatlands beyond environmental thresholds for stable microform states, triggering a shift to potentially unstable states and resulting in a loss of resilience (Scheffer and Carpenter, 2003; van Nes and Scheffer, 2005; Kéfi *et al.*, 2013; Page and Baird, 2016). Improved knowledge of peatland development mechanisms should lead to a better understanding of likely environmental thresholds for state shifts (Hilbert *et al.*, 2000; Kéfi *et al.*, 2013), and therefore the level of peatland resilience to climate warming (Belyea, 2009; Eppinga *et al.*, 2009b). Understanding how these mechanisms operate within HBL peatlands for which there has been limited research is particularly important, especially when considering the potential for changes within these extensive peatlands to feedback to global climate (Gagnon and Gough, 2005; Ruhland *et al.*, 2013; Delidjakova *et al.*, 2016).

1.2 Research Objectives

My research aims to provide a better understanding of mechanisms controlling peatland structure and function through analysis of field evidence from HBL peatlands. Specifically, I examine interactions among vegetation, hydrology, and nutrients for peatland microforms to test current hypotheses and assumptions of peatland development models. The question of how northern peatlands may respond to future climate change forms the basis for this research, and so I also assess the possible effects of environmental change on peatland structure and function. My research objectives are as follows:

- To test proposed mechanisms for spatial patterns within peatlands, including identifying possible feedbacks among variables, and establish whether proposed mechanisms are applicable to HBL peatlands (Chapter 3).
- To determine the effect of lichens on peat accumulation within the context of proposed peat development mechanisms (Chapter 4).
- To determine the effect of environmental change on peatland structure and function, examine how these changes may alter feedbacks within proposed peat development mechanisms, and determine potential for shifts in ecosystem state (Chapter 5).

1.3 Study Sites

My research for all three chapters was completed at sites located approximately 90 km west of Attawapiskat in the Hudson Bay Lowland (HBL), part of the Hudson Plains ecozone (Ecological Stratification Working Group, 1996), in northern Ontario, Canada (Figures 1.1 and 1.2). The De Beers Canada Victor Mine (52°49'06" N, 83°54'18" W; ~ 83 m elevation), an open pit diamond mine that became fully operational in 2008, provided a base camp for research in the area. The selected research sites provide examples of pristine peatland typical of the HBL area, and peatland that has been hydrologically impacted by mining activity, and allow a comparison of pristine peatland ecosystems and those impacted by environmental change.

The HBL landscape is dominated by peatlands (mainly bogs and fens) up to 3 m deep, in an interconnecting mosaic of rivers, water tracks and pools (Sjörs, 1959; Sjörs, 1963; Riley, 2011). The underlying geology is a flat limestone plain (Paleozoic carbonate rocks) with numerous kimberlite pipes occurring as vertical intrusions into the limestone (Martini, 1989). The limestone is overlain by marine clays and silts that were deposited following the retreat of the Laurentide Ice Sheet and marine incursion that formed the Tyrell Sea between 7000 and 8500 years BP (Martini, 1989; Dredge and Cowan, 1989). The region is experiencing rapid isostatic uplift and this has had a significant influence on the formation of the wetlands and peatlands across the HBL, with a regional chronosequence of peatlands from the coast of James Bay to inland areas (Glaser *et al.*, 2004a; Glaser *et al.*, 2004b; Martini, 2006; Riley, 2011; Packalen *et al.*, 2014). Variability in regional climate also contributes to the spatial distribution of peatland types and C storage in the HBL (Packalen *et al.*, 2016).

The nearest long-term climate station is located approximately 280 km WSW at Lansdowne House (52°14'N, 87°53W; 254 m elevation). Mean annual temperature is -1.3 °C and the mean annual precipitation is 700 mm, predominantly as snowfall in all months except July and August (1971 – 2000; Environment Canada, 2016). Permafrost in this part of the HBL is sporadic and discontinuous (Riley, 2011) but there is no permafrost at the selected research sites.

The main research site is accessed by a 1.5 km raised boardwalk (installed by the Ontario Ministry of Environment and Climate Change, OMOECC, referred to as MOE throughout this thesis) located almost 13 km south of Victor Mine and accessible only by helicopter (Figure 1.3). The MOE boardwalk crosses an ombrogenous raised bog (unofficially named MOE Bog, 52°41'36" N, 83°56'41" W; ~ 93 m elevation) through to a moderately-rich minerogenous fen (MOE Fen, 52°42'02" N, 83°57'18" W; ~ 91 m elevation;

Ulanowski and Branfireun, 2013; Ulanowski, 2014). The boardwalk joins two eddy covariance (EC) towers – one located near the apex of MOE Bog and the other tower located within MOE Fen (Humphreys *et al.*, 2014).

During a preliminary research trip to the HBL in summer 2012, I selected four sites along the boardwalk that represent the range of peatland types within this area. These sites were given the unofficial names of Bog, Ridge-Pool, Moss, and Fen (Figures 1.3 and 1.4). 'Bog' is located at the apex of MOE Bog near the EC tower and represents a treed bog with hummock-hollow microtopography. 'Ridge-pool' is a sequence of parallel ridges and pools (or 'flarks') perpendicular to the slope of the main bog. 'Moss' is located near the margin of MOE Bog and is a treed bog with open areas of hummock-hollow microtopography. 'Fen' is located within the MOE Fen near the EC tower and comprises a series of ridges and pools that are perpendicular to the slope.

My other study site is near a bioherm (fractured limestone outcrops that protrude to the peatland surface) located approximately 3 km from the main pit at Victor Mine (Figures 1.5 and 1.6). In 2007, Whittington and Price (2012; 2013) installed a series of well transects and piezometer nests around seven of the bioherms. Their results show pronounced water table drawdown at the bioherm locations due to dewatering at the mine site (e.g. depth to peatland water table ranging from 90 to 130 cm in a dry year and 30 to 130 cm in a wet year, and decreasing with distance from the bioherm). Their study was completed when the water table at the mining pit had only decreased to approximately 60 m below the surface. In summer 2013 the drawdown at the pit was >100 m with final drawdown likely to be ~150 m (2013, De Beers Canada hydrogeologists and environment lab, *personal communication*).

Transects from North Road Bioherm (NRB, unofficially named by Whittington and Price, 2012) to the surrounding peatland, and along ridge to pool transitions were selected during the preliminary research trip in 2012. The selected transects include areas of treed bog

with hummock-hollow microtopography and ridge to pool transitions similar to 'Bog' and 'Ridge-pool' at the pristine MOE sites. The selected research sites will allow for a study of how peatland structure and function may respond to future drier conditions predicted to occur with climate warming.



Figure 1.1 Map of North America showing the location and extent of the Hudson Plains ecozone in Canada. 1 = Hudson Bay Lowland (HBL), 2 = Coastal HBL (Ecological Stratification Working Group, 1996). Study sites marked with a star.



Figure 1.2 Location of study sites (near De Beers Canada Victor Mine) within the Hudson Bay Lowland in Canada.



Figure 1.3 Raised research boardwalk (~ 1.5 km long) connecting EC towers in MOE Bog and MOE Fen, with research locations shown.



Figure 1.4 MOE research sites (a) Bog, (b) Ridge-Pool, (c) Moss, and (d) Fen (photos taken August 2013).



Figure 1.5 Location of hydrologically impacted NRB site near Victor Mine. Main pit located ~1 km in direction of arrow.



Figure 1.6 NRB research site with small boardwalk located near Victor Mine. The raised bioherm is covered by dense trees (photo taken October 2013).
CHAPTER 2 - Literature Review

2.1 What are peatlands?

Peatlands are wetland ecosystems where almost constantly waterlogged conditions slow the decay of organic matter. As plant growth and litter production surpass decomposition, this organic matter slowly accumulates to form 'peat', a soil that is rich in carbon (C). As this process continues over thousands of years, the thickness of the peat increases and develops into distinct peat landforms. Bogs and fens are the dominant peat landforms, with their development depending on local topography, hydrology, nutrient regime, and climate (Moore and Bellamy, 1974; Ivanov, 1981; Winter, 1999; Glaser, 1992; Glaser *et al.*, 1997; Rydin and Jeglum, 2013).

Bogs may develop as distinct raised mounds of peat or spread across the landscape as blanket bogs. As the peat surface is raised above and often disconnected from the surrounding land in both cases, ombrogenous bogs depend solely on precipitation for water and nutrients (Rydin and Jeglum, 2013). *Sphagnum* moss is uniquely adapted to these nutrient-poor and acidic (pH ~ 4) ombrotrophic conditions, and as the dominant species is also essential in forming the structure of the bog itself (Halsey *et al.*, 2000; Turetsky *et al.*, 2012).

Fens are hydrologically connected to the surrounding landscape, receiving water and nutrients from groundwater and/or upslope sources ('geogenous' wetlands - Winter, 1999; Rydin and Jeglum, 2013). Although these minerotrophic conditions vary depending on local hydrology, minerogenous fens are generally more species-rich than bogs (Rydin and Jeglum, 2013). Fens are often subdivided into poor, moderate, and rich according to alkalinity (pH 5 to 9), with further divisions based on hydrological setting (e.g. basin fen, fen track or 'ladder

fen') and plant species composition (Moore and Bellamy, 1974; Ivanov, 1981; Foster *et al.*, 1988a; Sjörs and Gunnarsson, 2002; Duval and Waddington, 2011; Duval *et al.*, 2012).

Peatland ecosystems range from the tropics to the subarctic, covering almost 4.5 million km² of the land surface (Yu *et al.*, 2010). Peatlands are dominant in northern latitudes however, due to prevailing cool and wet climate conditions (Tarnocai and Stolbovoy, 2006; Yu, 2012; Page and Baird, 2016). These northern peatlands cover ~ 4 million km² (Yu, 2012), extending across the boreal and subarctic ecoclimate zones in Canada and the northern portion of the USA, northern Europe, and Russia. The most southern limit is approximately 40°N latitude in North America and 50°N in Europe and Asia (Tarnocai and Stolbovoy, 2006). The extensive peatlands of the West Siberian Lowlands are the largest continuous expanse of northern peatland in the world, covering over 600,000 km² (Kremenetski *et al.*, 2003; Sheng *et al.*, 2004). Many northern peatlands are in areas of permafrost, ranging from continuous permafrost zones to discontinuous and sporadic permafrost zones (Turetsky *et al.*, 2002; Tarnocai and Stolbovoy, 2006; Bauer and Vitt, 2011).

2.2 Role in the global carbon cycle

Peatland ecosystems are acknowledged to be a critical component of the global C cycle, with estimates for current global peatland C stocks of ~ 500 to 600 Pg C (Gorham, 1991; Yu, 2012). This estimate is approximately one fifth of the global soil C pool which is around 3000 Pg C (Kuhry *et al.*, 2010; Batjes, 2014). Northern peatlands contain ~ 80 % of global peatland C (Yu, 2012), with ~ 150 Pg C in boreal and subarctic peatlands in Canada (Tarnocai, 2009).

Peatland ecosystems are recognised by the IPCC as a globally important C store (Ciais *et al.*, 2013). Photosynthesis in plants removes carbon dioxide (CO₂) from the atmosphere and this C is then stored within living plants and dead plant matter (or litter). Waterlogged conditions (high water tables) slow the decay of this organic matter and as peat

accumulates, C is effectively contained for long periods within the peatland. Long-term average rates of C accumulation in northern peatlands range from 17 g C m⁻² yr⁻¹ in minerogenous fens (Turunen *et al.*, 2002) and 19 to 25 g C m⁻² yr⁻¹ in ombrogenous bogs (Turunen *et al.*, 2004; Roulet *et al.*, 2007; van Bellen *et al.*, 2011). Peatlands also lose C, however, as CO₂ release through ecosystem respiration, as methane (CH₄) emissions, and as waterborne C (Roulet *et al.*, 1992; Fraser *et al.*, 2001b; Lafleur *et al.*, 2005a). Waterborne C may include dissolved organic C (DOC, annual flux range of 2 to 20 g m⁻² yr⁻¹), particulate organic C (POC), and dissolved inorganic C (DIC) (e.g. Moore, 2003; Olefeldt *et al.*, 2013). Fluxes of CH₄ from northern peatlands can be large (annual flux range of 1 to 20 g m⁻² yr⁻¹), with bogs and fens producing an average of ~ 0.1 g CH₄ m⁻² d⁻¹ and instantaneous fluxes ranging from 0.02 to 4 g CH₄ m⁻² d⁻¹ (Moore *et al.*, 2011; Turetsky *et al.*, 2014).

Most northern peatlands are thought to be net C sinks (Frolking *et al.*, 2011). For example, Roulet *et al.*, (2007) report average annual contemporary C accumulation (1998 to 2004) at Mer Bleue, an ombrogenous bog in Canada, to be around 21 g C m⁻² yr⁻¹. Nilsson *et al.*, (2008) estimated the annual net ecosystem C balance (NECB) of Degero Stormyr, a minerotrophic peatland in Sweden as a net C sink of 24 g C m⁻² yr⁻¹ during 2004 and 2005. Both studies highlight the annual variation in peatland C balance from a C sink to a source, even within short-time periods.

Due to their global extent and important role in the global C cycle (and therefore climate regulation), northern peatlands have been subject to an increasing number of studies over the past decade or so. Sites such as Mer Bleue bog in Ontario, Canada (e.g. Roulet *et al.*, 2007; Moore *et al.*, 2011), and Degero Stormyr (e.g. Nilsson *et al.*, 2008; Peichl *et al.*, 2014) and Stordalen Mire in Sweden (e.g. Christensen *et al.*, 2012; Olefeldt *et al.*, 2012; Olefeldt *et al.*, 2013), are just three examples of long-term peatland research sites. As new sites are established, including in the HBL (e.g. Humphreys *et al.*, 2014), data on C dynamics can be

compared across different sites and for multiple years (e.g. Lafleur *et al.*, 2003; Humphreys *et al.*, 2006; Lund *et al.*, 2010; Adkinson *et al.*, 2011).

2.3 Peatlands of the Hudson Bay Lowland (HBL)

The HBL peatlands comprise the second largest expanse of northern peatland in the world, extending over 250,000 km² (Riley, 2011). Most HBL peatlands (80 %) are in northern Ontario but they also extend to Manitoba, and to northern Quebec, east of James Bay. More than 90 % of the HBL land cover is peatland or wetland (Riley, 2011). Most of the HBL peatlands are bogs and fens occurring in a complex mosaic with bog pools and small lakes across the landscape (e.g. Sjörs, 1959; Sjörs, 1963; Glaser *et al.*, 2004a; Riley, 2011; Packalen *et al.*, 2016). In more northern parts of the HBL where permafrost is both discontinuous and continuous (Cowell *et al.*, 1978; Dyke and Sladen, 2010), peat plateau, palsa and tundra occur (12 % land cover).

The HBL is a basin of Paleozoic carbonate rocks (limestone, dolostone) surrounded by the Precambrian granite rocks of the Canadian Shield (Riley, 2011). Kimberlite pipes also occur as vertical intrusions into the limestone throughout the HBL. The peatlands are underlain by marine clays that were deposited following the retreat of the Laurentide Ice Sheet and marine incursion that formed the Tyrrell Sea between 7000 and 8500 years BP (Dredge and Cowan, 1989). The HBL began to emerge from the Tyrrell Sea approximately 6000 years BP due to isostatic uplift of the land (Dredge and Cowan, 1989), causing the formation of tidal marshes that eventually began to accumulate peat as fens (Glaser *et al.*, 2004a; Riley, 2011). As isostatic uplift continued and water drained toward Hudson Bay, *Sphagnum*-dominated peatlands established on drier fen hummocks (Klinger and Short, 1996; Hasley *et al.*, 2000; Glaser *et al.*, 2004b; Bunbury *et al.*, 2012). Over the last 6000 years, land continued to emerge creating a regional chronosequence of peatland types (Glaser *et al.*, 2004a and 2004b). Continued and rapid isostatic uplift has been an important factor in the formation of the extensive peatlands now present in the HBL. Webber *et al.*, (1970) state the rate of uplift for the past 1000 years as 1.2 m every 100 years, causing the peatlands to slope towards Hudson Bay with an average gradient of 1 m per km (Dyke and Sladen, 2010). Thus, peat is generally older and thicker further inland from Hudson Bay (Martini, 2006; Packalen *et al.*, 2016). Depth of peat for different peat types and within individual peat landforms varies however, with peat \sim 3 m deep recorded in bogs and less than 2 m in fens (Riley, 2011).

Rates of C accumulation for a bog in the Attawapiskat area of the HBL were high between 6700 to 5500 years BP (average 30.7 g C m⁻² yr⁻¹), corresponding to the transition from fen to *Sphagnum*-dominated bog (Bunbury *et al.*, 2012). This period of transition from a fen community to ombrogenous bog is consistent with studies of peat cores in other parts of the HBL by Jeglum and Cowell (1982), Klinger and Short (1996), and Glaser *et al.*, (2004b). From 5500 to 1000 years BP, rates of C accumulation declined, reaching an average value of 20.3 g C m⁻² yr⁻¹ between 1000 and 600 years BP (Bunbury *et al.*, 2012). These estimates of are within the range of 20 to 30 g C m⁻² yr⁻¹ reported by Gorham *et al.*, (2003). Analysis of 100 peat cores from across the HBL revealed an average peat accumulation rate of 18.5 g C m⁻² yr⁻¹ (Packalen *et al.*, 2014). Due to differing climate conditions across the HBL, C storage varies for both bogs and fens, with greater C stored as peat in warmer and wetter regions (Packalen *et al.*, 2016). Overall, the HBL peatlands currently store ~ 30 Pg C and are net C sinks (Packalen *et al.*, 2014; Humphreys *et al.*, 2014).

2.4 Peatland development – hypotheses and models

Initial hypotheses of peatland form and development were outlined by Ivanov (1981), Ingram (1978; 1982) and Clymo (1884). Ingram (1978) described a column of peat as having two distinct layers – an upper acrotelm and a lower catotelm, with the boundary defined as the lowest position of the water table. Clymo (1984) further defines the two layers based on relative rates of decomposition, where the upper acrotelm is mostly oxic and so rates of decay are faster than the lower and mostly anoxic catotelm. In Clymo's model of peat accumulation, plant matter is added to the catotelm (through net primary production, NPP) and then slowly buried as a mass of partially decomposed peat as the water table rises. The anoxic conditions in the catotelm slow the decay of the plant matter and so peat accumulates in the catotelm. As production exceeds decomposition the thickness of the peat slowly increases over time.

The presence of small-scale variations in surface elevation (microtopography), and hence the water table depth, on many northern peatlands suggests spatial variations in production and decomposition cause the rate of peat accumulation to differ across a peatland (Clymo, 1984). Dominant microforms are typically hummocks and hollows at a spatial scale of 1 m x 1 m (e.g. Cresto Aleina et al., 2015; Malhotra et al., 2016). These microforms may form distinct spatial patterns (or 'microtopes') within peat landforms (individual bogs and fens, or 'mesotopes') and at the landscape scale (bog-fen complex, or 'macrotope') (Belvea and Baird, 2006). Hummock-hollow microtopes may be spatially irregular or form sequences of parallel ridges and pools on slopes (e.g. Ivanov, 1981; Glaser et al., 1981; Foster et al., 1983; Foster et al., 1988a; Swanson and Grigal, 1988; McCarter and Price, 2017). Concentric ridges and pools may develop on raised bogs (e.g. Foster et al., 1988b; Couwenberg and Joosten, 2005), and maze-patterns may occur on peatlands with minimal topographic slope (e.g. Rietkerk et al., 2004b; Eppinga et al., 2008; Eppinga et al., 2009a). Microforms are often visually distinct due to differences in vegetation cover, including different species of Sphagnum moss in wet hollows and on elevated hummocks, and increased shrub and tree cover on hummocks (Andrus et al., 1983; Glaser, 1983; Swanson and Grigal, 1991; Belyea and Clymo, 1998; Andersen et al., 2011).

Belyea and Clymo (1998) hypothesise that despite differences in NPP and decay in hummocks and hollows, the local rate of burial (LRB) must be the same. If this differed for each microform then differences in surface elevation for hummocks and hollows would be extreme, certainly not consistent with observations of peat landscapes and in peat cores. Belyea and Clymo (1998) suggest that hummock growth is constrained by the growth of an adjacent hollow. Hummock NPP is greater than the hollow due to greater cover of vascular plants, particularly shrubs that prefer their roots to be above the water table. This greater hummock NPP is a positive feedback for hummock growth as surrounding hollows are unable to reach the same NPP due to higher water tables. But as the height of the hummock increases, the length of time that the acrotelm is exposed to decay increases. Hummock growth therefore slows, making LRB the same as adjacent hollows. This 'peat accumulation mechanism' is discussed further by Belyea and Clymo (2001), describing how this negative feedback between peat formation and acrotelm thickness in hummocks and hollows enables steady long-term rates of C accumulation in peatlands (Belyea and Clymo, 2001).

Various models have advanced the developing theory of peat accumulation to understand long-term processes, with most models based on the two-layer (or diplotelmic) column model of peat accumulation described by Hilbert *et al.*, (2000). These models allow for a better understanding of the relationships and possible feedbacks among vegetation, hydrology, and nutrients controlling peat accumulation. For example, Hilbert *et al.*, (2000) recognise the importance of a non-linear relationship between production and water table depth in their dynamic peat accumulation model (PAM). Frolking *et al.*, (2001) describe a model of peat decomposition (PDM) to test the hypothesis that long-term peat accumulation is linked to contemporary carbon flux dynamics. The Holocene Peat Model (HPM) developed by Frolking *et al.*, (2010) builds on PDM and PAM to include different decay rates for litter produced by various plant functional types (PFTs).

Other models have considered lateral peat expansion (e.g. Morris *et al.*, 2012), pool formation (e.g. Foster and Wright, 1990), and the spatial interaction of variables for the

formation of ridge-pool patterns in both ombrotrophic bogs and fens (e.g. Swanson and Grigal, 1988; Eppinga *et al.*, 2009a). For example, Eppinga *et al.*, (2009a) provide a model describing spatial interaction among vegetation, nutrients, and hydrology as the cause of ridge, hummock, lawn, and hollow patterns in peatlands. The model suggests that the spatial regularity of ridges and hollows could be driven by an evapotranspiration (ET)-induced feedback between ridge vegetation and nutrient availability ('nutrient accumulation mechanism' proposed by Rietkerk *et al.*, 2004b). The hypothesis that vegetation communities control the spatial variability of ET in wetlands is supported by Brown *et al.*, (2010), who also reported a link between microtopography and ET. Eppinga *et al.*, (2008) outline the results of an empirical test of this hypothesis in a Siberian bog. Field data supported model predictions, with higher concentrations of nutrients on hummocks than hollows, and a diurnal response of water table depth to ET.

Much work has been done to improve models of peatland growth through further theoretical and empirical studies. This has resulted in the addition of more realistic hydrological parameters to the models and a better understanding of complex peatland ecohydrology (Baird *et al.*, 2008; Morris *et al.*, 2011a; Morris *et al.*, 2011b). Models of peatland hydrology consider the role of hydrological flows (precipitation, surface water and groundwater) on biogeochemical processes in peatlands (mainly for bogs). Some of these models present conflicting ideas for groundwater flow within peatlands. For example, Ingram (1982) developed the 'groundwater mound hypothesis' (GMH) for a small raised bog in Scotland. This 'shallow-flow' hypothesis assumes that groundwater within the peat mound is controlled by the low permeability of peat (particularly in the catotelm) and that only horizontal flow occurs. Belyea and Baird (2006) reviewed the assumptions for the GMH and concluded that its application may be limited to a small number of peatlands with a constant size and shape (in equilibrium state). Siegel and Glaser (2006) also discuss the GMH and

conclude that application of the model may be limited to small symmetric raised bogs with simple boundary conditions (e.g. bordered by two parallel streams). The 'shallow-flow' model also contradicts the findings of various field studies of raised bog hydrology, for which an alternative 'groundwater-flow' hypothesis is proposed (e.g. Romanowicz *et al.*, 1993; Glaser *et al.*, 1997; Reeve *et al.*, 2000). These studies found considerable evidence of vertical flows within peatlands (although flows are very small due to low hydraulic conductivities), including flow reversals (e.g. Devito *et al.*, 1997; Fraser *et al.*, 2001a), and interactions with groundwater from underlying mineral substrates (e.g. Siegel and Glaser, 1987). This suggests complex and dynamic groundwater flow within peatlands, although the possible influence on biogeochemical processes and peatland development, including the formation of surface patterns and microtopography, is uncertain.

Although the two-layer model (one-dimensional) of peatland growth (Clymo, 1984) works well for ombrogenous bogs and is an important component of continuing theory and model development, there is much discussion on whether this is suitable for modelling other peatland processes. Most authors argue the two-layer model limits modelling of peatland ecohydrology, which can be temporally and spatially complex (Hilbert *et al.*, 2000; Holden and Burt, 2003; Morris and Waddington, 2011; Morris *et al.*, 2011b). Fens with more variable hydrological inputs (including a major groundwater component) will likely require a two-dimensional framework. Models of peatland development in fens may then be used with models for ombrotrophic peatlands to further understand landscape-scale peatland development. The development of two-dimensional models will be particularly important for the peatlands of the HBL, where the development of individual bogs and fens are linked through landscape-scale hydrological processes (Glaser *et al.*, 2006).

2.5 Vegetation and environment relationships

Microtopography and spatial surface patterns in peatlands are visually evident as distinct differences in vegetation. Environmental factors (alkalinity, nutrients, hydrology, elevation etc.) influencing patterns of peatland vegetation were initially identified by Sjörs (1948) and then explained further by Vitt and Slack (1984), Vitt and Chee (1990), Swanson and Grigal (1991), Charman (1993), Nordbakken (1996), Camill (1999), Andersen *et al.*, (2011) and Malhotra *et al.*, (2016), among others. The influence of water table on plant species composition has been shown by various researchers, particularly the importance of the water table or soil moisture on *Sphagnum* species (e.g. Ridolfi *et al.*, 2006; Rydin, 1993b; Schouwenaars and Gosen, 2007).

The relation between vegetation and factors controlling peat accumulation within different microforms is an important consideration in peatland development. Species composition influences litter quality (Belyea, 1996; Dorrepaal *et al.*, 2009; Moore *et al.*, 2007) and availability of recalcitrant material, and therefore the capacity for C accumulation in a peatland. *Sphagnum* is particularly important (e.g. Malmer *et al.*, 2005) as the litter is recalcitrant compared to that formed by most vascular plants (Johnson and Damman, 1993). Due to slower decay rates, peat accumulation will typically be greater in peatland microforms with a higher percentage cover of *Sphagnum* species, and particularly hummock species (e.g. Bengtsson *et al.*, 2016). Species composition also influences nutrient cycling within different microforms, with vascular plants considered to play a particularly important role for hummock formation (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a).

Microtopography and associated vegetation communities also affect the function of peatland systems. These effects are evident in the spatial variation of CH_4 fluxes from different microforms within a peatland. For example, Bubier *et al.*, (1993b) describe the difference in average CH_4 flux at hummocks and hollows, and the relation of water table

depth within each feature. CH₄ emissions are significantly larger from hollows than those from hummocks, partly due to greater CH₄ production rates in hollows (higher anaerobic respiration by methanogens) and greater oxidation of CH₄ in hummocks. Larger CH₄ emissions from hollows and pools have also been attributed to the greater cover of sedges that are typical of these microforms (Gignac *et al.*, 2004; Strack *et al.*, 2006a). Relationships between microtopography and the net ecosystem exchange (NEE) of CO₂ are less variable than CH₄, but components of NEE (e.g. gross primary productivity (GPP) and ecosystem respiration (ER)) may differ significantly across microforms (e.g. Moore *et al.*, 2002; Bubier *et al.*, 2003; Pelletier *et al.*, 2011; Laine *et al.*, 2012).

Models of peatland development include different plant communities as 'plant functional types' (PFTs) and these are generally considered to be a simple way of including vegetation-environment relationships in peatland development (Dorrepaal, 2007). The PFT classification used in models by Frolking *et al.*, (2010) is based on the ecological niche requirements of plant species in terms of nutrient availability and water table depth (Tuittila *et al.*, 2013). The model therefore includes minerotrophic sedges, ombrotrophic shrubs, and hummock *Sphagnum* as distinct PFTs.

Although lichens are a common feature of many northern peatlands (generally above $\sim 50^{\circ}$ latitude), their role in peatland structure and function is not well understood, and they are not included as PFTs in existing models of peatland development. Lichens are composite, symbiotic organisms comprising a fungus (mycobiont) and a photosynthetic partner such as algae and/or cyanobacteria (photobiont), and often cover extensive areas of raised bogs, palsa, and peat plateaus (Glaser and Janssens, 1986; Ahti and Oksanen, 1990; Brodo *et al.*, 2001). The fruticose lichens of *Cladonia* spp. are dominant in northern peatlands, including the HBL (Riley, 2011). These lichens form large mats over *Sphagnum* hummocks and upper lawn areas (Ahti and Oksanen, 1990; Nordbakken, 1996). For example, in raised peat bogs

and drier peatlands in the HBL, *Cladina stellaris* will establish and grow over *Sphagnum fuscum* hummocks with lichen cover up to 25 cm deep in places (*personal observation*). Lichens may establish on patches of peatland subject to persistent dry surface moisture conditions, and where there is limited nutrient availability for the growth of vascular plants, which would otherwise out-compete the lichens (Kershaw, 1977; Økland, 1992; Cornelissen *et al.*, 2001). The abundance and persistence of lichens in northern peatlands would suggest they play an important role in peatland development and yet this subject has received little attention in the literature.

2.6 Peatlands and Environmental Change

Significant increases in atmospheric concentrations of CO₂, CH₄, and nitrous oxide (N₂O) over the past 200 years have resulted in anthropogenic radiative forcing, causing climate warming (IPCC, 2014). Climate warming is likely to affect C cycle processes within terrestrial ecosystems including peatlands, potentially causing further increases in atmospheric CO₂. Although evidence for the effects of climate warming on terrestrial ecosystems is increasing, potential impacts on northern peatlands remain uncertain. Most studies suggest climate warming with prolonged periods of drought will result in drier surface peat and lower water tables (Hilbert et al., 2000; Riutta et al., 2007; Flanagan et al., 2011; Wu and Roulet, 2014; Thompson et al., 2017). Studies of northern peatlands with lower water tables due to drainage indicate a change in peatland structure (vegetation change from Sphagnum mosses to vascular plants, particularly woody shrubs, e.g. Weltzin et al., 2000; Talbot et al., 2010; Walker et al., 2015) and function (biogeochemical change including loss of C, e.g. Munir et al., 2014; Strack et al., 2008), although the effects of drainage on structure and function vary for different peatland sites. In addition to drier surface conditions and lower water tables, warmer temperatures will likely increase decomposition of deep peat deposits and release a significant amount of C to the atmosphere (Dorrepaal et al., 2009). Ise *et al.*, (2008) and Bridgham *et al.*, (2008) also propose this scenario of warming-induced decomposition of peat deposits and the release of large amounts of carbon. In contrast, Wilson *et al.*, (2016) suggest that although surface C (acrotelm) may be affected by climate warming, there may be little change in C storage in the catotelm. Charman *et al.*, (2013) also suggest an alternative scenario, of increased carbon sequestration due to increased primary productivity that is caused by a longer growing season and increased photosynthetically active radiation (decrease in cloud cover).

The uncertainty in how peatlands may respond to the effects of climate warming is due to our limited understanding of the complex feedbacks operating in peatlands that allow self-regulation and resilience to environmental change (Ivanov, 1981; Belyea and Malmer, 2004; Belyea, 2009). Peatlands are spatially heterogeneous ecosystems, with microforms occupying alternative stable states, either a wet stable state (hollows) or a dry stable state (hummocks) (Hilbert et al., 2000; Carpenter, 2001; Scheffer and Carpenter, 2003; Eppinga et al., 2009b). This spatial heterogeneity or 'patchiness' likely reduces the potential for catastrophic regime shifts (Scheffer et al., 2001; van Nes and Scheffer, 2005), which in peatlands may be a shift from an open pool or hollow dominated peatland, to a drier treed hummock dominated peatland (Eppinga et al., 2009b). The combination of spatial heterogeneity, self-regulating structure, localized flows and non-linearity in peatlands has led Belvea and Baird (2006) to describe peatlands as 'complex adaptive systems' (CAS) (Levin, 1998). CAS are steady or long-lasting as they can recover from perturbations that may push the system towards alternative stable states (e.g. van Nes and Scheffer, 2005; Carpenter, 2013; Kéfi et al., 2013; van de Leemput et al., 2015). CAS would seem to apply to peatlands although the mechanisms are not well understood (e.g. Hilbert et al., 2000; Rietkerk et al., 2004a; Eppinga et al., 2009b; Swindles et al., 2012; Morris et al., 2015). We do not know how feedback mechanisms will respond to changing environmental conditions (e.g.

vegetation-hydrology feedbacks) and there is currently insufficient knowledge to determine possible threshold conditions (or 'tipping points') for hydrology and vegetation that may push these systems out of a stable state (e.g. Eppinga *et al.*, 2009b; Scheffer *et al.*, 2012).

Climate change may have significant impacts on the peatlands of the HBL. These peatlands are sustained by a cool, wet climate influenced by the unimpeded movement of arctic air masses across the flat landscape (Martini, 2006; Riley, 2011). The cooling effect of persistent sea ice on Hudson Bay on the climate of the HBL (Rouse, 1991) is responsible for the distribution and extent of permafrost peatlands in the region, and the vegetation and hydrological characteristics (and therefore C storage) of non-permafrost bogs and fens (Packalen et al., 2016). However, researchers are now documenting increases in air and seasurface temperatures. Changes in the phenology and reductions in the extent of sea ice on Hudson Bay are noted to be amplifying regional warming (Gagnon and Gough, 2005; Hochheim and Barber, 2010). Rühland et al., (2013) recently revealed biological evidence of the rapid warming of the HBL. They evaluated paleolimnological records of lake-sediment cores to discover significant biological changes in lakes in the region since the onset of rapid warming in the mid-1990s. The effects of rapid warming on the HBL peatlands are yet to be determined. Also, as the HBL is remote with very limited infrastructure development, there have been very few opportunities to study the effects of drainage on peatland structure and function. Whittington and Price (2012; 2013) describe the hydrological changes in a peatland in the HBL that has been impacted by dewatering from a nearby mining operation (the De Beers Victor Diamond Mine) but no research has yet been done to understand the potential impact of this hydrological change (drainage) to peatland structure and function, at this site or any other location in the HBL. With any changes to the structure and function of the HBL peatlands having potentially significant consequences for global climate, there is clearly a need for increased research effort in this region (e.g. Yu, 2012; Gorham et al., 2012).

The unique ecology of the HBL and the importance of these peatlands as a C store has been recognised in the Far North Act (Bill 191, Statutes of Ontario 2010; Far North Science Advisory Panel, 2010), which outlines land-use planning objectives for the Far North of Ontario. One of the five objectives of the Act is 'the maintenance of biological diversity, ecological processes and ecological functions, including the storage and sequestration of carbon in the Far North'. There are many uncertainties and challenges that will need to be overcome to achieve this objective however (McLaughlin and Webster, 2013; McLaughlin and Webster, 2014), including the many gaps and uncertainties in our knowledge of peatland development mechanisms and response to environmental change.

2.7 Conclusions from literature review

This review confirms the need for further research to understand the relationship between the structure and function of northern peatlands (bogs and fens). Further empirical evidence would be beneficial for testing existing hypotheses and models of peat accumulation and understanding the complex feedback mechanisms within peatland systems. We still do not fully understand some of the more basic processes and feedbacks operating within peatland systems (e.g. plant species composition, hydrology and nutrient interactions) and particularly if these mechanisms are relevant to all northern peatlands. There is currently limited field evidence to support proposed small-scale structuring mechanisms for peatland development (e.g. Belyea and Clymo, 2001, Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a), and particularly if these mechanisms are applicable to HBL peatlands (Chapter 3).

Plant species composition is an important factor influencing peat accumulation, as it determines photosynthetic capacity, productivity and litter quality. Lichens are a common feature of many northern peatlands, often covering extensive areas of the peatland surface. However, there has been limited research on the role of lichen on peatland development (e.g. Malmer and Wallen, 1999), with most studies focusing on lichens within drier boreal forest ecosystems (e.g. Kershaw, 1977; Botting and Fredeen, 2006), the spectral properties of lichens (Neta *et al.*, 2011), and the importance of lichen as a food source for caribou (Boudreau and Payette, 2004; Dunford *et al.*, 2006). Further analysis of vegetation associations within peatlands, particularly the effect of lichen growth on peat accumulation is required (Chapter 4).

Climate warming will alter environmental conditions and therefore the feedback mechanisms that control peatland development. Models of peatland development (such as the HPM, Frolking *et al.*, 2010) allow for some manipulation of model parameters that control feedback mechanisms, thus simulating the predicted effects of climate change. However, field evidence to test the outputs and predictions of peatland development models and climate change scenarios is limited. Very few researchers present an analysis of how feedback mechanisms may be altered by changing environmental conditions using field data, and how this may then influence function (e.g. Belyea and Malmer, 2004; Eppinga *et al.*, 2009b). This represents a significant research gap, one that is fundamental to our knowledge of the future role of northern peatlands in global climate regulation. The question of whether peatlands are self-regulating systems is essential when considering the likely impacts of climate change and feedbacks to global climate. Understanding the response of peatland structure and function to environmental change is particularly important for the HBL peatlands, for which there has been limited research (Chapter 5).

CHAPTER 3 - Small-scale structuring mechanisms for surface patterns in peatlands of the Hudson Bay Lowland

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3.1 Context within thesis

As described in the literature review (Chapter 2), the development of microtopography (hummocks and hollows) and spatial surface patterns in northern peatlands may be explained by relationships and feedbacks among vegetation, hydrology and nutrients that control peat accumulation. These small-scale structuring mechanisms (microform to microtope scale) are described by several authors (e.g. Belyea and Clymo, 2001, Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a), and tested using field data and modelling studies. The proposed mechanisms present conditions and predictions that would benefit from further empirical evidence to support theoretical relationships for peatland structure and function. Research examining the structure and function of the vast and remote HBL peatlands is particularly limited, and none of the proposed mechanisms have been tested using data from the HBL.

In this chapter, I examine relationships among vegetation, hydrology, and nutrients for HBL peatlands within the context of proposed mechanisms for microform development and surface patterns. I test whether the conditions for these small-scale structuring mechanisms apply to HBL peatlands, specifically different ecohydrological settings within an ombrogenous bog and a minerogenous fen.

3.2 Abstract

Spatial surface patterns of hummocks, hollows, ridges, and pools (microtopography) are common features of many northern peatlands, and are particularly distinct within the vast and remote peatlands of the Hudson Bay Lowland (HBL). Various hypotheses and models describe how small-scale feedbacks among vegetation, hydrology, and nutrients cause spatial differences in peat accumulation and thus, the development of microtopography and spatial surface patterns. Empirical evidence to support conditions and predictions for proposed mechanisms remains limited however, and it is uncertain if the mechanisms apply to HBL peatlands. To test proposed mechanisms and model predictions, we investigated relationships and feedbacks controlling peatland structure and function in an ombrogenous bog and a minerogenous fen in the HBL. Our sites represent microtopography and surface patterns found in many northern peatlands, specifically spatially irregular hummocks and hollows, and patterns of parallel ridges and pools that are perpendicular to slope. We found the occurrence of different spatial patterns depends on position within a peat landform, with these differences attributed to varying ecohydrological setting related to landscape-scale hydrology. In turn, the ecohydrological setting influences the strength and direction of feedback mechanisms at the microform scale. Our data support the prediction of a positive feedback between plant productivity and acrotelm thickness for peat accumulation and hummock growth, and that this may be enhanced by water ponding on slopes to form distinct ridge-pool tracks. We did not find evidence of a feedback for hummock growth by evapotranspiration (ET)-driven transport of water and nutrients to hummocks. We suggest a combination of mechanisms operating at varying temporal and spatial scales are required for the development of surface patterns in HBL peatlands.

3.3 Introduction

Peatland ecosystems cover almost 4.5 million km² or 3 % of the global land area and are dominant in boreal and subarctic regions due to cool and moist climate conditions that are ideal for the accumulation of organic matter (Tarnocai, 2006; Yu et al., 2011). Although these northern carbon-rich ecosystems are mostly low-lying and may appear flat, small-scale variations in surface elevation (microtopography) are evident and often form distinct spatial patterns (microtopes) across the landscape (Belyea and Clymo, 1998; Couwenberg and Joosten, 2005; Belyea and Baird, 2006). The dominant microforms are typically hummocks and hollows at a spatial scale of 1 m x 1 m (e.g. Cresto Aleina et al., 2015; Malhotra et al., 2016) that may converge to form tracks of parallel ridges and pools on slopes (e.g. Ivanov, 1981; Glaser et al., 1981; Foster et al., 1983; Foster et al., 1988a; Swanson and Grigal, 1988; McCarter and Price, 2017), concentric ridges and pools (e.g. Foster et al., 1988b; Couwenberg and Joosten, 2005), maze-patterns on flat areas (e.g. Rietkerk et al., 2004b; Eppinga et al., 2008 and 2009a), or remain spatially irregular (e.g. Belyea and Clymo, 2001; Malhotra et al., 2016). These patterns are usually accentuated by differences in vegetation cover that correspond to environmental gradients, such as different species of Sphagnum moss in wet hollows and on elevated hummocks, and increased shrub and tree cover on hummocks (Andrus et al., 1983; Glaser, 1983; Swanson and Grigal, 1991; Andersen et al., 2011).

Surface patterns are particularly striking across the extensive peatlands of the Hudson Bay Lowland (HBL) in northern Ontario, Canada, with spatially variable patterns or microtopes evident within single peat landforms (e.g. a raised bog mesotope) and the wider landscape (e.g. bog-fen complex or macrotope) (Figure 3.1; Sjörs, 1959; Sjörs, 1963; Belyea and Baird, 2006; Riley, 2011). Approximately 6 % of the northern peatland C pool (~ 30 Pg C) is contained with these vast peatlands that extend over 250,000 km² (Riley, 2011; Packalen *et al.*, 2014). Peatland development in the HBL began after deglaciation around 8000 years ago, and since then the region has experienced rapid glacial isostatic uplift significantly influencing regional hydrology (Glaser *et al.*, 2004b; Packalen *et al.*, 2014). The resulting landscape comprises a complex mosaic of peat landforms (mostly bogs and fens) spread within a network of rivers and fen water tracks (Glaser *et al.*, 2004a; Riley, 2011).

Surface patterns within peatlands have been the subject of various studies (e.g. Glaser et al., 1981; Foster et al., 1983; Foster et al., 1988a; Foster et al., 1988b; Belyea and Clymo, 1998; Couwenberg and Joosten, 2005; Eppinga et al., 2008) but so far very few have examined structural patterns within the remote HBL peatlands. Sjörs (1959; 1963) and Riley (2011) provide a detailed account of surface patterns within HBL peatlands, describing relationships among vegetation, hydrology, and geomorphology that influence pattern formation, mostly at the landscape (mesotope to macrotope) scale. The important role of isostatic uplift in altering hydrogeologic setting and thus the development and morphology of peat landforms in the HBL is described by Glaser et al., (2004a and b). Variability in regional climate also contributes to the spatial distribution of peat landforms and stored C in the HBL (Packalen et al., 2016). But our knowledge of relationships and processes operating at smaller scales (e.g. microform to microtope scale - Belyea and Baird, 2006) in HBL peatlands is limited. Identifying ecohydrological and topographic mechanisms that control peatland structure is essential to understand biogeochemical function (e.g. CO₂ exchange), particularly for HBL peatlands which may be especially sensitive to environmental change, including the effects of climate warming (Gagnon and Gough, 2005; Ruhland et al., 2013; Delidjakova et al., 2016).

Various hypotheses and models for pattern formation in peatlands have been proposed, each describing mechanisms for small-scale variations in production and decomposition that cause the rate of peat accumulation to differ across a peatland (Clymo,

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1984). relationships These models describe and autogenic feedbacks among microtopography, hydrology, and vegetation at the microform-microtope scale within these spatially 'self-organised' ecosystems (Rietkerk et al., 2004a; Couwenberg and Joosten, 2005; Eppinga et al., 2009a; Eppinga et al., 2009b; Malhotra et al., 2016). These small-scale structuring mechanisms are described in several modelling studies, each focusing on different peatland surface patterns, and applied to peatlands in North America, northern Europe (Scotland and Sweden), and Western Siberia (Swanson and Grigal, 1988; Belyea and Clymo, 2001; Rietkerk et al., 2004b; Eppinga et al., 2008; Eppinga et al., 2009a).

Small-scale variations in peat accumulation may be caused by differences in hydrology and vegetation that alter local net primary production (NPP) and rates of decay (Belyea and Clymo, 1998; Malmer and Wallen, 1999). Hummock NPP is larger than in hollows due to greater cover and biomass of vascular plants (particularly shrubs) that prefer drier conditions above the water table. Larger hummock NPP increases input of plant matter added to the upper oxic acrotelm and then to the lower anoxic catotelm, slowly increasing the thickness of the acrotelm over time. The result is a positive feedback for hummock growth, with surrounding hollows unable to reach the same NPP due to high water tables constraining woody shrub growth. As the height of the hummock increases however, the length of time the acrotelm is exposed to decay increases. This slows hummock growth, reducing the difference in height between hummocks and adjacent hollows. Despite differences in NPP and decay in hummocks and hollows, the local rate of burial (or peat added to the catotelm) is therefore the same (Belyea and Clymo, 1998; Belyea and Clymo, 2001). The positive feedback between plant productivity and acrotelm thickness required for the 'peat accumulation mechanism' enables microforms to persist over time and for steady long-term rates of C accumulation (Belyea and Clymo, 2001).

The peat accumulation mechanism may be further enhanced by ponding of surface water upslope of hummocks that have lower hydraulic conductivity than hollows or pools (Swanson and Grigal, 1988). Water ponding further constrains hollow or pool NPP and increases hummock growth relative to the hollow or pool. This 'water ponding mechanism' is considered a significant control for the development of ridge-pool tracks (or 'ladder fens') that align perpendicular to the slope of raised peat domes (Foster *et al.*, 1983; Foster *et al.*, 1988a; Couwenberg and Joosten, 2005).

Greater vascular plant cover on hummocks may also drive diurnal changes in water table that result in hydraulic gradients between microforms, enabling nutrient transport from adjacent hollows or pools (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2008; Eppinga *et al.*, 2009a). This 'nutrient accumulation mechanism' assumes greater evapotranspiration (ET) rates for vascular plants causes the water table in hummocks and ridges to drop during the day. Due to smaller vascular plant cover and higher hydraulic conductivity of adjacent hollows and pools, the water table does not decrease as much, creating a hydraulic gradient between the hummock and the hollow. This hydraulic gradient causes water flow towards the hummock at night (when ET is zero). Consistent transport of water and nutrients (N and P) to hummocks causes nutrients to accumulate under the hummock that become locally available for increased growth of vascular plants. The positive feedback between plant productivity and nutrient availability facilitates a self-reinforcing system for hummock and ridge formation in peatlands (Eppinga *et al.*, 2009a).

Modelling studies based on theoretical assumptions and supported by limited field data, indicate that the proposed mechanisms for pattern formation in peatlands are plausible (e.g. Eppinga *et al.*, 2009a; Eppinga *et al.*, 2010; Morris *et al.*, 2012). It is not certain however, if the proposed mechanisms are applicable to all peatlands, or if only one or a combination of mechanisms are required to produce specific surface patterns within a

peatland (e.g. Eppinga *et al.*, 2009a). Variations in regional climate and local environmental conditions are also likely significant controls on which mechanisms may occur within peatlands and at different geographical locations (Eppinga *et al.*, 2010).

The peat accumulation and nutrient accumulation mechanisms also present seemingly contradictory conditions for hydraulic gradients at the microform-microtope scale. Rietkerk *et al.*, (2004b) and Eppinga *et al.*, (2008) highlight the importance of lateral water flow from hollows (or pools) to hummocks (ridges) for nutrients to accumulate under hummocks. In contrast, Belyea and Clymo (2001) suggest differential rates of submergence (or water level rise) at the acrotelm-catotelm boundary cause higher water tables under hummocks than hollows, resulting in a lateral flow of water from hummocks to hollows. These hydrological conditions cannot occur at the same time which means each mechanism is likely limited by peatland type (e.g. differing ecohydrology of bogs and fens), to different regional climates, or possibly seasonal factors influencing vegetation growth and hydrology. Position within different peat landforms (ecohydrological setting) is likely also an important factor for each mechanism, as this affects vegetation composition and therefore local production and decomposition rates, as well as the potential influence of slope (e.g. cross-scale processes and feedbacks - Belyea and Baird, 2006).

Small-scale structuring mechanisms enable spatial self-organisation in peatlands and ecosystem stability during periods of environmental change (Belyea and Clymo, 2001; Eppinga *et al.*, 2009b). Yet our understanding of these mechanisms remains limited. Considering the scale and importance of HBL peatlands as a C store, knowledge of which mechanisms may occur under different ecohydrological and climate conditions is essential. The objective of our work was to investigate proposed conditions and predictions for each mechanism using data collected from the HBL, and to determine which mechanisms may apply to bogs and fens, the main peat landforms within the HBL. We hypothesise that (a) relationships among vegetation, hydrology, and nutrients at the microform-microtope scale determine possible structuring mechanisms (Table 3.1), and (b) the occurrence of small-scale structuring mechanisms depends on peat landform type and ecohydrological setting within peat landforms (microtope-mesotope scale).

3.4 Methods

Site Description

The site is accessed by a ~ 1.5 km long raised boardwalk located approximately 90 km west of Attawapiskat and 13 km south of the De Beers Canada Victor Mine ($52^{\circ}49'06''$ N, $83^{\circ}54'18''$ W; ~ 83 m elevation) in northern Ontario, Canada. The boardwalk crosses an ombrogenous raised bog (unofficially named MOE Bog, $52^{\circ}41'36''$ N, $83^{\circ}56'41''$ W; ~ 93 m elevation) through to a moderately-rich minerogenous fen (MOE Fen, $52^{\circ}42'02''$ N, $83^{\circ}57'18''$ W; ~ 91 m elevation), the two dominant peatland types in the HBL (Riley, 2011; Ulanowski and Branfireun, 2013; Ulanowski, 2014; Humphreys *et al.*, 2014). The boardwalk joins two eddy covariance (EC) towers – one located near the apex of MOE Bog and the other tower located within MOE Fen. The site is located within the zone of discontinuous and sporadic permafrost (Riley, 2011) but there is no permafrost at the site.

Mean annual temperature is - 1.3 °C (1971-2000, Lansdowne House, 280 km WSW - Environment Canada, 2016) with daily averages ranging from - 22.3 °C in January and to 17.2 °C in July. Mean annual precipitation is ~ 700 mm, predominantly as snowfall in all months but July and August. During our study in 2013, total annual (and June through August) evapotranspiration (ET) in MOE Bog and MOE Fen was 347 (216) mm and 459 (225) mm, respectively (MOE tower, data not shown). In 2014, total annual (and June through August) ET in MOE Bog and MOE Fen was 362 (224) mm and 317 (226) mm, respectively. Mean annual (and June through August) temperature in 2013 and 2014 was -2.3

(14.6) °C and -2.6 (15.0) °C, respectively (MOE tower data, not shown). The site received ~ 410 mm precipitation in 2013 and ~ 600 mm in 2014 (MOE EC Tower, data not shown).

We selected four sites within the boardwalk area that represent distinct microtopes (hummock-hollow or ridge-pool complex) within MOE Bog and MOE Fen. The microtopes were identified based on clear visual contrasts in microtopography, dominant vegetation communities, hydrological conditions, and elevation, and were named Bog, Ridge-Pool, Moss, and Fen (Figure 3.1).

Bog is located at the apex of MOE Bog, approximately 150 m from the Bog EC tower. Bog has spatially variable hummock-hollow microtopography, with hummocks ~ 20 - 35 cm higher than hollows. Hummock vegetation includes *Sphagnum fuscum*, *Picea mariana*, *Chamaedaphne calyculata*, *Rhododendron groenlandicum*, *Vaccinium oxycoccos* and *Rubus chamaemorus* (see Table S3.1 for species list and nomenclature). Hollows typically comprise *Sphagnum rubellum*, *R. chamaemorus* and *Carex oligosperma*. There is also extensive lichen cover (mostly *Cladina stellaris* and *Cladina rangiferina*) on both hummocks and hollows.

Ridge-pool is a 100-m section of a large water track (~ 500 m length) within the MOE Bog. The water track (or 'ladder fen') comprises a sequence of ridges and pools (or flarks ranging from 8 to 15 m wide) that are perpendicular to the slope (average topographical slope of -0.0018; Ulanowski, 2014). The water track originates near the apex of MOE Bog before tapering off near the MOE Bog-Fen boundary. Ridges are ~ 2 to 3 m wide and are ~ 20 - 25 cm higher than adjacent pools. Vegetation on ridges comprises *S. fuscum, P. mariana, C. calyculata, R. groenlandicum,* and *V. oxycoccos*. Intermediate lawns occur on the downslope side of ridges with *S. rubellum, R. chamaemorus, Andromeda glaucophylla* and *Eriophorum vaginatum* the typical vegetation. Pool vegetation comprises *Sphagnum majus, C. oligosperma, Carex magellanica, Rhyncospora alba,* and *Tricophorum cespitosum*. Moss represents an area of spatially variable hummock-hollow microtopography near the MOE Bog-Fen boundary. On average, hummocks are ~ 20 - 25 cm higher than hollows. Hummock vegetation includes *S. fuscum*, *P. mariana*, *Maianthemum trifolium*, *C. calyculata*, *A. glaucophylla*, and *V. oxycoccos*. Hollows are wetter than those at Bog, and include *S. majus*, *C. oligosperma*, *C. magellanica*, *Carex pauciflora*, and *Scheuchzeria palustris*.

Fen is located within the large minerogenous MOE Fen (Ulanowski and Branfireun, 2013; Ulanowski, 2014), approximately 100 m from the Fen EC tower. The fen comprises a sequence of parallel ridges and pools that are perpendicular to the slope and flow of groundwater that drains towards a large tributary of the Nayshkootayaow River (average topographic slope of -0.0013, Ulanowski, 2014). Ridge vegetation includes *Dicranum fuscescens, Rhytidiadephus triquetrus, Tomentypnum nitens, Betula pumila, Larix laricina, A. glaucophylla, Rubus acaulis* and *C. calyculata.* Pools include *Scorpidium scorpioides, Menyanthes trifoliata, Equisetum* spp., *Carex lasiocarpa, C. magellanica,* and *Tricophorum alpinum.*

Data were collected from plots representing the dominant vegetation-microform types within each site (e.g. *Sphagnum*-sedge pool, *Sphagnum*-shrub hummock). To limit damage to the site and to enable surveys of otherwise inaccessible areas (e.g. floating *Sphagnum* mats in centre of pools), most plots were established along transects parallel to and within a short distance of the main boardwalk. Where necessary, short sections of additional boardwalk were built.

Surface Elevation Measurements

In 2014, we measured the surface elevation of all plots, transects, and wells (base and top) using a Topcon HiPer Differential Global Positioning System (DGPS), relative to the UTM Zone 17N NAD83 datum (referred to as meters above sea level, m.a.s.l., \pm 0.01 m

horizontal and 0.003 m vertical accuracy). These measurements were checked against elevations for the tower sites recorded using DGPS in 2013 and 2014.

Hydrology

Wells (slotted, 5 cm inside diameter PVC tubes, screened with a mesh cover) were installed within or near each plot and to represent the range of microforms within each site. Water table position was measured continuously (30-minute records) with a capacitance water level probe (Odyssey, Dataflow Systems, New Zealand, loggers calibrated each field season) through June to October in 2013 and 2014, and for three weeks in July 2015. Manual water table measurements were also recorded throughout the study period at all plots. Using the surface elevation measurements for each well, depth of water table below the surface (cm) was converted to water table elevation (m.a.s.l.) for analysis. Short periods where continuous data may have been affected by on-site disturbance (e.g. logger downloads, sampling, wildlife activity) were checked, and if necessary, data removed prior to analysis.

To measure continuous changes in peat moisture content in the acrotelm (above the water table), we installed two Water Content Reflectometers (Campbell Scientific TDR CS616, 30 cm probe length) connected to a CR10x datalogger in two ridges at Fen in July 2015. The probes were installed at ~ 10 – 15 cm depth in the side of each ridge. We also measured the moisture content of peat at 20 cm depth (volumetric water content, VWC %) using a Hydrosense 2 Soil Moisture Sensor fitted with a CS658 water content sensor (Campbell Scientific, 20 cm probe length) at all plots throughout the study period. Volumetric moisture content (%) was calculated from the period (µs) using a custom linear calibration curve of gravimetric moisture content (GWC, % of dry weight) for vegetation and peat samples from each plot ($r^2 = 0.57$ for y = mx + c, where y = VWC as %, m = slope (17.06), c = intercept (0), and x = period in µs).

To determine the distribution and sharpness of boundaries between microforms (hummocks, intermediate, and hollows or pools) at each site, we use the lowest 10 % of WTD measurements (recorded during July and August 2014 for each well), as an estimate of acrotelm thickness (similar to Eppinga *et al.*, 2008). We defined acrotelm thickness as the distance from the peat surface to minimum WTD (lowest 10 %) as this most closely represents the lower limit of the structurally variable acrotelm (or 'peat proper') as described by Clymo (1992).

Diurnal fluctuations in WT elevation may be used to estimate rates of evapotranspiration (ET) (or rates of groundwater consumption) in wetlands and riparian environments (White, 1932; Loheide *et al.*, 2005; Loheide, 2008; Gribovski *et al.*, 2010; Watras *et al.*, 2017). In peatlands, greater vascular plant cover on hummocks or ridges may increase ET rates relative to adjacent hollows or pools, potentially creating hydraulic gradients between microforms that may allow the flow water and nutrients from hollows or pools to hummocks or ridges (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2008; Eppinga *et al.*, 2009a). To determine if this hydrological mechanism for nutrient transport occurred at our sites in the HBL, we analysed diurnal fluctuations in WT elevation using MatLab R2016b. We selected periods with no recorded precipitation events or other on-site disturbance (e.g. logger downloads, sampling, data loss due to wildlife activity) during or 24 hours prior to the start of the period. This gave us four periods, each comprising 2-5 full days, during July and August 2013 and 2014. We applied a simple moving average to smooth data for these time periods, a minimal smoothing technique to remove sensor noise and fluctuations (1 mV equal to < 0.25 mm WT elevation change; Figure S3.1).

Horizontal hydraulic gradients for hummock-hollow pairs were calculated as the difference between WT elevations for each 30-minute interval, divided by the distance between pairs at each site. As described by Loheide *et al.*, (2005) and Eppinga *et al.*, (2008),

change in storage (mm) was calculated as the difference between the maximum and minimum WT elevation during the day (6am to midnight) and night (midnight to 6am) for the selected rain-free periods. Regressions (linear) of night and day changes in WT elevation indicate the rate of advection (mm d⁻¹). Values with adjusted r-square less than 0.3 were considered as zero change in WT elevation. Overall WT trend was calculated as a linear regression of the daily minimum WT for each rain-free period (Eppinga *et al.*, 2008). We also estimated the rate of peat groundwater consumed by ET (ET_G, mm d⁻¹) using equation 1 (White, 1932; Loheide *et al.*, 2005; Loheide, 2008; Carlson Mazur *et al.*, 2014);

$$ET_G = Sy * (\Delta s/t + R)$$
 (eq. 1)

Where Sy is the average specific yield (dimensionless) of the top 20-40 cm of peat (estimates based on mean values in Letts *et al.*, 2000 and Leclair *et al.*, 2015), Δ s (mm) is the daily change in storage calculated as the net rise or fall of the water table over 24 hours, and R is the net inflow rate (recovery or rate of advection, mm d⁻¹) calculated as the rate of change in water table at night when ET is presumed to be zero. As stated by Loheide *et al.*, (2005), ET_G refers to the component of ET that is derived from the saturated zone (peat groundwater and not surface moisture).

Nutrients

Water samples were taken on two sample days in late July and early August 2014, from vegetation-microform types at each site (3 samples per well on each sample day). Wells were purged ~ 48 hours before sampling and samples extracted with a peristaltic pump. Samples were filtered under vacuum (0.45 μ m Macheray-Nagel) within 24 hours, and stored in the dark at ~ 4 °C until analysis for dissolved organic carbon (DOC, mg L⁻¹) and major ions (Ca²⁺, Mg²⁺, K⁺, Na⁺, NO₃⁻-N, NH₄⁺-N, PO₄³⁻, SO₄²⁻, units mg L⁻¹) by Western University (Ecohydrology Lab and Biotron Institute for Experimental Climate Change), London, ON (detailed analysis and quality control procedures outlined in Ulanowski, 2014).

Nutrient availabilities for vegetation-microform types at each site were determined using Plant Root Simulator (PRSTM, Western Ag Inovation, Saskatoon, Saskatchewan, Canada) ion-exchange resin probes (Wood *et al.*, 2015; Wang *et al.*, 2016). Each sample comprised four pairs of probes (one probe adsorbing cations and the other adsorbing anions in each pair). The probes were buried at depths of 5-15 cm and ~ 20-35 cm in hummocks, and 5 - 15 cm in intermediate 'lawns' and hollows/pools, in triplicate plots at all sites. The upper probes in hummocks remained above the water table, whereas all probes in hollows/pools were beneath the water table. Probes in intermediate lawns and at ~ 20-35 cm in hummocks were located at or slightly above the water table, and were likely submerged during the burial period.

The probes were buried for 4 weeks from mid-July to mid-August 2014. During this period (every few days), we measured air and peat temperature at 10 and 20 cm below the surface, peat moisture content for 0 - 20 cm depth, and WTD. After removal, the probes were thoroughly cleaned and rinsed with deionised water, then stored in the dark at 4 °C until analysed according to Hangs *et al.*, (2004). Samples were extracted with 0.5 *M* HCl. Ammonium (NH4⁺-N) and nitrate (NO3⁻-N) were analysed colorimetrically using an automated flow injection analyser (Technicon Autoanalyzer II, Technicon Instrument Corporation, Tarrytown, New York, USA). Other nutrients (P, K, Ca, Mg, Fe, Al, Pb, B, Cu, Zn, S and Mn) were measured by inductively-coupled plasma spectrometry (Perkin Elmer Optima 3000-DV ICP, Perkin Elmer Inc., Shelton, Connecticut, USA). Nutrient availabilities were reported as µg per 10 cm⁻² of the membrane surface area per week, allowing a comparison of relative differences of *in-situ* nutrient availabilities for microforms within and across sites.

Productivity (Net Ecosystem CO₂ Exchange, NEE)

During the 2013 and 2014 growing seasons (June to August), CO₂ fluxes for different vegetation-microform types (triplicates) at each site were measured using clear plexiglass chambers (27.57 L volume, 0.055 m² basal area) fitted with fans and a cooling unit. A portable CO₂ analyser (EGM-4 Environmental Gas Analyser, PP Systems) was used to measure the change in headspace CO₂ concentration (ppm) at 10 s intervals for the first minute and at 30 s intervals for the final 2 minutes. Measurements were repeated for full-light, half-light, and dark conditions (using mesh and opaque shrouds over the chamber). A quantum PAR sensor (PP Systems) was used to record photosynthetic photon flux density (PPFD, μ mol m⁻² s⁻¹) at the same time as CO₂ concentration (Bubier *et al.*, 1998; Pelletier *et al.*, 2011). We measured air and peat temperature at 10 and 20 cm below the surface, peat moisture content, and water table depth, at the same time as all NEE sampling runs.

Net ecosystem exchange (NEE) of CO₂ (μ mol⁻¹ CO₂ m⁻² s⁻¹) was calculated as a linear regression of change in CO₂ concentration in the chamber headspace with time, as a function of volume, air temperature and pressure inside the chamber (Bubier *et al.*, 1998; Strack *et al.*, 2006b; Pelletier *et al.*, 2011). Data with r^2 values less than 0.5 were checked for measurement errors caused by equipment malfunction or weather conditions. Following the data quality check, most data with low r^2 values correspond to very low or no flux (not due to error) and were included in all subsequent analysis.

The relationship between NEE and PPFD was determined using a rectangular hyperbola curve in SigmaPlot 12.0 (equation 2, e.g. Frolking *et al.*, 1998). The sign convention is positive for CO_2 uptake and negative for CO_2 release to the atmosphere.

$$NEE = GP_{max} * \alpha * PPFD / ((\alpha * PPFD) + GP_{max}) + ER, \qquad (eq.2)$$

Where GP_{max} is the maximum gross photosynthetic CO₂ capture at maximum PPFD (µmol CO₂ m⁻² s⁻¹), α is the photosynthetic quantum efficiency (µmol CO₂ m⁻² s⁻¹) per µmol

PPFD m⁻² s⁻¹), and ER is dark ecosystem respiration (μ mol CO₂ m⁻² s⁻¹) (Bubier *et al.*, 2003). Net ecosystem production (NEP, μ mol CO₂ m⁻² s⁻¹) was calculated as gross primary production (GPP) minus ER. Statistical differences in the rectangular hyperbola parameters (GP_{max} and α) between vegetation-microform types at each site were determined from confidence intervals. Differences in GPP, ER, and NEP among vegetation-microform types and the significance of environmental factors (temperature, peat moisture, elevation, WTD) were assessed using Generalised Linear Models (GLM, fixed effects with repeated measures, IBM SPSS Statistics 23). All models shared the same structure where collar was designated as the subject and date as repeated measures, with a covariance components type and using the maximum likelihood method. All models were fit with a gamma distribution and log link. The best model fit was determined using Akaike's Information Criterion (AIC) and restricted -2 log-likelihood (-2logLL). The sequential Sidak method for multiple comparisons (pairwise) was used to determine significant differences between vegetation types and microforms.

Plant Community Composition

Plant community composition was measured at all NEE and PRS plots during July-August 2014 (n = 70). Using the point-intercept method, we recorded the number of times a metal rod (radius ~ 3 mm) 'hit' each plant species for 25 grid points within 0.5 m² quadrats (Larmola *et al.*, 2013). All vegetation was identified to the species level, with nomenclature for vascular plants and moss as Flora of North America (1993+) and Riley (2003), and nomenclature for lichens as Brodo *et al.*, (2001). Bare peat and litter were also recorded for each quadrat.

Species richness (total number of species per plot, alpha diversity), Simpson Diversity (D) and Shannon-Weiner Diversity (H') (evenness) were calculated for each individual quadrat. We also measured vascular green area (VGA) for each gas flux collar in 2013 and 2014. We recorded the total number of green leaves per species, along with the width and length of 20 leaves per species (or all leaves if less than 20). Species-specific formulae based on leaf geometry were applied to determine average leaf size (Wilson *et al.*, 2007). This was then multiplied by the number of leaves and divided by the collar surface area to give the green area index of a vascular plant species ($m^2 m^{-2}$) for the measurement period (mid-July to mid-August). The VGA of each collar was calculated by summing the green area index of all vascular plants present.

Differences in vegetation (species richness, diversity, VGA), WTD, WT elevation, surface elevation, nutrients (water chemistry and PRS probes), temperature, and soil moisture, between microforms and sites were assessed using ANOVAs or appropriate non-parametric tests (e.g. Kruskal-Wallis). Unless noted otherwise, all statistics were conducted using R version 3.3.1 (R Core Team 2016) or IBM SPSS Statistics 23.

3.5 Results

Elevation and Microtopography

Mean elevation (\pm standard deviation) decreased from 93.27 \pm 0.13 m.a.s.l. at Bog, to 92.88 \pm 0.12 m.a.s.l. at Ridge-Pool, 92.15 \pm 0.13 m.a.s.l. at Moss, and 91.74 \pm 0.09 m.a.s.l. at Fen (Figure 3.2a, p < 0.001). The frequency distributions of elevation at each site varied and were poor fits except for Fen (bimodal distribution) (Figure 3.2b). The distribution was approximately normal for Bog and Ridge-Pool, and skewed towards lower elevations for Moss.

All sites showed a bimodal distribution in acrotelm thickness, defined as the distance from the peat surface to the lowest 10 % of WTD measurements during July and August 2014 (Figure 3.3). Despite the inclusion of data for intermediate microforms at all sites (~ 30 % of the total number of observations at each site), this did not change the bimodal distribution.

Acrotelm thickness for hummocks increases from the margin to the apex of the bog, from - 25.7 cm to -30.7 cm and – 45.7 cm at Moss, Ridge-Pool and Fen respectively. Hollow/pool acrotelm thickness is largest at Bog (-22.9 cm) then Moss (-10.7 cm) and Ridge-Pool (-9.3 cm). Acrotelm thickness was smallest at Fen, with -23.1 cm for hummocks and -3.7 cm for pools.

Hydrology

Mean WTD (\pm standard error, July-August 2014) was significantly lower for Bog (-28.6 \pm 0.7 cm, p < 0.001) compared to Ridge-Pool (-13.6 \pm 0.6 cm), Moss (-14.5 \pm 0.9 cm) and Fen (-13.8 \pm 0.8 cm) (Figure 3.4a). For Bog, the range in WTD was significantly larger than Ridge-Pool and Fen (p < 0.05), and the variance was significantly larger than Ridge-Pool, Moss and Fen (p < 0.05). Mean WTD in July-August 2013 was slightly lower (-18.9 \pm 0.8 cm) than the 2014 mean WTD at Ridge-Pool but there were no significant differences between years for other sites.

Mean WT elevation (July-August 2013 and 2014) was highest at Bog, then Ridge-Pool, Moss and Fen (Figure 3.4b, 2014 data shown). The range in WT elevation was greatest at Bog (0.32 m in 2013 and 0.24 m in 2014), followed by Ridge-Pool (0.18 m in 2013, 0.14 m in 2014), Moss (0.11 m in 2013, 0.13 m in 2014) and Fen (0.10 m in 2013, 0.12 m in 2014). Each site showed a strong linear relationship between mean July-August WTD and surface elevation (Table 3.2), but the relationship for combined data from all sites was weak.

Mean July-August WT elevation was significantly different for microforms within each site, with mean hummock WT elevation higher than hollows/pools at all sites in both 2013 and 2014 (Figure 3.4). At Bog, mean WT elevation was slightly greater for some hollows than hummocks, possibly due to the greater range in WT elevations at this site compared to Ridge-Pool and Moss. At Ridge-Pool, mean WT elevation was significantly higher for wells (hummocks and hollows) located upslope, with a mean difference of 0.06 m in 2013 and 0.05 m in 2014 between the highest and lowest WT elevations. The difference in mean WT elevation between adjacent pools (separated by a ridge) was 0.04 m in 2013 but only 0.007 m in 2014. Mean horizontal hydraulic gradients from Bog to Moss (through the water track) were small (~ 0.002) and within the range reported for the same site by Ulanowski (2014). The mean horizontal hydraulic gradient was much smaller at Fen (< 0.0008) and likely close to the error margin of the WT elevation measurements (all gradients < 0.001).

Mean horizontal hydraulic gradients for hummock-hollow pairs at Fen and Ridge-Pool were also very small. Gradients were positive except for small negative gradients (minimum -0.004) in late July/early August 2013 and 2014 (Figures S3.2 and S3.3, 2013 data shown). Gradients at Moss remained positive in 2013 but were slightly negative (minimum -0.001) in early August 2014. Gradients at Bog remained positive during both 2013 and 2014. Greater gradients at all sites correspond to rainfall events. During rain-free periods, mean horizontal hydraulic gradients were less than 0.004 for hummock-hollow pairs at all sites except Bog (gradients < 0.013; Table S3.2).

Diurnal changes in WT elevation were observed at all sites from July through August 2013 and 2014, corresponding to evapotranspiration which ceases at night (e.g. Figure 3.5). During the day, water tables dropped in all microforms at all sites, with no significant differences in the mean change between sites, or for microforms within sites except at Ridge-Pool and Bog in 2013 (Table 3.3). During the night, water tables rose in hummocks at all sites except for Bog. Slight nighttime increases were recorded for pools/hollows at Fen, Moss and Ridge-Pool but there were no significant differences in the mean change for microforms within sites (except Fen and Ridge-Pool in 2013). Nighttime increases in WT elevation were greater for hummocks (ridges) at Fen compared to other sites, although the slope of the increase varied across the selected rain-free periods (Table S3.3). ET_G (mean \pm standard

error) for hummocks was $2.9 \pm 1.0 \text{ mm d}^{-1}$ at Fen, $2.1 \pm 0.7 \text{ mm d}^{-1}$ at Moss, $3.6 \pm 0.5 \text{ mm d}^{-1}$ at Ridge-Pool, and zero at Bog, although the uncertainty was quite large for all estimates (\pm 2.0 standard deviation).

Diurnal changes in VWC (%) at ~ 10 – 15 cm depth (above the water table) were also observed for two ridges at Fen in July 2015 (Figure S3.4), with a mean increase (VWC % \pm standard error) of 0.02 % \pm 0.02 during the night and a 1.15 % \pm 0.18 drop during the day.

Nutrients

Ca and Mg concentrations in water samples were significantly larger at Fen (mean Ca concentration of 39.7 mg L⁻¹ indicative of a moderately-rich fen, Bourbonniere, 2009) than other sites, whereas Bog had significantly larger concentrations of DOC, K, NH₄⁺, and total N (Table S3.4). We did not find any significant differences in water chemistry for different microforms within sites, except for significantly larger DOC concentrations in hummocks than pools at Fen. At Bog, DOC concentrations in lichen-shrub hummocks were larger than *Sphagnum*-spruce hummocks and lichen hollows (ANOVA, p < 0.01).

The PRS probes showed no significant differences in P, K or total N availability (as NH_4^+ , NO_3^- very low/close to detection limits) for microforms within sites, except significantly larger total N availability in hollows than hummocks at Moss (Figure 3.6). Ca and Mg availabilities were significantly larger in pools/hollows compared to the surface of adjacent hummocks at all sites. Zn availability was also larger in pools/hollows at all sites except Fen, and Mn was larger in pools at Ridge-Pool and Fen. Nutrient availabilities were similar at ~ 30 cm depth in hummocks and adjacent pools at all sites, except at Bog where Ca, Mg, and Zn availabilities in hummocks were significantly smaller than adjacent hollows.

Plant Community Composition

Species richness, Shannon diversity, and cover of graminoids and forbs were significantly greater at Fen than other sites (p < 0.03). *Sphagnum* cover was significantly
greater at Moss and Ridge-Pool than Fen and Bog (p < 0.03), and lichens were only recorded at Bog. VGA was significantly larger at Fen and Ridge-Pool than at Moss and Bog (p < 0.001, Table 3.4). This corresponds to vascular plant cover which was significantly greater at Fen (as graminoids and forbs) than other sites (p < 0.02). There were no differences in the cover of trees or shrubs among sites although the species composition differed (e.g. the shrubs *B. pumila* and *Salix* spp. at Fen but not other sites). Shrub cover on hummocks was significantly greater than lower microforms at all sites, and graminoid cover was significantly greater for pools/hollows than hummocks at all sites (p < 0.001). Shannon diversity was significantly greater for hummocks than pools at Fen, but not at other sites. There were no significant differences in species richness among microforms at each site.

Productivity (NEE)

NEE-PPFD relationships were similar for vegetation-microform types at each site, except the poor fit for lichen covered microforms at Bog (Table S3.5). Hummock GPP was significantly larger than hollows/pools at all sites, with GPP for hummocks (combined vegetation types) at Fen, Moss, and Ridge-Pool (means > 3.9 µmol CO₂ m⁻² s⁻¹) significantly larger than hummocks at Bog (mean 2.6 ± 0.21 µmol CO₂ m⁻² s⁻¹, Figure 3.7). GPP for hollows/pools at Fen and Moss (means > 2.6 µmol CO₂ m⁻² s⁻¹) was significantly larger than Ridge-Pool and Bog. Hummock ER was larger than hollows/pools at all sites except Bog, where ER did not differ among microforms. Hummock ER was greatest at Fen (mean -3.0 ± 0.3 µmol CO₂ m⁻² s⁻¹) than the other sites (means smaller than -2.2 µmol CO₂ m⁻² s⁻¹). NEP did not differ between microforms at Moss but was greater for hummocks than hollows/pools at Bog, Fen, and Ridge-Pool. The exception to this were *Eriophorum* tussocks in pools/intermediate microforms at Ridge-Pool where NEP was the same as hummocks. NEP was negative for hollows at Bog and positive for the other sites, with the largest NEP for hollows at Moss (mean 1.88 ± 0.16 µmol CO₂ m⁻² s⁻¹). Hummock NEP (combined vegetation

types) was largest at Ridge-Pool (mean $2.14 \pm 0.23 \ \mu$ mol CO₂ m⁻² s⁻¹) and smallest at Bog (mean $1.2 \pm 0.19 \ \mu$ mol CO₂ m⁻² s⁻¹). WTD and VGA were significant predictors for GPP at Fen and Bog, but at Moss and Ridge-Pool elevation was more significant (Figure 3.8). Peat temperatures (at 10 cm depth) were positively correlated to ER at all sites (warmer temperatures have larger ER) (Table S3.6). WTD was also significant for ER but at Bog and Fen only (deeper water tables have larger ER), and VGA significant at Fen only (larger VGA has larger ER).

3.6 Discussion

Our results support some of the fundamental conditions for the proposed mechanisms controlling peat accumulation (Table 3.1). While elevation and spatial distribution of microforms varied among HBL sites, acrotelm thickness had a consistently bimodal distribution, highlighting the dominance of two microform types (hummocks and hollows) at all sites (e.g. Eppinga *et al.*, 2008). Therefore, feedbacks between hummocks and hollows are likely critical in controlling changes in production and decomposition in HBL peatlands (Malmer and Wallen, 1999; Belyea and Clymo, 2001).

Contrasting vegetation composition, and particularly greater shrub cover on hummocks than hollows, was an important control for production across microforms. Hummock GPP (and NEP) was generally greater than hollows and pools (at all sites except Moss), which increases the potential input of plant matter to the acrotelm and then the catotelm, and therefore increases hummock height above the water table. The positive feedback between acrotelm thickness and plant productivity is a key requirement in the peat accumulation mechanism (Belyea and Clymo, 1998; Belyea and Clymo, 2001). This positive feedback for hummock growth is likely reinforced by water ponding upslope of linear ridges in water tracks, such as our Ridge-Pool site where WT elevation is significantly lower for pools downslope (Foster *et al.*, 1983; Foster *et al.*, 1988a; Swanson and Grigal, 1988). Greater vascular plant cover on hummocks is also required for the nutrient accumulation mechanism, to enable ET-driven nutrient transport to hummocks from adjacent hollows and pools (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a). Nutrient availabilities did not differ among microforms however, and since horizontal hydraulic gradients between microforms were very small and mostly positive, significant water flow from pools and hollows to hummocks is unlikely. The lack of sufficient hydraulic gradients between microforms is also problematic for the peat accumulation mechanism, where flow of water from hummocks to hollows is suggested to occur (Belyea and Clymo, 2001). Our data also suggest the strength and direction of feedbacks among vegetation and hydrology vary for the HBL sites due to different ecohydrological conditions (Malhotra *et al.*, 2016). We now explain this in further detail together with evidence for each of the proposed structuring mechanisms.

Peat accumulation mechanism

Species distribution in peatlands is strongly related to hydrological and chemical gradients, both at the peat landform (bogs and fens) and microform scale (Glaser *et al.*, 1981; Glaser, 1983; Vitt and Chee, 1990; Bubier *et al.*, 2006; Andersen *et al.*, 2011; Riley, 2011; Graham *et al.*, 2016). Distinct differences in WTD in hummocks and hollows, as shown by the bimodal distribution in acrotelm thickness at the HBL sites, restrict species growth to microform types (Andrus *et al.*, 1983; Rydin, 1986; Nordbakken, 1996). Thus, elevated hummocks with deeper water tables, hollows with shallower water tables, and intermediate 'lawns', each may be identified as having distinct vegetation communities (Belyea and Clymo, 1998; Laine *et al.*, 2012). These vegetation communities, in turn, provide important feedbacks to production and decomposition processes controlling microform development (Belyea, 1996; Belyea and Clymo, 1998; Loisel and Yu, 2013), and peatland C function (Bubier *et al.*, 2003; Riutta *et al.*, 2007; Pelletier *et al.*, 2011).

Our results show greater vascular plant cover (and VGA) relates to increased GPP and this is positively correlated to microform elevation, with hummock GPP larger than intermediate, hollows, and pools at all HBL sites (Figures 3.7 and 3.8). Although elevated hummocks have a thicker acrotelm where aerobic decay may be greater than hollows and pools with a thin or no acrotelm (Belyea, 1996), hummock NEP was positive and generally greater than hollows and pools. This larger hummock NEP suggests peat accumulation at the HBL sites is partly due to a positive feedback between acrotelm thickness and plant productivity, as described by Belyea and Clymo (2001). Exceptions to this were low or negative NEP for lichen-shrub hummocks at Bog, and similar NEP for hummocks and hollows at Moss, and *Eriophorum* tussocks in pools at Ridge-Pool. These exceptions may be explained by variation among sites of the significance of biotic and abiotic controls on GPP and ER, and consequently NEP.

GPP (and NEP) was positively correlated to vascular plant cover (and larger VGA) at all sites except Moss (Figure 3.8c). Higher water tables in hollows at Moss (lowest water tables < 10 cm below surface in summer) allowed sedges and forbs to grow well (e.g. *S. palustris* mean cover 12 % at Moss compared to 6 % at Ridge-Pool, data not shown), and hollow VGA was therefore comparable to hummocks. Hollow GPP remained small however, as higher water tables limited photosynthesis of vascular plants and moss (Weltzin *et al.*, 2000; Pelletier *et al.*, 2011). Species composition differed from that typical of hummocks at other sites, with slightly greater cover of forbs such as *M. trifolium* on hummocks at the expense of evergreen shrubs (e.g. *C. calyculata* and *R. groenlandicum* mean cover 15 % and 9 % at Ridge-Pool respectively, and each < 6 % at Moss, data not shown). Although net photosynthetic rates vary for individual species and depend on site hydrology and nutrient conditions (Leppälä *et al.*, 2008; Korrensalo *et al.*, 2016), rates are generally greater for deciduous species than evergreen species (Small, 1972; DeLucia and Schlesinger, 1995). Therefore, despite similar VGA, hummock GPP at Moss was still significantly larger than hollows. As suggested by small ER, decomposition in hollows may also have been reduced by high water tables, resulting in no differences in NEP for hummocks and hollows at this site (Belyea and Clymo, 1998). Similarly, small but dense *Eriophorum* tussocks at Ridge-Pool have larger VGA than both hummocks and *Sphagnum*-sedge pools. Although GPP for *Eriophorum* tussocks was smaller than hummocks, ER was also smaller due to high water tables, resulting in NEP comparable to hummocks (Figure 3.7).

At Bog, hummocks completely covered in thick lichen mats (~ 20 cm thick, mainly *C*. *stellaris*) had a small or negative NEP (Figure 3.7). ER did not differ for lichen-shrub or *Sphagnum*-shrub hummocks, but GPP was significantly smaller for lichen-shrub hummocks. As VGA was only slightly smaller for lichen-shrub than *Sphagnum*-shrub hummocks, smaller GPP is most likely due to the low productivity of lichens. Growth rates for *Sphagnum* species may be up to 10 mm yr⁻¹ (Lindholm, 1990) while lichen growth rates are ~ 3 to 6 mm yr⁻¹ (Helle *et al.*, 1983; Kumpula *et al.*, 2000). Lichens also decay quite rapidly (average *k* value of 0.2 yr⁻¹, Lang *et al.*, 2009b) compared to *Sphagnum* moss (average *k* value of 0.05 yr⁻¹, Bengtsson *et al.*, 2016). Therefore, since lichens may lower production and litter addition to the peat mass (Malmer and Wallen, 1999), the relationship between plant productivity and acrotelm thickness no longer applies. If production is less than decomposition, peat accumulation and therefore hummock growth will slow or cease.

Although WTD was not as significant a predictor for GPP as elevation and VGA at Moss and Ridge-Pool (Figure 3.8), there was a weak negative correlation for both sites (deeper water tables have larger GPP). GPP (and NEP) was also negatively correlated to WTD at Fen, but at Bog there was a weak positive correlation (deeper water tables have smaller GPP and NEP). These contrasting relationships are likely due to different species composition (in the bog and the fen) and diversity among sites, and constraints on species growth to different WTD and chemical requirements (e.g. Laine *et al.*, 2012; Duval *et al.*, 2012). Species richness for Fen (2014 mean = 13) was greater than the Bog, Ridge-Pool, and Moss sites combined (2014 mean = 7), which is mostly due to greater nutrient availability and alkalinity within minerotrophic fens compared to ombrotrophic bogs (Vitt and Chee, 1990; Glaser *et al.*, 1990). At Fen, hummocks (and ridges) were dominated by a large variety of moss species, forbs, large shrubs (e.g. *B. pumila, Salix* spp.), and trees (e.g. *L. laricina*), and the range in WTD was small (mean -13.8 cm, range from 6 cm above surface to -29 cm below surface). Consequently, GPP (and NEP) was larger for hummocks with deeper water tables. At Bog, deeper water tables with a greater range (mean WTD -28 cm, range from at surface to -51 cm below surface), coupled with less nutrient availability compared to Fen, limit species diversity to mostly evergreen shrubs and lichens with smaller GPP.

The peat accumulation mechanism assumes the rate of submergence of the catotelm increases (or water level rises) as the thickness of the acrotelm increases (more porous peat), and thus water levels are slightly higher in hummocks than hollows and pools (Belyea and Clymo, 2001; Morris *et al.*, 2011a). If this hypothesis is correct, then the difference in water levels between microforms would create a hydraulic gradient causing water flow from the hummock to the hollow. Our results showed hummock water table elevations were similar or slightly higher than adjacent hollows and pools, and except for slightly negative gradients at Ridge-Pool and Fen in late July/early August, horizontal hydraulic gradients were very small however (< 0.004 for all sites except Bog, < 0.013), and coupled with the low saturated hydraulic conductivity (*K*) of hummocks compared to hollows and pools, flow between microforms is likely restricted (Malmer and Wallen, 1999; Branham and Strack, 2014; Baird *et al.*, 2015). *K* values for the upper 50 cm of peat at Bog and Ridge-Pool are reported by Ulanowski (2014) as 7.22 m d⁻¹ (10⁻⁵ m s⁻¹) in ridges and 10.34 m d⁻¹ (10⁻⁴ m s⁻¹) in pools, and

at Fen, 5.87 m d⁻¹ (10⁻⁵ m s⁻¹) in ridges and 9.86 m d⁻¹ (10⁻⁴ m s⁻¹) in pools. These values decrease substantially at 1 m depth, to 0.05 m d⁻¹ (10⁻⁷ m s⁻¹) in ridges and 0.98 m d⁻¹ (10⁻⁵ m s⁻¹) in pools at Bog and Ridge-Pool, and to 0.59 m d⁻¹ (10⁻⁶ m s⁻¹) in ridges and 1.03 m d⁻¹ (10⁻⁵ m s⁻¹) in pools at Fen (Ulanowski, 2014). These values correspond to other studies showing a significant decrease in *K* with depth, and to variations in *K* among vegetation communities and microforms (McCarter and Price, 2017; Baird *et al.*, 2015; Whittington *et al.*, 2007; Branham and Strack, 2014). Similar hydraulic gradients (~ 0.012) were observed for hummocks and hollows at Mer Bleue bog in southern Ontario, which again, coupled with low *K*, were deemed too small for significant water flow between microforms (Wilson, 2012).

Nutrient accumulation mechanism

Our results suggest the nutrient accumulation mechanism does not influence the development of microform patterns at our HBL sites. We found no differences in nutrient availabilities in peatland water among microforms and notably, P concentrations were also very small or below detection limits. The small P concentrations at our HBL sites are similar to bogs in Sweden and Scotland, where tests of peatland water and plant tissues revealed no differences among microforms, and it was considered unlikely that the nutrient accumulation mechanism occurred at those sites (Eppinga *et al.*, 2010).

We did not test nutrient concentrations in plant tissues as species varied considerably across each site and for microforms within sites (e.g. different species on hummocks and in pools at Fen). Individual species, and plant functional types comprising similar species (e.g. graminoids, evergreen shrubs, forbs), can have varying nutrient concentrations that may not be directly related to nutrient availability within the soil (Güsewell and Koerselman, 2002; McJannet *et al.*, 1995; Wang and Moore, 2014). It may therefore be difficult to accurately attribute differences in nutrient concentration to species, or to nutrient availability in different

microforms. Instead, we chose to use PRS probes with an ion-exchange membrane to measure relative *in-situ* differences in nutrient availabilities of hummocks, hollows, and pools at each site (Wood *et al.*, 2015; Wang *et al.*, 2016). Probes were buried within the upper 15 cm of microforms, where it is assumed a localised increase in nutrient availability may be found if the nutrient accumulation mechanism were to occur (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a). We did not find any significant differences in nutrient availabilities using the PRS probes (Figure 3.6) but we cannot rule out potential differences in nutrient concentrations in plant tissues among microforms. Although the probes were buried for 4 weeks, this still represents short-term nutrient availability which can change considerably over the growing season and between years (Güsewell and Koerselman, 2002; Wang and Moore, 2014). Nutrient concentrations in plant tissues may represent a longer-term accumulation process of nutrient uptake by plants, particularly in nutrient-poor environments with a small dissolved nutrient pool (Eppinga *et al.*, 2010; Güsewell and Koerselman, 2002) but it is not clear how to deal with species differences.

As well as the lack of differences in nutrient concentrations between microforms at the HBL sites, our analysis did not support the proposed hydrological mechanism for greater nutrient availability in hummocks than hollows and pools. Localised accumulation of nutrients in hummocks is assumed to be caused by the flow of water, and therefore nutrients, to hummocks from adjacent hollows and pools (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a). This nutrient transport mechanism requires hummock ET to cause a sufficient drop in hummock WT compared to the hollow or pool, which is most likely to occur in ET dominated (high ET:Precip ratio) peatlands such as Siberia but not in precipitation dominated sites (low ET:Precip ratio, < 0.5) such as Sweden and Scotland (Eppinga *et al.*, 2010). ET:Precip ratios for the HBL MOE Bog and MOE Fen ranged from 0.5 to 1.1 (2013 and 2014 MOE EC Tower, data not shown). These high ET:Precip ratios are within the same range as Siberia (Eppinga *et al.*, 2010) and indicate the HBL sites are ET dominated peatlands.

Our results showed slightly negative horizontal hydraulic gradients in late July/early August at Fen and Ridge-Pool, meaning water tables in hummocks were lower than adjacent pools. Although water flow from pools to hummocks would therefore be possible during this period, the gradients were very small (ranging from 0 to -0.005). Hydraulic gradients may also be created by ET-driven diurnal changes in water table, allowing water flow from pools to hummocks for a short period (Eppinga *et al.*, 2008). We observed diurnal fluctuations in WT at all HBL sites, with significant nighttime increases in hummock WT elevation at Fen, and smaller increases at Moss and Ridge-Pool (Table 3.3). As vascular plant cover (VGA) and GPP (and NEP) were greater for hummocks at Fen and Ridge-Pool, we considered these the most likely sites for the nutrient accumulation mechanism to occur. The diurnal changes in WT elevation did not alter the magnitude or direction of hydraulic gradients between microforms at these sites however. Gradients were small (Table S3.2) and remained positive (except Ridge-Pool in late August 2014), meaning if flow between microforms was to occur it would be from hummocks to hollows. Due to low *K* values for peat below the water table, consistent flow between microforms was therefore unlikely.

Our analysis of diurnal fluctuations in water table also showed significant differences in ET_{G} for hummocks at each site, although the uncertainty was quite large for these estimates. As our data showed water flow between microforms was unlikely, ET_{G} is likely to represent the rise and fall of the water table within microforms, with differences between sites due to differences in WTD. ET_{G} estimates the rate of peat groundwater (change in water table) consumed by ET as direct water uptake by plants, but does not estimate changes in surface moisture (Loheide *et al.*, 2009; Carlson-Mazur *et al.*, 2014). Sites with shallow water tables and vegetation with deep roots (e.g. Ridge-Pool, Moss, and Fen) therefore show greater fluctuations in water table as ET and water tables are coupled (Romanov, 1961; Loheide et al., 2009; Lafleur et al., 2005b; Carlson-Mazur et al., 2014). At Bog, low or zero ET_G is most likely due to 'decoupling' of ET to the overall deeper water tables (mean WTD – 28.6 cm compared to mean WTD of -13 to -15 cm for Ridge-Pool, Moss and Fen). Although midday ET values at Bog are slightly smaller than Fen (through June to August, 2012 to 2014 - MOE tower data, not shown) and likely affect surface moisture, diurnal fluctuations in water table may be minimal, and so estimates of ET_G are low or zero (Carlson-Mazur et al., 2014). The extensive lichen cover with very low ET rates (< 1 mm d⁻¹, Leclair *et al.*, 2015) also contributes to the low or zero ET_G at Bog. Vascular plant and moss cover may be less on hummocks with thick lichen mats (Cornelissen et al., 2001, Lang et al., 2009a), that may also maintain cooler peat temperatures and reduce evaporation from the underlying peat (Leclair et al., 2015). ET driven transport of nutrients to hummocks covered by thick lichen mats is therefore very unlikely, and would indeed be detrimental for lichens. Any increases in nutrient availability in hummocks would favour the growth of vascular plants that would eventually outcompete slower-growing lichens (Kumpula et al., 2000; Kytöviita and Crittenden, 2007).

Water ponding mechanism

The water ponding mechanism assumes hydrological flow in ridge-pool tracks is restricted by elevated ridges, with water retention in upslope pools limiting NPP relative to ridges (Foster *et al.*, 1983; Foster *et al.*, 1988a; Swanson and Grigal, 1988). Higher WT elevations for wells located in pools upslope of ridges at Ridge-Pool suggest water flow is impeded by ridges and results in water ponding. Horizontal hydraulic gradients were small (~ 0.002) but similar to other studies at this site and other ridge-pool tracks in the HBL, which report flow of water downgradient (Ulanowksi, 2014; McCarter and Price, 2017). Significant differences in vegetation composition on ridges and pools are further evidence of contrasting

hydrological conditions, with greater shrub and tree cover (and VGA) on ridges. Ridge GPP is therefore larger than the *S. majus* and *Carex spp.*-dominated pools, and despite greater ER due to a thicker acrotelm, ridge NEP is larger. Our data for Ridge-Pool therefore support a positive feedback between acrotelm thickness and plant productivity required for the peat accumulation mechanism, and it is very likely that this feedback is enhanced by water ponding in upslope pools.

Water ponding upslope of ridges depends on low *K* at the level of the water table in ridges. *K* values for ridges (and hummocks) at Bog and Ridge-Pool decrease from 7.224 m d⁻¹ (10^{-5} m s⁻¹) at 50 cm depth to 0.051 m d⁻¹ (10^{-7} m s⁻¹) at 1 m depth (Ulanowski, 2014). Unless there are preferential flow pathways in deeper peat, the low *K* values for peat at 1 m depth in ridges would therefore restrict water flow (Dimitrov *et al.*, 2010). When water tables are high however, water flow through the upper part of ridges is possible. McCarter and Price (2017) highlight the importance of the vertical distribution of *K* values in ridges in connecting pools within ridge-pool tracks, with low water tables significantly limiting flow for potentially long time periods. Only during very wet periods (e.g. spring and autumn high flows), does hydrological connectivity between pools increase due to increasing transmissivity (Foster *et al.*, 1983; Quinton and Roulet, 1998; McCarter and Price, 2017). The potential for restricted flow, and therefore water ponding upslope of ridges over long periods, is important for long-term localised differences in peat accumulation in ridges and pools.

As well as seasonal changes in hydrological connectivity, annual variability in climate conditions may also be important for the water ponding mechanism. At Ridge-Pool we observed smaller differences in WT elevation between pools in 2014 than in 2013, most likely due to increased rainfall amounts in 2014 (~ 600 mm in 2014, ~ 410 mm in 2013, MOE EC Tower, data not shown). The only significant difference in GPP and NEP between 2013 and 2014 was for *Sphagnum*-only collars at Ridge-Pool, with smaller GPP and NEP in

2014. As there was no difference in GPP and NEP for *Sphagnum*-sedge collars between years, this may be due to higher water tables in 2014 having a negative impact on photosynthesis of *S. majus*, the dominant pool *Sphagnum* species (Weltzin *et al.*, 2000; Pelletier *et al.*, 2011). Ridge GPP and NEP did not differ between years. Higher water tables in ridge-pool sequences are likely to further constrain pool NEP relative to ridges, thus reinforcing the positive feedback (Foster *et al.*, 1983; Swanson and Grigal, 1988). In drier years, such as 2013, pool GPP and NEP is still smaller than hummocks but this slightly greater growth may prevent significant increases in hummock height relative to hollows (Belyea and Clymo, 2001).

The water ponding mechanism may also be important for the development of parallel ridges and pools at Fen, although due to much smaller hydraulic gradients (< 0.001) and overall lower *K* values (0.003 – 9.861 m d⁻¹, Ulanowski, 2014), rates of flow are likely smaller (Siegel and Glaser, 1987).

Importance of ecohydrological setting and landscape-scale hydrology

Our results indicate the development of different spatial patterns of microforms (or distinct microtopes) depend on position within a peat landform (the mesotope) (Foster *et al.*, 1988a; Foster *et al.*, 1988b; Foster and Wright, 1990; Belyea and Baird, 2006; Riley, 2011). Hummock-hollow microtopes occur in areas with minimal topographical slope, such as our sites Bog and Moss located at the apex and margin of MOE Bog respectively. In areas where there is sufficient topographical slope, water tracks may develop that result in a sequence of parallel ridges and pools aligned perpendicular to the direction of flow (e.g. Ridge-Pool; Foster *et al.*, 1983; Foster *et al.*, 1988a; Swanson and Grigal, 1988; McCarter and Price, 2017). The development of distinct microtopes is dependent on ecohydrological setting which in turn, influences processes controlling peat accumulation at the microform scale (Belyea and Baird, 2006). For example, the ecohydrological conditions required in the water ponding

mechanism only occur in ridge-pool tracks but not in areas with limited or no slope (e.g. Bog and Moss). Our results also suggest the strength and direction of feedbacks among vegetation and hydrology vary for sites with varying ecohydrological conditions (Malhotra *et al.*, 2016).

Although this study does not attempt to quantify the landscape-scale hydrology of the HBL, it is important to consider the influence of these large-scale processes on the ecohydrological setting of mesotopes, and consequently microtopes (Glaser et al., 1981; Foster et al., 1988a; Glaser et al., 2004b; Belyea and Baird, 2006; Riley, 2011). The patterning of raised bogs, fens, and water tracks (macrotopes) within this region of the HBL is similar to peatlands in northern Minnesota, US, and western Labrador, Canada, where surface drainage is noted as an important control for the development of peat landforms (Glaser et al., 1981; Foster et al., 1983; Foster et al., 1988a; Glaser, 1989; Glaser, 1992). Surface drainage at the HBL sites is generally towards stream and river systems (Glaser et al., 2004a; Glaser et al., 2004b; Riley, 2011), with groundwater flow in MOE Fen greatest near a large tributary to the Nayshkootayaow River (within 100-200 m; Ulanowski, 2014). As our site (Fen) was located further from the tributary (> 200 m), hydraulic gradients were smaller, and therefore groundwater flow is likely slower. Although flow may be slow, this is likely important for the development of parallel ridges that are perpendicular to flow, where water ponding restricts production (NEP) in pools upslope of ridges. Quicker flow would likely prevent this mechanism from occurring, as preferential flow pathways are more likely to form, enabling flow through ridges and potentially forming rivulets nearer tributaries (Foster et al., 1983; Ulanowski, 2014; McCarter and Price, 2017).

Variable rates of flow within MOE Fen likely shape the adjacent MOE bog, which tapers to an ovoid or 'tear-drop' shape in closer proximity to the tributary (Glaser *et al.*, 1981; Glaser, 1992). Drainage pathways within MOE Bog then reflect the shape of the landform, with water tracks forming along slightly steeper inclines from the apex to the margin, and not

within the taper (Figure 3.1; Foster *et al.*, 1988a). The distinct microtopes (e.g. hummockhollow complex, ridge-pool track) within MOE Bog depend on the ecohydrological conditions created by these drainage pathways, which may also be altered by seasonal changes in hydrology. Shallower water tables in spring (including surface flooding) enhance drainage pathways and hydrological connectivity within and between peat landforms (Quinton and Roulet, 1998; Ulanowski, 2014). The effect of seasonal changes in hydrology on mechanisms controlling peat accumulation and the development of microforms and microtopes, remains uncertain however, and warrants further research.

3.7 Conclusions

The development of surface patterns of microforms and microtopes within the HBL peatlands may be explained by small-scale structuring mechanisms that control peat accumulation at the microform scale. Our data supports the conditions required for the peat accumulation mechanism, and depending on the ecohydrological setting, this may be enhanced through the water ponding mechanism. We did not find evidence of nutrient accumulation in hummocks relative to hollows or pools at any of our sites, and our analysis revealed no mechanism for ET-driven transport of water and nutrients to hummocks. We suggest a combination of mechanisms operating at varying temporal and spatial scales are required for the development of surface patterns in HBL peatlands, with further research into the influence of landscape-scale hydrology particularly important for the HBL peatlands.

3.8 Figures and Tables



Figure 3.1 Patterns within peatlands across the HBL landscape and location of four study sites (Bog, Ridge-pool, Moss, and Fen) along the 1.5 km boardwalk at the MOE research site. Location of MOE Bog and Fen eddy covariance (EC) towers shown. A large tributary of the Nayshkootayaow River is located ~500 m to the left of the Fen EC Tower in this photograph.



Figure 3.2 (a) Elevation (m.a.s.l.) of microforms along the MOE boardwalk (microforms within sites are significantly different if they have no lowercase letters in common - Kruskal-Wallis, p < 0.007), and (b) frequency distribution of elevation at (a) Bog (n = 28), (b) Ridge-Pool (n = 39), (c) Moss (n = 19), and (d) Fen (n = 22), with an almost equal number of observations (~ 30 to 37 %) for hummocks, hollows/pools, and intermediate microforms at each site. The black line shows the best model fit (μ = mean, σ = standard deviation, with parameter values) for each site: (a) Bog, normal distribution (W = 0.90, $\mu = 93.2$, $\sigma = 0.11$, p = 0.02), (b) Ridge-Pool, normal distribution (W = 0.95, $\mu = 92.8$, $\sigma = 0.12$, p = 0.125), (c) Moss, Johnson's S_I distribution (W = 0.93, $\theta = 91.98$, p = 0.216), and (d) Fen, bimodal fit ($\chi^2 = 27.6$, $\mu_1 = 91.66$, $\mu_2 = 91.79$, $\sigma_1 = 0.01$, $\sigma_2 = 0.07$, p = 0.009). Log-likelihood ratio and Shapiro-Wilk test used to determine significance of distribution model.



Figure 3.3 Frequency distribution of acrotelm thickness (estimated as lowest 10 % of WTD recorded during July and August 2014) for all microforms at (a) Bog (n = 76), (b) Ridge-Pool (n = 64), (c) Moss (n = 52), and (d) Fen (n = 69), with an almost equal number of observations (~ 30 to 36 %) for hummocks, hollows/pools, and intermediate microforms at each site. Negative values indicate water table below the surface. The black line shows a bimodal fit (normal mixture model, $\mu = \text{mean}$, $\sigma = \text{standard deviation}$, with parameter values for each site). Log-likelihood ratio used to determine significance of bimodal distribution compared to unimodal or multimodal model.



Figure 3.4 (a) Distribution of WTD (cm below surface, positive values indicate WT above surface) and, **(b)** Water table elevation (m.a.s.l.) for microforms at Bog, Ridge-Pool, Moss, and Fen (July-August 2014). WTD and WT elevation for microforms within sites are significantly different if they have no lowercase letters in common (Kruskal-Wallis, p < 0.001; for Moss – Mann-Whitney, p < 0.001). WTD are significantly different for the same microform type (hummocks or pools/hollows) across sites if they have no uppercase letters in common (Kruskal-Wallis, p < 0.05).



Figure 3.5 Diurnal variations in water table for (a) a ridge and (b) a pool at Fen, from 27 to 29 July 2014. Nighttime hours indicated by grey areas (approximate times for sunset and sunrise - data from MOE EC towers). For (a) ridges: input via advection at night (water table rises). Losses through ET exceed gains via advection during the day (water table drops). For (b) pools: loss or input via advection at night. Losses through ET exceed gains via advection during the day (water table drops) (Eppinga *et al.*, 2008).



Figure 3.6 Nutrient availability (mean supply rate in $\mu g/10 \text{ cm}^2/\text{week} \pm \text{standard error}$) for microforms at each site (PRSTM probes, RP = Ridge-Pool). Microforms within sites are significantly different if they have no lowercase letters in common (ANOVA, p < 0.05). Microforms across sites are significantly different if they have no uppercase letters in common (ANOVA, p < 0.05). No significant difference among microforms or across sites if no letters shown.



Figure 3.7 Mean GPP, ER and NEP for different vegetation-microform types at Bog, Ridge-Pool, Moss and Fen (2013 and 2014 combined data, standard error bars). Significant differences for vegetation-microform types within sites if no lowercase letters in common (GLM, p < 0.05).



Figure 3.8 Generalised linear model parameters for GPP predictor variables within sites (showing relative significance of predictor variables among sites): (a) Elevation, (b) WTD, (c) VGA. Model parameters are significantly different for sites with no letters in common (p < 0.05). * = model parameter not significant. Kruskal-Wallis test used to determine significant differences in elevation and WTD between sites (p < 0.05). Significant predictor variables for GPP at each site determined by Spearman's rank-order correlation.

Table 3.1 Proposed mechanisms for differential peat accumulation within peatlands and hypothesised environmental conditions and relationships, and likely occurrence at study sites in HBL. References: 1. Belyea and Clymo (1998, 2001), 2. Rietkerk *et al.*, (2004b), 3. Eppinga *et al.*, (2008, 2009a), 4. Swanson and Grigal (1988), 5. Ivanov (1981), 6. Eppinga *et al.*, (2010), 7. Foster *et al.*, (1983), 8. Foster *et al.*, (1988a).

| Mechanism | Main Feedback | Conditions | HBL Site |
|--|---|---|----------------------------------|
| Peat Accumulation ^{1,5} | Positive feedback between acrotelm thickness and plant productivity. | Greater vascular plant cover on hummocks than hollows or pools. Greater GPP for hummocks than hollows/pools. Greater nutrient availability in hollows than hummocks. WT elevations slightly higher in hummocks than hollows/pools due to differential submergence rates. Hydraulic gradients between microforms cause water flow from hummocks to hollows or pools. | Bog Ridge-Pool Moss Fen |
| Nutrient Accumulation ^{2,3,6} | Positive scale- dependent feedback between ET and nutrient accumulation. | ET induced hydraulic gradients between microforms enable consistent water flow from hollows or pools to hummocks. Larger nutrient concentrations in water under hummocks than hollows or pools. Greater nutrient availability on hummocks than hollows or pools. Greater vascular plant cover on hummocks than hollows or pools. Greater GPP for hummocks than hollows or pools. | Fen Ridge-Pool |
| Water Ponding on Slope ^{4,7,8} | Positive feedback between hydrology and plant productivity. | Greater vascular plant cover on ridges than pools. Lower hydraulic conductivity of peat within ridges slows/prevents water discharge to pools downslope. Surface and WT elevations are significantly greater upslope ridge-pool sequence. | Ridge-Pool Fen |

| Site | n | Intercept | Slope | r^2 | <i>p</i> -value |
|------------|----|-------------------|----------------|-------|-----------------|
| Bog | 16 | 7514.58 (996.43) | -80.84 (10.68) | 0.79 | < 0.0001 |
| Ridge-Pool | 17 | 9212.41 (844.17) | -99.32 (9.08) | 0.88 | < 0.0001 |
| Moss | 12 | 8844.47 (413.6) | -96.17 (4.48) | 0.97 | < 0.0001 |
| Fen | 12 | 7964.23 (1174.42) | -86.92 (12.79) | 0.80 | < 0.0001 |
| All sites | 57 | 870.61 (226.26) | -9.59 (2.44) | 0.21 | < 0.0002 |

Table 3.2 Simple linear regression model of mean July-August WT depth below surface (cm, 2014data) and surface elevation (m.a.s.l.) for each site. Standard error in parentheses.

| | | | Bog | | Ridge-Poo | 1 | Μ | OSS | F | en |
|------|-------|-------------|-------------|-------------|-------------|--------------|-------------|--------------|-------------|-------------|
| Year | | Hk | Hw | Hk | Int | Pl | Hk | Hw | Hk | Pl |
| | | -1.8 | -7.1 | -8.4 | -6.7 | -4.4 | -7.2 | -6.6 | -6.1 | -2.4 |
| | Day | (1.4) aA | (0.9) bB | (1.2) aA | (0.4) AB | (0.5) abB | (0.3) aA | (0.9) abA | (3.4) aA | (1.8) aA |
| 2013 | | | | | | | | | | |
| | | -0.9 | -0.3** | +0.6** | +0.7** | -0.8** | +0.2** | +0.3** | +2.3 | -1.9 |
| | Night | (0.1) | (0.2) | (0.5) | (0.3) | (0.3) | (0.3) | (0.3) | (1.1) | (0.5) |
| | | bA | bA | abA | В | abB | abA | bA | aA | aB |
| | | -8.0 | -6.7 | -6.9 | -5.1 | -4.3 | -6.2 | -4.2 | -4.5 | -8.0 |
| | Day | (0.6) | (0.6) | (1.2) | (0.7) | (0.5) | (1.1) | (0.4) | (0.7) | (1.8) |
| | | aA | aA | aA | А | aA | aA | aA | aA | aA |
| 2014 | | | | | | | | | | |
| | | -0.6* | -0.4* | +0.2** | +1.0** | +0.1* | +0.1** | -0.4* | +1.2* | +0.3** |
| | Night | (0.2) | (0.2) | (0.4) | (0.4) | (0.3) | (0.3) | (0.1) | (0.5) | (0.2) |
| | | bA | aA | abA | А | aA | abA | aA | aA | aA |

Table 3.3 Mean change in WT elevation (mm) from 6am to midnight (day), and midnight to 6am (night) for microforms at MOE sites during four rain-free periods from mid-July through August 2013 and 2014. Increases in WT elevation are highlighted in bold. Standard error in parentheses.

Statistical significance of daytime decrease or nighttime increase (difference) indicated by * p < 0.001, ** p < 0.05 (paired samples *t*-test, one-tailed). Mean values for microforms are significantly different between sites if they have no lowercase letters in common (Kruskal-Wallis, p < 0.04). Mean values for microforms are significantly different within sites if they have no uppercase letters in common (Kruskal-Wallis, p < 0.05).

| Site | General Vegetation Type | Microform | Vascular Plants | Nonvascular | VGA (m ² m ⁻²) | WTD (cm) | pН |
|----------------|----------------------------|--------------------------|--|--|--|---------------|--------------|
| | Lichen only | Hummock- Intermediate | R. groenlandicum C. calyculata C. oligosperma | C. stellaris C. rangiferina | 0.0 (0.0) | -14 (0.7) | 3.9 (0.1) |
| Bog | Lichen-shrub | Hummock | R. groenlandicum C. calyculata | C. stellaris C. rangiferina | 2.0 (0.4) | -33 (0.9) | 3.7 (0.0) |
| | Sphagnum-shrub | Hummock | R. groenlandicum C. calyculata R. chamaemorus V. oxycoccos | S. fuscum | 2.3 (0.4) | -18 (0.8) | 4.0 (0.0) |
| | Sphagnum only | Pool | C. magellanica ssp. irrigua T. cespitosum | S. majus S. papillosum | 0.1 (0.0) | 2.5 (0.3) | 4.3 (0.1) |
| | Sphagnum-sedge | Pool | C. oligosperma C. limosa C. pauciflora R. alba C. magellanica ssp. irrigua | S. majus S. papillosum | 2.2 (0.4) | 2.2 (0.2) | 4.3 (0.1) |
| Ridge- Pool | Eriophorum tussock | Pool- Intermediate | E. vaginatum V. oxycoccos | S. rubellum S. papillosum | | -1.8 (0.7) | 4.1 (0.1) |
| | Sphagnum-shrub | Intermediate | R. chamaemorus V. oxycoccos A. glaucophylla C. calyculata | S. rubellum S. capillifolium | 1.6 (0.4) | -12 (0.7) | 4.1 (0.1) |
| | Sphagnum-shrub | Hummock (ridge) | P. mariana C. calyculata R. groenlandicum M. trifolium | S. fuscum S. capillifolium | 3.9 (1.0) | -24 (0.7) | 4.1 (0.0) |
| | Sphagnum-sedge | Hollow | C. oligosperma C. magellanica S. palustris | S. majus | 1.8 (0.3) | -3 (0.3) | 4.3 (0.0) |
| Moss | Sphagnum-shrub | Hummock | M. trifolium C. calyculata A. glaucophylla V. oxycoccos | S. fuscum S. capillifolium | 1.8 (0.2) | -24 (0.9) | 4.1 (0.0) |
| Fen | Moss-shrub | Hummock (ridge) | B. pumila A. glaucophylla C. calyculata R. acaulis V. oxycoccos C. leptalea | D. fuscescens R. triquetrus T. nitens S. rubellum | 3.5 (0.9) | -21 (0.5) | 7.0 (0.0) |
| | Bogbean-sedge | Pool | M. trifoliata E. fluviatile. C. lasiocarpa T. alpinum | S. scorpioides | 3.6 (0.2) | 0.8 (0.5) | 7.0 (0.0) |

Table 3.4 Plot characteristics for NEE measurements (collar triplicates) at all four sites.

Major vascular plants and nonvascular bryophytes and lichens are listed (bold are species within collar for gas flux measurements). Mean (combined 2013 and 2014) Vascular Green Area (VGA) within collar for each vegetation-microform type. Mean values for 2013 and 2014 summer (June to August) pH and water table below surface (cm). Mean value for WTD recorded at same time as CO₂ measurements in 2013 and 2014. Standard error in parentheses.

3.9 Supplementary Figures and Tables



Figure S3.1 Sensitivity of Odyssey capacitance logger to changes in room temperature (stable water level and dry sensor after midday on 17/6). Raw value (mV) with 1 mV equivalent to < 0.25 mm change in water level.



Figure S3.2 Change in WT elevation (m.a.s.l.) and horizontal hydraulic gradient for hummock-hollow/pool pairs at (a) Bog, and (b) Ridge-Pool, from July-August 2013.



Figure S3.3 Change in WT elevation (m.a.s.l.) and horizontal hydraulic gradient for hummock-hollow/pool pairs at (c) Moss, and (d) Fen, from July-August 2013.



Figure S3.4 (a) and (b) Diurnal variations in VWC (%) at ~ 10 - 15 cm depth (above the water table) in two ridges at Fen during a rain-free period in July 2015, and (c) diurnal variations in WT elevation (m.a.s.l.) for Ridge A during the same period. Nighttime hours indicated by grey areas (approximate times for sunset and sunrise - data from MOE EC towers).

| Species | Botanical authority | Growth Form | English Common Name | Bog | RP | Moss | Fen |
|--------------------------------|-----------------------------|----------------|-----------------------------|-----|----|------|-----|
| Andromeda glaucophylla | L. (Link) DC. | Shrub | Bog rosemary | | * | * | * |
| Betula pumila | L. | Shrub | Bog birch | | | * | * |
| Caltha palustris | L. | Forb | Marsh marigold | | | | * |
| Carex chordorrhiza | L. | Sedge | Creeping sedge | | | | * |
| Carex diandra | Schrank. | Sedge | Lesser panicled sedge | | | | * |
| Carex interior | L. H. Bailey | Sedge | Inland sedge | | | | * |
| Carex lasicocarpa | Ehrh. | Sedge | Wire sedge | | | | * |
| Carex leptalea | Wahlenb. | Sedge | Bristle-stalked sedge | | | | * |
| Carex limosa | L. | Sedge | Mud sedge | | * | | * |
| Carex magellanica ssp. irrigua | Lam (Wahlenb.) Hulten | Sedge | Poor sedge | | * | * | |
| Carex oligosperma | Michx. | Sedge | Fewseed sedge | * | * | * | |
| Carex pauciflora | Lightf. | Sedge | Fewflower sedge | | * | * | |
| Carex tenuiflora | Wahlenb. | Sedge | Sparse-flowered sedge | | | | * |
| Chamaedaphne calyculata | (L.) Moench. | Shrub | Leatherleaf | * | * | * | * |
| Cladina rangiferina | ex F.H.Wigg. | Lichen | Reindeer lichen | * | | | |
| Cladina stellaris | (Opiz) Brodo | Lichen | Reindeer lichen | * | | | |
| Comarum palustre | L. | Forb | Marsh cinquefoil | | | | * |
| Dicranum fuscescens | Turner | Moss | Dicranum moss | | | | * |
| Drosera anglica | Huds. | Forb | English sundew | | * | | * |
| Drosera rotundifolia | L. | Forb | Roundleaf sundew | * | * | * | * |
| Eriophorum vaginatum | L. | Sedge | Tussock cottongrass | * | * | | |
| Eriophorum viridi-carinatum | (Engelm.) Fern. | Sedge | Green cottongrass | | | | * |
| Equisetum fluviatile | L. | Forb | Water horsetail | | | | * |
| Galium trifidum | L. | Forb | Small bedstraw | | | | * |
| Kalmia angustifolia | L. | Shrub | Sheep laurel | * | | | |
| Kalmia polifolia | Wangenh. | Shrub | Bog laurel | * | * | * | |
| Larix laricina | (Du Roi) K. Koch | Tree | Tamarack | | * | * | * |
| Maianthemum trifolium | (L.) Sloboda | Forb | Three-leaved solomon's seal | * | * | * | * |

Table S3.1 List of species and nomenclature for Bog, Ridge-Pool (RP), Moss and Fen.

| Species | Botanical authority | Growth Form | English Common Name | Bog | RP | Moss | Fen |
|----------------------------|----------------------------------|----------------|-------------------------|-----|----|------|-----|
| Menyanthes trifoliata | L. | Forb | Bogbean | | | | * |
| Muhlenbergia glomerata | (Willd.) Trin. | Grass | Marsh muhly | | | | * |
| Picea mariana | Britton, Sterns & Poggenb. | Tree | Black spruce | * | * | * | * |
| Polytrichum strictum | Brid. | Moss | Haircap moss | * | * | * | * |
| Rhododendron groenlandicum | (Oeder) Kron & Judd. | Shrub | Labrador tea | * | * | * | * |
| Rhytidiadelphus triquetrus | (Hedw.) Warnst. | Moss | Shaggy moss | | | | * |
| Rubus acaulis | L. (Michx.) Focke | Forb | Dwarf raspberry | | | | * |
| Rubus chamaemorus | L. | Forb | Cloudberry | * | * | | |
| Salix candida | Fluegge ex Willd. | Shrub | Sage-leaved willow | | | | * |
| Salix pedicullaris | Pursh | Shrub | Bog willow | | | | * |
| Sarracenia purpurea | L. | Forb | Pitcher plant | | * | * | |
| Scheuchzeria palustris | L. | Forb | Podgrass | | * | * | * |
| Scorpidium scorpioides | (Hedw.) Limpr. | Moss | Hooked scorpion-moss | | | | * |
| Sphagnum angustifolium | C.E.O. Jens. ex Russ. | Moss | Fine bog moss | | * | | |
| Sphagnum capillifolium | (Ehrh.) Hedw. | Moss | Acute-leaved bog moss | * | * | * | * |
| Sphagnum fuscum | (Schimp.) Klinggr. | Moss | Rusty bog moss | * | * | * | |
| Sphagnum magellanicum | Brid. | Moss | Magellanic bog moss | | * | * | |
| Sphagnum majus | (Russow) C.E.O. Jens. | Moss | Olive bog moss | | * | * | |
| Sphagnum papillosum | Lindb. | Moss | Papillose bog moss | | * | | |
| Sphagnum rubellum | Wils. | Moss | Red bog moss | * | * | * | * |
| Triantha glutinosa | (Michx.) Bak. | Forb | Sticky false asphodel | | | | * |
| Tricophorum alpinum | (L.) Pers. | Sedge | Alpine club-rush | | * | | * |
| Tricophorum cespitosum | (L.) Hartm. | Sedge | Tufted club-rush | | * | | |
| Tomenthypnum nitens | (Hedw.) Loeske | Moss | Fuzzy brown moss | | | | * |
| Vaccinium myrtilloides | Michx. | Shrub | Velvet-leaved blueberry | * | | | |
| Vaccinium oxycoccos | L. | Shrub | Small cranberry | * | * | * | * |
| Vaccinium uliginosum | L. | Shrub | Bog bilberrv | * | | | |

Table S3.2 Mean horizontal hydraulic gradients for hummock-hollow/pool pairs at each site during four rain-free periods in July-August 2013 and 2014. Standard error < 0.0001. * = gradients < 0.001 likely close to error margin for WT elevation and accuracy of surface elevation and WTD measurements.

| Time Period | | Bog | Ridge-Pool | Moss | Fen |
|-------------------|-------|--------|-------------------|-----------|---------|
| 20 21 July 2012 | DAY | 0.0097 | 0.0020 | 0.0009* | 0.0014 |
| 29-51 July 2015 | NIGHT | 0.0097 | 0.0017 | 0.0011 | 0.0011 |
| 22-24 August 2013 | DAY | 0.0130 | 0.0025 | 0.0035 | 0.0002* |
| | NIGHT | 0.0130 | 0.0023 | 0.0035 | 0.0002* |
| 26 20 July 2014 | DAY | 0.0015 | 0.0008* | 0.0006* | 0.0011 |
| 20-29 July 2014 | NIGHT | 0.0014 | 0.0008* | 0.0005* | 0.0013 |
| 20.24 August 2014 | DAY | 0.0019 | - 0.0020 | - 0.0006* | 0.0004* |
| 20-24 August 2014 | NIGHT | 0.0018 | - 0.0020 | - 0.0007* | 0.0005* |

| | | | | BOG | | | RIDO | GE-POOL | | | N | IOSS | | | J | FEN | |
|----------------|-------------------------------------|-----|--------------------------------|--------|-----------------|------|--------------------------------|---------|-----------------|-------|--------------------------------|--------|---------|------|--------------------------------|--------|-----------------|
| Period | Observation | F | Slope (mm d ⁻¹) | r² adj | <i>p</i> -value | F | Slope (mm d ⁻¹) | r² adj | <i>p</i> -value | F | Slope (mm d ⁻¹) | r² adj | p-value | F | Slope (mm d ⁻¹) | r² adj | <i>p</i> -value |
| | Night 29-30 July | 157 | -5.0 | 0.93 | < 0.001 | 1692 | +6.2 | 0.99 | < 0.001 | 55 | +3.2 | 0.83 | < 0.001 | - | 0 | - | - |
| 29-31 July | Night 30-31 July | 18 | -2.5 | 0.62 | 0.0015 | 72 | +5.6 | 0.87 | < 0.001 | 26 | +2.4 | 0.70 | < 0.001 | 2865 | +18.1 | 0.99 | < 0.001 |
| 301y 2013 | Overall trend (n = 3, df = 1, 1) | 88 | -6.3 | 0.97 | 0.0675 | 223 | -8.3 | 0.99 | 0.0426 | >5496 | -7.0 | 1 | < 0.001 | 4 | -3.8 | 0.78 | 0.3088 |
| | Night 22-23 August | 18 | -2.5 | 0.62 | 0.0015 | - | 0 | - | - | 27 | -1.8 | 0.71 | < 0.001 | - | 0 | - | - |
| 22-24 | Night 23-24 August | 170 | -4.0 | 0.94 | < 0.001 | 12 | +0.9 | 0.51 | 0.0052 | - | 0 | - | - | 33 | +7.6 | 0.75 | < 0.001 |
| August 2013 | Overall trend (n = 3, df = 1, 1) | Inf | -1.2 | 1 | < 0.001 | 456 | -6.7 | 0.99 | 0.0298 | 1496 | -7.3 | 0.99 | 0.0165 | - | 0 | - | - |
| | Night 26-27 July | 65 | -4.1 | 0.85 | < 0.001 | 60 | -10.3 | 0.84 | < 0.001 | 61 | +5.1 | 0.85 | < 0.001 | 12 | +11 | 0.50 | 0.0058 |
| 26-29 | Night 27-28 July | 7 | -0.8 | 0.33 | 0.0285 | - | 0 | - | - | 91 | -6.8 | 0.89 | < 0.001 | 1720 | +13.6 | 0.99 | < 0.001 |
| July 2014 | Night 28-29 July | - | 0 | - | - | 12 | -3.1 | 0.50 | 0.006 | 12 | +1.2 | 0.49 | 0.0069 | 6 | +3.4 | 0.31 | 0.0359 |
| | Overall trend* | - | -8.7 | - | - | - | -3.5 | - | - | - | -7.0 | - | - | - | -2.8 | - | - |
| | Night 19-20 August | 240 | -4.5 | 0.96 | < 0.001 | 21 | +2.4 | 0.65 | < 0.001 | - | 0 | - | - | 30 | +2.1 | 0.73 | < 0.001 |
| | Night 20-21 August | 195 | -5.0 | 0.95 | < 0.001 | 70 | +3.0 | 0.86 | < 0.001 | - | 0 | - | - | - | 0 | - | - |
| 20-24 | Night 21-22 August | 11 | -1.5 | 0.49 | 0.0069 | 136 | +3.3 | 0.92 | < 0.001 | 112 | +3.1 | 0.91 | < 0.001 | 44 | +2.2 | 0.80 | < 0.001 |
| August | Night 22-23 August | 11 | -1.5 | 0.49 | 0.0069 | 137 | +6.1 | 0.93 | < 0.001 | - | 0 | - | - | 7 | +0.5 | 0.33 | 0.0285 |
| 2014 | Night 23-24 August | 89 | -4.1 | 0.89 | < 0.001 | - | 0 | - | - | - | 0 | - | - | - | 0 | - | - |
| | Overall trend (n = 4, df = 1, 2) | 126 | -8.8 | 0.97 | 0.0078 | 68 | -5.2 | 0.95 | 0.0142 | 24 | -4.8 | 0.88 | 0.0382 | 99 | -3.8 | 0.97 | 0.0099 |

Table S3.3 Regressions (linear) of nighttime water table dynamics and overall trend in water table (WT elevation) for hummocks at MOE sites during four rain-free periods from mid-July through August 2013 and 2014 (method based on Eppinga *et al.*, 2008). Degrees of freedom (df) = 1,10 for all nighttime trends, *overall trend for 26-29 July 2014 limited to only 2 daytime minimum values for 27 and 28 July.

Table S3.4 Water chemistry at each site. Mean values (mg L⁻¹) for combined microforms at each site with standard error in parentheses. ND = not detectable. Sites with no lowercase letters in common are significantly different (ANOVA, p < 0.005, * = p < 0.04).

| | DOC | Ca ²⁺ | Mg ²⁺ | \mathbf{K}^{+} | Na ⁺ | NO3 ⁻ N | NH4 ⁺ - N | Total N (NO3 ⁻ -N + NH4 ⁺ -N) | PO4 ³⁻ | SO 4 ²⁻ |
|--|-----------------|------------------|------------------|------------------|-----------------|--------------------|-------------------------|---|-------------------|---------------------------|
| Bog (<i>n</i> = 24) | 65.8 | 7.5 | 0.3 | 1.0 | 3.8 | 0.1 | 2.8 | 3.5 | 0.8 | 0.3 |
| | (2.8) c | (0.7) b | (0.0) c | (0.1) a* | (0.5) ab* | (0.0) a | (0.6) a | (0.8) b* | (0.5) a | (0.1) a |
| Ridge- Pool (<i>n</i> = 18) | 43.7 (2.3) b | 5.6 (0.5) b | 0.3 (0.0) c | 0.6 (0.1) ab* | 2.6 (0.5) b* | 0.1 (0.0) a | 0.9 (0.3) b | 1.0 (0.2) ab* | ND | 0.2 (0.0) a |
| Moss (<i>n</i> = 18) | 47.6 | 7.3 | 0.5 | 0.5 | 2.3 | 0.1 | 0.8 | 1.4 | 0.2 | 0.2 |
| | (1.5) b | (0.7) b | (0.1) b | (0.1) b* | (0.4) ab* | (0.0) a | (0.3) b | (0.6) ab* | (0.1) a | (0.0) a |
| Fen (<i>n</i> = 18) | 16.3 | 39.7 | 4.9 | 0.7 | 3.7 | 0.1 | 0.7 | 1.0 | 0.1 | 0.2 |
| | (0.8) a | (2.6) a | (0.4) a | (0.1) ab* | (0.4) a* | (0.0) a | (0.1) b | (0.2) a* | (0.0) a | (0.1) a |

Table S3.5 NEE-PPFD rectangular hyperbola curve fit parameters for vegetation-microform types at each study site (combined 2013 and 2014 data, mean values for GPP and ER, μ mol CO₂ m⁻² s⁻¹, $a = \mu$ mol CO₂ m⁻² s⁻¹ per μ mol PPFD m⁻² s⁻¹).

| Site | General Vegetation Type | Microform | n | α | GP _{max} | r^2 | GPP | ER |
|------------|-------------------------|----------------------|-----|-------------|-------------------|-------|----------------|------------------|
| | Lichen only** | Hummock-Intermediate | 90 | 0.00 (0.01) | 0.72 (0.38) | 0.07 | 0.43 (0.15) aA | -1.05 (0.13) aA |
| Bog | Lichen-shrub | Hummock | 81 | 0.01 (0.00) | 2.24 (0.44) | 0.46 | 1.36 (0.14) bA | -1.40 (0.17) aA |
| | Sphagnum-shrub | Hummock | 71 | 0.01 (0.00) | 8.28 (0.80) | 0.85 | 3.91 (0.27) cA | -1.39 (0.16) aA |
| | Sphagnum only | Pool | 101 | 0.11 (1.02) | 0.50 (0.13) | 0.16 | 0.46 (0.08) aB | -0.24 (0.10) aA |
| | Sphagnum-sedge | Pool | 107 | 0.01 (0.00) | 4.50 (0.61) | 0.64 | 2.34 (0.18) bB | -1.02 (0.15) bA |
| Ridge-Pool | Eriophorum tussock | Intermediate | 116 | 0.01 (0.00) | 5.21 (0.67) | 0.63 | 2.75 (0.22) bA | -0.83 (0.11) bA |
| | Sphagnum-shrub | Intermediate | 99 | 0.01 (0.00) | 5.82 (0.74) | 0.75 | 2.91 (0.18) bA | -1.09 (0.16) bA |
| | Sphagnum-spruce | Hummock (ridge) | 114 | 0.02 (0.01) | 6.23 (0.69) | 0.66 | 3.90 (0.24) cB | -1.89 (0.22) cAB |
| Masa | Sphagnum-sedge | Hollow | 90 | 0.01 (0.00) | 5.97 (1.17) | 0.67 | 2.57 (0.24) aA | -0.69 (0.17) aA |
| MOSS | Sphagnum-shrub | Hummock | 93 | 0.01 (0.00) | 8.21 (1.07) | 0.76 | 4.08 (0.27) bB | -2.26 (0.26) bBC |
| Fon | Bogbean-sedge | Pool | 102 | 0.02 (0.01) | 4.16 (0.56) | 0.53 | 2.81 (0.19) aA | -1.98 (0.18) aB |
| ren | Moss-shrub | Hummock (ridge) | 104 | 0.02 (0.01) | 9.38 (1.59) | 0.59 | 4.60 (0.33) bB | -3.04 (0.32) bC |

*Note the poor fit of the rectangular hyperbola (**no fit) for these vegetation-microform types.

Standard error in parentheses. Parameters for <u>veg-microform types</u> within sites are significantly different if they have no lowercase letters in common (p < 0.05). Parameters are significantly different for the <u>same microforms</u> across sites if they have no uppercase letters in common (p < 0.05). Statistical differences in α and GP_{max} were determined from confidence intervals (r^2). Generalised linear models (fixed effects with repeated measures) were used to assess differences in GPP and ER between veg-microform types within and across sites, and to determine relative significance of predictor variables.
Table S3.6 Generalised linear model (GLM – fixed effects) results for GPP, ER, and NEP at Bog, Ridge-Pool, Moss, and Fen. Standard error for model coefficient in parentheses. In the GLM, ER has positive values and therefore the positive relationship of ER and VGA (significant at Fen only) means larger VGA have greater ER. The negative relationship with WTD means deeper water tables have greater ER. * = significant at 95 % confidence interval

| | | BOG | | | | RIDGE-POOL | | | | MOSS | | | | FEN | | | |
|-----|--------------------|------|---------------------|-------|-----------------|------------|---------------------|------|-----------------|------|---------------------|-------|-----------------|-----|---------------------|-------|-----------------|
| | Model Term | F | Coefficient (SE) | t | <i>p</i> -value | F | Coefficient (SE) | t | <i>p</i> -value | F | Coefficient (SE) | t | <i>p</i> -value | F | Coefficient (SE) | t | <i>p</i> -value |
| GPP | Model | 19 | | | < 0.001 | 60 | | | < 0.001 | 18 | | | < 0.001 | 11 | | | < 0.001 |
| | VGA | 52 | 0.436 (0.06) | 7.2 | < 0.001* | 14 | 0.057 (0.01) | 3.8 | < 0.001* | 1.2 | 0.061 (0.05) | 1.0 | = 0.284 | 5.6 | 0.074 (0.03) | 2.3 | = 0.023* |
| | WTD | 9.2 | 0.026 (0.00) | 3.0 | = 0.003* | 1.1 | -0.004 (0.00) | -1.0 | = 0.288 | 0.5 | 0.004 (0.00) | 0.6 | = 0.502 | 8.9 | -0.029 (0.00) | -2.9 | = 0.005* |
| | Elevation | 0.5 | -0.794 (1.06) | -0.7 | = 0.459 | 48 | 4.441 (0.63) | 6.9 | < 0.001* | 16 | 2.476 (0.61) | 4.0 | < 0.001* | 1.1 | -2.202 (2.00) | -1.0 | = 0.283 |
| ER | Model | >900 | | | < 0.001 | 17 | | | < 0.001 | 718 | | | < 0.001 | 13 | | | < 0.001 |
| | VGA | 0.6 | -0.058 (0.07) | 0.7 | = 0.450 | 1.1 | 0.031 (0.02) | 1.0 | = 0.286 | 0.8 | 0.084 (0.09) | 0.91 | = 0.615 | 6.4 | 0.130 (0.05) | 2.5 | = 0.018* |
| | WTD | 122 | -0.040 (0.00) | -11.0 | < 0.001* | 2.2 | -0.012 (0.00) | -1.4 | = 0.144 | 124 | -0.005 (0.00) | -11.1 | = 1.000 | 20 | -0.065 (0.01) | -4.5 | < 0.001* |
| | Soil Temp 10 cm | 6.0 | 0.014 (0.00) | 2.4 | = 0.038* | 5.7 | 0.071 (0.02) | 2.3 | = 0.019* | 11 | 0.098 (0.02) | 3.3 | = 0.006* | 9.1 | 0.089 (0.02) | 3.0 | = 0.009* |
| | Elevation | 0.7 | 0.601 (0.69) | 0.8 | = 0.396 | 11 | 3.821 (1.12) | 3.4 | < 0.001* | 74 | 2.856 (0.32) | 8.6 | = 0.254 | 11 | -10.336 (3.01) | -3.4 | = 0.002* |
| NEP | Model | 71 | | | < 0.001 | 22 | | | < 0.001 | >900 | | | < 0.001 | 56 | | | < 0.001 |
| | VGA | 65 | 0.122 (0.15) | 8.1 | = 0.103 | 5.1 | 0.036 (0.01) | 2.2 | = 0.028* | >900 | 0.188 (0.00) | 557 | < 0.001* | 55 | 0.281 (0.03) | 7.4 | < 0.001* |
| | WTD | 12 | 0.018 (0.00) | 3.4 | = 0.004* | 0.5 | -0.003 (0.00) | -0.6 | = 0.499 | >900 | -0.022 (0.00) | -45 | < 0.001* | 105 | -0.104 (0.01) | -10.2 | < 0.001* |
| | Elevation | 73 | -1.715 (0.20) | -8.5 | = 0.044* | 19 | 3.551 (0.81) | 4.3 | < 0.001* | >900 | -3.324 (0.03) | -85 | < 0.001* | 100 | -21.616 (2.15) | -10.0 | < 0.001* |

CHAPTER 4 – Lichens: a limit to peat growth?

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4.1 Context within thesis

As indicated in the literature review, and demonstrated by the results of my analysis in Chapter 3, vegetation composition is an important factor influencing peat accumulation in HBL peatlands. Lichens are a common feature of many northern peatlands (above ~ 50° latitude), often covering large areas as mats up to 20 cm thick. Yet very few studies consider the potential effects of these lichens on peat accumulation (e.g. Malmer and Wallen, 1999). At one of my HBL sites (Bog), NEP for lichen covered hummocks was very small or negative, indicating significantly smaller production than *Sphagnum* dominated hummocks. If production is then exceeded by decomposition, peat accumulation in lichen covered hummocks may slow or cease.

In this chapter, I assess the effect of thick lichen mats (predominantly *C. stellaris*) on the structure (e.g. vegetation composition) and biogeochemical function (production and decomposition) of an ombrotrophic bog in the HBL. I examine indicators and possible mechanisms for potential contrasts in decomposition (e.g. leachate chemistry, peat age-depth relationships, peat chemical composition) for peat in *Sphagnum* hummocks and under lichen mats. I then discuss the balance of production and decomposition in lichen dominated areas and the potential consequences for peat accumulation.

4.2 Abstract

The fruticose lichens Cladina stellaris and Cladina rangiferina form thick mats on hummocks in bogs in the Hudson Bay Lowland (HBL). Lichens cover large areas of northern peatlands but their role within peatland ecosystems is poorly understood. We investigated the potential effect of these mat-forming lichens on peat production and decomposition processes, using field data from an ombrogenous bog in the HBL and laboratory analyses. We hypothesise that (a) production in lichen-shrub hummocks is less than Sphagnum-shrub hummocks, (b) the decay of lichen litter is faster than Sphagnum moss so the mass litter input to the peat profile is reduced, and (c) faster decomposition of the underlying peat is stimulated by lichen leachates. In combination, this means that in lichen-dominated hummocks the production of new material added to the peat column is less and the decomposition of residual peat is greater, hence limiting the accumulation of peat. We found that thick lichen mats alter vegetation composition in peatlands, reducing Sphagnum cover and inhibiting the growth of small shrubs. Coupled with low lichen productivity that is constrained by moisture conditions, production for lichen-dominated hummocks is significantly smaller than Sphagnum hummocks. We found no evidence to suggest leachates from lichen enhance decomposition processes in peatlands but larger bulk densities for peat under lichen mats does indicate a loss of structural integrity and potential collapse of the peat column. Coupled with smaller production and faster lichen decay that results in very little or no addition of mass to the peat column, local peat accumulation in lichen dominated hummocks ceases, representing a possible temporary limit to peat growth.

4.3 Introduction

The peatlands of the Hudson Bay Lowland (HBL), Canada, extend over 250,000 km² and are globally important carbon (C) stores, containing ~ 30 Pg C, or approximately 6 % of the northern peatland C pool (Packalen *et al.*, 2014). Lichen can be a substantial vegetation cover on raised bogs

within the HBL and other northern peatlands (Glaser and Janssens, 1986; Ahti and Oksanen, 1990; Malmer and Wallen, 1999; Dunford *et al.*, 2006; Riley, 2011; Neta *et al.*, 2011). Glaser and Janssens (1986) note lichen cover to be over 80 % on bogs in southeastern Labrador, in northern New Brunswick, northeastern Newfoundland, and eastern Quebec. In the HBL, mats of predominantly *Cladina stellaris*, (Opiz) Brodo., and *Cladina rangiferina*, (L.) Weber ex F.H.Wigg., may be up to 20 cm thick and cover ~ 50 % of the peatland surface (OMOE, 2011; Humphreys *et al.*, 2014). Lichens are susceptible to fire and foraging by caribou, but long fire intervals and small caribou populations in the flat and wet HBL peatlands allow these mat-forming lichens to thrive (Payette, 1988; Boudreau and Payette, 2004; Magoun *et al.*, 2005; Riley, 2011). Although lichens cover large areas of peatland and may contribute significantly to global biogeochemical cycles (Elbert *et al.*, 2012; Porada *et al.*, 2013; Porada *et al.*, 2014), their role within peatland ecosystems is poorly understood, particularly their influence on peatland development and C cycling.

Dense lichen mats are associated with reduced moss and vascular plant cover (Crittenden, 2000; Cornelissen *et al.*, 2001, Lang *et al.*, 2009a), altering plant community structure, which is important for biogeochemical processes controlling peat production and decomposition (Belyea, 1996; Belyea and Malmer, 2004). Peatland development over time requires plant production (as net primary production, NPP) to exceed decomposition to enable accumulation of peat (Clymo, 1984). Assuming a two-layer structure for a peat column, Clymo (1984) describes how peat not lost to decay in the aerobic acrotelm is added to the anaerobic catotelm over time, resulting in peat growth. However, as the peat column increases in height, the thicker acrotelm is exposed to aerobic decay for a longer time period, and while decay in the catotelm continues, the rate of peat accumulation slows. This is a steady state for peatlands and represents 'the limit to peat bog growth' (Clymo, 1984). Various models have since been proposed to incorporate more detailed hydrological feedbacks and variable NPP (e.g. Belyea and Clymo, 1998; Hilbert *et al.*, 2000; Belyea and Clymo, 2001; Eppinga

et al., 2009a; Morris *et al.*, 2011a), but none consider the potential consequences of vegetation change from a *Sphagnum*-dominated surface to a lichen-dominated surface.

Since desiccation-tolerant lichens may be dry for prolonged periods (Rundel, 1988; Jonsson et al., 2008), their productivity is generally small when compared to bryophytes and vascular plants (Green et al., 2008). In addition to light and temperature constraints, photosynthesis in lichens is determined by water availability with net CO₂ exchange largely controlled by water content in the thallus (Kershaw, 1972; Lechowicz, 1978; Lechowicz, 1982; Green et al., 2008). Photosynthetic activity of the photobiont is therefore not only restricted to periods of optimal light intensity and temperature, but also when lichen thalli are partly hydrated (Gasulla et al., 2012). Photosynthesis in Sphagnum mosses is also constrained by moisture content but unlike lichens, relatively constant productivity is achieved through desiccation avoidance and hydraulic continuity with the water table (Rydin, 1993a; Schouwenaars and Gosen, 2007; Hájek and Vicherová, 2014). Consequently, growth rates for *Cladina* spp. with low C density, are estimated at 3 to 6 mm yr⁻¹ or approximately 11 % o the biomass production per year (Ouzilleau and Payette, 1975; Vasander, 1981; Helle et al., 1983; Kumpula et al., 2000), while growth rates for the hummock forming Sphagnum fuscum, (Schimp.) Klinggr., with greater C density, may be 10 mm yr⁻¹ or more (Lindholm, 1990). Lichen also decays quite rapidly (average k value of 0.2 yr⁻¹) compared to Sphagnum spp. (average k value of 0.05 yr⁻¹) and particularly when compared to hummock forming Sphagnum spp. such as S. fuscum (Lang et al., 2009b; Bengtsson et al., 2016). Coupled with very low litter addition from reduced vascular plant cover, the quantity of litter added to the peat profile in lichen hummocks is deemed insignificant (Malmer and Wallén, 1999), and considering constraints on productivity in lichens, production in lichen-dominated hummocks is therefore small.

Decomposition processes in peatlands are dependent on litter quantity and quality (for lichens this is mostly dead fungal biomass – Crittenden, 1991), and abiotic conditions (e.g. temperature, water table depth, pH). These factors affect the activity of microbial communities within the peat

(Strakova *et al.*, 2011; Preston *et al.*, 2012) and may be altered in lichen-dominated areas. As vascular plant cover may be reduced, the influence of root exudates and root turnover on decomposition may also decline (Crow and Wieder, 2005; Basiliko *et al.*, 2012). The organic matter and leachate chemistry of fungal lichens may differ from *Sphagnum* moss and are therefore likely to be important for decomposition in lichen-dominated areas (Williams and Crawford, 1983; Medvedeff *et al.*, 2015).

The chemical composition of leachates from different plant species vary due to significant variation in the secondary metabolites or 'chemical defence mechanisms' employed by different species (Pinsonneault *et al.*, 2016a). These leachates typically comprise dissolved organic carbon (DOC, including humic acids and a range of polyphenolic compounds), and enzymes such as phenol oxidases (Naumova *et al.*, 2013; Zagoskina *et al.*, 2013; Beckett *et al.*, 2013; Medvedeff *et al.*, 2015). *Cladina* species are rich in polyphenolic compounds such as usnic and perlatolic acids (Rundel, 1978; Hyvarinen *et al.*, 2003; Zagoskina *et al.*, 2013), which can leach in large quantities to underlying peat following rain events (Dudley and Lechowicz, 1987). It is possible that these lichen leachates stimulate (or prime) the consumption of recalcitrant C, increasing decomposition of underlying peat through increased microbial consumption of biologically available C (Stark and Hyvarinen, 2003). This 'priming effect' may be a competition mechanism (a form of allelopathy) to enable lichen establishment, particularly on *Sphagnum* peat that does not readily decay.

We hypothesise that in northern peatlands where lichens are present that (a) the productivity of lichen-shrub hummocks is less than *Sphagnum*-shrub hummocks, (b) the decay of lichen litter is faster than *Sphagnum* moss so the mass litter input to the peat profile is reduced, and (c) faster decomposition of the underlying peat is stimulated by lichen leachates. In combination, this means the production of new material added to the peat column is less and the decomposition of residual peat is greater, hence reducing the accumulation of peat (Figure 4.1) We investigate these potential differences in production and decomposition in lichen-dominated hummocks and *Sphagnum*-dominated hummocks through analysis of field data and laboratory analyses.

4.4 Methods

Study Site

Data were collected from sites in the remote HBL, approximately 90 km west of Attawapiskat in northern Ontario, Canada. Mean annual temperature is - 1.3 °C (1971-2010, Lansdowne House, 280 km WSW - Environment Canada, 2016) with daily averages ranging from - 22.3 °C in January and 17.2 °C in July. Mean annual precipitation is ~ 700 mm, predominantly as snowfall in all months but July and August.

Located almost 13 km south of the De Beers Canada Victor Mine (52°49'06" N, 83°54'18" W; ~ 83 m elevation), a 1.5 km raised boardwalk (installed by the Ontario Ministry of Environment and Climate Change, OMOECC, referred to as MOE) crosses a pristine ombrogenous raised bog (named MOE Bog, 52°41'36" N, 83°56'41" W; ~ 91 m elevation) through to a moderately-rich minerogenous fen (MOE Fen, 52°42'02" N, 83°57'18" W; ~ 88 m elevation), the two dominant peatland types in the HBL (Ulanowski and Branfireun, 2013; Ulanowski, 2014; Humphreys *et al.*, 2014). A research site was also established at North Road Bioherm (NRB, 52°51'22" N, 83°54'49" W; ~ 86 m elevation), a treed bog located approximately 3 km from Victor Mine (Whittington and Price, 2012). MOE Bog and NRB are ombrogenous peatlands with similar small-scale hummockhollow microtopography and *S. fuscum* and lichens as the dominant hummock vegetation cover (Table 4.1).

Vegetation Community Composition and Structure

Vegetation composition and structure of lichen-shrub (> 10 % *C. stellaris* cover, mat thickness ~ 15 cm) and *Sphagnum*-shrub (*S. fuscum* with < 10 % lichen cover) hummocks at MOE Bog were measured in July-August 2014. Vegetation was surveyed following a stratified random

sampling approach, with 34 quadrats placed randomly and evenly (17 quadrats each) on lichen-shrub and *Sphagnum*-shrub hummocks. We used the point-intercept method where, for 25 grid points in each 0.5 m² quadrat, we recorded the number of times a metal rod (radius ~ 3 mm) was in contact with each species and component (for leaf:stem ratios) (Larmola *et al.*, 2013). Canopy height (vascular plants), thickness of lichen mats, bare peat and litter were also recorded. All vegetation was identified to the species level, with nomenclature for vascular plants and moss as Flora of North America (1993+) and Riley (2003), and nomenclature for lichens as Brodo *et al.*, (2001) (see Table S4.1 for full species list and nomenclature).

For each quadrat, we calculated species richness (total number of species per plot, alpha diversity), Simpson Diversity (D) and Shannon-Weiner Diversity (H') (evenness), and assessed differences between lichen-shrub and *Sphagnum*-shrub hummocks using *t*-tests or Mann-Whitney rank sum tests. To examine differences in species composition and abundance, we used non-metric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix calculated from percentage cover in the R-library *vegan* (Oksanen *et al.*, 2016).

For each NEE collar (see below), we measured vascular green area (VGA) by recording the total number of green leaves per species, along with the width and length of 20 leaves per species (or all leaves if less than 20). Species-specific formulae based on leaf geometry were applied to determine average leaf size (Wilson *et al.*, 2007). This was then multiplied by the number of leaves and divided by the collar surface area to give the green area index of a vascular plant species (m² m⁻²) for the measurement period (mid-July to mid-August). The VGA index (m² m⁻²) of each collar was calculated by summing the green area index of all vascular plants present.

*Net Ecosystem CO*₂ *Exchange (NEE)*

We used closed chamber measurements of NEE to examine the productivity of lichen-shrub hummocks compared to *Sphagnum*-shrub hummocks under a range of environmental controls (e.g. lichen moisture content, temperature). Study plots representing dominant hummock vegetation were selected at the MOE Bog research location, with three collars, each of 0.055 m² area, installed for each vegetation type in summer 2012 (Table 4.1). CO₂ fluxes for each collar were measured during the 2013 and 2014 growing seasons (June to August) using closed chambers constructed of clear Plexiglas (27.57 L volume) and fitted with fans and a cooling unit. Change in headspace CO₂ concentration (ppm) was measured using a portable CO₂ analyser (EGM-4 Environmental Gas Analyser, PP Systems). Photosynthetic photon flux density (PPFD μ mol m⁻² s⁻¹) was measured at the same time as CO₂ using a quantum sensor (PAR-1, PP Systems). Measurements were recorded every 10 seconds for the first minute and then every 30 seconds for the final 2 minutes, for full-light, halflight, and dark conditions, using mesh and opaque shrouds over the chamber (Bubier *et al.*, 1998; Strack *et al.*, 2006b; Pelletier *et al.*, 2011).

We used a mini-chamber (0.79 L volume) to measure CO₂ fluxes from lichen only (*C. stellaris*) and to explore the effect of moisture on lichen CO₂ exchange. Three mini-collars, each of 0.0078 m² area, were installed in the three vegetation-microform types (lichen-only hummock, lichen-only intermediate, *Sphagnum*-only hummock), with six plots for each vegetation-microform type - three natural conditions, three experimental moisture conditions (total of 18 plots), at the NRB study site. Although water table depths are lower at NRB as a result of dewatering at Victor Mine (Whittington and Price, 2012), we considered it unlikely that this would significantly affect the CO₂ exchange of lichen mats on the peatland surface that depend solely on recent rainfall/precipitation for moisture needs (Jonsson *et al.*, 2008). The experimental plots were sprayed with variable amounts of de-ionised (DI) water and CO₂ measurements taken immediately after (as described above) and then repeated during the day as the lichen (or *Sphagnum*) dried naturally.

NEE of CO₂ (μ mol⁻¹ CO₂ m⁻² s⁻¹) was calculated from a linear regression of change in CO₂ concentration in the chamber headspace with time, as a function of chamber volume and temperature. Data with r^2 values less than 0.5 were checked for measurement errors caused by

equipment malfunction or weather conditions, and removed if poor quality. Remaining data with low r^2 values correspond to very low or no CO₂ flux (not due to error) and were included in the analysis.

We applied a rectangular hyperbola curve (equation 1, SigmaPlot 12.0) to determine the relationship between NEE and PPFD (Frolking *et al.*, 1998; Bubier *et al.*, 1999). The sign convention is positive for CO_2 uptake and negative for CO_2 release to the atmosphere.

$$NEE = GP_{max} * \alpha * PPFD / ((\alpha * PPFD) + GP_{max}) + ER, \qquad (eq.1)$$

where GP_{max} is the maximum gross photosynthetic CO₂ capture at maximum PPFD (µmol $CO_2 \text{ m}^{-1} \text{ s}^{-1}$), α is the photosynthetic quantum efficiency (initial slope of the curve, µmol $CO_2 \text{ m}^{-1} \text{ s}^{-1}$ per umol PPFD m⁻² s⁻¹) and ER is the dark ecosystem respiration (umol CO₂ m⁻¹ s⁻¹). Net ecosystem production (NEP, μ mol CO₂ m⁻¹ s⁻¹) was calculated as gross primary production (GPP) minus ER. Maximum rates of photosynthesis (PSN_{max}) were calculated from all GPP with PPFD greater than 1000 µmol m⁻² s⁻¹ (Bubier et al., 2003). Statistical differences in the rectangular hyperbola parameters (GP_{max} and α) between vegetation-microform types were determined from confidence intervals. Generalised linear models (GLM - fixed effects with repeated measures, IBM SPSS Statistics 23) were used to determine the significance of species and environmental factors (temperature, peat moisture, WTD) for NEP, GPP, PSN_{max} and ER. All models shared the same structure where collar was designated as the subject and date as repeated measures, and using the maximum likelihood method. All models were fit with a gamma distribution and log link and used the Satterthwaite approximation for the unbalanced design. Akaike's Information Criterion (AIC) and restricted -2 log-likelihood (-2logLL) were used to determine the best model fit. Separate GLMs for vegetation type and for abiotic variables were also used to determine the pure contribution of the two sets of predictor variables.

Decomposition (sample collection and lab analyses)

To determine potential differences in peat decomposition in lichen-shrub and Sphagnumshrub hummocks we used Fourier-Transform Infrared Spectrometry (FTIR) as a quantitative measure of decomposition (humification), and ²¹⁰Pb dating to estimate age-depth relationships and peat accumulation rates (Turunen et al., 2004; Beer et al., 2008; Broder et al., 2012; Hodgkins et al., 2014; Biester et al., 2014). Peat cores (to 30 cm depth) and intact lichen mats (~ 20 cm thick) were collected in July 2015 from six lichen-shrub hummocks (three C. stellaris and three C. rangiferina hummocks), and three Sphagnum-shrub hummocks (S. fuscum) at MOE Bog (four small intact cores were collected per hummock as field replicates). Samples were taken from each field replicate at 0-5 cm, 10-15 cm and 20-25 cm for Sphagnum-shrub, and 0-5 cm and 20-25 cm for peat under lichen mats. Samples were also taken from upper (0-5 cm) and lower (10-15 cm) lichen mats. All samples were sorted to remove roots and vascular plant material and homogenised to ensure representation of the replicate location and depth increment. For FTIR analysis, samples were oven dried at 50 °C for 24 hours or until dry before grinding through a 40-mesh sieve (Wiley Mini Mill 3383-L10). FTIR spectra were obtained using a FTIR spectrometer (Agilent Cary 670 FTIR Spectrometer). To determine differences in decomposition among samples, we calculated humification indices (HI, higher HI indicates increased decomposition) as ratios of absorbance at wavenumbers 1450, 1514, 1630, 1720, and 2920 cm⁻¹ (aliphatic, aromatic, and phenolic moieties) with respect to polysaccharides (1060 cm⁻¹) (structural group assignments given in Table S4.2). Differences in HI ratios between species were assessed using ANOVAs or appropriate non-parametric tests (e.g. Kruskal-Wallis).

For ²¹⁰Pb dating, additional intact peat cores (~ 1 m depth) were collected from a *Sphagnum*shrub hummock and a lichen-shrub hummock (*C. stellaris*) at MOE Bog. Dry samples at 2 cm increments for the first 20 cm and 5 cm increments thereafter were shipped to Flett Research Ltd (Winnipeg, Canada) for analysis. For ²¹⁰Pb dating, it is assumed ²¹⁰Pb concentrations (measured as ²¹⁰Pb activity in dry peat samples) decrease exponentially with peat depth, and that a low constant value represents the supported ²¹⁰Pb fraction formed within soil rather than from atmospheric deposition (Turetsky *et al.*, 2000; Turunen *et al.*, 2004). The age of each depth increment was calculated using the constant rate of supply (CRS) model (Appleby and Oldfield, 1978).

Chemical analyses of leachates

We explored potential biogeochemical mechanisms for enhanced decomposition by comparing the chemical composition of leachates collected from fresh vegetation and peat core samples (Pinsonneault *et al.*, 2016a). Leachates were prepared by soaking the samples in 60 ml DI water (1:3 sample:solution suspension) overnight (~ 12 hours) in the dark at room temperature (~ 20 °C). The leachates were immediately filtered through a 0.45 μ m binder-free filter paper (Macherey-Nagel) and stored at 4 °C in the dark until analysis a few days later.

Dissolved organic carbon (DOC, mg L⁻¹) and total dissolved nitrogen (TDN, mg L⁻¹) were measured using a Shimadzu V-CSN TOC/TN analyser. We used a LAMBDA Bio spectrophotometer (PerkinElmer) with a 1 cm path length cell, to measure UV absorbance at wavelengths of 250, 254, 365, 465, and 665 nm. Specific UV absorbance at 254 nm (SUVA₂₅₄) was calculated from the absorbance at 254 nm divided by the DOC concentration (mg L⁻¹) and the path length of the cell (cm), and is expressed as L mg C⁻¹ m⁻¹. To estimate aromaticity and molecular weight of each sample, the E2:E3 ratio was calculated by dividing absorbance at 250 nm by 365 nm (Peacock *et al.*, 2014).

Nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N) concentrations (mg L⁻¹) were determined using a Lachat QuikChem AE flow injection autoanalyzer (Lachat Instruments, USA) using the cadmium reduction method (QuikChem method 10-107-04-1-C; Lachat 2008) for NO₃⁻-N and the salicylate hypochlorite method (QuikChem method 10-107-06-2-C; Lachat 2008) for NH₄⁺-N.

Total soluble phenolic concentrations (TSP, mg L⁻¹) were determined for each sample as described by Pinsonneault *et al.*, (2016b). 250 μ L triplicates of each leachate sample (1:3

sample:solution) were added to clear microplate wells. 12.5 μ L Folin-Ciocalteau reagent (Sigma-Aldrich) was added, followed by 37.5 μ L sodium carbonate solution (Na₂CO₃, concentration 200 g L⁻¹). The reaction proceeded for 1.5 hour before measuring absorbance at 750 nm on a spectrophotometer (Infinite 200 Pro, Tecan). Total soluble phenolic concentrations for each sample were derived from a standard calibration curve of known concentrations from 0 to 40 mg L⁻¹.

Total phenol oxidase activities (PO, μ mol dicq g⁻¹ min⁻¹) were determined per Dunn *et al.*, (2014) and Pinsonneault *et al.*, (2016b). For each sample replicate, two 1 g samples were placed into two separate stomacher bags (sample and a control) and incubated at field temperatures overnight (~ 12 hours). 9 mL L-DOPA solution (prepared fresh, 10 nM dihydroxy phenylalanine, Sigma-Aldrich) or Milli-Q water (control) (both incubated to analysis temperature) were added to the stomacher bags and then incubated at field temperature for 10 minutes. Three replicates of each sample and three of each control were then immediately centrifuged for 5 minutes at 13,500 RPM to terminate the reaction. Aliquots of each sample and control were added to clear microplate wells and absorbance at 460 nm measured on a spectrophotometer (Infinite 200 Pro, Tecan).

Generalised linear models (GLM – both fixed and mixed effects, IBM SPSS Statistics 23) were used to determine the significance of species and abiotic variables (including temperature, pH, moisture content, WTD) on leachate chemistry. Apart from repeated measures (not required), model fit and structure was as described for NEE, with separate GLMs for species and for abiotic variables with multiple comparisons. To compare results for lichen-shrub and *Sphagnum*-shrub hummocks, peat depths of similar age were determined from ²¹⁰Pb dating. We consider the photosynthetically active surface of *Sphagnum* and lichen mats to be new growth and therefore of a similar age, termed 'age class A'. Peat samples from above the water table at 20 - 25 cm depth in *Sphagnum*-shrub hummocks at 0 - 5 cm depth, and were therefore termed 'age class B' for statistical comparisons.

Biodegradability Incubation

Potential differences in the biodegradability of DOC from lichen mats, peat under lichen mats, and peat from *Sphagnum*-shrub hummocks were determined using a water extraction and incubation technique described by Pinsonneault *et al.*, (2016a). Samples were taken from the same peat cores and lichen mats at the same depth intervals noted for other chemical analyses. Water soluble DOC was extracted using a 1:100 (dry weight) sample:solution suspension. Samples (4 g dry weight equivalent) were soaked in 400 mL DI water overnight (~ 12 hours) at room temperature (~ 20 °C) in the dark. The extracts were then filtered using a Whatman 41 filter paper to remove particulates, and then a 0.45 µm binder-free filter paper (Macherey-Nagel). A 20 mL aliquot of each filtered sample was taken for DOC concentrations and UV absorbance prior to the start of the incubation. Samples were then stored in the fridge until the start of the incubation a few days later.

The microbial inoculum was prepared one day prior to the start of the incubation and comprised a mix of organic matter samples (excluding lichen, to eliminate possible antimicrobial effect of additional lichen compounds), at 4:45 sample:solution (26.6 g organic matter to 300 mL DI water). The inoculum was left for ~ 12 hours in the dark at room temperature (~ 20 °C) then filtered through fibreglass wool. Two 20 mL aliquots of filtered inoculum were taken on day 1 of the incubation for DOC concentrations and UV absorbance measurements.

Each sample was incubated in triplicate with 200 mL water extract in a 250 mL mason jar with samples diluted to ensure standard DOC concentrations of 10 - 20 mg L⁻¹ per sample (to prevent excessive microbial growth, Hongve *et al.*, 2000; McDowell *et al.*, 2006). 2 mL of microbial inoculum and two 0.45 µm binder-free filter papers cut in half were added to each jar (papers provide a surface for microbial growth). Samples were incubated at room temperature (~ 20 °C) in the dark. Aliquots (20 mL) were taken on days 1, 3, 7, 14 and 28 of the incubation and filtered through 0.45 µm filter paper. DOC concentrations and UV absorbance were measured as described for other leachates. On days 3 and 26, CO_2 was measured by sealing the jars and sampling the headspace with a syringe at time 0, 120 mins, and 240 mins. CO_2 concentrations were measured on a Shimadzu Mini-2 gas chromatograph with a methanizer.

Ancillary Measurements

We measured air and peat temperature at 5, 10 and 20 cm below the surface at the same time as all NEE sampling runs, as well as during sample and peat core collection at all locations. We also measured moisture content of peat at 20 cm depth (volumetric water content, VWC %) using a Hydrosense 2 Soil Moisture Sensor fitted with a CS658 water content sensor (20 cm probe length, Campbell Scientific). Volumetric moisture content (%) was calculated from the period (μ s) using a custom linear calibration curve of gravimetric moisture content (GWC, % of dry weight) for vegetation and peat samples from all plots at MOE Bog ($r^2 = 0.57$ for y = mx + c, where y = VWC as %, m = slope (17.06), c = intercept (0), and x = period in μ s). Water table depth below the surface was measured in slotted PVC tubes (with a mesh screen) installed at each location, or during peat core extraction. We also measured the light available to *Sphagnum* moss under lichen mats, by placing a quantum sensor (PAR-1, PP Systems) at different depths in *C. stellaris* lichen mats.

Differences in WTD, peat temperature, and peat moisture between species (lichens and *Sphagnum*) were assessed using ANOVAs or appropriate non-parametric tests (e.g. Kruskal-Wallis). Unless noted otherwise, all statistics were conducted using R version 3.3.1 (R Core Team 2016) or IBM SPSS Statistics 23.

4.5 Results

Plant community composition

Lichen-shrub hummocks had significantly lower species richness, Shannon diversity and percentage shrub cover than *Sphagnum*-shrub hummocks (Figure 4.2, full species list and nomenclature in Table S4.1). Although VGA and shrub leaf:stem ratio were larger, and shrub canopy

height smaller for *Sphagnum*-shrub hummocks than lichen-shrub hummocks, the differences were not statistically significant (Table 4.1). *Chamaedaphne calyculata* and *Rhododendron groenlandicum* were the dominant species for lichen-shrub hummocks, although the percent cover for these species did not differ from *Sphagnum*-shrub hummocks. *Drosera rotundifolia, Polytrichum strictum, Rubus chamaemorus, Kalmia angustifolia, Kalmia polifolia,* and *Vaccinium* spp. were absent from hummocks with more than 30 % lichen cover. A best solution NMDS ordination of community composition was reached after 20 runs with a resulting stress of 0.14, indicating a good fit in 2D space (Figure 4.3). There was no overlap between lichen-shrub and *Sphagnum*-shrub dominated hummocks, with hierarchical clustering showing clear separation of the two communities.

NEE

NEE-PPFD relationships for each vegetation type (Table 4.2) were determined using pooled 2013 and 2014 data, as there was no significant variation between years for MOE Bog and insufficient data in 2013 for NRB. These combined data revealed variable GPP-PPFD relationships among vegetation types at MOE Bog (Figure 4.4). GPP was significantly larger for *Sphagnum*-shrub hummocks than lichen-shrub hummocks (p = 0.015) and lichen-only hummock-intermediate microforms (p < 0.001), with the GPP-PPFD rectangular hyperbola curve a poor fit for the latter. The GPP-PPFD relationship for lichen-only hummocks at NRB was also a poor fit (Figure 4.4).

At MOE Bog, PSN_{max} was significantly larger for *Sphagnum*-shrub hummocks than both lichen-shrub and lichen-only hummocks (p < 0.001), and significantly larger for lichen-shrub hummocks than lichen-only hummocks (p < 0.001). At NRB, PSN_{max} of lichen-only was significantly correlated to moisture content but there was no significant relationship for *Sphagnum* (Figure 4.5). ER did not vary significantly among veg-microform types at MOE Bog but due to significantly smaller GPP, mean NEP was negative for lichen-shrub hummocks (-0.045 ± 0.11 µmol $CO_2 m^{-2} s^{-1}$) and lichen-only hummock-intermediate microforms (-0.54 ± 0.14 µmol $CO_2 m^{-2} s^{-1}$). Mean NEP for *Sphagnum*-shrub hummocks was $2.5 \pm 0.23 \mu mol CO_2 m^{-2} s^{-1}$. Mean NEP for lichenonly plots at NRB was $-0.21 \pm 0.12 \mu mol CO_2 m^{-2} s^{-1}$, similar to MOE Bog.

Measurements of PPFD at various depths within thick lichen mats confirmed a significant reduction in light available to underlying *Sphagnum* moss at around 5 cm (Figure 4.6).

Decomposition

 210 Pb activity for the lichen core decreased exponentially from 45 dpm g⁻¹ to 0.5 dpm g⁻¹ at 30 cm, whereas the *Sphagnum* core decreased gradually from 16 dpm g⁻¹ to 0.5 dpm g⁻¹ at 95 cm (Figure 4.7a). The 210 Pb chronologies result in older age estimates for lichen hummocks compared to *Sphagnum* hummocks at comparable depths (Figure 4.7b).

Bulk densities were significantly larger for the upper 20 cm of peat under lichen mats (ranging from 0.04 to 0.2 g cm⁻³) compared to *Sphagnum* peat (< 0.05 g cm⁻³) (Figure 4.7c and Figure 4.8).

FTIR spectra are similar for all samples but the relative intensity of the bands differs for age class A, reflecting variations in the structure of organic matter for the photosynthetically active surface of *Sphagnum* moss and fungal lichens (e.g. more abundant polysaccharides, cellulose, aromatics and lignins; Lang *et al.*, 2009b; Figures S4.1). The 1450:1060 ratio (HIs) was significantly larger for lichen mats than *Sphagnum*, indicating greater humification in lichen mats compared to *Sphagnum* (p < 0.001, ANOVA). Greater recalcitrance of the *Sphagnum* surface was also indicated by larger aromatic content compared to both lichen species (*S. fuscum* mean 22.4 %, *C. stellaris* mean 15.1 %, and *C. rangiferina* mean 14.8 %, data not shown). Spectra for age class B (peat under lichen mats and at 20-25 cm in *Sphagnum*) were similar with no consistent differences in the intensity of the bands (Figure S4.2) or carbohydrate and aromatic content. HIs for *C. stellaris* mats, but not *C. rangiferina*, were smaller than the underlying peat indicating advanced decomposition in peat compared to both the upper surface of the lichen mat and the partially decayed lower layer (p < 0.05, ANOVA). We did not find a significant increase in HIs with peat depth, or any differences in

HIs for peat under lichen mats compared to *Sphagnum* hummocks, for age class B or any other depth comparisons (Table S4.3). We also found no statistically significant differences in DOC:TDN ratio (from leachates) with depth or for lichen peat compared to *Sphagnum* peat (Table 4.3).

Chemical composition of leachates

There were significant differences in the chemical composition of leachates from lichen mats compared to underlying peat. Leachate from lichen mats had larger DOC, TDN, and N-NH₄⁺ concentrations (p < 0.05), and smaller SUVA₂₅₄ values (mean < 1 L mg C⁻¹ m⁻¹ for upper and lower mat of both lichen species) than leachate from underlying peat (SUVA₂₅₄ mean values ranging from 3.2 to 4.6 L mg C⁻¹ m⁻¹ for all peat depths; Table 4.3). There were also significant differences between the upper and the lower part of lichen mats - notably, PO activity was significantly reduced in the lower part of lichen mats compared to the upper mat and underlying peat (p < 0.05), while TSP values were larger in the upper part of *C. stellaris* than the lower mat and underlying peat (p < 0.05). In contrast, values for leachates from *Sphagnum* dominated hummocks did not vary significantly with depth, except for an increase in SUVA₂₅₄ from a mean of 2.2 to 3.6 L mg C⁻¹ m⁻¹ (p < 0.005).

We calculated the ratio of TSP to DOC to reconcile the large DOC and TSP (recalcitrant material) with the small SUVA₂₅₄ values (indicating more biodegradable material) we obtained for lichen mats. A small TSP:DOC ratio denotes a smaller fraction of the DOC pool being comprised of recalcitrant, inhibitory TSP. The larger TSP:DOC ratio for peat under lichen mats (p < 0.005) indicates a greater fraction of recalcitrant TSP as shown by larger SUVA₂₅₄ values. The reduced PO activity recorded for the lower part of lichen mats corresponds with a significantly smaller TSP:DOC ratio (p < 0.005).

Species is a significant control for leachate composition from the photosynthetically active surface of lichen mats and *Sphagnum* (GLM age class A), but not for leachates from peat below lichen mats or at depth in *Sphagnum* hummocks (GLM age class B). DOC, TSP, TDN, NO₃⁻-N, and NH₄⁺-N concentrations were significantly larger in leachate from the surface of lichen mats than

Sphagnum (Figure 4.9). TSP, TDN and NO₃⁻-N concentrations were significantly larger from peat under lichen mats (*C. stellaris* only) compared to *Sphagnum* hummocks (Figure 4.10). The TSP:DOC ratio was also significantly larger for peat under lichen mats than *Sphagnum* hummocks (p< 0.005), but there were no significant differences between species for DOC or SUVA₂₅₄. We found no significant differences in PO activity between lichen hummocks and *Sphagnum* hummocks for age class A or B.

GLMs with abiotic predictor variables only, highlighted temperature as a significant effect for TSP (p = 0.015) and TSP:DOC ratio (p = 0.039) in leachate from age class A. Temperature was also a significant effect for TSP, TSP:DOC ratio, SUVA₂₅₄, TDN, and NO₃⁻-N (p < 0.05) for age class B, with WTD also important for TSP, TDN, and NO₃⁻-N (p < 0.05). We recorded cooler temperatures in peat under lichen mats than *Sphagnum* hummocks (p < 0.005, Kruskal-Wallis test, MOE Bog only). The surface moisture content of lichen mats was also significant effect on DOC, SUVA₂₅₄, TDN, NO₃⁻-N, and NH₄⁺-N (p < 0.001). We found no difference in VWC (%) in peat under lichen mats compared to *Sphagnum* hummocks (test at MOE Bog only). We found no significant abiotic controls for PO activity for either age class A or B, and contrary to other studies (e.g. Pind *et al.*, 1994), the relationship between PO activity and TSP was poor (Figure S4.3).

DOC Biodegradability

We found no significant differences in DOC biodegradability of peat under lichen mats or *Sphagnum* (Figure S4.4a). However, during the first 3 days of the incubation there was an overall decrease in E2:E3 ratios (triplicate averages) followed by an increase on day 14 for all samples (Figure S4.4c), indicating a change in the quality of DOC despite minimal or no changes in DOC quantity throughout the incubation period. SUVA₂₅₄ values of the initial and final samples were strongly correlated (Figure S4.5) and there was an overall slight increase during the incubation

(Figure S4.4b). No detectable change in CO₂ production was observed for any samples on day 3 or day 26 of the incubation period.

4.6 Discussion

To our knowledge, this is the first study to examine the effects of lichen on peat production and decomposition processes. We show that production for lichen-dominated hummocks is significantly lower, with smaller GPP for lichen-shrub hummocks than Sphagnum-shrub hummocks. Our results also confirm the dependence of lichen productivity on moisture conditions (Lechowicz, 1978; Lechowicz, 1982; Green et al., 2008). Consistent with studies showing fast decay rates for lichens (Moore, 1984; Lang et al., 2009b), our results indicate that DOC leached from lichen mats is significantly more biodegradable (smaller SUVA₂₅₄ values) than underlying peat, and when compared to the surface of Sphagnum hummocks. We also found larger HI 1450:1060 ratios for lichen mats indicating advanced decomposition. However, we did not find any evidence to support our hypothesis of enhanced decomposition of peat under lichen mats, except when compared to the lichen mat (both the upper and partially decayed lower mat). Our analyses show no difference in decomposition for peat under lichen mats compared to Sphagnum hummocks, and no evidence for increased PO activity as a potential mechanism for a priming effect. Despite this, NEP was slightly negative for lichen-shrub hummocks, indicating that during the growing season, these areas may function as a small C source to the atmosphere. We therefore suggest that local peat accumulation is effectively eliminated by significantly lower production in lichen-dominated hummocks, which is likely to be equal to or less than decomposition. This confirms our conceptual model in Figure 4.1, except for the hypotheses of advanced decomposition in stage C.

Productivity

Smaller production for lichen-dominated hummocks can be explained by changes in plant community composition due to the growth of a thick lichen mat. Lichen GPP (when moist) is smaller than *S. fuscum* but only by a small amount, with GPP for both species generally less than 2 μ mol CO₂ m⁻² s⁻¹ (e.g. Street *et al.*, 2012). It is therefore likely that the type and cover of shrubs enables significantly larger GPP for *Sphagnum*-shrub hummocks compared to lichen-shrub hummocks. This is consistent with our hypothesis that the growth of a lichen mat reduces the light available for *Sphagnum* moss and for low growing (or less competitive) shrubs such as *R. chamaemorus* and *K. polifolia*, resulting in their absence in lichen dominated areas. Species associated with thick lichen mats were *C. calyculata* and *R. groenlandicum*, both with faster growth rates and therefore the potential to grow above the lichen mat (Bartsch and Schwintzer, 1994; Hébert and Thiffault, 2011). Taller shrubs may not have larger leaf:stem ratios however, as shrubs (which may also be older in lichen covered areas) allocate biomass to woody stems in order to grow above thick lichen mats. Our analysis indicates that a smaller shrub leaf:stem ratio, coupled with a smaller number of shrub species, lowers VGA and consequently GPP in lichen-dominated areas.

As lichen productivity is also limited by moisture conditions, this may reduce the time lichens are photosynthetically active compared to *Sphagnum*. Both *Sphagnum* moss and lichens are poikilohydrous (Kappen and Valladares, 2007) but in contrast to the desiccation-tolerant lichens (Kranner *et al.*, 2008), *Sphagnum* mosses are generally intolerant to drought and therefore have functional traits to retain water for longer (Lindholm, 1990; Hájek and Vicherová, 2014). Although the photosynthetic capacity of *Sphagnum* is also strongly dependent on the water content of the capitula (Rydin and McDonald, 1985; Silvola, 1990), the ability to retain water enables photosynthesis for longer periods than for lichens which quickly dry out (Groulx and Lechowicz, 1987; Palmqvist *et al.*, 2008). Too much water can also be a problem for photosynthesis in lichens, with studies finding suppressed net photosynthesis at high thallus water contents (Lange and Tenhunen, 1981; Green *et al.*, 2008), and maximum water saturation causing the photobiont to die (Harris and Kershaw, 1971). A respiration response to recent rainfall (and experimental wetting) or over saturation and therefore delayed photosynthetic recovery, may also be the cause of the

'negative' GPP we frequently observed for *C. stellaris* (Groulx and Lechowicz, 1987). The 'optimum' moisture conditions for lichen photosynthesis may therefore be severely limited.

Lichen productivity is also affected by age, with photosynthesis in older (and thicker) lichens declining after around 15 years (Lechowicz, 1983), and becoming minimal at around 100 years depending on environmental conditions and disturbance (Kumpula *et al.*, 2000). We chose to measure GPP for *C. stellaris* mats around 20 cm thick to ensure we could compare hummocks where lichen is clearly the dominant vegetation. However, this means the small GPP we observed for *C. stellaris* may also be due to the age of the mat which we estimate at ~ 50 to 100 years at this location.

Similar to *Sphagnum* mosses, lichens are able to capture inorganic N and phosphorus (P) from rainfall, and are susceptible to excess nutrient loads (Aldous, 2002; Kytoviita and Crittenden, 2007; Makkonen *et al.*, 2007; Fritz *et al.*, 2014). We found greater TDN, NO₃⁻⁻N, and NH₄⁺-N concentrations in leachate from lichen mats than *S. fuscum*, and particularly for *C. stellaris* compared to *C. rangiferina*. Kytovitta and Crittenden (2007) found high nitrogen use efficiency and relative growth rates for *C. stellaris* compared to other lichen species, and suggest that this may enable its dominance in undisturbed nutrient-poor conditions.

Decomposition

Faster decay rates for lichen mats compared to *Sphagnum* (*S. fuscum*) are due to differences in the chemical composition of the fungal lichen and its growth function. DOC concentrations were significantly larger for leachate from lichen mats than *Sphagnum*. However, only a small fraction of the DOC consists of recalcitrant, inhibitory TSP (low TSP:DOC ratio), in contrast to *Sphagnum* (higher TSP:DOC ratio). Lang *et al.*, (2009b) and Bengtsson *et al.*, (2016) also found little to no measurable decomposition for *S. fuscum* samples in either the field or laboratory conditions. The recalcitrant nature of *S. fuscum* is key to its success as a hummock forming *Sphagnum* species in bogs, whereas lichens that readily decay occupy a role similar to vascular plants, in that they do not themselves form microtopographical structures in peatlands. Leachate from peat under lichen mats was similar in chemical composition to peat from *Sphagnum* hummocks, comprising recalcitrant carbon compounds typical of more advanced decomposition of peat at depth (Beer *et al.*, 2008; Leifeld *et al.*, 2012; Biester *et al.*, 2014). These chemical similarities may explain the lack of differences in the degree of decomposition in peat under lichen mats compared to *Sphagnum* hummocks (as indicated by FTIR HIs and DOC:TDN ratios). As the peat under lichen mats was most likely *S. fuscum* prior to the establishment and growth of the lichen mat above it, this would account for the similar chemical composition. We also only sampled shallow cores above the water table (to 30 cm). Tfaily *et al.*, (2014) showed that HIs did not differ significantly for the upper 30 cm of peat, with large increases in HI occurring below 50 cm. Potential differences in decomposition in the upper 30 cm of chemically similar lichen peat (which was previously *Sphagnum* spp.) and *Sphagnum* peat may therefore be difficult to detect using these methods.

The lack of differences in decomposition may also be explained by feedback mechanisms among abiotic factors (e.g. temperature) and the chemical composition of organic matter and leachates. Temperature is an important control on decomposition in peatlands (Davidson and Janssens, 2006; Dorrepaal *et al.*, 2009). Lichen mats insulate the underlying peat (through increased albedo), resulting in cooler temperatures that may reduce the rate of decomposition (Kershaw, 1977). This may also be significant for PO activity, an important factor for decomposition in peatlands (Freeman *et al.*, 2001; Freeman *et al.*, 2004), and which has been shown to be dependent on temperature (Pinsonneault *et al.*, 2016b). TSP:DOC ratios were significantly larger in peat under lichen mats, probably due to leaching from the lichen mat and indicating a greater fraction of recalcitrant TSP. According to Pind *et al.*, (1994), TSP decreases with increasing PO activity but we did not find this relationship in our data. This may be explained by the cooler temperatures in peat under lichen mats, resulting in no differences in PO activity in lichen-dominated hummocks compared to *Sphagnum* hummocks, despite the larger TSP:DOC ratios. We found larger N

concentrations (as NO_3 -N) in leachates from peat under lichen mats, possibly due to greater N in leachate from lichen mats. Sinsabaugh *et al.*, (2010) suggest that increased concentrations of N in soils may inhibit PO activity. We also found slightly lower pH values in peat under lichen mats (Table 1), most likely due to acids from lichen leachates, and this too may suppress PO activity (Pind *et al.*, 1994; Sinsabaugh *et al.*, 2010).

It is also possible that there are differences in microbial communities in lichen-shrub hummocks compared to *Sphagnum*-shrub hummocks. If lichen-shrub hummocks with reduced cover of woody shrubs are less lignin-rich than *Sphagnum*-shrub hummocks, this will result in a lower abundance of PO producers and therefore reduced PO activity and a larger TSP:DOC ratio (Pinsonneault *et al.*, 2016b). This would also support the suggestion by Stark *et al.*, (2007) that the microbial community in peat under lichen mats is adapted to leachate from the lichen mat and that these leachates are not allelopathic. Although there was evidence of microbial activity in both lichen and *Sphagnum* peat, as a change in DOC quality (E2:E3 ratios, Figure S4.4), our results do not indicate increased microbial respiration in peat under lichen mats (Stark and Hyvarinen, 2003). We suggest that this is due to the abiotic controls described above, and that these controls may be important feedback mechanisms for regulating decomposition processes in peatland areas with different vegetation cover. For areas dominated by lichen, these feedbacks may prevent too rapid decomposition of peat under slow-growing lichen mats that would be at greater risk of decay closer to the water table and in a continuously wet substrate (Dietz and Hartung, 1999).

Consequences for peat accumulation

In Figure 4.1, we presented a conceptual model of the role of lichen mats on peat accumulation over time. Our results support our hypothesis of smaller NPP for lichen-dominated hummocks, causing a gradual decrease in peat growth, as described for stage B and C of the model. We did not find evidence of advanced decomposition in peat under lichen mats (stage C) but our results did show significant differences in peat age, with peat immediately under lichen mats significantly older than *Sphagnum* peat at a comparable depth below the photosynthetically active surface. ²¹⁰Pb chronologies were derived using a Constant Rate of Supply (CRS) model and are considered conservative estimates for the upper 30 cm of both cores, with predicted ages below 30 cm to be considered with caution (Flett Research Ltd, Canada). Various studies have highlighted the need for caution in using ²¹⁰Pb dating in peat hummocks, particularly the upper part (age < 50 years) due to inconsistencies caused by the porous structure of *Sphagnum* mosses (e.g. Malmer and Holm, 1984; Turunen *et al.*, 2004). As such, and similar to the predicted ages, we consider the peat accumulation rates determined from ²¹⁰Pb dating as a conservative estimate of relative differences between *Sphagnum* and lichen-dominated hummocks. Peat accumulation was slower in the lichendominated hummock (~ 150-350 g C m⁻² yr⁻¹) than the *Sphagnum* hummock (~200-400 g C m⁻² yr⁻¹). Although these values seem quite large, they are within the range of recent peat accumulation rates for near surface peat (not long-term rates) reported for studies using the same ²¹⁰Pb dating method, in North America, Europe, and Asia (e.g. Wieder *et al.*, 1994; Sanders *et al.*, 1995; Ali *et al.*, 2008; Gao *et al.*, 2010; Olid *et al.*, 2016).

These differences in peat age and accumulation may be partly explained by the slow growth of lichens, with thick lichen mats (~ 20 cm) up to 200 years old (Kumpula *et al.*, 2000). Lichen mats also have distinct layers – the upper photosynthetically active layer and the lower layers of partly decayed and 'slimy' material (Stark *et al.*, 2007). The rate of production in lichen mats slows over time, until at around 100 years, the growth in the top of the mat is equal to the rate of decomposition in the lower mat (Morneau and Payette, 1989; Kumpula *et al.*, 2000). Thus, there may be little to no addition of mass to the underlying peat for a considerable time (~ 100 years). The significantly older peat under lichen mats is evidence for this decreased addition of mass to the lichen hummock. Since this cannot be explained by advanced decomposition in peat under lichen mats, it is likely due to slow production coupled with the more rapid decay of the lichen mat, thereby reducing the overall quantity of litter addition to the peat column over time. It is also likely that over the longer time

periods for decomposition, a loss of structural integrity in peat under the lichen mat may occur as indicated by the significantly larger bulk densities we obtained for lichen peat than *Sphagnum* peat. The mean bulk density for the upper 20 cm of *Sphagnum* peat was 0.03 g cm⁻³ but mean bulk densities for peat under lichen mats were 0.06 g cm⁻³ (*C. stellaris*) and 0.08 g cm⁻³ (*C. rangiferina*). Our results do not indicate advanced decomposition in peat under lichen mats so this increase in bulk density must be due to a collapse in the peat structure (and therefore a decrease in hummock height as noted in stage C, Figure 4.1.). We estimate this collapse may lower lichen hummocks by up to 10 cm, and since there is little to no organic matter being added to the peat column, this represents a significant limit to peat growth.

It is not certain how lichens establish and become dominant on hummocks in northern peatlands and we do not test this in our conceptual model (stage A to B in Figure 4.1.). It is possible that drier hummock conditions that may limit *Sphagnum* growth could allow lichens a brief opportunity to outcompete *Sphagnum* (Vasander, 1981; Lindholm, 1990; Jauhiainen *et al.*, 2002). These drier conditions prior to lichen establishment may also cause greater decomposition of the peat mass in *Sphagnum* hummocks, and as *Sphagnum* production may be small, peat accumulation will be reduced. This reduction in peat accumulation continues as lichen becomes the dominant hummock vegetation cover (stages B and C in Figure 4.1.).

For lichen-dominated hummocks, we not only need to consider the multiple layers in lichen mats but also the clearly defined physical boundary between the lichen mat and underlying peat. This boundary typically comprises a small amount of vascular plant litter merged with the decaying bottom of the lichen mat. Although *Sphagnum* also comprises an upper photosynthetically active surface that grows above lower partly decomposing remains, it is unusual to find significant contrasts (or clearly defined layers) in peat composition down the profile until the water table. Hummocks covered by lichen mats have multiple layers and boundaries, and therefore require a multi-layer

model beyond the two-layer model introduced by Ingram (1978) and Clymo (1984), an approach proposed by Morris *et al.*, (2011b).

Changes in production and decomposition in lichen-dominated hummocks may also have consequences for the development of hummock-hollow microtopography in peatlands. Belyea and Clymo (1998) suggest that the growth of the hummock is constrained by the growth of the hollow. As the height of a hummock increases (due to greater NPP), the thickness of the acrotelm increases and this lengthens the time that litter is exposed to aerobic decay, until the difference between larger NPP and faster decay make peat accumulation the same as in adjacent hollows. However, the lichen mat on a hummock indicates stagnation of hummock growth (NPP is reduced) and therefore it is smaller production and not increased decomposition that reduces the height of the hummock. The potential collapse in peat structure, as indicated by larger bulk densities for lichen-dominated hummocks, further constrains peat growth. Thus, we propose that for lichen-dominated hummocks, the growth of the hummock is constrained by the hummock, and not the hollow. The potential collapse in hummock structure may also account for the presence of thin lichen mats in some intermediate and hollow microforms.

4.7 Conclusions

Lichens are an important component of northern peatland vegetation communities, covering up to 50 % of the peatland surface in some areas of the HBL and other peatlands (Glaser and Janssens, 1986; Malmer and Wallen, 1999; Dunford *et al.*, 2006; Riley, 2011; Neta *et al.*, 2011; OMOE, 2011; Humphreys *et al.*, 2014). Fruticose, mat-forming lichens are considered a climax vegetation type in northern peatlands (Ahti and Oksanen, 1990; Nordbakken, 1996) and therefore represent an important stage in the development of peatlands over time. Peatland development models assume production to be greater than decomposition, resulting in the gradual accumulation of peat over time (Clymo, 1984). As the height of the peat surface above the water table increases, decay rates in the acrotelm are equal to or greater than production, representing the limit to peat growth. However, we show that due to smaller productivity, fast lichen decay rates, and a potential loss of peat structural integrity, mat-forming lichens reduce local peat accumulation to the point that peat growth is likely to cease.

4.8 Figures and Tables



Figure 4.1 Conceptual model showing the role of lichen on peat production and decomposition over time (peat column model based on Hilbert *et al.*, 2000), where α_A = acrotelm decay rate, α_C = catotelm decay rate, α_S = decay rate of *Sphagnum* layer under lichen mat, α_L = decay rate of lichen mat, NPP_{S+VP} = Net Primary Production (NPP) of *Sphagnum* moss and vascular plants, NPP_{L+VP} = NPP of lichen mat and vascular plants, and NPP_L = NPP of lichen only. Different size arrows represent hypothesised difference in magnitude of NPP and decay rates. *h* is the total peat thickness ($h_A + h_C$) where h_A = thickness of the acrotelm (distance between water table and peat surface) and h_C = thickness of the anoxic catotelm above a mineral substrate. A to C represent development stages over time:

A. Sphagnum-shrub hummock (with limited lichen cover). NPP_{S+VP} is greater than α_A , and as h_A increases over time so does *h* (peat accumulation according to Clymo, 1984).

B. h_L increases over time, reducing light available to underlying *Sphagnum* moss and small shrubs and forbs (e.g. *Vaccinium oxycoccos* L.). NPP_{S+VP} decreases, resulting in a decomposing *Sphagnum* layer directly under the lichen mat. NPP_L is small and dependent on moisture conditions, and coupled with a reduced vascular plant cover, NPP_{L+VP} of lichen-shrub hummocks is smaller than *Sphagnum*-shrub hummocks.

C. Fast decay rates for the lichen mat $(\alpha_{L1} + \alpha_{L2})$ and reduced vascular plant cover result in decreased addition of mass to a lichen-shrub hummock. Decomposition of peat under lichen mats (α_A) is enhanced due to increased phenol oxidases activity that enables the breakdown of phenolic compounds through increased microbial consumption (a 'priming' effect). h_A decreases over time due to reduced NPP_{L+VP} and faster decomposition of peat under the lichen mat (α_A) , thereby reducing *h*.



Figure 4.2 Boxplots showing significant differences in (a) shrub cover (t (31) = 2.98, p < 0.006, t-test) (b) species richness (U = 31, p < 0.001, Mann-Whitney test), and (c) Shannon diversity index (U = 51, p = 0.001, Mann-Whitney test), for lichen-shrub hummocks and *Sphagnum*-shrub hummocks.



Figure 4.3 NMDS ordination of a Bray-Curtis dissimilarity matrix generated from plant community composition of lichen-shrub hummocks (open circles, n = 17, > 10 % lichen cover) and *Sphagnum*-shrub hummocks (closed circles, n = 17, < 10 % lichen cover) at MOE Bog. Lines represent a cluster dendrogram from hierarchical clustering using average linkage methods, which shows clear separation of plant communities on hummocks dominated by either *Sphagnum* or lichen.



Figure 4.4 Relationship between gross primary productivity (GPP) and photosynthetic photon flux density (PPFD), fit with a rectangular hyperbola equation (2013 and 2014 combined data for each site) for (a) lichen-only (n = 59, a = 0.003, GP_{max} = 0.7, F = 1.2, p = 0.281), lichen-shrub (n = 54, a = 0.008, GP_{max} = 2.1, F = 6.2, p = 0.016), and *Sphagnum*-shrub (n = 52, a = 0.01, GP_{max} = 9.3, F = 85, p < 0.001) at MOE Bog, and (b) lichen-only (n = 117, a = 0.002, GP_{max} = 0.8, F = 2.1, p = 0.149) at NRB (mini-chamber). Numbers in parentheses indicate r^2 values for GPP-PPFD curve fit for each vegetation-microform type.



Figure 4.5 (a) Relationship between PSN_{max} and moisture content (% dry weight basis) of lichenonly (*C. stellaris*, linear curve, a = 0.005, F = 13.73, p < 0.001) and *Sphagnum*-only (*S. fuscum*, no significant fit, linear curve, F = 0.55, p = 0.47) at NRB, and (b) relationship between PSN_{max} and moisture content of lichen-only at NRB. Lichen moisture contents less than 50 % fit with linear curve (a = 0.06, F = 18.72, p < 0.001), and <u>excluding</u> measurements at 0 % moisture, n = 50. No significant fit for lichen moisture contents above 50 % (linear curve, F = 0.24, p = 0.627).



Figure 4.6 Light available to *Sphagnum* layer under lichen mats of variable thickness (PPFD at 0 cm are surface measurements, n = 58, a = 1424, b = 1.3, F = 488, p < 0.001).



Figure 4.7: (a) ²¹⁰Pb activity, (b) estimated peat accumulation rates, (c) estimated age (from CRS model), and (d) bulk density for each depth increment in *Sphagnum*-shrub hummocks and lichen-shrub hummocks (peat under lichen mats). The relationship between bulk density and the estimated age of peat is shown in (e). Peat at 20-25 cm depth in *Sphagnum*-shrub hummocks is comparable in age (approx. 25 - 30 years) to peat immediately under lichen mats at 0 - 5 cm depth as indicated by box on (c), and termed 'age class B' for statistical comparisons. Analysis by Flett Research Ltd, Canada.



Figure 4.8 Variability in peat bulk density (means with standard error) for the upper 20 cm of *Sphagnum*-shrub hummocks (*S. fuscum*) and lichen-shrub hummocks (upper 20 cm of peat immediately under lichen mats). Bulk density measured for 2 cm increments.


Figure 4.9 Model parameters for <u>age class A</u> (photosynthetically active surface of lichens and *Sphagnum*) for leachates: (a) PO activity, (b) TSP, (c) DOC, (d) TSP:DOC, (e) SUVA₂₅₄, (f) TDN, (g) NO₃⁻-N, and (h) NH₄⁺-N. Model coefficients for species are significantly different if they have no lowercase letters in common (p < 0.05). * = model parameter not significant.



Figure 4.10 Model parameters for <u>age class B</u> (peat 0-5 cm depth immediately under lichen mats and 20-25 cm depth in *Sphagnum*-shrub hummocks) for leachates: (**a**) PO activity, (**b**) TSP, (**c**) DOC, (**d**) TSP:DOC, (**e**) SUVA₂₅₄, (**f**) TDN, (**g**) NO₃⁻-N, and (**h**) NH₄⁺-N. Model coefficients for species are significantly different if they have no lowercase letters in common (p < 0.05). * = model parameter not significant.

| Site | General Vegetation Type | Vascular Plants | Nonvascular | VGA | Leaf:stem ratio | Shrub Height (cm) | WTD (cm) | pН |
|------------|-------------------------------|--|--|--------------|--------------------|-------------------------|---------------|--------------|
| | Lichen- only | R. groenlandicum C. calyculata C. oligosperma | C. stellaris (100 %) C. rangiferina | - | 1.75 (0.35) | 12.4 (2.0) | -14 (0.7) | 3.9 (0.1) |
| MOE Bog | Lichen- shrub | R. groenlandicum (20 %) C. calyculata | C. stellaris (66 %) C. rangiferina | 2.0 (0.4) | 1.90 (0.16) | 15.8 (5.1) | -33 (0.9) | 3.7 (0.0) |
| | <i>Sphagnum-</i> shrub | R. groenlandicum (14 %) C. calyculata (6 %) R. chamaemorus (18 %) V. oxycoccos (11 %) | S. fuscum (48 %) | 2.3 (0.4) | 3.34 (0.89) | 7.6 (1.7) | -18 (0.8) | 4.0 (0.0) |
| NRB | Lichen- only | R. groenlandicum C. calyculata | C. stellaris (100 %) | - | - | - | -125 (1.6) | 3.8 (0.0) |

Table 4.1 Plot and collar vegetation characteristics for NEE measurements at MOE Bog and NRB.

Microforms are all hummocks except for lichen-only which is intermediate (or low hummock). Major vascular plants and nonvascular bryophytes and lichens within plots are listed. Bold are species <u>within collar</u> for gas flux measurements with relative percent cover noted in parentheses (average for collar triplicates). Mean VGA (<u>within collar</u> only, 2013 and 2014 combined). Mean 2014 shrub leaf:stem ratio and shrub height for plot triplicates (standard error) at MOE Bog only. Mean values (standard error) for 2013 and 2014 summer (June to August) pH and water table below surface (cm). Mean value for WTD recorded at same time as CO₂ measurements.

 Table 4.2 NEE-PPFD rectangular hyperbola curve fit parameters for each vegetation-microform type.

| Site | General Vegetation Type | n | α | GP _{max} | r^2 | GPP | PSN _{max} | ER |
|------------|----------------------------|-----|----------------|-------------------|-------|---------------|--------------------|----------------|
| | Lichen-only** | 90 | 0.00 (0.01) | 0.72 (0.38) | 0.07 | 0.43 (0.15) a | 0.33 (0.27) a | -1.02 (0.13) a |
| MOE Bog | Lichen-shrub | 81 | 0.01 (0.00) | 2.24 (0.44) | 0.46 | 1.36 (0.14) b | 1.75 (0.20) b | -1.40 (0.17) a |
| | Sphagnum-shrub | 71 | 0.01 (0.00) | 8.28 (0.80) | 0.85 | 3.91 (0.27) c | 6.11 (0.34) c | -1.39 (0.16) a |
| NRB | Lichen-only* | 199 | 0.00 (0.00) | 0.90 (0.29) | 0.16 | 0.58 (0.08) | 0.72 (0.11) | -0.79 (0.07) |

*Note the poor fit of the rectangular hyperbola (**no fit) for these vegetation-microform types. Combined 2013 and 2014 data, mean values for GPP, PSN_{max} and ER, $\mu mol CO_2 m^{-2} s^{-1}$, $a = \mu mol CO_2 m^{-2} s^{-1}$ per $\mu mol PPFD m^{-2} s^{-1}$. Standard error in parentheses. Parameters for veg-microform types at MOE Bog are significantly different if they have no lowercase letters in common.

| Species | Depth (cm) | Age Class | DOC mg L ⁻¹ | SUVA254 L mg C ⁻¹ m ⁻¹ | TSP mg L ⁻¹ | TSP:DOC ratio | PO activity µmol dicq g ⁻¹ min ⁻¹ | TDN mg L ⁻¹ | DON mg L ⁻¹ | NO3 -N mg L ⁻¹ | NH4 ⁺ -N mg L ⁻¹ | % TDN which is DON | DOC:TDN ratio |
|---------------------------|---------------|--------------|---------------------------|---|---------------------------|------------------|---|---------------------------|---------------------------|------------------------------|---|--------------------------|------------------|
| <i>Sphagnum-</i> shrub | 0-5 | Α | 14.2 (1.3) | 2.2 (0.4) | 2.14 (0.34) | 0.15 | 0.117 (0.021) | 0.7 (0.1) | 0.42 (0.19) | 0.02 (0.00) | 0.05 (0.02) | 60 | 22 |
| | 10-15 | | 12.3 (0.9) | 3.3 (0.2) | 2.00 (0.13) | 0.16 | 0.086 (0.017) | 0.6 (0.1) | 0.47 (0.09) | 0.02 (0.00) | 0.07 (0.02) | 78 | 25 |
| | 20-25 | В | 15.8 (1.6) | 3.6 (0.3) | 2.79 (0.23) | 0.18 | 0.123 (0.021) | 0.6 (0.1) | 0.54 (0.05) | 0.02 (0.00) | 0.06 (0.01) | 90 | 29 |
| Lichen- shrub | 0-5 (L) | Α | 167.4 (24.5) | 0.8 (0.1) | 14.11 (1.36) | 0.08 | 0.114 (0.017) | 10.0 (1.2) | 4.77 (0.92) | 0.06 (0.01) | 4.77 (0.61) | 48 | 16 |
| | 10-15 (L) | | 98.4 (20.1) | 0.6 (0.1) | 4.99 (0.70) | 0.05 | 0.031 (0.005) | 2.3 (0.7) | 2.10 (0.76) | 0.04 (0.01) | 0.13 (0.03) | 91 | 22 |
| | 0-5 (P) | В | 17.6 (1.7) | 3.2 (0.2) | 6.50 (1.03) | 0.37 | 0.138 (0.029) | 1.0 (0.2) | 0.73 (0.05) | 0.14 (0.06) | 0.12 (0.02) | 73 | 55 |
| | 20-25 (P) | | 13.7 (1.3) | 3.7 (0.2) | 4.56 (0.20) | 0.41 | 0.102 (0.014) | 0.7 (0.1) | 0.62 (0.06) | 0.02 (0.00) | 0.10 (0.03) | 88 | 21 |
| Lichen- shrub | 0-5 (L) | Α | 45.1 (3.6) | 1.0 (0.0) | 7.20 (0.54) | 0.16 | 0.069 (0.007) | 1.5 (0.2) | 1.06 (0.18) | 0.04 (0.01) | 0.48 (0.11) | 71 | 35 |
| | 10-15 (L) | | 49.0 (5.0) | 0.8 (0.1) | 3.46 (0.27) | 0.07 | 0.018 (0.005) | 1.8 (0.6) | 1.70 (0.72) | 0.03 (0.00) | 0.43 (0.08) | 95 | 20 |
| | 0-5 (P) | В | 13.2 (2.0) | 3.8 (0.2) | 4.96 (0.62) | 0.38 | 0.100 (0.017) | 0.7 (0.1) | 0.60 (0.08) | 0.05 (0.01) | 0.09 (0.02) | 85 | 46 |
| | 20-25 (P) | | 10.9 (0.9) | 4.6 (0.1) | 5.62 (0.36) | 0.42 | 0.139 (0.022) | 0.6 (0.1) | 0.52 (0.06) | 0.02 (0.00) | 0.06 (0.02) | 87 | 21 |

Table 4.3 Leachate results for Sphagnum-shrub hummocks (S. fuscum) and lichen-shrub hummocks (C. stellaris and C. rangiferina) at MOEBog.

Mean values (n = 12) for species and depth at 3 plots (4 replicates at each plot) with standard error in parentheses. Depth marked with (L) indicates lichen mat, depth marked with (P) indicates peat below lichen mat. Age-class indicates depth increment of closest comparable age estimate based on ²¹⁰Pb dating: **A** – photosynthetically active surface of *Sphagnum* and lichens, **B** – *S. fuscum* 20-25 cm and peat at 0-5 cm (P) under lichen mats. All leachates obtained from 1:3 sample-solution except PO activity (1:10 sample-solution).

4.9 Supplementary Figures and Tables



Figure S4.1 FTIR spectral curves for **'age class A'** the upper photosynthetically active surface of *C*. *stellaris*, *C. rangiferina* and *S. fuscum*, with (**a**) representing all absorption bands with absorption peaks identified per Niemeyer *et al.*, (1992), Cocozza *et al.*, (2003), and Artz *et al.*, (2008), and (**b**) highlighting absorption peaks at 600 to 2000 cm⁻¹.



Figure S4.2 FTIR spectral curves for **'age class B'** – peat immediately under lichen mats (*C. stellaris* and *C. rangiferina*, 0-5 cm P) and *Sphagnum* (*S. fuscum*) at 20-25 cm, with (**a**) representing all absorption bands with absorption peaks (see S4.1 for references), and (**b**) highlighting absorption peaks at 600 to 2000 cm⁻¹.



Figure S4.3 Relationship between TSP and PO activity (mean values for species). Error bars show standard error. Note no curve fit.



Figure S4.4 (a) Percentage DOC remaining in leachates obtained from *C. stellaris, C. rangiferina*, and *S. fuscum*, and including peat material underneath the lichen mat, marked (P), (b) change in specific UV absorbance at 254 nm (SUVA₂₅₄, L mg C⁻¹ m⁻¹), and (c) change in E2:E3 absorbance ratio during a 28-day incubation. Error bars show standard error. Similar to other leachate samples from lichen mats, SUVA₂₅₄ values (day 1) were significantly lower than for peat underneath the mat (*C. stellaris* and *C. rangiferina* mean values < 1.2, *p* < 0.001, ANOVA).



Figure S4.5 Relationship between specific UV absorbance (SUVA₂₅₄, L mg C⁻¹ m⁻¹), on day 1 and day 28 of the incubation.

Table S4.1 List of species and nomenclature for lichen-shrub and *Sphagnum*-shrub hummockssurveyed at MOE Bog.

| Species | Botanical authority | Growth Form | English Common Name |
|----------------------------|----------------------------------|----------------|----------------------------|
| Carex oligosperma | Michx. | Sedge | Fewseed sedge |
| Carex pauciflora | Lightf. | Sedge | Fewflower sedge |
| Chamaedaphne calyculata | (L.) Moench. | Shrub | Leatherleaf |
| Cladina rangiferina | (L.) Weber ex F.H.Wigg. | Lichen | Reindeer lichen |
| Cladina stellaris | (Opiz) Brodo | Lichen | Reindeer lichen |
| Drosera rotundifolia | L. | Forb | Roundleaf sundew |
| Eriophorum vaginatum | L. | Sedge | Tussock cottongrass |
| Kalmia angustifolia | L. | Shrub | Sheep laurel |
| Kalmia polifolia | Wangenh. | Shrub | Bog laurel |
| Picea mariana | (Mill.) Brit., Sterns & Poggenb. | Tree | Black spruce |
| Polytrichum strictum | Brid. | Moss | Haircap moss |
| Rhododendron groenlandicum | (Oeder) Kron & Judd. | Shrub | Labrador tea |
| Rubus chamaemorus | L. | Forb | Cloudberry |
| Sphagnum fuscum | (Schimp.) H. Klinggr. | Moss | Rusty peat moss |
| Vaccinium myrtilloides | Michx. | Shrub | Velvet-leaved blueberry |
| Vaccinium oxycoccos | L. | Shrub | Small cranberry |
| Vaccinium uliginosum | L. | Shrub | Bog bilberry |

Table S4.2 Calculated FTIR ratios for humification indices (HI) according to Beer *et al.*, (2008) and Hodgkins *et al.*, (2014).

| Ratio | Indicative for |
|-----------|--|
| 2920/1060 | Aliphatics (lipids, fats, waxes)/polysaccharides |
| 1720/1060 | Carboxylic and aromatic esters/polysaccharides |
| 1630/1060 | Aromatics and aromatic or aliphatic carboxylates/polysaccharides |
| 1515/1060 | Aromatic C=C or C=O of amides/polysaccharides |
| 1450/1060 | Phenolic and aliphatic structures/polysaccharides |

| Species | Depth (cm) | Age Class | Von Post Score | 2920/1060 | 1720/1060 | 1630/1060 | 1514/1060 | 1450/1060 |
|--------------|---------------|--------------|----------------------|-------------|-------------|--------------|--------------|--------------|
| | 0-5 | А | H1/H2 | 0.38 (0.01) | 0.51 (0.01) | 0.44 (0.01)* | 0.26 (0.00) | 0.35 (0.00) |
| S fuscum | 10-15 | | H2 | 0.38 (0.01) | 0.48 (0.01) | 0.42 (0.01) | 0.24 (0.00) | 0.34 (0.01) |
| 5. juscum | 20-25 | В | H3 | 0.42 (0.01) | 0.52 (0.02) | 0.52 (0.02) | 0.26 (0.01) | 0.37 (0.01) |
| | 25-30 | | H3 | 0.36 (0.02) | 0.49 (0.02) | 0.48 (0.04) | 0.26 (0.02) | 0.36 (0.02) |
| | 0-5 (L) | А | - | 0.35 (0.01) | 0.32 (0.01) | 0.45 (0.01)* | 0.19 (0.00)* | 0.44 (0.00)* |
| | 10-15 (L) | | - | 0.36 (0.01) | 0.35 (0.02) | 0.43 (0.01) | 0.20 (0.01) | 0.45 (0.01) |
| C stallaria | 0-5 (P) | В | H3/H4 | 0.33 (0.02) | 0.47 (0.01) | 0.52 (0.02) | 0.24 (0.01) | 0.36 (0.01) |
| C. stettarts | 10-15 (P) | | H4 | 0.34 (0.00) | 0.48 (0.01) | 0.49 (0.02) | 0.24 (0.01) | 0.35 (0.01) |
| | 20-25 (P) | | Н5 | 0.34 (0.01) | 0.47 (0.01) | 0.48 (0.00) | 0.23 (0.00) | 0.35 (0.01) |
| | 25-30 (P) | | Н5 | 0.31 (0.02) | 0.48 (0.01) | 0.54 (0.03) | 0.25 (0.02) | 0.37 (0.02) |
| | 0-5 (L) | А | - | 0.41 (0.01) | 0.40 (0.01) | 0.38 (0.00) | 0.18 (0.00)* | 0.42 (0.01)* |
| | 10-15 (L) | | - | 0.45 (0.01) | 0.39 (0.02) | 0.40 (0.02) | 0.20 (0.01) | 0.42 (0.01) |
| С. | 0-5 (P) | В | H5/H6 | 0.40 (0.05) | 0.57 (0.04) | 0.65 (0.07) | 0.33 (0.03) | 0.47 (0.04) |
| rangiferina | 10-15 (P) | | H6 | 0.34 (0.02) | 0.50 (0.02) | 0.56 (0.06) | 0.25 (0.03) | 0.37 (0.03) |
| | 20-25 (P) | | H7 | 0.43 (0.04) | 0.57 (0.04) | 0.63 (0.07) | 0.33 (0.04) | 0.44 (0.05) |
| | 25-30 (P) | | H7 | 0.40 (0.06) | 0.57 (0.07) | 0.64 (0.10) | 0.34 (0.06) | 0.45 (0.07) |

Table S4.3 Humification indices (HI) of peat and lichen samples calculated from FTIR spectra (mean values for species-depth with standard error in parentheses).

Depth marked with an (L) indicates lichen mat and (P) indicates peat under lichen mat. Significant differences between lichens and *Sphagnum* for age class A are in bold, and * indicates no significant difference between marked species (p < 0.001, ANOVA).

CHAPTER 5 – An ombrogenous bog in the Hudson Bay Lowland demonstrates resilience to drier conditions caused by short-term drainage

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5.1 Context within thesis

As described in the literature review, the effects of environmental change (including climate warming) on peatlands remain uncertain. This uncertainty is due to complex feedbacks among peatland structure and function that control peat accumulation. In Chapter 3 I highlight the variability in the strength and direction of some of these feedbacks within the context of proposed structuring mechanisms for microtopography in pristine peatlands in the HBL, including the effect of different vegetation composition (see Chapter 4). I also demonstrate the importance of ecohydrological setting for different structuring mechanisms and the development of spatial patterns in peatlands. Climate warming will alter the ecohydrology of northern peatlands, with prolonged periods of drought likely to result in drier surface conditions and lower water tables. This will test the range and thresholds for feedback mechanisms controlling peat accumulation. Knowledge of environmental thresholds is needed to determine the limits for self-regulation in peatlands and potential ecosystem shifts to stable or unstable states.

In this chapter, I examine peatland structure and function in an ombrogenous bog subject to gradual drainage over ~ 7 years compared to a pristine site. I assess vegetation composition, cover, and functional traits (e.g. vascular green area, leaf:stem ratio), production (NEE), and indicators for decomposition (e.g. leachate chemistry, peat chemical composition). My analysis places field evidence within the context of potential shifts in ecosystem state.

5.2 Abstract

The vast peatlands of the Hudson Bay Lowland (HBL) are globally important carbon (C) stores but climate change poses a significant risk to peatland biogeochemical processes in this region. Peatlands may be described as self-regulating systems, maintaining long-term stability due to feedbacks between biological and hydrological processes. Drier conditions associated with climate warming may test peatland resilience, with shifts in ecosystem state likely to occur if environmental thresholds are passed. Yet our knowledge of potential changes to peatland structure and function, and particularly thresholds for changes in ecosystem state, is limited. To determine the effect of drier conditions on peatland structure and function, we compare two ombrogenous treed bogs in the HBL - a pristine bog (MOE) and a bog (NRB) subject to ~ 7 years' gradual drainage (water table ~ 1 m below hummock surface at the time of study). At NRB, plant production was significantly reduced, most likely due to small changes in vegetation structure (e.g. shrub leaf:stem ratios) caused by lower water tables and reduced moisture content of surface peat. We found vegetation response to hydrological change was dependent on microform, with no significant differences in species composition for hummocks and intermediate microforms at NRB and MOE. Dry pools at NRB comprise mostly bare peat and litter, in stark contrast to Sphagnum- and sedge-dominated pools at MOE. NEP was negative (i.e. C emission) from the dry pools, but despite smaller production, NEP for hummocks and intermediate microforms was positive, indicating large areas of the drained site likely remain a small C sink. Although NRB has been drained for ~ 7 years, our results did not indicate significantly advanced decomposition. Our results indicate that except for dry pools, hydrological thresholds for a shift in ecosystem state have not yet been reached at NRB. This highlights the resilience of these peatlands to lower water tables and drier surface conditions, a response that may be considered analogous to future climate change.

5.3 Introduction

Peatland ecosystems cover almost 4.5 million km² or 3 % of the global land area and are a significant long-term terrestrial carbon (C) store (Yu, 2012). Peatlands are common ecosystems in boreal and subarctic regions, where bogs and fens may merge to form massive continuous peatland complexes that dominate the landscape. As the second largest area of continuous northern peatland in the world, the Hudson Bay Lowland (HBL), Canada, extends over 250,000 km² of low topographic relief (Glaser et al., 2004a; Riley, 2011). Approximately 6% of the northern C pool (~ 30 Pg C) is contained within the HBL peatlands, making them globally important C stores (Packalen et al., 2014). Yet due to anthropogenic-driven climate warming, the cool and wet climate conditions that have enabled C accumulation within the HBL peatlands for thousands of years are now changing (Far North Science Advisory Panel, 2010). Resulting changes to the HBL peatlands may be intensified by feedbacks to regional climate warming, as the reduction of sea-ice on Hudson Bay further increases regional temperatures (Gagnon and Gough, 2005; Ruhland et al., 2013; Delidjakova et al., 2016). The HBL peatlands are also at risk from land-use change and disturbance due to proposed economic development (e.g. mining and transportation) within this remote region (Far North Science Advisory Panel, 2010). Alterations to peatland hydrology, vegetation, and biogeochemical function caused by these development pressures may exacerbate the risks posed by climate change.

The accumulation of organic matter in peatlands is dependent on shallow water tables that limit decomposition relative to production (Clymo, 1984). In non-permafrost bogs, warmer and drier climate conditions with prolonged periods of drought will likely result in drier surface peat and deeper (lower) water tables (Hilbert *et al.*, 2000; Riutta *et al.*, 2007; Flanagan *et al.*, 2011; McLaughlin and Webster, 2014; Thompson *et al.*, 2017). For bogs that depend on precipitation for water and nutrients, drier conditions could alter both peatland structure and function (Wu and Roulet, 2014). Coupled with increasing temperatures, drier peat is subject to an increase in oxic decomposition by increased microbial growth and enzyme activity (Ise et al., 2008; Fenner and Freeman, 2011; Jassey et al., 2013). This breakdown of organic matter increases potential loss of C from the ecosystem as carbon dioxide (CO₂) release to the atmosphere (e.g. Munir *et al.*, 2014), or in some peatlands, as waterborne C loss (Fenner et al., 2007; Strack et al., 2008). Vegetation change is also likely, with drier conditions predicted to favour the growth of vascular plants, particularly woody shrubs, over Sphagnum mosses and lichens (Weltzin et al., 2000; Cornelissen et al., 2001; Talbot et al., 2010; Walker et al., 2015). The high water holding capacity and recalcitrance of Sphagnum mosses is important for peat accumulation in bogs (Turetsky et al., 2008), but a significant shift to vascular plants with more decomposable litter could increase decomposition relative to production, regardless of the likely increase in CO₂ uptake (Bragazza et al., 2012; Ward et al., 2013; Ward et al., 2015; Del Giudice and Lindo, 2017). Lichens can be a dominant vegetation cover on bogs in the HBL (Riley, 2011; Neta et al., 2011), and due to their thickness (lichen mats may be up to 20 cm thick) and higher albedo compared to vascular plants, decrease energy absorption and reduce evaporation from the underlying peat (Stoy et al., 2012; Porada et al., 2016). Consequently, a reduction in lichen cover relative to vascular plants (which depending on water availability, will likely outcompete lichens owing to their root system and canopy shading effect) could increase peat warming and drying.

The loss of peatland C due to climate change may be offset however, by autogenic processes (including negative feedbacks) that regulate peatland response to environmental change (Belyea and Baird, 2006; Belyea, 2009; Swindles *et al.*, 2012; Loisel and Yu, 2013; Morris *et al.*, 2015). These 'self-regulating' mechanisms include hydrological feedbacks that enable peatlands to regulate water loss under drought conditions, such as increased peat permeability because of decomposition, or increased surface tension that reduces evaporative losses (Price, 2003; Kettridge and Waddington, 2014; Waddington *et al.*, 2015; Nijp *et al.*, 2017). Small-scale variations in surface elevation (microtopography) across peatlands are due to feedbacks among vegetation, hydrology, and nutrients

that cause differential rates of peat accumulation (Belyea and Clymo, 2001; Rietkerk *et al.*, 2004b). Microforms (hummocks and hollows) comprise different species of *Sphagnum* moss that are adapted to small variations (i.e. long-term average) in depth to water table (Rydin, 1986; Rydin, 1993b; Belyea, 1996; Schouwenaars and Gosen, 2007; Bengtsson *et al.*, 2016). Woody shrubs and trees are typically confined to elevated hummocks with limited cover in hollows that are at or close to the water table (Glaser, 1983). The distribution of vegetation communities with different functional traits (e.g. green biomass, leaf area) across different microforms is a significant control for biogeochemical function, including CO₂ and methane (CH₄) exchange (Bubier *et al.*, 1993b; Bubier, 1995; Laine *et al.*, 2012; Cresto-Aleina *et al.*, 2015).

As both structure and function differ, hummocks and hollows (which also show a bimodal distribution in HBL peatlands, Figure 3.3 in Chapter 3 of this thesis) can be described as occupying alternate stable states within peatlands, with hummocks and hollows representing dry and wet stable states, respectively (e.g. Hilbert *et al.*, 2000; van de Koppel *et al.*, 2001; van Nes and Scheffer, 2005; Eppinga *et al.*, 2009a). A feedback between vascular plant growth (particularly shrubs) and increased litter available to add to the peat mass, further increases the height of the hummock above the water table (Belyea and Clymo, 1998; Belyea and Clymo, 2001). Hummock growth is constrained however by the growth of the adjacent hollow, as the difference between decomposition in the hummock and production in the adjacent hollow, decreases (Belyea and Clymo, 1998). This negative feedback permits steady long-term peat accumulation across microforms and is thought to increase peatland resilience to disturbance (Belyea and Clymo, 2001; Belyea and Malmer, 2004). The resilience of bogs in future climate change scenarios is shown by Wu and Roulet (2014), but knowledge of environmental thresholds (bifurcation points or 'tipping points') for known stable states, particularly with increasing pressures from infrastructure development, remains limited (Hilbert *et al.*, 2000; Belyea, 2009; Scheffer *et al.*, 2012; Kéfi *et al.*, 2016).

Changes in vegetation community will depend on species tolerances and optima to environmental variables (Andersen *et al.*, 2011; Graham *et al.*, 2016). For example, although graminoids (sedges) may benefit from warmer temperatures, their growth will likely be restricted to shallower water tables (Talbot *et al.*, 2010; Laine *et al.*, 2012; Dieleman *et al.*, 2015). As microforms allow species to occupy niches along environmental gradients in peatlands, environmental change may simply cause a spatial shift in vegetation communities and lateral extent of microforms (Belyea and Clymo, 2001). For example, if drier conditions and greater vascular plant cover enable production to exceed decomposition, peat accumulation will likely transform drier hollows to lawn or hummock communities (Belyea and Clymo, 2001; Breeuwer *et al.*, 2009).

Understanding the effects of long-term drought and more severe decreases in water table on peatland vegetation communities will help determine species tolerance thresholds, and if these may be exceeded in future drier climate conditions. If thresholds are exceeded we may observe shifts to non-peatland vegetation communities, and coupled with biogeochemical changes, a potentially significant effect on ecosystem function (Laine *et al.*, 1995; Pasquet *et al.*, 2014). Due to the range of feedbacks operating within peatland ecosystems however, our understanding of potential thresholds for ecosystem shifts is poor (Belyea, 2009). It is therefore important to determine the range of conditions for existing stable states, and to identify indicators of low resilience or potentially unstable states (e.g. Scheffer *et al.*, 2012; Kéfi *et al.*, 2013; van de Leemput *et al.*, 2015; Lindenmayer *et al.*, 2016) and likely thresholds for shifts to alternate and potentially non-peatland states.

Here, we examine the ecological effects of hydrological change in ombrogenous bogs located in the Attawapiskat River Basin area of the HBL, Canada. We compare a pristine ombrogenous treed bog with a similar bog that has been subject to gradual lowering of the water table for approximately seven years prior to (and during) our study (Whittington and Price, 2012). Lower water tables expose deeper peat to oxic conditions and reduce the moisture content of surface peat through a loss in surface tension and reduced evapotranspiration (ET) (Schwärzel *et al.*, 2006; McCarter and Price, 2014). So, although precipitation amounts during the study period may not reflect a future climate change scenario (i.e. less precipitation), peat surface moisture is still reduced. The drained site therefore allows us to study the potential effects of drier peatland conditions (short-term) likely in a future climate change scenario (e.g. Whittington and Price, 2006; Wu and Roulet, 2014).

We examine differences in peatland structure (vegetation and hydrology) and biogeochemical function (production and decomposition) to determine potential for ecosystem shifts. Specifically, our objectives were to (1) determine relationships among vegetation, hydrology, and nutrients, and possible changes to these relationships due to drainage, and (2) identify potential hydrological thresholds (water table depth) for changes in production and decomposition that may result in shifts in ecosystem state. We hypothesise that in a bog with lower water tables and drier surface conditions, there will be (1) a decrease in *Sphagnum* cover and an increase in vascular plants (particularly woody shrubs), (2) advanced decomposition in both shallow (above the water table) and deeper peat (i.e. usually below the water table in pristine bogs) that has been exposed to aerobic conditions, and that this leads to (3) lower or potentially negative net ecosystem production (NEP) (i.e. C emission), and (4) these changes in structure and function represent a shift to an unstable state.

5.4 Methods

Site Description

The study was conducted in the HBL, approximately 90 km west of Attawapiskat in northern Ontario, Canada. The main research site is located ~ 13 km south of the De Beers Canada Victor Mine (52°49'06" N, 83°54'18" W; ~ 83 m elevation) and comprises an ombrogenous raised bog (unofficially named MOE Bog, 52°41'36" N, 83°56'41" W; ~ 93 m elevation) and a moderately-rich minerogenous fen (MOE Fen, 52°42'02" N, 83°57'18" W; ~ 91 m elevation; Ulanowski and Branfireun, 2013; Ulanowski, 2014; Humphreys *et al.* 2014). A 1.5 km raised boardwalk (installed

by the Ontario Ministry of Environment and Climate Change, OMOECC, referred to as MOE) crosses the site, joining two eddy covariance (EC) towers – one located near the apex of MOE Bog and the other tower located within MOE Fen (Humphreys *et al.*, 2014). We collected data from two locations near the apex of the MOE Bog, unofficially named 'Bog' and 'Ridge-Pool'.

A research site was also established at North Road Bioherm (NRB, unofficially named by Whittington and Price, 2012), an area of treed bog near a bioherm (a fractured limestone outcrop formed from an ancient coral reef - Cowell, 1983) located approximately 3 km from Victor Mine. Peatlands in the HBL are underlain by low permeability marine sediments (Riley, 2011) but bioherms represent a connection to the regional groundwater due to reduced or no cover of marine sediment. Consequently, a drop in regional groundwater levels due to dewatering at the mine has resulted in a significant gradual decrease in peatland water tables (Whittington and Price, 2012; 2013). Initial drainage began ~ 7 years prior to this study (2012 to 2014), with a decline in water tables during this period (Whittington and Price, 2012).

Temperatures in this part of the HBL range from -22.3 °C in January to 17.2 °C in July (daily averages), with an annual mean of - 1.3 °C (1971-2000, Lansdowne House, 280 km WSW - Environment Canada, 2016). The area receives ~ 700 mm precipitation (mean annual), which falls as snow in all months except July and August. During our study in 2013 and 2014, the sites received ~409 mm and ~600 mm rain, respectively. Mean annual (and June through August) temperature in 2013 and 2014 was -2.3 (14.6) °C and -2.6 (15.0) °C, respectively (MOE EC Towers, data not shown). Although located in the zone of discontinuous and sporadic permafrost (Riley, 2011), there is no permafrost at the research sites.

The microtopography (hummock-hollow, and ridge-pool sequences) is similar at the hydrologically impacted NRB (subject to ~ 7 years' gradual drainage) and the pristine MOE site, so we assume the sites would have had similar vegetation prior to drainage at NRB (Figure 5.1). Vegetation surveys completed as part of the Environment Impact Assessment (EIA) for De Beers

Canada Victor Mine also indicate similar species composition at the NRB and MOE sites (AMEC, 2004). This allows for a direct comparison of similar general vegetation-microform types at each site (e.g. *Sphagnum*-sedge pool, lichen-shrub hummock, *Sphagnum*-shrub hummock). Data were therefore collected from plots representing similar vegetation-microform types at each site. To limit damage to the sites and to enable surveys of otherwise inaccessible areas (e.g. floating *Sphagnum* mats in centre of pools), most plots were established along transects parallel to and within a short distance of raised boardwalks.

CO₂ Gas Exchange Measurements

Three collars, each of 0.055 m⁻² area, were installed in each vegetation-microform type at each site in summer 2012, with all measurements completed during the 2013 and 2014 growing seasons (June to August). CO₂ fluxes for each collar were measured using clear Plexiglas chambers (27.57 L volume) fitted with fans and a cooling unit. CO₂ concentration (ppm) in the chamber headspace was measured with a portable CO₂ analyser (EGM-4 Environmental Gas Analyser, PP Systems). Photosynthetic photon flux density (PPFD, μ mol m⁻² s⁻¹) was measured at the same time as CO₂ using a quantum sensor (PAR-1, PP Systems). Measurements were recorded at 10-s intervals for the first minute and at 30-s intervals for the final 2 minutes, and repeated for full-light, half-light, and dark conditions by placing mesh and opaque shrouds over the chamber (Bubier *et al.*, 1998; Strack *et al.*, 2006b; Pelletier *et al.*, 2011; Munir *et al.*, 2015).

CO₂ flux rates (net ecosystem exchange, NEE µmol CO₂ m⁻² s⁻¹) were calculated from the linear change in CO₂ concentration in the chamber headspace with time, as a function of chamber volume and temperature (Bubier *et al.*, 1998; Pelletier *et al.*, 2011). Data with r^2 values less than 0.5 were checked for measurement errors caused by equipment malfunction or weather conditions. Following the data quality check, most data with low r^2 values correspond to very low or no flux (not due to error) and were included in all subsequent analyses.

The relationship between NEE and PPFD was determined using a rectangular hyperbola curve in SigmaPlot 12.0 (equation 1, Frolking *et al.*, 1998). The sign convention is positive for CO_2 uptake and negative for CO_2 release to the atmosphere.

$$NEE = GP_{max} * \alpha * PPFD / ((\alpha * PPFD) + GP_{max}) + ER, \qquad (eq. 1)$$

where GP_{max} is the maximum gross photosynthetic CO_2 (µmol CO_2 m⁻² s⁻¹) captured at maximum PPFD, α is the photosynthetic quantum efficiency (µmol CO_2 m⁻² s⁻¹ per µmol PPFD m⁻² s⁻¹), and ER is dark ecosystem respiration (µmol CO_2 m⁻² s⁻¹). Net ecosystem production (NEP, µmol CO_2 m⁻² s⁻¹) was calculated as gross primary production (GPP) minus ER. Maximum rates of photosynthesis (PSN_{max}, µmol CO_2 m⁻² s⁻¹) were calculated from all GPP with PPFD greater than 1000 µmol m⁻² s⁻¹ (Bubier *et al.*, 2003). Statistical differences in the rectangular hyperbola parameters (GP_{max} and α) between vegetation-microform types at each site were determined from confidence intervals. We used generalised linear models (GLM – fixed effects with repeated measures, IBM SPSS Statistics 23) to determine the significance of vegetation and environmental factors (temperature, peat moisture, WTD) for GPP, ER, and NEP. Model structure assigned collar as the subject and date as repeated measures. All models were fit with a gamma distribution and log link and used the Satterthwaite approximation for the unbalanced design. Akaike's Information Criterion (AIC) and restricted -2 log-likelihood (-2logLL) were used to determine the best model fit.

Nutrients

Water samples were taken from wells (purged ~ 48 hours before sampling) representing each vegetation-microform type (triplicates) at each site, on two sample days in late July and early August 2014 (3 samples per well on each sample day). Samples were extracted from the wells using a peristaltic pump, filtered under vacuum (0.45 μ m Macheray-Nagel) within 24 hours, and stored in the dark at ~ 4 °C until analysis for dissolved organic carbon (DOC, mg L⁻¹) and major ions (Ca²⁺, Mg²⁺, K⁺, Na⁺, NO₃⁻-N, NH₄⁺-N, PO₄³⁻, SO₄²⁻, units mg L⁻¹) by Western University (Ecohydrology

Lab and Biotron Institute for Experimental Climate Change), London, ON (detailed analysis and quality control procedures outlined in Ulanowski, 2014).

Plant Root Simulator (PRSTM) ion-exchange resin probes (Western Ag Inovation, Saskatoon, Saskatchewan, Canada) were used to determine relative differences in nutrient availabilities in different vegetation-microform types at each site (Wood *et al.*, 2015; Wang *et al.*, 2016). Each sample comprised four pairs of probes (one probe adsorbing cations and the other adsorbing anions in each pair), placed at depths of 5 - 15 cm in hummocks, intermediate 'lawns' and hollows/pools, and ~ 20-35 cm in hummocks, in triplicate plots at each site. The probes were buried for a 4-week period from mid-July to mid-August 2014. At the MOE sites, the upper probes in hummocks remained above the water table, whereas all probes in hollows/pools were beneath the water table. Probes in intermediate lawns and at ~ 20-35 cm in hummocks were located at or just above the water table and were likely submerged during the burial period. At NRB, all probes were above the water table during the burial period.

After removal, the probes were thoroughly cleaned, rinsed with deionised water, and stored in the dark at 4 °C until analysed. Samples were extracted with 0.5 *M* HCl, and ammonium (NH4⁺-N) and nitrate (NO₃⁻-N) analysed colorimetrically using an automated flow injection analyser (Technicon Autoanalyzer II, Technicon Instrument Corporation, Tarrytown, New York, USA). Other nutrients (P, K, Ca, Mg, Fe, Al, Pb, B, Cu, Zn, S and Mn) were measured by inductivelycoupled plasma spectrometry (Perkin Elmer Optima 3000-DV ICP, Perkin Elmer Inc., Shelton, Connecticut, USA; Hangs *et al.*, 2004). Nutrient availabilities were reported as μ g per 10 cm⁻² of the membrane surface area per week, and enabled a comparison of relative differences in *in-situ* nutrient availabilities for vegetation-microform types at each site.

Plant Community Composition

Plant community composition and structure was measured at all NEE and PRS plots in July-August 2014 using the point-intercept method (n = 27 quadrats at MOE Bog/RP and 27 quadrats at NRB). We recorded the number of times a metal rod (radius ~ 3 mm) 'hit' each plant species and component (for shrub leaf:stem ratio) for 25 grid points within 0.5 m² quadrats (Larmola *et al.*, 2013). Canopy height (vascular plants) and thickness of lichen mats were also recorded. All vegetation was identified to the species level, with nomenclature for vascular plants as Flora of North America (1993+) and Riley (2003), and nomenclature for lichens as Brodo *et al.*, (2001) (see Table S5.1 for species list and nomenclature). Bare peat and litter were also recorded for each quadrat.

To examine differences in species composition and abundance at each site, we used nonmetric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix calculated from percentage cover in the R-library *vegan* (Oksanen *et al.*, 2016). Species richness (total number of species per plot, alpha diversity), Simpson Diversity (D) and Shannon-Weiner Diversity (H') (evenness) were calculated for each individual quadrat.

We measured vascular green area (VGA) for each NEE collar by recording the total number of green leaves per species, along with the width and length of 20 leaves per species (or all leaves if less than 20). Species-specific formulae based on leaf geometry were applied to determine average leaf size (Wilson *et al.*, 2007). This was then multiplied by the number of leaves and divided by the collar surface area to give the green area index of a vascular plant species (m² m⁻²) for the measurement period (mid-July to mid-August). The VGA index (m² m⁻²) of each collar was calculated by summing the green area index of all vascular plants present.

Peat Core Collection and Chemical Analyses

In July 2015, shallow peat cores (to 30 cm depth) were collected from three *Sphagnum* hummocks (*S. fuscum*) and six lichen hummocks (three *C. rangiferina* and three *C. stellaris*) at MOE Bog, and the same at NRB. Four intact cores were collected per hummock as field replicates. Samples were taken from each field replicate at 0-5 cm, 10-15 cm and 20-25 cm for *S. fuscum*, 0-5 cm and 10-15 cm from intact *C. rangiferina* and *C. stellaris* lichen mats, and from 0-5 cm and 20-25 cm peat under the lichen mat. All samples were sorted to remove roots and vascular plant material,

and then homogenised to ensure representation of the replicate location and depth increment. These homogenised samples were used for all subsequent analyses.

Leachates were prepared by soaking the moss, lichen and peat samples in 60 mL de-ionised water (1:3 sample:solution suspension) for ~12 hours in the dark at room temperature (~20 °C) (according to Pinsonneault *et al.* 2016a). Mixing was done intermittently. The leachates were immediately filtered through a 0.45 μ m binder-free filter paper (Macherey-Nagel) and stored in the fridge until analysis.

DOC and total dissolved nitrogen (TDN) concentrations (mg L⁻¹) were measured using a Shimadzu V-CSN TOC/TN analyser. UV absorbance at wavelengths of 250, 254, 365, 465, and 665 nm was measured using a LAMBDA Bio spectrophotometer (PerkinElmer) with a 1 cm path length cell. Specific UV absorbance at 254 nm (SUVA₂₅₄) was calculated from the UV absorbance at 254 nm divided by the DOC concentration and the path length of the cell of the spectrophotometer (cm), and is expressed as L mg C⁻¹ m⁻¹.

 $NO_3^{-}-N$ and $NH_4^{+}-N$ concentrations (mg L⁻¹) were determined using a Lachat QuikChem AE flow injection autoanalyzer (Lachat Instruments, USA) using the cadmium reduction method (QuikChem method 10-107-04-1-C; Lachat 2008) for $NO_3^{-}-N$ and the salicylate hypochlorite method (QuikChem method 10-107-06-2-C; Lachat 2008) for $NH_4^{+}-N$.

Total soluble phenolic concentrations (mg L⁻¹) were determined for each sample according to Pinsonneault *et al.*, (2016b). We added 250 μ L triplicates of each leachate sample (1:3 sample:solution) to clear microplate wells, followed by 12.5 μ L Folin-Ciocalteau reagent (Sigma-Aldrich), and then 37.5 μ L sodium carbonate solution (Na₂CO₃, concentration 200 g L⁻¹). The reaction proceeded for 1.5 hour before absorbance was measured at 750 nm on a spectrophotometer (Infinite 200 Pro, Tecan). Total soluble phenolic concentrations for each sample were derived from a standard calibration curve prepared using laboratory standards of known concentration (0 to 40 mg L⁻¹). Total phenol oxidase activities were determined according to Dunn *et al.*, (2014). For each sample replicate, two 1 g samples were placed into two separate stomacher bags (sample and a control) and incubated at field temperatures overnight (~12 hours). 9 mL L-DOPA solution (10 nM dihydroxy phenylalanine, Sigma-Aldrich) or Milli-Q water (control) (both incubated to analysis temperature) were added to the stomacher bags and then incubated at field temperature for 10 minutes. Three replicates of each sample and three of each control were then immediately centrifuged for 5 minutes at 13,500 RPM to terminate the reaction. Aliquots of each sample and control were added to clear microplate wells and absorbance at 460 nm measured on a spectrophotometer (Infinite 200 Pro, Tecan).

Generalised linear models (GLM – fixed effects, IBM SPSS Statistics 23) were used to determine the effect of environmental factors (temperature, pH, moisture content, WTD) on phenolics, PO activity, DOC, SUVA₂₅₄, DON, NH₄⁺-N and NO₃⁻-N. All models were fit with a gamma distribution and log link and using the Satterthwaite approximation for the unbalanced design. Akaike's Information Criterion (AIC) and restricted -2 log-likelihood (-2logLL) were both used to determine the best model fit.

Peat samples for FTIR analysis were taken from intact shallow peat cores from the same locations as the cores used for the above analyses (same sample plots). Samples for each depth increment were sorted to remove roots and vascular plant material, and then homogenised to ensure representation of the replicate location and depth increment. Samples were oven dried at 50 ° Celsius for 24 hours or until dry. Each sample was then ground through a 40-mesh sieve (Wiley Mini Mill 3383-L10) and placed into a small sample envelope. FTIR spectra were obtained using a FTIR spectrometer (Agilent Cary 670 FTIR Spectrometer). To determine differences in decomposition among samples for each site, we calculated humification indices (HI, higher HI indicates increased decomposition) as ratios of absorbance at wavenumbers 1450, 1514, 1630, 1720, and 2920 cm⁻¹

(aliphatic, aromatic, and phenolic moieties) with respect to polysaccharides (1060 cm⁻¹) (structural group assignments given in Table S5.3).

Ancillary Measurements

We measured air and peat temperature at 10 and 20 cm below the surface, peat moisture content, and water table depth, at the same time as NEE sampling runs, as well as during the PRS probe burial period. Water table depth below the surface was measured in wells (slotted PVC tubes) installed at each location, either manually, or from continuous logger measurements using capacitance water level probes (Odyssey, Dataflow Systems, New Zealand, loggers calibrated each field season). Moisture content of peat at 20 cm depth (volumetric water content, VWC %) was measured using a Hydrosense 2 Soil Moisture Sensor fitted with a CS658 water content sensor (20 cm probe length, Campbell Scientific). Volumetric moisture content (%) was calculated from the period (μ s) using a custom linear calibration curve of gravimetric moisture content (GWC, % of dry weight) for vegetation and peat samples from plots at each site (y = mx + c, where y = VWC as %, m = slope, c = intercept (0), and x = period in μ s, for MOE: $r^2 = 0.57$, m = 17.06, and NRB: $r^2 = 0.64$, m = 8.91). Microtopography of all plots and wells was determined from surface elevation measured using a Topcon HiPer Differential Global Positioning System (DGPS), relative to the UTM Zone 17N NAD83 datum (referred to as meters above sea level, m.a.s.l.) (\pm 0.01 horizontal and 0.003 vertical accuracy).

Differences in vegetation (e.g. species richness, diversity, leaf:stem ratio, VGA), WTD, nutrients (water chemistry and PRS probes), temperature, and soil moisture, between microforms and sites were assessed using two sample *t*-tests, ANOVAs or appropriate non-parametric tests (e.g. Kruskal-Wallis). Unless noted otherwise all statistics were conducted using IBM SPSS Statistics 23 or R version 3.3.1 (R Core Team 2016).

5.5 Results

Differences in water table, peat moisture and temperature

Water tables were significantly lower for all microforms at NRB than the MOE sites (Figure 5.2a). Mean WTD (cm, \pm standard error) was -93.4 \pm 6.1 cm and -28.2 \pm 3.7 cm for hummocks at NRB and MOE respectively. Mean WTD for hollows/pools was -37 \pm 4.2 cm at NRB and -4.4 \pm 2.9 cm at MOE. The distribution of WTD values for hollows/pools at NRB ranged from ~ -20 to -50 cm below the surface, matching hummocks at the MOE sites.

Peat moisture content (% VWC) of the upper 20 cm of all microforms was also significantly less at NRB compared to the MOE sites (Figure 5.2b). The difference between mean peat moisture content (% VWC) at NRB and MOE was smallest for hummocks (9.7 %) and largest for intermediate microforms (21.5 %). At both sites, lichen covered hummocks had significantly greater surface peat moisture contents (peat under lichen mats, MOE mean 83.6 ± 1.9 % VWC, NRB mean 81.3 ± 1.5 % VWC) than *Sphagnum* hummocks (MOE mean 76.9 ± 3.5 % VWC, NRB mean 69.9 ± 2.9 % VWC).

Peat temperature (at 20 cm depth) did not differ significantly for microforms at each site, except for slightly cooler temperatures recorded for intermediate microforms at NRB than MOE sites (Figure 5.2c). Peat temperatures did not vary among microforms within the MOE sites, except for cooler temperatures for peat in lichen covered hummocks (mean 6.7 ± 0.5 °C) compared to *Sphagnum* hummocks (mean 9.8 ± 0.8 °C). At NRB peat temperatures were warmer in intermediate (mean 10.6 ± 0.4 °C) and hollows/pools (mean 11.9 ± 0.7 °C) than hummocks (mean 8.9 ± 0.7 °C), and as found for MOE, peat temperatures were cooler in lichen covered hummocks (mean 10.3 ± 0.2 °C) compared to *Sphagnum* hummocks (mean 12.3 ± 0.6 °C).

Vegetation

An NMDS ordination of plant community composition showed no distinction between the NRB or MOE sites, except for pool communities (Figure 5.3). Hierarchical clustering revealed five

distinct clusters, with clusters A to C representing major vegetation-microform types present at both sites (e.g. *Sphagnum*-spruce hummocks), and clusters D and E represent *Sphagnum*-sedge pools at the MOE site and bare peat pools at the NRB site. Species groups were significantly concordant (5 groups, Kendall's *W*, p < 0.04) with 2 groups matching clusters A and B and 3 groups dispersed through clusters C, D and E.

Species richness and Shannon's diversity (evenness) were significantly less in hollows/pools at NRB compared to MOE sites, but there were no significant differences for hummocks or intermediate microforms (Figure S5.1). However, hummocks and intermediate microforms at NRB had significantly smaller *Sphagnum* spp. cover (%) compared to the same microforms at MOE sites (Figure 5.4a). Forb cover (e.g. *R. chamaemorus, M. trifolium*) was also significantly less for hummocks at NRB than MOE sites but there were no differences for intermediate microforms (Figure 5.4b). *Sphagnum* spp. and forbs were absent in hollows/pools at the NRB site. Although there were no significant differences in percentage shrub cover (e.g. *C. calyculata, R. groenlandicum*) between sites, shrub leaf:stem ratios were significantly smaller for hummocks and intermediate microforms at NRB (Figures 5.4 c and d). VGA was also smaller for all microforms at NRB (mean VGA = 3.9 and 1.7 for *Sphagnum*-spruce hummocks at MOE and NRB, respectively, Table S5.2). There were no differences in percentage cover of graminoids, lichens, or trees between sites. Litter cover was significantly greater in intermediate microforms and pools at NRB compared to MOE (data not shown).

NEE measurements

NEE and GPP-PPFD relationships were similar for vegetation-microform types at each site (Figure S5.2 and Table S5.2), except the poor fit for *Sphagnum*-only pools at MOE (Ridge-Pool) and NRB. Mean GPP (μ mol CO₂ m⁻² s⁻¹, \pm standard error) was significantly smaller for *Sphagnum*-spruce hummocks (2.1 \pm 0.1 μ mol CO₂ m⁻² s⁻¹) and *Sphagnum*-shrub intermediate microforms (1.9 \pm 0.1 μ mol CO₂ m⁻² s⁻¹) at NRB compared to MOE (3.9 \pm 0.2 μ mol CO₂ m⁻² s⁻¹ for *Sphagnum*-spruce

hummocks and $2.9 \pm 0.2 \ \mu$ mol CO₂ m⁻² s⁻¹ for *Sphagnum*-shrub intermediate) (Figure 5.5). GPP did not differ between sites for *Eriophorum* tussocks or for *Sphagnum* only pools. Smaller GPP for *Sphagnum*-spruce hummocks and *Sphagnum*-shrub intermediate microforms corresponds to significantly reduced NEP for these microforms at NRB (< 1 μ mol CO₂ m⁻² s⁻¹). Although ER was significantly greater for *Eriophorum* tussocks at NRB than MOE, this did not change NEP between sites. However, significantly greater ER coupled with small GPP resulted in negative NEP for *Sphagnum* only pools at NRB (mean -0.4 ± 0.08 μ mol CO₂ m⁻² s⁻¹).

GLMs showed VGA was the most significant predictor for GPP, ER, and NEP at both sites, with a larger VGA corresponding to greater GPP, ER and NEP (Table 5.1). The models showed WTD was weakly significant for GPP at MOE but not NRB, with lower water tables corresponding to greater GPP at MOE (Figure 5.6). The weak negative relationship between ER and WTD at MOE indicates lower water tables have greater ER. At NRB the model coefficient is significant but very small indicating a weak positive relationship where lower water tables (> 1 m below the surface) have smaller ER. Although statistically significant, VWC was a weak predictor for GPP at MOE (larger VWC have smaller GPP) and this relationship was weaker at NRB. Smaller VWC corresponded to greater ER at NRB but not MOE. Warmer soil temperature corresponded to greater ER at NRB but not MOE.

Decomposition

FTIR spectra are similar for all hummock samples at both sites, with multiple peaks between 600 and 2000 cm⁻¹, and between 2800 and 3500 cm⁻¹ (Figures S5.5 and S5.6). The relative intensity of bands differs for *Sphagnum* hummocks, with consistently higher peaks for the NRB sites compared to the MOE sites (Figure S5.5). The intensity of bands did not differ for lichen hummocks at the NRB or MOE sites (Figure S5.6). There were no significant differences in humification indices (HIs, Table S5.3) for peat samples from *Sphagnum* or lichen hummocks at NRB or MOE, except for the 2920/1060 ratio for peat under lichen mats (*C. stellaris*) (Table S5.4). The higher 2920/1030 ratio

for peat under lichen mats at NRB indicates increased peat humification. We also found no significant differences in HI ratios with depth (same species and site) except for larger 2920/1030 ratios at 20-30 cm compared to 0-20 cm in *Sphagnum* hummocks at NRB.

Nutrients

Analysis of water samples from wells revealed Ca concentrations were significantly smaller in all major vegetation-microform types at NRB compared to MOE (Figure S5.3). NO₃⁻-N concentrations were greater in all vegetation-microform types at NRB compared to MOE but there were no differences in NH₄⁺-N concentrations (except smaller concentrations for lichen hummocks and hollows at NRB). DOC concentrations did not differ between sites except for significantly smaller concentrations for lichen hummocks and hollows at NRB than MOE. K concentrations were significantly larger at MOE than NRB for all microforms except intermediate where there was no difference between sites.

The PRS probes showed total N (as NH₄⁺-N) and K availabilities were significantly greater in pools at NRB compared to MOE sites (Figure S5.4). Conversely, for intermediate microforms (*Sphagnum*-shrub), total N (as NH₄⁺-N) availability was significantly larger at the MOE site than NRB. Fe, Zn, Al, and Mn availabilities were significantly larger in MOE pools compared to NRB (note Mn not detected in NRB pools). Mn availability was also significantly larger in intermediate microforms at the MOE site. We found no significant differences in nutrient availabilities for *Sphagnum* hummocks or lichen hummocks or hollows at MOE and NRB.

Nutrient availabilities did not vary significantly for different microforms within the NRB or MOE site, except for larger Ca, Mg, Fe, Mn, and Zn availabilities in pools at the MOE sites, and significantly larger total N (as NH₄⁺-N) in pools at NRB. We also found K availability was significantly smaller in lichen hummocks and hollows compared to *Sphagnum* intermediate microforms and hummocks at NRB but not the MOE site.

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Chemical composition of leachates

DOC concentrations were significantly smaller in leachates from *Sphagnum* hummocks at the NRB site compared to the MOE site but the opposite was found for peat under lichen mats, with larger DOC concentrations at NRB compared to the MOE site (Figure 5.7a). TON concentrations were significantly greater at NRB than MOE (Figure 5.7b) but there were no differences in N-NO₃ or N-NH₄ at either site. DOC:TDN ratios for *Sphagnum* hummocks were significantly lower at the NRB site indicating increased decomposition, but there were no significant differences in C:N ratio between sites for peat under lichen mats (Figure 5.7c). In contrast, SUVA₂₅₄ values were significantly lower (indicating more biodegradable DOC) for peat under lichen mats at the NRB site compared to the MOE site (Figure 5.7d). There were no significant differences in SUVA₂₅₄ values between sites for *Sphagnum* hummocks.

There were no significant differences between sites for mean TSP, except for lichen hummocks (*C. stellaris*) where TSP concentration was larger at the MOE site than the NRB site (Figure 5.8a). However, the relative proportion of DOC comprising TSP (as indicated by the TSP:DOC ratio) is significantly smaller in peat under lichen mats at NRB compared to the MOE site, and significantly larger for *Sphagnum* hummocks at NRB compared to the MOE site (Figure 5.8b). We found no differences in PO activity between sites (Figure 5.8c).

5.6 Discussion

To determine peatland resilience to environmental change, we compared the ecological and biogeochemical conditions of a bog subject to a gradual lowering of the water table over 7 years (NRB), with a pristine bog (MOE). We found changes in vegetation were dependent on microform, with the most significant difference in dry pools at NRB. These pools comprised mostly bare peat and litter, and consequently, had negative NEP (i.e. C emission). NEP was smaller for hummocks and intermediate microforms at NRB than MOE but remained positive (i.e. C sink). This is likely due

to less *Sphagnum* cover (and drier surface peat as indicated by smaller VWC) and smaller leaf:stem ratios for woody shrubs at NRB. Contrary to our hypothesis, we did not find greater vascular plant cover (woody shrubs) at NRB. We also did not find evidence of significantly advanced decomposition at NRB, except for dry pools. Our analysis suggests bogs in the HBL are resilient to short-term hydrological changes. Dry pools at NRB represent a shift to an unstable ecosystem state, but the limited changes in structure and function for hummocks and intermediate microforms do not indicate a similar shift. It is likely that the resilience of these microforms has been reduced however, with ecosystem shifts possible if drainage was to continue long-term.

Vegetation

Species composition did not differ for hummocks and intermediate microforms at MOE and NRB, with distinct species assemblages associated with microform type regardless of water table depth. The exception to this were pools at NRB, where vegetation cover was less than 12 % (as *R alba*), resulting in a surface of mostly bare peat and litter. This is a stark contrast to pools at MOE but as pool species such as *S. majus* (that forms floating *Sphagnum* mats) are slow to recover from prolonged desiccation (Rydin and McDonald, 1985; Hájek and Vicherová, 2014; Bu *et al.*, 2013), their absence in a dry pool (mean WTD -37 cm) is not surprising. We did not observe greater graminoid cover (sedges) in any microforms at NRB, most likely due to the lower water tables at NRB being outside the range of tolerance for most peatland species (Weltzin *et al.*, 2003; Talbot *et al.*, 2010; Laine *et al.*, 2012). Mean peat moisture at the surface (~ 20 cm depth) was 67.4 % for *Eriophorum* tussocks at NRB (compared to 92 % at MOE), slightly drier than the range (> 70 %) noted for increased *E. vaginatum* growth at an extracted peatland in Quebec (Lavoie *et al.*, 2005). Although frequently observed for disturbed bogs and fens (Tuittila *et al.*, 1999; Tuittila *et al.*, 2000; Lavoie *et al.*, 2005), lower water tables and peat moisture content at NRB may prevent the rapid expansion of *E. vaginatum* within the bare peat pools.

Shrub cover did not differ for hummocks at MOE or NRB but we did observe smaller shrub leaf:stem ratio and VGA at NRB, and cover of *Sphagnum* spp. and forbs were also less. This suggests reduced water availability (WTD ~ 90 cm below the surface and reduced surface moisture) at NRB is having an adverse effect on hummock vegetation structure, including more resilient *Sphagnum* spp. such as *S. fuscum* (Rydin and McDonald, 1985; Toet *et al.*, 2006; Hájek and Vicherová, 2014). The lack of greater shrub cover (and vascular plants) after 7 years of drainage however, is contrary to other studies (Weltzin *et al.*, 2000; Munir *et al.*, 2014) but may be explained by differences in peatland type (e.g. nutrient limitation in bogs), and the magnitude and period of drainage. Regional climate may also be important. For example, Munir *et al.*, (2014) found increased shrub cover in a treed bog in northern Alberta ~ 10 years after initial drainage. Although the period of drainage was similar to NRB, the hydrological conditions (water tables ~ 80 cm below the surface) were likely not the result of a gradual decrease in water tables as at NRB. The climate is also slightly warmer and drier than the HBL sites, therefore providing more favourable conditions for shrub growth.

CO₂ Exchange

Despite only small changes in vegetation structure for hummocks and intermediate microforms at NRB, GPP was significantly smaller (means $< 2.1 \ \mu \text{mol} \ \text{m}^{-2} \ \text{s}^{-1}$) than equivalent microforms at MOE (means $> 2.9 \ \mu \text{mol} \ \text{m}^{-2} \ \text{s}^{-1}$). Our results show GPP was positively correlated to VGA which was smaller at NRB due to smaller shrub leaf[°]stem ratios and the absence of forbs such as *M. trifolium* and *S. palustris*. Smaller GPP at NRB may also be due to low peat moisture contents at the surface of hummocks and intermediate microforms, causing periods of water stress and decreased photosynthesis in *S. fuscum* and *S. rubellum* (Wallen *et al.*, 1988; Silvola, 1990). GPP for *Eriophorum* tussocks (*E. vaginatum*) in intermediate microforms did not differ between sites despite a mean WTD of -32 cm at NRB compared to 0.2 cm at MOE. While hydrological conditions may not

support the expansion of *E. vaginatum* at NRB, similar GPP suggests photosynthesis of established *Eriophorum* tussocks with a deep root system (Wein, 1973) is maintained.

GPP in pools at NRB was small owing to the collars containing only bare peat and litter (no vegetation cover) but there was no difference when compared to MOE pools (GPP at both sites < 1 μ mol CO₂ m⁻² s⁻¹). It is possible that higher water tables in MOE pools in 2014 had a negative impact on photosynthesis of *S. majus* and vascular plants (*S. palustris, Carex* spp.), thereby reducing overall GPP for MOE pools (Weltzin *et al.*, 2000; Pelletier *et al.*, 2011). At NRB, we also noted small dark patches of possibly algae or lichen on the surface of the dry pond but as this was often indistinguishable from litter, it was recorded as such. This may be a reason for the small GPP in collars with no apparent vegetation cover in NRB pools.

Hummocks at MOE had greater ER than NRB despite significantly lower water tables at NRB. At both sites, we found a strong positive relationship between ER and VGA but relationships for WTD and peat moisture content were weak. This differs to other studies where ER was closely related to WTD and not vegetation structure (e.g. Laine *et al.*, 2009). We also found a strong positive relationship between ER and peat temperature at the NRB site but not at MOE. This suggests that although ER was greater for hummocks than intermediate microforms and pools at MOE, this was not due to peat temperature (which did not vary for microforms). Greater ER for MOE hummocks may therefore be explained by larger VGA which is a strong control for ER at both sites. VGA does not explain greater ER for pools with little vegetation cover at NRB, and as peat temperatures did not vary significantly between sites, this is most likely due to lower WTD and peat moisture content.

Although GPP was significantly smaller for hummocks and intermediate microforms at NRB, the lack of differences in ER (or smaller ER) compared to MOE, mean NEP remained positive (a C sink). For pools at NRB however, NEP was negative, indicating these areas of the site are a C source to the atmosphere.
Decomposition

We found few differences in water chemistry, leachate chemistry, or nutrient availabilities between sites with the only statistically significant results dependant on microform. NH_4^+ -N availability (PRS probes at 15 cm depth) was significantly larger for NRB pools than MOE pools. This indicates mineralisation of the dry and bare peat surface that is also subject to rewetting after rainfall events, particularly in spring and autumn (Knorr and Blodau, 2009; Laine *et al.*, 2013). Larger NO_3^- -N concentrations in water samples at NRB, for all microforms, also suggest advanced decomposition at this site (Glatzel *et al.*, 2006; Reiche *et al.*, 2009; Laine *et al.*, 2013). A larger FTIR ratio (2920/1060) for peat at 20-30 cm depth compared to 0-20 cm suggests advanced decomposition of deeper peat in *Sphagnum* hummocks at NRB. As HI ratios did not vary with depth at MOE, this suggests lower water tables at NRB have increased the rate of decomposition.

Although DOC concentrations have been noted to increase in drained peatlands (e.g. Strack *et al.*, 2008), we did not find larger concentrations at NRB. We did find DOC concentrations were reduced in leachates from *Sphagnum* hummocks at NRB compared to MOE. This suggests consistently lower water tables and smaller vegetation productivity (as indicated by smaller GPP) may reduce DOC production at NRB (Freeman *et al.*, 2004). It is also likely the recalcitrant nature of *S. fuscum* (Lang *et al.*, 2009b; Bengtsson *et al.*, 2016), the dominant hummock-forming species at both sites, inhibits DOC production at NRB. The higher TSP:DOC ratios in leachates from *Sphagnum* hummocks at NRB indicate the DOC contains a larger fraction of recalcitrant, inhibitory TSP, which does suggest more advanced decomposition at NRB. We did not find any difference in PO (enzyme) activity between sites however, which contrasts to other studies where advanced decomposition in peatlands subject to drought is thought to be due to increased PO activity (Fenner and Freeman, 2011). The lack of difference in PO activity may be explained by a difference in N concentrations in leachates from *Sphagnum* hummocks (larger concentrations at NRB than MOE), with larger N likely to inhibit PO activity (Sinsabaugh *et al.*, 2010). In contrast to *Sphagnum*

hummocks, DOC concentrations in leachates from lichen hummocks were larger at NRB than MOE and contained a smaller fraction of recalcitrant TSP. This could indicate less advanced decomposition for lichen hummocks at NRB (more biologically available C), or may be due to increased leaching from lichen mats following a rainfall event on the day before the samples were collected at NRB (Dudley and Lechowicz, 1987). We recorded larger peat moisture contents (by 10-15 % VWC), and cooler temperatures (by ~ 3°C) in peat under lichen mats compared to *Sphagnum* hummocks at both sites, which could have slowed decomposition.

Temperature is an important control for decomposition in peatlands (Davidson and Janssens, 2006; Dorrepaal *et al.*, 2009) but there were no differences in peat temperatures (at 20 cm depth) at NRB or MOE (only for different vegetation-microform types within each site). Our results therefore show potential effects of lower water tables and peat moisture contents on indicators of decomposition but not the combined effects of hydrological change and temperature.

Potential shifts in ecosystem state

Belyea and Clymo (2001) suggest the relationship between peat accumulation and WTD as a parabola (or 'humpbacked'). Plant production determines organic matter input to the catotelm and therefore peat growth, but is limited by water stress at both high and low WTD (Belyea and Clymo, 2001; Ridolfi *et al.*, 2006). Peat growth is therefore optimal at intermediate acrotelm thickness (Hilbert *et al.*, 2000; Belyea and Clymo, 2001). Our results showed GPP was largest where water tables were ~ 20 cm below the surface, and that GPP declines as WTD is greater or less than this optimum range (Figure 5.6). If we assume minimum WTD as an estimate of acrotelm thickness (Clymo, 1992), and GPP as an indicator of plant production and therefore potential organic matter input and peat growth, our results support the described relationship.

Figure 5.9 shows the GPP-WTD relationship as a conceptual diagram of peat accumulation as change in production (GPP) with WTD (based on Hilbert *et al.*, 2000, Belyea and Clymo, 2001 and Eppinga *et al.*, 2009a), with potential tipping points for changes in peat accumulation identified at

both MOE and NRB. Different microforms at MOE and NRB are also identified as occupying specific points on two separate curves. Our results showed NEP is positive for both hollows/pools and hummocks at MOE, so we assume production exceeds decomposition and that these microforms represent a stable wet state and a stable dry state (Hilbert *et al.*, 2000; Belyea and Clymo, 2001; Eppinga *et al.*, 2009a; Eppinga *et al.*, 2009b). Although the WTD for dry pools was within the same range as hummocks at MOE, NEP was negative, indicating decomposition exceeds production. It is therefore likely that these pools represent an unstable dry state (Figure 5.10, based on Lindenmayer *et al.*, 2016). NEP was positive for hummocks at NRB despite indications of advanced decomposition, suggesting these microforms occupy a stable dry state although with reduced resilience (e.g. R₂ or R₃ for hummocks, Figure 5.10), therefore increasing the potential for shifts to alternative unstable and stable states, including non-peatland states (Figure 5.10; Hilbert *et al.*, 2000; Belyea and Clymo, 2001; Eppinga *et al.*, 2009b; Scheffer *et al.*, 2012; Lindenmayer *et al.*, 2016).

Although hydrological thresholds for vegetation change have been passed for certain microforms (e.g. dry pools at NRB), either thresholds for vegetation change across the site have not been reached, or there is a delayed vegetation response. As most peatland species are persistent, vegetation succession (allogenic and autogenic) in peatlands can be slow, often taking decades, even in response to external forcing (e.g. change in climate) (Nordbakken, 2000; Hughes and Barber, 2004). The rate of vegetation change does depend on the degree of change in boundary conditions however, with rapid successional changes observed following drainage (Strack *et al.*, 2006b; Munir *et al.*, 2014), and also fire (Kuhry, 1994; Benscoter and Vitt, 2008; Kettridge *et al.*, 2015). Whether dry pools at NRB are eventually colonised by peatland hummock species (e.g. *C. calyculata, S. fuscum*) or undergo succession to forest species (e.g. *Populus* spp., *Alnus* spp., *Geocaulon lividum*, and *Pleurozium* spp. from the nearby raised bioherm), will determine the shift to a stable peatland dry state or an alternative non-peatland state (Figure 5.10). Although water tables will likely increase at NRB when dewatering at the mine stops (Whittington and Price, 2012), we can hypothesise the

effect of continued decreases in water table as a decline in *Sphagnum* and forb cover on hummocks. Shrub and tree species tolerant of drier conditions (e.g. *P. mariana, R. groenlandicum, E. nigrum*) may slowly increase cover but this would likely lead to slower rates of peat accumulation and a potential shift to a non-peatland state. Lower water tables may also cause compression of the peat and subsidence, therefore reducing distance to the water table (Price and Schlotzhauer, 1999; Strack *et al.*, 2006b). This feedback would mediate the effects of drainage at NRB and potentially prevent shifts to non-peatland states.

5.7 Conclusions

Our results suggest bogs in the HBL are resilient when subject to significant (although shortterm) drainage but this resilience depends on microtopography. After the water table was lowered by ~ 60 cm over 7 years of drainage, *Sphagnum* spp. and forb cover were less and shrub leaf:stem ratios were smaller for hummocks and intermediate microforms, but there were no significant changes in shrub, graminoid, or tree cover, and no differences in species composition. Although plant production was smaller for hummocks and intermediate microforms, NEP was positive, indicating large areas of the drained site remain a C sink. In contrast, lowering the water table by ~ 30 cm in pools caused an almost complete loss of vegetation cover, with ~ 85 % of the surface comprising bare peat or litter. Consequently, NEP was negative (i.e. C emission). We found some indication of advanced decomposition caused by drainage but this varied for different microforms. Except for dry pools, our results indicate hydrological thresholds for shifts in ecosystem state have not yet been reached at NRB.

5.8 Figures and Tables



Figure 5.1 Aerial photographs of (a) pristine MOE site (Bog and Ridge-Pool, photo taken August 2013) and (b) hydrologically impacted NRB sites (photo taken October 2013).



Figure 5.2 (a) Mean WTD, (b) peat moisture, and (c) peat temperature, for microforms at MOE (Bog and Ridge-Pool) and NRB (n = 27 plots at each site, mean values June to August 2014). Different lowercase letters indicate significant differences among microforms at each site (p < 0.05, ANOVA and Tukey's post hoc test). Sites are significantly different (same microform) if they have no uppercase letters in common (p < 0.05, *t*-test, per Levene's test for equality of variances).



Figure 5.3 NMDS ordination (2D stress = 0.09) of a Bray-Curtis dissimilarity matrix generated from plant community composition of plots at NRB and MOE (Bog and Ridge-Pool) sites. Dashed circles represent community clusters from hierarchical clustering using average linkage methods: A – lichen-shrub hummocks and hollows, B – *Sphagnum*-spruce hummocks, C – *Sphagnum*-sedge-shrub intermediate microforms, D – *Sphagnum*-sedge pools at the MOE site, E – '*Sphagnum*-sedge' pools at the NRB site.



Figure 5.4 Boxplots showing cover (abundance as %) of (a) *Sphagnum* spp., (b) forbs, (c) shrubs, and (d) shrub leaf:stem ratio for microforms at MOE (Bog and Ridge-Pool) and NRB (n = 27 plots at each site, 2014). Different lowercase letters indicate significant differences among microforms at each site (p < 0.05, ANOVA and Tukey's post hoc test). Sites are significantly different (same microform) if they have no uppercase letters in common (p < 0.05, *t*-test, per Levene's test for equality of variances).



Figure 5.5 Differences in NEP, GPP, and ER (mean \pm standard error, 2013 and 2014 combined data) for vegetation-microform types at MOE (Ridge-Pool) and NRB. Different lowercase letters indicate significant differences among microforms at each site (p < 0.05, GLM). Sites are significantly different (same microform) if they have no uppercase letters in common (p < 0.05, GLM).



Figure 5.6 Relationship of GPP to WTD (cm below the surface) at MOE (Ridge-Pool) and NRB, each fitted with a quadratic polynomial (MOE: a = -0.13, b = -0.0026, F = 55.9, p < 0.0001, NRB: a = -0.03, b = -0.0002, F = 11.7, p < 0.0001).



Figure 5.7 Leachate results for peat samples from lichen and *Sphagnum* hummocks at MOE (Bog) and NRB: (a) DOC concentration, (b) TON concentration, (c) DOC:TDN ratio, and (d) SUVA₂₅₄. Samples from peat depths of similar age (age class B, 0-5 cm under lichen mats and 20-25 cm for *Sphagnum* hummocks). Shaded boxes and different lowercase letters indicate significant differences between sites (same species) (GLM, p < 0.05). * indicates no significant difference.



Figure 5.8 Leachate results for peat samples from lichen and *Sphagnum* hummocks at MOE (Bog) and NRB: (a) total toluble phenolics (TSP), (b) TSP:DOC ratio, and (c) phenol oxidases (PO) activity. Samples from peat depths of similar age (age class B, 0-5 cm under lichen mats and 20-25 cm for *Sphagnum* hummocks). Shaded boxes and different lowercase letters indicate significant differences between sites (same species) (GLM, p < 0.05). * indicates no significant difference.



Figure 5.9 Conceptual diagram of the peat accumulation mechanism (adapted from Eppinga *et al.*, 2009a, and Hilbert *et al.*, 2000). The purple curve represents change in production at the MOE site and the grey curve the drained NRB site (based on GPP-WTD curves in Figure 5.6). Black lines show loss through decomposition. Larger open circles (dashed for NRB) indicate the range of conditions for hollows and hummocks at each site (larger circles for hummocks indicating greater stability). The small black circles are tipping points for peat accumulation, where production exceeds decomposition (hollows become hummocks) or decomposition exceeds production.



Figure 5.10 Conceptual model of multiple alternative stable states in peatlands as determined by ecosystem change, and relationship to ecosystem resilience (based on Lindenmayer *et al.*, 2016). R1 to R3 represent the loss of resilience over time either due to sudden, rapid effects or slow and/or cumulative effects (e.g. hummocks at NRB).

| Table 5.1 Generalised linear model (GLM – fixed effects) results for GPP, ER, and NEP at MOE |
|---|
| (Ridge-Pool) and NRB. Standard error for model coefficient in parentheses. In the GLM, ER has |
| positive values and therefore the positive relationship of ER and VGA at both sites means larger |
| VGA have greater ER. The negative relationship with WTD at MOE means lower water tables have |
| greater ER. The negative relationship of GPP and WTD at MOE means lower WTD have larger |
| GPP. At NRB the model coefficient for ER and WTD is significant but very small indicating a weak |
| positive relationship where lower water tables (> 1 m below the surface) have smaller ER. The |
| relationship is negative for ER where $WTD < 1$ m at NRB (deeper water tables have greater ER). * |
| = significant |

| | | | MOE Ridge | NRB | | | | | |
|-----|--------------------|------|---------------------|-------|-----------------|-------|---------------------|--------|-----------------|
| | Model Term | F | Coefficient (SE) | t | <i>p</i> -value | F | Coefficient (SE) | t | <i>p</i> -value |
| GPP | Model | 24.7 | | | < 0.001 | 49.9 | | | < 0.001 |
| | VGA | 15.6 | 0.151 (0.04) | 3.95 | < 0.001* | 65.8 | 0.222 (0.02) | 8.11 | < 0.001* |
| | WTD | 10.8 | - 0.021 (0.00) | -3.29 | < 0.001* | 2.3 | - 0.002 (0.00) | - 1.51 | = 0.130 |
| | VWC 20 cm | 3.2 | - 0.011 (0.00) | -1.80 | = 0.023* | 7.0 | - 0.008 (0.00) | - 2.65 | = 0.009* |
| | Soil Temp 10 cm | 5.3 | - 0.053 (0.02) | -2.30 | = 0.074 | 2.9 | 0.022 (0.01) | 1.70 | = 0.090 |
| ER | Model | 14.5 | | | < 0.001 | >100 | | | < 0.001 |
| | VGA | 4.3 | 0.148 (0.07) | 2.07 | = 0.042* | 17.7 | 0.126 (0.03) | 4.20 | < 0.001* |
| | WTD | 12.2 | - 0.041 (0.01) | -3.49 | < 0.001* | 20.9 | 0.002 (0.00) | 4.56 | < 0.001* |
| | VWC 20 cm | 0.0 | - 0.007 (0.01) | -0.64 | = 0.521 | 50.0 | - 0.011 (0.00) | - 7.07 | < 0.001* |
| | Soil Temp 10 cm | 0.4 | - 0.013 (0.04) | -0.30 | = 0.760 | 274.2 | 0.095 (0.00) | 16.55 | < 0.001* |
| NEP | Model | 8.4 | | | < 0.001 | 11.4 | | | < 0.001 |
| | VGA | 9.9 | 0.155 (0.04) | 3.14 | = 0.002* | 7.4 | 0.102 (0.03) | 2.72 | = 0.009* |
| | WTD | 3.0 | - 0.014 (0.00) | -1.75 | = 0.086 | 2.6 | 0.003 (0.00) | 1.59 | = 0.114 |
| | VWC 20 cm | 5.9 | - 0.003 (0.00) | -0.45 | = 0.653 | 20.7 | - 0.019 (0.00) | - 4.54 | < 0.000* |
| | Soil Temp 10 cm | 0.2 | - 0.065 (0.02) | -2.42 | = 0.019* | 0.3 | - 0.011 (0.02) | - 0.52 | = 0.604 |

5.9 Supplementary Figures and Tables



Figure S5.1 (a) Vegetation species richness and (b) Shannon's Diversity Index for microforms at MOE (Bog and Ridge-Pool) and NRB (n = 27 plots at each site, 2014). Different lowercase letters indicate significant differences among microforms at each site (p < 0.05, ANOVA and Tukey's post hoc test). Sites are significantly different (same microform) if they have no uppercase letters in common (p < 0.05, *t*-test, per Levene's test for equality of variances).



Figure S5.2 Relationship between gross primary productivity (GPP) and photosynthetic photon flux density (PPFD) for vegetation-microform types at NRB and MOE (Ridge-Pool), fitted with a rectangular hyperbola equation, (a) *Sphagnum*-spruce hummocks: MOE n = 75, a = 0.01, GP_{max} = 6.78, F = 26.5, p < 0.0001; NRB n = 120, a = 0.005, GP_{max} = 5.73, F = 132.8, p < 0.0001, (b) *Sphagnum*-shrub intermediate: MOE n = 66, a = 0.008, GP_{max} = 6.76, F = 58.1, p < 0.0001; NRB n = 116, a = 0.009, GP_{max} = 3.3, F = 23.9, p < 0.0001, (c) *Eriophorum* tussocks: MOE n = 77, a = 0.01, GP_{max} = 5.42, F = 29.6, p < 0.0001; NRB n = 118, a = 0.008, GP_{max} = 6.5, F = 107.6, p < 0.0001, (d) *Sphagnum*-only pool: no fit.



Figure S5.3 Water chemistry (mean \pm standard error) for vegetation-microforms at MOE (Bog and Ridge-Pool) and NRB: (a) Total N, (b) DOC, (c) NH₄⁺-N, (d) NO₃⁻-N, (e) K⁺, and (f) Ca²⁺. Sites are significantly different (same vegetation-microform type) if they have no uppercase letters in common (*p* < 0.05, ANOVA).



Figure S5.4 Nutrient availability (mean supply rate \pm standard error, PRSTM probes) in upper 20 cm of vegetation-microform types at MOE (Bog and Ridge-Pool) and NRB: (a) Total N, (b) NH₄⁺-N, (c) NO₃⁻-N, (d) K, and (e) Ca. Sites are significantly different (same veg-microform type) if they have no uppercase letters in common (*p* < 0.05, ANOVA).



Figure S5.5 FTIR spectra for *Sphagnum*-spruce hummocks at MOE (Bog) and NRB, at (a) 10-15 cm, and (b) 25-30 cm. Absorption peaks identified according to Niemeyer *et al.*, (1992), Cocozza *et al.*, (2003), and Artz *et al.*, (2008).



Figure S5.6 FTIR spectra for peat at 0-5 and 25-30 cm depth under lichen mats (lichen-shrub hummocks) at MOE (Bog) and NRB. Two lichen species are shown: (a) and (c) *Cladina stellaris*, and (b) and (d) *Cladina rangiferina*.

Botanical Growth English MOE MOE NRB **Species** authority Form **Common Name** Bog RP Andromeda glaucophylla L. (Link) DC. Shrub Bog rosemary * * Carex limosa Sedge Mud sedge L. Lam (Wahlenb.) Carex magellanica ssp. irrigua Sedge Poor sedge * * Hulten Fewseed sedge * * Carex oligosperma Michx. Sedge Lightf. Fewflower sedge * Carex pauciflora Sedge * Chamaedaphne calyculata (L.) Moench. Shrub Leatherleaf * (L.) Weber ex Cladina rangiferina Lichen Reindeer lichen * F.H.Wigg. * Cladina stellaris (Opiz) Brodo Reindeer lichen Lichen Drosera anglica Huds. Forb English sundew * Roundleaf * * Drosera rotundifolia L. Forb sundew Shrub Empetrum nigrum L. Crowberry Tussock * * Eriophorum vaginatum L. Sedge cottongrass Kalmia angustifolia L. Shrub Sheep laurel * * * Kalmia polifolia Wangenh. Shrub Bog laurel Larix laricina (Du Roi) K. Koch Tree Tamarack Three-leaved Maianthemum trifolium (L.) Sloboda Forb * * solomon's seal (Mill.) Britton, Tree Black spruce * Picea mariana Sterns & Poggenb. * * Polytrichum strictum Brid. Moss Haircap moss (Oeder) Kron & * Rhododendron groenlandicum Shrub Labrador tea * Judd. Rhyncospora alba (L.) Vahl, Enum. Sedge White beaksedge * * Rubus chamaemorus L. Forb Cloudberry * * Forb Pitcher plant * * Sarracenia purpurea L. Scheuchzeria palustris Forb Podgrass * L. C.E.O. Jens. ex Sphagnum angustifolium Moss Fine bog moss Russ. Acute-leaved bog * Sphagnum capillifolium (Ehrh.) Hedw. Moss * moss Sphagnum fuscum (Schimp.) Klinggr. Moss Rusty bog moss * * * Magellanic bog Sphagnum magellanicum Brid. Moss moss (Russow) C.E.O. Sphagnum majus Moss Olive bog moss Jens. Papillose bog Sphagnum papillosum Lindb. * Moss

Table S5.1 List of species and nomenclature for MOE (Bog and Ridge-Pool) and NRB.

moss

| Species | Botanical authority | Growth Form | English Common Name | MOE Bog | MOE RP | NRB |
|------------------------|------------------------|----------------|----------------------------|------------|-----------|-----|
| Sphagnum rubellum | Wils. | Moss | Red bog moss | * | * | * |
| Tricophorum alpinum | (L.) Pers. | Sedge | Alpine club-rush | | * | |
| Tricophorum cespitosum | (L.) Hartm. | Sedge | Tufted club-rush | | * | * |
| Vaccinium myrtilloides | Michx. | Shrub | Velvet-leaved blueberry | * | | * |
| Vaccinium oxycoccos | L. | Shrub | Small cranberry | * | * | * |
| Vaccinium uliginosum | L. | Shrub | Bog bilberry | * | | * |

Table S5.2 NEE plot characteristics and NEE-PPFD rectangular hyperbola curve fit parameters for vegetation-microform types at MOE (Ridge-Pool) and NRB (combined 2013 and 2014 data).

| Site | Vegetation-Microform Type | Vascular Plants | Nonvascular | VGA (m ² m ⁻²) | WTD (cm) | рН | n | α (μmol CO ₂ m ⁻² s ⁻¹) | GP _{max} (µmol CO ₂ m ⁻² s ⁻¹) | <i>r</i> ² |
|------|---------------------------------|--|--|---------------------------------------|--------------|--------------|-----|--|--|-----------------------|
| MOE | Sphagnum only pool | C. magellanica ssp. irrigua T. cespitosum | S. majus S. papillosum | 0.1 (0.0) | 2.5 (0.3) | 4.3 (0.1) | 101 | 0.11 (1.02) | 0.50 (0.13) | 0.16 |
| | Sphagnum-sedge pool | C. oligosperma C. limosa C. pauciflora R. alba C. magellanica ssp. irrigua | S. majus S. papillosum | 2.2 (0.4) | 2.2 (0.2) | 4.3 (0.1) | 107 | 0.01 (0.00) | 4.50 (0.61) | 0.64 |
| | Eriophorum tussock intermediate | E. vaginatum V. oxycoccos | S. rubellum S. papillosum | 5.8 (1.8) | -1.8 (0.7) | 4.1 (0.1) | 116 | 0.01 (0.00) | 5.21 (0.67) | 0.63 |
| | Sphagnum-shrub intermediate | R. chamaemorus V. oxycoccos A. glaucophylla C. calyculata | S. rubellum S. capillifolium | 1.6 (0.4) | -12.0 (0.7) | 4.1 (0.1) | 99 | 0.01 (0.00) | 5.82 (0.74) | 0.75 |
| | Sphagnum-spruce hummock | P. mariana C. calyculata R. groenlandicum M. trifolium | S. fuscum S. capillifolium | 3.9 (1.0) | -24.0 (0.7) | 4.1 (0.0) | 114 | 0.02 (0.01) | 6.23 (0.69) | 0.66 |
| | 'Sphagnum' only pool | R. alba | - | 0.0 (0.0) | -27.9 (1.3) | 4.9 (0.0) | 144 | 0.00 (0.00) | 0.93 (0.36) | 0.12 |
| | Eriophorum tussock intermediate | E. vaginatum V. oxycoccos | S. rubellum | 3.2 (0.5) | -39.9 (1.1) | 4.4 (0.0) | 179 | 0.01 (0.00) | 6.15 (0.74) | 0.69 |
| NRB | Sphagnum-shrub intermediate | R. chamaemorus V. oxycoccos C. calyculata | S. rubellum | 1.4 (0.2) | -67.5 (3.5) | 4.3 (0.1) | 175 | 0.01 (0.00) | 3.08 (0.36) | 0.52 |
| | Sphagnum-spruce hummock | P. mariana C. calyculata R. groenlandicum | S. fuscum | 1.7 (0.2) | -124.6 (1.7) | 4.0 (0.0) | 184 | 0.01 (0.00) | 5.00 (0.66) | 0.66 |

Standard error in parentheses. Major vascular plants and nonvascular bryophytes are listed (bold are species within collar for gas flux measurements). Mean Vascular Green Area (VGA) within collar for each vegetation-microform type (triplicates, 2013 and 2014). Mean values for 2013 and 2014 summer (June to August) pH and WTD (cm below surface). Mean WTD recorded at same time as CO_2 measurements in 2013 and 2014. Statistical differences in α and GP_{max} were determined from confidence intervals (r^2).

*Note the poor fit of the rectangular hyperbola (**no fit) for these vegetation-microform types.

Table S5.3 Calculated FTIR absorbance ratios for humification indices (HI) according to Beer *et al.*, (2008) and Hodgkins *et al.*, (2014).

| Ratio | Indicative for |
|-----------|--|
| 2920/1060 | Aliphatics (lipids, fats, waxes)/polysaccharides |
| 1720/1060 | Carboxylic and aromatic esters/polysaccharides |
| 1630/1060 | Aromatics and aromatic or aliphatic carboxylates/polysaccharides |
| 1515/1060 | Aromatic C=C or C=O of amides/polysaccharides |
| 1450/1060 | Phenolic and aliphatic structures/polysaccharides |

Table S5.4 Humification indices (HI) of peat samples from *Sphagnum*-spruce and lichen-shrub hummocks (peat under lichen mats) at MOE (Bog) and NRB, calculated from FTIR spectra (mean values for species-depth with standard error in parentheses). Significant differences between sites marked in bold (*t*-test, p < 0.05). Significant difference between depth increments for same species and site marked with * (*t*-test, p < 0.05).

| Species | Depth (cm) | Von Po | Von Post Score | | 2920/1060 | | 1720/1060 | | 1630/1060 | | 1514/1060 | | 1450/1060 | |
|-------------------|---------------|--------|----------------|----------------|-----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|--|
| • | | MOE | NRB | MOE | NRB | MOE | NRB | MOE | NRB | MOE | NRB | MOE | NRB | |
| S. fuscum | 10-15 | H2 | H2 | 0.38 (0.01) | 0.36* (0.01) | 0.48 (0.01) | 0.48 (0.01) | 0.42 (0.01) | 0.41 (0.02) | 0.24 (0.00) | 0.24 (0.01) | 0.34 (0.01) | 0.33 (0.01) | |
| | 20-25 | Н3 | H2/H3 | 0.42 (0.01) | 0.40* (0.02) | 0.52 (0.02) | 0.49 (0.01) | 0.52 (0.02) | 0.47 (0.04) | 0.26 (0.01) | 0.25 (0.02) | 0.37 (0.01) | 0.37 (0.03) | |
| | 25-30 | Н3 | H3/H4 | 0.36 (0.02) | 0.39* (0.01) | 0.49 (0.02) | 0.48 (0.01) | 0.48 (0.04) | 0.45 (0.01) | 0.26 (0.02) | 0.24 (0.00) | 0.36 (0.02) | 0.35 (0.00) | |
| C. stellaris | 0-5 | H3/H4 | H4/H5 | 0.33 (0.02) | 0.44 (0.02) | 0.47 (0.01) | 0.50 (0.03) | 0.52 (0.02) | 0.56 (0.06) | 0.24 (0.01) | 0.28 (0.02) | 0.36 (0.01) | 0.42 (0.03) | |
| | 10-15 | H4 | Н5 | 0.34 (0.00) | 0.40 (0.01) | 0.48 (0.01) | 0.49 (0.02) | 0.49 (0.02) | 0.49 (0.02) | 0.24 (0.01) | 0.25 (0.01) | 0.35 (0.01) | 0.37 (0.02) | |
| | 20-25 | Н5 | Н5 | 0.34 (0.01) | 0.43 (0.01) | 0.47 (0.01) | 0.49 (0.01) | 0.48 (0.00) | 0.49 (0.02) | 0.23 (0.00) | 0.25 (0.01) | 0.35 (0.01) | 0.37 (0.01) | |
| | 25-30 | Н5 | H6 | 0.31 (0.02) | 0.42 (0.05) | 0.48 (0.01) | 0.49 (0.03) | 0.54 (0.03) | 0.48 (0.04) | 0.25 (0.02) | 0.25 (0.03) | 0.37 (0.02) | 0.37 (0.03) | |
| C. rangiferina | 0-5 | H5/H6 | H3/H4 | 0.40 (0.05) | 0.36 (0.11) | 0.57 (0.04) | 0.52 (0.07) | 0.65 (0.07) | 0.61 (0.10) | 0.33 (0.03) | 0.32 (0.06) | 0.47 (0.04) | 0.46 (0.07) | |
| | 10-15 | H6 | H4 | 0.34 (0.02) | 0.34 (0.04) | 0.50 (0.02) | 0.49 (0.03) | 0.56 (0.06) | 0.48 (0.05) | 0.25 (0.03) | 0.24 (0.02) | 0.37 (0.03) | 0.36 (0.02) | |
| | 20-25 | H7 | H4/H5 | 0.43 (0.04) | 0.29 (0.06) | 0.57 (0.04) | 0.48 (0.00) | 0.63 (0.07) | 0.48 (0.01) | 0.33 (0.04) | 0.25 (0.00) | 0.44 (0.05) | 0.37 (0.00) | |
| | 25-30 | H7 | Н5 | 0.40 (0.06) | 0.37 (0.06) | 0.57 (0.07) | 0.51 (0.00) | 0.64 (0.10) | 0.52 (0.01) | 0.34 (0.06) | 0.27 (0.01) | 0.45 (0.07) | 0.40 (0.01) | |

CHAPTER 6 – Conclusions and directions for future research

6.1 Conclusions

The peatlands of the Hudson Bay Lowland (HBL) are the world's second largest expanse of northern peatland and are globally important carbon (C) stores. Bogs and fens cover this extensive landscape, interspersed with meandering rivers, water tracks, and pools. Within these bogs and fens, small-scale variations in surface elevation (microtopography) form distinct spatial patterns accentuated by different vegetation cover related to water table depth. These differences in microform structure and biogeochemical function are thought to enable peatlands to occupy alternate dry and wet stable states, and therefore increase resilience to environmental change (Hilbert et al., 2000; Belyea and Clymo, 2001; Belyea and Malmer, 2004; Eppinga et al., 2009b). Various models describe mechanisms controlling peatland structure and function but with limited field evidence to support model conditions and predictions (e.g. Belyea and Clymo, 2001; Eppinga et al., 2008; Eppinga et al., 2009a; Eppinga et al., 2010). Given the risk climate change poses to northern peatlands and their massive C stores, it is important to gain a better understanding of mechanisms controlling peatland structure and function, and the potential for shifts in ecosystem state if environmental thresholds are passed. It is particularly important to understand how these structuring mechanisms operate within the remote HBL peatlands for which there has been limited research, and where owing to their extent, changes in biogeochemical processes could feedback to global climate. In this thesis, I have examined relationships among vegetation, hydrology, and nutrients, to determine controls on peatland structure and function, and how hydrological change (drier conditions) may affect these controls in the vast peatlands of the HBL.

In Chapter 3, I test whether conditions for proposed structuring mechanisms apply to peatlands in the HBL. Surface patterns in the HBL are spatially variable, particularly for different ecohydrological settings. On ombrogenous bogs, hummocks and hollows may be spatially irregular,

but occasionally, hummocks may converge to form ridges that align perpendicular to slope, creating narrow tracks of parallel ridges and pools on bogs, or extended ridges and pools in minerogenous fens (Glaser *et al.*, 1981; Foster *et al.*, 1983; Foster *et al.*, 1988a; Eppinga *et al.*, 2009a). One of the objectives of my research in Chapter 3 was to determine if different spatial patterns may be dependent on ecohydrological setting within a peat landform (Couwenberg and Joosten, 2005; Belyea and Baird, 2006; Malhotra *et al.*, 2016). My research sites in the HBL, allowed a study of the structure and function of hummocks and hollows at the apex and margin of a bog, a narrow ridge-pool track in a bog, and ridge-pool sequence in a fen. My analysis of these sites suggests ecohydrological setting is important for the development of different spatial patterns, and the strength and direction of relationships among vegetation, hydrology, and nutrients. As discussed by Belyea and Baird (2006), I posit that ecohydrological setting is important for feedback mechanisms controlling microform development in northern peatlands.

I found distinctive spatial patterns in the HBL may be partially explained by feedbacks among vegetation and hydrology that cause differential rates of peat accumulation at the microform scale, as described by Belyea and Clymo (1998; 2001). Contrasting vegetation composition, and particularly greater shrub cover (and vascular green area, VGA) on hummocks positioned above the water table, was an important control for production across microforms and sites. As net ecosystem production (NEP) represents an estimate of the amount of organic C available for accumulation in an ecosystem (with positive NEP indicating a C sink and negative NEP a C source), a larger NEP for hummocks than hollows and pools indicates greater availability of plant matter to add to the peat column (acrotelm and then the catotelm). This enables hummocks to increase in height above the water table, while in hollows, shrub growth is constrained by shallow water tables resulting in smaller NEP. These contrasts in vegetation, hydrology, and production for hummocks and hollows, are fundamental requirements for the peat accumulation mechanism and the assumption of a positive feedback between plant productivity and acrotelm thickness described by Belyea and Clymo (1998; 2001).

My results also lend support to the reinforcement of this positive feedback for hummock growth by water ponding upslope of linear ridges in ridge-pool water tracks in bogs (Glaser *et al.*, 1981; Foster *et al.*, 1988a; Swanson and Grigal, 1988). Water table elevations were higher for wells located upslope of ridges, indicating water flow is impeded by the low hydraulic conductivity (K) of peat at the level of the water table in ridges. Although water ponding may influence the development of parallel ridges and pools in minerogenous fens, the hydraulic gradients were very small, and coupled with overall lower K values, rates of flow are likely slower than for water tracks on bogs.

The accumulation of nutrients, through evapotranspiration (ET)-induced transport of water (and nutrients) to hummocks with greater vascular plant cover, is another proposed mechanism for greater production and therefore hummock growth relative to hollows (Rietkerk *et al.*, 2004b; Eppinga *et al.*, 2009a). My analysis shows no difference in nutrient availabilities for different microforms however, and no hydrological mechanism for nutrient transport, leading me to conclude this mechanism does not influence the development of microform patterns in the HBL.

In Chapter 4, I explore the effect of lichen mats on peat accumulation, a topic that has so far received very little attention in the peatland research community. My results in Chapter 3 show NEP for lichen-dominated hummocks was very small or negative, indicating smaller production than *Sphagnum*-dominated hummocks. Some studies suggest leachates from lichen mats may influence decomposition (Stark and Hyvarinen, 2003) but the effects, and the mechanisms for this, remain uncertain. I hypothesised therefore, that local peat accumulation in lichen-dominated hummocks would be less than *Sphagnum* hummocks, due to the low productivity of lichens, smaller mass litter input due to faster decay of lichen litter, and faster decomposition of underlying peat stimulated by lichen leachates. I also developed a conceptual model proposing the effect of lichen mats on peat growth over time.

My results support the conditions and predictions outlined in this model, except for the hypothesised increase in the rate of decomposition in peat under lichen mats. Analysis of peat chemical composition, biodegradability, and leachate chemistry including enzyme activity (phenol oxidases), did not indicate advanced decomposition in peat under lichen mats. My results show thick lichen mats alter vegetation composition in peatlands however, with significantly less or no cover of Sphagnum spp., forbs, and small shrubs. I also confirm the dependence of lichen productivity on surface moisture conditions, and that when coupled with smaller vascular plant cover, production for lichen-dominated hummocks is significantly smaller than *Sphagnum* hummocks. I therefore conclude that due to smaller production and the fast decay of lichen mats, local peat accumulation is reduced to the point that peat growth is likely to cease. Large bulk density values for peat under lichen mats suggest a loss of structural integrity and a collapse in hummock elevation, although the mechanism for this change in peat structure remains elusive. My analysis suggests lichens represent a temporary limit to peat growth, and I therefore propose lichens are an important feedback in the development of microtopography in peatlands. Belyea and Clymo (1998) suggest the growth of a hummock is constrained by the hollow, due to relative differences in production and longer exposure of the aerobic hummock acrotelm to decay. Where there are extensive lichen mats with a localised reduction in peat accumulation however, the growth of hummock is constrained by the hummock, and not the hollow.

In Chapter 5, I examine changes in peatland structure and function in a hydrologically impacted peatland relative to a pristine site. As demonstrated in Chapter 3, the relationship between hydrology and vegetation is an essential component of structuring mechanisms that control peatland structure and function. Climate warming will likely alter the ecohydrology of northern peatlands, with prolonged periods of drought causing drier conditions on the surface of peatlands and lower water tables. As changes in hydrology affect vegetation, peatland function (biogeochemical processes) may also be altered. Drier conditions caused by climate warming may therefore test the self-regulating behaviour of peatlands, where shifts from a dry stable state (hummocks) and a wet stable state (hollows) enable steady long-term rates of peat accumulation (Hilbert et al., 2000; Belyea and Clymo, 2001; Eppinga et al., 2009a). My objective in Chapter 5 was to determine potential environmental thresholds (hydrology) for changes in peatland structure and function, and to ascertain whether shifts in ecosystem state may occur if thresholds are passed (van Nes and Scheffer, 2005; Scheffer et al., 2012). My results indicate bogs in the HBL are resilient however, with no significant changes in species composition or cover of shrubs, graminoids, or trees in a bog subject to 7 years' drainage. Drier surface conditions (reduced peat moisture content) due to a gradual lowering of water tables (current water tables ~ 1 m below hummock surface) in hummocks and intermediate microforms caused a reduction in Sphagnum spp. and forb cover, and shrub leaf:stem ratios were smaller. Gross primary production (GPP) was smaller, but NEP was positive, indicating large areas of the drained site likely remain a C sink. Analysis of peat chemical composition, leachate chemistry, and nutrient availabilities also revealed few contrasts between the drained and pristine sites, indicating drainage has not significantly advanced decomposition for these microforms. In contrast, greater NH₄⁺-N availability in pools comprising mostly bare peat and litter (< 15 % vegetation cover) suggests advanced decomposition. NEP was also negative, indicating these areas are a C source to the atmosphere. Except for dry pools, I conclude that hydrological thresholds for shifts in ecosystem state have not yet been reached at the drained bog.

The overall objective of my research was to provide a better understanding of mechanisms controlling peatland structure and function through analysis of field evidence from HBL peatlands. My results lend support to the peat accumulation mechanism described by Belyea and Clymo (1998; 2001), and indicate water ponding upslope of elevated ridges enhances the feedback between plant production and acrotelm thickness, enabling the development of parallel ridges and pools in water tracks (Foster *et al.*, 1988a; Swanson and Grigal, 1988). I found no evidence to support the nutrient accumulation mechanism in HBL peatlands. I also demonstrate the importance of lichen mats in

reducing local peat accumulation and propose lichens play an important role for microform development in the HBL.

Knowledge of mechanisms controlling the structure and function of HBL peatlands is crucial when considering the potential effects of environmental change. My research indicates bogs in the HBL may be resilient to hydrological change (drier conditions caused by drainage) that could occur as a result of climate warming. Although this is in agreement with some recent modelling studies (e.g. Wu and Roulet, 2014) and supports the proposed self-regulating behaviour of peatlands (Belyea and Clymo, 2001; Belyea, 2009), many other studies suggest much greater peatland sensitivity to climate change and consequently, much greater potential C loss (e.g. Ise *et al.*, 2008; Bridgham *et al.*, 2008; Dorrepaal *et al.*, 2009; Fenner and Freeman, 2011). It is important to note my results are limited to the effect of hydrological change on peatland structure and function, and not temperature. However, the lack of substantial changes in vegetation, CO₂ exchange, and indicators of significantly advanced decomposition, at a bog that has been subject to significantly lower water tables and surface peat moisture content for 7 years, indicates some resilience to hydrological change. This highlights the potentially complex response of peatlands to environmental and climate change as described by Belyea (2009).

6.2 Directions for future research

The fate of northern peatlands in the face of environmental and climate change is uncertain. Not only does climate warming pose a significant risk, increasing development for infrastructure and mining, particularly in the remote HBL, could exacerbate this risk through increased degradation and a loss of resilience. My research in this thesis provides knowledge of the current state of bogs and fens in the HBL, and provides insight into possible mechanisms and feedbacks controlling structure and function. Yet there remain many unanswered questions, for which further research is needed.

My research highlights the importance of hydrology on peat surface patterns in the HBL, but this is a short-term study that was limited to the main growing season over 2 years. Analysis of longterm hydrological trends, including the influence of spring snowmelt and increased rainfall in autumn, is required to fully understand hydrological controls on vegetation composition and structure and biogeochemical function. My study is also limited to small-scale hydrological processes (microform scale). In the HBL, landscape-scale hydrology is likely a major control for the development of peat landforms (bogs and fens) (e.g. Glaser *et al.*, 2004a and Glaser *et al.*, 2004b). As spatial patterns are dependent on ecohydrological setting that is determined by the type of landform (bog or fen) and position within the landform (apex of bog, slope, margin), further knowledge of hydrological controls at the landscape-scale would be beneficial.

Lichens cover large areas of northern peatlands (above 50° latitude) but their role in the ecosystem is poorly understood. My research suggests local peat accumulation is effectively eliminated through reduced production caused by the low productivity of lichens and a decrease in the cover of Sphagnum spp., forbs and small shrubs. Although I found no indication for advanced decomposition, large bulk density values suggest there is a loss of structural integrity in peat under lichen mats, and yet the cause is not certain. Further research on the effect of lichens (including the chemical composition of leachates) on peat production, decomposition, and structure certainly warrants further research, particularly when considering their importance in the ecosystem for wildfire and herbivores. Wildfire and caribou grazing/trampling are often cited as disturbance factors that impact establishment and growth of lichens in dry boreal forests and peatlands (Foster and Glaser, 1986; Treter 1995; Boudreau and Payette, 2004; Dunford et al., 2006). Yet we do not understand the role of feedbacks between lichens (establishment, growth, and removal) and caribou grazing and wildfire, on peatland development. Climate change may also alter vegetation composition in peatlands, with increased growth of vascular plants potentially reducing lichen cover. As my research suggests lichens may play an important role in autogenic succession in northern peatlands, it will be important to understand the consequences of their loss on peatland development.

My research highlights the uncertainties in predicting the response of peatlands to environmental and climate change. We do not fully understand the combined effects of long-term drought and warmer temperatures on peatland vegetation, and the consequences for biogeochemical function. Field studies are restricted to hydrological change (except the 'SPRUCE' experiment, Hanson *et al.*, 2016) and studies of temperature change are limited to laboratory-based mesocosms which do not allow for natural vegetation dispersion and colonisation, and often do not include hydrology (except Bridgham *et al.*, 2008). Predicting future changes to peatlands requires a modelling approach and many studies provide detailed analyses (e.g. Frolking *et al.*, 2010; Wu, 2012; Quillet *et al.*, 2013; Wu and Roulet, 2014). Further field evidence (particularly from remote peatlands such as the HBL), and laboratory-based studies that test the combined effects of temperature and hydrology, will aid in the development of model conditions and corroborate model predictions. This research would also help inform land-use planning decisions in Ontario's Far North, where further development of the HBL peatlands for infrastructure and resource use (e.g. mining) are likely to occur.

Lastly, my research presents an analysis of contemporary processes influencing microform development in the HBL. Knowledge of the effects of these processes on long-term peat accumulation and development could be improved by relating my results to an analysis of changes (vegetation, hydrology, and C accumulation) observed in the palaeoecological record. By understanding the historical effects of climate forcing, and disentangling these effects from internal processes, we may predict with greater accuracy the effects of future changes to northern peatlands.

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