POST-FIRE CHRONOSEQUENCE ANALYSIS OF PEATLAND BOG VEGETATION COMMUNITIES ACROSS HYDROGEOLOGICAL SETTINGS

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TITLE: Post-Fire Chronosequence Analysis of Peatland Bog Vegetation Communities Across Hydrogeological Settings

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ABSTRACT

Canada's Boreal Plains peatlands comprise 2.1% of the world's terrestrial carbon store and are vital water supplies for adjacent upland ecosystems in this sub-humid climate. Projections indicate that future drought and wildfire events will be more frequent and severe, enhancing moisture deficits and threatening the functional role of peatlands as net carbon sinks. Peatland margins existing at the peatland-upland interface have been identified as deep smouldering hotspots on the landscape, where margin carbon loss accounts for 50 to 90% of total peatland carbon loss, dependent on hydrogeological setting. Previous chronosequence analysis of peatland bog recovery from wildfire disturbance has chronicled a return to carbon sink status within 20 years, but has not included margins nor peatlands located in coarse or heterogeneous-textured hydrogeological settings with varying degrees of groundwater connectivity. This analysis identifies and describes margin vegetation communities and recovery trajectories with time since fire and across hydrogeological settings. No significant differences were identified in margin area over time or margin peat depths across hydrogeological settings. Margin canopy composition consists of mixed coniferous and broadleaf deciduous species, with enhanced litterfall characterizing the dominant early to mid successional ground layer composition. Both peatland bog middle and margin vegetation communities were found to be dominated by feathermoss growth ~60 years following wildfire, which represents an accelerated trajectory from previous chronosequence analyses. Increased peatland and margin fuel loads with time since fire are also demonstrated using aboveground biomass calculations. Restoration practitioners can use this study to identify recovery milestones and altered trajectories, with their associated feedbacks, that perpetuate a broadleaf canopy and limited *Sphagnum* moss paludification. Fire managers should include confined peatlands in coarse-textured hydrogeological settings with deep smouldering margins in their management considerations and consider intervention (forest treatments) to open the canopy and prevent legacy carbon losses by severe wildfires.

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Basal diameter	BD
Biomass	BM
Boreal Plains	BP
Canopy closure	CC
Coarse	C
Coarse - Heterogeneous	CH
Diameter breast height	DBH
Diversity	Div
Fine	F
Moraine - Fine	MF
Moraine - Heterogeneous	MH
Non-Metric Multidimensional Scaling	NMDS
Peat depth	PD
Richness	Rich
Split Moving Window	SMW
Squared Euclidean Distance	SED
Time since fire	TSF
Water table depth	WTD

DECLARATION OF ACADEMIC ACHIEVEMENT

This main chapters of this thesis (2 and 3) have been prepared as independent manuscripts for submission to peer-reviewed academic journals. There is a fair degree of repetition in the introduction and methods to make each of the chapters stand-alone documents.

The work presented in this thesis is the result of collaborative research, with the contributions of the candidate including site selection and vegetation survey data collection and analysis. GIS assistance was provided by Craig Allison and significant field assistance by Sophie Wilkinson, Rebekah Ingram and Cameron McCann. Categorization of sites into hydrogeological settings was completed by Rebekah Ingram. Dr. Paul Moore significantly contributed to the experimental design and data analysis.

CHAPTER 1: INTRODUCTION

1.1 Boreal Plains Peatlands

Boreal Plains (BP) wetlands account for up to 50% of the landscape, with a high density of small depression ponds and peatlands underlain by deep glacial deposits (Kuhry *et al*., 1993; Devito *et al*., 2012). The peatlands, geogenous fens and ombrogenous bogs with at least 40 cm of organic soil, are important water and carbon stores with an estimated 48 Pg carbon, representing 2.1% of the world's terrestrial carbon (Zoltai and Vitt, 1995; Vitt *et al*., 2000). The rate of peatland initiation in this region peaked around 6,000 years ago, following an initial deglacial lag (Zoltai and Vitt, 1990; Halsey *et al*., 1998; Gorham *et al*., 2007). Although carbon accumulation has slowed in the last 3,000 years with permafrost development and as the current southern extent of peatlands was reached, continental peatlands continue to increase their carbon storage today by an estimated 7.1 Tg carbon yr^{-1} (over last 1,000 years), indicating that the BP region remains a net carbon sink (Vitt *et al*., 2000).

Early peat forming communities on the BP varied from marshes and swamps to wet fens formed via terrestrialization, infilling of shallow waterbodies, or paludification, direct establishment of peat in areas formerly occupied by upland vegetation (Bauer *et al*, 2003; Kuhry and Turunen, 2006). A successional gradient from marsh to minerotrophic rich fen to ombrotrophic bog communities isolated from nutrient rich groundwater (ombrotrophication) with time has been documented in many study peatlands in this region (Zoltai and Vitt, 1990; Halsey *et al*., 1998). Associated species dominance at each stage shows an abundance of ground layer monocots in marsh and fen communities to an increasing abundance of non-vascular bryophytes including brown mosses in rich fens and *Sphagnum* mosses in poor fens and bogs (Kuhry *et al*., 1993; Bauer *et al*., 2003). This successional trajectory may not proceed unidirectionally, but rather via transitions to alternate stable states (Granath *et al*., 2010). A rapid shift may arise and be sustained through positive autogenic feedbacks or disturbances, such as drought or wildfire.

1.1.1 *Sphagnum* mosses as keystone species

The invasion and expansion of keystone *Sphagnum* moss species plays a key role in ombrotrophication, or the successional gradient from fen to bog peatlands (Granath *et al*., 2010). In the BP, the formation of extensive peat deposits relies on only about six *Sphagnum* species, with most carbon sequestered within belowground *Sphagnum* biomass (Halsey *et al*., 1998). Ecophysiological traits of *Sphagnum* that allow it to efficiently store carbon and form extensive peat deposits include its high specific yield, ability to acidify its environment, further perpetuating *Sphagnum* expansion, and its relatively high composition of lignin-like compounds slowing rates of decomposition (Halsey *et al*., 2000).

There are three primary gradients within peatlands: microtopographical variation creating hummock-hollow landforms, peatland expanse to margin and degree of minerotrophy (Graham *et al*., 2015). Within the *Sphagnum* genus, species composition and associated community structure, or microtopography, is important in regulating peatland water tables and rates of peat accumulation versus decomposition (Belyea and Clymo, 2001; Malhotra *et al.*, 2016). Each *Sphagnum* species is adapted to niches within the microtopographical gradient (Gignac *et al*, 1991). Species of Section Acutifolia (*e.g. Sphagnum fuscum*) are densely packed, adapted to maintaining high moisture contents via external capillary flow with increasing distance from the water table (Wagner and Titus, 1984). Hollow species tend to be of Section Cuspidata (*e.g. Sphagnum angustifolium*), favouring constant connection to the water table. Later successional species of bogs, particularly feathermosses (*e.g. Pleurozium schreberi*) can also inhabit hummock positions, preferably in drier sites with greater shading from the black spruce (*Picea mariana*) canopy (Bisbee *et al*., 2001; Mulligan and Gignac, 2001). Peatland species and microforms arise through successional processes and interaction between biotic and abiotic elements of the system. Ecohydrological feedbacks act to maintain carbon and water storage function of these systems, increasing their resilience to disturbances such as periodic drought or wildfire (Waddington *et al*., 2015).

1.1.2 The importance of feedbacks in maintaining peatlands

The vulnerability of carbon stored in BP peatlands to decomposition or wildfire combustion is primarily controlled by water table depth (WTD) and associated moisture content of near-surface peat (Thompson and Waddington, 2013b). For fen peatlands, the water table is maintained by groundwater inputs and these systems are generally considered resilient, apart from severe disturbances (prolonged drought) that may impact the regional water table. Bog peatlands, with ephemeral to no groundwater connection, rely on key negative hydrological feedbacks that maintain or stabilize local water tables and associated species such as *Sphagnum* mosses adapted to periodic water table drawdown (Kettridge and Waddington, 2014; Waddington *et al*., 2015).

1.1.2.1 Negative feedbacks

The WTD – moss surface resistance and albedo feedback occurs when near-surface tensions in *Sphagnum* mosses increase with water table decline (specifically declines > 0.4 m), and an evaporative cap is created at the moss surface, limiting further evaporation and desiccation (Thompson and Waddington, 2008; Kettridge and Waddington, 2014; Waddington *et al*., 2015). Similarly, the WTD – transmissivity feedback describes the ability of a peatland to prevent lateral water losses through the margins existing at the peatland-upland interface, where generally higher bulk density, lower hydraulic conductivity peat acts as a low transmissivity curtain. Lastly, the WTD – peat deformation feedback describes the movement of the peat surface with seasonal water table fluctuations, which dampens changes in WTD relative to the peat surface and maintains capillary connection to the moss capitula.

Bryophyte and vascular plant species distribution and associated microtopography within peatlands are also important drivers in maintaining water tables, with microtopographical shifts to more abundant hummock species, that are better able to retain moisture, acting as an adaptation to prolonged drought (Strack *et al*., 2009; Moore *et al*., 2015). Overall, these feedbacks increase the resilience of these systems to disturbance (Waddington *et al*., 2015; Moore and Waddington, 2015).

1.1.2.2 Positive feedbacks

The positive hydrological feedbacks are those that can reinforce an external perturbation, such as drought, and hence could result in runaway consequences (Waddington *et al*., 2015). The two with the most influence include the WTD – afforestation/shrubification feedback, which describes increased tree and shrub encroachment into successionally drier peatlands (those mounded further and further from the water table with time), which results in increased evapotranspiration and shading, changes in ground layer species composition to increased feathermoss over *Sphagnum* composition, and overall reinforces water table declines (Kettridge *et al*., 2013; Waddington *et al.,* 2015). The second is the WTD – specific yield feedback whereby specific yield declines sharply with depth in the peat profile (dependent on the degree of humification and hence peat porosity and bulk density), limiting the ability of peat to regulate fluctuations in water table with depth. If the water table drops, further water withdrawals from the peatland result in proportionally greater water table declines.

1.2 Disturbance Regimes

1.2.1 Climate Change and Drought

Climate acts as a primary control on peatland distribution and expansion, with BP peatlands existing today in a sub-humid climate characterized by frequent moisture deficits (precipitation < potential evapotranspiration; Gignac *et al*., 1991; Devito *et al*., 2012). There are large inter-annual variations in the climate cycle of this region, with roughly decadal drought cycles. The ability of peatlands in this climatic setting to conserve and supply water to surrounding upland ecosystems likely acts as a buffer against ecosystem collapse during drought cycles (Kettridge *et al*., 2015; Thompson *et al*., 2015a). Climate projections indicate that the frequency and intensity of drought will increase under future temperature and precipitation regimes in the BP, with projected increases in evapotranspiration expected to exceed increases in precipitation (Collins *et al*., 2013; Price *et al*., 2013).

A modelling study of peatland sensitivity to future climate warming has indicated that ~60% of Canadian peatland area and 51% of the associated carbon storage is expected to be severely to extremely severely affected by climate change (Tarnocai, 2006). The most dramatic changes are expected at the current extents of peatland distribution, namely within permafrost peatlands of the subarctic and southern boreal peatlands. Climate warming is expected to increase vapour pressure deficits, evapotranspiration and summer moisture deficits within continental peatlands, leading to water table drawdown (Roulet *et al*, 1992; Ise *et al*., 2008). In turn, vegetation community shifts, greater peat decomposition rates and a net release of carbon to the atmosphere could occur (Gorham, 1991; Strack and Waddington, 2007).

1.2.2 Wildfire

Coupled with future climate projections and the potential impact on continental peatland water tables, there is a further concern that peatland carbon stocks will be more vulnerable to future combustion from wildfire (Turetsky *et al*., 2011). In the BP, wildfire is a significant peatland disturbance, consuming up to 1850 km^2 yr^{-1}, releasing 5.9 Tg carbon to the atmosphere via direct combustion (Turetsky *et al*., 2004; Turetsky *et al*., 2015). On an areal basis, average combustion rates from a peat fire are 2.4 kg carbon m^{-2}, which is equivalent to ~100 to 140 years of carbon storage (Benscoter and Wieder, 2003; Turetsky *et al*, 2011). Projections indicate that wildfire frequency and severity will increase in the future, with an increase in area burned in Canada by up to 118% by 2100 (Flannigan *et al*., 2005). In addition, individual fire intensity may increase and fire seasons will be longer (Flannigan *et al*., 2013). Although BP peatlands have co-evolved with a modern wildfire return interval of ~120 years (Turetsky *et al*., 2004; Wieder *et al*., 2009), changes in this disturbance regime has implications for fire management and peatland ecosystems as net sinks of carbon (Turetsky *et al*., 2002; Wieder *et al*., 2009; Turetsky *et al*., 2011; Johnston *et al*., 2015).

Peatland fires are generally dominated by smouldering combustion below the surface (Turetsky *et al*., 2015). These fires can persist for long periods in relatively lower temperature and higher moisture conditions than those needed to propagate flaming combustion. Hydrophysical properties of pristine peat such as low bulk density and high specific yield maintain peatland conditions too wet to ignite or sustain smouldering (Benscoter *et al*., 2011). However, when disturbances or fluctuating water tables alter these peat properties, peatlands become more vulnerable to smouldering combustion (Rein *et al*., 2008). A key component to peatland resilience to wildfire disturbance is a cover of *Sphagnum* moss, which maintains high surface water contents regardless of groundwater connection and thereby limits combustion (Shetler *et al*., 2008).

Studies of compound disturbances, such as peatland recovery from wildfire in previously drained systems, can draw inferences of potential impacts of wildfires on peat combustion in a drier climate future (Turetsky *et al*., 2011; Sherwood *et al*, 2013; Kettridge *et al*., 2015). Drained sites have exhibited up to nine times the depth of burn of undrained sites, attributable to increased tree cover, greater peat bulk densities, lower specific yield and lower surface moisture contents at the drained location (Turetsky *et al*., 2011; Sherwood *et al*, 2013). Severe combustion of surface peat layers can, in turn, impact hydrophysical and moisture retention properties of the newly exposed peat, specifically via the WTD – specific yield feedback whereby this new peat tends to have even higher bulk density and lower specific yield, leading to large water table fluctuations not favourable to the *Sphagnum* moss recolonization (Price and Whitehead, 2001; Kettridge *et al*., 2013; Thompson and Waddington, 2013a; Thompson *et al*., 2014; Lukenbach *et al*., 2016). The combustion of deep peat into potential legacy carbon stores that have not been a part of the active carbon cycle for centuries to millennia not only has implications for long-term recovery of these systems back to carbon sinks but also the feedbacks of these ecosystems on climate (Turetsky *et al*., 2015).

1.2.2.1 Intra and inter-peatland variation in burn severity

Peatlands with differing groundwater connection (fens and bogs), underlying surficial deposits, topographical positions and sizes (perimeter to area ratios) experience differing burn severities (Zoltai *et al*., 1998; Lukenbach *et al.*, 2015a; Hokanson *et al*., 2016). Bogs have been the focus of many studies on burn severity likely because of their isolation from groundwater regimes and assumption that they will be more susceptible to surface drying and combustion. Peat combustion recorded within BP bogs ranges from 1.8 to 4.9 kg carbon m^{-2} (Zoltai *et al*., 1998; Turetsky and Wieder, 2001; Turetsky *et al*., 2002; Benscoter and Wieder, 2003; Shetler *et al*., 2008).

Within-peatland variability in combustion can occur from heterogeneities in species composition and hydrology within microtopographic landforms, especially prevalent in bogs (Benscoter and Wieder, 2003; Thompson and Waddington, 2013b). Hollow species (Section Cuspidata) grow closer to the water table and form a looser arrangement of stems, leaving them more susceptible to desiccation and severe burning during drought periods. Post-fire microtopography is often accentuated by greater burn depths observed in hollows versus hummock landforms, as well as an increase in the hollow microform abundance (Benscoter and Wieder, 2003). The resulting heterogeneity of the ground layer can result in a variety of successional trajectories at the plot-scale (Benscoter *et al*., 2005; Benscoter, 2006; Lukenbach *et al*., 2015a).

Another variation in burn severity within a peatland system could arise from differences in hydrophysical and associated species properties in margins (peatland-upland transition zones) versus the interior, or middle, of the peatland (Bhatti *et al.,* 2006; Bauer *et al*., 2009; Lukenbach *et al*., 2015a). Peatland margins tend not to exhibit the hummock-hollow microtopography seen in middles and margin species diversity can be variable, with a mixture of peatland, riparian and upland species present, possibly due to increased pH, cation and nutrient concentrations from the influence of mineral substrates (Bauer *et al*., 2009; Graham *et al*., 2015; Paradis *et al*., 2015). Although aboveground carbon biomass capable of carrying a crown fire has been shown to decrease along the upland to peatland interface, total ecosystem carbon increases due to the larger influence of soil carbon stocks (Bhatti *et al.,* 2006). WTD in peatland margins is generally lower (Hartshorn *et al*., 2003; Bhatti *et al*., 2006), leading to more decomposed, denser peat at these interface locations. This peat has a lower specific yield and, as such, is prone to further water table drawdown in periods of drought or high demand by adjacent upland forest ecosystems (Ferone and Devito, 2004; Petrone *et al*., 2007; Waddington *et al*., 2015). These margin peat properties can help to maintain the groundwater mound in raised bogs via the WTD – transmissivity feedback and buffer the system from surrounding upland minerotrophic water (Ingram 1982; Howie *et al*., 2013; Waddington *et al*., 2015), however they can also make margin peat vulnerable to severe smouldering in wildfires. Depth of burn in peatland margins with ephemeral groundwater connection can be up to eight times greater than that exhibited in middles (10 to 85 kg carbon m^{-2}), with margin carbon loss accounting for 50 to 90% of the total peatland carbon loss (Lukenbach *et al*., 2015a; Hokanson *et al*., 2016).

Similar to drained peatland scenarios, this severe margin smouldering can suspend the key negative feedback mechanisms that stabilize the water table and facilitate keystone *Sphagnum* moss regrowth (Lukenbach *et al*., 2016; Waddington *et al*., 2015). Margins may then be prone to runaway positive feedbacks such as afforestation, possibly by atypical deciduous species, and limited water table regulation which can lead to an ecosystem regime shift to a swamp-like system, with key peatland carbon accumulation and water conservation mechanisms lost (Kettridge *et al*., 2015, Lukenbach *et al*., 2015b; Waddington *et al*., 2015).

This potential regime shift in peatlands is similar to what has been predicted by Schneider *et al*. (2015), who discuss peripheral ingress of terrestrial vegetation in western boreal peatlands likely to undergo more severe drought conditions in future climate scenarios. Upland deciduous species encroachment will likely lead to increased evapotranspiration rates and will therefore form a positive feedback for drying. Ingress may be counteracted by periodic flooding, with the extent of this likely to determine whether *Sphagnum* mosses can regain a competitive advantage, water chemistry impacts notwithstanding.

1.3 Peatland Resilience and Recovery

Peatland resilience to drought and/or wildfire disturbance is primarily controlled by negative hydrological feedback mechanisms acting to maintain high moisture contents in surface peat, even under periodic drought conditions (Turetsky *et al*., 2015; Waddington *et al*., 2015). Surface moisture governs water, nutrient, gas and heat fluxes from the peat profile as well as composition and structure of the overlying vegetation community and the susceptibility to drought and combustion (Zoltai *et al*., 1998). Peatlands with stable water tables (groundwater connection) or adaptations that maintain high surface moisture (namely *Sphagnum* species that maintain capillary connection to the water table) could be considered resilient. Disturbance regimes such as periodic drought or wildfire may act to release stored carbon from these systems, but disturbances are also important ecosystem maintenance tools. For example, heterogeneity promoted by differential peat combustion promotes biodiversity, carbon accumulation and can increase overall system resilience to subsequent disturbance regimes (Benscoter and Vitt, 2008; Benscoter *et al*., 2015).

Peatland (bog) recovery and succession from wildfire disturbance depends largely on the ability of *Sphagnum* moss to recolonize burned peat areas. Lukenbach *et al.* (2016) observed a decreasing post-fire moss water availability present with increasing burn severity of *Sphagnum fuscum* hummocks. Benscoter and Vitt (2008) observed that *Sphagnum angustifolium* hollows were quick to recolonize after fire irrespective of burn severity. The hydrophysical properties of this post-fire peat surface have been postulated as the primary indicator of recovery trajectory (Lukenbach *et al*., 2016). Successful re-establishment of *Sphagnum* has been observed in sites where pore-water pressures of the exposed peat surface do not exceed -100 mb at any point in the summer (Price and Whitehead, 2001). In other words, there must be a stable water table present, and hollows are more likely to recolonize before hummocks given their proximity to this water table (Benscoter, 2006). Similarly, the susceptibility of hollows to disturbance and their ability to support a wide range of species leads to a broader range of post-fire successional trajectories (Benscoter *et al*., 2005).

Full recovery of *Sphagnum* mosses, and hence return of peatlands to carbon sink status, has been recorded in BP bogs 20 years after wildfire (Zoltai *et al*., 1998; Benscoter and Vitt, 2008; Wieder *et al*., 2009). Early colonizers include *Polytrichum* mosses (0 to 20 years) and later successional ground cover is dominated by feathermosses (*e.g. Pleurozium schreberi*) after ~80 years (Benscoter and Vitt, 2008). Feathermoss invasion is facilitated by the gradual loss of hummock-hollow microtopography from the peatland system (Benscoter *et al*., 2015). With the peat surface becoming more homogeneous in elevation and community composition, surface drying due to peat accretion and increased shading from the denser black spruce (*Picea mariana*) canopy facilitates feathermoss establishment. Functional diversity of the peatland system is maximized when *Sphagnum* mosses assume their positions within the hummock-hollow microforms (20 to 80 years), allowing the peatland to accumulate carbon and effectively conserve water (Benscoter and Vitt, 2008; Wieder *et al*., 2009).

Later successional peatlands in generally drier hydrological settings with high feathermoss cover before fire can be more vulnerable to combustion, with areas of low burn severities exhibiting low post-fire water availability and hence low post-fire moss recolonization (Benscoter and Vitt, 2007; Benscoter *et al*., 2011; Lukenbach *et al*., 2015b; Lukenbach *et al*., 2016). This has also been attributed to hydrophobic properties of burnt feathermosses, which act to limit peatland evaporation post-fire (Kettridge *et al*., 2014). Alternatively, areas with high feathermoss burn severity tend to result in full combustion of the feathermoss structure and earlier recolonization by pioneer *Polytrichum* moss species (Lukenbach *et al*., 2015b). The successional stage and ground layer species present before wildfire interacts with burn severity to determine the peat hydrophysical properties and hence vegetation recovery trajectory. This is especially true for peatland margins, where hummock-hollow microtopography is less prevalent and therefore species distribution may play a more integral role in determining the post-fire recovery (Lukenbach *et al*., 2016).

Compound disturbances of drainage and wildfire, resulting in severe combustion of peat carbon stores, has chronicled an altered successional pathway of peatlands that encompasses a regime shift to a swamp-like broadleaf deciduous canopy with a higher fire frequency that could eventually yield an upland ecosystem (Kettridge *et al*., 2013). This deciduous species recruitment and altered successional trajectory has also been noted in severely burned black spruce forests of Alaska (Johnstone *et al*., 2010; Gibson *et al.*, 2016). Because the fire return interval (~120 years) is within the lifespan of early colonizing tree species, this initial cohort may determine the canopy composition for the duration of the fire-free interval (Wieder *et al*., 2009). Species traits such as litter quantity, quality and evapotranspiration of deciduous versus coniferous species can further modify environmental conditions to support their continued dominance.

Peatland margin recovery from severe wildfire has been examined by Lukenbach *et al*. (2015b and 2017). Severe combustion of dense margin peat (possibly into legacy carbon stores) can lead to loss of negative feedback mechanisms that act to stabilize the water table at these locations after burning (Waddington *et al*., 2015). For example, loss of dense margin peat in coarse-textured systems could result in failure of the WTD –

transmissivity feedback and increased lateral water losses from the margins (Lukenbach *et al*., 2015b). A stable water table, and hence high post-fire water availability, acts as a primary control on moss recolonization post-fire (Lukenbach *et al*., 2016). Furthermore, there is the possibility of higher nutrient availability and greater competition from surrounding upland and riparian species in these systems, which also may prevent peatland moss species from re-establishing (Lukenbach *et al*., 2016). These margin processes have not been studied more than three years post-fire in the BP.

1.4 Vulnerable Peatlands

Johnston *et al*. (2015), using the same chronosequence analysis as Benscoter and Vitt (2008) and Wieder *et al*. (2009), investigated surface and canopy fuel conditions present in forested bogs and hence their vulnerability to future wildfires. Fuel loads were characterized using biomass equations the authors developed specific to bog black spruce. They found that canopy fuel loads increased with time since fire, and black spruce recovery ~80 years post-fire provided enough fuel to support active crown fires between 10 to 40% of days in a typical Alberta fire season. Surface fuel loads remained generally constant throughout the chronosequence, attributed to rapid growth rates of *Sphagnum* species which can bury any dead-down woody debris or litter at the surface. Bog peatlands have been extensively studied due to their isolation from groundwater (or only ephemeral connection), causing them to experience local water table drawdowns more readily in dry years (Hokanson *et al*., 2016). This drying effect combined with black spruce afforestation in later successional bogs leads to reduced *Sphagnum* moss cover and enhanced feathermoss and lichen cover which provide conditions ideal for igniting and propagating fire across and into the peat profile, likely representing a deep smouldering “hotspot” on the landscape (Shetler *et al*., 2008). Wildfire rate of spread modelling found that propagation of fire across and into a drought-stressed peat profile could result in deep smouldering of all sites that were susceptible to initial ignition (Johnston *et al*., 2015; Thompson *et al*., 2015b). This study did not account for the probability of fire moving from a surrounding upland forest into a forested bog (propagation across the interface/margin).

Within peatland systems, vulnerability is not only a function of the local WTD and hence surface moisture conditions, but also of variations in microtopography, associated species distributions, and peat profile bulk densities across the peatland (Benscoter and Wieder, 2003; Miyanishi and Johnson, 2012; Hokanson *et al*., 2016; Lukenbach *et al*., 2016). The higher the bulk density (typical of peatland margins), the lower the specific yield, the more susceptible to enhanced water table fluctuations and the greater the potential for surface drying and deep smouldering combustion, as discussed in Section 1.2.2.

Identifying future climatic conditions, hydrogeological setting and several key features such as the perimeter to area ratio and specific margin characteristics of peatlands vulnerable to severe combustion within the BP landscape is an important research objective for the resource extraction and fire management industries. The chronosequence, or space-for-time substitution, approach taken previously by Benscoter and Vitt (2008), Wieder *et al.* (2009) and Johnston *et al.* (2015) is one viable method for investigating peatland recovery within various hydrogeological settings. This approach could help indicate where vulnerable peatlands exist on the landscape, which could then inform conservation and fire treatment efforts or refine carbon accounting and hydrological models. Furthermore, the risk of peatland area loss via ingress of peatland margins can be evaluated in the context of recent (previous 120 years) and potential future climate scenarios.

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CHAPTER 2: CHARACTERIZING THE PEATLAND-UPLAND INTERFACE OF BOREAL PLAINS BOGS

2.1 Introduction

Across North America, numerous studies have characterized vegetation communities within the peatland-upland interface, or the peatland margins, and their relationship to abiotic gradients such as peat depth, water table depth and biogeochemistry (Hartshorn *et al.,* 2003; Bhatti *et al.,* 2006; Berg *et al.,* 2009; Pellerin *et al.,* 2009; Howie and van Meerveld, 2013; Dimitrov *et al.,* 2014, Paradis *et al.,* 2015). In the Boreal Plains (BP), this vegetation ecotone has been qualitatively described as a “swamp,” or a wetland community dominated by minerotrophic groundwater and characterized by tall woody vegetation (Warner and Rubec 1997; Bauer *et al.*, 2009). Similar to ephemeral draws (*e.g.* Devito *et al*., 2012) it is believed the soil structure and storage dynamics of these peat swamp margins can promote surface saturation and lateral flow as well as vegetation community assemblages to moderate evaporation losses (Riddell, 2008). As such they can play a role in long-term stability of ecosystems by providing critical hydrological connection (effective surface water catchment) between uplands and peatlands (Devito *et al*., 2005). Moreover, it has been postulated that peatland margins and their associated peat properties play an important role in autogenic feedback processes (specifically the water table depth – transmissivity feedback) which act to maintain peatland water tables during periods of drought (Waddington *et al*., 2015). Briefly, water table fluctuations characteristic of BP peatland margins can lead to more decomposed, denser peat with a lower saturated hydraulic conductivity (Hartshorn *et al*., 2003; Bhatti *et al*., 2006), thereby potentially reducing lateral water losses during drought conditions. However, future climate change impacts, such as more frequent or prolonged drought cycles and severe wildfire events (Flannigan *et al*., 2013), may undermine the ability of peatland margins to maintain peatland water tables. These zones are prone to further water table drawdown in periods of drought or high demand by adjacent upland forest ecosystems (Ferone and Devito, 2004; Petrone *et al*., 2007). These drier conditions, coupled with denser margin peat, can cause peatland margins to become deep smouldering "hotspots" during wildfire, with carbon loss from the margins accounting for 50 to 90% of total peatland carbon loss (Hokanson *et al.*, 2016; Lukenbach *et al*., 2015a). Furthermore, areas of deep peat smouldering have been shown to exhibit an ecosystem regime shift post-fire, where runaway positive feedbacks abound and key peatland species (*Sphagnum* moss) and their associated ecosystem functions (carbon accumulation, water storage) are lost (Kettridge *et al.*, 2015; Lukenbach *et al*., 2015b). Nevertheless, despite margin importance for water and carbon cycling, little quantifiable work has been conducted to identify and describe these ecotones or assess their prevalence on the landscape, variation across hydrogeological settings and changes in vegetation community composition with time since fire. We argue that there is an urgent research need to characterize, identify and describe BP peatland margins to further our understanding of their ecological functions and role in maintaining the resilience of peatland ecosystems to disturbances.

Using a transect-based sampling approach, 26 peatlands were investigated in 2016 to determine the ubiquity of margin ecotones and distribution of margin widths across the BP landscape. The relationship between margin width and abiotic factors such as hydrogeological setting and peat depth was also examined. Although we expected peatland margin communities to experience differing vegetation recovery dynamics at each of the peatland middle to margin and margin to upland forest transitions, we hypothesized that overall peatland recovery could be described by an increase in peatland middle area with time since fire, as *Sphagnum* mosses recover and paludify margin swamp communities. Moreover, the extent of peatland recovery with time was expected to be modified by hydrogeological setting. We hypothesized that peatlands which are more susceptible to drought (*e.g.* coarse-textured, potentially perched peatlands) would show decreased recovery rates and potential ingress of swamp vegetation with time since fire, due to deep smouldering of vulnerable margin peat. This would indicate an overall loss of peatland area, likely to be accentuated in a drier climate future. These vulnerable peatlands could switch from net carbon sinks to sources, with further positive climate feedbacks accelerating this cycle of deep smouldering, limited recovery and peatland area loss.

2.2 Methods

2.2.1 Site Selection

A chronosequence, or space-for-time substitution, approach was adopted for selecting peatland study sites that represent stages in wildfire recovery, from five to greater than 112 years since the most recent wildfire. This covers a range of peatland recovery stages within a typical fire return interval (~120 years; Turetsky *et al*., 2004; Wieder *et al*., 2009). Study sites were chosen in proximity to Red Earth Creek and Wabasca, Alberta, within the Central Mixedwood Natural Subregion (Figure 2.1). This subregion is characterized by its continental sub-humid climate, with cold winters and short, warm summers (Natural Regions Committee, 2006). Average temperatures range from -18.7 ^{o}C in the winter to 15.9 ^{o}C in the summer. Mean annual precipitation is 478 mm, of which 336 mm falls during the growing season. This region has pronounced annual and decadal cycles of water availability, however the average year operates at a moisture deficit, where annual potential evapotranspiration exceeds precipitation (Devito *et al.*, 2012).

Site selection involved the use of historical aerial imagery (provided by Alberta Environment and Parks) coupled with Ducks Unlimited Wetland

Inventories, Alberta Surficial Geology and Canadian National Fire Database mapping datasets (Canadian Forest Service, 2011; Fenton *et al.*, 2013). The intention was to capture peatlands located in a wide variety of hydrogeological settings, and hence with potentially varying degrees of groundwater connection and deep smouldering potential. The hydrogeological settings used can be categorized based on the surficial geology and predominant sediment textures: coarse (C; glaciofluvial or outwash deposits), coarse heterogeneous (CH; moraine deposits with glaciofluvial influence predominating), moraine heterogeneous (MH), moraine with predominately fine deposits (MF) and fine-textured (F; glaciolacustrine deposits), as per the Alberta Surficial Geology mapping dataset, modified by field-based soil texture data (Fenton *et al.*, 2013). Historical aerial photographs (1940 to present) of study sites were used to qualitatively assess the peatland type, signs of wildfire and subsequent recovery over time (Government of Alberta, 2016). This included an evaluation of peatland canopy composition (shrubby or forested, deciduous or coniferous), shape and size (Appendix 1).

Field investigation was carried out from May to August 2016, evaluating peat hydrophysical properties and vegetation recovery status of the selected 26 study sites, with a focus on the peatland margins (Table 2.1). All peatlands assessed were identified as treed bogs (ecosite BM-i1), using the ecosite classification of a black spruce (*Picea mariana*) dominated vegetation canopy and *Sphagnum* moss dominated ground layer, with ericaceous shrubs such as Labrador tea (*Rhododendron groenlandicum*) and bog cranberry (*Vaccinium vitis-idaea*) also prominent (Beckingham and Archibald, 1996). Later successional peatlands had a dominant groundcover of feathermoss species (*Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*), indicative of greater shading from the black spruce canopy (Mulligan and Gignac, 2001).

2.2.2 Transect Vegetation Surveys and Split Moving Window Analysis

A transect-based sampling approach was used, with transects running from the upland forest vegetation community into the peatland middle, hence covering the location of potential margin ecotones. When field assessors were standing within a selected bog study site, a random number generator was used to determine the orientation of each transect. In some cases, a disturbance such as a cutline intersected the transect and a new orientation was selected. Every effort was made to capture at least 10 m of homogeneous bog vegetation and homogeneous upland vegetation at each end of the transect, hence each transect differed in length depending on the width of the perceived margin ecotone. Ground layer vegetation plots measuring 0.5 m by 0.5 m were spaced at 1 m intervals for all transects less than 60 m in length, otherwise spacing was adjusted to 2 or 3 m for longer transects. Species presence or absence was recorded in each plot. A tree stand density survey was also conducted, identifying and describing the nearest tree to each plot location on each side of the transect (up to 5 m away). In addition, as many as nine auger holes were characterized along each transect to record peat depth and various peat and sediment properties used for site categorization.

This transect sampling approach was evaluated using a Split Moving Window (SMW) statistical method, which indicates where transitions in vegetation assemblages are occurring (Ludwig and Cornelius 1987; Cornelius and Reynolds 1991). This method has been shown to detect biological boundaries along abiotic gradients in many ecosystems (Boughton *et al.*, 2006; Camarero *et al.*, 2006), and has been shown to detect landscape-level changes in vegetation communities with more efficacy than a detrended correspondence analysis in the case of a fen peatland in Ohio, USA (Choesin and Boerner, 2002). It has also been used by Paradis *et al.* (2015) to described the lagg (margin) ecotone in raised bogs of eastern Canada.

For each transect, vegetation plots were separated into two datasets: non-vascular and vascular species (including trees). For each dataset, a window was drawn around an even number of plots. Windows varied in widths (6, 8, 10, 12, 14, 16 or 18 plots, selected to account for a variety of peatland margin widths) and each window was split in half. A dissimilarity index, Squared Euclidian Distance (SED), was calculated as a comparison of the two halves of each window (Appendix 3). Windows were then moved along the transect from start to finish. SED was chosen due to its efficacy at identifying ecotone transitions in several other studies, as well as its ability to discern the margin ecotone location of these peatland study sites, as compared to other diversity indices such as Sorensen's Index (Erdos *et al.,* 2014; Appendix 3).

Areas with disproportionately high dissimilarity between two window halves can be represented by peaks on a plot of SED versus the location of that window mid-point on the transect. Once all seven window sizes were evaluated, a pooled average Z score was calculated for each of the two datasets by running 1000 Monte Carlo simulations on randomized transect data (Cornelius and Reynolds, 1991). Final plots averaged the Z score values from the non-vascular and vascular datasets at each window location on the transect. Any Z score value of greater than two standard deviations above the mean was chosen to represent a significant peak and hence the transition points in the vegetation community. All statistical analyses were completed with a program written in RStudio version 0.99.484 (R Core Team, 2016).

2.3 Results

2.3.1 Margin Location as Determined by SMW Analysis

The location (or absence) of a margin in the 26 selected study sites is indicated by peaks on the dissimilarity plots where average Z score values are greater than two standard deviations above the mean (Appendix 2). These results compare reasonably well to field-determined margin locations, with the average margin width being adjusted by 3.7 m from that determined in the field. SMW average Z score peaks, and hence margin ecotone boundaries, can be interpreted in various ways. Three trends were noted in the results and demonstrated in Figure 2.2: a) at least two distinct peaks which indicate the boundaries of the margin ecotone; b) a sustained peak where the average Z scores throughout the margin are sustained near or above 2 standard deviations; and finally, c) one distinct peak, indicating an upland-peatland transition with no separate margin ecotone.

The width of SMW-determined margin ecotones varies from 0 m (no margin) to 60 m, with an average width of 12 m. There are no clear trends in margin width over time (linear regression $r^2 = 0.007$; Figure 2.3; Table 2.2). An estimate of the margin area in relation to the total peatland area was obtained by assuming uniform margin width around each peatland. There was no trend identified in this margin area to peatland area ratio over time (linear regression $r^2 = 0.091$, Figure 2.4; Table 2.2). Margin widths were log-transformed to satisfy the assumption of normality in conducting analysis of variance (ANOVA). There was no statistically significant difference between log-transformed margin widths in the five hydrogeological settings, as determined by one-way ANOVA ($F(4) = 0.870$, $p = 0.498$; Figure 2.5; Table 2.2). There were statistically significant differences between the margin area to peatland area ratio across the five hydrogeological settings, as determined by one-way ANOVA (*F*(4) = 6.474, *p* = 0.001; Figure 2.6; Table 2.2). Specifically, peatland margins located in fine-textured deposits were determined to have significantly lower margin area to total peatland area ratios than those located in fine-textured moraine, heterogenous moraine and heterogeneous coarse deposits, as determined by a Tukey post-hoc test. This is likely due to the gentle slopes and generally larger (expansive) sizes of peatlands located in fine-textured deposits, versus the greater topography and smaller (confined) sizes of peatlands located in moraine and glaciofluvial deposits. Figure 2.7 illustrates the relationship between total peatland area (log-transformed) and the proportion of margin area across hydrogeological settings. In addition, three peatland study sites (in blue) are illustrated from Hokanson *et al.* (2016), including the proportion of margin carbon loss from these sites measured post-fire.

2.3.2 Margin Widths and Associated Peat Depth

Applying SMW-determined margin ecotone boundaries to transect-based measurements of peat depth illustrates how the margin ecotone differs in structure from peatland middles (Appendix 2). Peat depth measurements were log-transformed to satisfy the assumption of normality in conducting statistical analysis. Not unexpectedly, margin peat depths were determined to be significantly lower than middle peat depths, as determined by a t-test (t = -4.155, p = 5.94 x 10^{-5}; Figure 2.8; Table 2.2). The mean margin peat depth was 0.54 m, however the range of margin peat depths recorded was 0.02 to 2.46 m. Across hydrogeological settings, there was no statistically significant difference in log-transformed peat depths, as determined by one-way ANOVA (*F*(4) = 1.482, *p* = 0.222; Figure 2.9; Table 2.2).

2.4 Discussion

2.4.1 Margin Ecotone Dynamics with Time Since Wildfire

Split moving window analysis has identified and described margin ecotones in 22 of the 26 peatland bog study sites examined in the BP. The extent and associated peat properties of this ecotone vary from site to site, however there were no distinct trends noted across the chronosequence analysis. It appears the margin ecotone does not increase or decrease in area over the course of one fire return interval, assuming study sites at different recovery stages are appropriate replicates of each other. This result does not support the hypothesis that peatland middle vegetation communities, specifically *Sphagnum* moss, recovers and expands into the margin swamp ecotone with increasing time since wildfire. Nor that the margin ecotone expands into the peatland middle in the case of coarse-textured (potentially drier and more vulnerable) peatlands.

Further research into this question could be conducted by examining the botanical origin of peat within the identified margin ecotones. If *Sphagnum* moss were found below the uppermost charcoal layer (most recent fire), this would support the hypothesis that the margin ecotone has established on what was formally a peatland middle vegetation community. In addition, this analysis has only examined a single fire return interval. Further research could be undertaken to assess margin peat properties and botanical origin back through several previous wildfire events to similarly identify *Sphagnum* moss peat.

2.4.2 Margin Peat Depths across Hydrogeological Settings

Across the five hydrogeological settings that were investigated, there were no statistically significant differences found between margin ecotone peat depths. The range of peat depths that were identified in margin ecotones (0.02 to 2.46 m) supports the work of Lukenbach *et al*. (2015a) and Hokanson *et al*. (2016) that vulnerable margin peat can represent a significant carbon store and the recovery of margin ecotones is of concern in returning the peatland to a carbon sink post-fire. The peatlands located in coarse-textured deposits at high topographical positions (*e.g.* ephemerally perched) are those that have been previously identified as most vulnerable to deep margin smouldering, contributing up to 90% of the total peatland carbon loss during wildfire (Lukenbach *et al*., 2015a; Hokanson *et al*., 2016; Figure 2.7). The larger the peatland, the less influential margin peat is on carbon losses during wildfire, however even an expansive fine-textured system has been reported to contribute 51% of carbon loss from margin areas, which represented only 5% of the total peatland area (Hokanson *et al.,* 2016). This demonstrates the importance of margin carbon stores across all peatlands, but the enhanced effect of carbon loss in confined systems with deep peat is of great concern.

2.4.3 Applications of Research

Implications of this research can be extended to fire managers developing strategies under future, drier climate scenarios. Peatland treatments for wildfire abatement and community protection should consider areas with numerous confined peatlands (moraine and glaciofluvial deposits) identified as having greater margin area to total peatland area ratios, combined with deep margin peat that is more vulnerable to severe smouldering (Figure 2.7). Fire fighting efforts could benefit from this knowledge at a landscape scale, both in terms of cost savings from allocating necessary resources in areas which are likely to be deep smouldering hotspots, but also in terms of carbon savings by protecting vulnerable margin peat reserves from the impact of severe smouldering.

Although no significant changes in margin width or area were identified over time in this chronosequence analysis, we further hypothesize that future climate scenarios with an enhanced moisture deficit in the region will not only lead to more frequent and severe wildfires (Flannigan *et al*., 2005), but will also increase peatland burn severities and further alter recovery trajectories of margin and peatland vegetation communities. In turn, it is expected that the total area of peatlands that are most vulnerable to wildfire (*e.g.* confined, potentially perched peatlands) will shrink and legacy carbon stores in these systems will be lost.

Considerable research is also being invested into the question of how to restore peatland ecosystems following disturbance. Constructing confined peatland ecosystems following large-scale mining disturbance has many benefits including preserving water quality (*e.g.* creating perched peatland systems above salt-contaminated groundwater) and increasing the area of wetland-forestland interface across the reconstructed landscape (Devito *et al*., 2012). It has been suggested that creating multiple small perched systems may be the ideal way to increase the size of this interface. However, given the vulnerability of these smaller, confined peatlands to wildfire, there is the potential to catastrophically alter their hydrological role and ecosystem integrity when this disturbance occurs on the reclaimed landscape (Lukenbach *et al.*, 2016). Further understanding the role of peatland margin vegetation ecotones in sustaining peatland autogenic feedback mechanisms that promote paludification and recovery is needed. Characterizing the vegetation communities of these margin swamps, including indicative species, canopy properties and biomass accumulation with time will help fulfill this goal.

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Table 2.1: Chronological list of bog study sites including approximate time since wildfire and hydrogeological setting, modified by predominant sediment textures.

Site Name	Easting	Northing	Zone	Area* (ha)	Time Since Fire** (years)	Fire Year	Hydrogeological Setting***
Utik1904	591471	6216082	11N	0.4	>112	~1904	Moraine - Fine
Utik1905	592774	6214080	11N	1.2	>111	~1905	Moraine - Het
Utik1916	593009	6214108	11N	0.7	>100	~1916	Coarse - Het
NWab1920	686086	6209980	11N	34.1	>96	~1920	Fine
Utik1935	619549	6194079	11N	35.7	81	1935	Fine
Haig1940A	553240	6306764	11N	1.0	>76	~1940	Moraine - Fine
Loon1940	618032	6328292	11N	6.9	>76	~1940	Coarse
Haig1940B	553337	6308376	11N	0.4	>76	~1940	Coarse - Het
SWab1940A	335410	6199670	12N	26.1	76	1940	Fine
SWab1940B	333471	6200089	12N	136.2	76	1940	Fine
Peli1950	349205	6185797	12N	0.7	>66	~1950	Moraine - Fine
Utik1956A	595669	6211969	11N	0.6	60	1956	Coarse - Het
Utik1956B	595802	6210662	11N	0.6	60	1956	Moraine - Fine
NWab1982	682434	6214709	11N	129.7	34	1982	Fine
Ottr1982A	568475	6269535	11N	1.4	34	1982	Moraine - Fine
Ottr1982B	576971	6267292	11N	0.2	34	1982	Moraine - Het
RECr1982	605355	6249569	11N	307.0	34	1982	Fine
Peli1999	352797	6186502	12N	3.1	17	1999	Fine
Ottr2001A	570778	6266861	11N	1.0	15	2001	Moraine - Het

Site Name	**Easting**	**Northing**	**Zone**	**Area* (ha)**	**Time Since Fire** (years)**	**Fire Year**	**Hydrogeological Setting*****
Ottr2001B	569649	6266860	11N	0.4	15	2001	Moraine - Fine
Ottr2001C	569914	6266709	11N	1.7	15	2001	Moraine - Het
Loon2002	634588	6329101	11N	6.6	14	2002	Fine
Utik2011A	614429	6205313	11N	5.4	5	2011	Fine
Utik2011B	596223	6207777	11N	1.1	5	2011	Moraine - Het
Utik2011C	580739	6219560	11N	0.5	5	2011	Coarse
Utik2011D	598997	6220012	11N	0.4	5	2011	Coarse - Het

*For sites >5.0 ha in area, the peatlands are generally expansive systems and the mapped portion of the peatland used to calculate the area is an underestimate of the entire peatland area.

**Years Since Fire: Determined by using the Canadian Forest Service National Fire Database and aerial photographs as primary evidence, followed by tree age data (Canadian Forest Service, 2011). When the date is uncertain, the ">" symbol is used.

*** Hydrogeological Setting: Categorized using the Alberta Surficial Geology mapping dataset and confirmed using field-based soil texture data from sediment analysis along the transect (Fenton *et al.*, 2013). "Het" stands for heterogeneous (mixed coarse and fine materials).

Table 2.2: Summary statistics from t-test, ANOVA and regression analysis. Statistical significance of each test is indicated by an asterisk (*) following the *p* or r^2 value.

<table>
<tr><th colspan="5">T-test/ANOVA</th></tr>
<tr><th>Figure</th><th>Description</th><th>Data transformation</th><th>Test Statistic</th><th>Significance</th></tr>
<tr><td>2.5</td><td>Boxplot of margin widths by hydrogeological setting</td><td>Log-transformed</td><td>$F(4) = 0.870$</td><td>$p = 0.498$</td></tr>
<tr><td>2.6</td><td>Boxplot of the ratio of margin area (assumed uniform around the entire peatland) to total peatland area by hydrogeological setting</td><td>None</td><td>$F(4) = 6.474$</td><td>$p = 0.001$*</td></tr>
<tr><td>2.8</td><td>Boxplot of margin versus middle peat depths</td><td>Log-transformed</td><td>$t = -4.155$</td><td>$p = 5.94 \times 10^{-5}$*</td></tr>
<tr><td>2.9</td><td>Boxplot of margin peat depths by hydrogeological setting</td><td>Log-transformed</td><td>$F(4) = 1.482$</td><td>$p = 0.222$</td></tr>
<tr><th colspan="5">Regression</th></tr>
<tr><th>Figure</th><th>Description</th><th colspan="2">Trendline Equation</th><th>Coefficient</th></tr>
<tr><td>2.3</td><td>Margin widths with time since fire and across hydrogeological settings</td><td colspan="2">$y = -0.029x + 13.025$</td><td>$r^2 = 0.007$</td></tr>
<tr><td>2.4</td><td>The ratio of margin area (assumed uniform around the entire peatland) to total peatland area with time since fire and across hydrogeological settings</td><td colspan="2">$y = -0.002x + 0.433$</td><td>$r^2 = 0.091$</td></tr>
</table>

Figure 2.1: Study area overview showing the nearest towns (red stars) and chronosequence study sites (blue polygons).

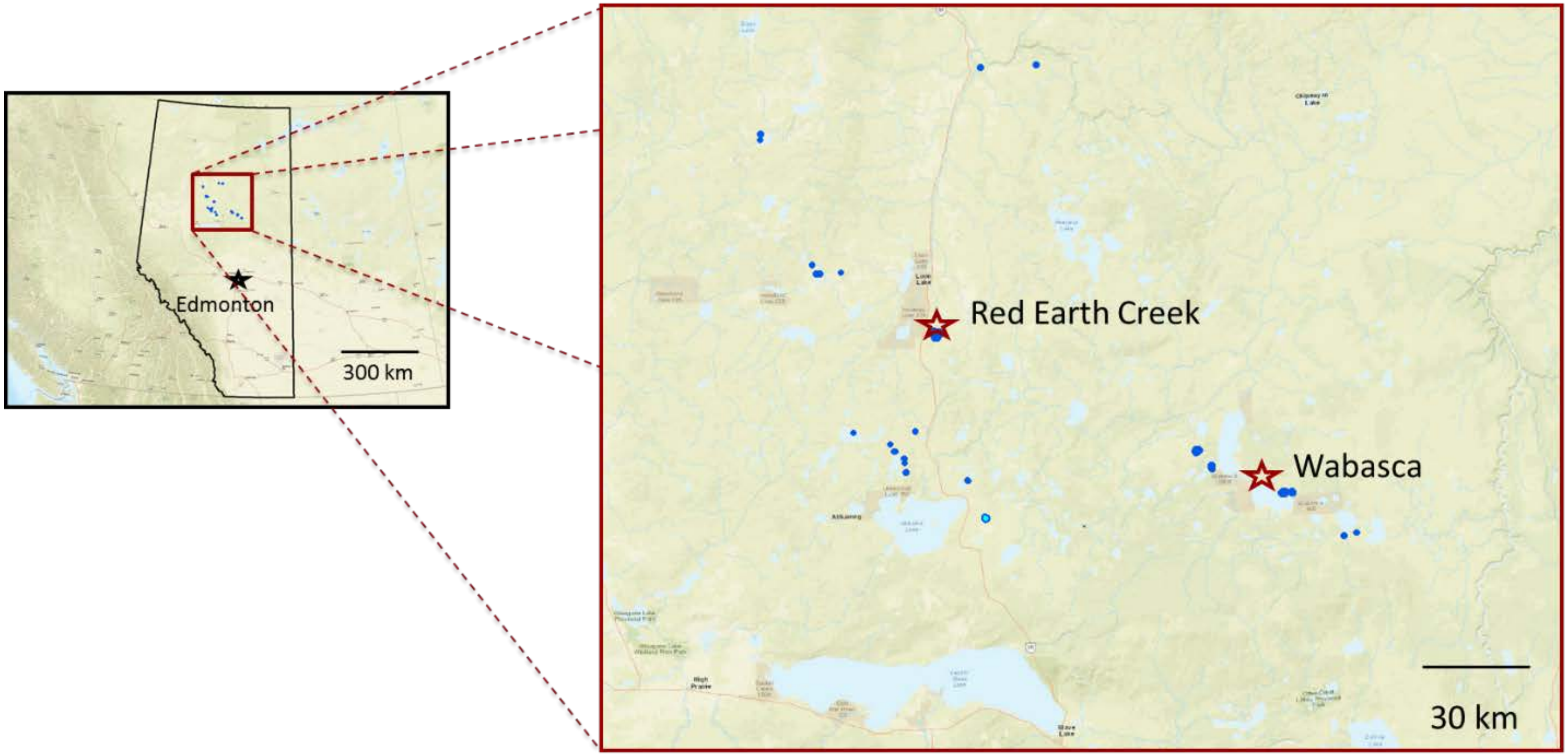
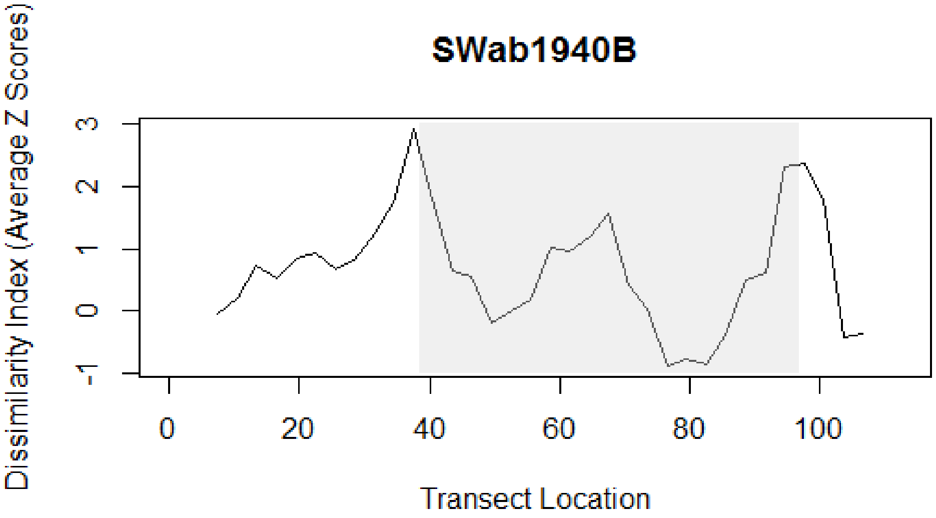


Figure 2.2: Overview of SMW dissimilarity index results, showing three common trends. Calculated using Squared Euclidian Distance average Z Scores from window sizes 6, 8, 10, 12, 14, 16 and 18 plots. Margin location (area between peaks) is indicated by shading.

a) Two distinct peaks show ecotone boundaries.



b) One sustained peak identifies ecotone as zone of high dissimilarity

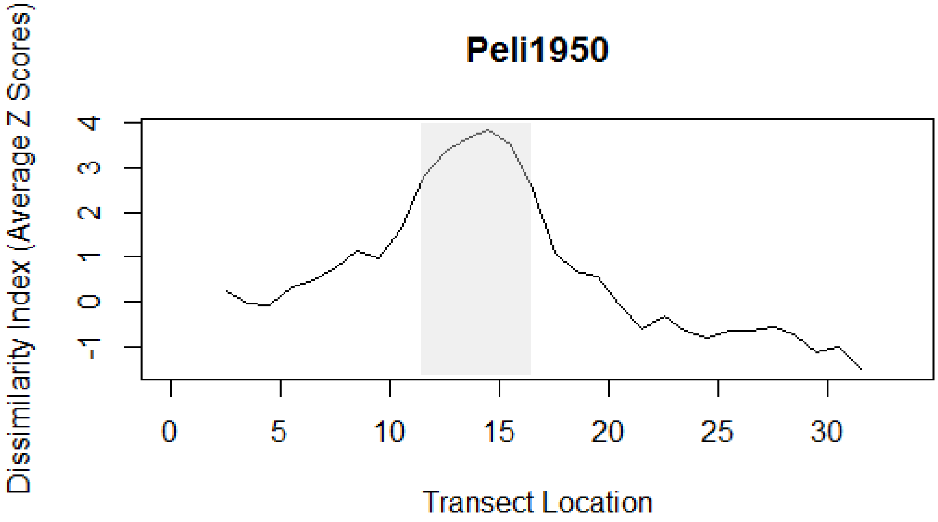


Figure 2.2 (continued):

c) One peak indicates no margin ecotone is present, vegetation community shifts from upland to peatland.

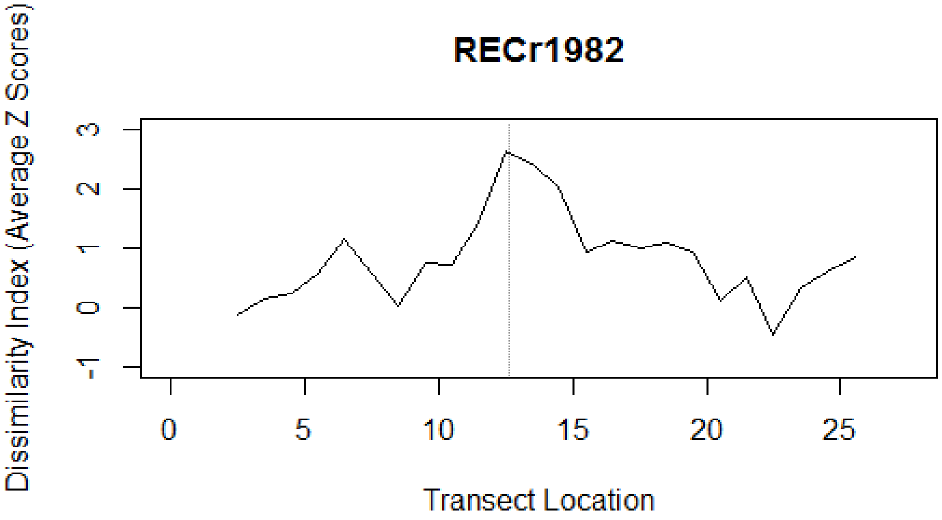


Figure 2.3: Margin widths with time since fire and across hydrogeological settings. The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.

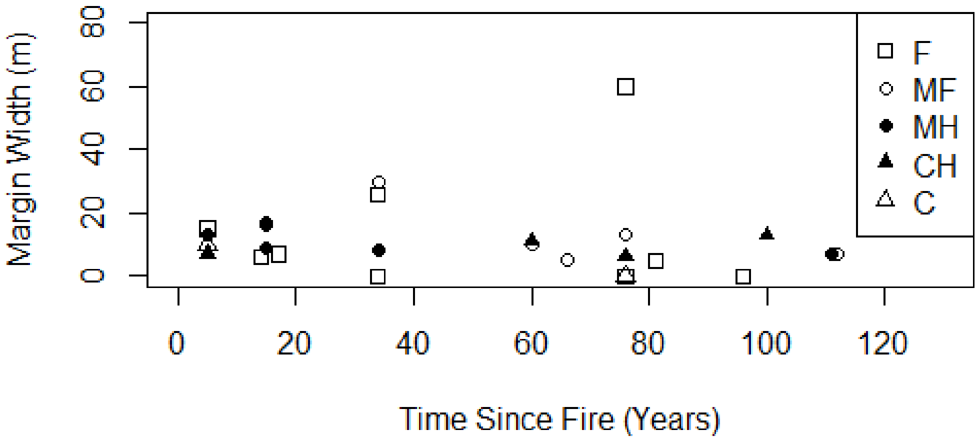


Figure 2.4: The ratio of margin area (assumed uniform around the entire peatland) to total peatland area with time since fire and across hydrogeological settings. The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.

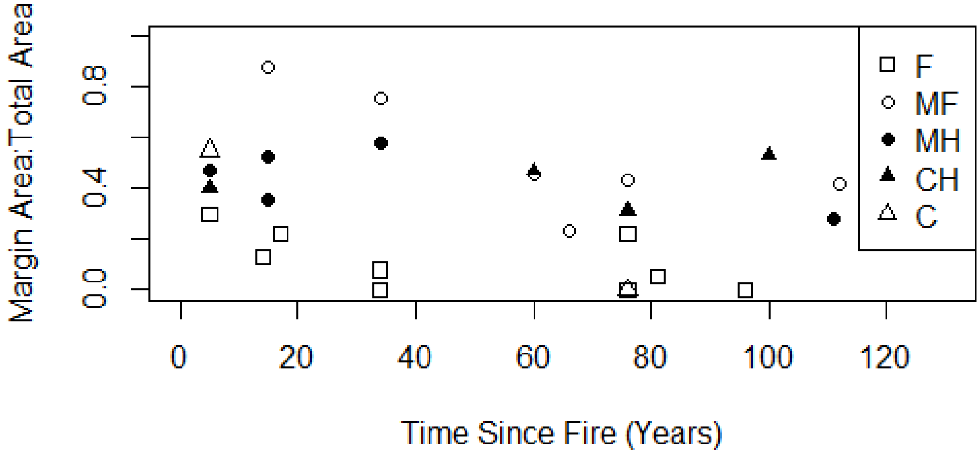


Figure 2.5: Boxplot of margin widths by hydrogeological setting. There were no significant differences identified between the log-transformed values of each group (*F*(4) = 0.870, *p* = 0.498). The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.

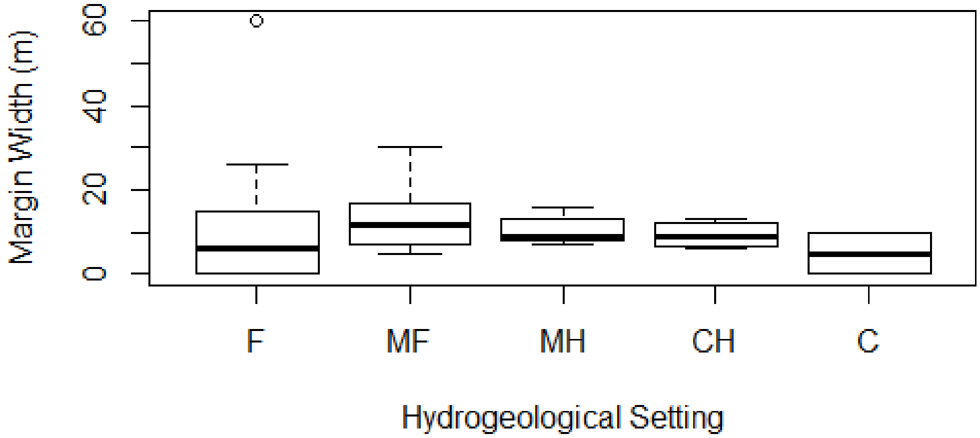


Figure 2.6: Boxplot of the ratio of margin area (assumed uniform around the entire peatland) to total peatland area by hydrogeological setting. Significant differences between groups are represented by lettering (a and b) above each boxplot (*F*(4) = 6.474, *p* = 0.001). The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.

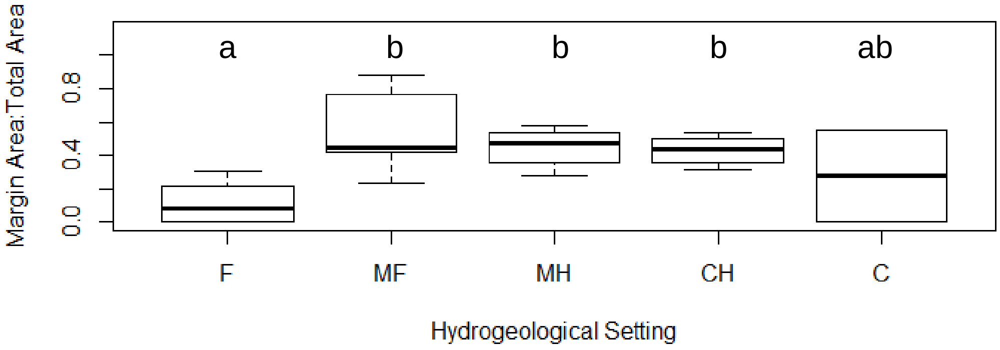


Figure 2.7: The proportion of peatland margin area (assumed uniform around the entire peatland) versus total peatland area (log-scale) for each of the 26 study sites (black), as well as three additional study sites from Hokanson *et al.* (2016) in blue. Reported carbon loss values from these additional sites are also included.

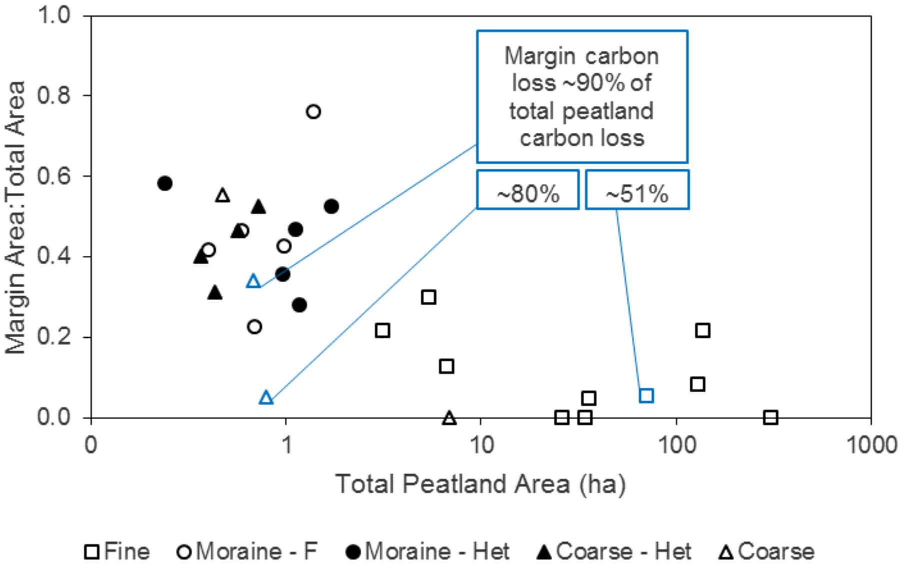


Figure 2.8: Boxplot of margin versus middle peat depths. Log-transformed values of each group were determined to be significantly different (*t*(4) = -4.155, *p* = 5.94 x 10^{-5}).

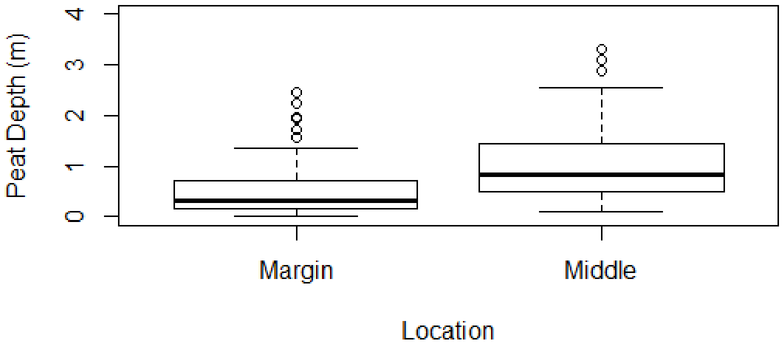
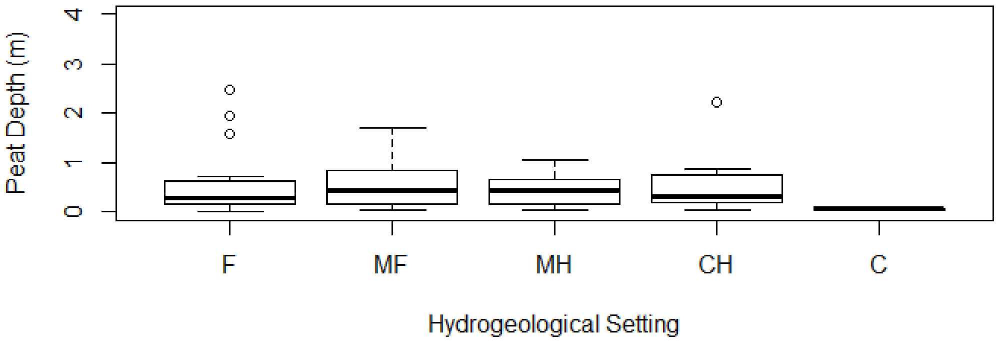


Figure 2.9: Boxplot of margin peat depths by hydrogeological setting. There were no significant differences identified between the log-transformed values of each group (*F*(4) = 1.482, *p* = 0.222). The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.



CHAPTER 3: POST-FIRE RECOVERY TRAJECTORIES OF PEATLAND BOG VEGETATION COMMUNITIES

3.1 Introduction

Boreal Plains (BP) carbon stores within peatland-upland transition zones, or margins, have been identified as vulnerable to wildfire disturbance, with carbon loss estimates ranging from 10 to 85 kg m^{-2} during wildfire and accounting for 50 to 90% of total peatland carbon loss (Lukenbach *et al.*, 2015a; Hokanson *et al*., 2016). High margin peat bulk densities and susceptibility of margin peat to low water table positions, with associated low moisture contents, have been identified as primary controls on deep smouldering (Benscoter *et al*., 2011; Lukenbach *et al*., 2015a). Across the landscape, hydrogeological setting has also been indicated as a primary control on peatland margin depth of burn (Hokanson *et al.,* 2016). Confined peatlands in high topographic positions prone to isolation from groundwater flow systems (*e.g.* ephemerally perched systems) experience greater vulnerability to deep smouldering than expansive or low-lying peatlands connected to groundwater flow systems. Coincidentally, confined peatland systems have a higher proportion of margin area to total peatland area (see Chapter 2), causing enhanced margin carbon loss during wildfire in these locations. Given the fire return interval for peatlands in this region is estimated at ~120 years (Turetsky *et al*., 2004; Wieder *et al*., 2009), legacy carbon lost due to deep smouldering may not be balanced by between-fire carbon sequestration (Lukenbach *et al.,* 2015b). This is primarily dependent on the recolonization and recovery of carbon-accumulating margin vegetation. Lukenbach *et al*. (2016) found that pre-fire species cover can interact with burn severity to alter post-fire water availability and hence bryophyte recovery in the peatland interior, or middle. Consequently, there is concern that high nutrient availability and greater competition from upland species may limit recovery of bryophytes in peatland margins (Bauer *et al*., 2009; Graham *et al*., 2015; Paradis *et al*., 2015; Depante, 2016). Immediately following wildfire, Lukenbach *et al*. (2017) found that peatland-dwelling bryophyte recolonization was observed at sites where hydrological conditions were moderated by larger-scale groundwater flow (connectivity). Limited peatland bryophyte recovery was observed in sites that were disconnected from groundwater systems and therefore experienced flooding during wet periods (as is frequently the case post-fire) and enhanced water table declines in drought periods – often referred to as a 'flashy' water table. As such, the ability of peatland margins to accumulate peat and return to carbon sinks post-fire may be compromised. This margin vegetation recovery, however, has not been examined more than three years post-fire at the landscape scale. Consequently, there is a need to characterize peatland margin indicator species, recovery trajectories and differences in structure and function over time and across hydrogeological settings to provide insight into how these elements of the landscape may promote resilience to wildfire disturbance.

Where ground layer species composition is of upmost importance in peatland middles, with *Sphagnum* mosses adapted for various water conservation and carbon sequestration roles (Wagner and Titus, 1984; Gignac *et al*, 1991; Waddington *et al*., 2015), the margin swamp that has been described in the literature alludes to an ecosystem dominated by broadleaf deciduous trees and shrubs and a ground layer characterized less by peatland bryophytes and more by marsh-loving grasses, sedges and forbs (Warner and Rubec 1997; Bauer *et al.*, 2009). It follows that the function of this ecotone may be focused less on carbon accumulation and more on seasonal water use and conservation, canopy shading, snow accretion, and species biodiversity. The aim of this research is to examine these margin ecotone species, properties and functions, as well as their recovery trajectories with time since wildfire, in greater detail using a chronosequence, or space-for-time substitution, approach.

Peatland middle ground layer species recovery trajectories have been analyzed by Benscoter and Vitt (2008) using a similar chronosequence approach. The stability of the water table post-fire is a primary control on the ability of *Sphagnum* mosses to recolonize burned peat areas (Price and Whitehead, 2001; Lukenbach *et al*., 2016). For this reason, hollows are more likely to recolonize before hummocks (Benscoter, 2006). Full recovery of *Sphagnum* mosses, and hence the return of the peatlands to a carbon sink status, has been recorded in BP bogs 20 years after wildfire (Zoltai *et al*., 1998; Benscoter and Vitt, 2008; Wieder *et al*., 2009). This period represents the greatest functional diversity of peatland ecosystems. Early successional (0 to 20 years) colonizers include *Polytrichum* mosses and later successional (>80 years) ground cover is dominated by feathermosses (*Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*; Benscoter and Vitt, 2008). From our investigation of peatland margin vegetation communities, we hypothesized that these ecotones exhibit a recovery trajectory that mimics that of peatland middles, with distinct indicator species (early, mid and later successional) which can be related to ecosystem functions promoting overall resilience.

Following from wildfire recovery trajectories, mature peatlands have been extensively studied to assess their vulnerability to future wildfires, potentially in a drier climate future with more frequent and severe fire events (Flannigan *et al*., 2005). From the canopy perspective, black spruce canopy fuel loads ~80 years post-fire can provide enough fuel to support active crown fires between 10 to 40% of days in a typical Alberta fire season (Johnston *et al*., 2015). Surface fuel loads show less vulnerability with time, attributed to the rapid growth rate of *Sphagnum* species which bury any dead-down woody debris or litter at the surface. Through severe burning, resultant hydrophobicity and low post-fire water availability (Kettridge *et al*., 2014), later successional feathermoss dominated peatlands (Benscoter and Vitt, 2007; Benscoter *et al*., 2011; Miller *et al.,* 2015), and especially those in coarse-textured, drier hydrological settings (*e.g.* potentially perched peatlands; Lukenbach *et al*., 2015b; Lukenbach *et al*., 2016), are likely most vulnerable to severe smouldering and slower rates of moss recolonization. In peatland margins, no trends have yet been identified regarding species composition and burn severity, however, lack of *Sphagnum* cover, associated hummock-hollow microtopography, and diverse species traits that govern litter and peat quantity, quality, as well as evapotranspiration and fuel load of the deciduous versus coniferous canopy, may play a more integral role in determining wildfire vulnerability (Lukenbach *et al*., 2016). Through our work, we hypothesized that the vegetation canopy fuel load and ground layer composition of peatland margins will promote the spread of wildfire from surrounding uplands into peatland ecosystems with increasing time since wildfire. Furthermore, we anticipated that the successional trajectories of peatland margin vegetation communities are likely modified by hydrogeological setting to potentially enhance fuel loads of coarse-textured, drier (*e.g.* potentially perched) peatland margins.

3.2 Methods

3.2.1 Site Selection

Peatlands that have burned in the past five to greater than 112 years were selected to represent a chronosequence of wildfire recovery study sites in proximity to Red Earth Creek and Wabasca, Alberta (see Chapter 2, Figure 2.1). This area is located within the Central Mixedwood Natural Subregion and is characterized by its continental sub-humid climate, with cold winters and short, warm summers (Natural Regions Committee, 2006). The average temperature ranges from -18.7 ^{o}C in winter to 15.9 ^{o}C in summer. Mean annual precipitation is 478 mm, of which 336 mm falls during the growing season. This region has pronounced annual and decadal cycles of water availability, however, the average year operates at a moisture deficit, where annual potential evapotranspiration exceeds precipitation (Devito *et al.*, 2012).

Site selection involved the use of historical aerial imagery (provided by Alberta Environment and Parks) coupled with Ducks Unlimited Wetland Inventories, Alberta Surficial Geology and Canadian National Fire Database mapping datasets (Canadian Forest Service, 2011; Fenton *et al.*, 2013). The intention was to capture peatlands located in a wide variety of hydrogeological settings, and hence with potentially varying degrees of groundwater connection and deep smouldering potential. The hydrogeological settings used can be categorized based on the surficial geology and predominant sediment textures: coarse (C; glaciofluvial or outwash deposits), coarse heterogeneous (CH; moraine deposits with glaciofluvial influence predominating), moraine heterogeneous (MH), moraine with predominately fine deposits (MF) and fine-textured (F; glaciolacustrine deposits), as per the Alberta Surficial Geology mapping dataset, modified by field-based soil texture data (Fenton *et al.*, 2013). Historical aerial photographs (1940 to present) of study sites were used to qualitatively assess peatland type, signs of wildfire and subsequent recovery over time (Government of Alberta, 2016). This included an evaluation of peatland canopy composition (shrubby or forested, deciduous or coniferous), shape and size (Appendix 1).

Field investigation was carried out from May to August 2016, inventorying species composition, abundance and biomass of the selected 26 study sites, with a focus on peatland margins (refer to Chapter 2, Table 2.1 for study site list). All peatlands assessed were identified as treed bogs (ecosite BM-i1), using the ecosite classification of a black spruce (*Picea mariana*) dominated vegetation canopy and *Sphagnum* moss dominated ground layer, with ericaceous shrubs such as Labrador tea (*Rhododendron groenlandicum*) and bog cranberry (*Vaccinium vitis-idaea*) also prominent (Beckingham and Archibald, 1996). Later successional peatlands had a dominant groundcover of feathermoss species, indicative of greater shading from the black spruce canopy (Mulligan and Gignac, 2001).

2.2.2 Margin and Middle Vegetation Plots

Vegetation plots were assessed in each of the 26 study sites at the margin and middle (typically at the end of a 30 to 60 m transect) locations. Species composition and abundance was assessed for the ground layer (plants <0.5 m in height) and the tree/tall shrub layer (woody plants >0.5 m in height). Ground layer assessments included two strata: non-vascular bryophytes and lichens as well as vascular graminoid, forb and dwarf shrub species present in six 0.5 m by 0.5 m plots in each of the margin, middle hummock and middle hollow locations. Tree and tall shrub composition, age and biomass was assessed using 2 m by 10 m plots and measuring stem density, basal diameter (BD), diameter breast height (DBH) and collecting basal disks or tree cores from multiple trees for estimation of age and annual radial growth. BD was measured above any root collar swelling to avoid bias towards large stem diameters and allometric biomass equations were used to relate these measurements to total aboveground tree biomass (Wieder *et al*., 2009; Lambert *et al*., 2005; Schiks *et al*., 2016; Appendix 3). Biomass was only calculated on sites where greater than 20 years had passed since the previous wildfire, to avoid issues with small tree diameters and to address research questions related to fuel loading and vulnerability to future wildfires. Tall shrub fuels were measured 0.15 m above the stem base to estimate biomass via foliage and stem allometric equations (Connolly and Grigal, 1983; Appendix 3). In addition, ground layer plot vegetation was harvested in sites greater than 60 years of age to calculate total aboveground biomass and the contribution of understory vegetation to this value. These samples were dried in the lab until a steady mass was obtained, representing the dry biomass. Canopy closure photographs were taken at each vegetation plot location using a digital camera pointed skyward from 0.5 m height. These photos were processed by a program created in ArcGIS ModelBuilder that removed the blue colour band and isolated tree, stem and leaf pixels from sky pixels, providing a percentage canopy closure value.

Tree ages were estimated by drying, sanding and scanning tree cookie and core cross-sections at a high resolution into WebPlotDigitizer, a program which allows the user to add points corresponding to each ring location along a line from tree cookie/core middle to edge and then conversion of this two-dimensional plot (ring width distances) to millimetre values which correspond to annual radial growth (Rohatgi, 2017). The number of rings corresponds to tree age. In peatland study sites where time since fire is unknown, site age was estimated using the age of the oldest sampled tree from middle and margin plots (refer to Chapter 2, Table 2.1 for study site list and ages).

Vegetation plot data were analyzed using indicator species analysis and ordination in the form of Non-Metric Multidimensional Scaling (NMDS) to identify trends in margin versus middle (hummock and hollow) plot composition over time and across hydrogeological settings. Using the method of Dufrene and Legendre (1997), species indicator values were calculated to identify characteristic species by location and over distinct recovery stages. This method accounts for both relative abundance and relative frequency/constancy of species. All statistical analyses were completed in RStudio version 0.99.484 using the vegan and labdsv packages (R Core Team, 2016; Roberts 2016; Oksanen *et al*., 2017). Plots from margins, hummocks and hollows of each site were averaged to provide a reliable estimate of site composition. Comparisons of species richness, Shannon-Wiener diversity, biomass, canopy closure and indicator species were performed to identify differences between margin and middle plots, over time and across hydrogeological settings.

2.2.3 Non-Metric Multidimensional Scaling

NMDS analysis using the Bray-Curtis dissimilarity index (or 1-Sorensen's index) was chosen for the ability of this index to discern differences in community data better than other ordination techniques which may employ Euclidian dissimilarity indices (Faith *et al.,* 1987; Oksanen 2015; Appendix 3). The Bray-Curtis index is applied to rank orders of species in communities (versus absolute abundances) and is therefore robust in avoiding problems of ambiguous shared absences in community data. Stress is reduced in the final plot by using 100 random starts to reposition the points in two dimensions until a threshold of ~0.2 is reached. This is also a method that has been employed in BP peatland middles to characterize ground layer vegetation recovery trajectories following wildfire disturbance (Benscoter and Vitt, 2008).

Clusters were imposed on the NMDS ordination from known margin versus middle groups and hydrogeological settings. Multiple regression was used to fit contours and/or vectors of explanatory variables (*e.g.* species richness, diversity, time since fire, canopy closure, biomass and peat depth) onto the NMDS biplot for each of the site-averaged margin and middle abundances to associate these variables with variations in plant community composition. Comparisons were made of both linear and non-linear correlations between the explanatory variable and ordination. Permutation tests were employed to test the significance of the explanatory variable. Finally, a continuous (contour-based) plot of recovery over time was also completed for both the margin and middle plots to aid in visualizing recovery trajectories.

3.3 Results

3.3.1 Aboveground Tree/Tall Shrub Biomass and Canopy Properties

Margin and middle tree/tall shrub stand densities and species composition were measured at all sites. The square-root of stand density values was used to satisfy the assumption of normality in conducting statistical analysis. Margin vegetation plots were identified to have significantly greater stand densities than middle vegetation plots, as determined by a t-test (t = 3.582, p = 0.001; Figure 3.1; Table 3.1). To enhance this analysis across the chronosequence, distinct time steps that roughly correspond to the recovery stages following wildfire described by Benscoter and Vitt (2008), <20 years, 20 to 70 years and >70 years since fire, were compared to represent stages in wildfire recovery. The proportions of each tree/tall shrub species that represent average stand densities at these recovery stages demonstrates structural differences in margin and middle vegetation canopies (Figure 3.2; Table 3.1). Middle plots appear to experience a flush of opportunistic species growth in the first 20 years, including jackpine (*Pinus banksianna*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*) and black spruce. After 20 years, characteristic bog black spruce trees assume dominance of peatland middle vegetation plots (Figure 3.2b; Table 3.1).

Margin plots have higher diversity at all recovery stages, with black spruce, willows (*Salix* sp.) and paper birch predominating (Figure 3.2a; Table 3.1). This is indicative of the margin being a swamp-like ecotone, with influence from the peatland likely causing black spruce prevalence more than is typical in a deciduous swamp community (Warner and Rubec 1997). Opportunistic occurrences of jackpine and trembling aspen (*Populus* *tremuloides*) also seem to occur in younger seral sites, likely from upland influence (*e.g.* post-fire germination of serotinous jackpine cones or clonal growth of aspen trees). White spruce, balsam poplar (*Populus balsamifera*) and green alder (*Alnus crispa*) were also noted in margins, with no distinct trends of opportunism over time from the limited data available.

Prior to statistical analysis, biomass values were log-transformed to satisfy the assumption of normality. Margin vegetation plots were identified to have significantly greater tree/tall shrub biomass than middle vegetation plots, as determined by a t-test (t = 4.679, p = 5.08 x 10^{-5}; Appendix 3c; Table 3.1). Both log-transformed margin and middle biomass values across the five hydrogeological settings were determined to not be significantly different, as determined by one-way ANOVA (margin: $F(4)$ = 0.664, p = 0.629 and middle: $F(4)$ = 2.434, p = 0.104; Appendix 3c; Table 3.1). There are no clear trends in margin or middle biomass over time (margin linear regression r^2 = 0.253 and middle linear regression r^2 = 0.321; Figure 3.3; Table 3.1). By fitting a smoothing spline to each distribution, it appears that biomass values level off after ~60 years following wildfire. In terms of total aboveground biomass, harvesting and drying of vegetation from ground layer plots determined that ground layer biomass represents a small (average 0.71%) proportion of total margin biomass. In peatland middles, ground layer biomass averaged 8.63% of total aboveground biomass, with Labrador tea shrubs representing the greater contribution to total aboveground biomass (Figure 3.4).

Concomitant with tree/tall shrub biomass results, overstory canopy closure analysis was conducted to investigate trends over time and potential correlations with biomass and understory species abundance. Using third order polynomial trendlines, correlations were identified between canopy closure in both margin and middle plots with time since fire (margin r^2: 0.703 and middle r^2: 0.704; Figure 3.5; Table 3.1). There is also a significant linear correlation between peatland middle canopy closure and tree/tall shrub biomass (r^2: 0.729; Figure 3.6; Table 3.1). This was not the case in peatland margins, where canopy closure appears to remain quite high regardless of biomass, possibly due to the broadleaf composition of the canopy (r^2: 0.170; Figure 3.6; Table 3.1). The relationship between the abundance of various understory species and canopy closure was assessed to determine if shading might play a role in understory species distribution. A significant linear correlation was found between canopy closure and the abundance of feathermoss species in peatland middles (r^2: 0.867; Figure 3.7; Table 3.1). This trend has been previously identified in the literature (Bisbee *et al.*, 2001; Mulligan and Gignac, 2001). However, the correlation was not significant in peatland margins for feathermoss or any other understory species (r^2: 0.230; Figure 3.7; Table 3.1).

3.3.2 Margin and Middle Vegetation Ground Layer Plot Analysis

Species richness values were log-transformed to satisfy the assumption of normality in conducting statistical analysis. Margin vegetation plots were identified to have significantly greater species richness than middle vegetation plots, as determined by a t-test ($t = 2.497$, $p = 0.016$; Appendix 3e; Table 3.1). Accounting for evenness of margin versus middle vegetation communities, Shannon-Wiener Diversity Index calculations were also compared for site-averaged margin and middle plots (Appendix 3). There were no statistically significant differences in diversity between the two groups, likely due to the presence of rare margin species (unevenness) which do not contribute to overall diversity of these plots in the way they contribute to greater species richness ($t = 1.739$, $p = 0.090$; Appendix 3f; Table 3.1). Margin species diversity was not determined to be statistically different across hydrogeological settings ($F(4) = 1.641$, $p = 0.213$; Appendix 3g; Table 3.1). Middle species diversity values across hydrogeological settings were determined to be significantly different, as determined by one-way ANOVA ($F(4) = 4.463$, $p = 0.009$; Appendix 3g; Table 3.1). Specifically, peatland middles located in fine-textured deposits (including moraine deposits with predominantly fine sediments) were determined to have higher species diversity than those located in coarse-textured deposits, as determined by a Tukey post-hoc test. There are no clear trends in margin or middle species diversity over time (margin linear regression $r^2 = 0.029$

and middle linear regression $r^2 = 0.003$; Figure 3.8; Table 3.1). By fitting a smoothing spline to each distribution, it appears that both margin and middle species diversity are maximized from 15 to 40 years post-fire, however margin plots also show increased species diversity towards the end of the chronosequence (~100 years).

Indicator species analysis was run on site-averaged margin and middle vegetation plot data (Table 3.2). To enhance this analysis across the chronosequence, distinct time steps that roughly correspond to recovery stages following wildfire described by Benscoter and Vitt (2008), <20 years, 20 to 70 years and >70 years since fire, were run and species groups corresponding to true/pioneer mosses, *Sphagnum* mosses and feathermosses clustered together (Table 3.3). These clusters represent species assemblages at distinct recovery stages for peatland middle vegetation communities, as identified by Benscoter and Vitt (2008). This analysis failed to identify the *Sphagnum* recovery stage (20 to 80 years post-fire) that was described by Benscoter and Vitt (2008; Table 3.3), likely due to the presence of *Sphagnum* moss across all age categories and therefore the role of *Sphagnum* mosses as more generalist than specialist species in peatland middles that were assessed in this study. The early successional pioneer moss stage and later successional feathermoss stage was clearly identified in this analysis.

Margin indicator species analysis identified a suite of vegetation strata (trees, shrubs, forbs, graminoids, ferns and mosses) and represent the keystone or characteristic species of this ecotone (Tables 3.2 and 3.3). In addition to the broadleaf (swamp-like) cover that was apparent from tree plot analysis, aspen and willows were also identified in early successional sites as low (< 0.5 m height) vascular species. On the ground layer, facultative wetland species such as bluejoint (*Calamagrostis canadensis*) and common horsetail (*Equisetum arvense*) support the association of peatland margins with swamp communities, however there are also several upland forbs, such as bunchberry (*Cornus canadensis*) and wild strawberry (*Fragaria virginiana*), and shrubs, such as twinflower (*Linnaea borealis*), wild rose (*Rosa woodsii*) and dwarf raspberry (*Rubus pubescens*), which act as a reminder that margin ecotones exist in a transition zone and lends characteristics from both surrounding peatland and upland vegetation communities.

3.3.3 Correlation of Vegetation Assemblages with Explanatory Variables

In running NMDS analysis of margin and middle vegetation plots, it was determined that the margin of one site, Ottr2001B, represented a significant outlier, plotting far from the cluster of remaining margin and middle plots in the ordination. This site was excluded from future NMDS analysis. Sites that were identified as having no discernible margin ecotone using SMW analysis (see Section 2.3.1, Appendix 2) were also excluded from NMDS margin analysis. Figure 3.9 shows the NMDS ordination biplot of margin and middle site-averaged vegetation abundance data. Species code names used in the ordination are described in Appendix 4. Margins and middles appear to cluster distinctly from each other, with the exception of slight overlap in the case of two sites, Utik1905 and Haig1940B. Further investigation of these sites and the NMDS biplot showed that they are later successional margins with high feathermoss abundances. As will be investigated in more detail, feathermoss prevalence in both later successional margin and middle vegetation communities could explain the overlap in this analysis.

Similar clustering of hydrogeological settings was run on the NMDS ordination biplots isolated for both margin and middle site-averaged species abundances to examine if any hydrogeological settings had distinct species assemblages that could be identified and further investigated (Figures 3.10 and 3.11). No clear clusters of sites across hydrogeological settings were identified as there was significant overlap of all clusters.

To examine the relation of margin biplot axes with explanatory variables of time since fire, species richness, diversity, canopy closure, tree/tall shrub biomass and maximum peat depth recorded in augering surveys, vector analysis was conducted (Figure 3.12). Time since fire (Age) explained the variation in margin composition along the two first axes (r^2 = 0.785, p = 0.001), and it was primarily correlated with the first axis. This trajectory of recovery is examined further below. Similarly, canopy closure (CC) was a strong predictor for the two first axes (r^2 = 0.560, p = 0.001). Tree/tall shrub biomass was a weaker predictor, and more correlated with the second axis (r^2 = 0.461, p = 0.051). Species richness (Rich), Shannon-Wiener diversity (Div) and peat depth (MaxPD) did not have statistically significant correlations with the biplot axes and are not displayed (Rich r^2 = 0.112, p = 0.337, Div r^2 = 0.201, p = 0.131 and MaxPD r^2 = 0.047, p = 0.670).

Analysis of peatland middle biplot axes with explanatory variables was also conducted (Figure 3.13). Time since fire (Age) explained the variation in middle composition along the two first axes (r^2 = 0.6027, p = 0.001), and it was mainly correlated with the second axis. This trajectory of recovery is examined further below. Tree/tall shrub biomass (BM), canopy closure (CC) and species richness (Rich) were even stronger predictors for the first two axes (BM r^2 = 0.802, p = 0.001, CC r^2 = 0.756, p = 0.001 and Rich r^2 = 0.677, p = 0.001). Species richness, Shannon-Wiener diversity and age were all more correlated with the second axis, while biomass appears to be evenly correlated to both biplot axes. Diversity is a weaker predictor of the biplot axes (r^2 = 0.356, p = 0.007).

3.3.4 Trajectories in Margin Vegetation Community Recovery

More specific analysis of margin vegetation community recovery following wildfire was conducted using contours of time since fire imposed on the margin NMDS biplot (Figure 3.14), and an additional plot with only ground layer bryophyte and lichen species isolated (Figure 3.15). This shows time as a continuous rather than a discrete variable (Benscoter and Vitt, 2008) and illustrates recovery trajectories of the studied peatland margin vegetation communities. Species code names used in the ordination are described in Appendix 4. If only indicator species (Tables 3.2 and 3.3) are accounted for, a further simplified recovery trajectory for peatland margins is presented in Figure 3.17 (summary statistics in Table 3.1). This includes litter and combined vascular abundances as significant groups. Vascular species are relatively more diverse and represent more indicator species in margin plots than middle plots, while litter was considered important as this was a dominant ground layer feature across early to mid successional sites. It is also an indicator of overstory broadleaf canopy in margin plots shedding leaves every fall and the contribution to margin peat as a significant component of litter versus decomposed *Sphagnum* moss.

Similar NMDS biplot contours and simplified recovery trajectories of studied peatland middles are presented in Figures 3.16 and 3.17 (summary statistics in Table 3.1). Significant species groupings follow Benscoter and Vitt (2008): true/pioneer mosses, *Sphagnum* mosses, feathermosses and vascular species.

It is apparent that, in both margins and middles, feathermoss species play an important role in later successional communities (Figure 3.17). In early successional margin communities, true/pioneer moss species are present and seem to compete with the litter layer for the first ~40 years. At 40 years, feathermoss species establish and take over from true/pioneer mosses, however the litter layer remains prominent until ~60 years post-fire. After 60 years, feathermoss species dominate the entire ground cover. Above the ground layer, vascular species appear to represent a greater abundance in the first ~40 years of the chronosequence and decline from that point onwards.

In peatland middles, very similar patterns are shown in ground layer trajectories, except for *Sphagnum* moss prevalence over litter cover (Figure 3.17). Feathermoss species overtake true/pioneer mosses after ~35 years, however *Sphagnum* mosses are the dominant ground layer species from ~8 to 60 years post-fire. Feathermosses become dominant at 60 years and remain until the end of the chronosequence analysis (120 years). Vascular cover is slightly higher in the first half of the chronosequence, but overall there is no notable shift in vascular abundance over time.

3.4 Discussion

3.4.1 Margin Ecotone Recovery Following Wildfire Disturbance

The margin swamp community that has previously been described in the literature is one dominated by broadleaf deciduous trees and shrubs and a ground layer composed of a mixture of non-*Sphagnum* bryophytes, grasses, sedges and forbs (Warner and Rubec 1997; Bauer *et al.*, 2009). This analysis of BP peatland bog margins across hydrogeological settings provides a conclusive analysis of margin vegetation community composition as well as successional changes over the course of one fire return interval. This builds on analysis by Lukenbach *et al.* (2017), where margin bryophyte recovery immediately following wildfire was determined to be controlled by degree of groundwater connectivity. In their work, peatland-dwelling bryophyte species were observed in margins with strong groundwater connectivity (fine-textured sites), versus limited peatland bryophyte recovery in margins that were disconnected from groundwater flow systems (coarse-textured, ephemerally perched peatlands) and therefore experienced enhanced depth of burn and flashy water tables post-fire (Hokanson *et al*., 2016; Lukenbach *et al*., 2015a). Beyond this analysis of the initial three years following wildfire, this study details characteristic ground layer species of BP peatland bog margin vegetation communities, including those indicative of recovery stages over time (Tables 3.2 and 3.3). These species represent a mixture of both facultative wetland species and typical upland vegetation that could be found in either an aspen or pine dominated community (Beckingham and Archibald, 1996). The overstory of a mid to later successional margin community consists of ~50% black and white spruce conifers and 50% deciduous broadleaf species including aspen, birch and willows. This composition reflects the position of the margin ecotone at the interface between upland and peatland communities, with species that are characteristic of both communities inhabiting the margin. As a result, margin communities were found to be very species-rich, although with similar diversity to middle communities given the prevalence of numerous rare species (low abundance, limited occurrences) in margins. None-the-less, characterization of margins as distinct ecotones with a separate species composition from peatland middles increases the biodiversity and hence functional diversity of the entire peatland ecosystem.

Vegetation structure in BP peatland bog margins differs from that of middles, from canopy composition and closure to ground layer species assemblages. Nutrient availability was not measured as part of this study, however there is likely an effect of soil nutrients and pH on vegetation assemblages which occur in margin versus middle communities, due to the influence of the relatively nutrient-rich upland mineral soil in proximity to margins (Depante, 2016). Being nutrient poor with low pH, bog peatland vegetation communities are sustained due to species competitive exclusion, with a homogeneous ground layer of tolerant ericaceous shrubs and *Sphagnum* mosses, and a canopy of black spruce trees which are able to withstand relatively high water tables. The margins are more species-rich (albeit with several rare species that cause considerable unevenness), with an emphasis on overstory tree and tall shrub diversity. The canopy is dominated by a mixture of coniferous and deciduous broadleaf species and canopy closure consistently remains higher in margin plots than middle plots throughout the chronosequence (Figures 3.2 and 3.5). Species opportunism (*e.g.* clonal growth in aspen) and facilitation has also been recorded among broadleaf trees and shrubs encroaching into peatlands from surrounding upland ecosystems, representing a positive feedback further facilitating this broadleaf margin recovery trajectory (Wieder *et al*., 2009; Holmgren *et al*., 2015; Schneider *et al*. 2015; Depante, 2016). It is likely that this canopy shading and water table drawdown from enhanced evapotranspiration in margins limits light and water availability for *Sphagnum* mosses, excluding them from recolonizing the margin ecotone from within the peatland (Bisbee *et al.*, 2001). Similarly, photo-inhibition favours feathermoss colonization in later successional peatlands, with a weaker correlation identified in margins (Figure 3.7).

Broadleaf species in the studied margin canopies bring seasonality to their functional roles in the ecosystem. In early spring, it is likely that high water tables from snowmelt in margin areas are reinforced by decreased evapotranspiration from the broadleaf canopy. When leaves emerge, drawdown of margin water tables would be caused by greater evapotranspiration demands of the aspen, birch and willow canopy throughout the warm summer months (Petrone *et al*., 2007; Depante, 2016). In fall, when drought water table levels are often experienced after high summer temperatures, leaf-fall of the deciduous species could counteract drought stress in peatlands by again limiting evapotranspiration demand in time for winter dormancy and snow accretion, with associated water table rebound. While *Sphagnum* moss can act as an evaporative cap in peatlands experiencing drought stress (Kettridge and Waddington, 2014), broadleaf canopy shading may also assist in limiting evaporation water losses in peatland margins. Relative strengths of these feedback mechanisms would be species specific (shading ability versus transpiration demand) and will change with time since fire (Kettridge *et al*., 2013).

From the ground layer perspective, early successional colonization of true moss species has been noted in both peatland margins and middles. This study has developed a better understanding of ground layer trajectories of margin vegetation communities beyond pioneer and opportunistic species establishment (Lukenbach *et al*., 2017). Although there are various vascular and fern species that were identified as indicative margin vegetation assemblages (Table 3.2), the dominant ground cover in early to mid successional margin communities was litter (Figure 3.17). This is due to shedding leaves from the deciduous canopy and likely contributes to the quantity and quality (physical and hydrological characteristics) of margin peat. It is also possible that litter can act as an evaporative cap at the ground surface, further serving a role that *Sphagnum* mosses fulfil in peatland middles (Kettridge and Waddington, 2014).

It is apparent that each margin vegetation component, its associated structure and larger ecological function, can be derived for the ground layer bryophytes, vascular/fern species and canopy assemblages (with litter also playing a role from canopy leaf-fall). This supports the hypothesis that, similar to peatland middle vegetation assemblages, peatland margins have characteristic species which play important roles in maintaining the integrity of this ecotonal community, and likely in maintaining the water and energy balances of the larger peatland ecosystems (*e.g.* Waddington *et al*., 2015). Further investigation into margin peat physical and hydrological properties, as well as individual species properties such as transpiration rates and surface evaporation rates from the litter layer, can help enhance this understanding of the role of margin communities in maintaining resilient peatland ecosystems across the landscape.

3.4.2 Vulnerable Margin Ecotones

Feathermoss ground layer dominance after ~60 years in both peatland margins and middles is a notable finding, given this is 20 years earlier than identified in the chronosequence analysis by Benscoter and Vitt (2008). It is possible that by sampling sites across a wide array of hydrogeological settings, and particularly by targeting coarse-textured, drier (*e.g.* potentially perched) peatlands, we have discovered an accelerated successional pathway in several sites which was a driving force of the recovery rates of this chronosequence analysis. With chronicled data on vulnerability of feathermoss dominated peatlands to wildfires (Benscoter and Vitt, 2007; Benscoter *et al*., 2011; Lukenbach *et al*., 2015b; Lukenbach *et al*., 2016), this feathermoss prevalence along the ground layer of peatland margins highlights further concern for ignition and deep smouldering of these peat reserves during wildfire. Coupled with this, it has been found that canopy fuel loads (biomass) of peatland margins are consistently higher than those of peatland middles across this entire chronosequence study. This reinforces the hypothesis that margin ecotones are capable of transmitting fire across the interface from surrounding uplands into peatland vegetation communities. Calculated tree/tall shrub biomass in peatland margins was found to generally increase with time since fire, but levelled off after ~60 years around 125,000 kg ha^{-1}. Peatland middle calculated tree/tall shrub biomass values followed a similar trend, with significant spread to the data, however average biomass values after ~60 years were considerably less, at 50,000 kg ha^{-1}. Wieder *et al.* (2009) have also found BP peatland black spruce biomass values levelled off at ~57,500 kg ha^{-1} 80 years post-fire. This further demonstrates that fuel loads in this chronosequence analysis represent an accelerated recovery trajectory with time since fire. The quality of woody fuels in margin vegetation communities, given the diversity of overstory margin species, should be evaluated in future research to identify fire danger, especially in the early spring and fall when deciduous species have no leaves and are not actively transpiring water.

3.4.3 Implications for Land Management

Restoration planning can incorporate these study findings by applying the detailed species recovery trajectories for both peatland margin and middle communities, which appear to maintain spatial representation over time (margin area to peatland area ratio, see Chapter 2), to understand recovery stages and potential milestones which may indicate success or alternate recovery trajectories in long-term monitoring projects. For example, *Sphagnum* presence in peatland bogs has been noted within 20 years following wildfire in this and other chronosequence analyses (Benscoter and Vitt, 2008). In terms of restoring ecosystem function, and especially the functions of carbon and water storage/supply for upland forests, this would represent a landmark stage in recovery that should be the goal for restoration managers. If the opportunistic canopy of aspen, birch and willow species that might colonize a site immediately following disturbance has not dissipated in the first 20 years, then it is likely that this community is at risk of developing a broadleaf canopy and enhanced litterfall in the longer term. This can perpetuate as a positive feedback and mimic the recovery trajectory of margin communities and that of collapsed peatland ecosystems, which accumulate dense, vulnerable peat with a flashy water table and limited carbon sequestration and water storage in the longer term (Kettridge *et al*., 2015).

From the opposite end of the chronosequence, it could be argued that feathermoss prevalence in later successional (>60 years) peatlands and their associated margin communities can be linked to increased canopy closure (as supported by Bisbee *et al.*, 2001 and Mulligan and Gignac, 2001). Hence, mechanical methods of opening the canopy in these communities might be a tool in promoting *Sphagnum* dominance over feathermoss in peatland middles, and possibly a tool in encouraging paludification, or expansion of the peatland into margin swamp ecotones. Further research into this area is vital in understanding how to manage increasing wildfire prevalence and severity in a drier climate future (Flannigan *et al*., 2005), as well as in a landscape where wildfires are a natural occurrence which have historically occurred every ~120 years (Turetsky *et al*., 2004; Wieder *et al*., 2009) but are now suppressed by humans to protect communities, resources and infrastructure. If we are limiting fire occurrence on the landscape, and subsequently accumulating greater fuel loads, then vulnerable peatlands which store large quantities of carbon could benefit from forest treatments (such as thinning) to open the vegetation canopy, promote *Sphagnum* moss prevalence and thereby prevent severe smouldering, catastrophic carbon losses and potential human losses (communities, infrastructure) that result from large-scale wildfires.

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Table 3.1: Summary statistics from t-test, ANOVA and regression analysis. Statistical significance of each test is indicated by an asterisk (*) following the *p* or r^2 value.

T-test/ANOVA				
Figure	**Description**	**Data transformation**	**Test Statistic**	**Significance**
3.1	Boxplot of margin and middle tree/tall shrub stand densities	Square root	$t = 3.582$	$p = 0.001$*
Appendix 3c	Boxplot of margin and middle tree/tall shrub calculated biomass	Log-transformed	$t = 4.679$	$p = 5.08\text{x}10^{-5}$*
Appendix 3d	Boxplots of margin and middle tree/tall shrub calculated biomass by hydrogeological setting	Log-transformed	Margin: $F(4) = 0.664$ Middle: $F(4) = 2.434$	$p = 0.629$ $p = 0.104$
Appendix 3e	Boxplot of margin versus middle species richness	Log-transformed	$t = 2.497$	$p = 0.016$*
Appendix 3f	Boxplot of margin and middle species diversity, calculated using the site-averaged Shannon-Wiener Diversity Index	None	$t = 1.739$	$p = 0.090$
Appendix 3g	Boxplots of margin and middle species diversity, calculated using the site-averaged Shannon-Wiener Diversity Index, by hydrogeological setting	None	Margin: $F(4) = 1.641$ Middle: $F(4) = 4.463$	$p = 0.213$ $p = 0.009$*

Regression

Figure	Description	Trendline Equation	Coefficient
3.3	Margin and middle tree/tall shrub biomass with time since fire	Margin: $y = 754.47x + 47815$ Middle: $y = 469.06x + 7784.5$	$r^2 = 0.131$ $r^2 = 0.182$
3.5	Margin and middle canopy closure with time since fire	Margin: $y = 0.0002x^3 - 0.052x^2 + 3.484x - 0.827$ Middle: $y = -0.0001x^3 + 0.016x^2 - 0.112x + 4.619$	$r^2 = 0.703$* $r^2 = 0.704$*
3.6	Margin and middle canopy closure versus tree/tall shrub calculated biomass	Margin: $y = 0.00007x + 62.467$ Middle: $y = 0.0005x + 13.44$	$r^2 = 0.170$ $r^2 = 0.729$*
3.7	Margin and middle canopy closure versus feathermoss species abundances in the understory	Margin: $y = 0.473x - 3.538$ Middle: $y = 1.4x - 6.757$	$r^2 = 0.230$ $r^2 = 0.867$*
3.8	Margin and middle species diversity, calculated using the site-averaged Shannon-Wiener Diversity, with time since fire	Margin: $y = -0.0019x + 2.070$ Middle: $y = -0.0006x + 1.806$	$r^2 = 0.029$ $r^2 = 0.003$
3.17	A simplified illustration of the margin and middle vegetation community recovery trajectory using indicator species and including litter abundance	Margin: True Moss: $y = 0.00002x^3 - 0.0004x^2 - 0.380x + 29.919$ Litter: $y = 0.0002x^3 - 0.036x^2 + 1.680x + 30.118$ Feathermoss: $y = -0.0004x^3 + 0.052x^2 - 1.27x + 6.574$ Vascular: $y = 0.0004x^3 - 0.064x^2 + 2.089x + 64.392$	 $r^2 = 0.269$ $r^2 = 0.059$ $r^2 = 0.782$* $r^2 = 0.459$

3.17 (cont'd)	A simplified illustration of the margin and middle vegetation community recovery trajectory using indicator species and including litter abundance	Middle: True Moss: $y = 0.00001x^3 + 0.0042x^2 - 0.581x + 26.61$ Sphagnum: $y = 0.0003x^3 - 0.054x^2 + 2.703x + 5.053$ Feathermoss: $y =-0.0002x^3 + 0.029x^2 - 0.506x + 2.236$ Vascular: $y = 0.0002x^3 - 0.036x^2 + 1.443x + 66.656$	$r^2 = 0.749$* $r^2 = 0.222$ $r^2 = 0.687$* $r^2 = 0.168$

Table 3.2: Indicator species identified, in priority order with their associated indicator values and probability, for each of the margin and middle site-averaged species abundances.

Margin Indicator Species

Species Code	Scientific Name	Common Name	Vegetation Stratum	Indicator Value	Probability
CORNCAN	*Cornus canadensis*	Bunchberry	Forb	0.619	0.001
EQUIARV	*Equisetum arvense*	Common horsetail	Fern	0.602	0.001
CALACAN	*Calamagrostis canadensis*	Bluejoint	Graminoid	0.524	0.001
LINNBOR	*Linnaea borealis*	Twinflower	Shrub	0.524	0.001
EPILANG	*Epilobium angustifolium*	Fireweed	Forb	0.381	0.003
ORTHOBT	*Orthotrichum obtusifolium*	Obtuseleaf aspen moss	Moss	0.333	0.003
ROSAWOO	*Rosa woodsii*	Wild rose	Shrub	0.333	0.003
RUBUPUB	*Rubus pubescens*	Dwarf raspberry	Shrub	0.333	0.003
VIOLCAN	*Viola canadensis*	Canada violet	Forb	0.333	0.001
MARCPOL	*Marchantia polymorpha*	Liverwort	Liverwort	0.276	0.022
SPHARIP	*Sphagnum riparium*	Streamside peat moss	Moss	0.191	0.033
FRAGVIR	*Fragaria virginiana*	Wild strawberry	Forb	0.191	0.034

Middle Indicator Species

Species Code	Scientific Name	Common Name	Vegetation Stratum	Indicator Value	Probability
SPHAFUS	*Sphagnum fuscum*	Rusty peat moss	Moss	0.881	0.001
RHODGRO	*Rhododendron groenlandicum*	Labrador tea	Shrub	0.841	0.001
RUBUCHA	*Rubus chamaemorus*	Cloudberry	Forb	0.833	0.001
VACCVIT	*Vaccinium vitis-idaea*	Bog cranberry	Shrub	0.785	0.001

Middle Indicator Species (continued)					
Species Code	**Scientific Name**	**Common Name**	**Vegetation Stratum**	**Indicator Value**	**Probability**
SPHAANG	*Sphagnum angustifolium*	Sphagnum	Moss	0.710	0.001
CLADSP.	*Cladina* sp.	Reindeer lichen	Lichen	0.683	0.001
OXYCMIC	*Oxycoccus microcarpus*	Small bog cranberry	Shrub	0.615	0.001
LICHEN	Lichen sp.	Lichen	Lichen	0.324	0.032
CHAMCAL	*Chamaedaphne calyculata*	Leatherleaf	Shrub	0.308	0.014
SPHACAP	*Sphagnum capillifolium*	Red peat moss	Moss	0.231	0.033

Table 3.3: Indicator species, with their associated indicator values and probability, for customized recovery stages based on those developed by Benscoter and Vitt (2008): <20 years, 20-70 years and >70 years since fire. Moss species were grouped corresponding to true/pioneer mosses, *Sphagnum* mosses and feathermosses to correspond to each of the three recovery stages, respectively, in peatland bogs.

Margin Indicator Species						
Age Range	**Species Code**	**Scientific Name**	**Common Name**	**Vegetation Stratum**	**Indicator Value**	**Probability**
<20 years	EPILANG	*Epilobium angustifolium*	Fireweed	Forb	0.733	0.001
	SALISP.	*Salix* sp.	Willows	Shrubs	0.498	0.048
	POPUTRE	*Populus tremuloides*	Trembling aspen	Tree	0.486	0.035
20-70 years	LINNBOR	*Linnaea borealis*	Twinflower	Shrub	0.624	0.023
>70 years	HYLOSPL PLEUSCH PTILCRI	*Hylocomium splendens,* *Pleurozium schreberi,* *Ptilium crista-castrensis*	Feathermosses	Mosses	0.624	0.023
	VIOLREN	*Viola renifolia*	Kidney-leaved violet	Forb	0.6367	0.011
Middle Indicator Species						
Age Range	**Species Code**	**Scientific Name**	**Common Name**	**Vegetation Stratum**	**Indicator Value**	**Probability**
<20 years	AULAPAL CERAPUR DICRUND POLYSTR POLYCOM	*Aulacomnium palustre,* *Ceratodon purpureus,* *Dicranum undulatum,* *Polytrichum strictum,* *Polytrichum commune*	True/pioneer mosses	Mosses	0.668	0.001
>70 years	HYLOSPL PLEUSCH PTILCRI	*Hylocomium splendens,* *Pleurozium schreberi,* *Ptilium crista-castrensis*	Feathermosses	Mosses	0.678	0.001

Figure 3.1: Boxplot of margin and middle tree/tall shrub stand densities. Square root-transformed values of each group were determined to be significantly different (*t*(4) = 3.582, *p* = 0.001).

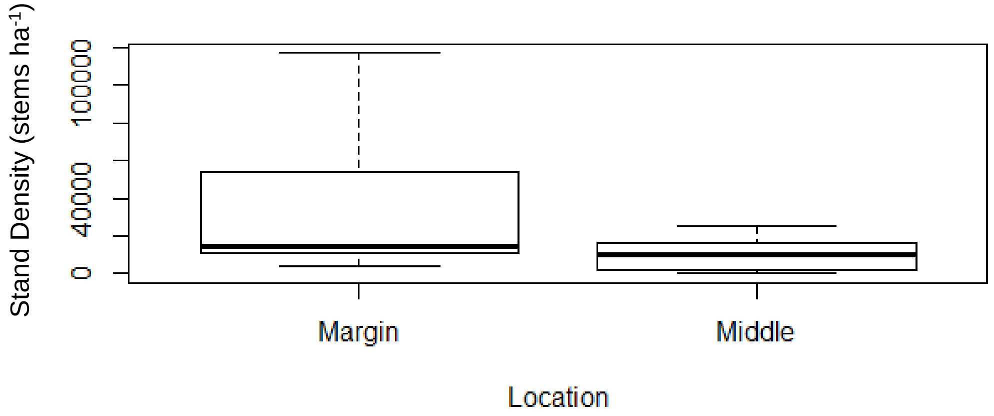
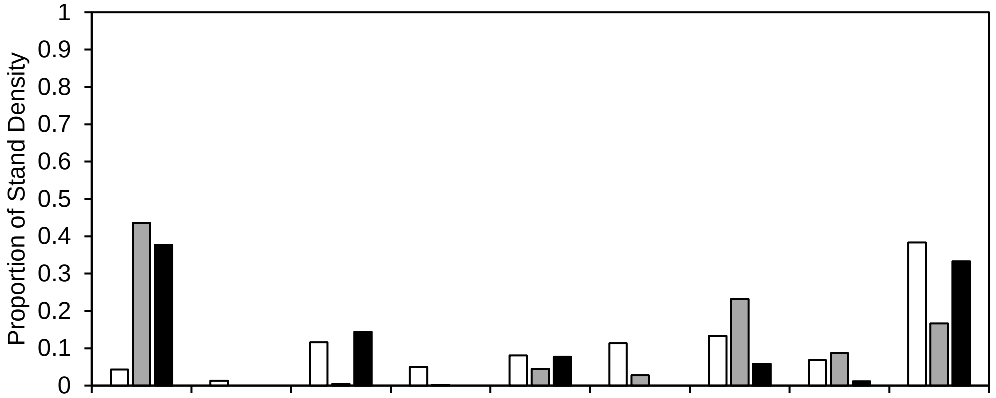


Figure 3.2: Margin and middle tree/tall shrub species proportions of total stand density at each recovery stage (<20 years, 20 to 70 years and >70 years) following wildfire. TSF indicates time since fire.

a) Margin



b) Middle

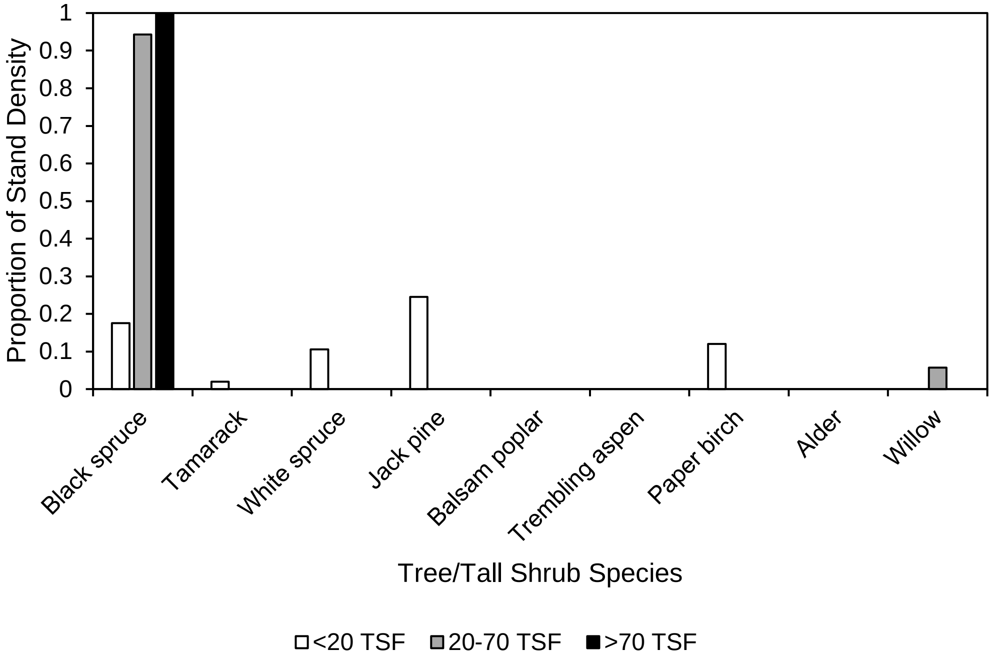


Figure 3.3: Margin and middle tree/tall shrub biomass with time since fire and a smoothing spline fit to each of the margin (blue) and middle (red) distributions.

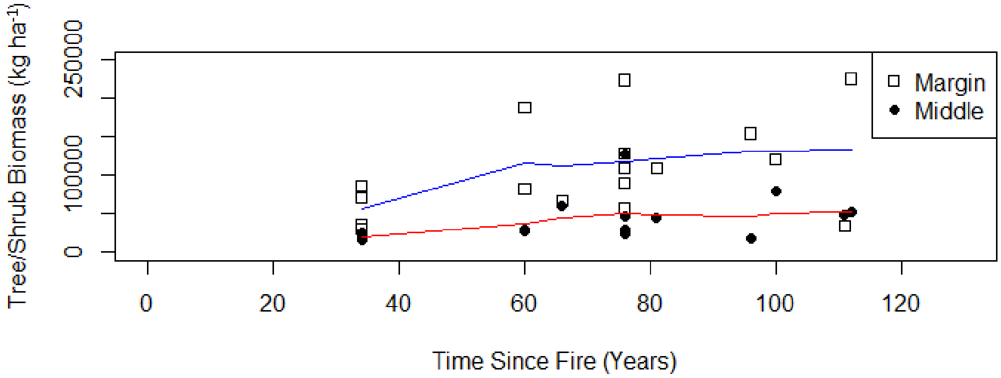


Figure 3.4: Margin versus middle site-averaged total aboveground biomass, including the harvested ground layer vegetation and tree/tall shrub biomass calculated using allometric equations.

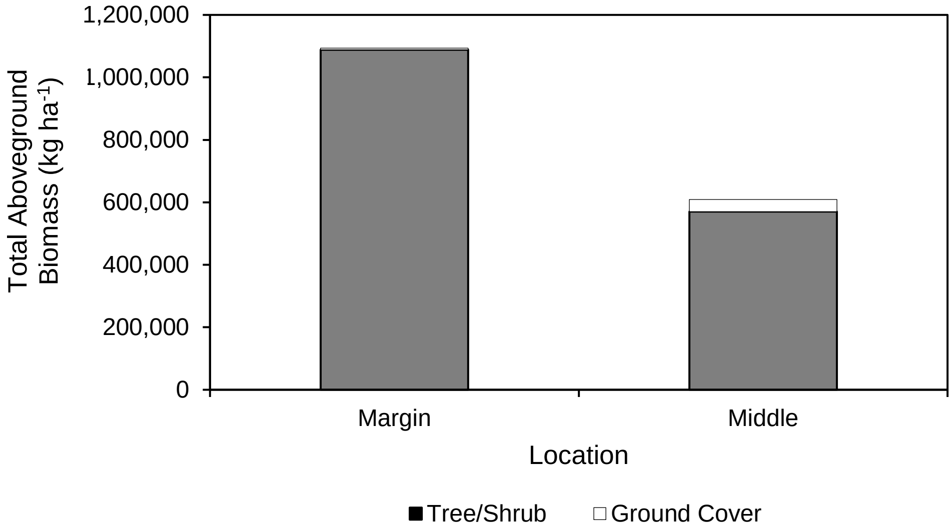


Figure 3.5: Margin and middle canopy closure with time since fire. Third order polynomial curves have been fit to each distribution. Equations are given in Table 3.1.

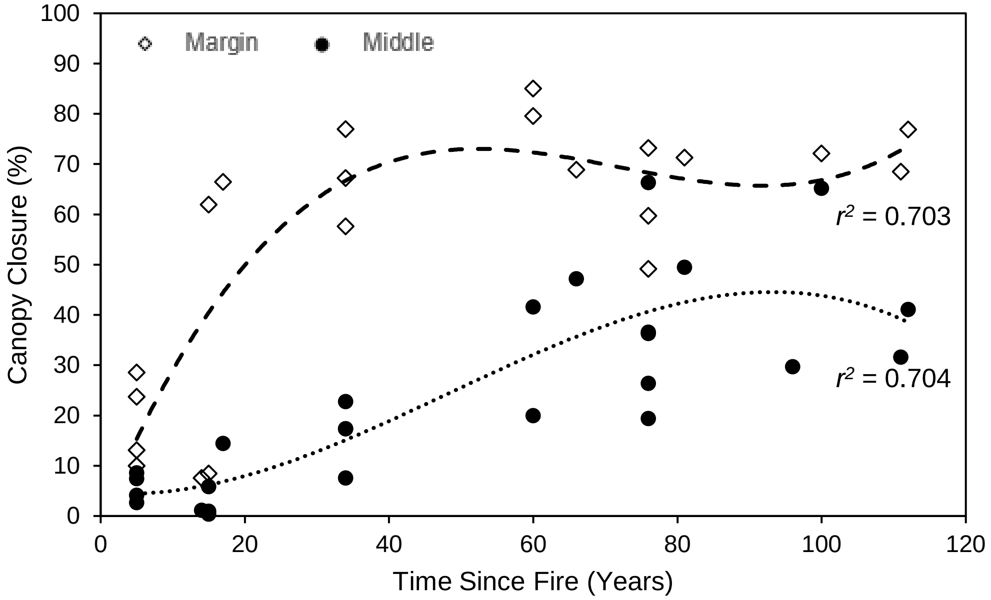


Figure 3.6: Margin and middle canopy closure versus tree/tall shrub calculated biomass. Linear regressions have been fit to each distribution. Equations are given in Table 3.1.

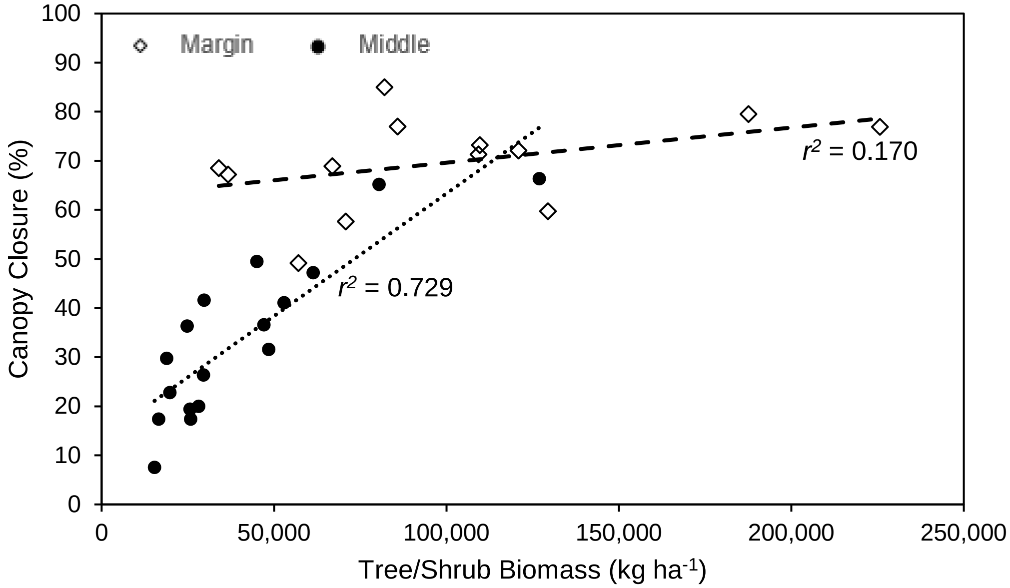


Figure 3.7: Margin and middle canopy closure versus feathermoss species abundances in the understory. Linear regressions have been fit to each distribution. Equations are given in Table 3.1.

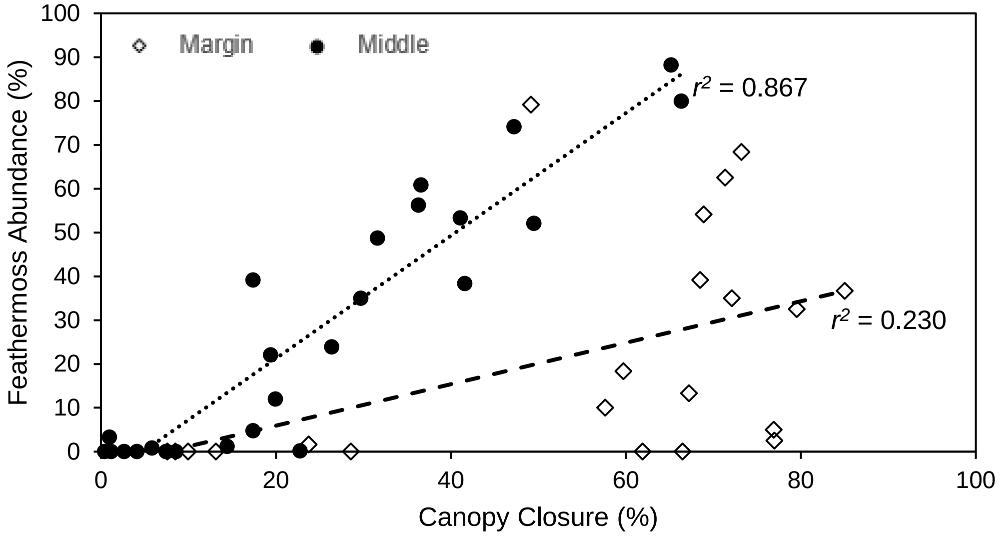


Figure 3.8: Margin and middle species diversity, calculated using the site-averaged Shannon-Wiener Diversity Index, with time since fire and a smoothing spline fit to each of the margin (blue) and middle (red) distributions.

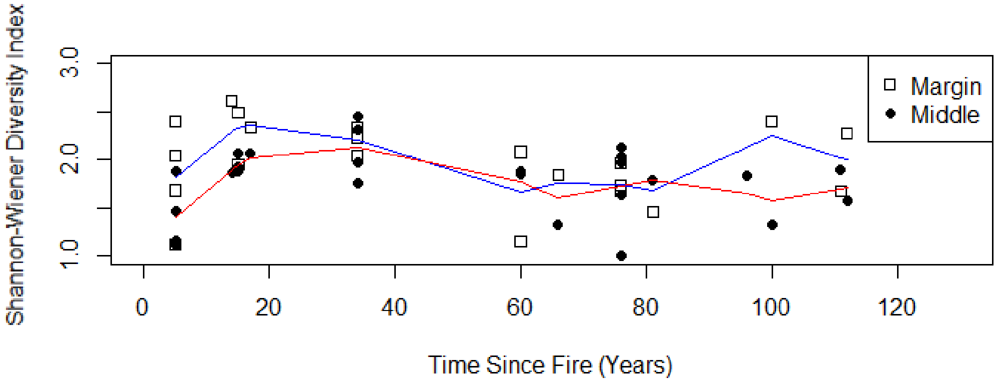


Figure 3.9: NMDS biplot illustrating the site-averaged vegetation abundances at margin and middle sites (n = 47) along the first two axes (stress = 0.143). Colors are used to differentiate margins (red) from middles (blue). Clusters were imposed upon groups, as shown by the black outlines. See Appendix 4 for species names.

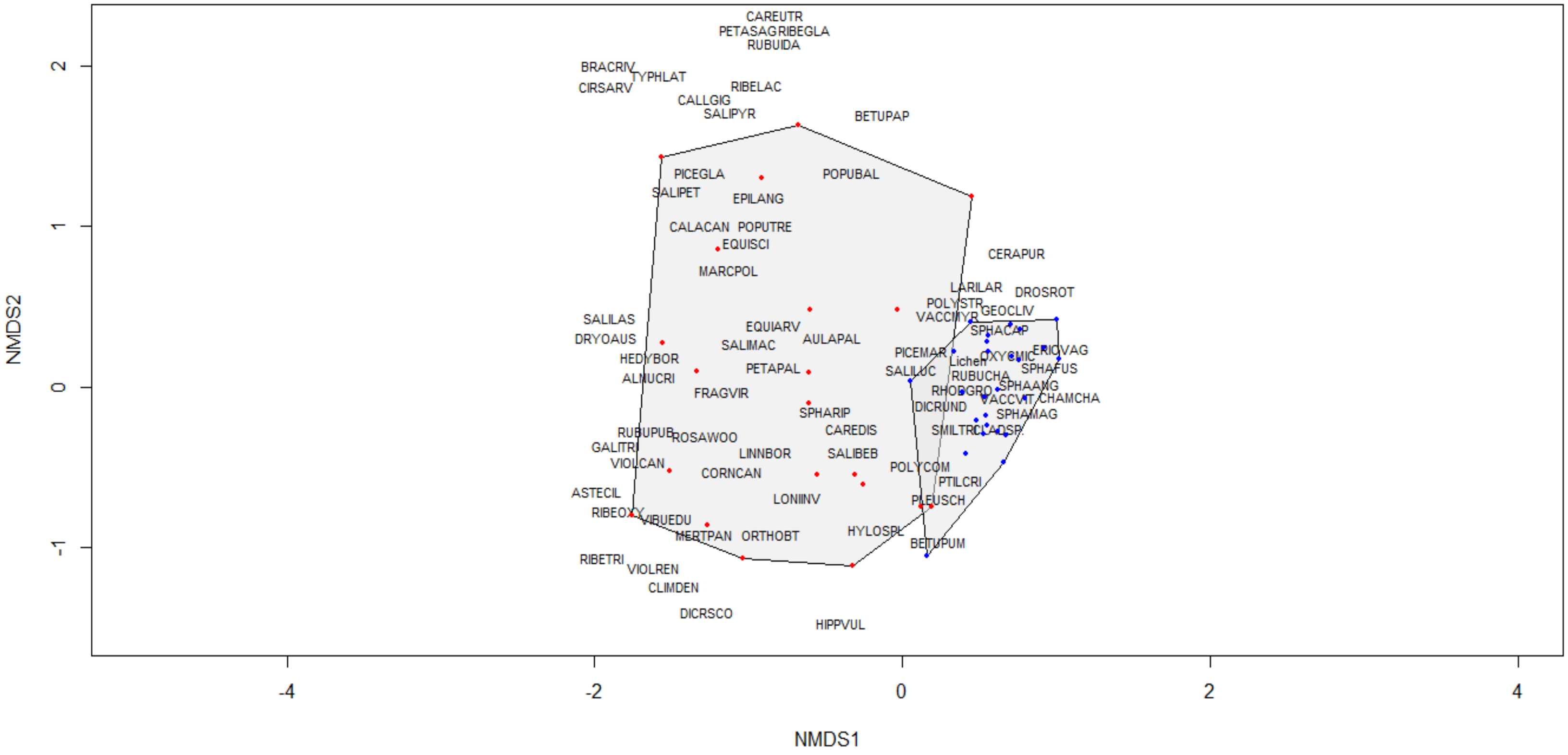


Figure 3.10: NMDS biplot illustrating the site-averaged vegetation abundances at margin sites only (n = 21) along the first two axes (stress = 0.165). Colors are used to differentiate fine (red), moraine (blue) and coarse (green) hydrogeological settings shown as clusters. See Appendix 4 for species names.

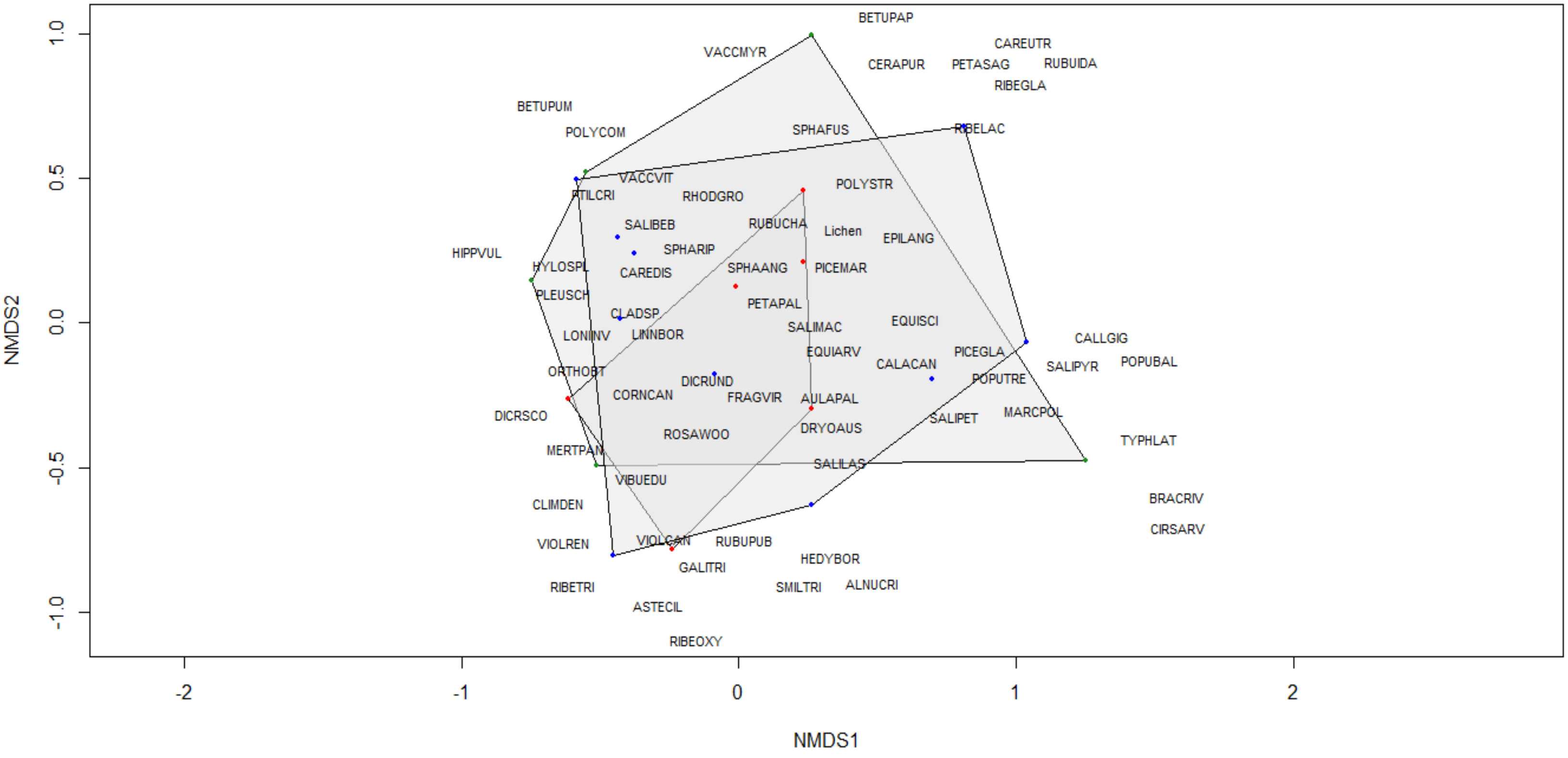


Figure 3.11: NMDS biplot illustrating the site-averaged vegetation abundances at middle sites only (n = 26) along the first two axes (stress = 0.153). Colors are used to differentiate fine (red), moraine (blue) and coarse (green) hydrogeological settings shown as clusters. See Appendix 4 for species names.

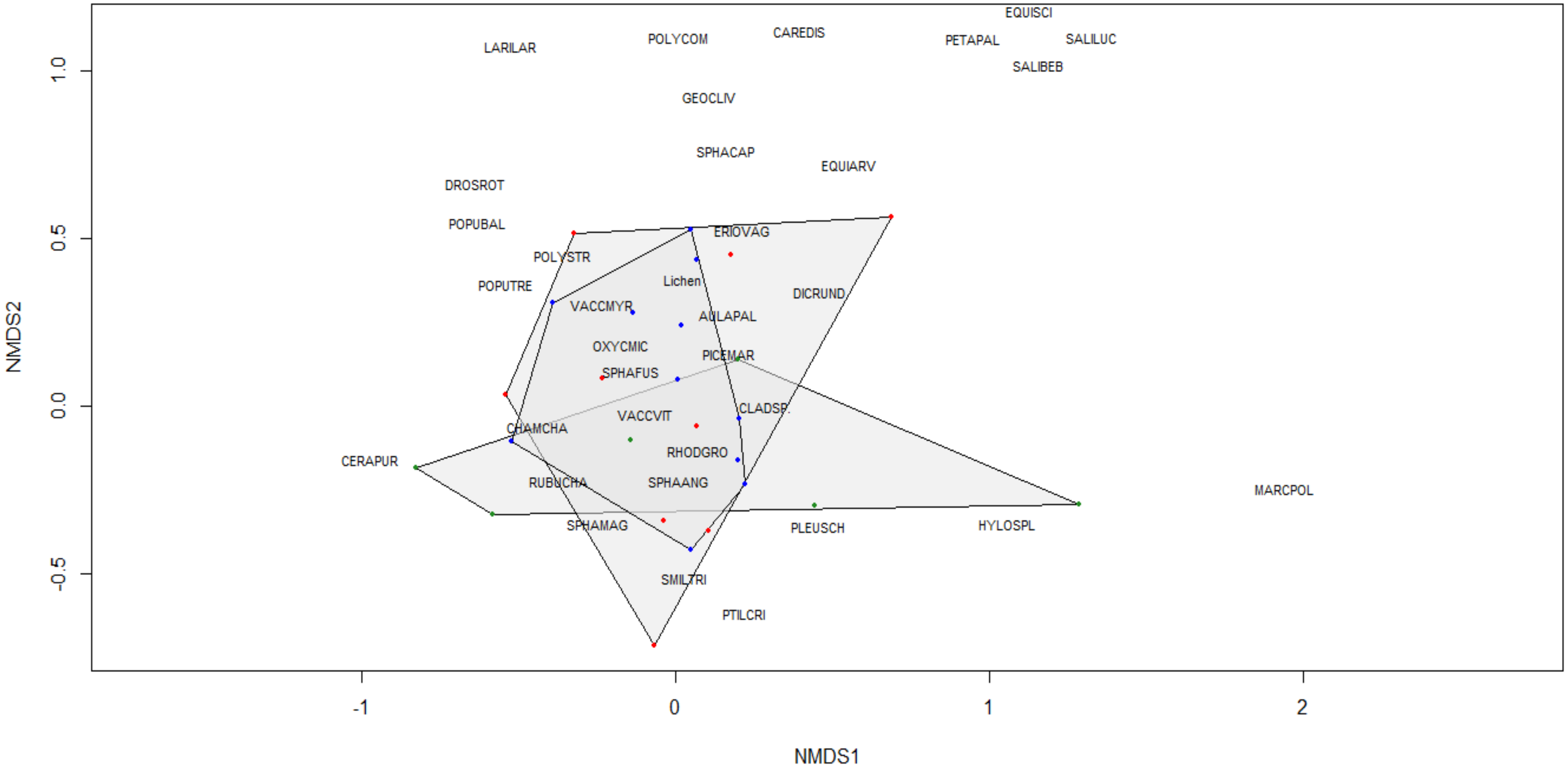


Figure 3.12: NMDS biplot illustrating the site-averaged vegetation abundances at margin sites only (n = 21) along the first two axes (stress = 0.247). Vectors have been fit to the plot representing explanatory variables measured in margin plots. Arrows are the direction of the gradients and arrow lengths indicate the strength of the correlation. See text for statistical results and Appendix 4 for species names.

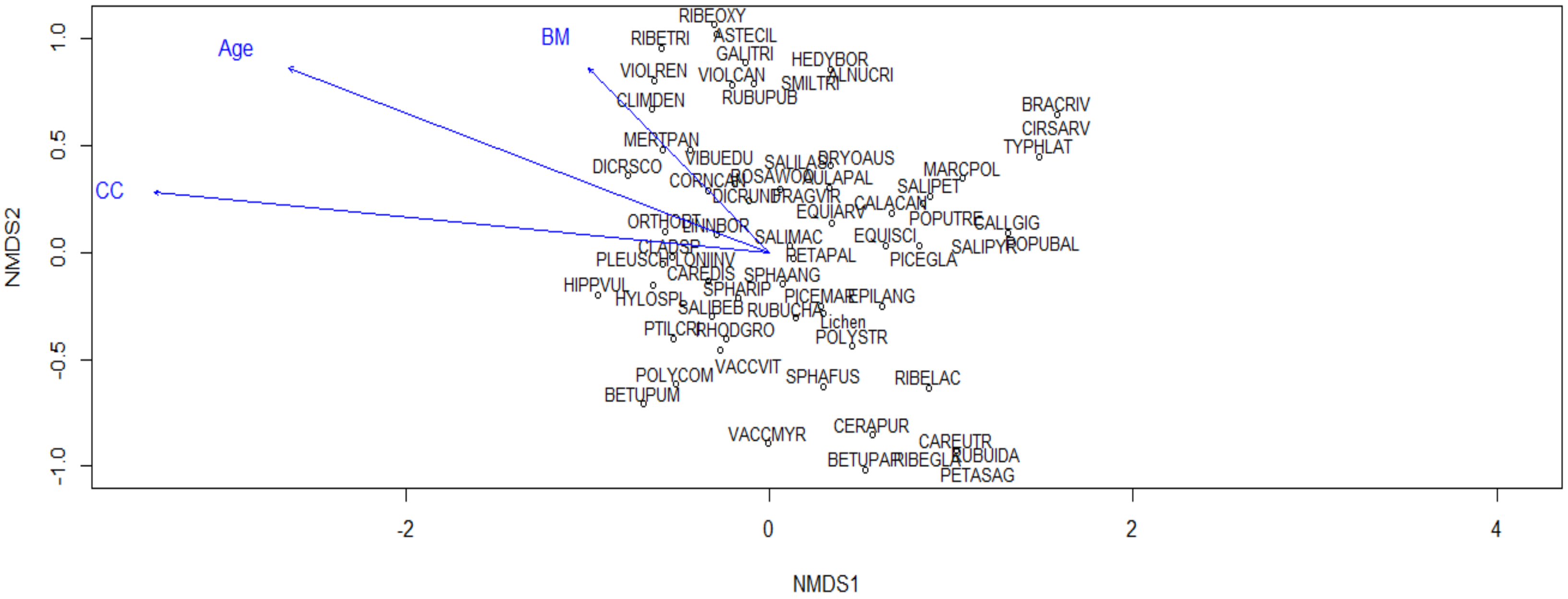


Figure 3.13: NMDS biplot illustrating the site-averaged vegetation abundances at middle sites only (n = 26) along the first two axes (stress = 0.163). Vectors have been fit to the plot representing explanatory variables measured in middle plots. Arrows are the direction of the gradients and arrow lengths indicate the strength of the correlation. See text for statistical results and Appendix 4 for species names.

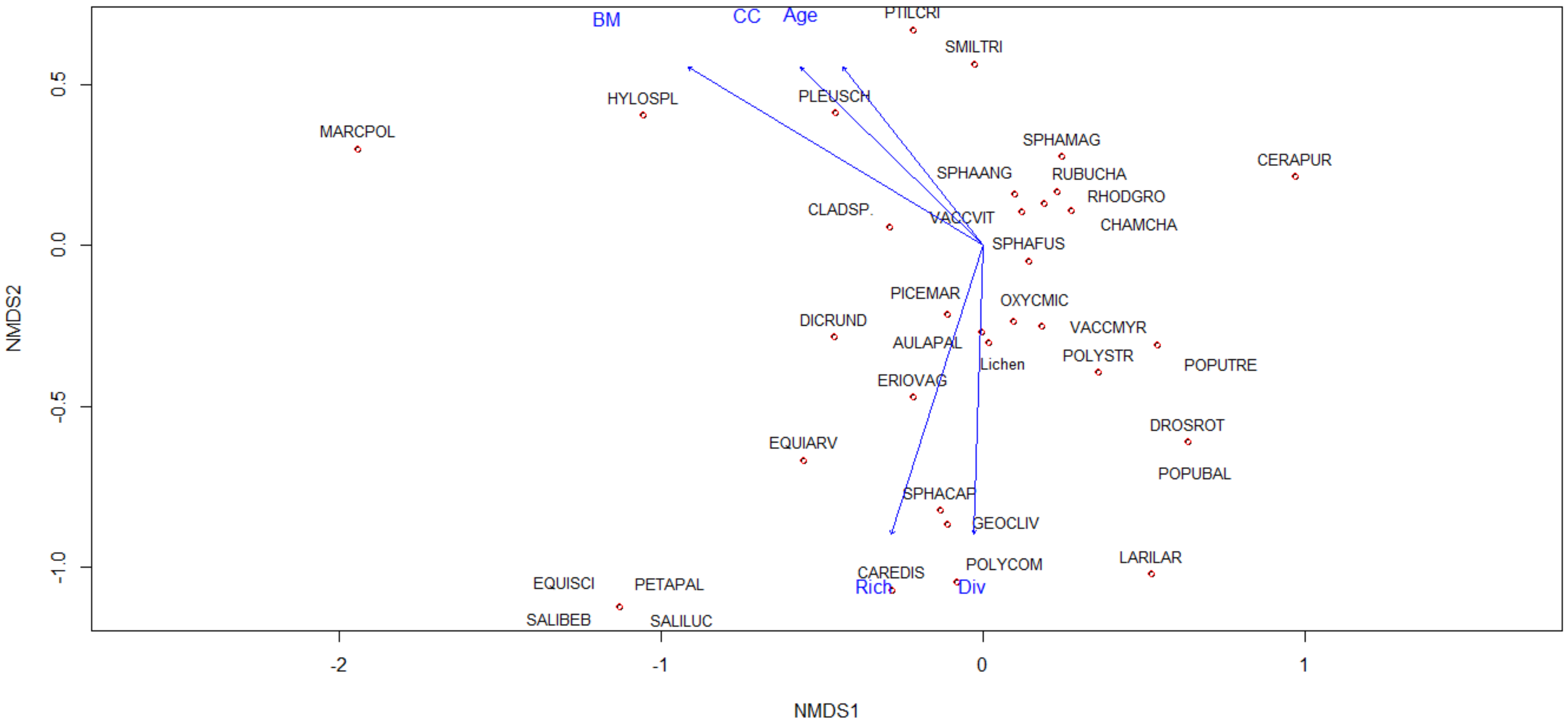


Figure 3.14: NMDS biplot illustrating the site-averaged vegetation abundances at margin sites only (n = 21) along the first two axes (stress = 0.247). Age has a significant non-linear correlation with the first NMDS axis (r^2 = 0.861). Contour lines of time since fire (years) are shown to indicate the trajectory of vegetation community recovery in studied peatland margins. See Appendix 4 for species names.

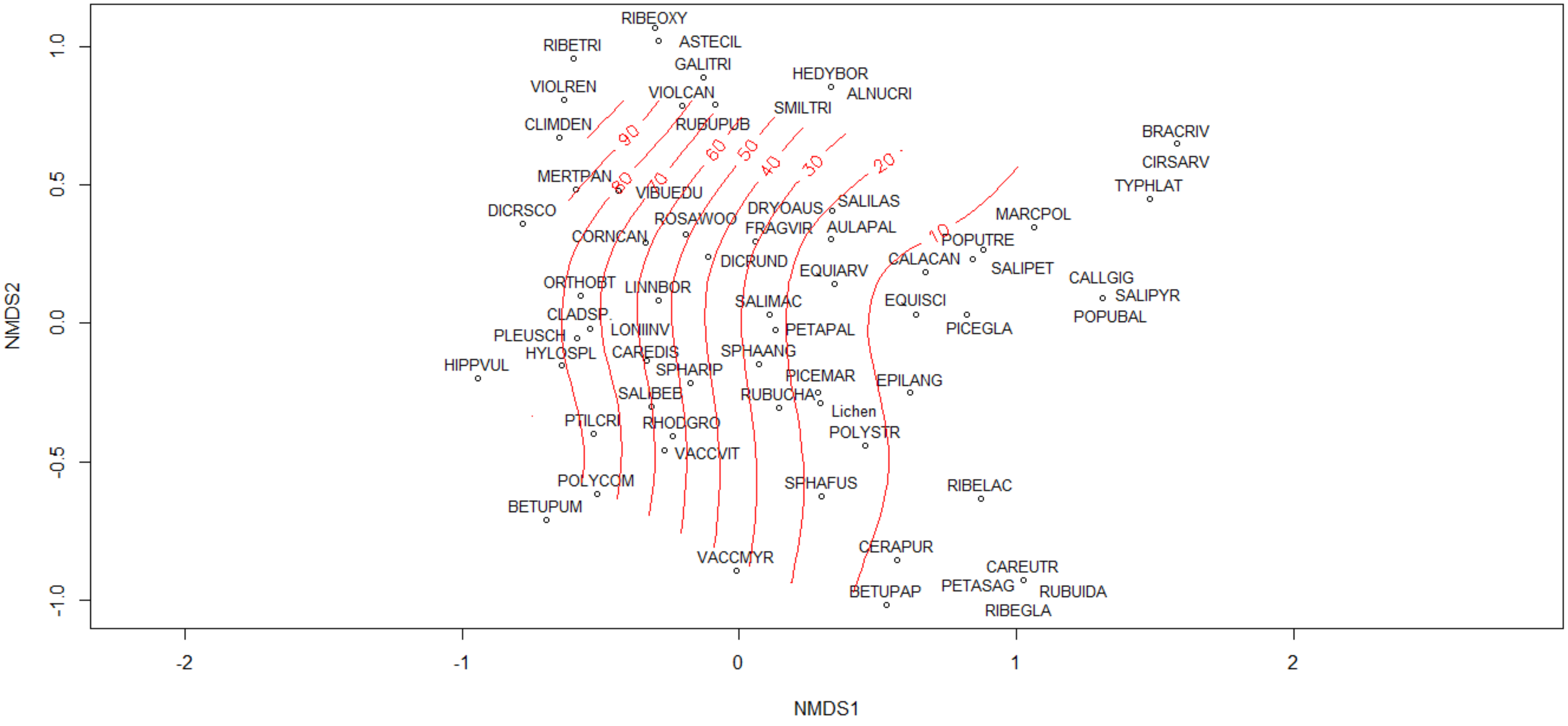


Figure 3.15: NMDS biplot illustrating the site-averaged vegetation abundances of margin ground layer bryophyte species only (n = 20) along the first two axes (stress = 0.123). Age has a significant corrleation with the first NMDS axis (r^2 = 0.789). Contour lines of time since fire (years) are shown to indicate the trajectory of vegetation community recovery. See Appendix 4 for species names.

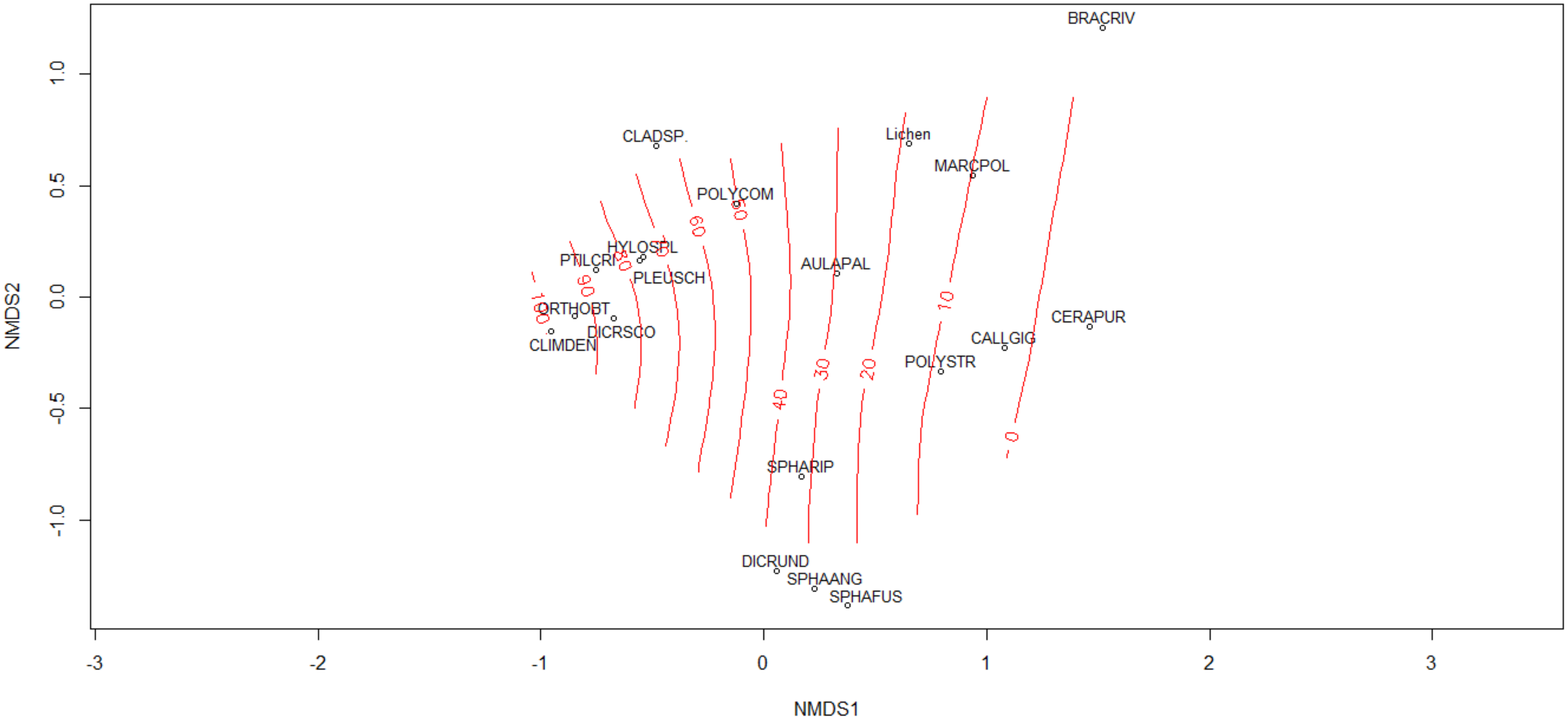


Figure 3.16: NMDS biplot illustrating the site-averaged vegetation abundances at middle sites only (n = 26) along the first two axes (stress = 0.163). Age has a significant non-linear corrleation with the second NMDS axis (r^2 = 0.603). Contour lines of time since fire (years) are shown to indicate the trajectory of vegetation community recovery in studied peatland middles. See Appendix 4 for species names.

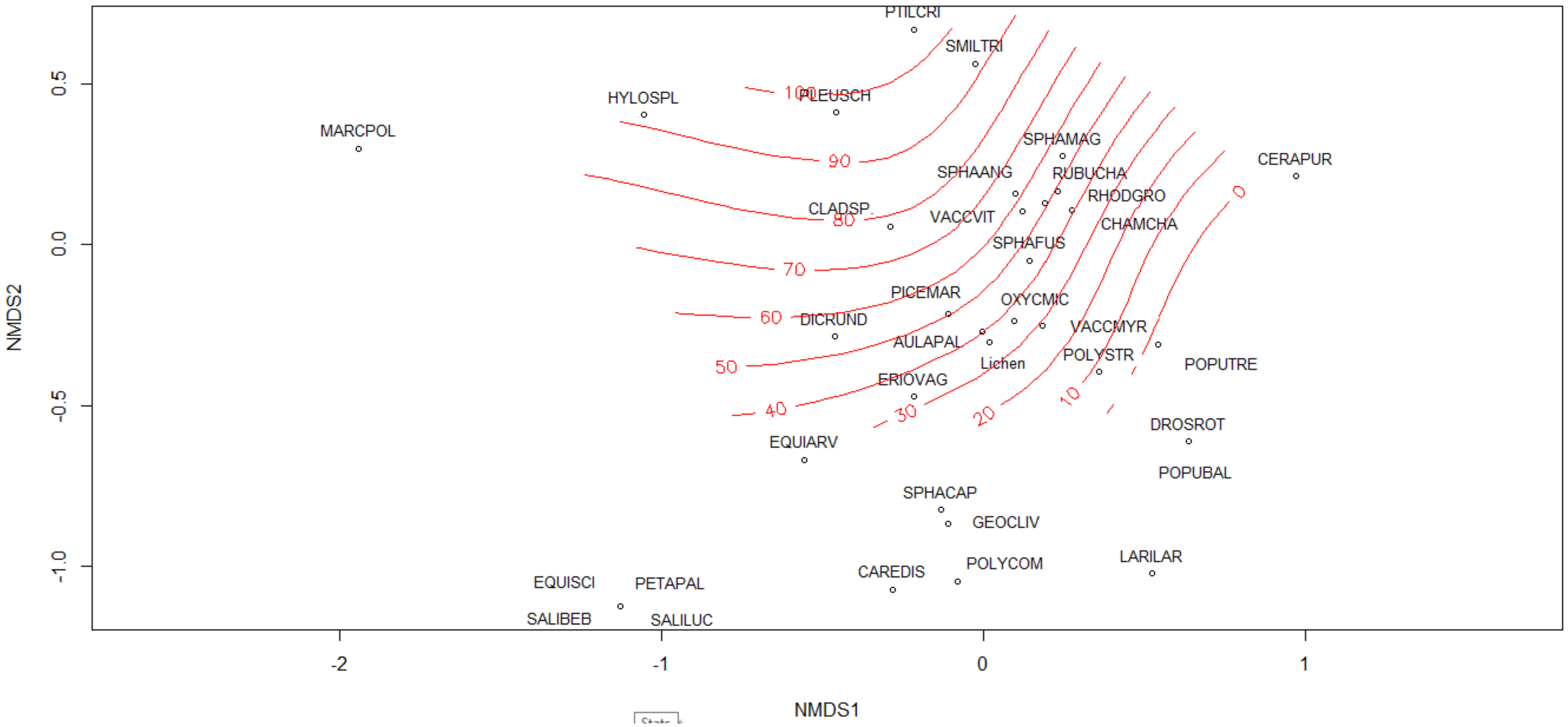
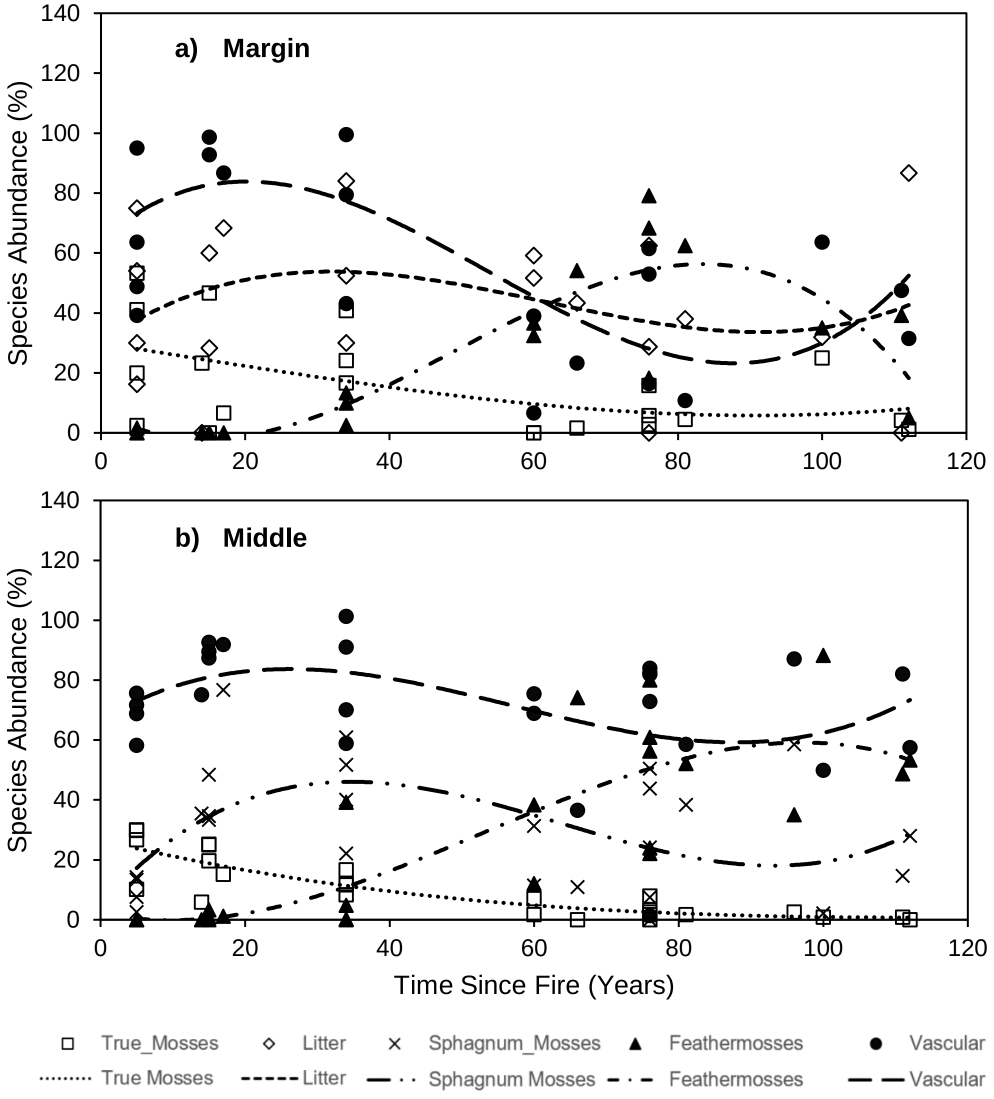


Figure 3.17: A simplified illustration of the margin and middle vegetation community recovery trajectories using indicator species and including litter abundance. Individual points represent site-averaged values of abundance for each species group. Groups include true mosses (all moss species except *Sphagnum* and feathermosses), *Sphagnum* mosses, feathermosses and vascular plants (ferns, graminoids, forbs and low shrubs) identified at each site. Third order polynomial trendlines have been fit to each species group (see Table 3.1 for associated equations and coefficients).



CHAPTER 4: CONCLUSION

Peat combustion and wildfire recovery in Boreal Plains peatland margins has been examined in recent studies to enhance our understanding of the carbon storage dynamics at this peatland-upland interface. Carbon loss during wildfire in peatland margins with ephemeral groundwater connection can account for up to 90% of total peatland carbon loss (Lukenbach *et al*., 2015; Hokanson *et al*., 2016). This severe smouldering in peatland margins can suspend key negative feedback mechanisms which stabilize the water table and facilitate keystone *Sphagnum* moss regrowth (Waddington *et al*., 2015; Lukenbach *et al*., 2016; Lukenbach *et al*., 2017). Margins are then prone to runaway positive feedbacks, such as afforestation by broadleaf deciduous species and limited water table regulation, which perpetuates an alternate recovery trajectory to a swamp-like ecosystem. In drained peatlands that have experienced similarly severe smouldering, this trajectory has been called a regime shift due to limited recovery of peatland bryophytes (particularly *Sphagnum* mosses; Kettridge *et al*., 2015).

This alternate recovery trajectory at the peatland-upland interface, with peatland margins successionally developing a mixed coniferous-deciduous canopy and experiencing limited bryophyte recovery until they reach a later successional feathermoss dominated stage (~60 years), is presented for the first time in this study. The enhanced rate of recovery noted in this chronosequence analysis, as compared to Benscoter and Vitt (2008) and

Wieder *et al.* (2009), has been attributed to the wider variety of hydrogeological settings that were sampled in this study. The intention was to capture landscape variability and particularly to focus on confined, potentially perched peatlands, with greater proportion of margin area and associated margin vulnerability to deep smouldering. Soil texture and surficial geology mapping (Fenton *et al.*, 2013) from this chronosequence analysis has identified study sites with coarse deposits and layering of fine and coarse sediments (heterogeneous coarse and heterogeneous moraine deposits), which may interact with local groundwater systems in similar ways as previously identified in vulnerable peatland ecosystems.

A conceptual model of each of the peatland middle and margin recovery trajectories, with the associated feedback mechanisms which underlie the ecosystem, is presented in Figure 4.1. By combining knowledge on peatland ecosystem collapse (Kettridge *et al*., 2015) with this study of margin area and species assemblages over time, it is proposed that maintenance of peatland ecosystems relies on the ability of *Sphagnum* mosses to recolonize peatland middle vegetation communities and maintain the transition boundary with the margins, where it appears that the broadleaf canopy acts to exclude *Sphagnum* moss paludification. In the past, over the course of development of these peatland ecosystems and especially in wetter climate cycles, *Sphagnum* mosses could expand outwards and increase peatland area between fire cycles. It appears that now, and especially at this southern extent of their range, peatlands are just able to maintain their aerial extent and carbon storage between fire events. The cycle of deep smouldering in peatland margins, and especially in peatlands which have a higher proportion of margin area, could eventually lead to ecosystem collapse when the integrity of the entire peatland becomes compromised by compounded wildfire events, severe smouldering further and further into the peatland and inability to recover water table regulation and associated *Sphagnum* moss recolonization functions. This is illustrated by the ‘peatland collapse’ conceptual model shown in Figure 4.1, where the integrity of the peatland margin has been undermined (loss of legacy carbon stores) and hence the integrity of the entire peatland ecosystem has collapsed. This scenario would be reinforced by runaway positive feedbacks and loss of key negative autogenic feedbacks, as shown in Figure 4.1. Further research into the fire danger of the margin ground layer (feathermoss) and canopy fuels could enhance this analysis to determine the fire risk under future climate projections and the likelihood for an accelerated fire return interval. Forest management practices (*e.g.* Fire Smart) to prevent these legacy carbon losses, and associated risk of peatlands becoming carbon sources to the atmosphere, could include forest treatments (such as thinning) which will open the tree canopy and promote *Sphagnum* moss paludification. Further research should examine the response and success of *Sphagnum* moss recovery and persistence under various forest treatment options.

4.1 References

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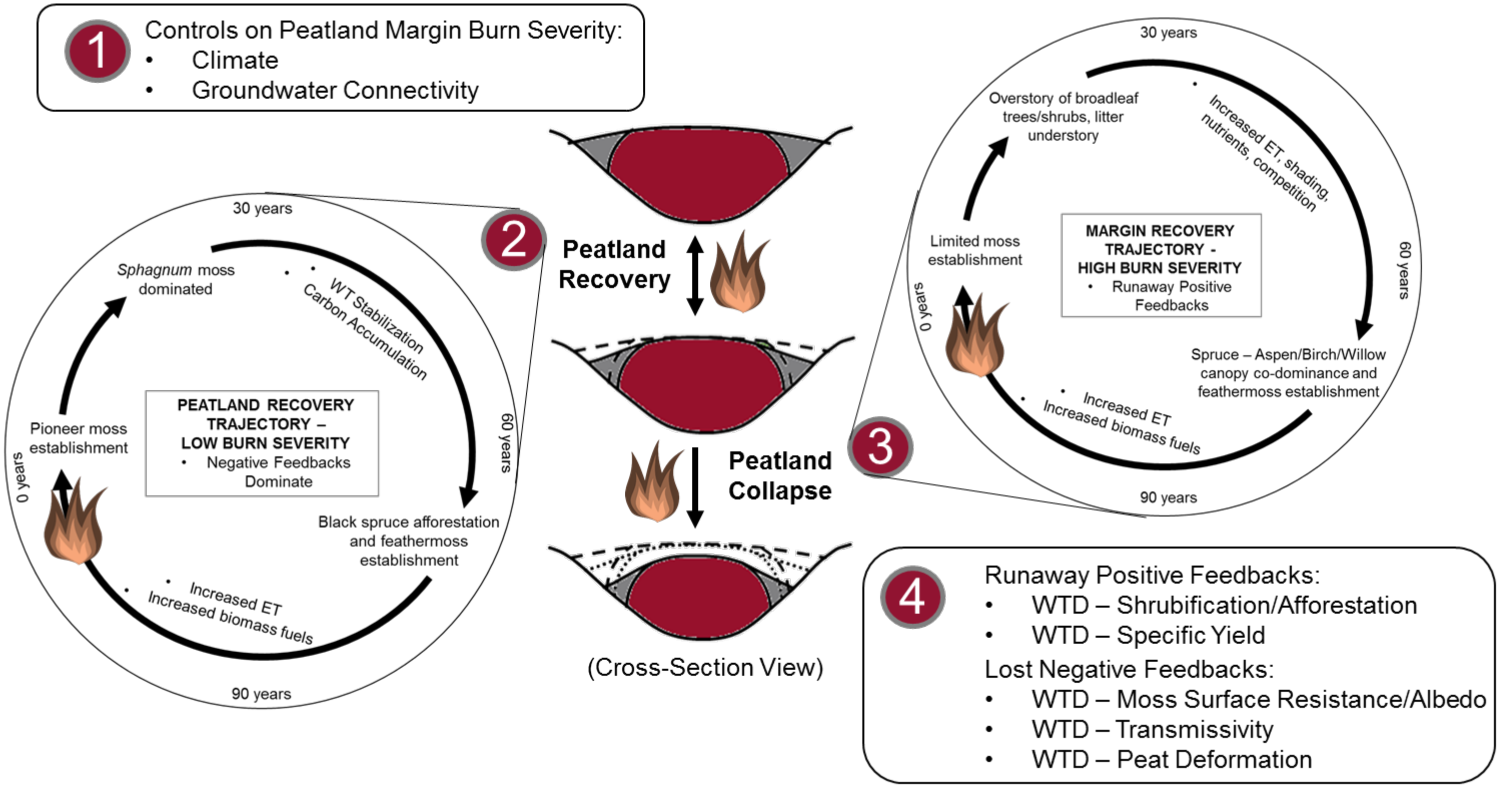
Figure 4.1: Conceptual model of peatland margin and middle vegetation community recovery trajectories with time since fire, including the key water table depth (WTD) feedbacks (see Waddington *et al*., 2015) which act to maintain the ecosystem integrity and an illustration (peatland cross-section) of what could occur if compounded drought and wildfire events, of increasing severity, lead to catastrophic margin smouldering and peatland ecosystem collapse. In the cross-section view, the maroon colour represents middle peat, while the grey colour represents vulnerable margin peat.



Appendix 1: Aerial images of each study site taken at various times from 1950 to 2012 (Government of Alberta, 2016).

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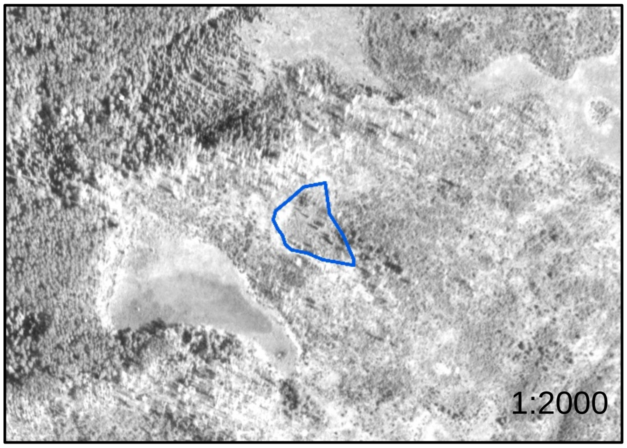

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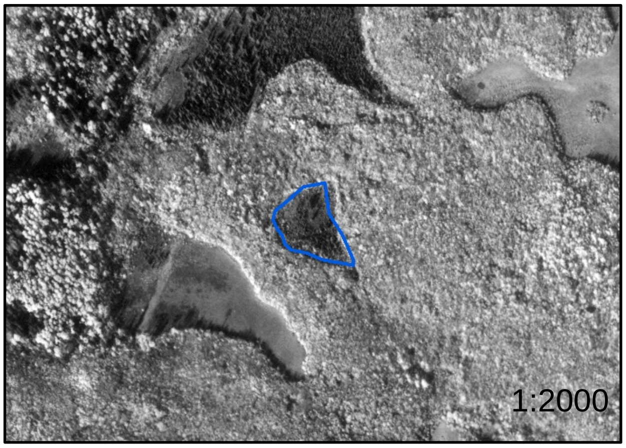

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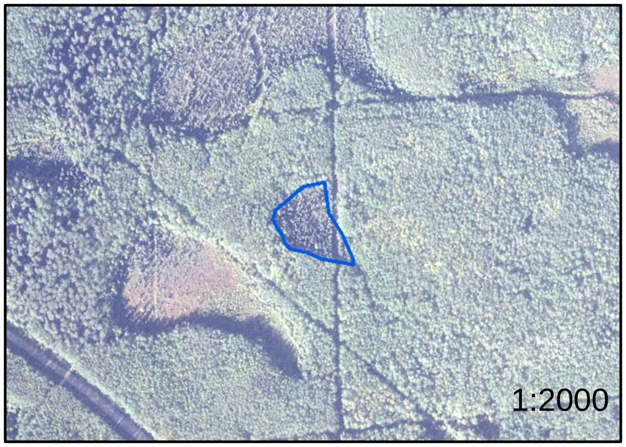

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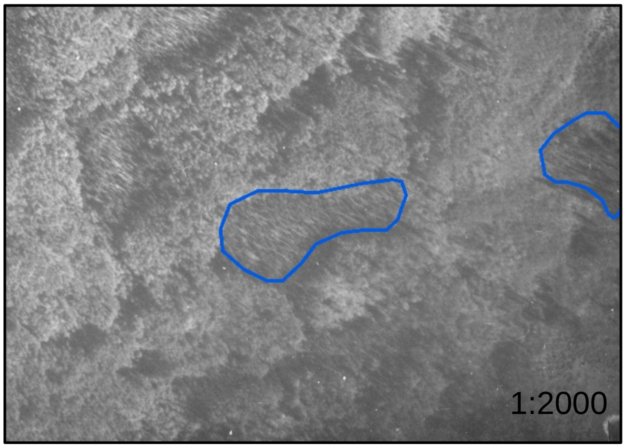

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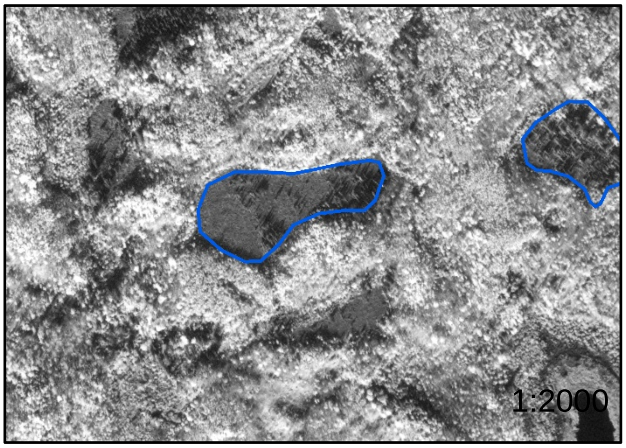

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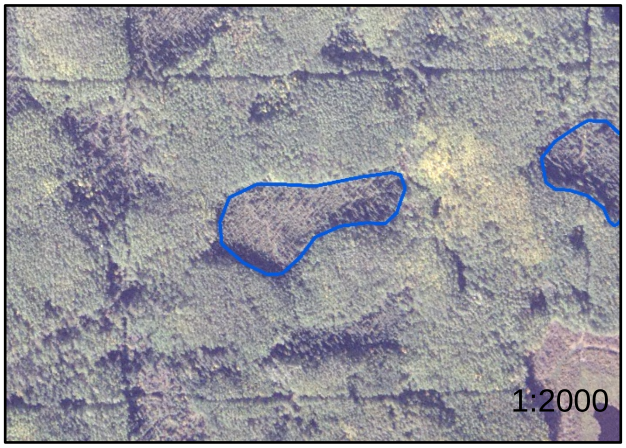

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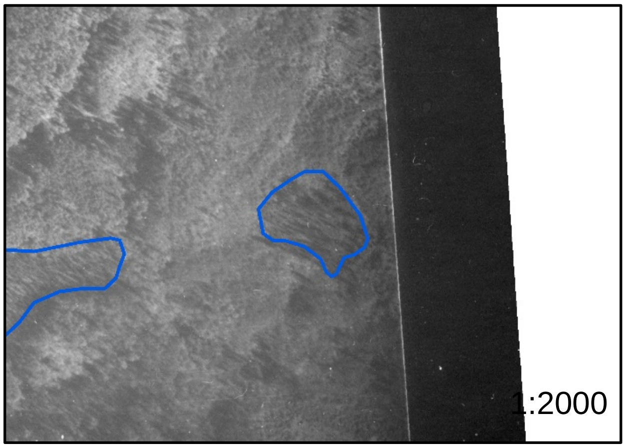

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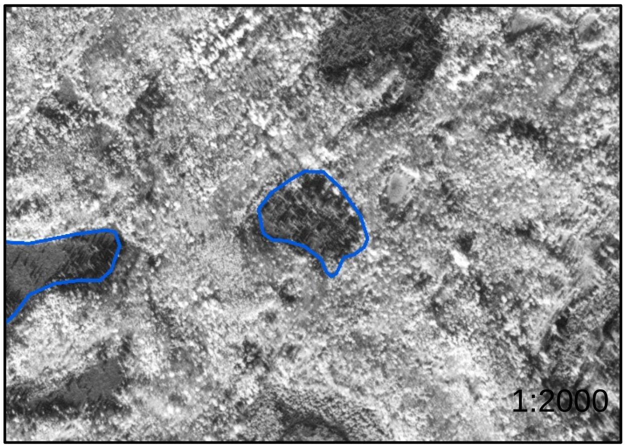

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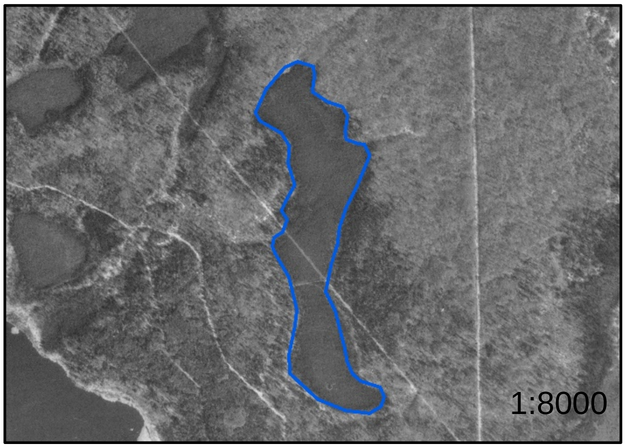

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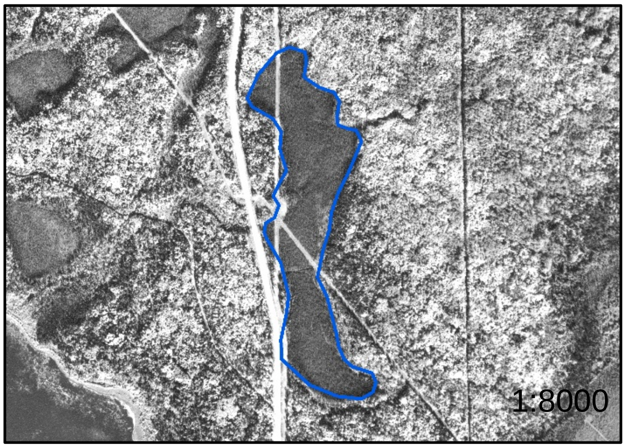

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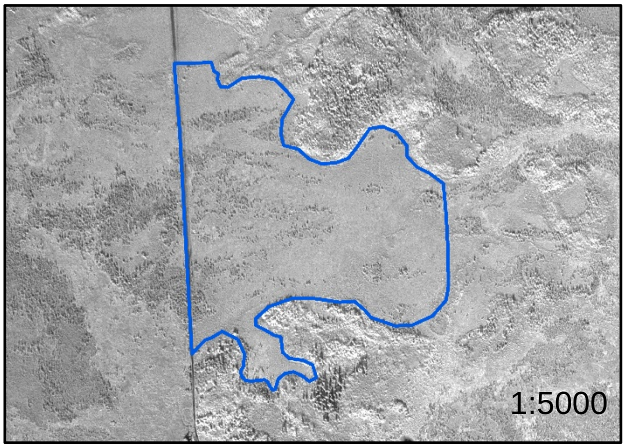

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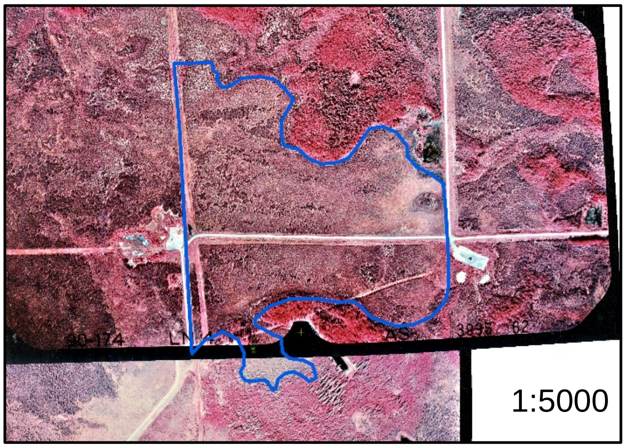

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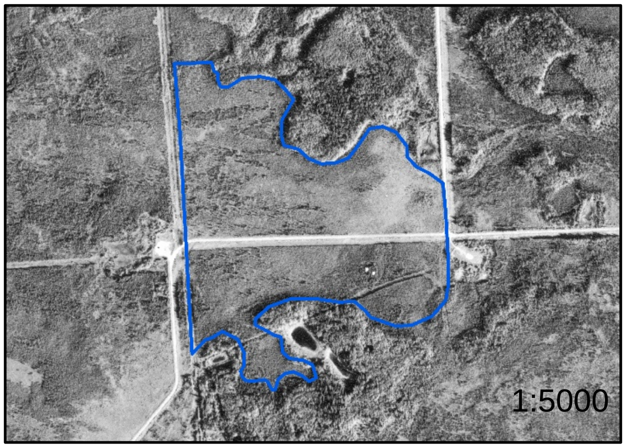

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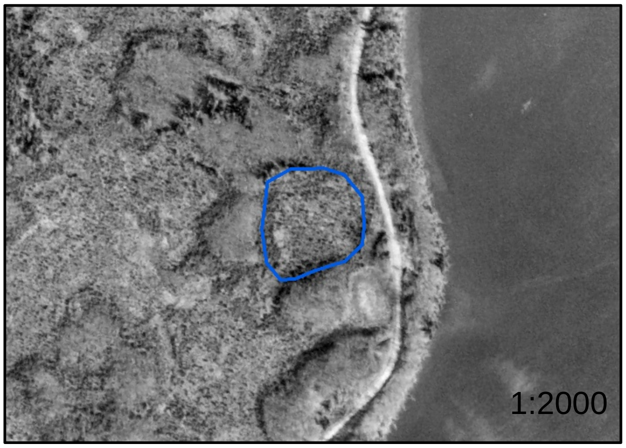

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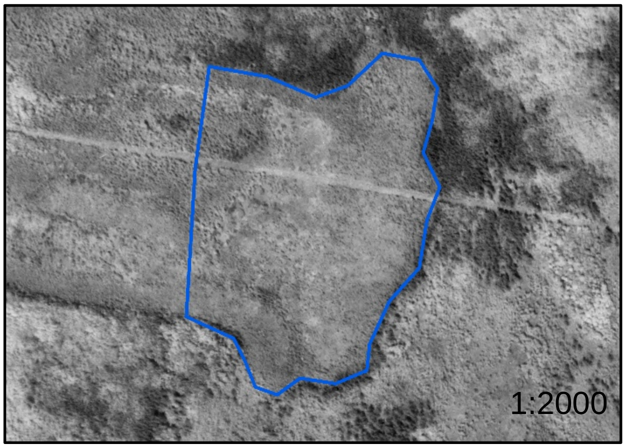

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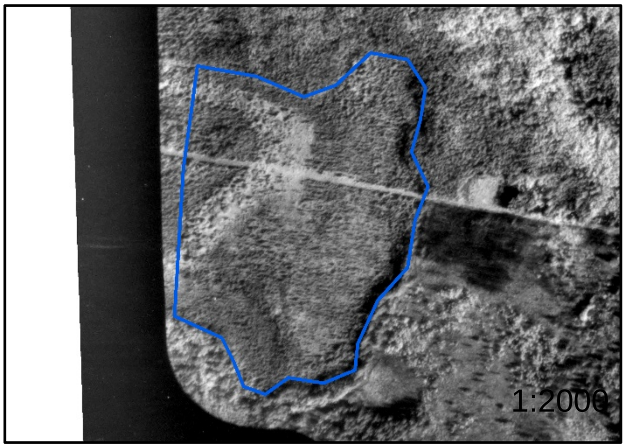

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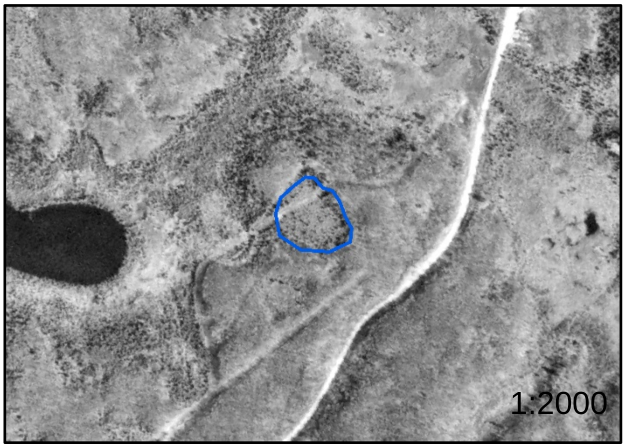

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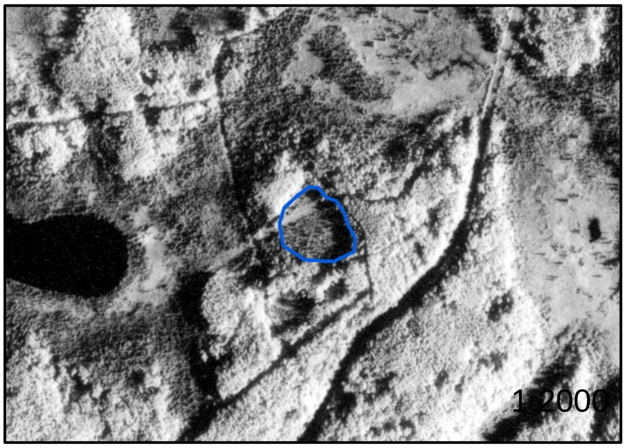

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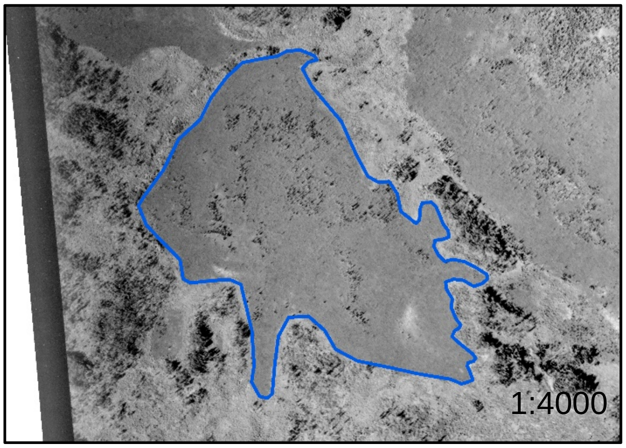

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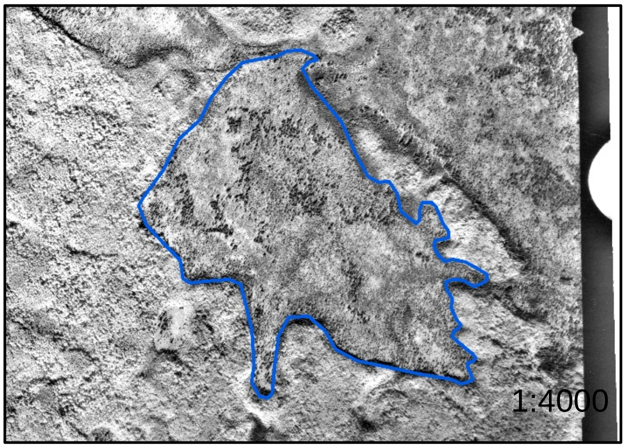

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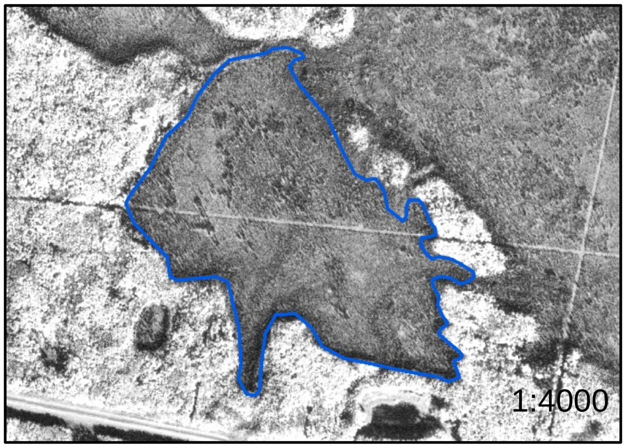

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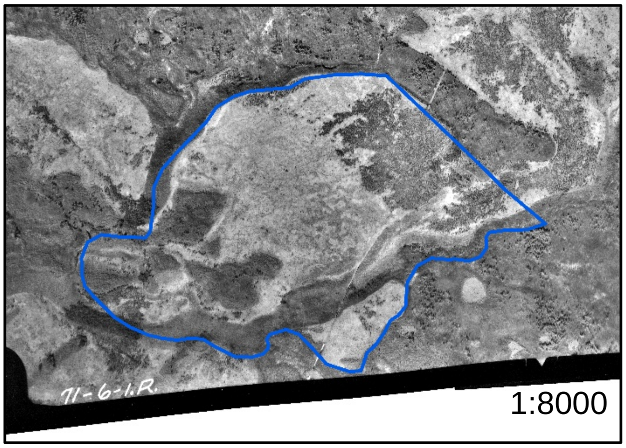

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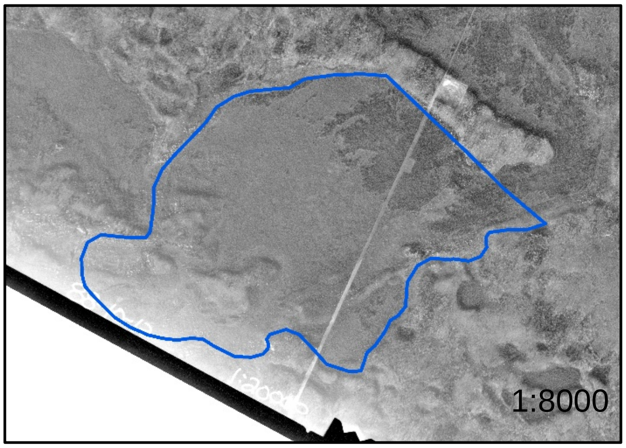

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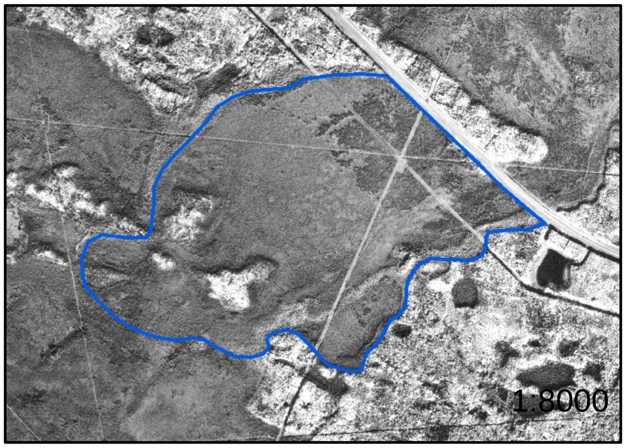

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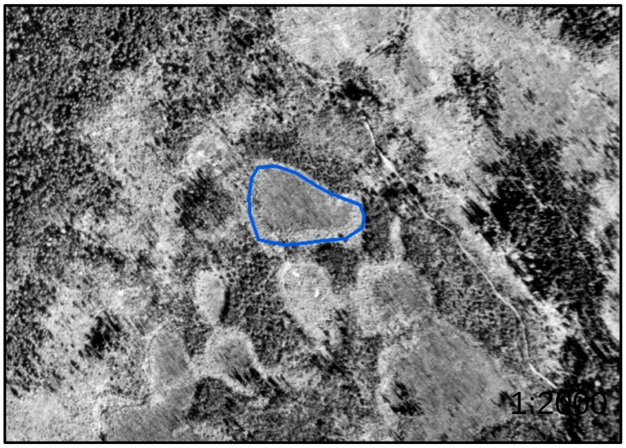

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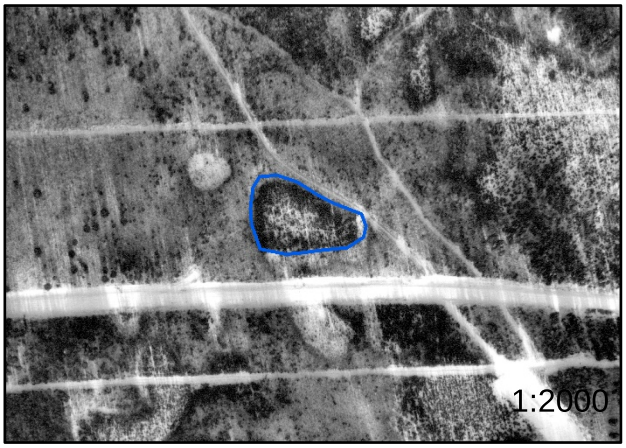

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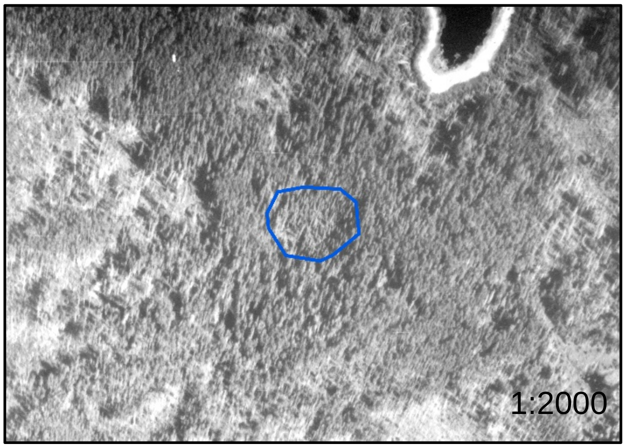

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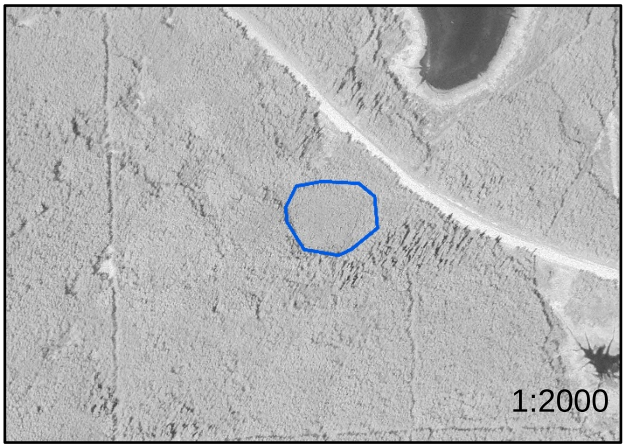

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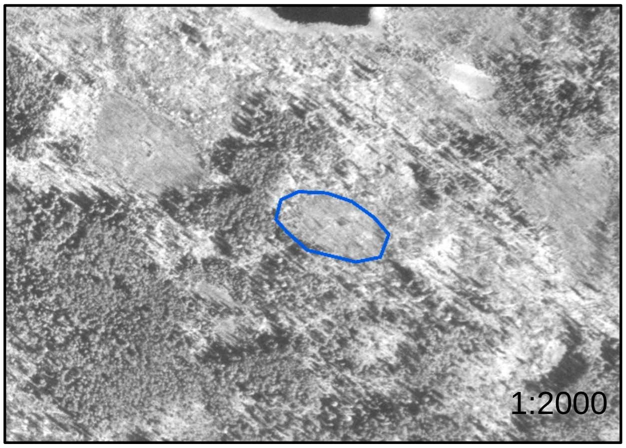

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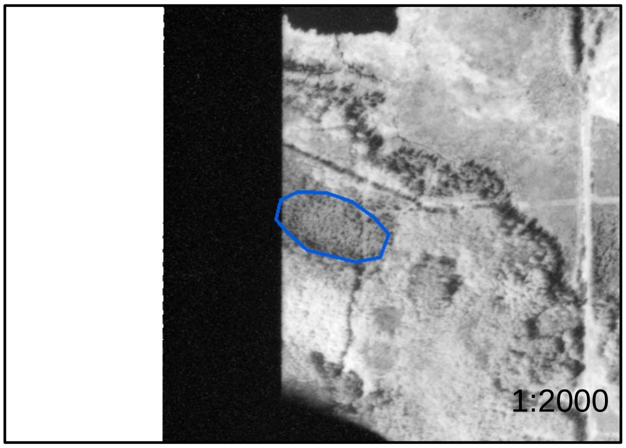

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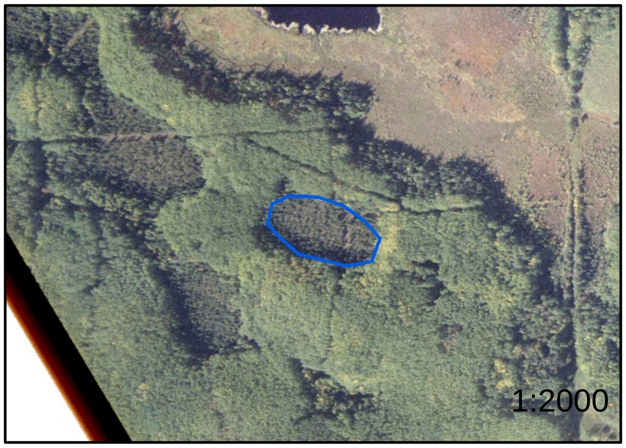

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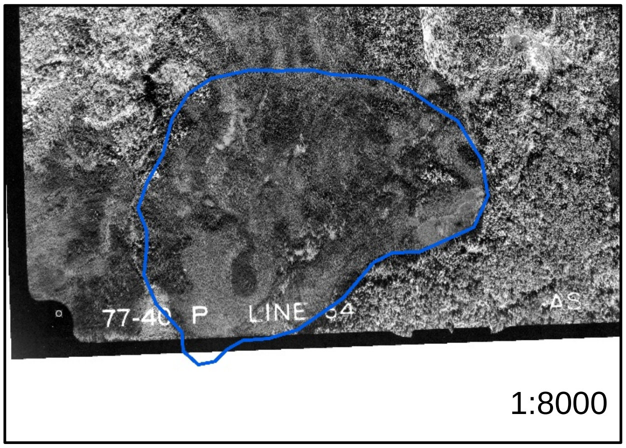

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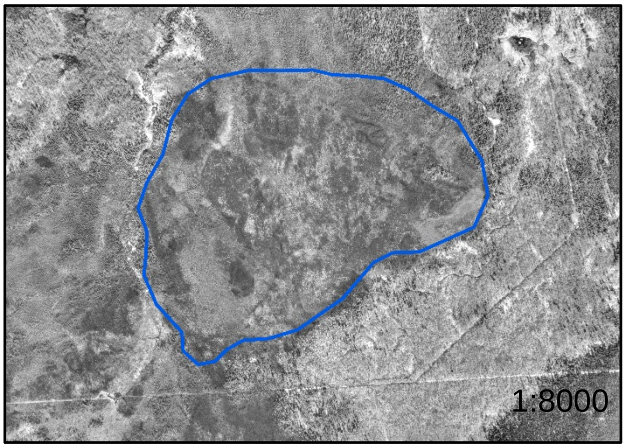

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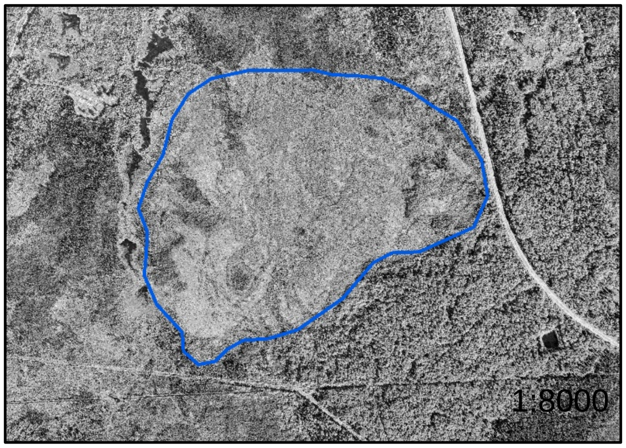

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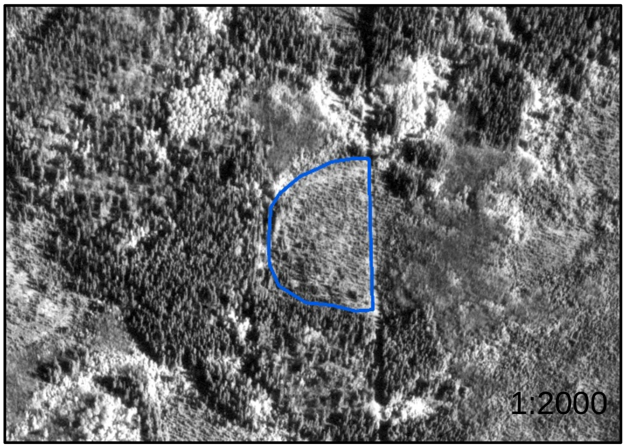

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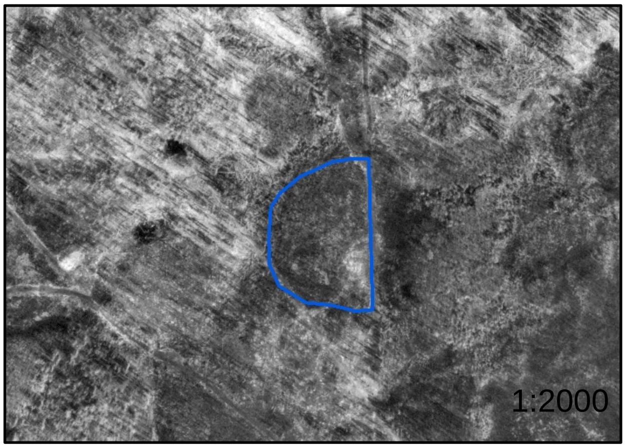

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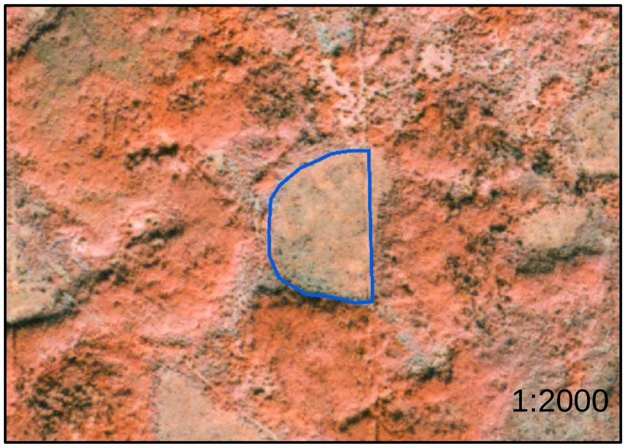

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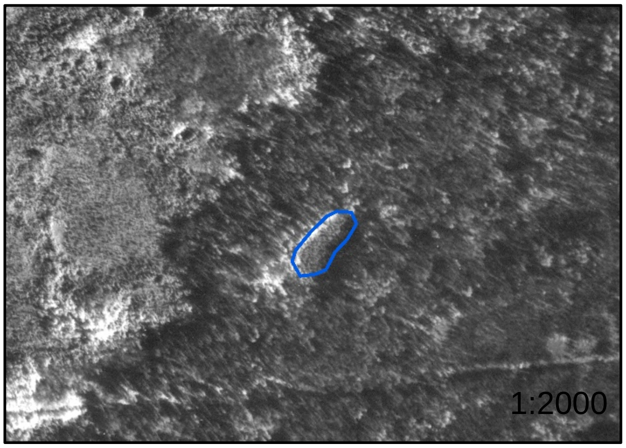

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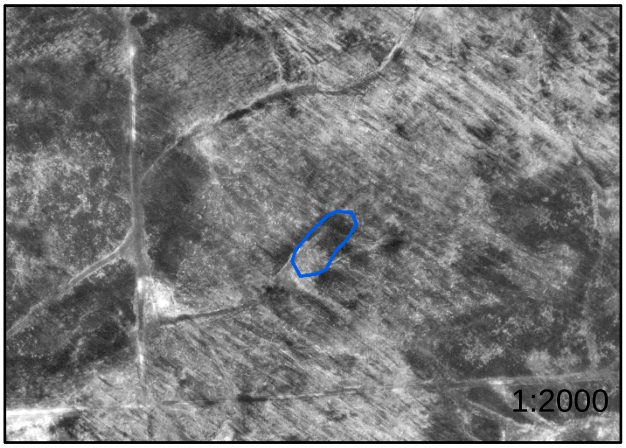
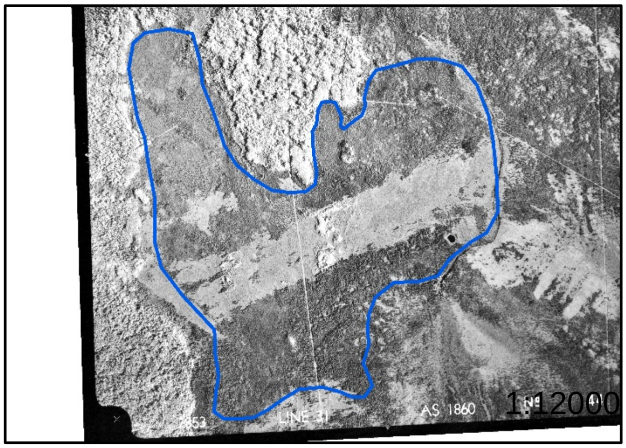


Image Date: May 14, 1983

Image Date: Aug 16, 2008

Appendix 1 (continued):

RECr1982



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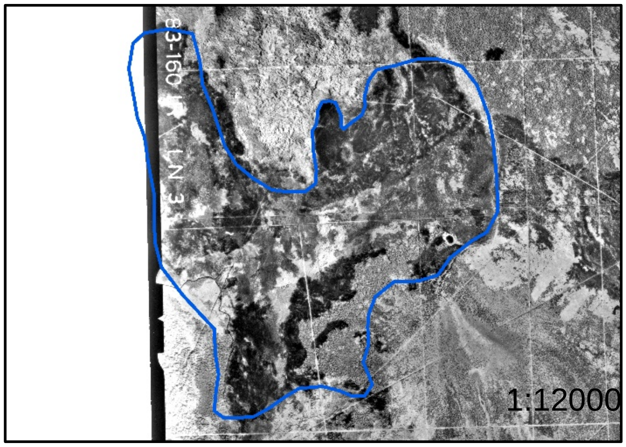


Image Date: Jun 29, 1983

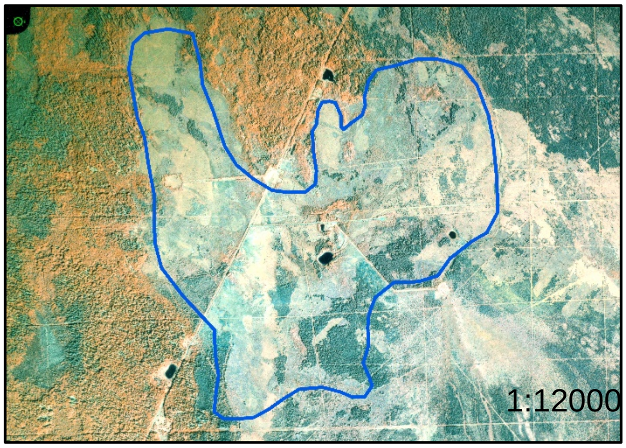
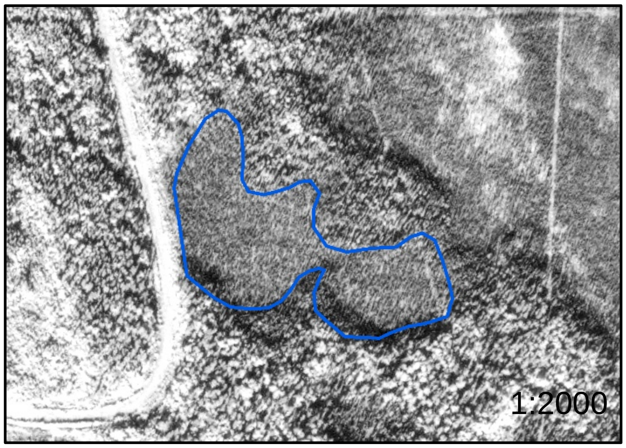


Image Date: Aug 16, 2008

Appendix 1 (continued):

Peli1999



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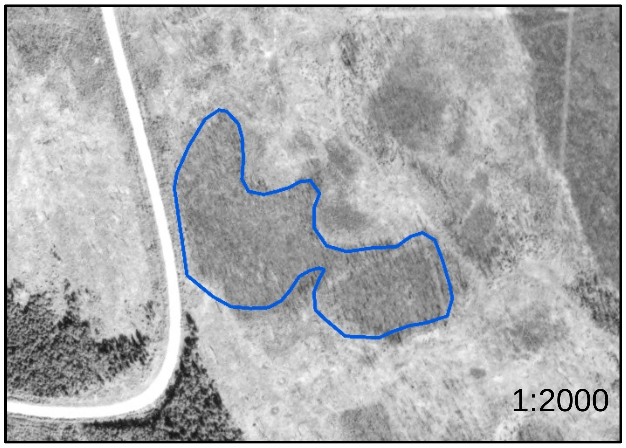

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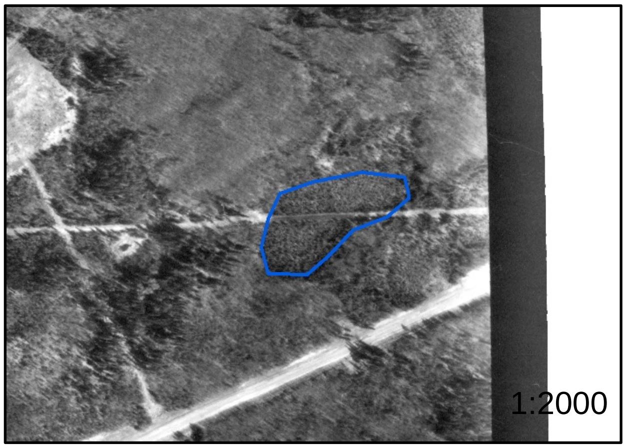
Appendix 1 (continued):

Ottr2001A



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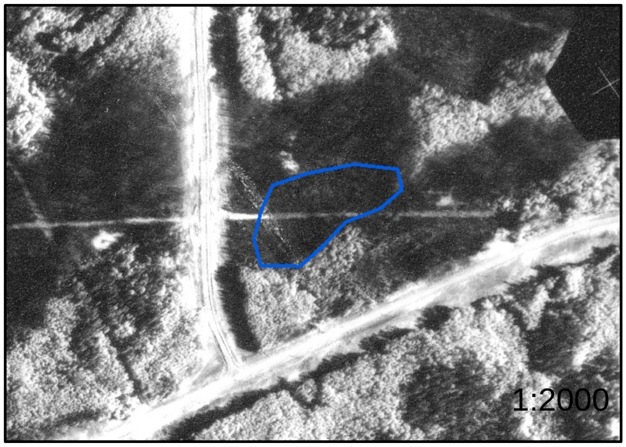
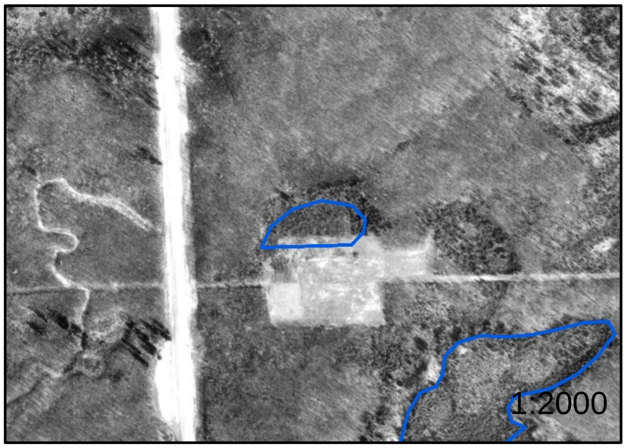


Image Date: Jul 8, 2001

Image Date: Aug 16, 2008

Appendix 1 (continued):

Ottr2001B



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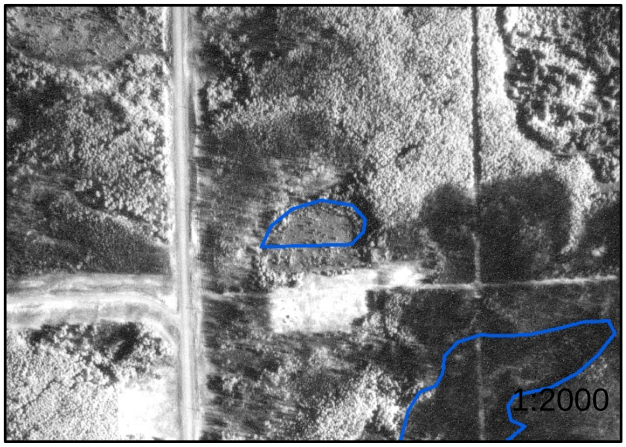

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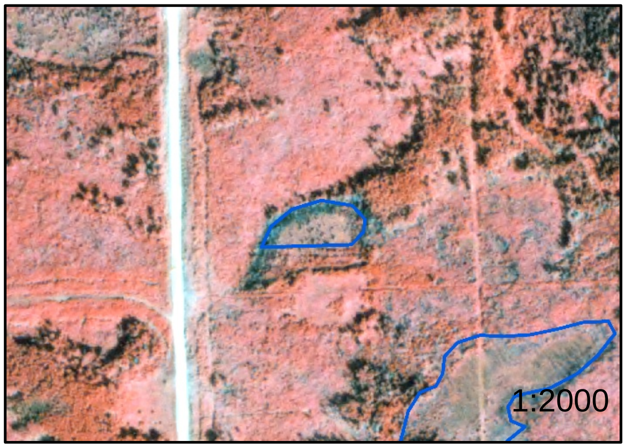

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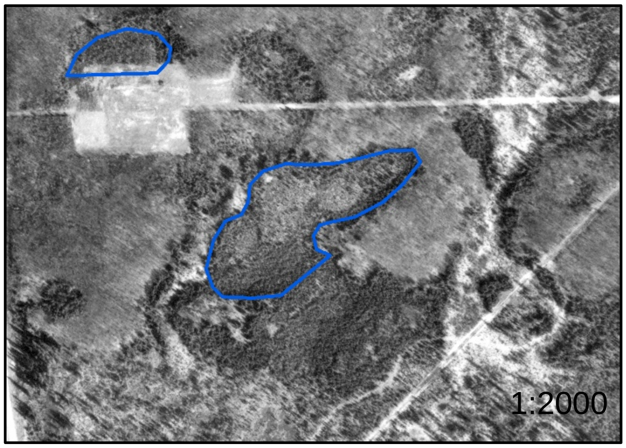
Ottr2001C



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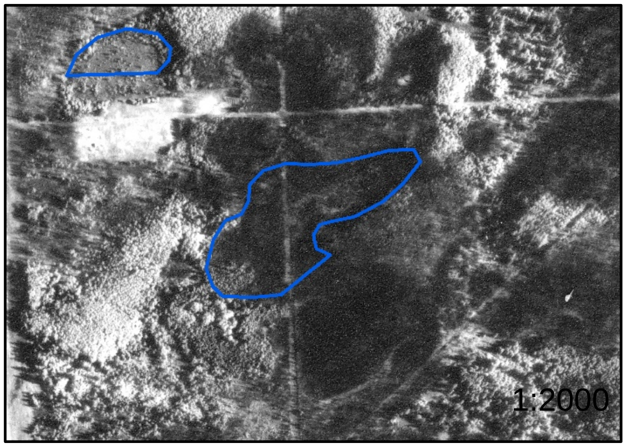

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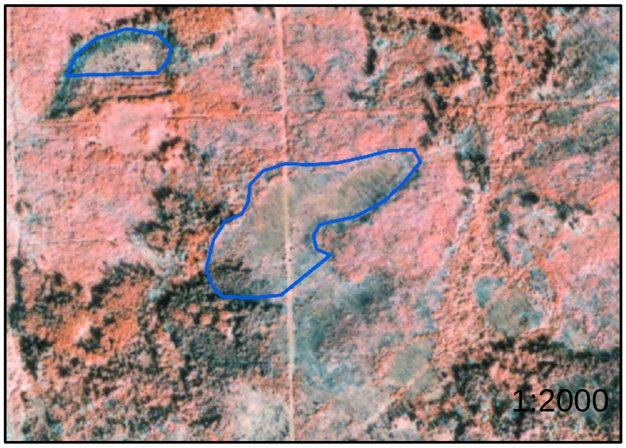

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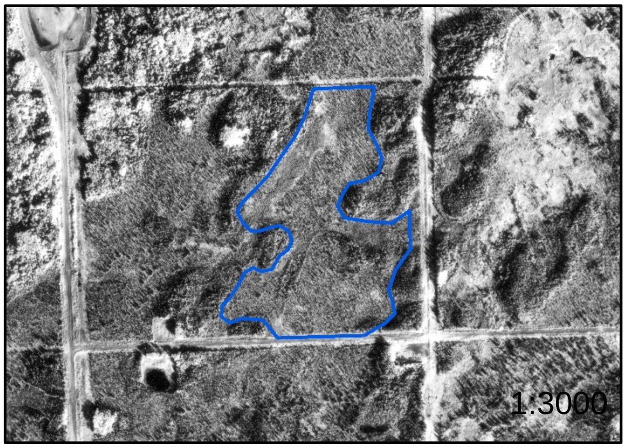

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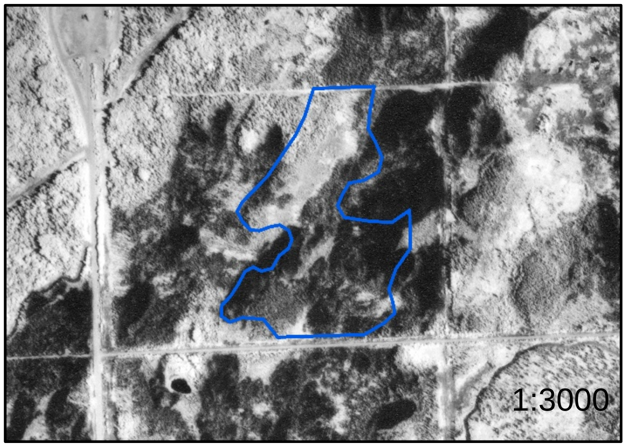

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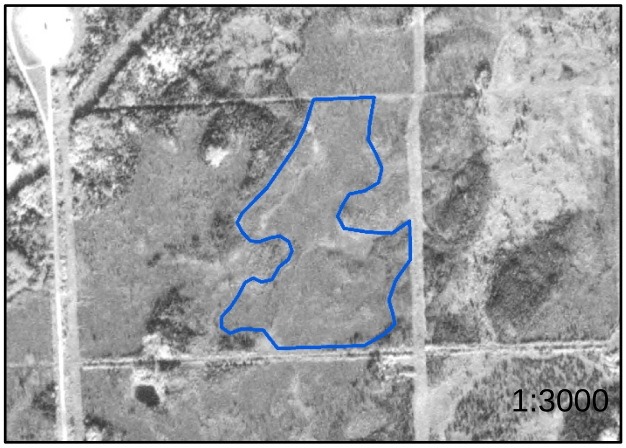

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Appendix 1 (continued):

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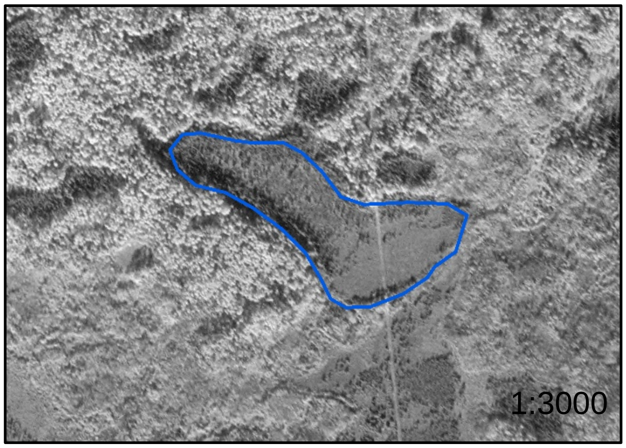

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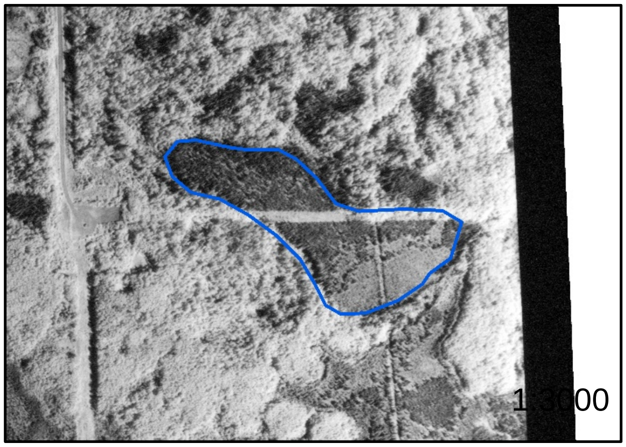

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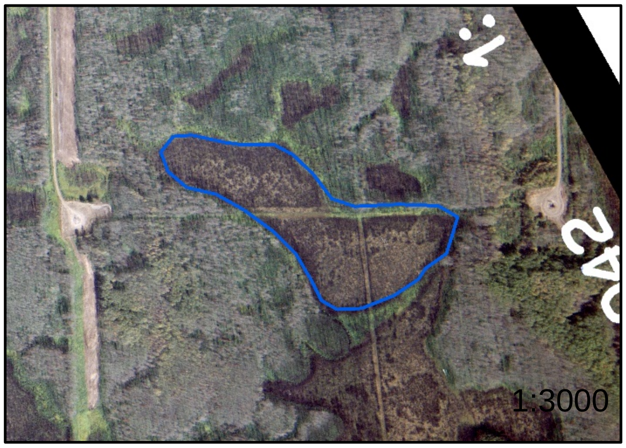

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Appendix 1 (continued):

Utik2011B

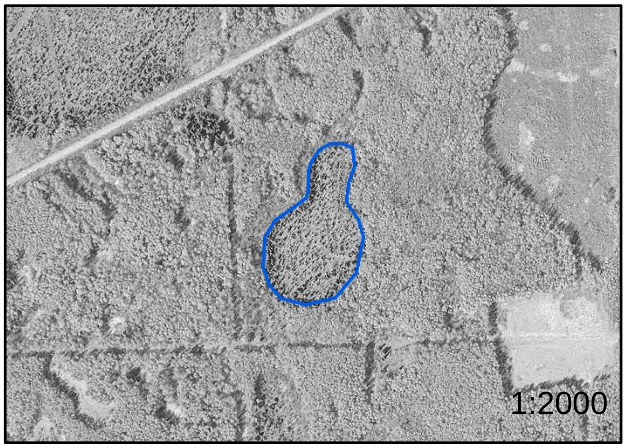
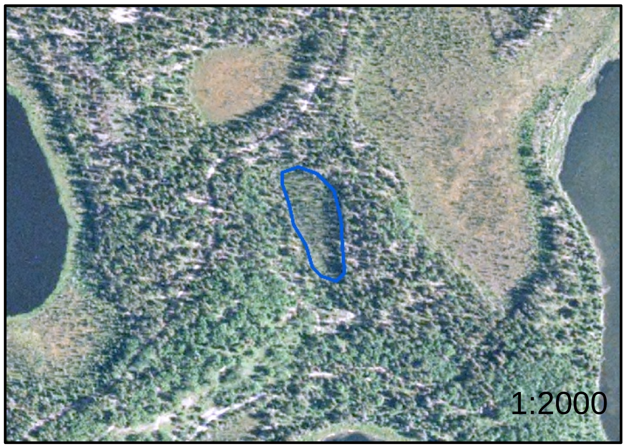


Image Date: May 29, 2000

Image Date: Sept 7, 2011

Appendix 1 (continued):

Utik2011C



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Appendix 1 (continued):

Utik2011D

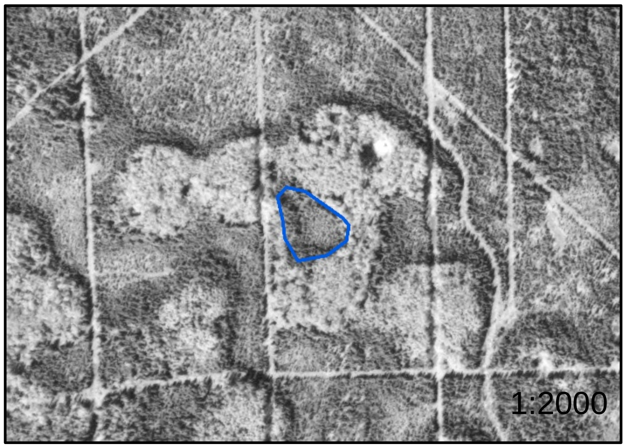


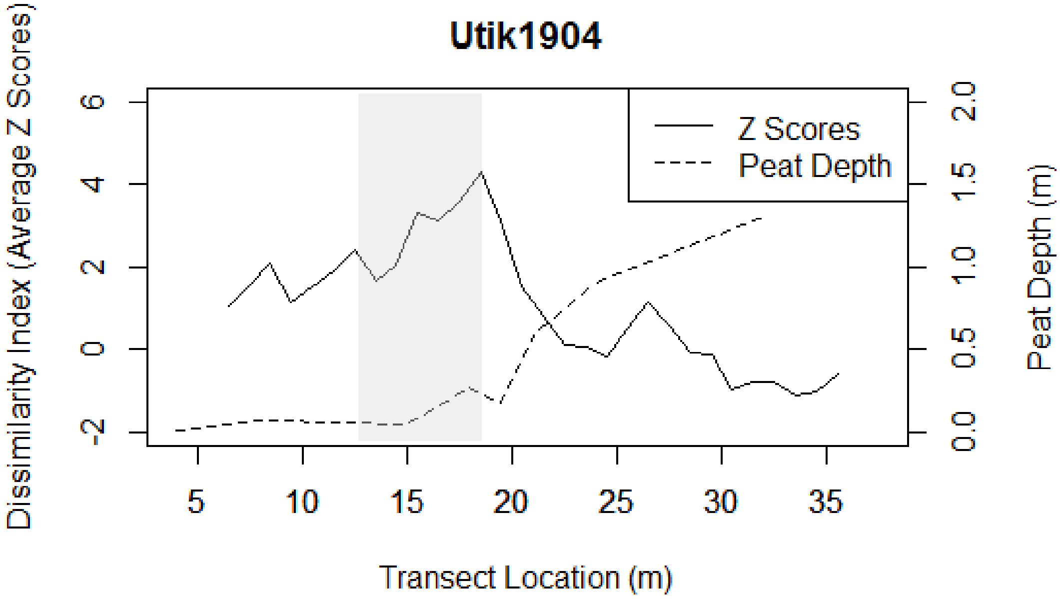
Image Date: May 29, 2000

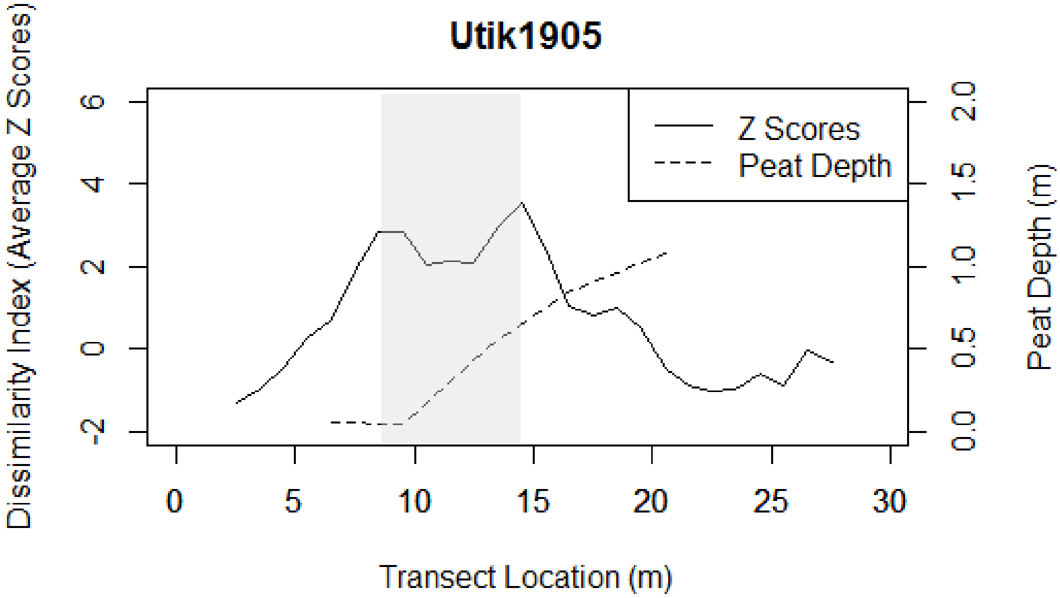
Image Date: Sept 7, 2011

References

Government of Alberta. 2016. Air Photo Distribution Centre. Minister of Environment and Parks, Government of Alberta. http://aep.alberta.ca/forms-maps-services/air-photos/default.aspx.

Appendix 2: SMW dissimilarity index results, in chronological order, calculated using SED average Z Scores from window sizes 6, 8, 10, 12, 14, 16 and 18 plots. Margin location is indicated by shading. Peat depth profiles are indicated by the dashed line and secondary axis.





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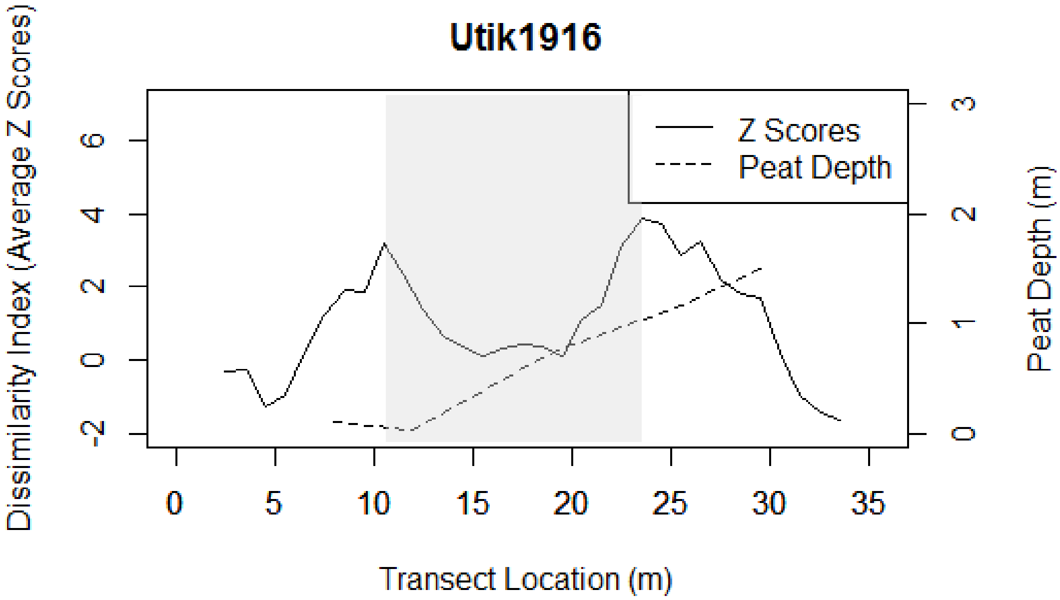

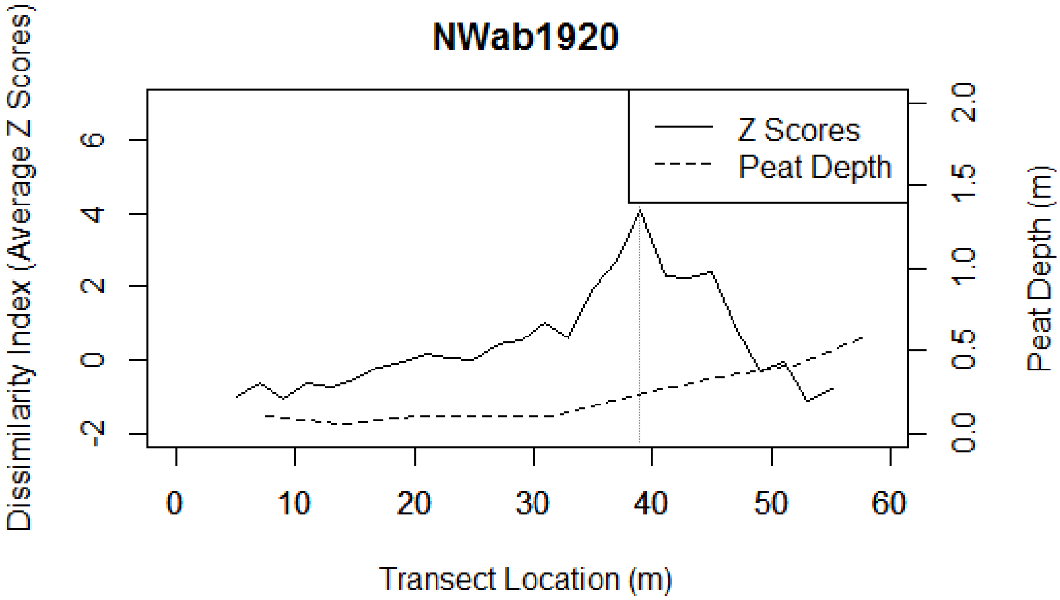

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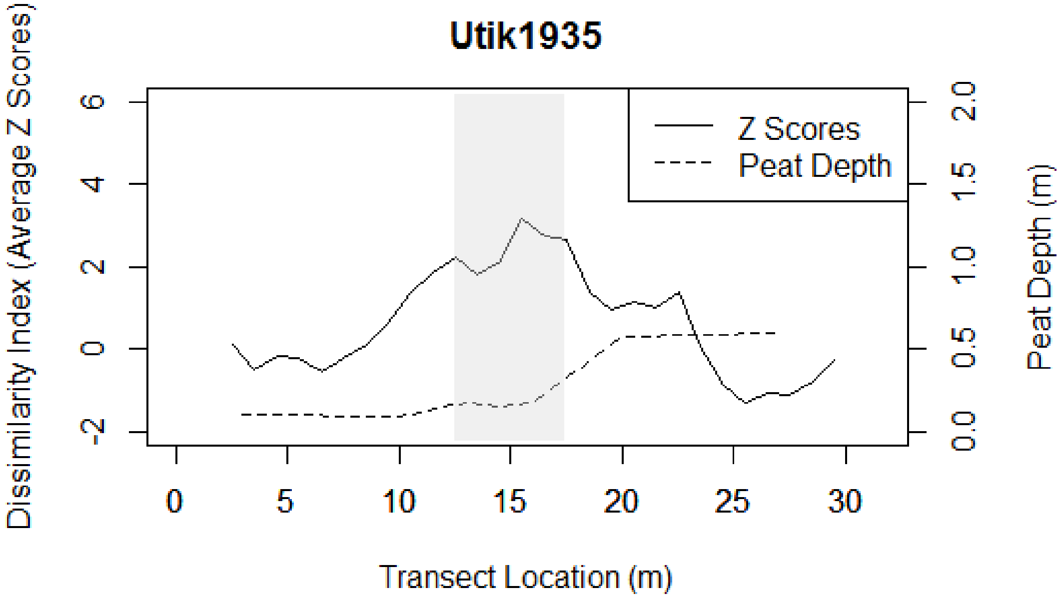

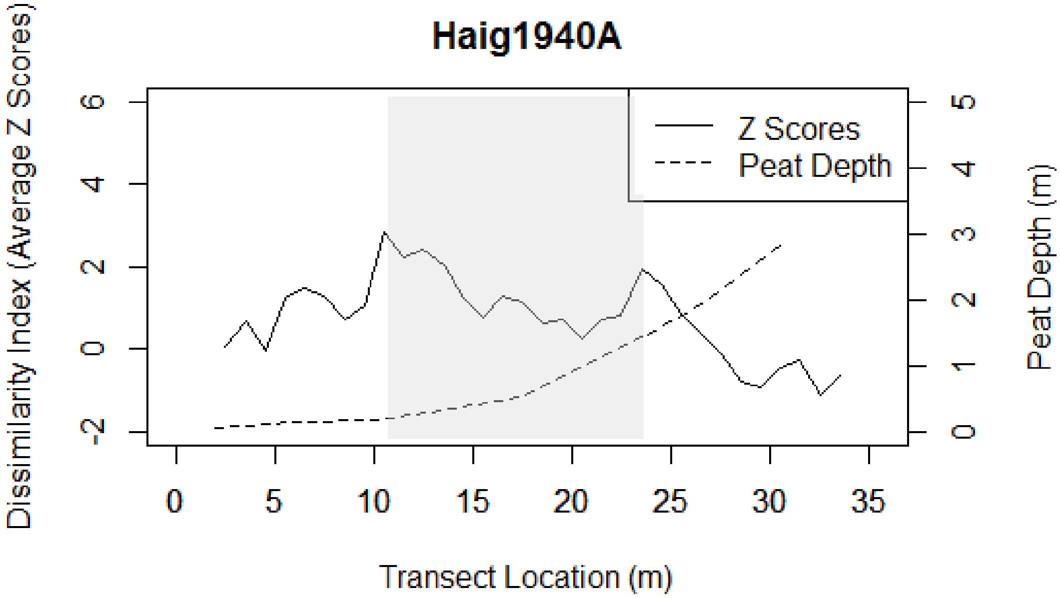

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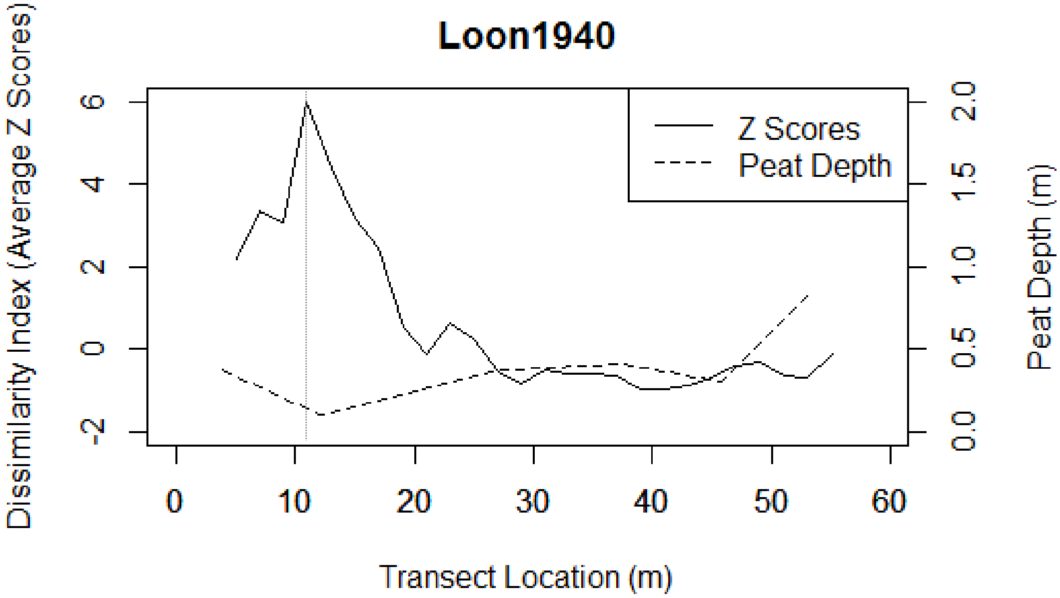

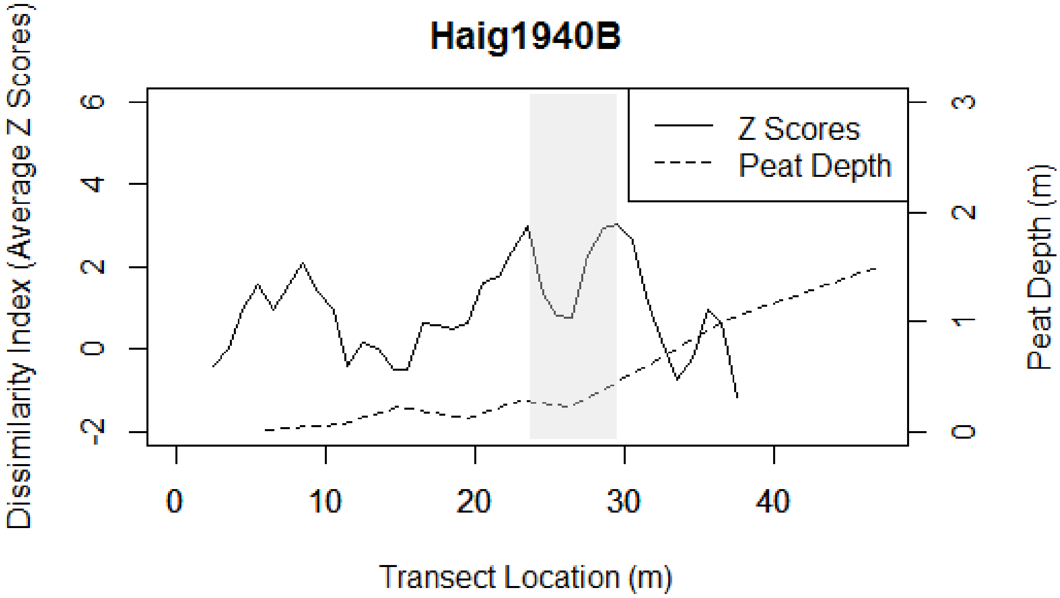

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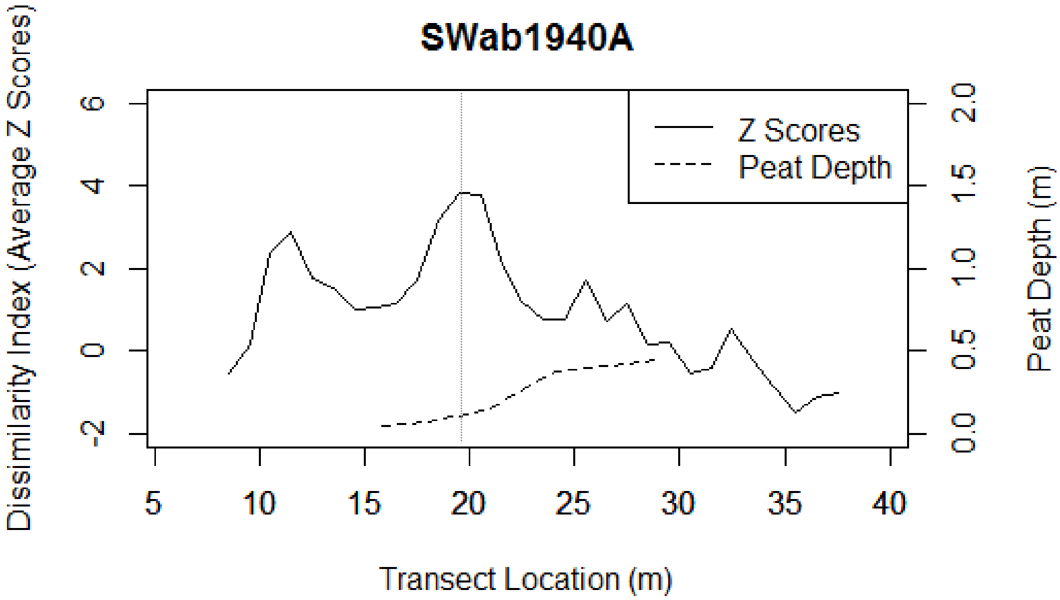

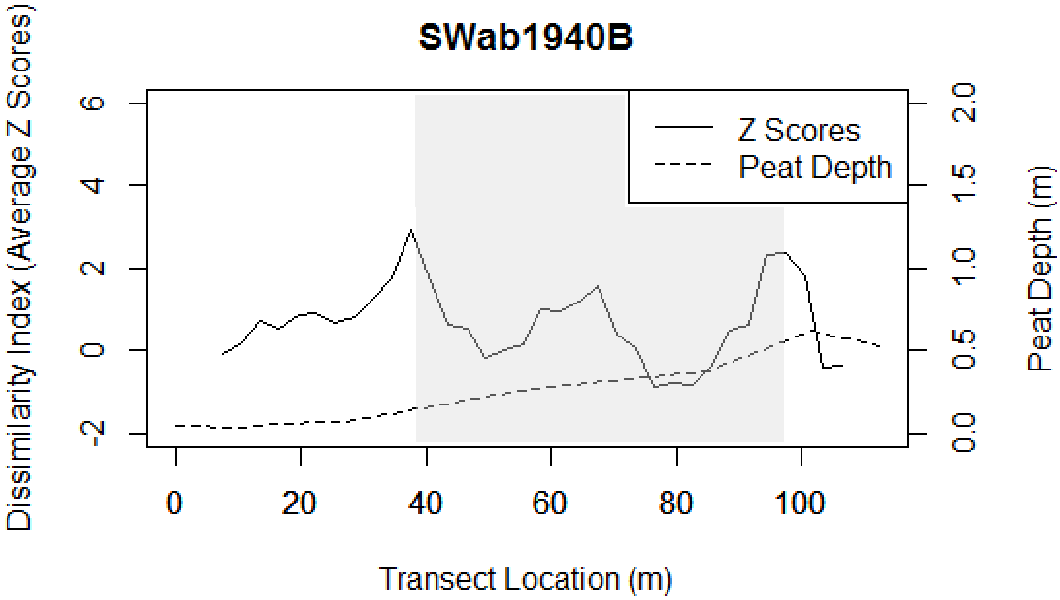

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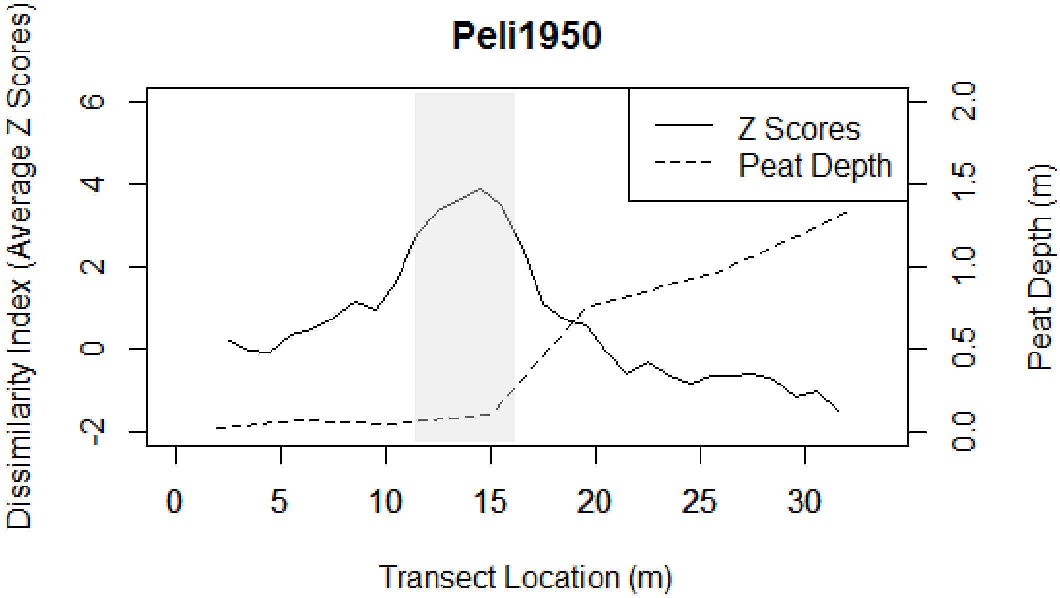

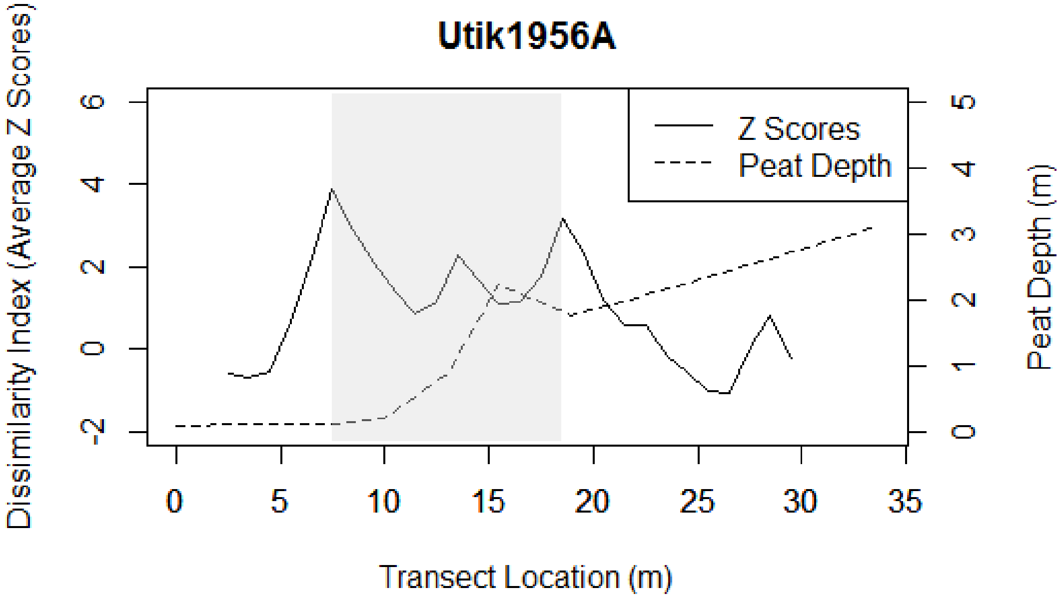

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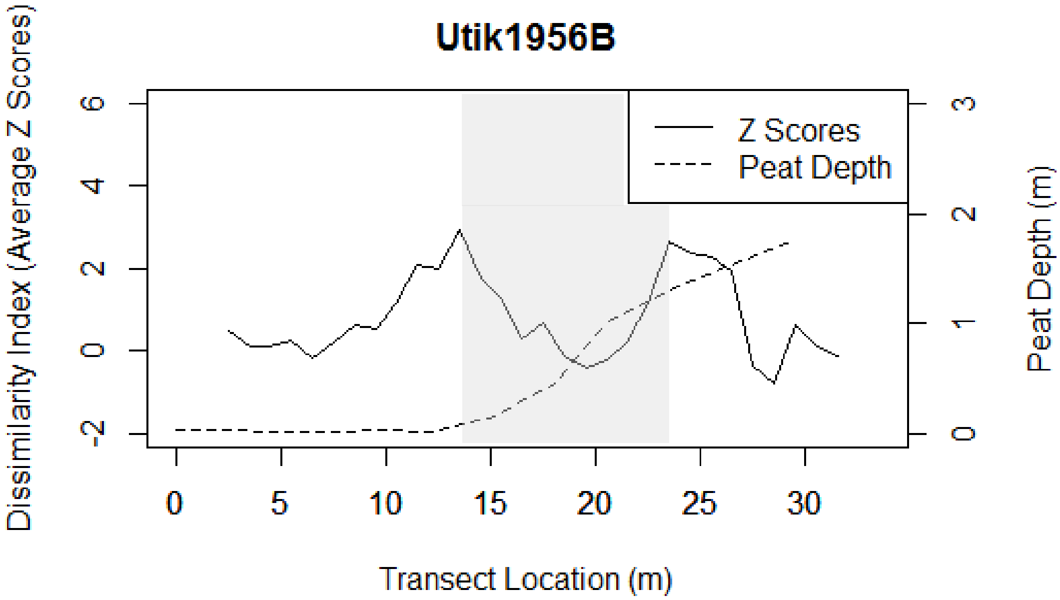

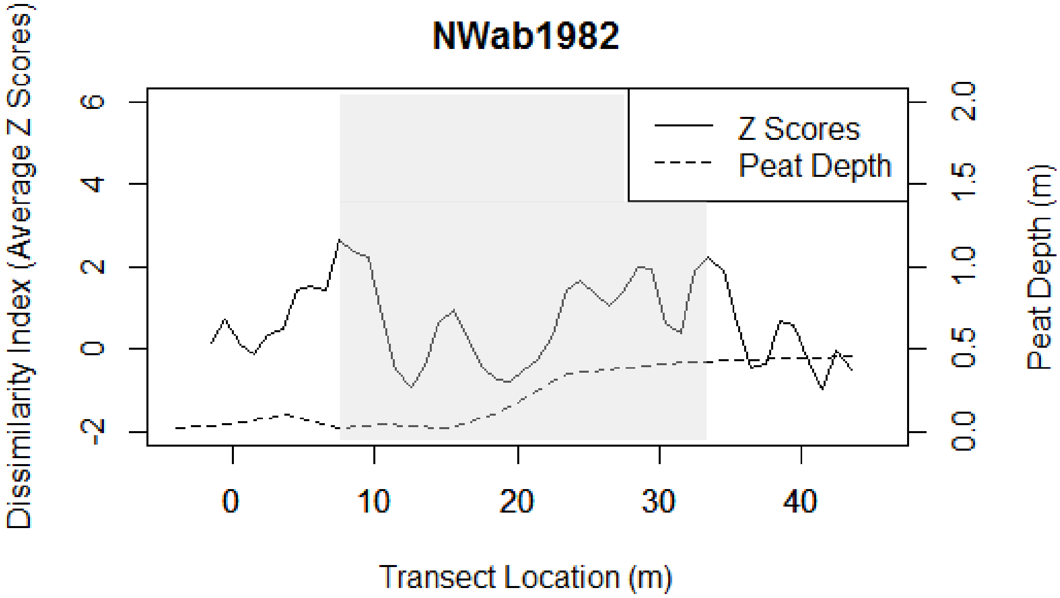

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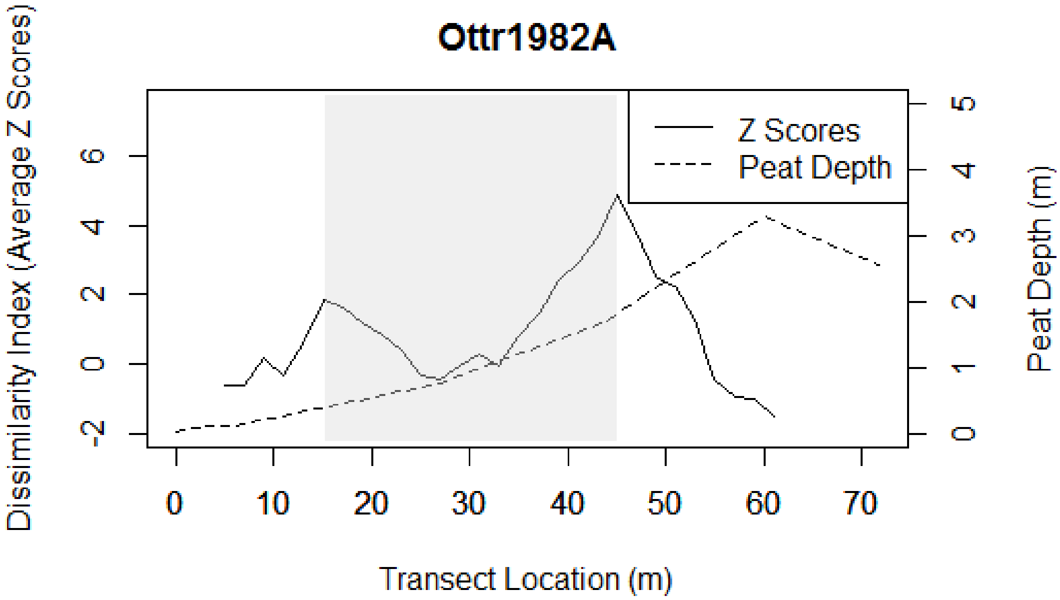

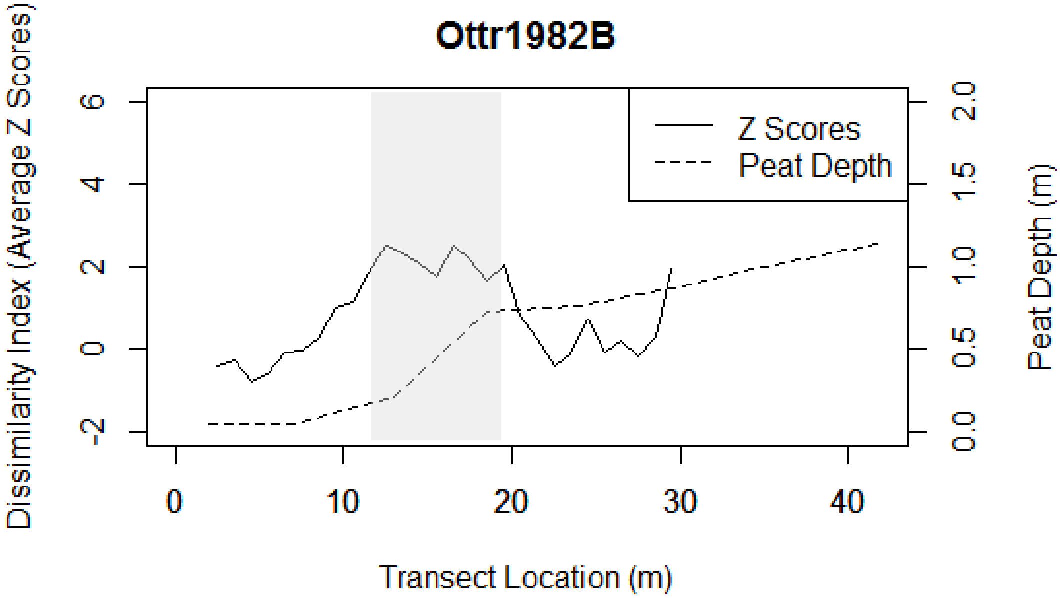

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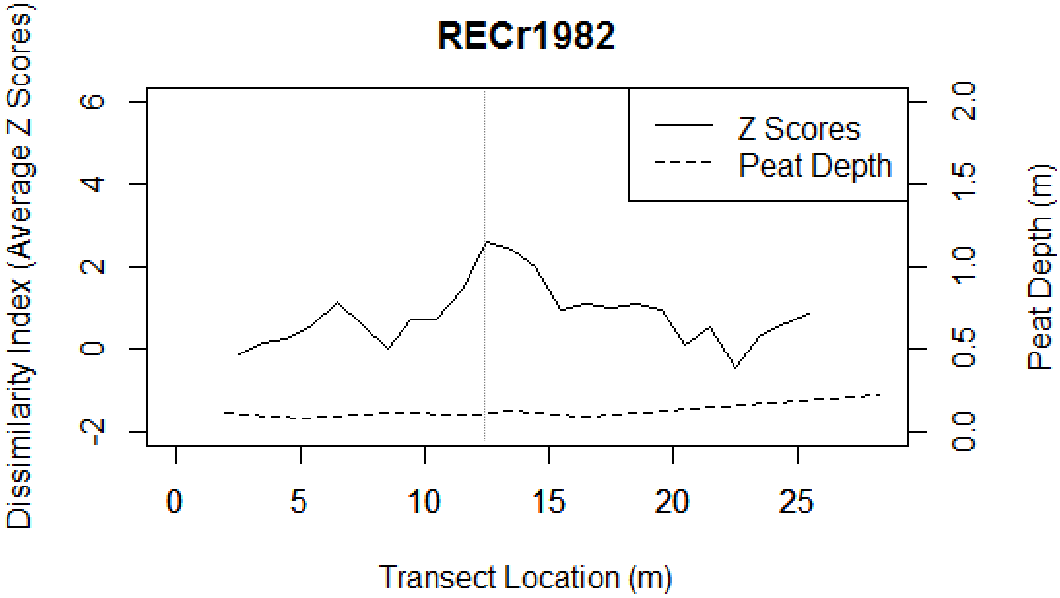

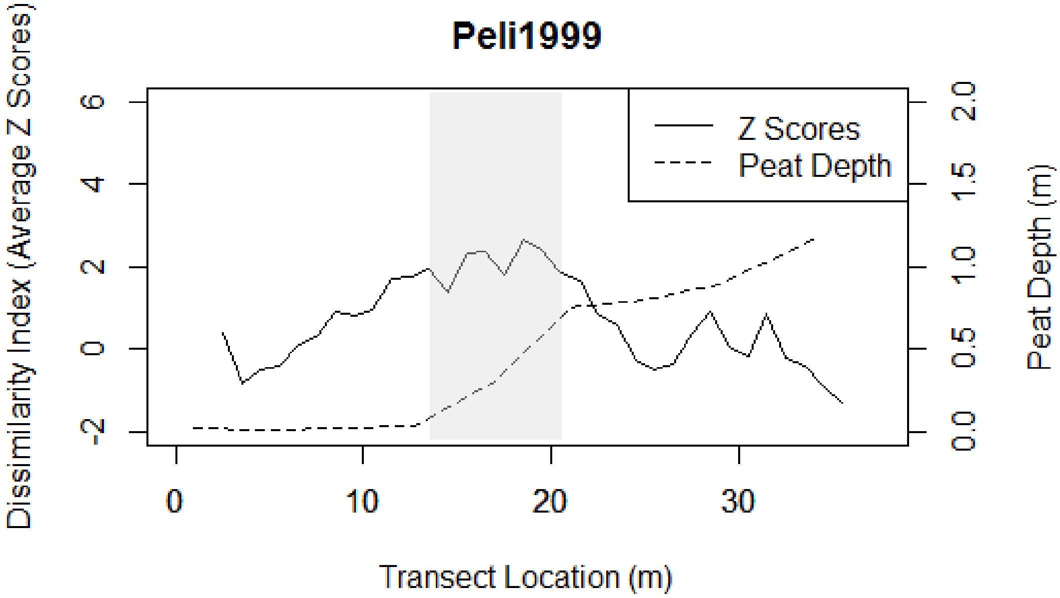

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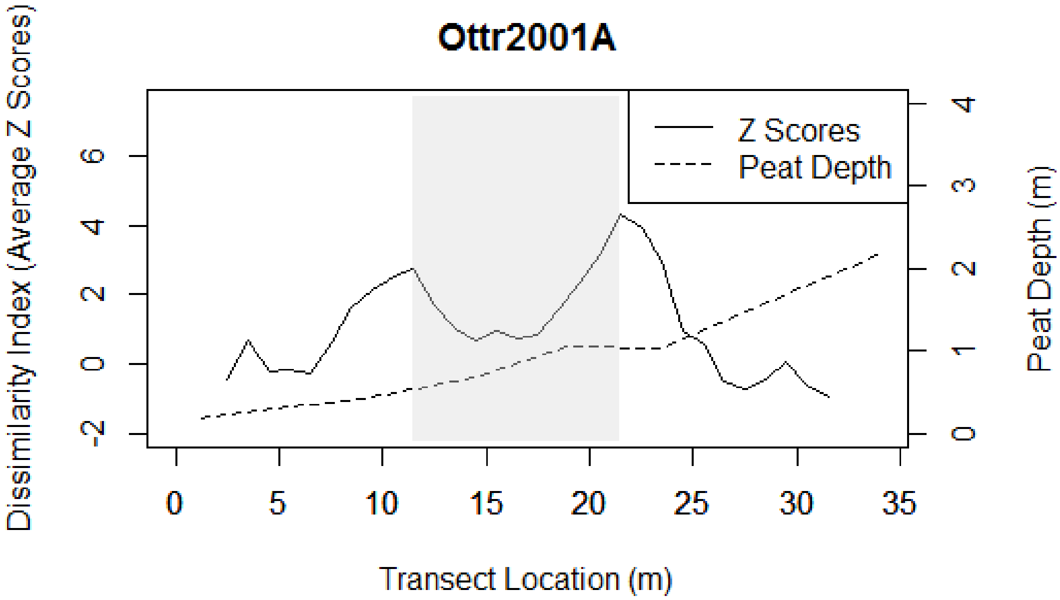

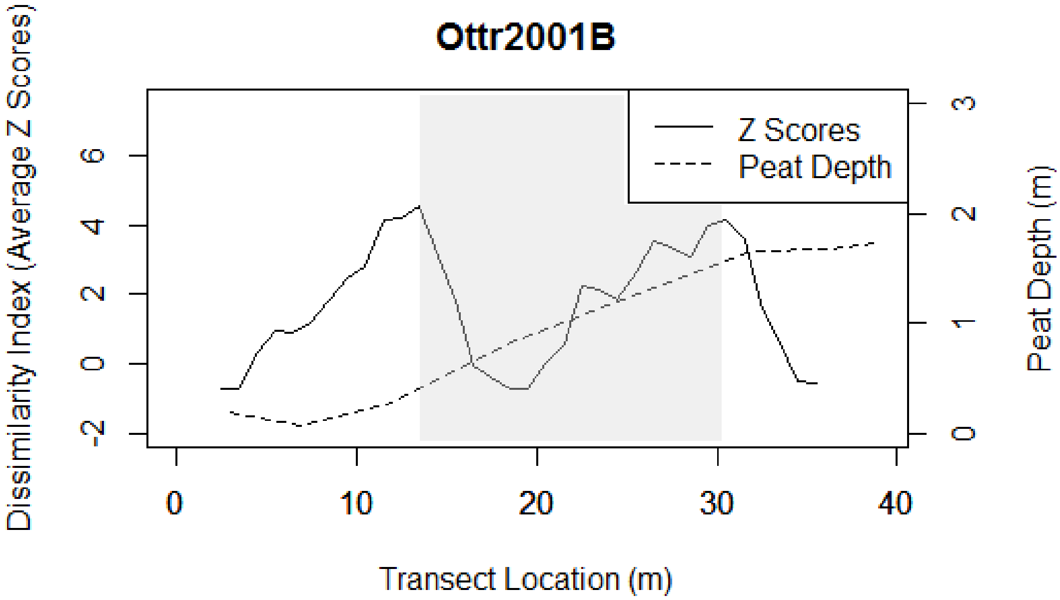

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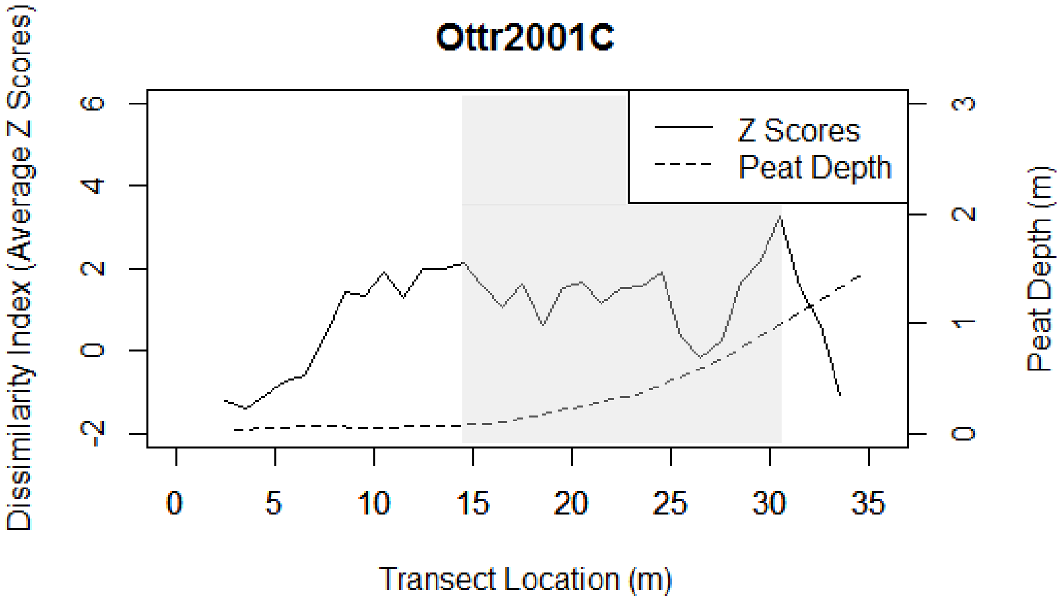

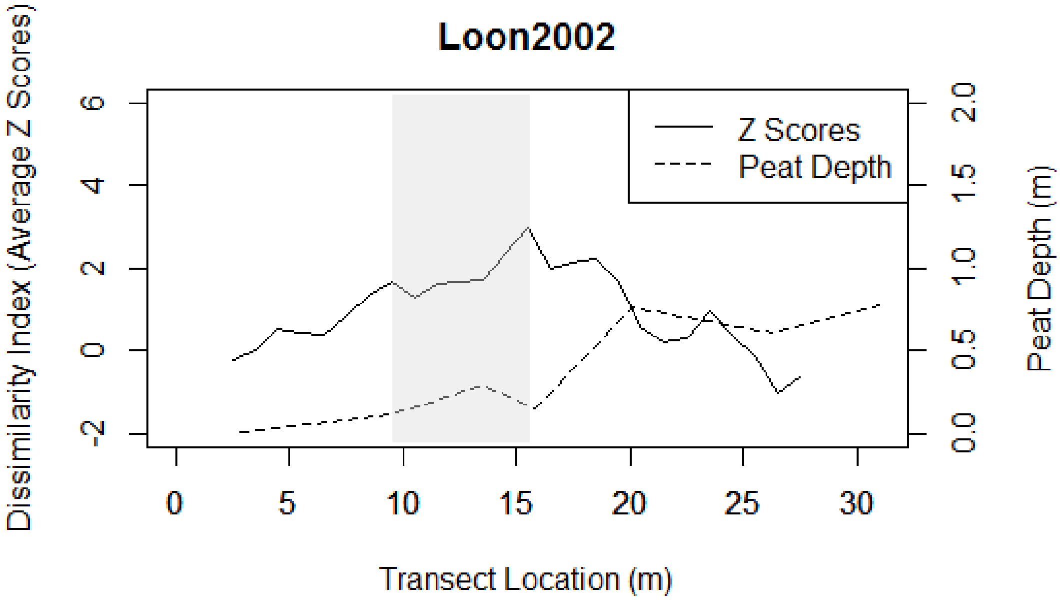

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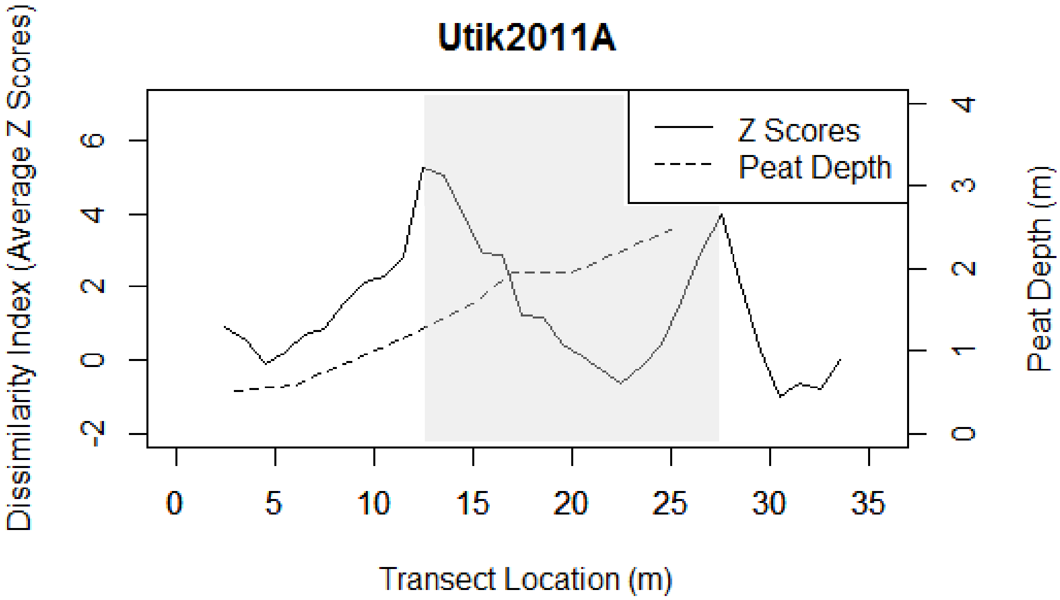

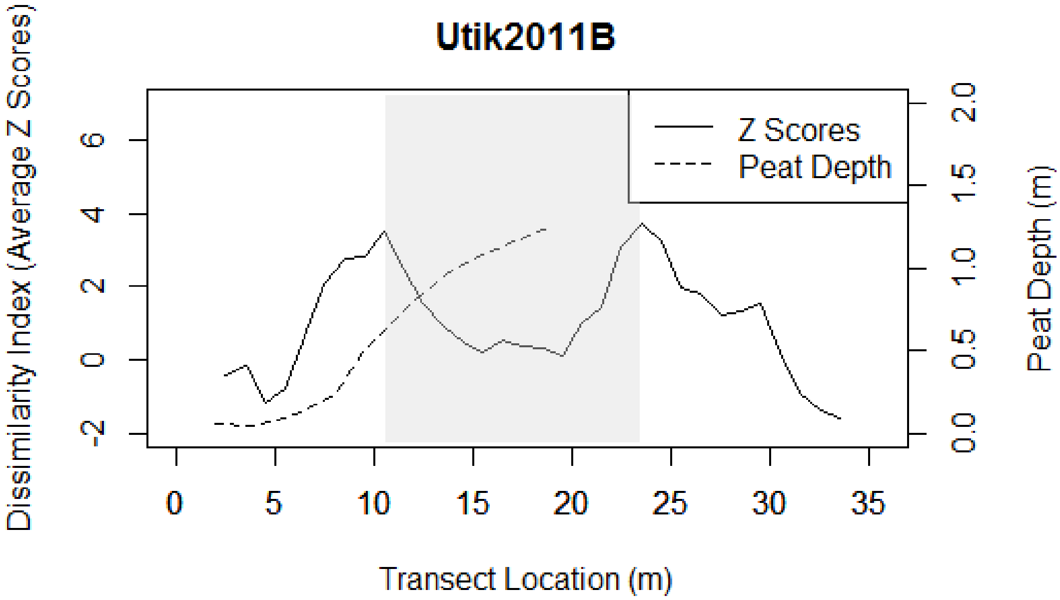

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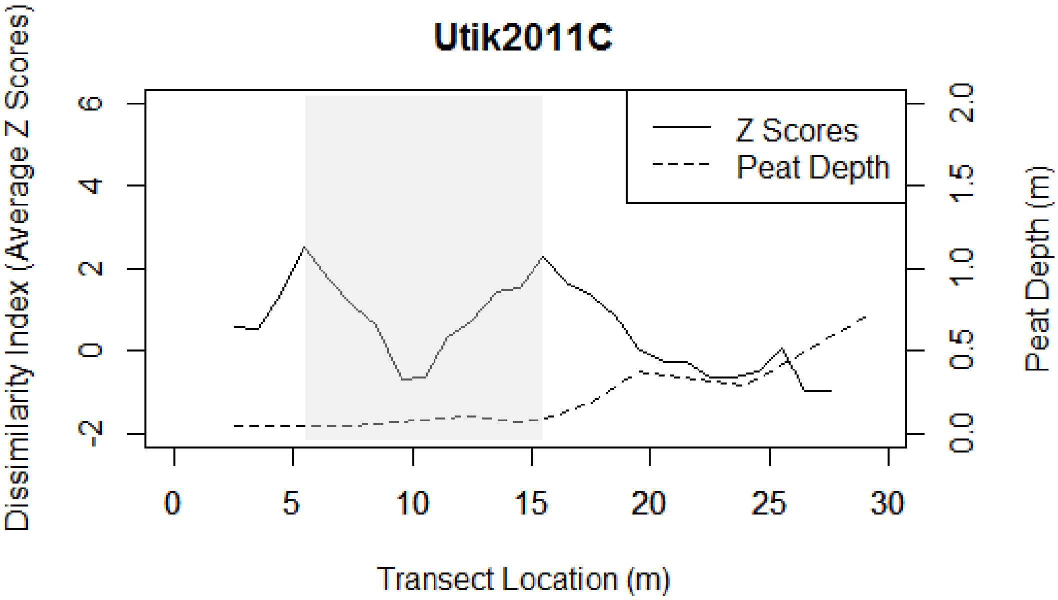
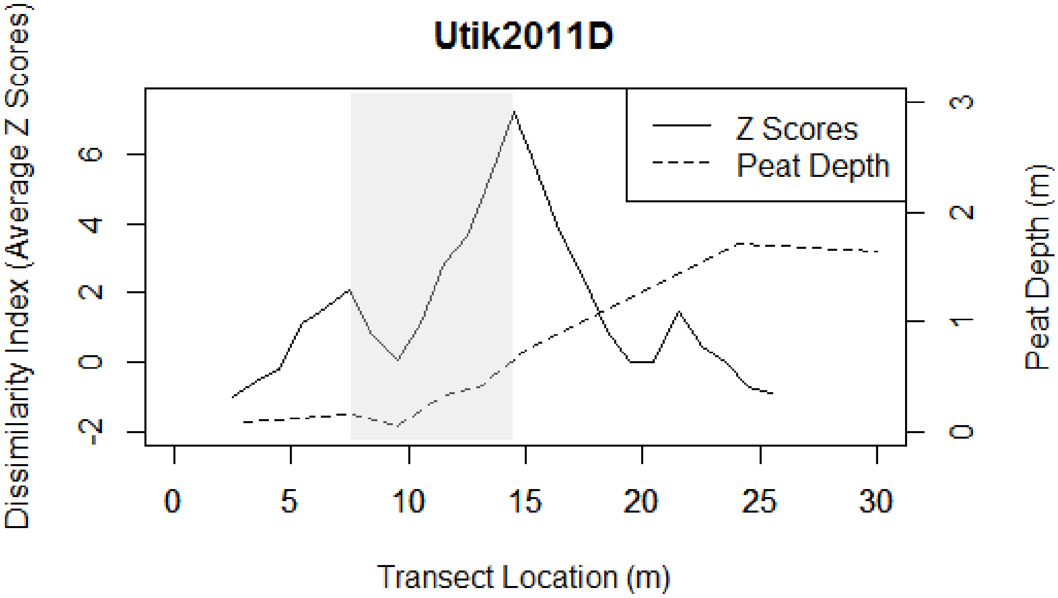




Appendix 3: Equations and additional figures.

3a) Species Diversity/Similarity Indices

Squared Euclidian Distance (SED):

$$SED = \sum_{i=1}^{n} (x_i - y_i)^2$$

Where *x* and *y* are species plot counts/abundances or summed window counts/abundances (for SMW analysis).

Bray-Curtis Dissimilarity Index (or 1-Sorensen's Similarity Index):

$$BC = 1 - \frac{R_{xy}}{R_x + R_y}$$

Where R is the species count/richness of plots *x* and *y*.

Shannon-Wiener Diversity Index:

$$SW = \sum_{i=1}^{n} p_i[ln(p_i)]$$

Where p_i is the proportion/abundance of species *i.*

Appendix 3 (continued):

3b) Tree/tall shrub biomass calculations

<u>Black Spruce Total Biomass (g)</u>

BM = 169.1 x BD + 146.5 X BD^2

Appropriate for black spruce trees with > 0.04 m BD.

Source: Wieder *et al.*, 2009.

<u>Tamarack Total Biomass (kg)</u>

ln(BM) = (-3.394) + [2.517 x ln(BD)]

Appropriate for tamarack trees with 0.01 – 0.15 m BD.

Source: Schiks *et al*., 2016.

<u>White Spruce Total Biomass (g)</u>

Wood Dry Biomass (g) = [0.0359 x ($DBH^{2.5775}$)] x 1000

Bark Dry Biomass (g) = [0.0116 x ($DBH^{2.3022}$)] x 1000

Stem Dry Biomass (g) = Wood + Bark

Foliage Dry Biomass (g) = [0.1601 x ($DBH^{1.467}$)] x 1000

Branches Dry Biomass (g) = [0.0283 x ($DBH^{2.0823}$)] x 1000

Crown Dry Biomass (g) = Foliage + Branches

Total Dry Biomass (g) = Stem + Crown

Appropriate for white spruce trees with 0.02 – 0.52 m BD.

Source: Lambert *et al*., 2005.

Appendix 3 (continued):

Jackpine Total Biomass (g)

Wood Dry Biomass (g) = [0.0804 x (DBH$^{2.4041}$)] x 1000

Bark Dry Biomass (g) = [0.0184 x (DBH$^{2.0703}$)] x 1000

Stem Dry Biomass (g) = Wood + Bark

Foliage Dry Biomass (g) = [0.0389 x (DBH$^{1.729}$)] x 1000

Branches Dry Biomass (g) = [0.0079 x (DBH$^{2.4155}$)] x 1000

Crown Dry Biomass (g) = Foliage + Branches

Total Dry Biomass (g) = Stem + Crown

Appropriate for jackpine trees with 0.02 – 0.41 m BD.

Source: Lambert *et al*., 2005.

Balsam Poplar Total Biomass (g)

Wood Dry Biomass (g) = [0.0359 x (DBH$^{2.5775}$)] x 1000

Bark Dry Biomass (g) = [0.0116 x (DBH$^{2.3022}$)] x 1000

Stem Dry Biomass (g) = Wood + Bark

Foliage Dry Biomass (g) = [0.1601 x (DBH$^{1.467}$)] x 1000

Branches Dry Biomass (g) = [0.0283 x (DBH$^{2.0823}$)] x 1000

Crown Dry Biomass (g) = Foliage + Branches

Total Dry Biomass (g) = Stem + Crown

Appropriate for balsam poplar trees with 0.02 – 0.52 m BD.

Source: Lambert *et al*., 2005.

Appendix 3 (continued):

Trembling Aspen Total Biomass (g)

Wood Dry Biomass (g) = $[0.0605 \times (DBH^{2.475})] \times 1000$

Bark Dry Biomass (g) = $[0.0168 \times (DBH^{2.3949})] \times 1000$

Stem Dry Biomass (g) = Wood + Bark

Foliage Dry Biomass (g) = $[0.0261 \times (DBH^{1.6304})] \times 1000$

Branches Dry Biomass (g) = $[0.008 \times (DBH^{2.5214})] \times 1000$

Crown Dry Biomass (g) = Foliage + Branches

Total Dry Biomass (g) = Stem + Crown

Appropriate for trembling aspen trees with 0.01 – 0.47 m BD.

Source: Lambert *et al*., 2005.

Paper Birch Total Biomass (g)

Wood Dry Biomass (g) = $[0.0593 \times (DBH^{2.5026})] \times 1000$

Bark Dry Biomass (g) = $[0.0153 \times (DBH^{2.4053})] \times 1000$

Stem Dry Biomass (g) = Wood + Bark

Foliage Dry Biomass (g) = $[0.0546 \times (DBH^{1.6351})] \times 1000$

Branches Dry Biomass (g) = $[0.0135 \times (DBH^{2.5532})] \times 1000$

Crown Dry Biomass (g) = Foliage + Branches

Total Dry Biomass (g) = Stem + Crown

Appropriate for paper birch trees with 0.02 – 0.44 m BD.

Source: Lambert *et al*., 2005.

Appendix 3 (continued):

Alder Total Biomass (g)

$BM = 33.722 \times BD^{2.712}$

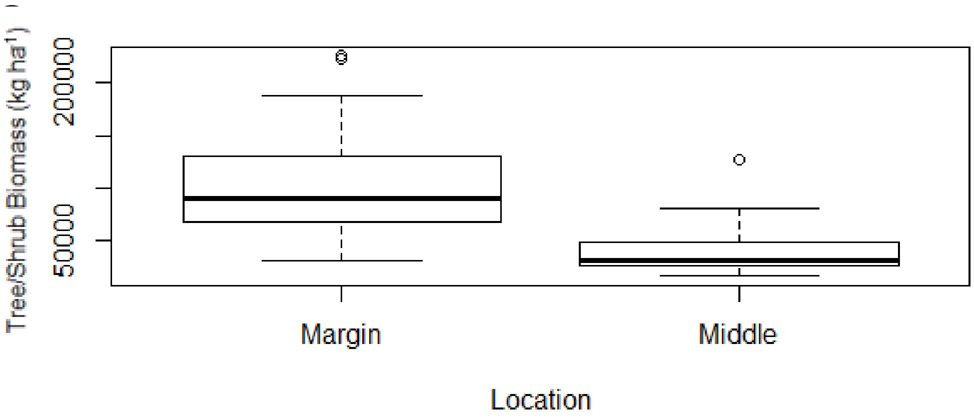
Source: Connolly and Grigal, 1983.

Willow Total Biomass (g)

$BM = 60.153 \times BD^{2.202}$

Source: Connolly and Grigal, 1983.

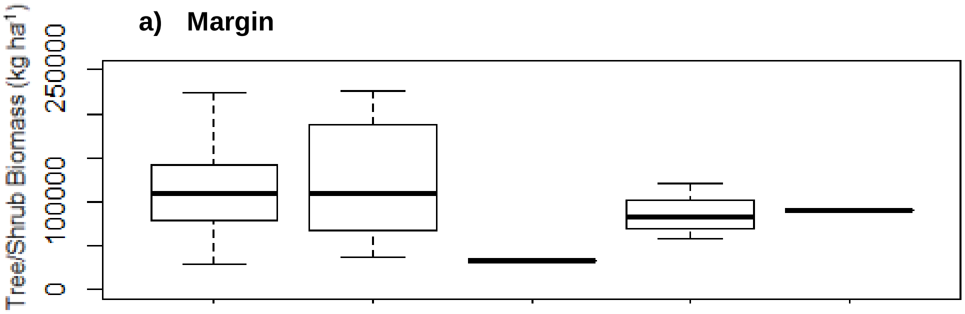
3c) Boxplot of margin and middle tree/tall shrub calculated biomass. Log-transformed values of each group were determined to be significantly different ($t(4) = 4.6789$, $p = 5.08 \times 10^{-5}$).



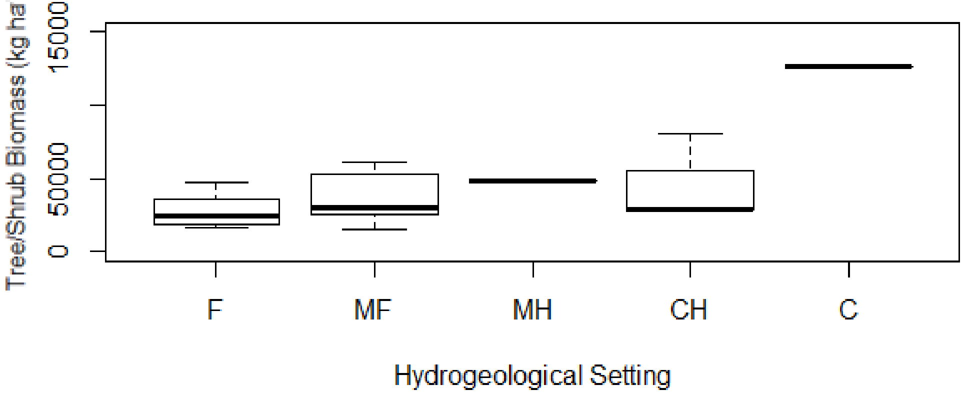
Appendix 3 (continued):

3d) Boxplots of margin and middle tree/tall shrub calculated biomass by hydrogeological setting. There were no significant differences identified between the log-transformed values of each group (margin *F*(4) = 0.664, *p* = 0.629 and middle *F*(4) = 2.434, *p* = 0.104). The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.

a) Margin

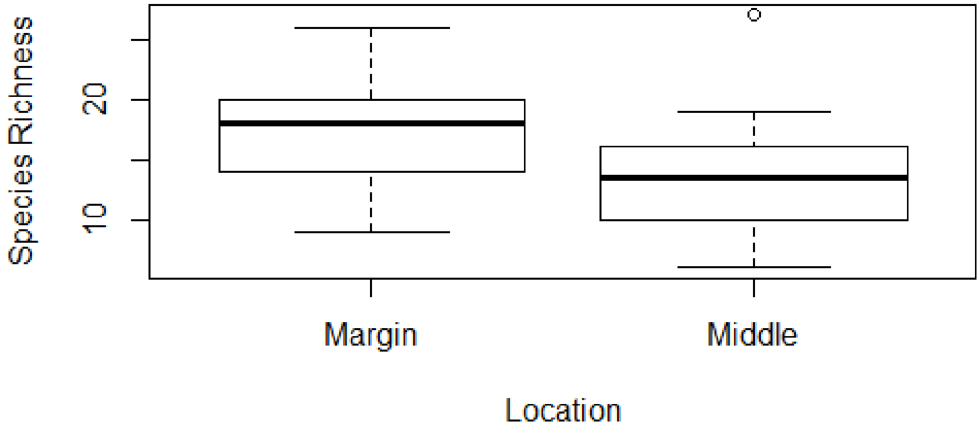


b) Middle

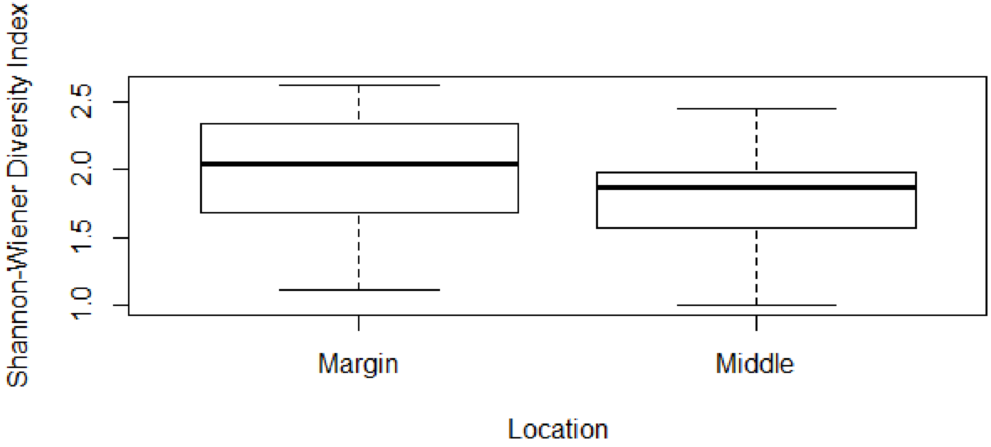


Appendix 3 (continued):

3e) Boxplot of margin versus middle species richness. Log-transformed values of each group were determined to be significantly different (*t*(4) = 2.4965, *p* = 0.016).



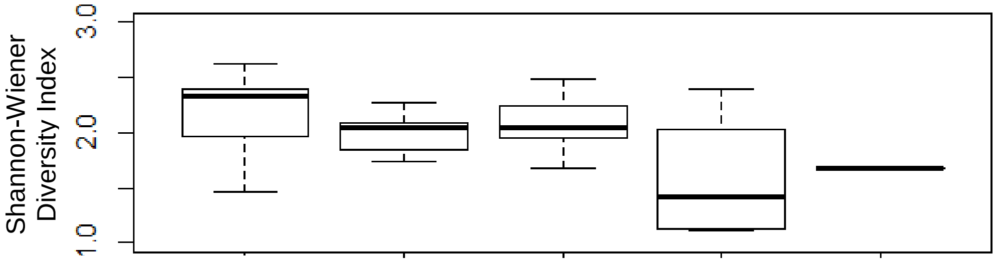
3f) Boxplot of margin and middle species diversity, calculated using the site-averaged Shannon-Wiener Diversity Index. There were no significant differences identified between each group (*t* = 1.7386, *p* = 0.090).



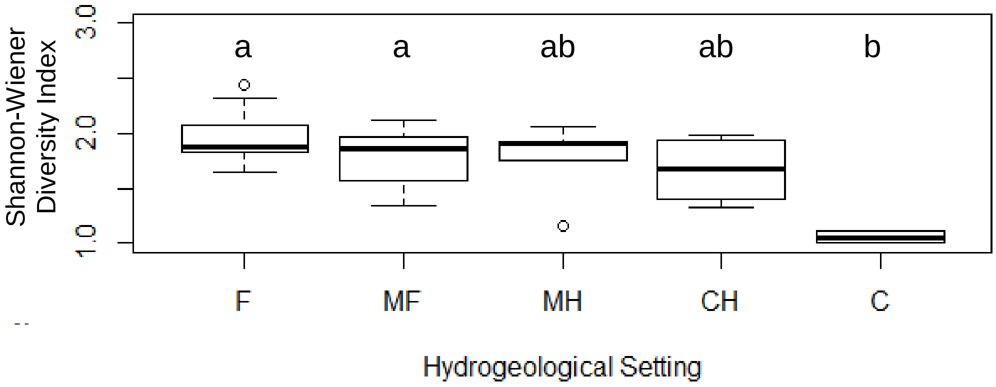
Appendix 3 (continued):

3g) Boxplots of margin and middle species diversity, calculated using the site-averaged Shannon-Wiener Diversity Index, by hydrogeological setting. Significant differences between groups are represented by lettering (a and b) above each boxplot (margin *F*(4) = 1.641, *p* = 0.213 and middle *F*(4) = 4.463, *p* = 0.009). The hydrogeological settings are as follows: F = Fine, MF = Moraine Fine, MH = Moraine Heterogeneous, CH = Coarse Heterogeneous, C = Coarse.

a) Margin



b) Middle



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Appendix 4: Species inventory.

Vegetation Stratum	Species Code	Scientific Name	Common Name
Ground Cover (Bryophytes/Lichens)	AULAPAL	*Aulacomnium palustre*	Aulacomnium moss
	BRACRIV	*Brachythecium rivulare*	Brachythecium moss
	CALLGIG	*Calliergon giganteum*	Giant calliergon moss
	CERAPUR	*Ceratodon purpureus*	Firemoss
	CLADSP.	*Cladonia* sp.	Reindeer lichen
	CLIMDEN	*Climacium dendroides*	Tree moss
	DICRSCO	*Dicranum scoparium*	Broom forkmoss
	DICRUND	*Dicranum undulatum*	Wavy dicranum moss
	HYLOSPL	*Hylocomium splendens*	Stair-step feathermoss
	MARCPOL	*Marchantia polymorpha*	Common liverwort
	ORTHOBT	*Orthotrichum obtusifolium*	Obtuseleaf aspen moss
	PLEUSCH	*Pleurozium schreberi*	Red-stem feathermoss
	POLYCOM	*Polytrichum commune*	Common haircap
	POLYSTR	*Polytrichum strictum*	Strict haircap
	PTILCRI	*Ptilium crista-castrensis*	Knight's plume feathermoss
	SPHAANG	*Sphagnum angustifolium*	Fine peat moss
	SPHACAP	*Sphagnum capillifolium*	Red peat moss
	SPHAFUS	*Sphagnum fuscum*	Rusty peat moss
	SPHAMAG	*Sphagnum magellanicum*	Magellan's peat moss
	SPHARIP	*Sphagnum riparium*	Streamside peat moss
	Lichen		Lichen

Vegetation Stratum	**Species Code**	**Scientific Name**	**Common Name**
Ferns	EQUIARV	*Equisetum arvense*	Common horsetail
	EQUISCI	*Equisetum scirpoides*	Dwarf scouring rush
	DRYOAUS	*Dryopteris australis*	Wood fern
Graminoids	CALACAN	*Calamagrostis canadensis*	Bluejoint
	CAREDIS	*Carex disperma*	Softleaf sedge
	CAREUTR	*Carex utriculata*	Bottle sedge
	ERIOVAG	*Eriophorum vaginatum*	Cottongrass
	TYPHLAT	*Typha latifolia*	Cattail
Forbs	ASTECIL	*Aster ciliolatus*	Fringed blue aster
	CHAMCHA	*Chamaedaphne calyculata*	Leatherleaf
	CIRSARV	*Cirsium arvense*	Canada thistle
	CORNCAN	*Cornus canadensis*	Bunchberry
	DROSROT	*Drosera rotundifolia*	Common sundew
	EPILANG	*Epilobium angustifolium*	Fireweed
	FRAGVIR	*Fragaria virginiana*	Wild strawberry
	GALITRI	*Galium triflorum*	Bedstraw
	GEOCLIV	*Geocaulon lividum*	Northern bastard toadflax
	HEDYBOR	*Hedysarum boreale*	Boreal sweet-vetch
	HIPPVUL	*Hippuris vulgaris*	Common mare's tail
	MERTPAN	*Mertensia paniculata*	Tall lungwort
	OXYCMIC	*Oxycoccus microcarpus*	Small bog cranberry
	PETAPAL	*Petasites palmatus*	Palmate-leaved coltsfoot
	PETASAG	*Petasites sagittatus*	Coltsfoot
	RUBUCHA	*Rubus chamaemorus*	Cloudberry
	RUBUPUB	*Rubus pubescens*	Dwarf raspberry

Vegetation Stratum	**Species Code**	**Scientific Name**	**Common Name**
Forbs (continued)	SMILTRI	*Smilacina trifolia*	Three-leaved false Soloman's seal
	VIOLCAN	*Viola canadensis*	Canada violet
	VIOLREN	*Viola renifolia*	Kidney-leaved violet
Shrubs	BETUPUM	*Betula pumila*	Bog birch
	LINNBOR	*Linnaea borealis*	Twinflower
	LONIINV	*Lonicera involucrata*	Bracted honeysuckle
	RHODGRO	*Rhododendron groenlandicum*	Labrador tea
	RIBEGLA	*Ribes glandulosum*	Skunk currant
	RIBELAC	*Ribes lacustre*	Black gooseberry
	RIBEOXY	*Ribes oxyacanthoides*	Canadian gooseberry
	RIBETRI	*Ribes triste*	Swamp redcurrant
	ROSAWOO	*Rosa woodsii*	Wild rose
	RUBUIDA	*Rubus idaeus*	Raspberry
	SALIBEB	*Salix bebbiana*	Bebb's willow
	SALILAS	*Salix lasiandra*	Pacific willow
	SALILUC	*Salix lucida*	Shining willow
	SALIMAC	*Salix maccalliana*	McCalla's willow
	SALIPET	*Salix petiolaris*	Basket willow
	SALIPYR	*Salix pyrifolia*	Balsam willow
	VACCMYR	*Vaccinium myrtilloides*	Common blueberry
	VACCVIT	*Vaccinium vitis-idaea*	Bog cranberry
	VIBUEDU	*Vibernum edule*	Lowbush cranberry

Vegetation Stratum	**Species Code**	**Scientific Name**	**Common Name**
Tall Shrubs/Trees	ALNUCRI	*Alnus crispa*	Green alder
	BETUPAP	*Betula papyrifera*	Paper birch
	LARILAR	*Larix laricina*	Larch/Tamarack
	PICEGLA	*Picea glauca*	White spruce
	PICEMAR	*Picea mariana*	Black spruce
	PINUBAN	*Pinus banksiana*	Jackpine
	POPUBAL	*Populus balsamifera*	Balsam poplar
	POPUTRE	*Populus tremuloides*	Trembling aspen