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Musical chairs in a boreal peatland:
how permafrost thaw reverses successional processes

By

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THESIS

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the
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Abstract

The current climate trends indicate amplified high latitude warming. Boreal peatlands can be found within those high latitudes and have important functions hydrologically, ecologically and also in terms of carbon cycling. Peatland's are wetlands that have accumulated more than 40 cm of peat and can range from minerotrophic fens to ombrotrophic bogs. Naturally, a rich fen can be converted to a bog once groundwater sources are cut off by *Sphagnum* spp. In areas underlain by discontinuous permafrost, landscape changes are occurring particularly rapidly as the permafrost there is sensitive to both vertical and horizontal thaw. The purpose of this thesis is to determine whether permafrost thaw can lead to the reversal of successional pathways, converting a bog into a fen by increasing hydrological connectivity. The study was conducted in the northern boreal peatlands of the Northwest Territories sampling from rich fens, poor fens and collapse scar bogs, while examining how different levels of hydrological connections (isolated, ephemerally connected or fully connected) impacted species community. We concluded that bogs are resilient to increased connectivity due to permafrost thaw, as they did not increase in richness with increased connectivity. Fens meanwhile showed great variation in richness with increased connectivity. Although there were no whole sale differences in species community, rich fen species have begun encroaching into the fully connected collapse scar bog, providing support for the reversal of the normal autogenic pathway. If no whole scale changes could be found in species composition, pH and nitrate both increased with connectivity, which indicates that we are seeing differences in water chemistry. Finally, flooding simulations were used to determine whether frequency of inundation of a fully connected bog by fen water was predicting soil water chemistry

and species composition. The data indicates that flooding alone cannot explain the presence of rich fen species and we speculate that nutrients are being released with permafrost thaw. Boreal peatlands are unique habitats and these changes in permafrost may eventually lead to the conversion of these wetlands and the loss of ecosystem functions.

Statement of authorship

I state that the findings presented in this thesis, with the exception of the following, were completed by me during my master's under the supervision of Dr. J. Baltzer. This thesis was formatted in a manuscript style and all co-authors are acknowledged at the beginning of each chapter. In Chapter 2 and 4 remote sensing data was provided by W. Quinton and was orthorectified and atmospherically corrected by L. Chasmer. J. Baltzer helped develop the experimental designs for all the different chapters, while A. Spring, L. Chasmer and W. Quinton contributed ideas for Chapter 4. W. Quinton provided Figure 2.2 on permafrost thaw between 1977 and 2008. A. Spring did a flooding model using water table elevation data provided by W. Quinton for Chapter 4. He also provided figures 4.1, 4.5 and 4.6, which used spectral imagery and digitized permafrost plateau extent that was provided by L. Chasmer.

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I would like to dedicate this thesis to my loved ones who answered the sat phone calls and sent their good wishes while I explored the great white north. Also to everyone, friends and family who gave their encouragement so I could get these words onto the page.

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Chapter 1

Introduction to boreal peatlands in a discontinuous permafrost landscape

Mélissa M. Fafard

1.1 Background

1.1.1 Boreal Peatlands

Wetlands are ecosystems where aquatic processes such as poorly drained soils, aquatic vegetation, and standing water can be found. Wetlands are divided into two sub categories: mineral and organic. Peatlands are organic wetlands, where more than 40 cm of peat has accumulated. Peatlands are unique in their hydrology, capacity for carbon storage, and the flora that inhabit them (National Wetlands Working Group 1997). They extend across 12% of Canada's land area, of which 97% are found in the boreal forest (Tarnocai, 2006). The rate of decomposition is very slow, due to the cold and often anoxic environment, which allows carbon to accumulate as peat (Vitt et al. 1994; Beilman and Robinson 2003) and makes them an important environment for net carbon storage (Volney and Fleming 2000). Another consequence of having low nutrient and anoxic environments is that the plants that are found in peatlands are adapted to these conditions and rely on them for survival (Locky and Bayley 2006). The peat is composed mainly of *Sphagnum* spp. but also contains a variety of bryoflora (such as *Hylocomium splendens* and *Tomenthypnum nitens*), which are responsible for 20 to 48% of wetland production. The insulation provided by the peat leads to cold soils, often underlain by permafrost (ground that is below 0°C for more than two years; French and Slaymaker 1993).

1.1.2 Peatland types

There are two types of peatlands in the mosaic-like northern landscape that are of interest for this thesis: bogs and fens. Each of these land formations has a specific

hydrological function (Quinton et al. 2009), as well as particular flora that is unique to them (Camill 1999a; Beilman 2001). However, there is some overlap as to what qualifies as a bog and what qualifies as a fen. The key differences between them can be broken down into three sections: 1) species richness; 2) pH; and 3) hydrologic function - the difference in pH being the clearest distinction between the three (Wheeler and Proctor 2000). As each land formation has a specific hydrological and ecological role, changing the proportional cover of each will affect the basin's hydrology (Quinton et al. 2003) as well as species composition (Weltzin et al. 2003). Tarnocai (2006) created a model that looked at the sensitivity of Canadian peatlands and found that due to their large areal extent, 60% of bogs and fens will be impacted by climate change. The following defines the characteristics that will be used to describe these different peatland types for this thesis (also see Table 1).

Bogs are acidic, as they are precipitation fed, and are characterized by a surficial water table (Tarnocai 2006). In areas underlain by permafrost, bogs can be classified as internal or connected collapse scars. Internal collapse scar bogs, also referred to as closed bogs or in the case of this study as isolated bogs, are usually round in shape, found within the plateau, and fully surrounded by permafrost. As a consequence, these bogs are hydrologically isolated. Connected collapse scars are created when the permafrost surrounding these bogs thaws and hydrologically connects them to other bogs or fens. They can be referred to as connected or open bogs. Like the isolated bogs, connected bogs do not have any permafrost beneath them (Vitt et al. 1995; Camill 1999b). Both of these types of bog are dominated by *Sphagnum* spp. and are quite species-poor. This is in part due to the ability of *Sphagnum* spp. to acidify the soil by releasing H⁺ ions through

cation exchange (Clymo 1963), which decreases microbial activity and reduces nutrient availability to vascular plants (Pouliot et al. 2011; Millett et al. 2012). Being primarily rain water fed and containing species that acidify the soil, bogs have very low pH ranging from <4.8-5.5 (National Wetlands Working Group 1997; Wheeler and Proctor 2000).

Peat plateaus are bogs that have been elevated by the formation of permafrost (Tarnocai 2006). Because of the volumetric expansion of water when it freezes, the ground surface of peat plateaus is 0.5-1.5 meters above the water table (Camill 1999a). The canopy usually consists of black spruce (*Picea mariana*), with feather mosses, *Sphagnum* spp., ericaceous shrubs, and forbs in the understory. The canopy height is greatest near the center of the plateau and is reduced as it gets closer to the edges (Chasmer et al. 2011). Loss of ice-rich permafrost underlying the plateau will lead to ground surface subsidence. When this subsidence occurs, the plateau lowers at the edges resulting in tree mortality as it is now at the water surface and forest conversion into a permafrost-free wetland (Chasmer et al., 2010; Wright, et al., 2008 Camill, 1999; Halsey et al., 1995).

Fens can be classified as poor, moderate, or rich based on their species composition, nutritional characteristics, and species richness (Vitt et al. 1994). In relative terms, they are typically species-rich, with a great abundance and diversity of brown mosses, and have a pH higher than 5.5. Hydrologically, like bogs, the water table is at or very close to the surface; however, their water source is comprised not only of precipitation but also of mineral-rich groundwater. This groundwater source is one of the key factors in determining spatial patterns in species distribution for a fen (Vitt et al. 1994; Barry et al. 2008). Poor fens are often an intermediate between rich fens and bogs,

having both brown mosses and *Sphagnum* spp. (Kuhry et al. 1993). More plant species can be found in fens than bogs, including a wide variety of sedges (Vitt et al. 1994; Wheeler and Proctor 2000; Tarnocai 2006), brown mosses, trees, and shrubs (National Wetlands Working Group 1997). In these high nutrient systems, we also find marshes that often border fens. Marshes can be mineral or organic wetlands (Locky and Bayley 2006) that have shallow water and high nutrients; they are characterized by emergent aquatic macrophytes (National Wetlands Working Group 1997).

1.1.3 Discontinuous Permafrost

The spatial extent of permafrost can vary substantially and is used to determine which zone it belongs to (>90% being continuous, between 50-90% discontinuous, and 10-50% sporadic permafrost, Jorgenson et al. 2001). Continuous permafrost can vary in depth from 100 to 1000 meters and is found where the mean annual air temperature (MAAT) is below -8°C (French and Slaymaker 1993). Discontinuous permafrost found in the more southern areas in the boreal zone is thin (5-15 m, Quinton et al. 2009) and warm (> -0.3°C , (Smith et al. 2005)). Finally, sporadic permafrost is restricted to small lenses found in peatlands in areas further south (Zoltai 1995).

Discontinuous permafrost soils have a natural cycle of aggradation and degradation of permafrost. Because of the properties of peat as an insulator, discontinuous permafrost can be found within regions where temperatures would not normally permit its formation. During the winter the peat is wet and cold air is able to pass through, cooling the soil underneath. During the summer, the dry peat will insulate the ground from further warming (Zoltai 1993). Therefore, disturbances to the peat may

reduce insulation of the ground, accelerating thaw. Due to the increasing trend in temperatures, once this permafrost thaws air temperatures are now too high for it to aggregate in that area again (Shur and Jorgenson 2007).

There has been a rapid increase in permafrost degradation in the discontinuous zone (Camill 2005). Studies are finding that permafrost thaw is a widespread Pan-arctic phenomenon with evidence of this found in Canada (Halsey et al. 1995; Jorgenson and Osterkamp 2005), Alaska (Jorgenson et al. 2001), Russia (Romanovsky et al. 2010), as well as Sweden (Johansson et al. 2006). An important consequence of permafrost thaw is that it will lead to the transition of peat plateaus into collapse scar bogs. At first, as the permafrost thaws, the plateau's edge will subside into the adjacent wetlands creating small channels. Eventually, these channels will lead to two wetlands becoming one very large fully connected feature (Zoltai 1993; Quinton et al. 2011). This will lead to ecosystem changes such as: wetter environments, increased hydrological connections and thus wetland conversion both for hydrological and ecological functions, and changes in water flow and runoff (Camill 1999b).

1.1.4 Vegetation shifts

With the current rates of permafrost degradation, it is important to fully understand the current species succession that takes place in these systems. Species succession refers to how vegetation develops due to modification of the local environment (Zobel 1988). There are two main processes that will be examined in a northern boreal peatlands: autogenic and allogenic forces (Lamentowicz et al. 2008).

Naturally peatlands will develop through autogenic factors, which are biotic interactions such as plant species succession through competition (Lamentowicz et al. 2008). There is a typical succession from marshes, to rich fens, to *Sphagnum* bogs (Klinger and Short 1996). Rich fens are the natural habitats of brown mosses such as *Scorpidium* species. These species require a higher abundance of nutrients that are most often provided through access to ground water. If for some reason this ground water source is restricted, *Sphagnum* species will have a competitive advantage over the other rich fen plant species. *Sphagnum* spp. are known for their ability to acidify the soil locally and also for their tolerance to minerotrophic soils such as those found in fens (Kooijman 1992; Laine et al. 2011). Acidification is the trigger for this succession; colonizing species such as *Sphagnum riparium* will establish first (Laine et al. 2011) and may use the vascular plants for the stability in their rooting system and protection (Pouliot et al. 2011). Once colonizing species have established, hummock species (such as *Sphagnum fuscum*) will start creating microtopography via hummock formation. This will raise the peat above the water table, cut off access to groundwater sources, and continue to make the environment unsuitable for other vascular plants by acidifying the soil and reducing nutrient sources for vascular and non-vascular plants (Zobel 1988). With increased *Sphagnum* spp. presence, the habitat will then become dependent on the biotic aspects (such as acidification and competition) rather than solely on the hydrology of the system (Vitt et al. 1975; Klinger and Short 1996). These processes will eventually lead to the conversion from a rich fen to a poor fen and finally to a bog stable state (Klinger and Short 1996). As mentioned previously, discontinuous permafrost has a natural cycle of aggradation and degradation. Therefore, within autogenic forces there is

also the ability to transform a peat plateau into a bog, or vice-versa. The degradation of permafrost on a peat plateau can occur naturally because of fire, wind, disease, depression in the ground surface, or permafrost topography, and will lead to the creation of a collapse scar bog (Zoltai 1972). The aggradation of permafrost starts with the formation of ice lenses during cold conditions or in well insulated soils. This initiates when *Sphagnum* spp. creates a hummock that is above the water table, which gives a substrate for trees to begin to colonize. The shade from the trees, combined with the insulating properties of peat will lead to the formation of the ice lens and eventually the development of permafrost (Vitt et al. 1994).

The transition from a fen to a bog is often viewed as unidirectional, or at least so it seems through autogenic processes (Zobel 1988). However, with increasing temperatures, allogenic factors (abiotic forces such as climate change) must be considered when examining species succession (Fig 2.1). Increased temperatures will lead to increased permafrost degradation, which means that peat plateaus will be converted into collapse scar bogs at a greater rate than they can form (Zoltai 1993; Beilman and Robinson 2003; Shur and Jorgenson 2007). Peat plateaus serve to hydrologically isolate neighboring wetlands, but when the permafrost underneath the plateaus thaws channels can be created between adjacent wetlands. This leads to increased hydrological connectivity and the potential for alteration in water chemistry, or even the return of ground water sources (Hughes and Dumayne-Peaty 2002). The added nutrient inputs from groundwater sources will have two consequences: first, inundation by nutrient rich water will lead to the decrease of *Sphagnum* spp. (Granath et al. 2010), and secondly, these nutrient rich waters will also give a competitive advantage to

vascular plants and enable them to colonize within the bog (Berendse et al. 2001). In theory, this will lead to the reversal of the autogenic pathway and to the conversion of a bog back into a fen.

1.1.5 Study site

The research was conducted in the Scotty Creek research basin, 50 km south of Fort Simpson in the Northwest Territories (61° 18'N; 121° 18'W). The area is characterized as a high boreal wetland region underlain by discontinuous permafrost. It has a dry continental climate and the Canadian Climate Normals stations recorded a mean annual air temperature of -3.2°C between 1971 - 2000 and an annual precipitation average of 369 mm of which approximately 50% is snow (MSC 2013). Scotty Creek drains 152 km² of peatland and is located in the Mackenzie River Basin, within the 140,000 km² of the Hay River Lowlands (Quinton et al. 2009). These peatland complexes are composed of different land formations that are in a dynamic state - the prominent formations being peat plateaus, bogs, and fens (channel and basin). Peat plateaus are the most abundant, representing 43% of the land area at Scotty Creek in 2009, and are populated by *Picea mariana* (black spruce). Bogs can be found both within plateaus and near their edges, and are dominated by *Sphagnum* spp. (Quinton et al. 2009). Channel fens have wide channels with species such as sedges and aquatic plants, while basin fens are more restricted in their hydrology; they are found within permafrost plateaus and contain species such as *Larix*, *Betula* and *Carex* spp. (National Wetlands Working Group 1997). Fens and bogs occupy 21% and 26% of the region, respectively (Quinton et al. 2009). The intimate hydrological and ecological relationship of these land formations and

the associated physical structure provided by the discontinuous permafrost is at the core of the present issue.

1.2 Objectives

Although many studies have been done on vegetation shifts in the tundra (Blok et al., 2010; Chapin et al., 2010; Yi et al., 2007), changes taking place in subarctic wetlands underlain with discontinuous permafrost are poorly documented. Due to the rate of the warming-induced changes, it is critical to assess the current state of the flora and predict future trajectories. By gaining knowledge of the present situation it is possible to understand the dynamics of a peatland mosaic, as well as future peatland functions. This includes species succession that would lead to increased methane sources (Blok et al., 2010). The objectives of this thesis are to examine species succession in boreal peatlands in the context of permafrost thaw and characterize the role of hydrological connectivity within an ecological framework. Overall, the three goals are to:

- 1) Document natural vegetation communities in bogs and fens
- 2) Quantify vegetation changes associated with hydrological connectivity
- 3) Identify environmental variables underlying these changes

Chapter 2 examines the community composition and structure of different wetland types in a boreal peatland and assesses how permafrost thaw induced hydrological connectivity may be impacting composition, richness, and structure. This chapter demonstrates that while the system still appears to be driven largely by autogenic succession, some evidence exists for encroachment of fen vegetation into well connected bogs. Chapter 3 delves into the mechanisms underlying species separation, specifically water chemistry and whether hydrological connectivity is impacting water chemistry. It

provides some evidence of changing water chemistry conditions in bogs that have undergone dramatic rates of thaw, and consequently increased connectivity. Chapter 4 delves into a case study of one of the bogs that has exhibited radical change, using flood modelling to assess whether increasing connectivity and thus easier movement of surface water drives the vegetation and water chemistry changes observed in chapter 2 and 3.

Table 1.1: Wetland characteristics, based on hydrology, pH and species richness

	Organic wetland (Peatland)				Mineral or organic wetland
	Bogs		Fens		Marsh
	Collapse scar	Peat plateau	Poor	Rich	
Hydrologic function	Ombrogenous ¹ Surficial water table ⁴	0.5-1.5 meters above water table ⁶ Permafrost ⁷	Minerogenous ¹ Surficial water table ⁴	Minerogenous ¹ Surficial water table ⁴	Minerogenous Shallow water ¹
pH	4-4.8 ^{1,2}	-	<5.5 ⁵	>5.5 ⁵	Circumneutral to highly alkaline ¹
Species richness	<i>Sphagnum</i> spp. ¹ Ericoids ¹ Dwarf shrubs ¹ Lichens ¹ <i>Picea mariana</i> ³ <i>Ledum groenlandicum</i> ⁵	<i>Picea mariana</i> ⁶ Feather moss ⁶ <i>Sphagnum</i> spp. ⁶ Ericoid shrubs ⁶ Forbs ⁶ Lichens ⁶	<i>Sphagnum</i> spp. ^{1,5} Ericoids ¹ Sedges ¹ Brown moss ¹ <i>Picea mariana</i> ¹	Sedges ¹ Brown moss: (Such as <i>Drepanocladus</i> spp.) ¹ Shrubs and trees ¹ : <i>Betula</i> spp. ¹ . <i>Salix</i> spp. ¹ . <i>Larix Laricina</i> ¹	Emergent aquatic ¹ Macrophytes ¹ Rushes ¹ Reeds ¹ Grasses ¹ Sedges ¹ Shrubs ¹ Herbs ¹ Brown moss ¹

¹ National Wetlands Working Group, 1997

² Wheeler & Proctor, 2000

³ Chasmer et al. 2011

⁴ Vitt et al. 1994

⁵ Vitt, 2006

⁶ Camill et al. 1999

⁷ Tarnocai 2006

⁸ Locky and Bayley 2006

Chapter 2
**Change and permafrost degradation in a boreal peatland: impacts on ground
vegetation**

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Keywords: Climate change, Permafrost, Allogenic succession, Species community, Peatlands, Bogs, Fens, Non-metric multidimensional scaling, *Sphagnum*, Species succession, Collapse scar bogs

Primary research article

Abstract

Peatlands are often influenced by both autogenic (internal) and allogenic (external) forces. Through autogenic influences there is a natural unidirectional trajectory between wetland types, where a rich fen will transition to a poor fen and finally to a bog. However, through allogenic influences, this natural trajectory can be reversed. The aim of this study was to examine autogenic and allogenic successional trajectories within a boreal peatland in the Northwest Territories. This site is facing rapid changes attributable to climate warming-induced permafrost thaw. We were interested in the potential role of permafrost thaw in the reversal of the typical autogenic successional trajectory, via increased above ground hydrological connectivity of bogs that were previously hydrologically isolated. Using high-resolution aerial imagery and a LiDAR digital elevation model (DEM), the degree of hydrological connectivity of wetlands was assessed and used as a basis for wetland selection. Within each wetland, lichens, vascular, and non-vascular plants were identified to the species level. The different wetland types were identified based on species composition and water chemistry; we were then able to compare the effects of hydrological connectivity on species composition in rich fens, poor fens, and collapse scar bogs. Species accumulation curves and richness indices revealed increased species richness with increased connection as a function of wetland type. Rich fens had the highest species richness and showed the greatest response to increased hydrological connectivity as would be expected in autogenic succession. However, bogs showed resilience to increased permafrost thaw in their species composition, which suggests that permafrost-thaw induced changes in hydrological connectivity may not be a critical allogenic successional force. Although no

differences in species composition were detected with the non-metric multidimensional scaling (NMDS), rich fen species were found in fully connected bogs. This suggests that with increased thaw more dramatic changes in species communities may be expected, which could lead to wetland conversion and alteration of wetland function.

2.1 Introduction

Peatlands are acidic wetlands, with 40 cm of peat or more, that are characterized by their extremely slow decomposition rates, low nitrogen availability, and the unique composition of plants associated with them (Wieder et al. 2006). Due to these slow decomposition rates peatlands are an important player in carbon cycling (Vitt 2006; Tarnocai 2006; Ruckstuhl et al. 2008); Canadian peatlands contain 147.11 Gt of organic carbon (Tarnocai 2009). However, different peatland types have different capacities for carbon storage (Tarnocai 2009) and methane release (Mahmood and Strack 2011). These peatlands come in ecological and hydrological gradients from geogenous and mesotrophic with relatively high plant diversity (fens) to ombrotrophic and oligotrophic with extremely low plant diversity (bogs) (Kuhry et al. 1993; Camill 1999a; Vitt 2006); these gradients markedly impact their function.

Peatland ecological theory indicates that autogenic forces (internal influences) will lead to the species conversion from rich fens (fens dominated by true mosses; Vitt et al. 2009), to poor fens (fens dominated by *Sphagnum* mosses; Vitt et al. 2009), and finally to bogs (dominated by *Sphagnum* spp. mosses and very acidic; National Wetlands Working Group, 1997) (Zobel 1988; Kuhry et al. 1993; Hughes and Dumayne-Peaty 2002; Granath et al. 2010; Hájková et al. 2012; Tuittila et al. 2012) (Fig 2.1). Peatland conversion usually starts when groundwater sources are cut off in a rich fen. This can happen through many mechanisms, the primary one being autogenic accumulation of peat, which will raise the ground surface above the water table (Kuhry et al. 1993; Granath et al. 2010; Hájková et al. 2012; Tuittila et al. 2012). The raised peat permits the colonization of *Sphagnum* spp, which acidifies the soil surface resulting in poor fen

conditions. With further accumulation of *Sphagnum* spp., the peatland will become completely isolated from its ground water source leading to bog-like conditions (Kuhry et al. 1993; Granath et al. 2010; Hájková et al. 2012; Tuittila et al. 2012). Often, without new input of nutrient rich waters this autogenic process is not reversible (Zobel 1988).

However, in northern peatlands there is often another player to consider in this ecological pathway: permafrost. Permafrost (perennially cryotic ground; French and Slaymaker 1993) is an essential part of the ecosystems where it is present. Permafrost controls water storage and runoff (Quinton et al. 2011; Bauer and Vitt 2011), and traps carbon stores and nutrients (Keuper et al. 2012). Across the latitudinal extent of permafrost, continuity is variable: discontinuous permafrost is found at the southern limit of permafrost range, and has an areal extent of 50 – 90% (Vitt et al. 1994; Beilman and Robinson 2003; Jorgenson et al. 2010).

The presence of permafrost in the discontinuous zone is controlled by the past and present climate. Under a cooler climate there is a balance between ombrotrophication (conversion of a fen to a bog; creating permafrost plateaus) and the creation of collapse scar bogs. However, warmer climates will shift this balance towards collapse scar bogs. Permafrost plateaus are formed by the thickening of a *Sphagnum* mat. This serves the dual purpose of lifting the *Sphagnum* above the water table (1 to 2 meters) (Quinton et al. 2003), thereby creating a dry, insulating layer at the ground surface, and in the Northwest Territories, facilitating the establishment of *Picea mariana*. Individuals of *P. mariana* will offer shade and reduce incident radiation, which further cools the soil locally and facilitates the development of persistent ice lenses. This will eventually lead to permafrost aggradation and to the formation of a permafrost plateau (Zoltai 1995; Arlen-

Pouliot and Bhiry 2005; Vardy et al. 2005). Conversely, the permafrost underlying the plateau can thaw and create a collapse scar bog (Beilman 2001), known as paludification.

In the zone of discontinuous permafrost, plateaus acts as a barrier between bogs and fens, where permafrost is absent. Permafrost thus restricts ground and surface water flow, which in turn determines storage capacities and drainage (Quinton et al. 2003). This barrier to water flow will be lost if permafrost thaws, leading to many impacts on the system including modifications to hydrology (Quinton et al. 2009), changing vegetation structure (Camill 1999a), and potentially removing spatial heterogeneity of this peatland mosaic (Turetsky 2004). As discontinuous permafrost can be especially vulnerable to further warming as it can be ice rich (Quinton et al. 2011), thin (5-15 m; Quinton et al. 2009) and warm ($>-0.3^{\circ}\text{C}$; Smith et al. 2005), these permafrost peatlands are very reliant on the climate to keep their successional processes (Arlen-Pouliot and Bhiry 2005).

Recently increased temperatures have led to circumpolar permafrost thaw, which can have marked implications on ecosystem functions and services (Jorgenson et al. 2001; Beilman and Robinson 2003; Tarnocai 2009). Increased temperatures are predicted for many areas of the world, however high latitude warming is especially dramatic - twice as fast as the global average (IPCC 2007). With increased warming, the rate of conversion of permafrost plateaus to bogs and fens is increasing (Vitt et al. 1994; Camill et al. 2010; Quinton et al. 2011; Baltzer et al. 2014). Where permafrost thaws, it can create connections between wetlands. There are different degrees of connection that are possible amongst the wetlands. A bog can begin as completely isolated (surrounded by permafrost as to be hydrologically isolated), however permafrost thaw can erode passages between wetlands, leading to ephemeral connections during spring (following snow melt)

and summer (during increased rain fall events) (Wright et al. 2008). These channels may expand further such that they become wide and permanent throughout the whole year, facilitating substantial hydrological exchanges (Vitt et al. 1994). A change in hydrology can induce the otherwise difficult reversal of autogenic succession from a bog to a poor fen (Hughes and Dumayne-Peaty 2002; Granath et al. 2010; Tuittila et al. 2012) by bringing the return of the nutrient-rich groundwater source through flooding (Asada et al. 2005; Hájková et al. 2012), through permafrost thaw (Keuper et al. 2012) or via the new surface water interactions (i.e. between a bog and a fen).

A series of rich fens, poor fens and collapse scar bogs were sampled within a boreal peatland complex in the zone of discontinuous permafrost. The amount of permafrost that has thawed in the region of study is considerable; over the last 60 years there's been a 27% decrease of permafrost plateau area (Fig 2.2). Species composition and abundance was characterized in bogs, poor fens, and rich fens that were isolated, ephemerally connected, or fully connected to address the following objectives:

1. Characterize vegetation in these wetlands and how it relates to hydrological connectivity
2. Identify changes in successional pathways and species community attributable to permafrost thaw and increased connectivity

The conversion and amalgamation of these peatlands can lead to complete changes in hydrological and ecological functions, as fens and bogs have very distinct communities. This in turn can lead to changes in soil moisture, permafrost stability, as well as ecosystem carbon and nitrogen storage (Turetsky et al. 2010). Temperatures are increasing rapidly (IPCC 2007) and understanding peatland successional pathways can

help establish future trajectories for carbon dynamics and ecosystem processes (Camill 1999a; Strack et al. 2006; Granath et al. 2010). Although much research has been done in the tundra concerning plant species shifting in the face of climate change (Chapin et al. 1995; Schuur et al. 2007; Blok et al. 2010), much less is known for boreal peatlands within the discontinuous permafrost zone, which is changing very rapidly as temperatures are warming (Quinton et al. 2011).

2.2 Methods

2.2.1 Site description

Scotty Creek is a 152 km² drainage basin in the lower Liard River Valley in the Northwest Territories (61° 18'N; 121°18'W), roughly 50 km south of Fort Simpson (Quinton et al. 2009). The area is in the boreal wetland region (Tarnocai et al. 2002) underlain with discontinuous permafrost (Heginbottom and Radburn 1992), and is prone to thawing both vertically and horizontally. The site has a dry continental climate and data from 1971-2000 indicate that the area has a mean annual air temperature of -3.2°C, and an annual average of 369 mm of precipitation, 224 mm of which is snow (MSC 2013). The landscape in 2011 consisted of 21% fens, 24% connected bogs, 4% isolated bogs and 43% peat plateaus (Chasmer et al. 2011), although Scotty Creek is a dynamic peatland mosaic and these ratios are changing.

2.2.2 Experimental design

Using the orthorectified LiDAR DEM data acquired on the 1 October 2010 from WorldView2, 30 wetlands were selected before fieldwork began. Of these wetlands: 10 were fully connected, 10 were ephemerally connected, and 10 were completely isolated

from surface water interactions. Because treed permafrost plateaus surround areas where permafrost is absent, it is possible to see the level of connection using remote sensing data. However once ground truthing was performed in 2012 only seven of the 10 isolated wetlands were completely isolated and met the criteria for this study. Therefore, only 27 total sites were sampled. From the remote sensing data, all the sites were thought to be bogs, however based on water chemistry and species composition it was determined that rich fens, poor fens, and collapse scar bogs were sampled (National Wetlands Working Group 1997). No isolated rich or poor fens were found. At each of these sampling sites, five one meter square quadrats were established (one for each of the cardinal directions as well as one at the center) (Appendix 2.1). The distance of each quadrat from the center was randomly determined based on the maximum diameter of each site.

2.2.3 Field measurements

At each quadrat vascular and non-vascular plants were identified to species level using flora for Northwestern North America (Hulten 1968; Porsild and Cody 1980; Johnson et al. 1995; Vitt et al. 2007). Herbarium voucher specimens are stored in the Wilfrid Laurier University Herbarium and voucher numbers for all species collected can be found in the Appendix 2.2. Species abundance was recorded and verified at three points in the summer (mid-June, as well as beginning and end of July); the abundance that was used for analysis was the final recorded data from the end of July. In addition, woody shrubs were counted and recorded in height categories (0-50 cm, 50-100 cm, 150-200 cm, 200+ cm) to examine structural differences among wetlands. Pictures were taken at each of these quadrats, along with field observations including: GPS coordinate, water table depth, and canopy cover.

2.2.4 Statistical analysis

To examine differences in species composition between quadrats, three sets of Non-Metric Multidimensional Scaling (NMDS) analyses were performed using the Vegan Package (Oksanen et al. 2013) in R. The first NMDS was calculated based on species abundance (% cover) and served to examine species composition. The second looked at shrub structure across sites. The third was a presence/absence NMDS based on the abundance data that was transformed into 1 and 0's; this last NMDS served to see if structure differed from composition.

The data for each of these were standardized; each species column was divided by the maximum abundance value for that species (Jackson 1993). Standardization was required as certain species such as bryophytes had a much greater abundance than vascular species and would skew the analysis (Schuur et al. 2007). For all the NMDS, the Bray-Curtis similarities was used with a $k=3$, which was decided based on a stress test. The stress test examines how many dimensions are necessary to properly explain the data, when the curve falls below a certain point it means that more dimensions would be superfluous, we decided to use <0.2 as the cut off as the values were in the lower range of 0.2, still useable (Clarke 1993) and there was very little difference between the stress of dimension 4 and 5 (Appendix 2.7).

Following this, the abundance NMDS was further tested with a 2 way ANOVA (Analysis of Variance) on the NMDS 1 as it was the primary axis. This was done to test whether the visual differences we saw in the NMDS analysis were statistically significant. The factors were wetland type (rich fen, poor fen, collapse scar bog) and

connectivity (fully connected and ephemerally connected). As it was not a full factorial design, isolated bogs were excluded from the ANOVA. The data met the normality and homogeneity conditions as determined by Shapiro-Wilk and Bartlett test, as well as visual assessment of whether the data met the assumptions. Finally, Tukey HSD test was performed as a post-hoc analysis.

The previous NMDS showed the data for every quadrat, to see if plant composition was similar within one site or within one wetland without the noise from every quadrat; the abundance for each species was summed into one data point that included abundance at all five quadrats for one site. An NMDS was then calculated using these combined site data.

Another important aspect to consider when two adjacent peatlands connect with one another is how similar is their species composition; if within site species variability is high but among site species composition is similar than hydrological connection should not lead to overall changes. If however one site has very homogenous composition amongst its quadrats but very different species composition than the adjacent sites, than connections would have a higher chance of species conversion. Therefore the scores from the abundance NMDS were used to calculate variance between the 5 quadrats and then between the different sites within one peatland type. Variance by site was then plotted against variance by peatland type.

To minimize the noise from having individual species, and to further visualize patterns within the species communities found at the different wetlands, species were combined into functional groups established by Camill (1999). The total percent

abundance for each functional group was determined at each quadrat. The data was then standardized with the same technique as with the NMDS to reduce the importance of abundant species. Afterwards the mean and standard error for each site was calculated using the abundance at the 5 quadrats.

To examine shrub structure, the number of stems was counted for each of the following size categories (0-50 cm, 50-100 cm, 100-150 cm, 150-200 cm, 200+ cm) and for each of the quadrats. Mean and standard errors were calculated for each wetland type, for each size category. A NMDS was also calculated to test if the shrub structure differed between wetlands.

As one of the main differences between bogs and fens is which types of moss are present, linear regressions were performed using abundance of *Sphagnum* moss and brown moss as predictors of other functional groups. For the regression between brown moss and *Sphagnum* spp., the abundance of brown moss was log transformed to meet the assumptions for the linear regression of homogenous variance and distribution.

To quantify species richness, species accumulation curves were calculated using the `specaccum` function with the random permutation method in R and plotted along with their confidence interval. All curves were compared at the 14th meter mark to have comparative richness. To examine diversity, the Shannon diversity index and the Simpson diversity index were calculated using the `Vegan` package in R (Oksanen et al. 2013), for all three wetland types (see Appendix 2.11 for diversity index calculation). The Shannon-Wiener index was used as it is more sensitive to differences in species community and to minor species, while the Simpson index was used as it is more

sensitive to more abundant species (Risvold and Fonda 2001). First the diversity was calculated at each site (all five quadrats) using the abundance data. This was done for all three indices. Once the diversity was obtained for a site, it was analyzed through a fully factorial, two-way ANOVA with wetland type and degree of connectivity as the main effects and their interaction. Assumptions of normality and homogeneity were tested using the Shapiro-Wilk test and the Bartlett test, as well as visually. Post hoc analysis was conducted using Tukey HSD tests.

After determining the richness for each of the peatland sites, it was necessary to know if the sites were becoming fully connected or if they had lost hydrological connection. We were thus able to see if the peatlands were going through allogenic succession or autogenic succession. At Scotty Creek, permafrost plateaus surround the bogs and fens, plateaus being treed it is possible to have a clear outline of where the edges of the bogs and fens are based on the presence of *Picea mariana*. Therefore, if the permafrost thaws the trees on the edges will also die and if there's aggradation of permafrost the trees will be able to colonize. We can therefore see how much a bog has expanded or shrunk based on the presence of the permafrost plateau that have been photographed using aerial imagery. To do this, polygons were created from both the 1977 aerial photos of the site and the 2010 LiDAR DEM data. The contours of each wetland site were traced along the forest edge and the area calculated in ArcGIS. The ratio between site extent in 1977 and in 2010 was then obtained and errors calculated.

To test for allogenic changes, a table was created listing all the unexpected species by wetland type. Species that are found outside of their expected habitat can be an indication that some change is happening within these environments. The flora of North

America, the e-flora of BC and PeatNet were used in order to determine which habitat was considered to be expected (Flora of North America Editorial Committee 1993; Vitt et al. 2011; Klinkenberg 2013). Once unexpected species were identified the ratio was calculated between observed species and unexpected species for each type of bog (isolated, ephemerally connected and fully connected) and plotted as mean and standard error per degree of connectivity and peatland type. These differences were then analyzed with a Kruskal-Wallis analysis, as they did not meet the assumptions of an ANOVA.

2.3 Results

2.3.1 Species composition in boreal wetlands

2.3.1.1 Species composition

The different species found at Scotty Creek were divided into functional groups to visualize species composition by wetland type. There is a progressive transition from aquatic, lawn and hummock *Sphagnum* spp. in the bogs, to hummock and lawn *Sphagnum* spp. and aquatic brown mosses in poor fens, to predominantly aquatic and hummock brown mosses in the rich fen (Fig 2.3a). There is an increase in emergent forb abundance going from collapse scar bogs, to poor and rich fens. The marsh, located at the opening of the fully connected collapse scar bog had a great abundance of aquatic forbs, as well as sedge species (Fig.2.3d). Ericoids are generalists and are found in all the different wetland types, whereas trees and deciduous shrubs become most abundant in the rich fens (Fig. 2.3c). This corroborated with the shrub structure analysis which showed that rich fens had the highest number of stems above 50 cm and were the only sites to have any stems higher than 100 cm (Fig. 2.4). Most lichens are found in the poor fen with

the exception of the connected collapse scars and the fully connected rich fen, which also have a small abundance of lichens (Fig. 2.3b).

Examining the relationships between these different functional groups, there is an overall negative trend between the proportional abundance of *Sphagnum* spp. and that of brown mosses and emergent forbs, while brown mosses had a positive relationship with emergent herbs (Fig 2.5).

To test the significance of the patterns in species functional group and see if these patterns were also correlated to hydrological connectivity, a NMDS was performed. There is a significant separation among the three wetland types: rich fen, poor fen and collapse scar bogs (Fig 2.6). However, no significant difference was found between the different levels of connection.

Another NMDS was performed on presence/absence data to see if there was a difference in structure as well as in composition. In this NMDS the poor fen and the collapse scar bogs sites merged together, whereas the rich fen species were still clearly separate (Appendix 2.8). This indicates that species abundance rather than composition drives differences between poor fens and bogs.

Examining variance among sites and wetlands, fully connected rich fens had high variance in species composition among other rich fen sites, being the only wetland type to have more variance among wetlands (other fully connected rich fens) than among the different quadrats within a site. This suggests that there is substantial landscape variation in the fully connected fen vegetation community. This was not the case for ephemerally connected rich fens, which were closer in species composition among than within sites

suggesting that species variation was largely driven by environmental gradient within a wetland (Appendix 2.10). Meanwhile poor fens and bogs sites clustered, with isolated bogs having very little variation among quadrats or wetlands. In other words, bogs were very homogenous in their species composition both within and among wetlands.

2.3.1.2 *Species richness*

Richness and diversity were quantified to assess the contribution of hydrological connection to these diversity indices, as the results from the NMDS indicated that there was no role of hydrological connectivity in determining vegetation community composition and structure. There was a difference in diversity based on wetland type (Table 2.1). The Shannon index demonstrated that fully connected rich fens had the highest diversity and collapse scar bogs the lowest, with the poor fen intermediate in diversity (Tukey's HSD test: poor fen-rich fen $p=0.026$, poor fen-collapse scar $p=0.009$, rich fen-collapse scar $p<0.0001$). There were very few differences driven by hydrological connectivity. The Shannon index showed a marginal difference between fully connected and ephemerally connected rich fens ($p=0.064$), which was also the case for the Simpson inverse index ($p=0.04$). The Simpson index found a marginal difference between fully connected collapse scar bogs and ephemerally connected ones ($p=0.065$).

Differences became more apparent when species richness was examined (Fig 2.7). As was the case for the NMDS, species richness varied among wetland types, with rich fens having the highest species richness and the collapse scar bogs the lowest richness. But there was also a difference in connectivity, where rich fens showed the most response, with the fully connected fens having 16 species more than the ephemerally connected fens and the connected fens over ten species more than the isolated bogs. Poor

fens and bogs, however, showed no differences between their fully connected and their ephemerally connected sites. Although there was more of a difference between isolated and fully connected/ephemerally connected curves, there was still a lot of overlap.

2.3.2 Identify changes in successional pathways and species community

2.3.2.1 *Autogenic succession*

The previous question established that there was indeed a difference in species composition among wetland types. However, it is important to relate these differences back to ecological pathways. Originally it was expected that fully connected wetlands would differ from ephemerally connected ones because of altered hydrological inputs. This was not the case for plant species community composition or structure; however there was an increase in richness attributable to increased connectivity for rich fens. To further explore the mechanism behind this change in richness aerial photos from 1977 were compared with recent remote sensing data from 2010 (Fig. 2.9). What was found was that the fully connected rich fens examined had a larger extent in 1977 than in 2010. This is not the case for bogs, which have been increasing in area due to permafrost thaw (Fig 2.10). Generally, it was found that both poor fen and rich fens in question are shrinking in area. This is indicative of wetlands as expected through autogenic succession, where *Sphagnum* hummocks are cutting off groundwater sources and leading to smaller areas, but could also potentially be leading to reforestation.

2.3.2.2 *Allogenic changes*

While the NMDS analysis did not detect a difference in community composition or structure between the different levels of connection (Fig. 2.6), there were some notable

species occurrences indicative of the beginning of compositional changes. Specifically, unexpected species were found in bogs, these species all belonging normally in a rich fen. By examining the distribution of those species most were found in fully connected bogs (although this difference was not statistically significant), this to the exception of one isolated site which had a very high proportion of rich fen species and a higher pH. These factors and the sites position in the NMDS (Appendix 2.9) lead to the conclusion that it was in fact an isolated poor fen and not an isolated bog (Fig. 2.11). The species outside their habitat for the collapse scar bogs were usually rich fen brown mosses, as well as one marsh species *Utricularia intermedia*.

2.4 Discussion

In this chapter, I demonstrate that bogs, fens and poor fens have very distinct species communities, which is most evident in the type of bryophytes and shrubs that are present in each, as well as the lower diversity in bogs particularly when compared with fens. Although no difference was found in species community composition attributable to different levels of hydrological connectivity, there was a difference in richness where fully connected rich fens had over 16 more species than the ephemerally connected ones. Bogs and poor fens were very resilient to changes in richness with increased connectivity, bogs showing no difference in number of species between fully connected and ephemerally connected and poor fens only a difference of 5 species.

In this chapter, I also examine successional pathways. Ephemerally connected rich fens in this study have been shrinking since 1977 as the wetlands have become more isolated with forest expansion. In contrast, bogs have been expanding due to increased rates of permafrost thaw and conversion of permafrost plateaus to bogs. While no

statistical difference in community was measured, many rich fen species were found in fully connected bogs, which could be a sign of the initiation of allogenic successional processes.

2.4.1 Species community in boreal peatlands

The NMDS analysis in this study showed a clear separation by wetland types, where each wetland had its own distinct species community composition and structure. Along with the presence of key indicator species, this separation supports the wetland classification that was assigned to the different sites. In line with what Beilman (2001) and Andersen (2011) found, the main difference between the flora from bogs and those from poor fens were in the abundance rather than in the composition of species. In contrast, rich fens support a very distinct community when compared with the other two wetlands. One of the most notable differences in species composition comes from the bryophytes, where there is a progression from an abundance of aquatic *Sphagnum* spp. in the bogs, to increases in hummock *Sphagnum* spp. in the poor fen, to a brown moss-dominated community in the rich fen. This is consistent with the findings of Locky & Bayley (2006) who showed that brown mosses were present in minerotrophic peatlands and *Sphagnum* spp. in oligotrophic ones. The presence of *Sphagnum* spp. is negatively correlated to presence of other functional groups such as forbs, shrubs and trees; therefore bogs, which are dominated by *Sphagnum* spp., tend to be very species poor. This is most likely due to *Sphagnum* spp. engineering their environment in order to make it more acidic and less hospitable to other species (Clymo 1963).

Rich fens supported a great diversity of shrubs, brown mosses, emergent forbs and trees. Fens are thought to have greater variability in their flora but also in their water chemistry (Vitt et al. 2009), this leads to a higher variability among fens compared to the poor fen and the collapse scar bogs that were clumped together and are more homogenous in their composition.

2.4.2 Species richness in boreal peatlands

While there were no clear differences in species composition attributable to hydrological connectivity, species richness was impacted by hydrological connection for rich fens. We expected this result as it fits with our autogenic succession model, where a decrease in connection can lead to changes in water chemistry. However, bogs remained extremely resilient to increased connection, which was unexpected. Some of the reason bogs could be so resilient is the same reason why their richness is the lowest. Bogs are populated by *Sphagnum* spp. which will engineer their environment: increasing acidity, altering water relations and capturing and immobilizing nutrients (Malmer et al. 2003). This genus is more resistant to environmental changes than other mosses (Lang et al. 2009) and good at surviving in nutrient rich conditions (Hotes et al. 2010).

2.4.3 Autogenic succession in a rich fen

After considering the loss of richness between ephemerally connected rich fens and fully connected ones it was necessary to confirm if they were becoming further connected through allogenic succession attributable to permafrost thaw (going from ephemerally to fully connected) or following the normal autogenic pathway (going from fully to ephemerally connected). Comparison of wetland extent between historical and

current day aerial imagery indicated that the ephemerally connected rich fens are reducing in size and slowly becoming isolated as the areas surrounding them are becoming reforested (Fig. 2.9). This could be an indication of normal autogenic succession that, coupled with the loss of richness, seems to indicate that the rich fens are converting into bogs. However, a loss of area could also be caused by the fens draining their water into the larger fen, this would allow trees and shrubs to regrow and look like the fens are shrinking through remote sensing. If the rich fens are becoming drier, this could make them more vulnerable to change (Turetsky et al. 2012). Further work is necessary to determine if the fens are becoming drained, if there's been an increased presence of trees in the last few years and finally if this is seen at other sites at Scotty Creek.

2.4.4 Allogenic succession in a fully connected collapse scar bog

Does permafrost thaw lead to allogenic succession? It is difficult to separate the effects of allogenic and autogenic succession. Simply looking at the NMDS it would seem as though there is no difference between fully connected and ephemerally connected wetlands. However by examining species that do not belong in their respective habitat, we can gain some perspective regarding changes in these communities. Most changes were found in poor fens, which is normal as they are transition sites. Their pH being between 5 and 6 they are extremely sensitive to acidification (Wetzel 2001), therefore it should be expected that they have both rich fen species from their original state and bog species from their stable-state community. However, when species that are normally only found in nutrient rich areas such as *Scorpidium scorpioides* (Kooijman 1992) are found in bogs, this could be a sign that there is an increase in nutrients and that

allogenic succession could be happening, reverting a bog into a fen community. The average for unexpected species is higher in fully connected bogs, which supports our initial theory, but this difference wasn't statistically significant. Nutrients are drivers of change in these systems both for fens and bogs (Andersen et al. 2011), if there is enough rich water input the ombrotrophy can be reversed (Hughes and Dumayne-Peaty 2002). We hypothesize that it may be a question of thresholds and that presently nutrient inputs attributable to permafrost thaw have not been sufficient to drive comprehensive change in the species composition or that insufficient time has passed to facilitate this transition. Another hypothesis is that permafrost thaw and hydrological changes may be happening faster than plant community can keep up.

2.5 Conclusion

We found that species community differs greatly among wetland types, rich fens having a higher richness than bogs. Rich fens are also more susceptible to changes in hydrological connection and this could be caused by autogenic succession turning the ephemerally connected rich fens into bogs or rich fens reducing in size due to reforestation. Evidence has been found of allogenic succession in fully connected collapse scar bogs but the mechanism for how these rich fen species are being found in these bogs remains unclear.

The clear distinction between the different wetland communities is in agreement with northern plant communities having low functional redundancy (Chapin et al. 1995; Turetsky et al. 2012). If permafrost thaw leads to a change in peatland type (from a bog to a fen) this could have a significant effect on the overall species diversity given the very different species composition in these wetlands. Such effects could alter the

biogeochemistry (Kooijman and Hedenäs 2009), decomposition (Camill 1999b), primary productivity (Johansson et al. 2006), carbon sequestration and surface energy budgets of these systems (Camill 2005). It could also lead to the conversion of wetland communities, which in turn would result in changing plant community composition and ecosystem function.

2.6 Acknowledgements

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Table 2.1: Average mean and standard error measurement (SEM) of the species diversity indices found across the three wetland types (rich fen, poor fen and collapse scar bog) and the three connection types (fully connected, ephemerally connected, isolated). A two-way ANOVA between sites was completed for the rich fen, poor fen and collapse scar, omitting isolated sites. Letters indicate where there is significance ($\alpha < 0.05$), letters in italics were marginally significant ($\alpha < 0.07$). Richness (\pm confidence interval) was also added using the data taken off the species accumulation curves (Fig 2.7).

	Rich fen-Fully connected	Rich fen- Connected	Poor fen-Fully connected	Poor fen- Connected	Collapse scar- Fully connected	Collapse scar- Connected	Isolated
Shannon index	2.26 ± 0.05 ^{ad}	1.95 ± 0.08 ^{bd}	1.9 ± 0.08 ^a	1.78 ± 0.04 ^c	1.52 ± 0.05 ^a	1.39 ± 0.09 ^{bc}	1.14 ± 0.12
Simpson index	0.86 ± 0.01	0.79 ± 0.03 ^a	0.81 ± 0.02 ^b	0.75 ± 0.02 ^c	0.69 ± 0.03 ^{bd}	0.57 ± 0.04 ^{cade}	0.56 ± 0.05 ^e
Simpson inverse index	7.42 ± 0.45 ^{ab}	5.30 ± 0.49 ^b	5.69 ± 0.6 ^c	4.75 ± 0.27	3.86 ± 0.35 ^{acd}	3.79 ± 0.41	2.62 ± 0.31 ^d
Species richness	54.93 ± 2	38.53 ± 1	47.53 ± 2	42.73 ± 7	34.35 ± 10	33.93 ± 2	25.43 ± 6

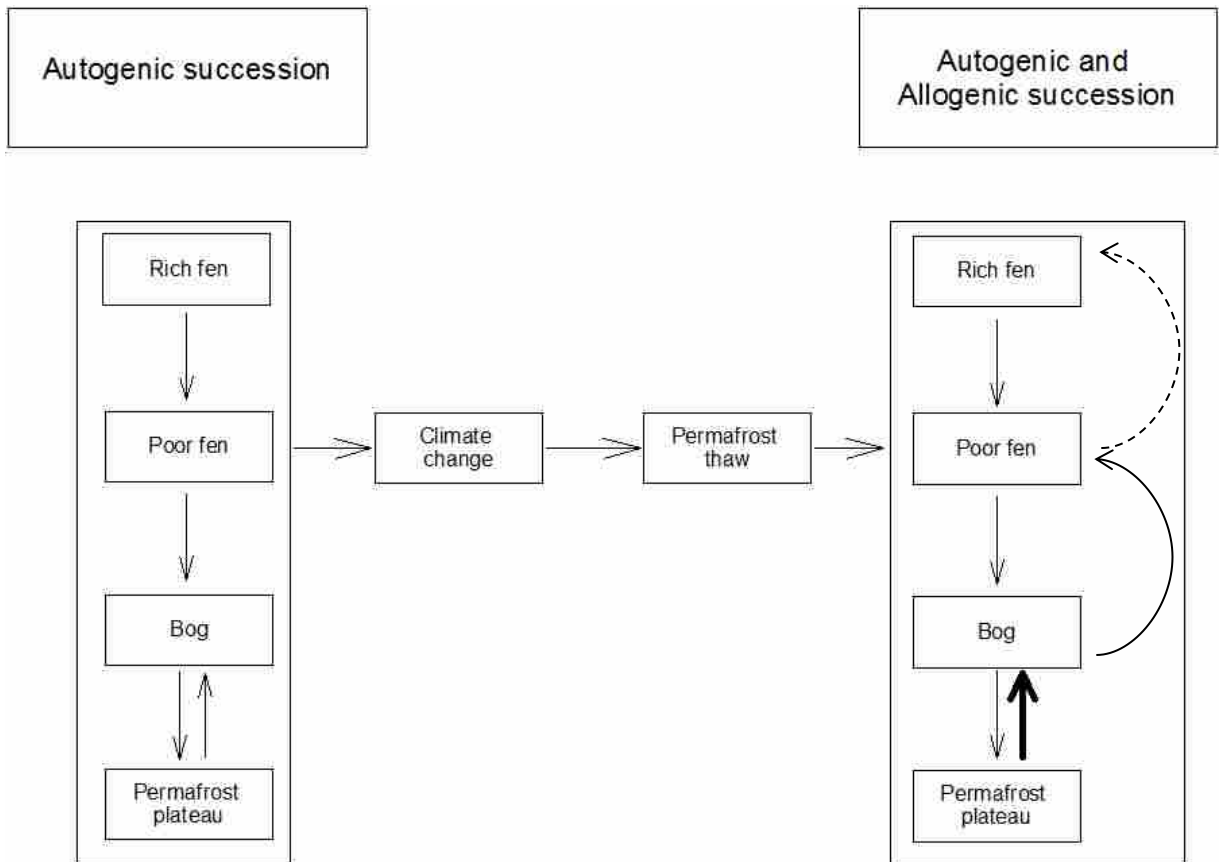


Figure 2.1: Successional pathway described following both autogenic and allogenic succession. In the normal autogenic succession a rich fen will turn into a bog through reduction in nutrient rich water sources. In a permafrost landscape a bog can turn into a permafrost plateau when sufficient insulation has built up or the permafrost plateau can collapse into a bog due to permafrost thaw. These two processes are normally balanced. With increased temperatures, we expect to see an increase in permafrost thaw. We hypothesize that this will reverse the normal autogenic processes, returning nutrient rich waters and reverting a bog back into a fen, due to the increased hydrological connections between peatlands. We also expect to see an increase in permafrost plateau degradation.

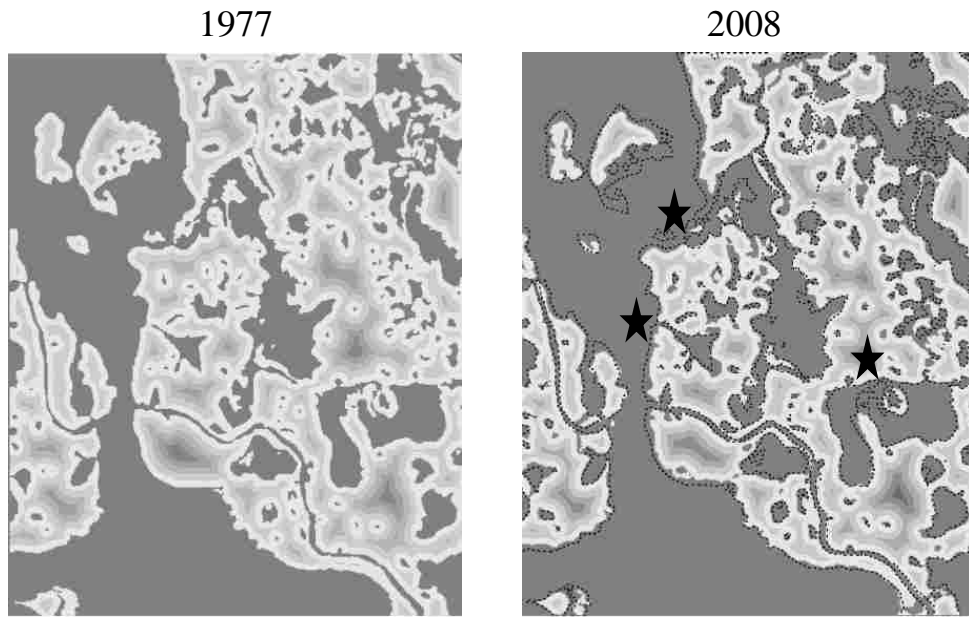


Figure 2.2: Permafrost plateau thaw between 1977 and 2008. Stars indicate areas that have shown extensive thaw, while the dotted line in the 2008 figure represents the 1977 extent of permafrost. (Credit W. Quinton)

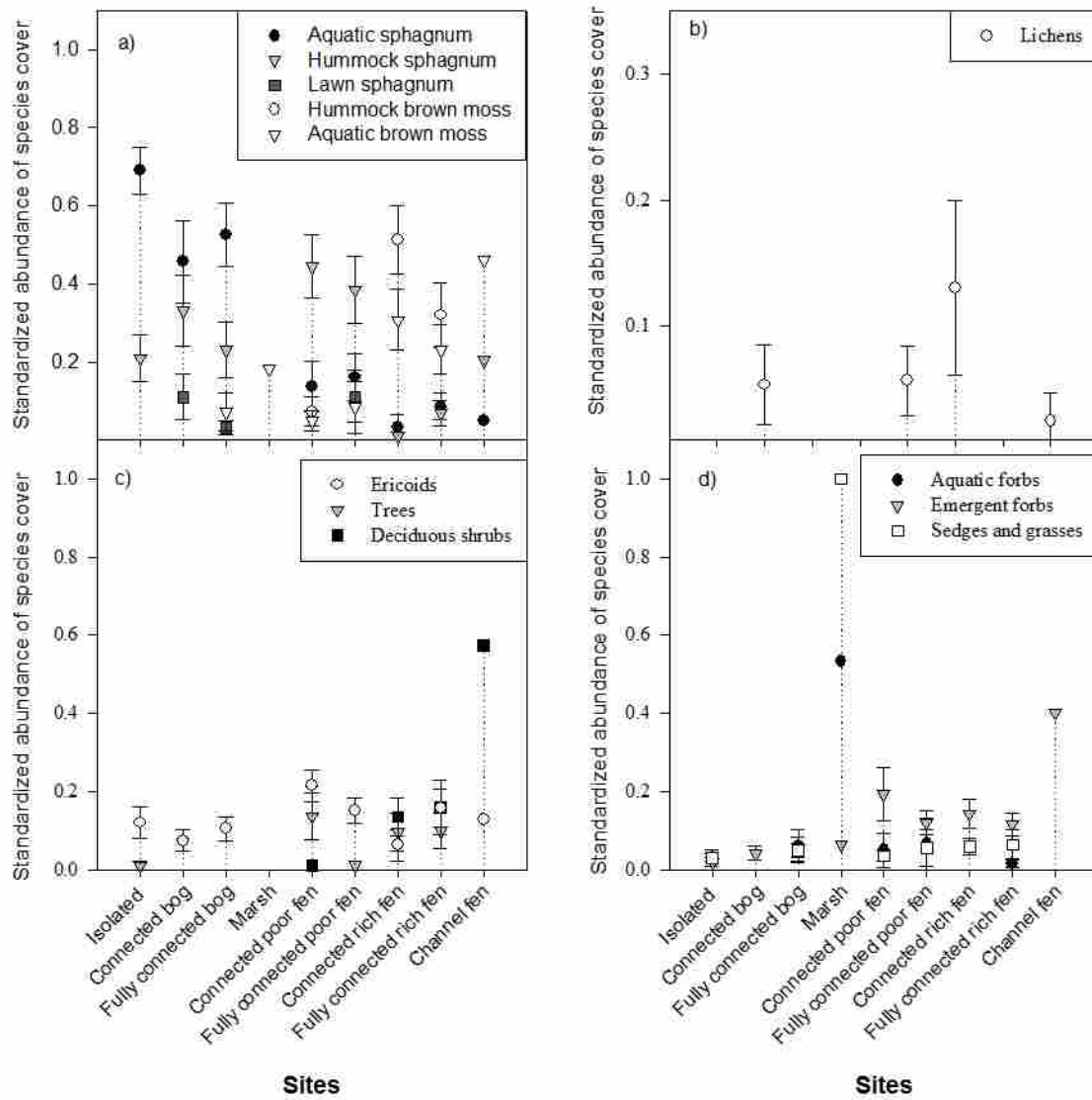


Figure 2.3: Standardized abundance (+/- SEM) of species found at Scotty Creek at their different sites and their different functional groups. a) Bryophyte abundance (aquatic *Sphagnum*, hummock and lawn spp., hummock and aquatic brown mosses) b) Lichen abundance c) Ericoids, trees and deciduous shrub abundance d) Aquatic and emergent forbs, sedges and grasses abundance

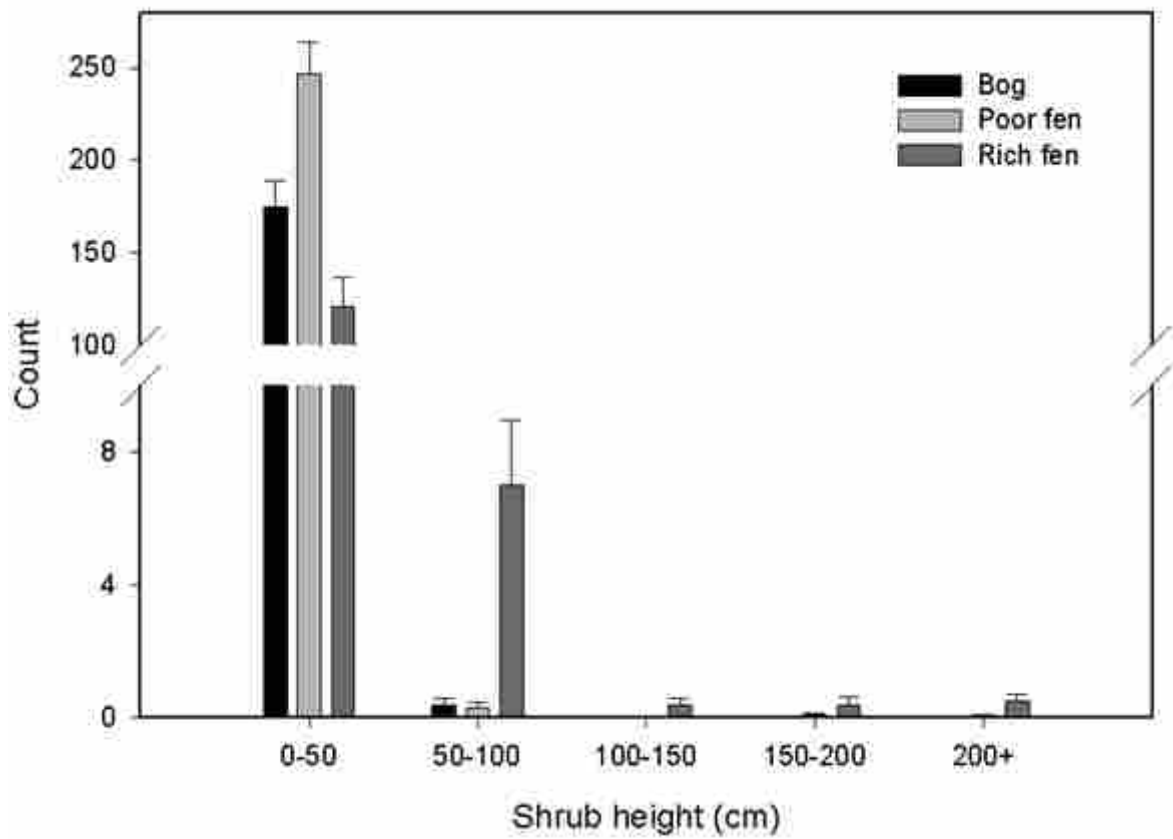


Figure 2.4: Mean shrub structure (+/- SEM) of sites divided by size category and wetland type. A scale break was used for the 0-50 cm category to clearly see the other categories that had much smaller value. An NMDS was done on shrub structure and found a significant difference between rich fen species community and poor fens/bog species community.

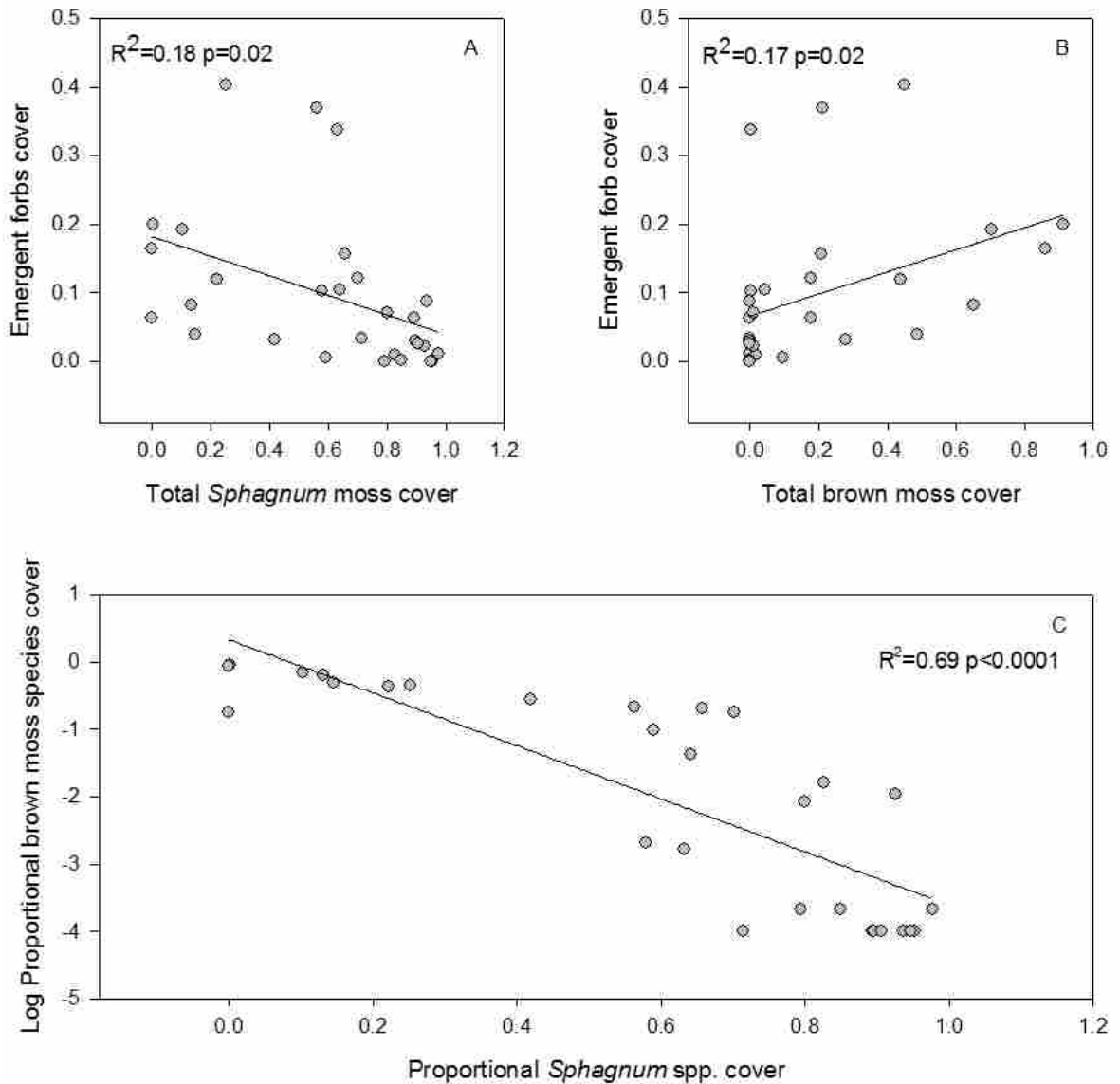


Figure 2.5: Linear regression of relationship among functional groups found at Scotty Creek. Panel A and B met assumptions for equal variance and homogenous distribution, while panel C) had to be log transformed. A) Proportional *Sphagnum* spp. with emergent forb cover B) Proportional brown moss cover with emergent forb cover C) Proportional *Sphagnum* spp. cover with log brown moss cover. Data represents mean abundance of the 5 quadrats at each site. *Sphagnum* spp. includes the species found within these functional groups: lawn, hummock and aquatic. Brown moss cover includes: hummock and aquatic species. Total herb cover includes: emergent forbs, sedges and grasses and aquatic forbs species.

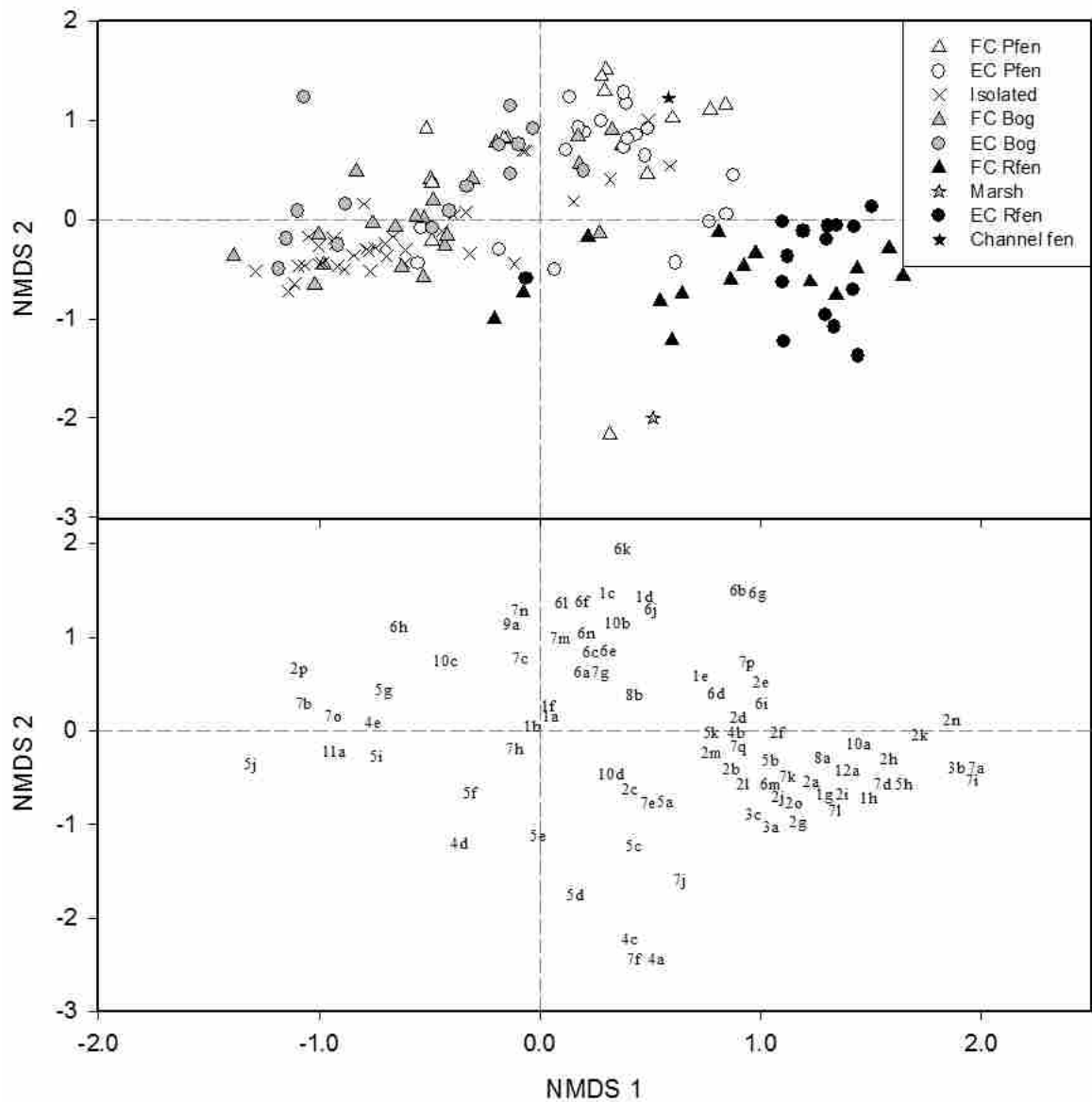


Figure 2.6: Panel a) is a NMDS based on the abundance of plant species of all sites, $k=3$, Bray-Curtis ordination, $p<0.001$ between the different wetland types. Panel b) represent the species map of the NMDS in panel a). 1=Ericoid, 2=Aquatic brown mosses 3=Deciduous shrubs 4=Forb-aquatic 5=Sedge and grass 6=Lichens 7=Emergent forbs 8=Trees 9=Lawn *Sphagnum* 10=Hummock *Sphagnum* 11= *Sphagnum* aquatic and 12=Brown moss hummock. Letters next to the numbers in panel b) refer to specific species and can be found in Appendix 2.2.

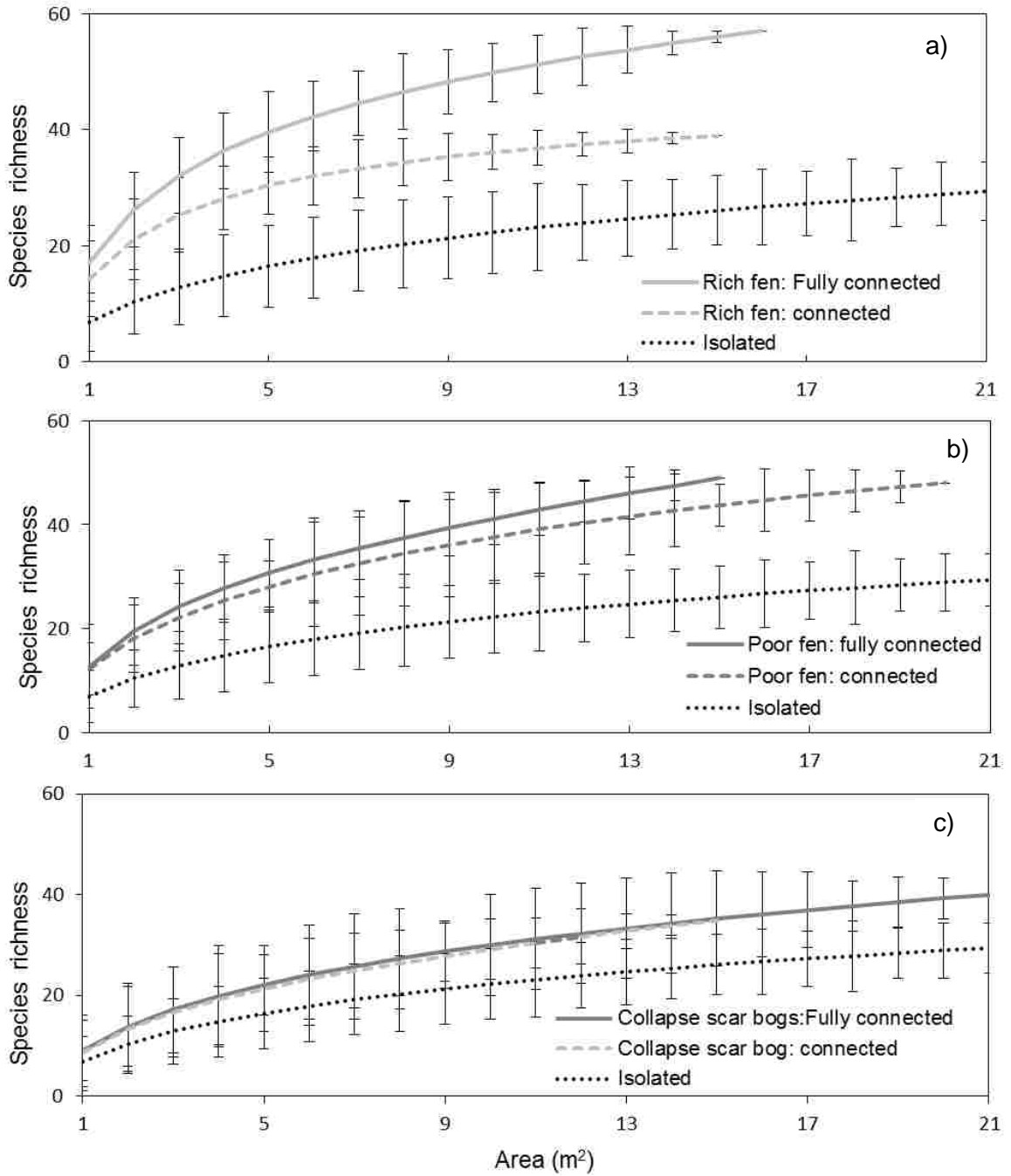


Figure 2.7: Species accumulation curve, depicting species richness per m² in the three wetland types and the three connection types found at Scotty Creek. The confidence intervals from the standard deviation are also depicted.

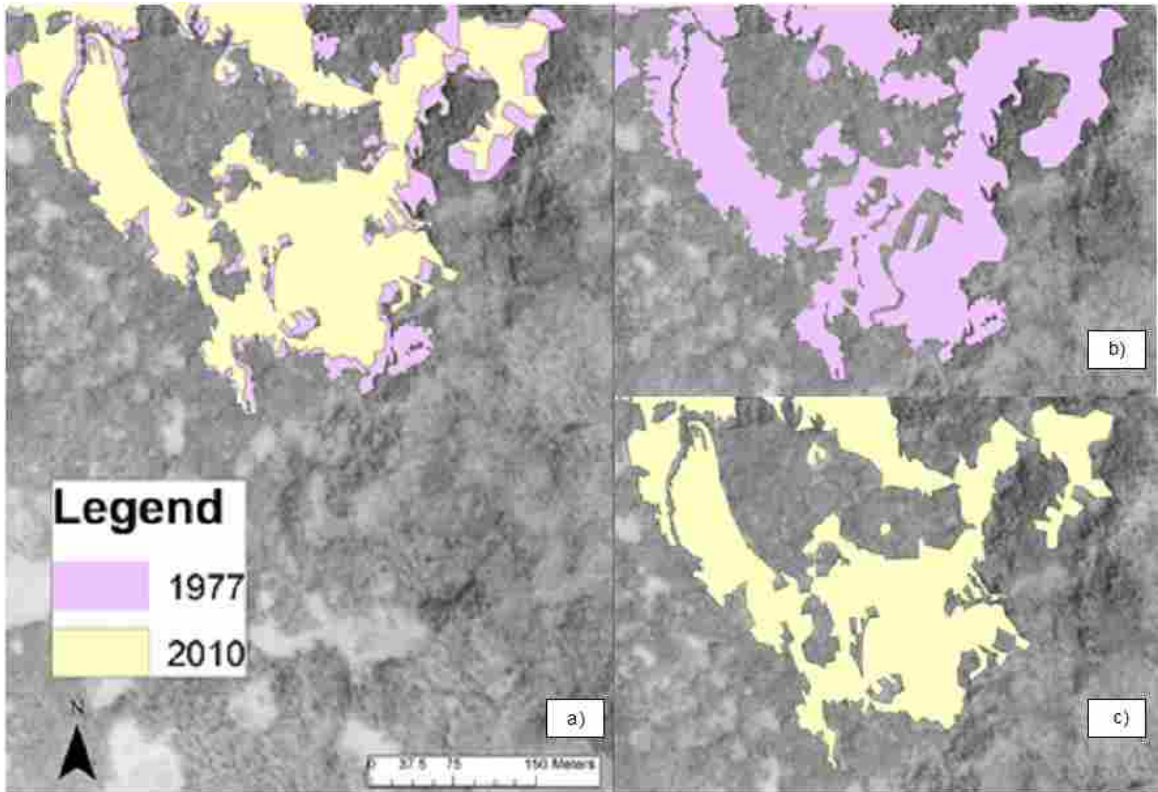


Figure 2.8: Map of the fully connected rich fens at Scotty Creek. Fen extent was obtained by digitalizing the outlines of fens in 1977 and in 2010. This was made possible as the permafrost extent corresponds with the forest extent at this site. The darker shade of purple indicates aerial photo extents from 1977, the lighter or hollow area represents the extents of the fens in 2010.

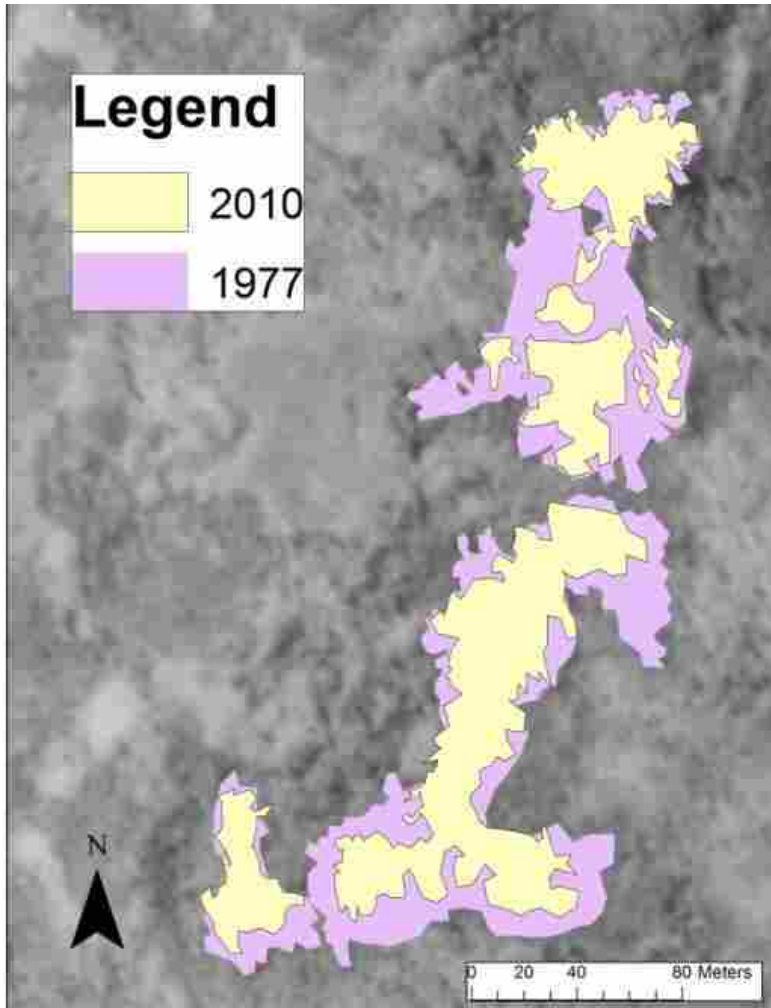


Figure 2.9: Map of the ephemerally connected rich fens at Scotty Creek. These outlines were obtained by digitalizing the outlines of fens in 1977 and in 2010. This was made possible as the permafrost extent corresponds with the forest extent at this site. The darker shade of purple indicates aerial photo extents from 1977, the lighter or hollow area represents the extents of the fens in 2010.

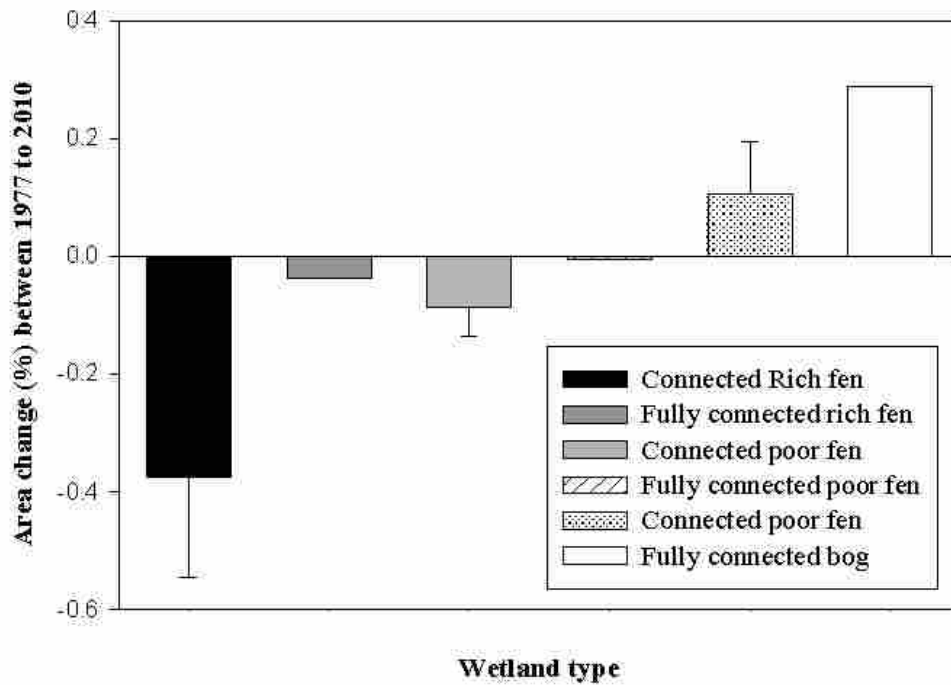


Figure 2.10: Area difference between 2010 and 1977 (+/- SEM) for each of the different wetlands at Scotty Creek.

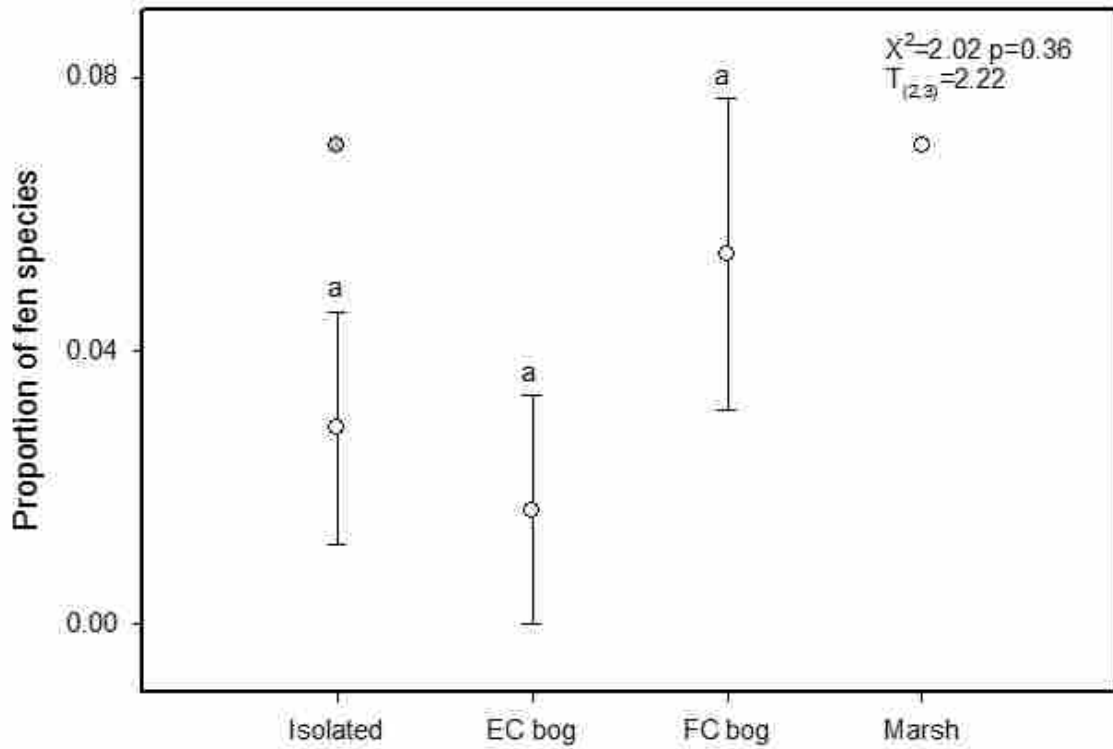
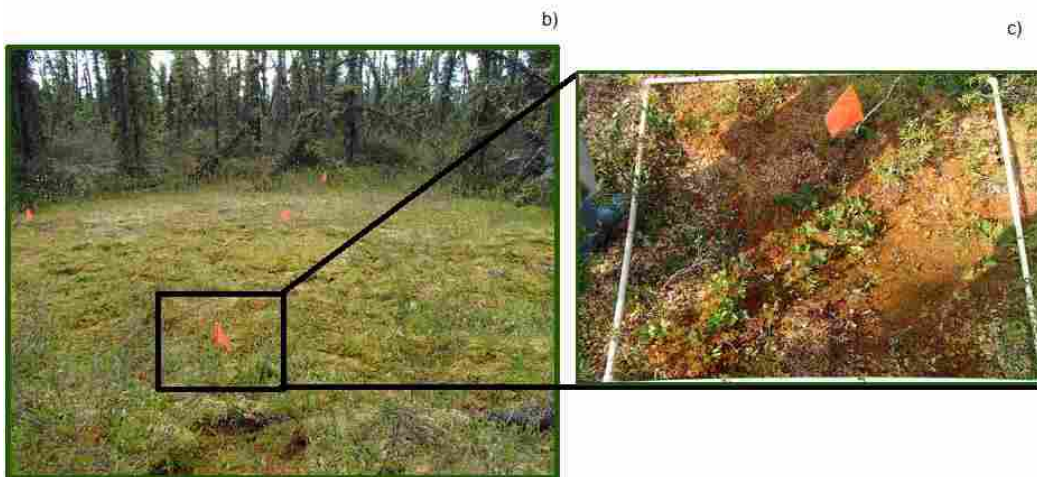
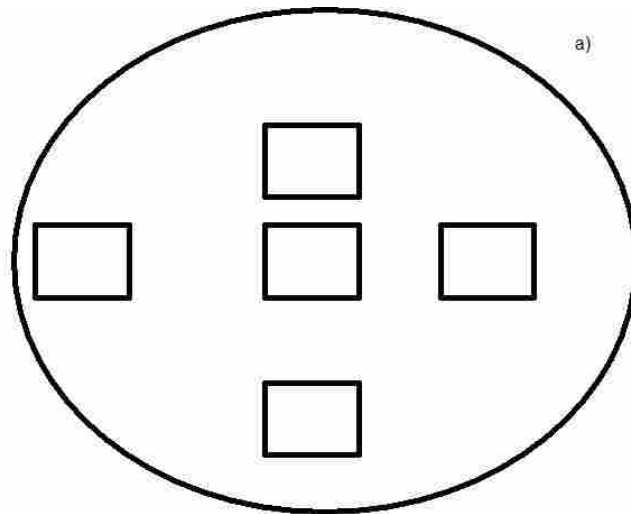


Figure 2.11: Proportion of fen species in the different types of wetlands. Grey circle in isolated category depicts outlier, which was an isolated site whose vegetation was closer to that of a fen than a bog and therefore would normally have a higher proportion of fen species. Kruskal Wallis test performed but no differences were found between any of the categories.

Appendix 2.1: Sampling design, a) main bog with the five quadrats in the cardinal directions randomly placed from the middle b) Photo of one of the sites c) close up of the one meter quadrat



Appendix 2.2: Herbarium and phytoimage references. Species found in Scotty Creek, within the functional groups established by Camill (1999). The number/letters combination corresponds to the identification number of the species from the NMDS species map. Numbers with hashtags indicate the ID number of the species in the Wilfrid Laurier University herbarium, in the Scotty Creek collection. DOL numbers are the reference numbers associated with the species picture at the Phytoimage website (<http://phytoimages.siu.edu/index.html>, keyword: Scotty Creek).

Functional group	Species
Ericoid	<i>Andromeda polifolia</i> (1a, #11, DOL66444, DOL66413, DOL66402, DOL66442), <i>Andromeda calyculata</i> (1b, #7, DOL66357), <i>Kalmia polifolia</i> (1c, #15, DOL66440), <i>Ledum de palustre var. decumbens</i> (1d, #14, DOL66376), <i>Rhododendron groenlandicum</i> (1e, #40, DOL66390, DOL66355), <i>Vaccinium microcarpum</i> (1f, #16, DOL66441, DOL66425), <i>Vaccinium uliginosum</i> (1g, #36, DOL66384), <i>Vaccinium vitis-idaea</i> (1h, #23)
Brown moss-Aquatic	<i>Aulacomnium palustre</i> (2a, #73, DOL66470), <i>Calliergon giganteum</i> (2b, #72, #95, DOL66416, DOL66389), <i>Calliergon stramineum</i> (2c, #84, DOL66458), <i>Campylium stellatum</i> (2d), <i>Dicranum fragiliifolium</i> (2e, #86), <i>Dicranum undulatum</i> (2f, #97), <i>Drepanocladus aduncus</i> (2g, #75, DOL66454), <i>Sanionia uncinata</i> (2h, #82, DOL66393), <i>Hylocomium splendens</i> (2i, #74, DOL66388), <i>Paludella squarrosa</i> (2j, #83, DOL66373), <i>Platydictya jungermannoides</i> (2k, #79, DOL66420), <i>Polytrichum juniperinum</i> (2l), <i>Polytrichum strictum</i> (2m, #88, DOL66434), <i>Pylaisiella polyantha</i> (2n, #80), <i>Plagiomnium ellipticum</i> (2o, #76, DOL66411), <i>Scorpius scorpioides</i> (2p, #81, DOL66350)
Deciduous shrub	<i>Betula glandulosa</i> (3a, #4, DOL66401, DOL66380), <i>Salix bebbiana</i> (3b, DOL66455), <i>Salix pedicellaris</i> (3c, #1, DOL66365, DOL66378, DOL66356, DOL66451, DOL66395)
Forb-Aquatic	<i>Calla palustris</i> (4a, #17, DOL66359), <i>Lemna minor</i> (4b), <i>Lemna Trisulca</i> (4c), <i>Menyanthes trifoliata</i> (4d, #27, DOL66439, DOL66445), <i>Utricularia intermedia</i> (4e, #12)
Sedge and grass	<i>Carex disperma</i> (5a, #34, DOL66428), <i>Carex gynocrates</i> (5b, #32, DOL66399), <i>Carex lenticularis var. lipocarpa</i> (5c, #18), <i>Carex limosa</i> (5d, #25, DOL66386), <i>Carex microptera</i> (5e, #33, DOL66463), <i>Carex utriculata</i> (5f, #38, DOL66417), <i>Eriophorum brachyanterum</i> (5g, #20, DOL66464), <i>Danthonia intermedia</i> (5h, #56), <i>Eriophorum viridicarinatum</i> (5i, #8, DOL66426, DOL66379), <i>Eriophorum vaginatum</i> (5j, #19, DOL66407), <i>Trichophorum alpinum</i> (5k, #41, DOL66391, DOL66409)
Lichen and liverwort	<i>Cetraria icelandica</i> (6a), <i>Cladina fragilis</i> (6b), <i>Cladina mitis</i> (6c, #99, DOL66396), <i>Cladina rangifera</i> (6d, #100, DOL66419), <i>Cladonia borealis</i> (6e, #101, DOL66374), <i>Cladonia chlorophaea</i> (6f, #102), <i>Cladonia cornuta</i> (6g, #103), <i>Cladonia gracilis</i> (6h, #104,

	DOL66353), <i>Cladonia verticillata</i> (6i, #105), <i>Flavocentraria nivalis</i> (6j, #106, DOL66438), <i>Icmadophila ericetorum</i> (6k, #68, DOL66364), <i>Leiomylia anomala</i> (6l, #71, DOL66431), <i>Peltigera aptosa</i> (6m, #69), <i>Lophozia ventricosa</i> (6n, #67, #92)
Forb-emergent	<i>Cornus canadensis</i> (7a, #59, DOL66429), <i>Droseratum anglica</i> (7b, #39, #43, DOL66392, DOL66368), <i>Drosera rotundifolia</i> (7c, #9, DOL66370), <i>Equisetum fluviatile</i> (7d, #10, DOL66358), <i>Equisetum palustre</i> (7e, #13), <i>Galium trifidum</i> (7f, #24), <i>Geocaulon lividum</i> (7g, #28, DOL66466, DOL66400, DOL66450), <i>Maianthemum trifolium</i> (7h, #5, #54, DOL66375, DOL66361), <i>Pedicularis sp</i> (7i, #21), <i>Comarum palustre</i> (7j, #46), <i>Pyrola asarifolia</i> (7k, #37, DOL66360, DOL66363), <i>Rubus arcticus</i> (7l, #47, DOL66381), <i>Rubus chamaemorus</i> (7m, #3, #52, DOL66447, DOL66460), <i>Sarracenia purpurea</i> (7n, #44, DOL66446, DOL66404), <i>Scheuchzeria palustris</i> (7o, #26, #45, DOL66405), <i>Spiranthes romanzoffiana</i> (7p, #29, #42, DOL66352), <i>Triglochin maritime</i> (7q, DOL66452)
Trees	<i>Larix laricina</i> (8a, #60, DOL66397), <i>Picea mariana</i> (8b, DOL66415, DOL66351)
Sphagnum-Lawn	<i>Sphagnum angustifolium</i> (9a, #70, #94, #93, DOL66427, DOL66354)
Sphagnum-Hummock	<i>Sphagnum capillifolium</i> (10a, #66), <i>Sphagnum fuscum</i> (10b, #78, DOL66430, DOL66410), <i>Sphagnum magellanicum</i> (10c, #87, #96, DOL66398, DOL66461), <i>Sphagnum warnstorffii</i> (10d, #85, DOL66435)
Sphagnum-Aquatic	<i>Sphagnum riparium</i> (11a, #65, #89, #90, #91, DOL66453)
Brown moss-Hummock	<i>Tomentypnum nitens</i> (12a, #77, DOL66377)

Appendix 2.3: Species composition that fit the expected habitat of the different wetlands found within the sampling area of Scotty Creek

Wetlands	<i>Species composition</i>
Rich fen	<p>Sphagnum sp: <i>Sphagnum warnstorffii</i></p> <p>Brown mosses: <i>Tomenthypnum nitens</i>, <i>Calliergon giganteum</i>, <i>Aulacomnium palustre</i>, <i>Dicranum fragiliifolium</i>, <i>Drepanocladus aduncus</i>, <i>Sanionia uncinata</i>, <i>Paludella squarrosa</i>, <i>Platydictya jungermannoides</i>, <i>Polytrichum juniperinum</i>, <i>Polytrichum strictum</i>, <i>Pylaisiella polyantha</i>, <i>Plagiomnium ellipticum</i>,</p> <p>Sedges and grass: <i>Carex disperma</i>, <i>Carex gynocrates</i>, <i>Carex utriculata</i>, <i>Danthonia intermedia</i></p> <p>Forbs emegent: <i>Cornus canadensis</i>, <i>Comarum palustre</i>, <i>Pyrola asarifolia</i>, <i>Rubus arcticus</i>, <i>Equisetum fluviatile</i>, <i>Equisetum palustre</i>, <i>Pedicularis spp.</i>,</p> <p>Lichens: <i>Cladina rangifera</i>, <i>Cladonia chlorophaea</i>, <i>Peltigera aptosa</i></p> <p>Deciduous shrubs: <i>Betula glandulosa</i>, <i>Salix bebbiana</i>, <i>Salix pedicellaris</i></p> <p>Ericoids: <i>Vaccinium uliginosum</i>, <i>Vaccinium vitis-idaea</i></p>
Poor fen	<p>Sphagnum spp. <i>Sphagnum magellanicum</i>, <i>Sphagnum angustifolium</i>, <i>Sphagnum riparium</i></p> <p>Brown moss: <i>Aulacomnium palustre</i>, <i>Calliergon giganteum</i>, <i>Dicranum fragiliifolium</i>, <i>Platydictya jungermannoides</i>, <i>Polytrichum strictum</i></p> <p>Sedges: <i>Eriophorum viridicarinatum</i></p> <p>Forbs-emergents: <i>Equisetum fluviatile</i>, <i>Equisetum palustre</i>, <i>Spiranthes romanzoffiana</i>, <i>Triglochin maritime</i>, <i>Comarum palustre</i></p> <p>Forb aquatic: <i>Lemna minor</i></p> <p>Lichens: <i>Cladina fragilis</i>, <i>Cladina mitis</i>, <i>Cladina rangifera</i>, <i>Cladonia borealis</i>, <i>Cladonia chlorophaea</i>, <i>Cladonia cornuta</i>, <i>Cladonia gracilis</i>, <i>Cladonia verticillata</i>, <i>Cetraria icelandica</i>, <i>Flavocentraria nivalis</i>, <i>Icmadophila ericetorum</i>,</p> <p>Deciduous shrubs: <i>Betula glandulosa</i></p> <p>Ericoids: <i>Kalmia polifolia</i>, <i>Ledum de palustre var. decumbens</i>, <i>Andromeda polifolia</i>,</p>
Collapse scar	<p>Sphagnum sp: <i>Sphagnum fuscum</i>, <i>Sphagnum magellanicum</i>, <i>Sphagnum angustifolium</i>, <i>Sphagnum riparium</i></p> <p>Brown moss: <i>Aulacomnium palustre</i></p> <p>Sedges: <i>Eriophorum brachyanterum</i>, <i>Eriophorum vaginatum</i>, <i>Eriophorum viridicarinatum</i>, <i>Carex limosa</i>, <i>Carex utriculata</i></p> <p>Lichens: <i>Cladonia borealis</i>, <i>Cladonia chlorophaea</i></p> <p>Liverwort: <i>Leiomylia anomala</i></p> <p>Eriocoids: <i>Rubus chamaemorus</i>, <i>Andromeda polifolia</i>, <i>Kalmia polifolia</i>,</p> <p>Forbs-emergent: <i>Scheuchzeria palustri</i>, <i>Rubus chamaemorus</i></p> <p>Deciduous shrub: <i>Salix pedicellaris</i></p> <p>Forb-aquatic: <i>Lemna trisulca</i></p> <p>Isolated: <i>Carex disperma</i>, <i>Carex gynocrates</i>, <i>Carex microptera</i>, <i>Eriophorum brachyanterum</i>, <i>Eriophorum vaginatum</i>, <i>Eriophorum viridicarinatum</i>, <i>Kalmia polifolia</i>, <i>Ledum de palustre var. decumbens</i>, <i>Polytrichum strictum</i>, <i>Salix pedicellaris</i>, <i>Scheuchzeria palustri</i>, <i>Sphagnum riparium</i></p>
Generalist	<p>Forbs-emergent: <i>Drosera anglica</i>, <i>Drosera rotundifolia</i>, <i>Geocaulon lividum</i>,</p>

Maianthemum trifolium, Sarracenia purpurea

Forb-aquatic: *Menyanthes trifoliata*

Tree: *Picea mariana, Larix laricina*

Ericoids: *Rhododendron groenlandicum, Andromeda calyculata,*

Brown moss: *Calliergon stramineum, Dicranum undulatum*

Lichen and liverwort: *Lophozia ventricosa,*

Sedges: *Carex lenticularis var. lipocarpa, Trichophorum alpinum*

Marsh

Forb-aquatic: *Calla palustris, Lemna trisulca, Utricularia intermedia*

Forb-emergent: *Galium trifidum, Comarum palustre, Rubus arcticus,*

Sedges: *Carex microptera*

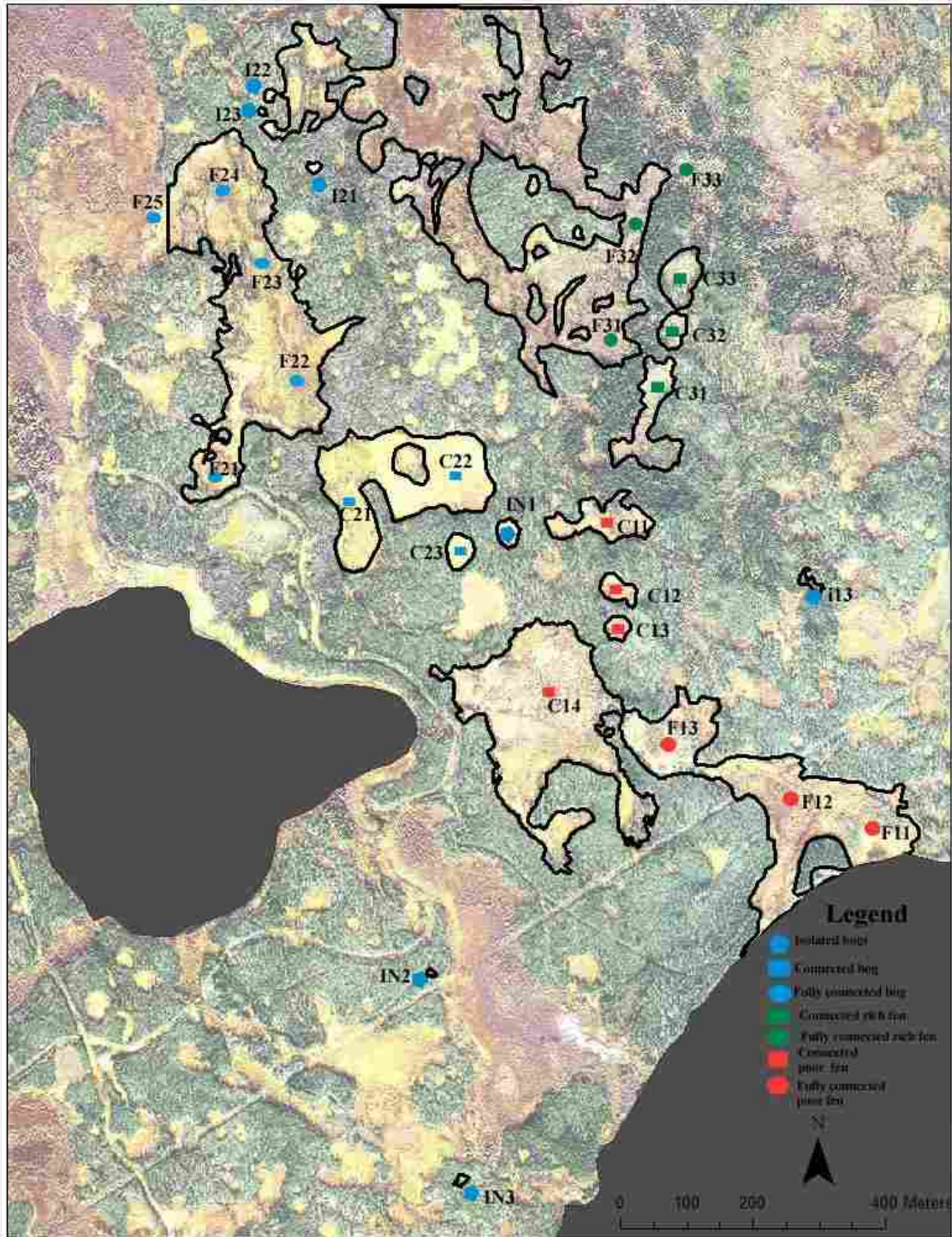
Appendix 2.4: Shrub species by size category at sites found at Scotty Creek

	0-50 cm	50-100 cm	100-150 cm	150-200 cm	200+ cm
Rich fen	<i>Salix pedicellaris</i> , <i>Larix laricina</i> , <i>Betulosa glandulosa</i> , <i>Vaccinium uliginosum</i> , <i>Vaccinium vitis-idea</i> , <i>Rhododendron groenlandicum</i>	<i>Salix pedicellaris</i> , <i>Betulosa glandulosa</i> , <i>Andromeda chamydaphne</i> , <i>Larix laricina</i>	<i>Betula glandulosa</i> , <i>Salix pedicellaris</i> , <i>Larix laricina</i> ,	<i>Salix pedicellaris</i> , <i>Betula glandulosa</i>	<i>Larix laricina</i> <i>Salix pedicellaris</i> , <i>Picea mariana</i>
Poor fen and Collapse scar bog	<i>Ledum decumbense</i> , <i>Kalmia polifolia</i> , <i>Andromeda polifolia</i> , <i>Picea mariana</i> , <i>Andromeda chamydaphne</i> , <i>Vaccinium microcarpus</i>	<i>Picea mariana</i>	<i>Picea mariana</i>		

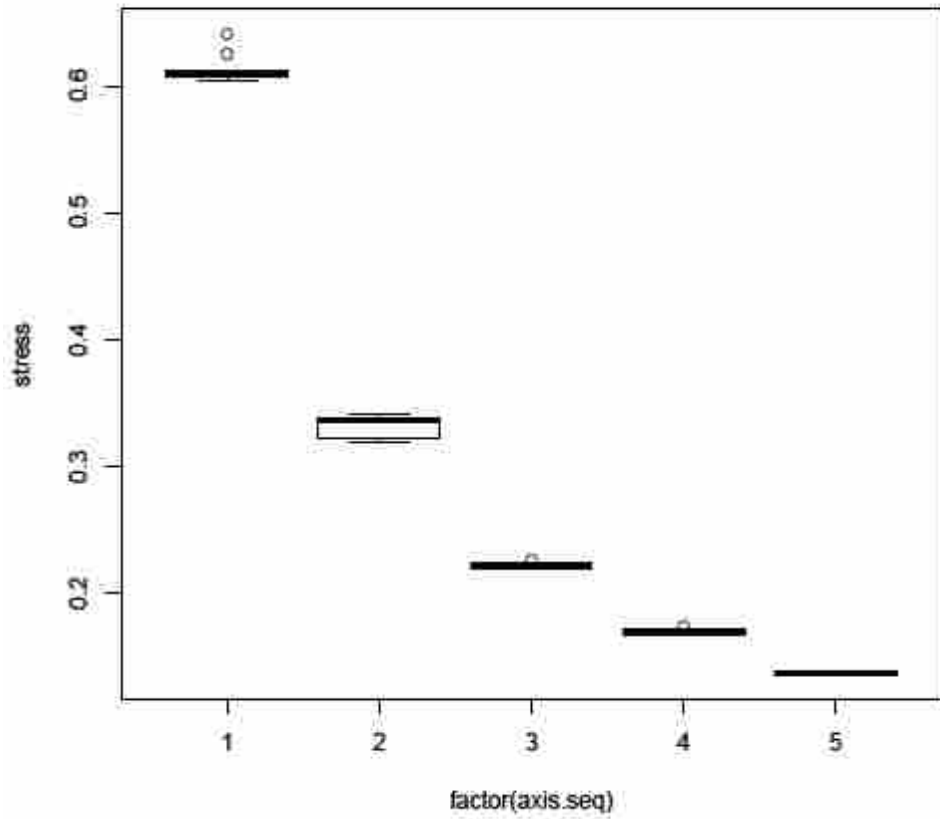
Appendix 2.5: Unexpected species, where they are found and where they normally would be found.

Wetland	Exceptions and site number	Rich fen	Poor fen	Collapse scar	Marsh	Peat plateau
Rich fen	<i>Andromeda polifolia</i> (F31,F32) <i>Carex limosa</i> (F31,F32) <i>Hylocomium splendens</i> (plateau?) <i>Sphagnum capillifolium</i> (plateau) <i>Sphagnum fuscum</i> (C31,F31) <i>Sphagnum riparium</i> (C31)		X X	X X X X		X X
Poor fen	<i>Campylium stellatum</i> (C14) <i>Carex limosa</i> (F13, C11, C13) <i>Leiomylia anomala</i> (F11-12, C12-C13) <i>Paludella squarrosa</i> (C14,C11,F12) <i>Eriophorum vaginatum</i> (F12) <i>Drepanocladus aduncus</i> (C11,F13) <i>Sanionia uncinata</i> (C11) <i>Rubus chamaemorus</i> (F11-12-13, C11-12-13-14) <i>Scheuchzeria palustri</i> (C14) <i>Scorpius scorpioides</i> (C14) <i>Sphagnum fuscum</i> (F11-12-13, C11-12-13-14) <i>Tomenthypnum nitens</i> (I13, C14, C11, F13)	X X X X X X		X X X X X X		
Collapse scar	<i>Paludella squarrosa</i> (F22) <i>Drepanocladus aduncus</i> (I13,I21) <i>Scorpius scorpioides</i> (F23-24) <i>Sphagnum warnstorffii</i> (C22,I13) <i>Tomenthypnum nitens</i> (I13) <i>Utricularia intermedia</i> (F23) <i>Vaccinium vitis-idaea</i> (IN3)	X X X X X X			X	
Generalist	<i>Vaccinium microcarpum</i>	X	X	X	X	
Marsh	<i>Drepanocladus aduncus</i> (F25)	X				

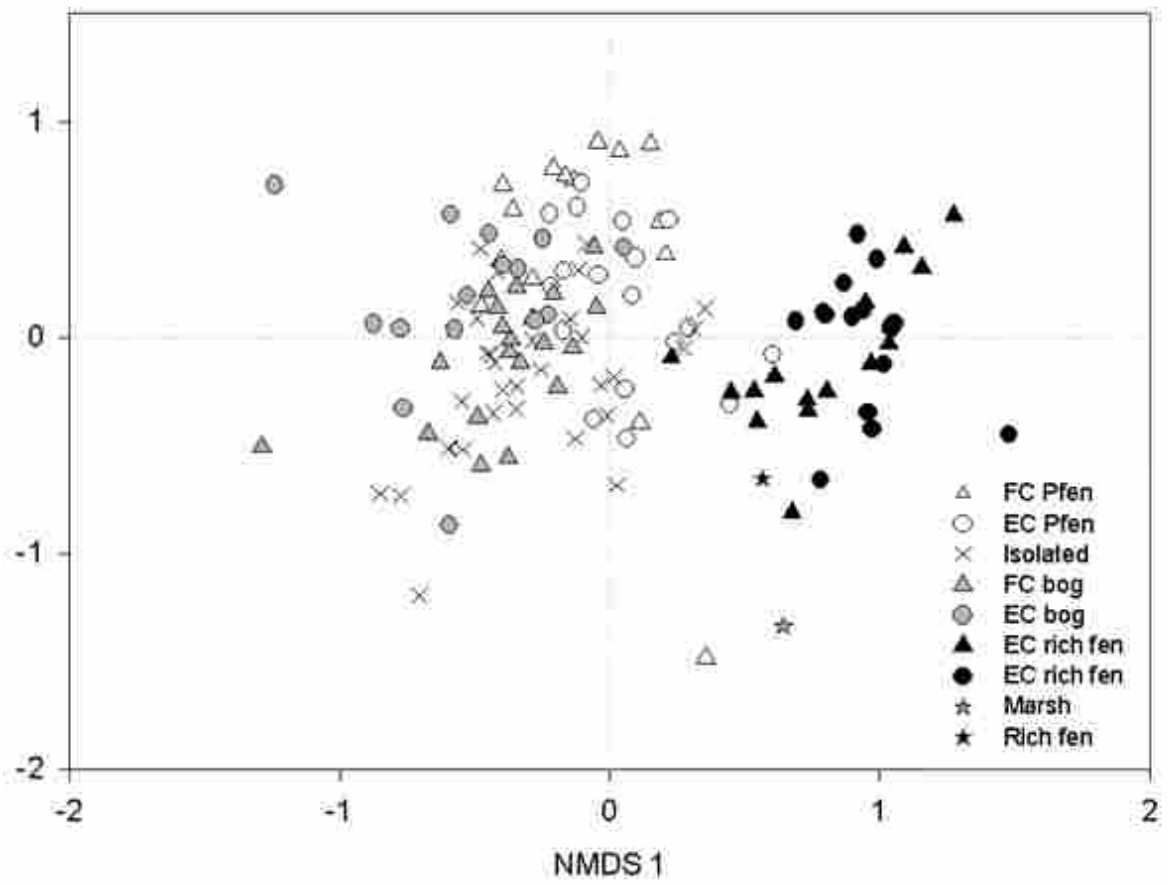
Appendix 2.6: Scotty Creek (NWT) sampling design. Blue is for collapse scar bogs, green for rich fens and red for poor fens. Pentagons are isolated wetlands, circles are fully connected wetlands and squares are connected wetlands. Letters and numbers correspond to the site names



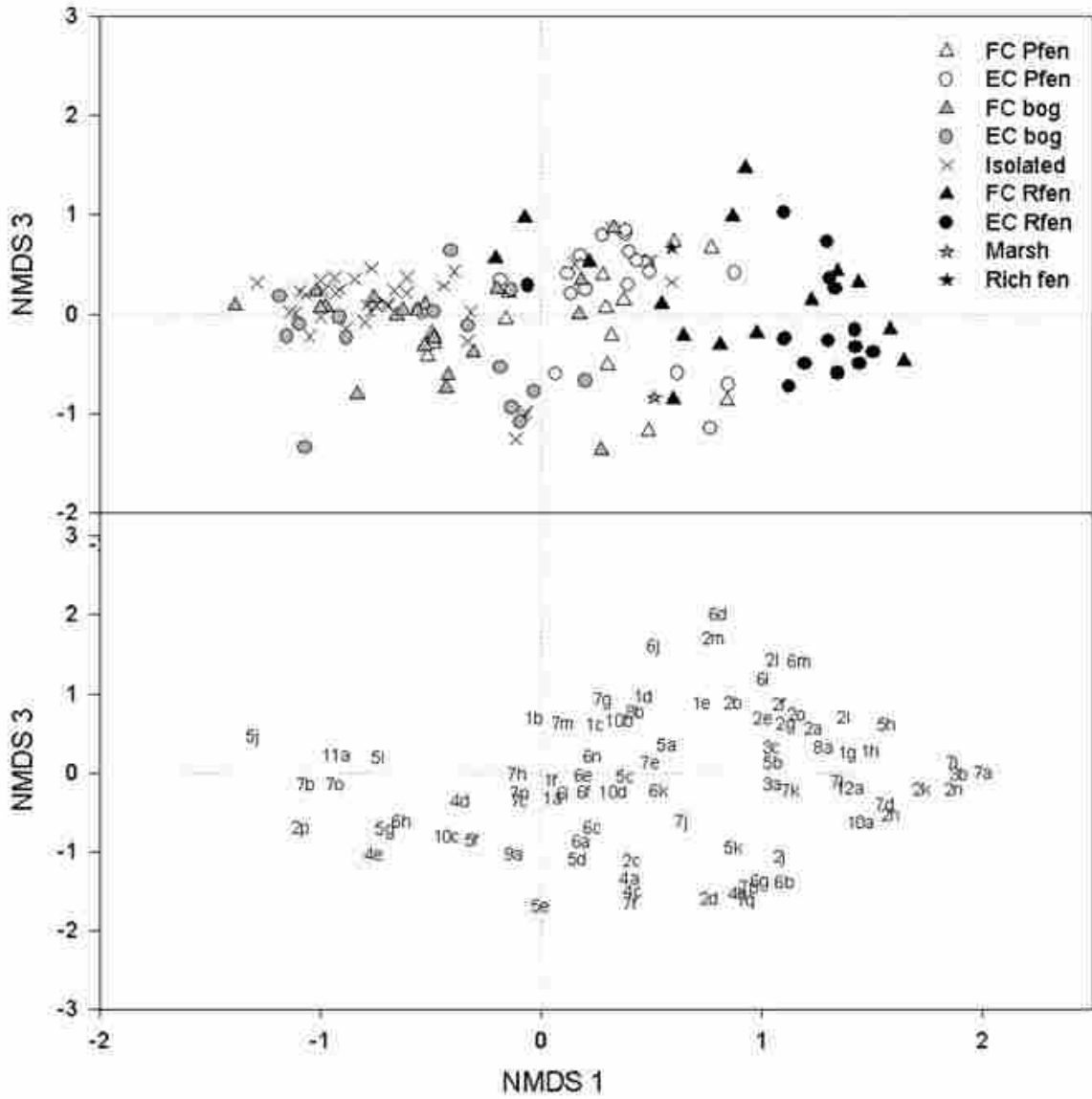
Appendix 2.7: Scree plot that was performed to see how many dimensions were necessary for the NMDS. Based on this plot, k would be 3.



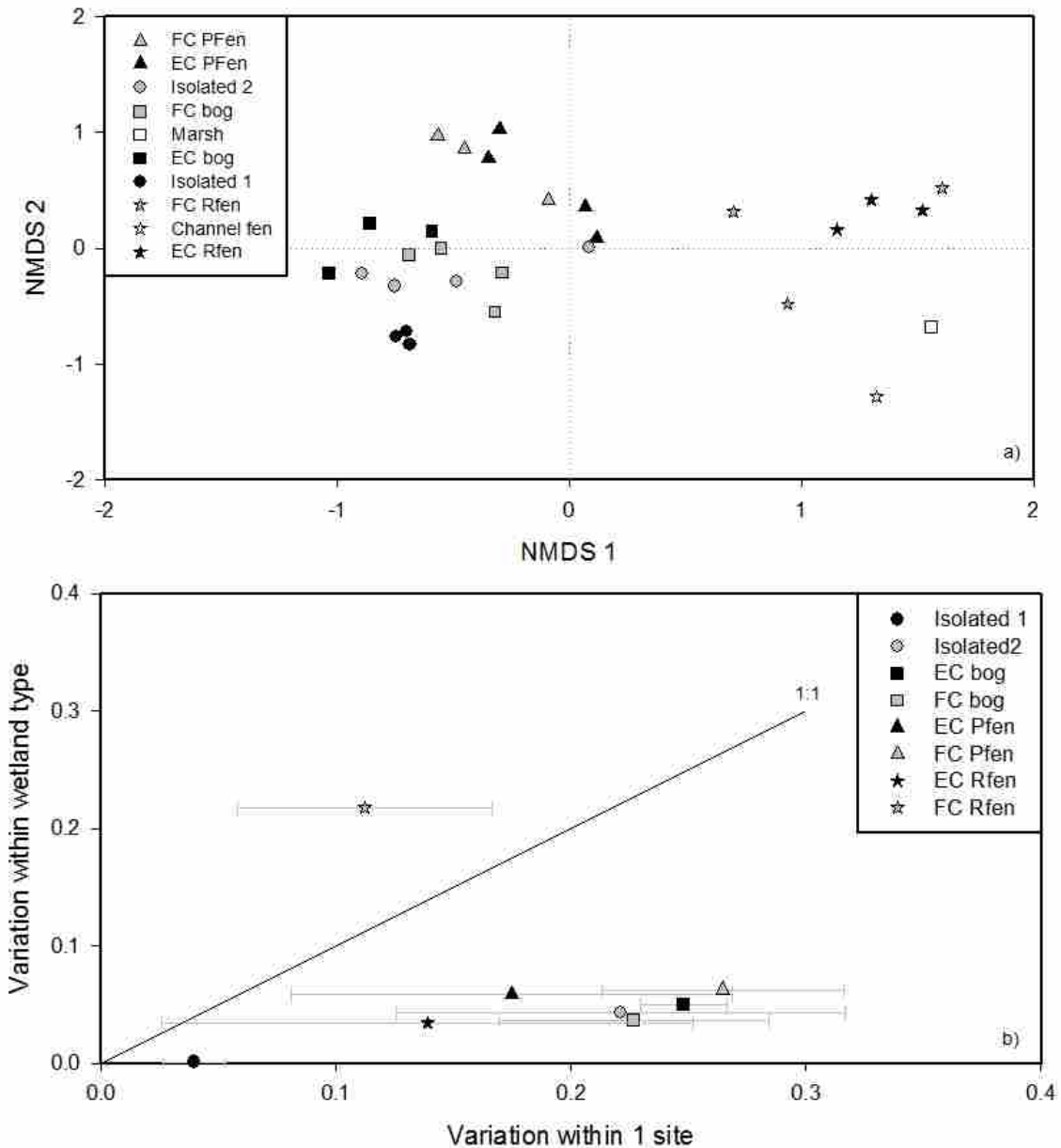
Appendix 2.8: Presence absence NMDS. An NMDS of the species found at Scotty Creek, based on presence absence data. k=3, ordination based on Bray-Curtis



Appendix 2.9: NMDS 1-3 of abundance of the species found at Scotty Creek. k=3, ordination based on Bray-Curtis. Bottom panel is the species map. 1=Ericoid, 2=Aquatic brown mosses 3=Deciduous shrubs 4=Forb-aquatic 5=Sedge and grass 6=Lichens 7=Emergent forbs 8=Trees 9=Lawn *Sphagnum* 10=Hummock *Sphagnum* 11= *Sphagnum* aquatic and 12=Brown moss hummock. For specific species refer to Appendix 2.2.



Appendix 2.10: Panel a) is an abundance NMDS where all 5 quadrats have been combined as one point to represent the site to examine variance between sites; Panel b) is a regression between site variation (variation between the 5 quadrats) and wetland type variation (the variation between the different sites (ex: 3 sites that comprise ephemerally connected bogs)). Trend indicates 1:1 ratio. Isolated 1 are the isolated nearest the bogs, isolated 2 the sites closest to the poor fens. EC=ephemerally connected, FC=fully connected, Rfen=rich fen, Pfen=poor fen



Appendix 2.11: Equations for diversity indices, where p_i is the proportion of species i

$$H = - \sum_{i=1}^S p_i \log_b p_i$$

Shannon diversity index

$$D_1 = 1 - \sum_{i=1}^S p_i^2$$

Simpson diversity index

$$D_2 = \frac{1}{\sum_{i=1}^S p_i^2}$$

Inverse Simpson diversity index

Chapter 3

Whodunit: Finding the environmental variables responsible for peatland species distributions

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Keywords: Water chemistry, Climate change, Permafrost, Allogenic succession, Species community, Bogs, Fens, Species succession, Collapse scar bogs, Water table, conductivity, nutrients, pH

Primary research article

Abstract

Peatlands exist across a gradient of environmental conditions, where water chemistry is an important predictor for species richness and composition, as well as peatland function. Changes to water chemistry can thus result in the alteration of plant communities. In northern areas where it is present, permafrost will serve to isolate peatlands from one another. This isolation is changing as climate warming is thawing permafrost. The purpose of this chapter is to characterize water chemistry in three different peatland types (rich fens, poor fens and bogs) found at a site where permafrost thaw is occurring rapidly and assess whether greater hydrological connectivity (associated with permafrost thaw) will lead to changes in water chemistry and species composition. Important peatland predictors were identified and water chemistry was measured to examine differences among peatland types. Rich fens had higher pH, nutrients and conductivity than bogs and poor fens. Dissolved oxygen was an important predictor of species composition for bogs and poor fens. Increased hydrological connectivity led to increases in pH and nitrate for bogs, which suggests that permafrost thaw is driving water chemistry changes potentially through novel surface water interactions. Here we show that water chemistry is changing with permafrost thaw and suggest that these changes can lead to wetland conversion and eventually to changes in species composition.

3.1 Introduction

Peatlands are unique ecosystems due to their low decomposition rates and capacity to accumulate carbon as peat (Wieder et al. 2006). Peat accumulation makes peatlands one of the largest terrestrial carbon sinks and these ecosystems thus play a significant role in the global carbon cycle (Tarnocai 2006). Peatlands also serve globally important hydrological functions, such as flood attenuation (Holden 2005). Finally, from a biodiversity perspective, peatlands are home to a range of specialized and even rare plant species (Camill 1999a; Beilman 2001; Locky and Bayley 2006). However, rapid and amplified high latitude warming is driving changes in these peatlands (IPCC 2007), with the potential to release sequestered carbon (Tarnocai 2006), alter in basin hydrology (Quinton et al. 2011) and potentially drive species loss. Understanding and predicting these changes is important given the globally important functions of these systems.

Peatlands are highly variable in terms of plant species composition and structure; from relatively nutrient and species rich fens to nutrient and species poor bogs (National Wetlands Working Group 1997). These floristic differences among peatland types are also reflected in their water chemistry; bogs have low pH (3-5), lower temperatures than other peatlands (Whitehouse and Bayley 2005), lower nutrient availability and are precipitation fed, while fens have high pH (>5), higher nutrient availability (National Wetlands Working Group 1997), higher conductivity (Vitt and Chee 1990) and are groundwater fed (National Wetlands Working Group 1997). Water chemistry is important in determining species composition and with the rapid changes occurring in the landscape due to permafrost thaw it is unclear how species composition will respond (Camill 1999b; Whitehouse and Bayley 2005).

One mechanism that may impact water chemistry (and in turn species composition) is permafrost thaw. Permafrost (ground that is below 0°C for more than two years, French and Slaymaker 1993) affects basin hydrology by driving patterns of drainage and runoff. In the discontinuous zone, where permafrost only covers 50-90% of the area, areas in peatlands with permafrost will be elevated above the water table, due to the volumetric expansion of peat when water is converted into ice (Camill 1999b). This creates a hydraulic gradient between permafrost plateaus and bogs or fens where permafrost is absent, thereby isolating wetlands hydrologically. Some of these bogs are normally completely surrounded by permafrost plateaus and therefore the only water input comes from the plateau's runoff or precipitation (Quinton et al. 2009). However, as permafrost thaws further, channels will connect permafrost free wetlands that were previously separated by permafrost. These channels can lead to contact with groundwater sources, which was previously inaccessible due to the presence of permafrost, as well as with new surface water interactions between nutrient rich fen water and nutrient poor acidic bog water. In ecological succession, decreased groundwater sources will lead to the conversion of a fen into a bog (Malmer 1986), therefore with increased groundwater inputs, caused by permafrost thaw, it is expected that the reverse will happen where a bog converts back into a fen (Vardy et al. 2005; Lamentowicz et al. 2008). In Chapter 2 we examined the effects of permafrost thaw induced increases in hydrological connectivity on plant species composition. We determined that although some unexpected species were identified there were no detectable differences in plant communities attributable to permafrost thaw. In this chapter I examine whether water chemistry is responding to increased hydrological conductivity, as it could be a necessary precursor to species

composition changes. To do this we compare different levels of hydrological connections from isolated to fully connected peatlands. The objectives for this chapter are to first examine if water chemistry impacts plant species composition and second to see if water chemistry changes with wetland type and assess the impact of increased hydrological connectivity (induced by permafrost thaw) on water chemistry.

3.2 Methods

3.2.1 Field measurements

Data was collected from the Scotty Creek field site described in Chapters 1 and 2. Water chemistry was sampled at the same 27 sites that were established in Chapter 2 for quantifying species abundance. Specifically, at each of the five quadrats per site, the abundance of vascular and non-vascular plants was measured. Following this, a Professional Plus Water Quality Instrument (YSI Inc, #6050000, USA) was used to quantify water chemistry (pH, conductivity ($\mu\text{S}/\text{cm}$), nitrate (NO_3) (mg/L) and ammonium (NH_4) (mg/L)). Measurements were made at the beginning of July 2012, as species abundance was recorded. The instrument was calibrated in the field the first day of sampling. The measurements were performed in open water where it was possible and when none was available the peat was dug out until the water table was found and the measurements taken. After doing a one-way univariate analysis of variance (ANOVA), no statistical difference was found between NO_3 or NH_4 samples that were collected from the open water and those collected after digging up the peat. This analysis was done on all the samples, as well as a separate analysis on the isolated bogs excluding the one that was more like a poor fen than a bog described in Chapter 2. Water table and bulk density were also measured. The water table was recorded at the end of June at the same time as

the initial species assessment. It was measured as the top of the peat being zero and then down to the surface of the water table, which could always be reached manually without the help of other tools.

Soil samples at each quadrat was collected from the first 10 cm of peat at the end of July for quantification of bulk density and sealed into metal tins. The bulk density samples were collected near the end of the field season to allow for rapid transport back to the laboratory for analysis. Once back in the lab the bulk density tins were then weighed. Following this they were saturated by adding water till it reached the rim of the tin and weighed. The samples were dried in an oven at 105°C and left for 2 days to dry. They were then weighed daily until their weight was constant. The initial, saturated and dry weight were recorded and used to calculate the bulk density of these samples.

3.2.2 Statistical analysis

To determine differences in water chemistry among wetland types and assess their influence on species distribution, I conducted a non-metric multidimensional scaling analysis (see Chapter 2) followed by an envfit analysis. An envfit function, from the Vegan package in R (Oksanen et al. 2013), uses a NMDS matrix and examines the strength and direction of correlations between environmental variables and site loadings. This allows us to see if the environmental variables are associated with different sites by visualizing them as vectors, where the longer the vector the greater impact it has on determining species abundance (Oksanen et al. 2013).

Analysis of variance was used to quantify the response of water chemistry to increased hydrological connectivity across wetland types. Dependent variables included:

dissolved oxygen (DO) (mg/L), water table (cm), water temperature ($^{\circ}\text{C}$), NO_3 (mg/L), NH_4 (mg/L), pH, conductivity ($\mu\text{s}/\text{cm}$) and bulk density (kg/m^3). Independent variables included wetland types, degree of connectivity, and their interaction. Only the ephemerally connected and fully connected wetlands were included as only the bog wetland type had an isolated category. For the two-way ANOVA, the data was transformed in order to meet the assumptions of the analysis. The following variables required Log_{10} transformations: NO_3 , DO, and bulk density. Conductivity and ammonium required a square root transformation. Finally, surface water temperatures were squared and pH was \ln transformed. It should be noted that the results of the analysis were consistent with or without transformation.

3.3 Results

3.3.1 Water chemistry impacts on plant species composition

The environmental fit takes different environmental parameters such as pH and conductivity and associates them with sites where they are most abundant (Fig. 3.1). Different peatland types have different important environmental conditions, where the most characteristic variables for the rich fens were high conductivity, pH, nitrate, and ammonium. In the poor fen bulk density and water table depth were key drivers and for the collapse scar bogs temperature and dissolved oxygen determine species compositional abundance. Comparing the environmental variables to species composition from Chapter 2 (Fig. 2.6), the increased conductivity, pH, nitrate and ammonium support a much richer plant community, containing many shrub species, brown mosses and trees. Meanwhile, where pH, nitrate and conductivity are low and where the main predictor is water table

there are fewer species, if we compare those sites with the NMDS1 in Chapter 2 (Fig. 2.6).

3.3.2 Water chemistry differences among peatland type and the role of hydrological connectivity on water chemistry

Conductivity only varied by wetland type and not as a function of hydrological connectivity, the rich fen having the highest (~120 $\mu\text{s}/\text{cm}$) and the bogs the lowest conductivity (~20 $\mu\text{s}/\text{cm}$) (Fig. 3.2a). pH had similar values for bogs and poor fens (between 4.5 and 5) but was much higher for rich fens (~6.5) (Fig 3.2b). However, fully connected bogs had significantly higher pH values than ephemerally connected bogs and these values were similar to that of a poor fen. Nitrate showed no real pattern for wetland type but showed a marginally significant increase between ephemerally and fully connected bogs, where the nitrate concentration in the fully connected bog was similar to both poor fens and rich fens. No trends were found between wetland types for DO and water table depth but fully connected rich fens had the lowest dissolved oxygen and ephemerally connected poor fens had the deepest water table. Finally, there was a significant decrease in bulk density between connected and fully connected bogs.

It is important to mention that our NO_3 values were high for northern peatlands; however they do fit within the literature values, although falling in the upper end of that range (Fig. 3.4). This brings up a problem in sampling methodology, where there isn't a uniform way of sampling in the literature and therefore some sources use pore water, some surface water and others bring their samples back to the lab where they can be filtered, which makes comparisons difficult. As the values that were obtained at Scotty

Creek were all done on the same calibration and fell into similar ranges then they can be used to compare the effects of increased permafrost thaw.

3.4 Discussion

In this chapter, I demonstrated that rich fens have very different water chemistry than poor fens and bogs. Some of the important predictors that distinguish the rich fens from the others include increased conductivity, pH and nutrients (NO_3 and NH_4). Unlike in Chapter 2 where no difference was found in species composition with increased degrees of hydrological connectivity, here we find evidence of allogenic changes in pH and nitrate between ephemerally connected and fully connected bogs.

3.4.1 Water chemistry by wetland type

The envfit confirms that the peatlands were well characterized as they correspond with the literature, where rich fens were predicted by and had the highest conductivity, pH (Wheeler and Proctor 2000; Mulligan and Gignac 2001; Whitehouse and Bayley 2005; Johnston and Brown 2013; Sasaki et al. 2013) and nutrients (Wheeler and Proctor 2000; Chapin et al. 2004). In Chapter 2 rich fens had a very distinct and rich species composition. Here we see a similar trend, where rich fens had very different water chemistry than the two other peatland types. This could be due to the presence of groundwater. Fens are minerotrophic, which means that they are groundwater fed, while bogs are ombrotrophic, precipitation fed (Weltzin et al. 2003). Groundwater has more ions, therefore it will have a higher conductivity (Johnston and Brown 2013), which will neutralize the pH (Weltzin et al. 2003). A higher pH will lead to greater microbial activity, which in turn will lead to increased nitrification (Shammas 1986).

Meanwhile, water table was an important predictor for bogs and poor fens (Camill 1999a; Laine et al. 2007). These peatlands supported a poorer species community (Chapter 2), which consisted of many *Sphagnum* mosses whose presence and species composition will depend on the position of the water table and whether it is at the surface or if it is hummocky (Laiho 2006; Wojtuń et al. 2013; Jiroušek et al. 2013). For example, poor fens had large hummocks of *Sphagnum fuscum*, which led to a deeper water table, while bogs had high abundance of aquatic *Sphagnum* spp., which leads to a surficial water table (Chapter 2). A raised water table will lead to the conversion of plant communities that prefer wetter conditions (Oomes et al. 1996). Alternatively, a deep water table will be favourable for shrub species (Bubier et al. 2006), which are very abundant in the rich fens (Chapter 2).

As we are seeing very different water chemistry amongst the peatland types, the increase in permafrost thaw can lead to ecosystem conversion. Initially as permafrost thaws and creates further connections, there will be a spike in conductivity in bogs that corresponds to when high cation fen water (Vitt and Chee 1990) gets introduced due to the presence of groundwater (Johnston and Brown 2013) or surface water flooding (Asada et al. 2005). As groundwater seems to be responsible for most of the differences between the peatlands (increased pH, nitrification, temperature etc.), its presence in a bog could lead to habitat changes. The question is now: is permafrost thaw leading to enough input of nutrient rich water to show evidence of allogenic change?

3.4.2 Water chemistry and hydrological connection

Unlike in Chapter 2, where species composition did not differ by degrees of hydrological connectivity, here pH and nitrate showed an increase between ephemerally connected bogs and fully connected ones. Not only did these variables increase between the levels of connection among their own peatland type, but nitrate concentrations in fully connected bogs were similar to those found in the fully connected rich fens and pH in fully connected bogs was similar to the pH in ephemerally connected poor fens. This is evidence of allogenic changes and with time we would expect these bogs to revert back towards fen-like plant communities (Arlen-Pouliot and Bhiry 2005; Lamentowicz et al. 2008), which Chapter 2 provides some evidence for.

However, the other water chemistry variables did not vary systematically among wetland types or levels of hydrological connection. This could be due to the fact that there hasn't been enough permafrost thaw between the wetlands or that there hasn't been enough time since it thawed for the water chemistry (such as conductivity, NH_4 dissolved oxygen etc.) to respond to such changes (Halsey et al. 1995). Another possibility is that there were not enough novel water interactions and that a major event needs to happen before there is an entire change in water chemistry. These events can range from fires (Lamentowicz et al. 2008) to flooding (Asada et al. 2005; Granath et al. 2010). Flooding has been known to happen at Scotty Creek within the fully connected bog and will be further studied in Chapter 4.

3.5 Conclusion

This chapter examined how water chemistry influenced species distribution and it was found that high conductivity, pH, nitrate and ammonium were correlated with rich

fen sites and species, deep water table and high dissolved oxygen with poor fen sites and warm temperatures with bogs. It also demonstrates that although we did not see extensive species change with connectivity in Chapter 2, that water chemistry is responding to permafrost thaw. This was evidenced by pH and nitrate in fully connected bogs being similar to pH and nitrate in poor fens. We have also similar trends between conductivity, pH and nitrate and that these were important elements in determining peatland composition.

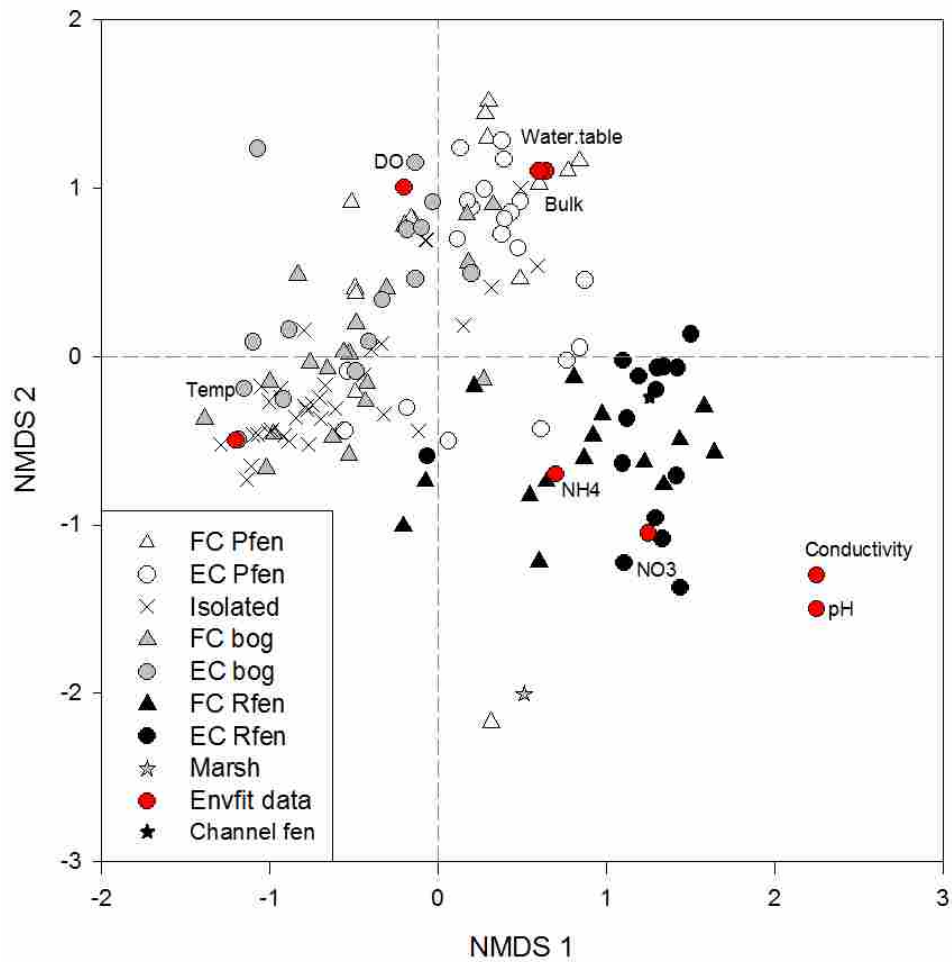


Figure 3.1: Envfit of the data at Scotty Creek by peatland and hydrological connectivity, showing the distribution of important environmental predictors. FC=fully connected, EC=ephemerally connected, Pfen=poor fen, Rfen=rich fen.

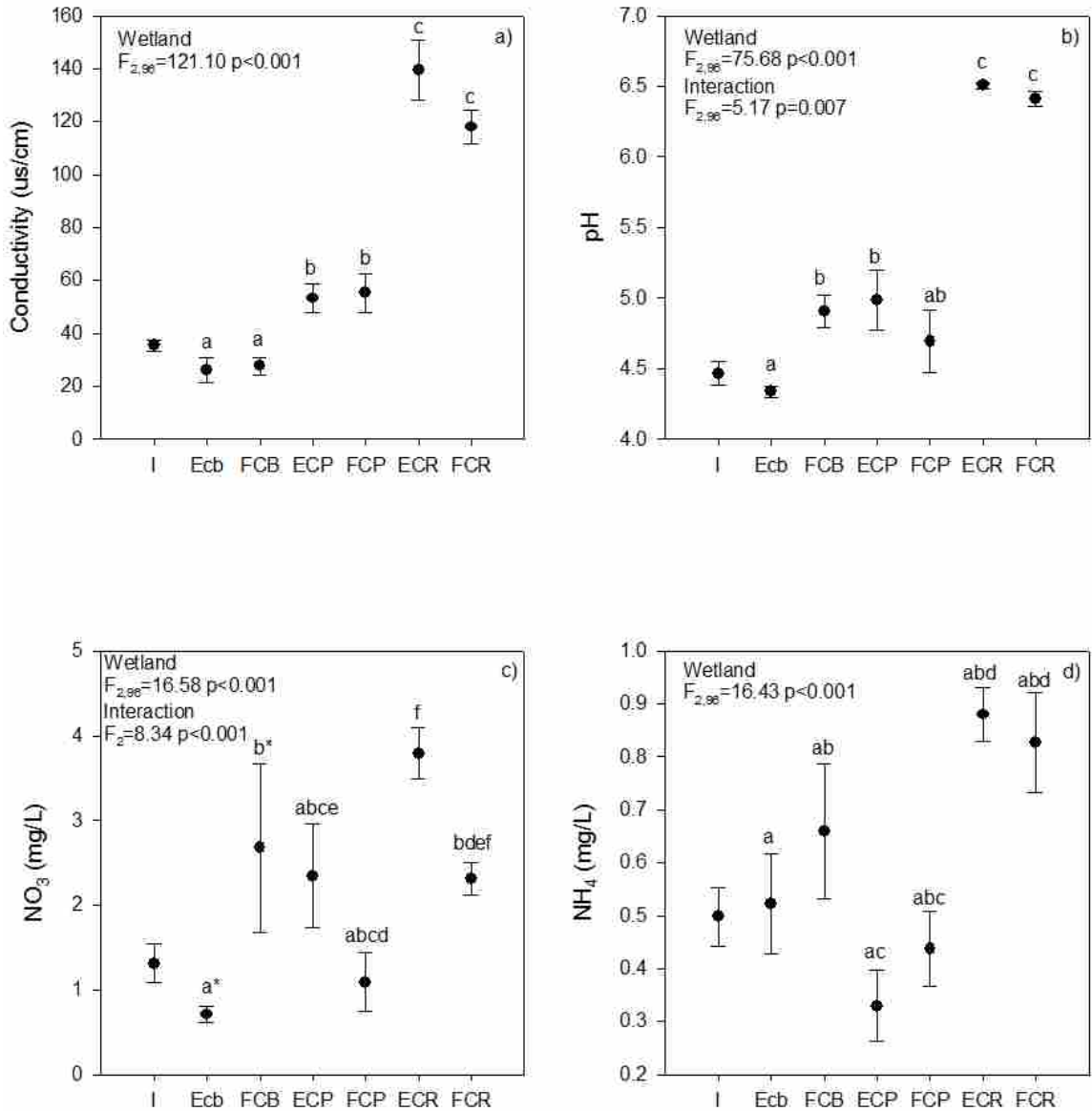


Figure 3.2: Average environmental predictor per peatland type (+/- SEM). Two-way ANOVA for the ephemerally connected and fully connected peatlands. Isolated bogs were excluded in this analysis as it wouldn't be a fully factorial analysis were they included. FC= fully connected, EC=ephemerally connected, P=poor fen, R=rich fen, B=bog, *=marginal significance $p=0.05$.

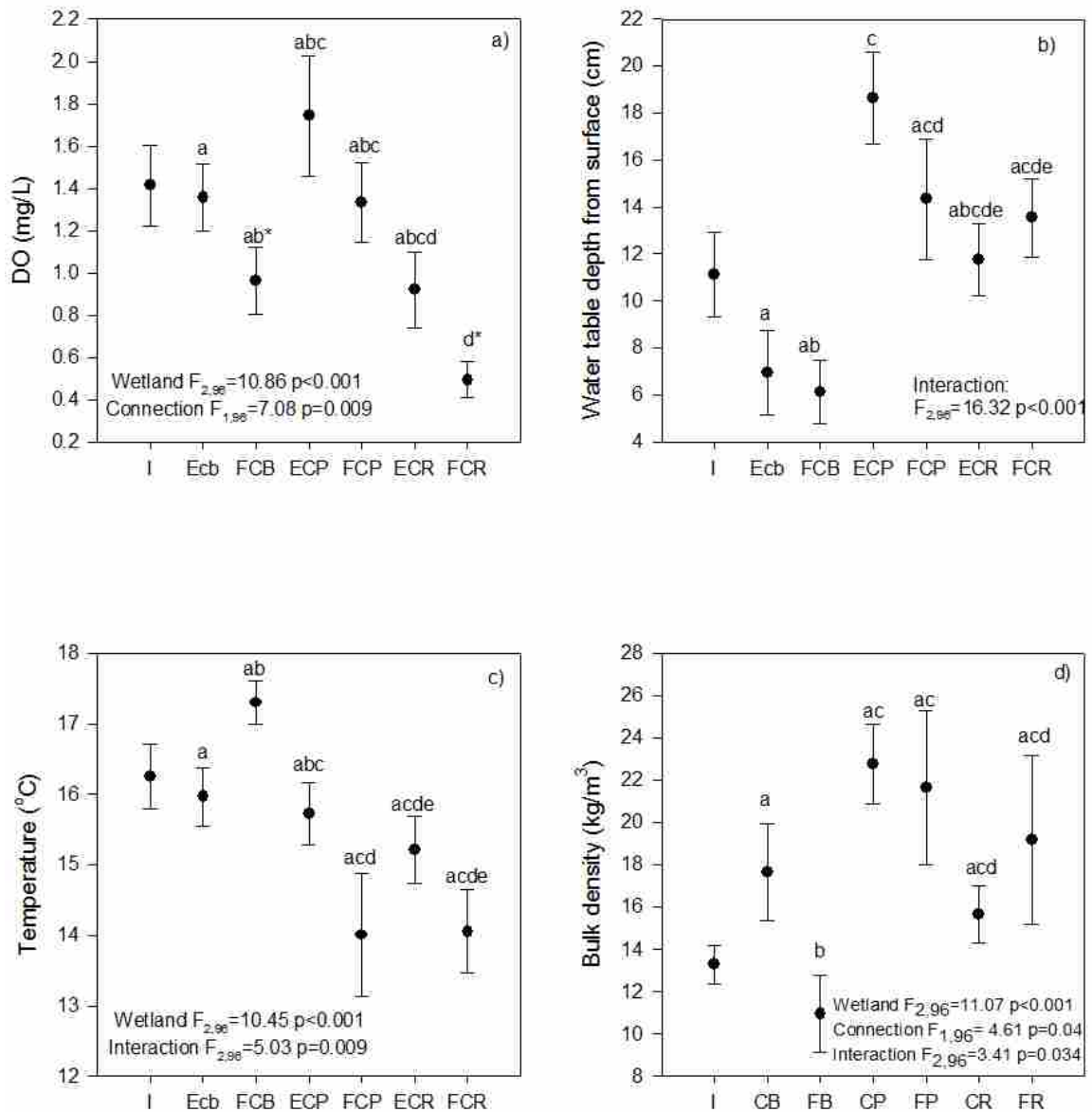


Figure 3.3: Average environmental predictor per peatland type (+/- SEM). Two-way ANOVA for the ephemerally connected and fully connected peatlands, standard error shown. *=marginal significance $p=0.05$. FC=fully connected, EC=ephemerally connected, P=poor fen, R=rich fen, B=bog

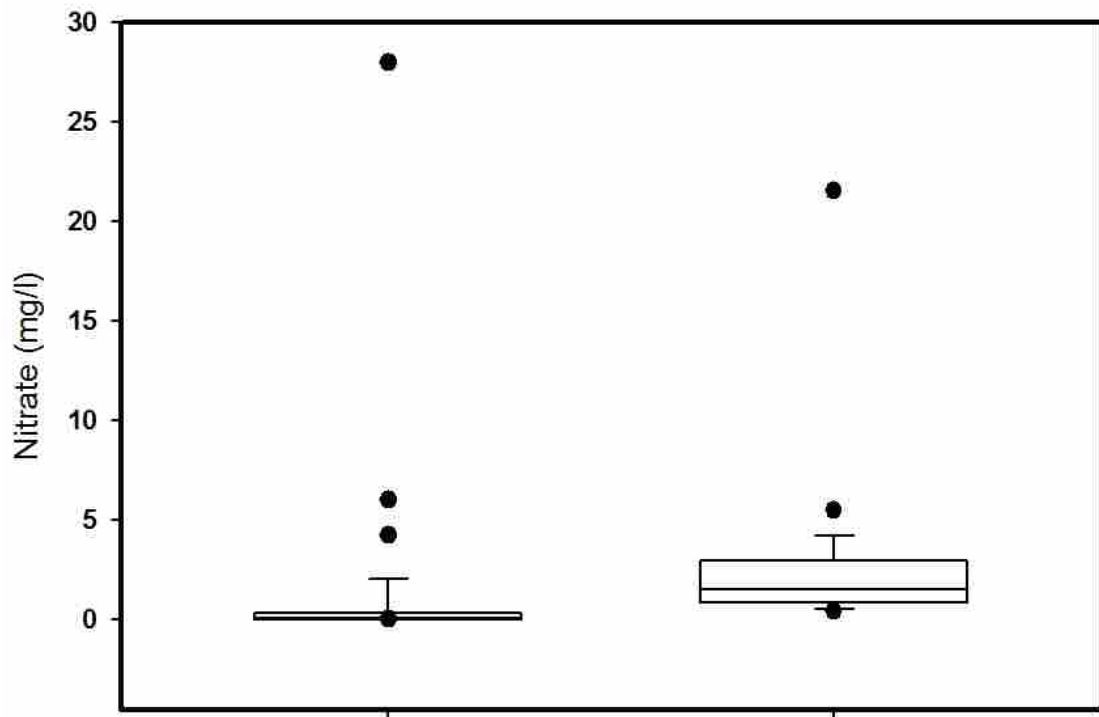


Figure 3.4: Box plot of nitrate (mg/l) values found in the literature compared to those found at the Scotty Creek sites.

Chapter 4

Hidden nutrients: A Case Study in Bog-Fen Succession

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Primary research article

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Abstract

In northern boreal peatlands, permafrost controls water flow in the landscape and isolates proximal wetlands from one another. The warming climate is driving permafrost thaw, which creates channels connecting wetlands to one another. Allogenic forces such as this can reverse the normal autogenic successional pathway so that a bog reverts into a fen. However, we know little about the effects of increased permafrost thaw as an allogenic force. The purpose of this chapter is to examine mechanisms of peatland species community reversal. This was done using a detailed case study examining the response of a single large bog to permafrost thaw-induced connectivity. Specifically, this bog recently merged with a channel fen as a result of permafrost thaw breaching the separating plateau. Water chemistry and species abundance data were collected for fully connected (3 sites), ephemerally connected (3 sites), and isolated bogs (7 sites). A flooding model was also developed as a tool to examine permafrost thaw and flooding as mechanisms for altering peatland species communities. Water chemistry did not change with respect to increased degrees of connectivity between ephemerally connected and isolated bogs. Of the water chemistry properties measured only pH, nitrate, and temperature differed between ephemerally connected and fully connected bogs. This suggests that increased hydrological connectivity is not a strong enough mechanism on its own to engineer species composition changes. The bog demonstrated a gradient of fen-like conditions from the mouth of the fen to the southern distal end of the bog, yet when the flooding model was tested between 2003-2012 even under the highest water levels measured (2007 and 2011) the fen water only penetrated approximately a hundred and seventy meters down the bog. As such, flooding alone could only explain increased

proportions of fen species at the site closest to the fen/marsh interface suggesting that hydrological connectivity can't be the only important factor in converting species composition to that normally found in a fen. Other possible drivers of observed change are also reviewed in this chapter.

4.1 Introduction

Peatlands are ecosystems where nitrogen is limited, and water chemistry is a key driver of plant community composition and structure (Chapter 2 and 3, Locky and Bayley 2006). Species richness is enhanced by a more neutral pH and greater nutrient availability, resulting in greater structural complexity; the two end points on this peatland gradient being fens and bogs. The differences between these two end points often stem from differential access to groundwater; bogs are isolated and precipitation fed, while fens are groundwater fed (Chapter 3, National Wetlands Working Group 1997; Locky and Bayley 2006; Vitt 2006; Vitt et al. 2009). As these two end points are very different from one another and have plant communities adapted to their ecosystems, altering water chemistry can lead to a complete transformation of peatland type. Unidirectional succession from a fen to a bog occurs naturally when access to groundwater becomes increasingly restricted by an accumulation of *Sphagnum* spp., eventually leading to the acidification of that peatland and to its conversion into a bog. Once this has happened, reversal of the process does not occur readily (Clymo 1963, Fig. 2.8).

Peatlands such as those described above can be found within the discontinuous permafrost zone (perennially cryotic ground that is found between 50-90% of the area). Frozen peat will volumetrically expand above the surrounding wetlands, as water turns into ice (Vitt et al. 1994; Quinton et al. 2011). The establishment of permafrost stores water and nutrients, and is also able to control runoff and isolate permafrost-free areas from one another (Camill 1999a; Jorgenson et al. 2010; Quinton et al. 2011). This isolation will serve to keep all these wetlands and the wetland's hydrological and ecological functions separated and is thus important in a boreal peatland mosaic where

fens and bogs are permafrost free and surrounded by areas where permafrost is present, known as permafrost plateaus.

Discontinuous permafrost in the boreal zone is ice-rich (Quinton et al. 2011) – meaning there is a high proportion of peat plateaus where water is volumetrically expanded into ice. The permafrost here is also relatively thin (Quinton et al. 2009) and warm (Smith et al. 2005), which makes it extremely vulnerable to climate warming that is currently happening rapidly at high latitudes (IPCC 2007; Tarnocai 2009; Scheffer et al. 2012). These increased temperatures can lead to permafrost degradation. Chasmer et al. (2011) found that the extent of permafrost plateaus has reduced by 27% over a period of 60 years at a site in the Northwest Territories, Canada. When it is present in peatlands, permafrost serves as a barrier to water exchanges; once it thaws, the peatlands will be able to interact hydrologically with one another. This could lead to the reversal of natural successional processes if the two connecting peatlands have varying chemical and biological composition, such as that of a fen and a bog (Hughes and Dumayne-Peaty 2002).

Such successional reversal can be accomplished via flooding events. Asada et al. (2005), studied vegetation pre- and post-damming of a peatland complex in the Experimental Lakes Area (Ontario, Canada). The area was left flooded for most of the summer, draining it in the fall, and repeated this protocol for a period of 9 years. They found that there was a decrease in bog vegetation and increase in typical fen and marsh species at the end of their study. A study by Granath et al. (2010) also supports successional reversal; they found that *Sphagnum fuscum*, a species of peat moss that establishes in bogs, was severely damaged after being kept submerged for only 25 days in

nutrient rich waters. In contrast, Mitchell & Niering (1993) found that although forests were being converted into fens due to beaver flooding, bog vegetation was not affected after three decades of the initial flooding. Although effects of flooding in wetlands are known, permafrost thaw as the mechanism of change is less well studied and this disturbance is becoming increasingly widespread (Vitt et al. 1994; Camill 1999a; Jorgenson et al. 2001; Beilman and Robinson 2003; Tarnocai 2009; Quinton et al. 2011; Baltzer et al. 2014).

The objective of this study is to examine the role of flooding in driving distribution of non-bog plant species in a recently connected bog and quantify its impact on wetland conversion. In studies in the previous chapters, many different wetland types were sampled at Scotty Creek (NWT); within those wetlands, it was found that the fully connected bogs contained many rich fen species, although complete compositional shifts were not detected. Presently, the site for this case study is one continuous bog unit that extends for approximately half a kilometer and is hydrologically connected not only to the other bogs, but also to the nutrient rich waters of a marsh bordering a fen at the northern tip of the bog (Fig. 4.1). Major increases in connectivity occurred between 1970 and 1977. With the knowledge that there is a source of nutrient rich water directly connected to the collapse scar bogs, our hypothesis is that the frequency and/or extent of surficial flooding of a bog by fen water drives fen vegetation distribution and associated water chemistry.

It is crucial to understand the responses of these wetlands to increased hydrological connectivity and in turn flooding events. Each wetland type has an important ecological and hydrological function and further permafrost thaw can lead to

the eventual amalgamation and possible conversion of these different wetlands. One implication of peatland conversion is species loss; as this system is rather species poor, this would have a considerable impact on overall ecosystem services and functions such as changes in soil moisture, permafrost stability, as well as ecosystem carbon and nitrogen storage (Chapin et al. 1995; Turetsky et al. 2010; Turetsky et al. 2012).

4.2 Method

4.2.1 Field measurement

The study was conducted at Scotty Creek (NWT), which was described in Chapters 1 and 2. Here, the focus is restricted to a set of fully connected bogs that have recently become connected to a channel fen, and these bogs were found to contain species typical of rich fens rather than vegetation characteristic of bogs. Four sites were selected along the fully connected collapse scar bog. The different sites were delimited by areas that were hypothesized to have been once separate and isolated bogs judging by the shape of the bogs and permafrost thaw in aerial imagery. At each of these sites, five quadrats were placed; one at the center of the bog, and one in each of the four cardinal directions at a randomized distance from center. A quadrat was also placed directly within the fen near its connection through the northernmost end of the series of collapse scar bog sites. At each of these sites, both vascular and non-vascular species were identified and their abundance measured in the first two weeks of July 2012. Using a Professional Plus Water Quality Instrument (YSI Inc, #6050000) the following environmental parameters were recorded: pH, ammonium, nitrate, temperature, dissolved oxygen (DO) and conductivity. This methodology was also followed for three

ephemerally connected and seven isolated bogs; these wetlands were initially sampled in Chapter 2 and used here for comparative purposes.

4.2.2 Remote sensing

4.2.2.1 Surface reflectance data

Using WorldView2 data acquired on 23 August 2010, I explored patterns of fen spectral signatures within this bog. The image was mosaicked and colour balanced in Geomatica OrthoEngine and orthorectified using LIDAR DEM (Digital Elevation Model) data collected in October 2010 (Chasmer et al. 2014). WorldView2 has eight spectral bands (coastal, blue, green, yellow, red, red edge, near infrared 1 and 2). It is possible to determine spectral signature with a precision of 2 m pixels using these bands. For this chapter we used the surface reflectance calculated from the atmospheric corrections done on WorldView2 data. The surface reflectance layer was previously used in Chasmer et al. (2013), which provides greater detail on correction methodology and data transformation. This layer was qualitatively able to show vegetation type by spectral radiance.

4.2.2.2 Flood modeling

To examine potential extent of fen water incursion into the bog, I developed a simple model that coupled DEM and fen water level data. The DEM shows that the bog is higher in elevation than the fen; thus, under normal conditions water will flow down this hydraulic gradient toward the fen. In order for fen water to enter the bog it must exceed a certain water table elevation, which in this case was 268.7 m above sea level (a.s.l.). The elevation at the water level recorder was known, however, it was situated at a well 20 meters away from the mouth of the bog - too far from the bog to determine

flooding potential. To determine the extent of fen water incursion into the bog, I had to convert relative water level data to elevational data. This was accomplished by determining the water level at the well for the exact time at which the LiDAR data was acquired. This allowed for an absolute elevation to be determined for that point, the correction for which could then be applied to water level data across the years. There was a small difference in elevation between the location of the well and the mouth of the bog, and as such I applied an elevation correction to all water level data to emulate water levels at the mouth of the bog. An elevation contour map of the bog was created using ArcGIS and I quantified how many times during each season and year the elevation of the water table at the mouth of the bog exceeded each elevation contour. This was done by creating a contour line of the DEM in ArcGIS based on maximum water table elevation recorded at the well, minimum elevation needed to enter the bog and an elevation between the two.

4.2.2.3 Permafrost thaw

Quantifying the extent of permafrost thaw through time was important, both to see which areas had always been bogs, which areas had previously been isolated, and which areas experienced the most extensive and rapid thaw. Permafrost extent from 1947, 1970, 1977 and 2000 were digitized manually in ArcGIS using aerial photos (1947, 1970, 1977) and IKONOS multispectral satellite image (2000, 2008) (Chasmer et al. 2010; Chasmer et al. 2011). This was possible because permafrost plateaus are treed and surround the collapse scar bogs (Camill 1999a), therefore by tracing the forest-wetland interfaces it is possible to determine the extent of permafrost through time.

4.2.3 Statistical analysis

A univariate analysis of variance (ANOVA) was used to determine whether the degree of connectivity determines water chemistry. Dependent variables included: dissolved oxygen (mg/L), water temperature (°C), nitrate (mg/L), ammonium (mg/L), pH and conductivity (µs/cm). The independent variable was the degree of connectivity. Only the isolated, ephemerally connected, and fully connected wetlands were included as the marsh site had no replication of measurement in the wetland. It is depicted in figures for reference only. Only ammonium and DO met the assumptions of the ANOVA. Transformations failed and thus the remainder of the environmental variables were tested using the Kruskal Wallis test with the Kruskal function from the agricolae package in R (Mendiburu 2013). Proportional fen species abundance has already been calculated in Chapter 2 and illustrated in Figure 2.11.

Species were classified into three groups: bog, fen/marsh, or generalist species. The classification was determined with the help of floras (Flora of North America Editorial Committee 1993; Vitt et al. 2011; Klinkenberg 2013) and their description of the species expected habitat. These categories were used to compare differences in vegetation (with a Kruskal Wallis analysis) with differences in spectral imagery, as there was a darker green band coincident with the colouration of fen vegetation that extended the length of the bog.

To examine changes in species composition and environmental variables with distance from the fen, I conducted linear regression analyses. Distance, following the path of least hydrological resistance, between each site and the opening of the fen was measured in ArcGIS and used as the predictor. Dependent variables included

conductivity and pH, which were found to be important water chemistry variables in Chapter 3.

4.3 Results

4.3.1 Increased connectivity and its effects on peatlands

In general, increased connectivity corresponded with changes in water chemistry (Fig. 4.2). From an isolated bog to a fully connected bog or marsh/fen, the data demonstrate an increase in pH, temperature, nitrate and ammonium (although the marsh/fen sampling point had a low ammonium reading), a decrease in DO, and no trend with conductivity. The ANOVA (for DO and ammonium) and Kruskal Wallis (pH, temperature, nitrate, and conductivity) indicated that both pH and temperature showed a significant increase between fully connected and isolated/ephemerally connected bogs. Nitrate increased between fully connected and ephemerally connected bogs but was similar between fully connected and isolated bogs. Overall, even when pH and temperature showed an increase between connections, no difference was found between isolated sites and ephemerally connected ones. No statistical differences were found with the ANOVA between proportions of fen species between different levels of connection.

4.3.2 Flooding events

As expected, there was a decrease in fen-like conditions as distance from the marsh/fen increased; specifically, lower pH and conductivity were found at sites further from the marsh/fen (Fig. 4.3). This is suggestive of differential frequencies of flooding events. The flood model was used to quantify how far the nutrient rich fen waters could potentially reach in the bog. The highest the fen water elevation got in the last decade

was 268.9 m a.s.l. and this happened during a springtime flooding event. This corresponds to an infiltration of approximately 170 meters into the bog and only covers a small fraction (approximately one eighth of the bog) (Fig 4.4). There were never fen water levels high enough to flood the entire bog (Table 4.1).

4.3.3 Spectral imagery and ground truthing

Spectral imagery clearly depicts a band of greenish vegetation similar to the spectral signature of fen vegetation. This extends the length of the bog (Fig. 4.5). This was corroborated with ground truthing, as rich fen species were found throughout this band (Fig. 4.6). Furthermore, there was a significantly higher proportional representation of fen species at the sites found within the green spectral band compared to sites found outside this band but within the bog (Fig. 4.7).

4.3.4 Permafrost thaw

The fully connected bog has been fully connected since 1977, however, the extent of connection is variable with time; more southerly bogs have been connected to the marsh/fen for the shortest time. Most of the sampling sites were on areas that have always been bogs according to the aerial image analysis, therefore any rich fen species would be a result of allogenic changes (Fig. 4.1).

4.4 Discussion

4.4.1 Thresholds and allogenic succession

Allogenic successional theory tells us that increased external forcing in the form of permafrost thaw and increased connectivity should eventually convert a bog into a fen

peatland system (Arlen-Pouliot and Bhiry 2005; Lamentowicz et al. 2008). In this study the initial hypothesis was that permafrost thaw serves as that external force, and both water chemistry and fen species' proportions agree with this theory to some degree (Fig. 4.2, Fig. 2.11). Although generally there is an increase in fen-like conditions with increased hydrological connectivity, it is not always significant; when it is present, it is not significant for every level of connection. Isolated and ephemerally connected bogs had similar water chemistry and species composition; however, we did see an increase in nitrate, pH, and temperature between ephemerally connected and fully connected bogs. This suggests that connection to the fen is an important driver of these changes. The marsh/fen habitat is very different than the other three categories for both water chemistry and species composition.

The lack of strong differences in water chemistry between the different levels of hydrological connection may simply be attributable to the bogs high resilience to change; therefore this comes down to a question of thresholds. Scheffer et al. (2001) examined how thresholds can influence species composition. If an ecosystem has two stable states (in this case a bog or a fen) there needs to be a catastrophic event that will tip the equilibrium in favour of the other stable state. When comparing most water chemistry variables amongst connection level there isn't a difference, which may be attributable to insufficient interactions between bog and fen waters. As ephemerally connected bogs are only connected during the spring or summer time, there could simply be not enough water exchange. Fully connected bogs, being connected all year round, already lead to communities closer to those found in fens, but to have that whole sale species community change that we haven't been able to capture in Chapter 2, there needs to be that

catastrophic event that will be able to tip the balance and start ecosystem conversions (Scheffer et al. 2001; ACIA 2004; Granath et al. 2010). In the case of this study, flooding serves as the catastrophic force driving species change, which has been known to cause a shift from bog to fen characteristics in other systems (Asada et al. 2005; Bauer and Vitt 2011).

There is an increase in fen like composition at the sites closer to the mouth of the marsh/fen. These changes include: increased pH and conductivity (Fig. 4.3), as well as presence of rich fen species (Fig.4.6). The relationship between the distance from a site to the marsh/fen and both the biotic and abiotic characteristics of that site indicate that surficial flooding could be responsible for the observed changes in this bog. Surficial flooding has been shown to reverse the normal successional pathway of a fen to a bog (Asada et al. 2005; Vitt 2006; Bauer and Vitt 2011). The potential for flooding from the fen/marsh into the fully connected bog has been recorded by the data loggers at this site between 2003 and 2012 (Table 4.1). Fen/marsh water was found to minimally encroach into the bog for most years except for 2004 and 2009 (no data was available for 2008). However, important flooding events only happened in 2007 and 2011 and were the only times water did more than encroach; these were the years that reached the maximum extent described in our model. Therefore, it could be that flooding is not constant enough to cause these changes.

In order to quantify whether or not flooding could be responsible for the varying conditions, we looked at the maximum penetration of water flow from the marsh/fen into the bog during one of these flooding events, which corresponds to a time when the water elevation was higher than the elevation at the mouth of the bog. The water was found to

extend through many of the quadrats in the first (northernmost) site, but did not extend further under maximum flooding conditions. DEM and water level data did not indicate that nutrient rich water from the marsh/fen was going very far into the bog. It is also important to mention that our model showed the furthest possible extent the fen water could penetrate into the bog as it does not take into account hydraulic head, where the water table in the bog would be higher and would be pushing fen water further into the fen. Despite this, rich fen species were found throughout the bog, thus flooding of bog vegetation cannot fully explain the distribution of fen vegetation in the bog. Similarly, the spectral imagery clearly shows an extended green colored band (the same spectral signature of fens) going from the mouth of the fen all the way down the bog. Ground truthing verified that rich fen species such as *Utricularia intermedia*, *Scorpius scorpioides*, and *Paludella squarrosa* were found throughout this band and much further than was possible if flooding alone were driving these changes. Sites found within this band also contained more fen like species than those found outside of it. As we only have data for the last decade, it could be possible that one major flooding event within the last fifty years could bring in the necessary nutrients. However, looking at precipitation data available in Quinton et al. (2009), we can see that, aside for one year in the 1980's that was extremely wet (precipitation at least 200 mm more than the mean), the last decade have been amongst the wetter years. We also lack the data to see if that extremely wet year was in the form of snow or rain, and if it was one main precipitation event or many. We therefore think there must be another process at play driving the vegetation and water chemistry characteristics of this site.

4.4.2 Potential mechanisms of change

If flooding is not solely responsible for the increase in rich fen species, permafrost thaw itself could be an important mechanism of change. Keuper et al. (2012) performed a study where they quantified nutrients released by permafrost as it thaws. They found that permafrost had plant - available nitrogen concentrations that were seven times higher than in rooting soil, which could potentially be used by species such as *Rubus chamaemorus* or other deep rooting species (these values ranged from 8 mg N/m² in rooting zone to 31 mg N/m² in permafrost soil for nitrate and 30 to 252 mg N/m² for ammonium) and therefore areas with increased thaw could support more fen like species with their higher nutrient concentrations. Figure 4.5 shows that the green band corresponds closely to areas that have always been bog; therefore, it could be that the nitrogen trapped in the permafrost is being released throughout the bog and that long-term addition of nitrate with constantly degrading permafrost edges is important in driving changes in plant community. This might also explain why changes have been restricted to this band where permafrost thaw has been extensive and that widespread changes have not been more dramatic after 50 years. Permafrost thaw can also lead to the discharge of both dissolved organic carbon and dissolved organic matter (Frey and Mcclelland 2009), which are important in determining peatland gradients (Gąbka and Lamentowicz 2008). Combined with increased nutrients and dissolved organic carbons, this could sufficiently lower the ecosystem's resilience so that if a major event were to happen the threshold will be exceeded and there will be reversal of peatland type. Permafrost has been thawing extensively at Scotty Creek - plateaus having been reduced by 27% over 60 years (Chasmer et al. 2011).

4.4 Conclusion

Chapter 2 determined that each wetland had a specific and distinct species community and that while fens were going through autogenic processes (decreasing in richness as autogenic succession decreased hydrological connection), bogs were extremely resilient to increased hydrological connectivity attributable to permafrost thaw. Chapter 3 demonstrated that rich fens have distinct environmental conditions from poor fens and bogs, and that there is some evidence of allogenic changes happening in bogs, where pH and nitrate differed between ephemerally connected and fully connected sites. These increases are related; as connections are increasing there is increased conductivity that neutralizes the pH, which in turn increases nitrate (Appendix 4.1). It also showed that conductivity is an important predictor for fens but that there was not a predictor that was found for bogs; it is possible that *Sphagnum* spp. could be engineering their ecosystem. In this Case Study we determined that flooding events associated with increased hydrological connectivity may be insufficiently large to convert a bog back into a fen. Despite this, this reversal appears to be occurring. Although flooding also cannot account for whole ecosystem changes it could play some part in changing the peatland, but what causes the reversal requires further research. This can be concluded by the shift in fen-like conditions for sites closer to the mouth of the marsh/fen. However, since rich fen species are being found further into the bog than can be explained by flooding this means that new water interactions are not the only factor to consider. Our hypothesis is that the permafrost itself is releasing nutrients and dissolved organic matter as it thaws, which means that permafrost thaw will both increase water interactions but also increase nutrient concentrations. Evidenced by the significant change in pH, it is most likely that

water chemistry will be the first to change and species community will follow. As the different peatlands have different species communities and different environmental conditions, the conversion of one of these peatlands to another would lead to wetland redistribution, changes in species, and in ecosystem functions.

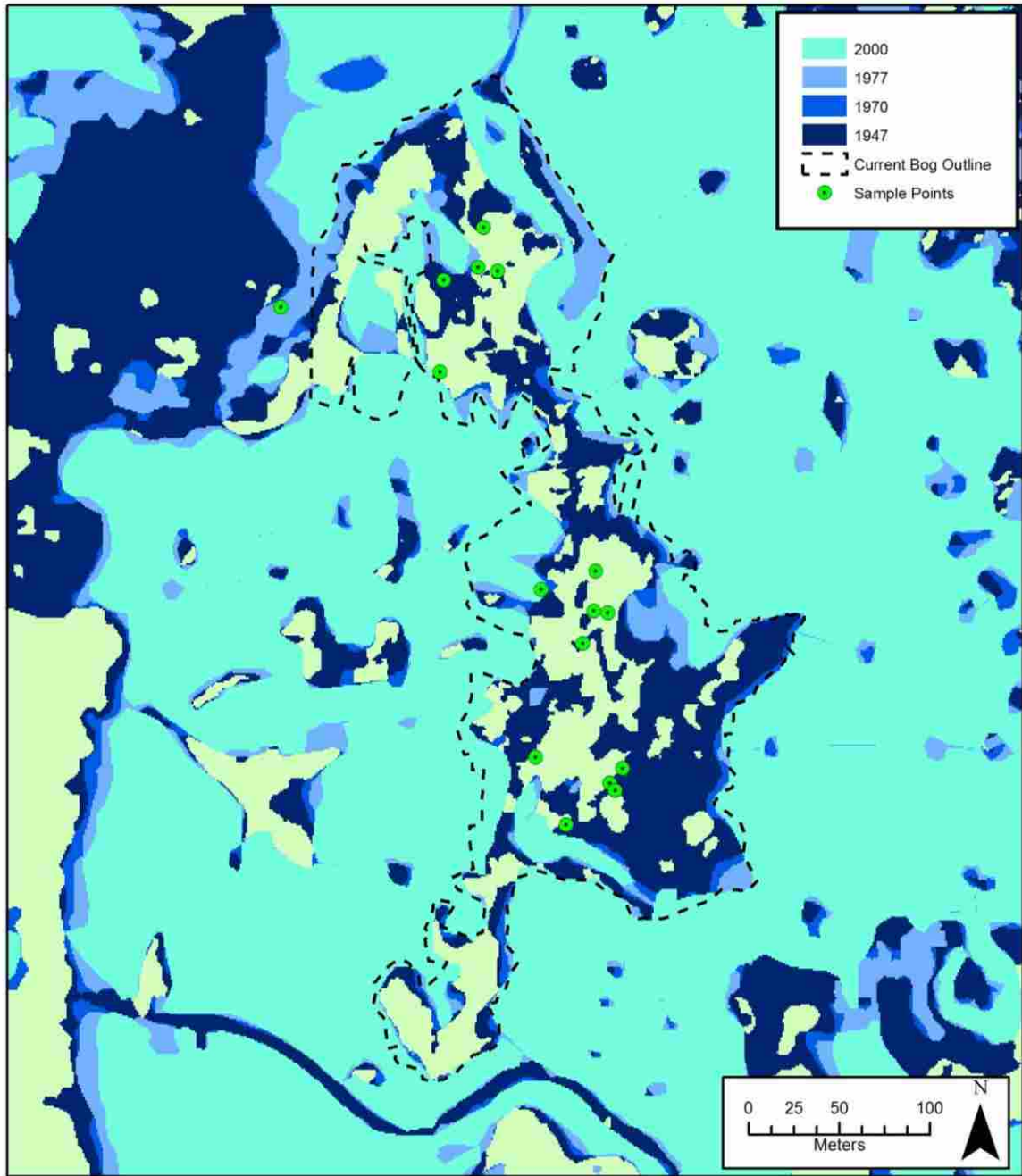


Figure 4.1: Permafrost thaw through the years (1947, 1970, 1977, 2000 and 2010) at study collapse scar bog site in Scotty Creek (NWT), green dots correspond to sampling points. The edge of the plateaus were manually digitized using aerial photos (1947, 1970, 1977), IKONOS multispectral satellite image (2000) and WorldView 2 (2010) imagery. 1947-2010 was digitalized by L. Chasmer, while 2010 was done by M. Fafard.

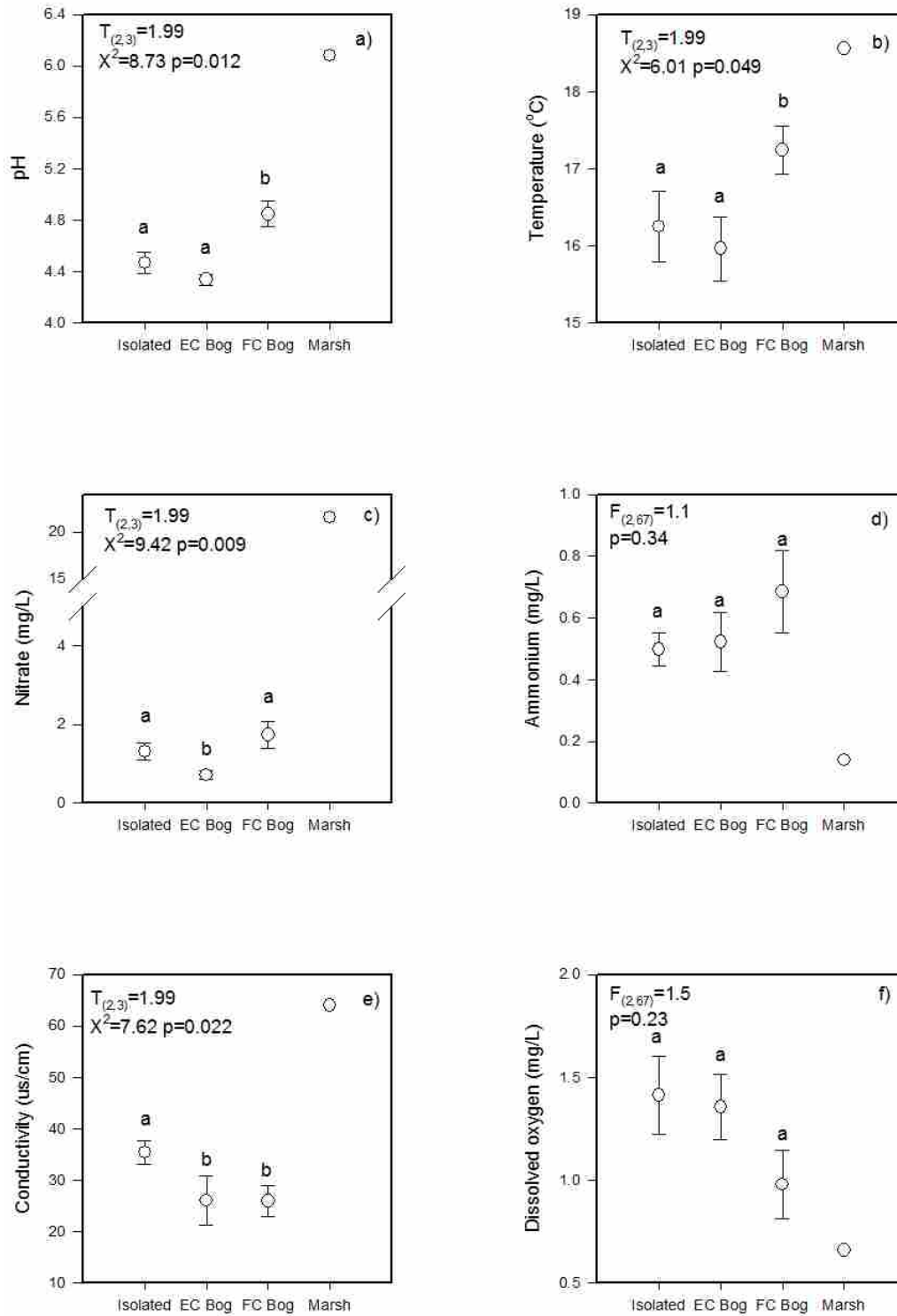


Figure 4.2: Mean (+/- SE) water chemistry parameters as a function of wetland type a) pH b) Temperature (°C) c) Nitrate (mg/L) d) Ammonium (mg/L) e) Conductivity (µs/cm) f) dissolved oxygen (mg/L). ANOVA or Kruskal-Wallis results are indicated on each panel as well as posthoc analysis. See figure 2.11 for fen proportion analysis.

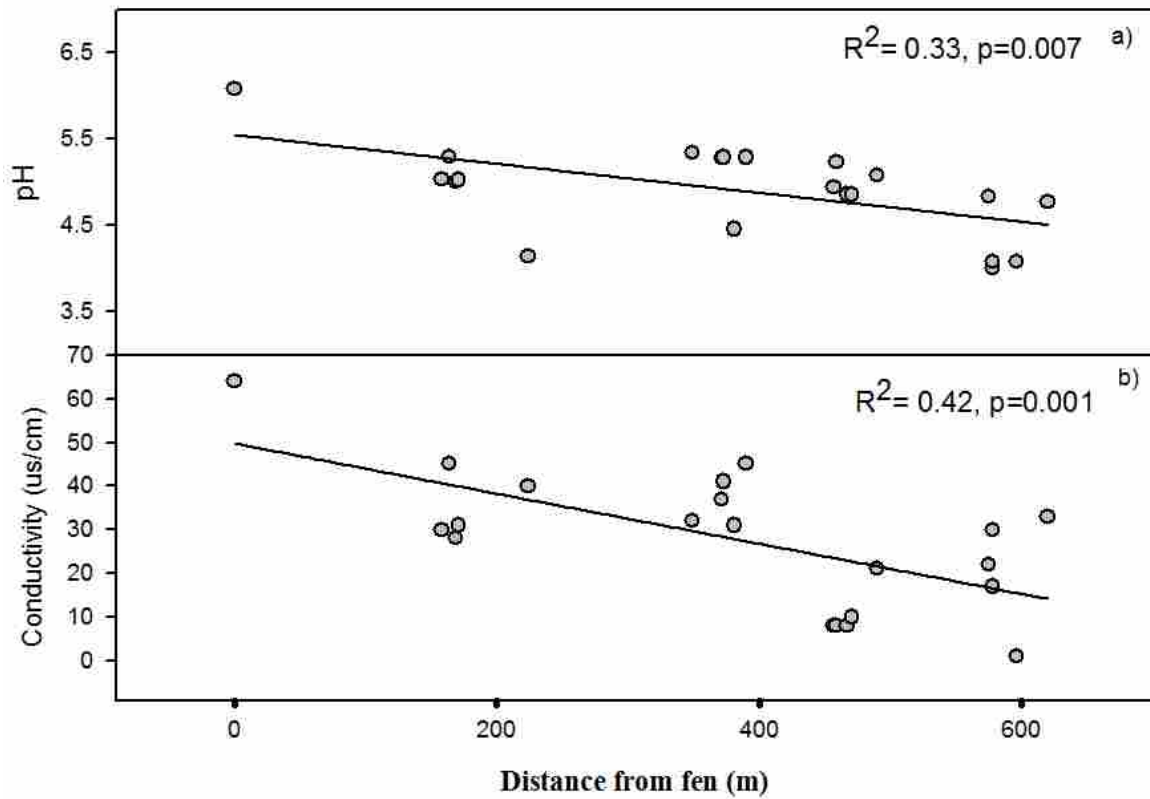


Figure 4.3: Linear regression between environmental variables within a fully connected collapse scar bog at Scotty Creek (NWT) and their distance to the connected fen. Assumptions for the linear regression were met. Distance was calculated as the path of least resistance hydrologically in ArcGIS. Panel a) pH with distance ($R^2=0.33, p=0.007$). Panel b) conductivity ($\mu\text{S/cm}$) with distance ($R^2=0.42, p=0.001$)

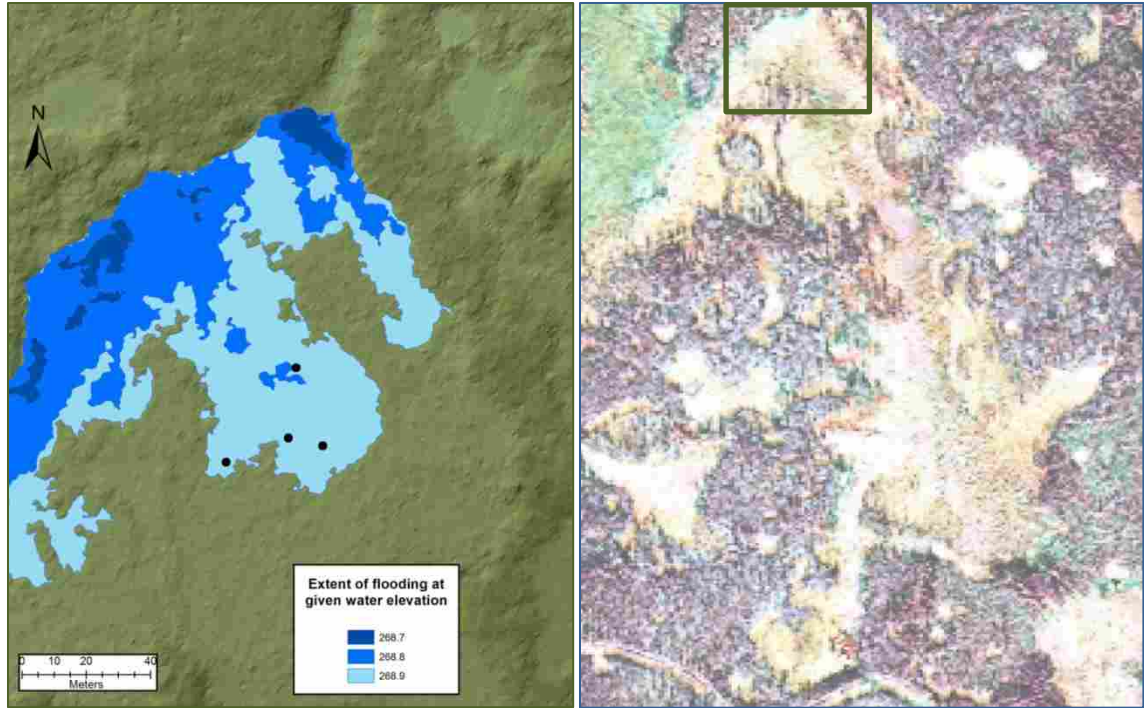


Figure 4.4: Left) Flooding extent into the studied bog indicating the elevation of the flood and distance the water will reach. The left panel is a close up of the northwestern tip of the bog, which is directly attached to the fen. This area is represented by a green square in the right panel. Right) WorldView2 image of the fully collapse scar bog at Scotty Creek (NWT). The greenish area at the top represents the fen like vegetation, with the yellow colour being more bog like. The smaller image represents a flooding model in the region.

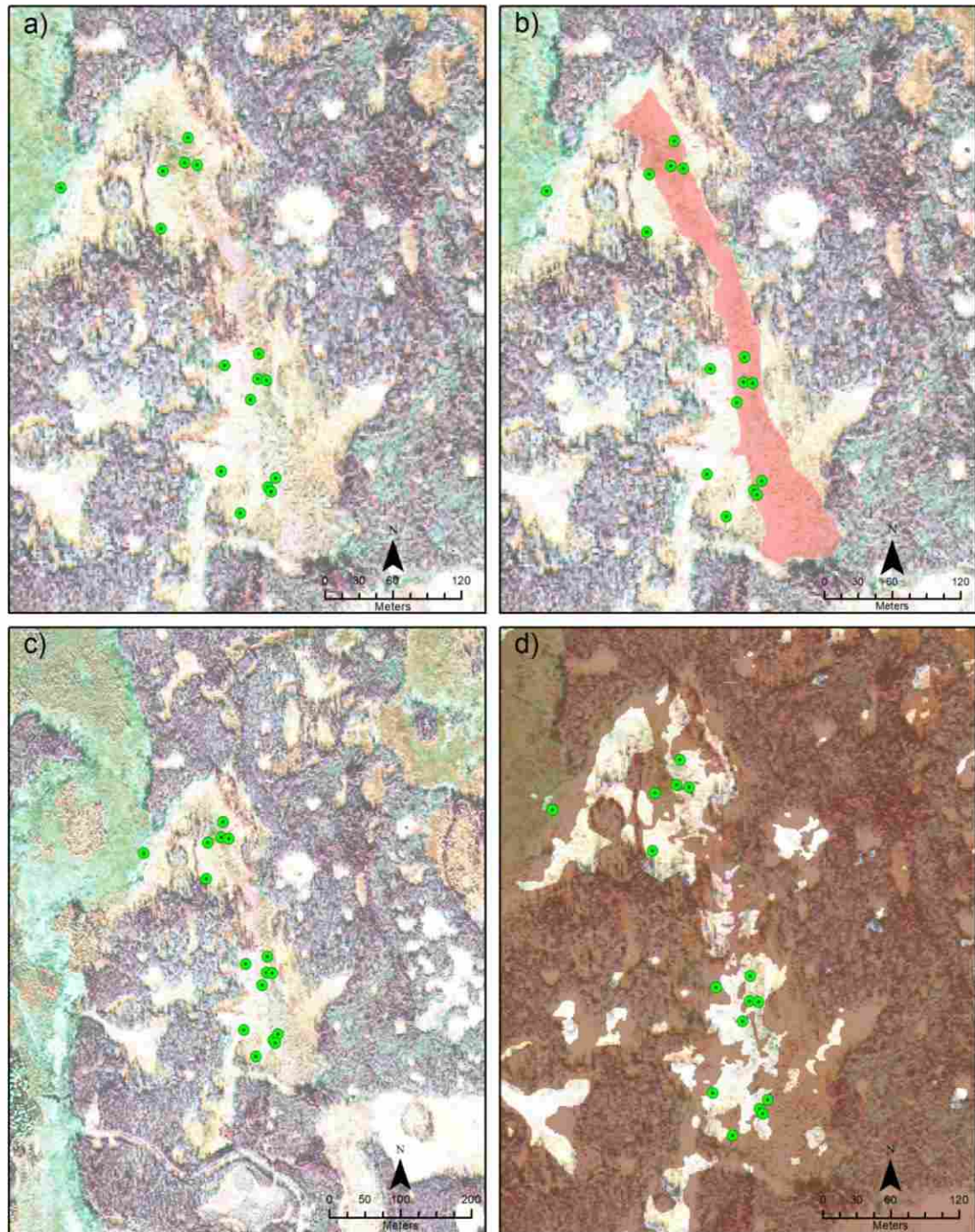


Figure 4.5: a) Fully connected bog found at Scotty Creek (NWT), sampling points are portrayed as the green dots. Area highlighted in panel b) corresponds to a darker green colour that is also found in the fen (clearly seen in panel c) and happens to have many high nutrient species. Panel d) looks at the extent of permafrost from 1947, which was digitalized using aerial photos. The lighter colours represents the bog and the darker the permafrost extent in 1947.

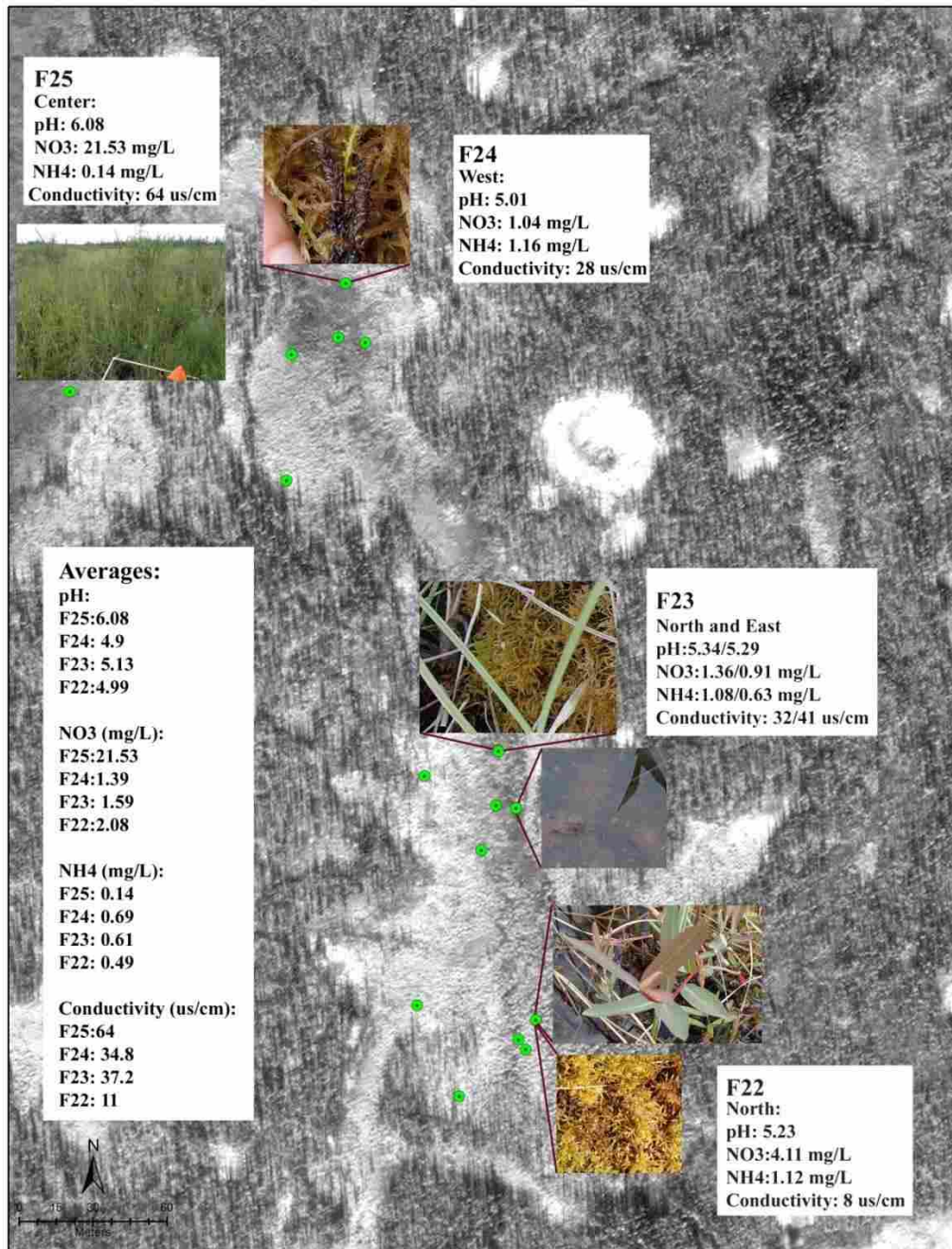


Figure 4.6: Study site along with species that are normally not found in a bog and the environmental characteristics at those quadrats along with averages at the sites. F25 was a single measurement point so an average couldn't be calculated.

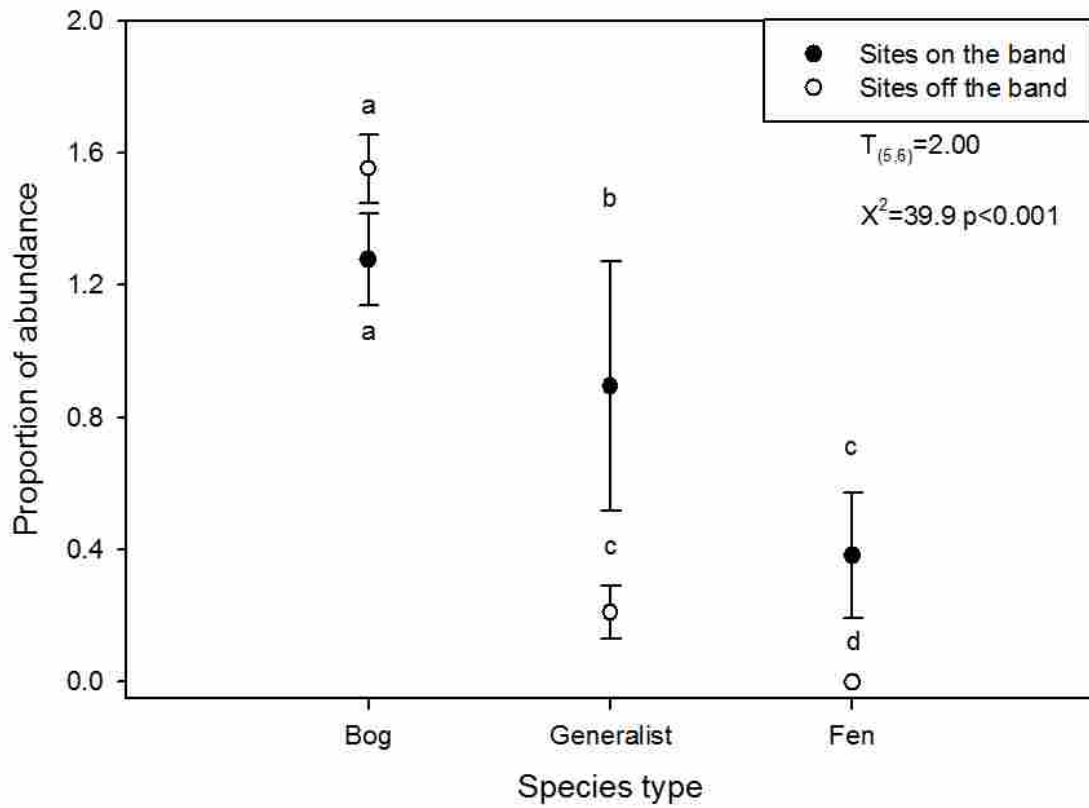
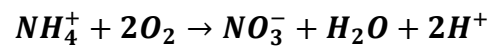


Figure 4.6: Mean (+/- SE) proportional abundance by species type within and outside of the green spectral band depicted in Fig 4.5. Species were found within the fully connected bog at Scotty Creek (NWT). Kruskal Wallis results are presented. Lowercase letters correspond with posthoc differences.

Table 4.1: Flooding model, based on water table elevation within a channel fen connected to a fully connected bog at Scotty Creek (NWT). This table represents the percentage of how often water table met or exceed the elevation categories during a given year.

Flood Situations	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Water encroachment Water level above 268.7 m a.s.l.	5%	0%	13%	32%	99%	NA	0%	100%	100%	30%
Partial submersion Water level above 268.8 m a.s.l.	0%	0%	0%	0%	84%	NA	0%	0%	98%	0%
Maximum extent of flooding into the bog Water level above 268.9 m a.s.l.	0%	0%	0%	0%	84%	NA	0%	0%	93%	0%

Appendix 4. 1 : Nitrification equation found in Wetzel 2001



Chapter 5

Conclusions and integrative biology

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In this thesis, the role of permafrost thaw on plant succession was examined both through species community composition and environmental parameters. Although species community did not show a distinct difference between the different levels of hydrological connectivity (fully connected, ephemerally connected, and isolated peatlands), there was a difference in species richness between connected and fully connected rich fen sites as expected under autogenic successional theory (Zobel 1988). It was also found that bogs are extremely resilient to changes in permafrost thaw, but even with this high tolerance, rich fen species are starting to colonize. Conductivity was shown as an important predictor of species community for fens and fully connected peatlands, while bogs and isolated peatlands rely more on species composition and water table as drivers of environmental conditions. There is evidence of allogenic changes found in differences in water chemistry, where increasing the connectivity of a bog results in higher pH and nitrate. Flooding, permafrost thaw, and nutrient inputs are all mechanisms for engineering changes in peatland plant species composition.

By characterizing the different communities of species found within these different wetlands, it will be possible to continue monitoring communities at Scotty Creek to assess when and if a threshold has been passed resulting in more extensive homogenization of vegetation. By knowing which environmental parameters affect species composition, it is possible to further understand how climate change may impact peatlands as a whole. For instance, Chapter 3 identified increased connectivity that we hypothesized was brought on by increased groundwater as an important predictor of species community. With increased permafrost thaw resulting from climate change, there will be greater access to groundwater and this in turn will affect community composition.

This thesis integrated aspects of 1) hydrology and ecology, 2) field-based and remote sensing techniques, and 3) related them back to global changes in climate.

Permafrost is an incredibly important aspect of boreal peatlands as it controls drainage and moisture, and has been studied extensively (Quinton et al. 2003; Johansson et al. 2006; IPCC 2007; Schuur et al. 2007; Quinton et al. 2009; Jorgenson et al. 2010; Quinton et al. 2011). However, this thesis served to describe how permafrost thaw related changes in hydrology drive species composition and environmental conditions. Permafrost thaw leads to increased connectivity between wetlands and also the potential release of nutrients. In Chapter 2, rich fens are losing species in ephemerally connected sites, which can relate back to hydrology and how these sites are losing access to ground water sources. At bog sites, increased permafrost thaw could be leading to the reversal of wetland succession as it may help bring in nutrients. Chapter 3 looked at water chemistry data and found that environmental conditions may be changing more quickly than species composition as evidence of allogenic changes could be seen with pH and nitrate. Chapter 3 also found that increased connectivity (which in turn indicates high conductivity as cation rich water is indicative of groundwater) impacts almost every aspect of fen water chemistry; however, for this study we did not have a true quantification of the amount of groundwater at the different sites. Future work should be done to test specifically for increased species richness and groundwater presence. Finally, Chapter 4 examined flooding events and found that these events did not last long enough to make a significant impact on species composition, but that other aspects of permafrost thaw may drive important biogeochemical changes.

The second integrative aspect of my research is combining both field based approaches for modeling and remote sensing. Chapter 2 found a decrease in richness for ephemerally connected rich fen sites based on ground survey data. To be able to fully understand species succession it was necessary to look at past historic photos, which permitted us to find that ephemerally connected rich fen sites were in fact shrinking. This is a further example that the data that was collected in the field is a valuable tool for models and can lay the groundwork for future predictions. Chapter 4 was able to rule out flooding as the main cause for the presence of rich fen species by combining modeling approaches with field-based survey data. By integrating these two approaches, it was possible to facilitate broader interpretation of the ground based data and validate remote sensing patterns.

Finally, my work examined the effects of permafrost thaw on ground vegetation, which relates back to the broader issue of climate change. The more temperature rises, the more permafrost will thaw - this can eventually push these ecosystems beyond their threshold and lead to complete species composition change and the conversion of wetlands. Peatland conversion and loss of species can impact the carbon balance, as fens are known to release more methane than bogs further aggravating climate change (Strack et al. 2006; Mahmood and Strack 2011).

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