Edge influence from linear disturbances and recovery of understory communities in boreal forests

by

Laureen Francesca Inocian Echiverri

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Conservation Biology

Department of Renewable Resources
University of Alberta

Abstract

Forest fragmentation is one of the leading causes of global biodiversity loss and is only expected to increase with the continued rise of anthropogenic disturbances. An important environmental consequence of fragmentation is edge influence—the set of ecological changes which occur at the interface of a forest and the adjacent non-forested patch. In the boreal forests of western Canada, seismic lines are one of the primary drivers of forest fragmentation. Seismic lines are narrow, linear disturbances used to locate fossil fuel reserves. Seismic lines are slow to recover and tend to persist in the landscape, contributing to their long-term widespread presence. To facilitate seismic line recovery, mounding is currently being applied to create micro-sites for tree establishment. In this thesis, I examine the edge influence of seismic lines on understory communities and assess the impacts of restoration efforts. Specifically, my objectives are to: 1) assess how edge influence from multiple seismic lines interacts and affects the understory communities of treed fens, 2) explore the mechanisms driving edge influence on the understory vegetation by examining the population- and individual-level performance of an herbaceous annual, *Melampyrum lineare,* in xeric, pine-dominated stands, and 3) assess the impact of mounding on understory community recovery in treed fens. To address these objectives, I sampled seismic lines and the adjacent forest in treed fens and pine-dominated stands in northeastern Alberta.

Despite their narrow nature, I found that seismic lines had a significant edge influence on the understory vegetation in treed peatlands. In addition, I found evidence of edge interaction when multiple seismic lines were in proximity. For example, in poor fens, multiple seismic lines had a strengthening edge interaction: single seismic lines did not have an edge influence on vegetation, while multiple seismic lines led to higher tree density in the adjacent fen. In xeric,

pine-dominated stands, I found a sealing effect at the edges of wider and older seismic lines, with woody vegetation increasing in abundance at the edge. In addition, I found that the population-level performance of *Melampyrum lineare* was shaped by the presence of seismic lines—with higher population density and seed production on the seismic lines. In contrast, at the individual-level, performance was primarily shaped by the vegetation surrounding each individual. Finally, while seismic lines left to recover naturally showed promising results, with the re-establishment of a peat-accumulating understory community, I found that attempts to re-create micro-sites for tree establishment on seismic lines only set back the recovery of understory communities in treed peatlands. Overall, these results show the complex impacts of fragmentation and the importance of evaluating the effects of restoration techniques, prior to their widespread use. Considering these results, I recommend 1) utilizing recent technology to prevent or minimize any additional creation of conventional and/or low impact seismic lines and 2) minimizing or preventing any additional disturbance on existing seismic lines.

Preface

Chapter 2 of this thesis has been submitted for publication as:

Echiverri, L.F.I., Macdonald, S.E., Nielsen, S.E. 2021. Neighboring edges: evidence of edge interaction of linear disturbances on vegetation in treed fens. Applied Vegetation Science. I was responsible for data collection, analysis, and manuscript composition. S.E. Macdonald and S.E. Nielsen were involved with research design and contributed to analyses and manuscript edits.

Chapter 4 of this thesis has been published as:

Echiverri, L.F.I., Macdonald, S.E., Nielsen, S.E. 2020. Disturbing to restore? Effects of mounding on understory communities on seismic lines in treed peatlands. Canadian Journal of Forest Research **50** (12): 1340-1351. I was responsible for data collection, analysis, and manuscript composition. S.E. Macdonald and S.E. Nielsen were involved with research design and contributed to analyses and manuscript edits.

Dedication

To my Titas,

Rosalie S.E. Yanong and Angeli S.R. Echiverri,

your resilience in the face of adversity

is my inspiration.

Acknowledgements

I would first like to thank my supervisors, Drs. Scott Nielsen and Ellen Macdonald. Thank you, Scott, for giving me the opportunity to explore treed peatlands and pine stands for my PhD! Thank you for your guidance throughout my research and for always reminding me to see the broader picture—to think beyond the provincial applications of my research. Thank you, Ellen, for generously sharing your wisdom and time! Thank you for helping me improve my research and writing skills. I have learned so much from you, not just with research, but also in teaching and project management. And as always, thank you for your patience, guidance, and constant support.

I am also grateful to my committee member, Dr. Anne McIntosh. Thank you for your valuable feedback and encouragement. Your positive emails helped buoy me through the final write-up of my thesis. I would also like to thank the external examiners, Drs. Viktoria Wagner and Dr. Martin Diekmann, and the exam chair, Dr. René Belland. Thank you for taking the time to be a part of the examining committee.

For their assistance in the field, I would like to thank Jennifer Buss, Anna Duke, Marcel Schneider, Fionnuala Carroll, Neal Josephs, Allison Roth, Renae Shewan, Victoria Colyn, Amanda Kadatz, Olivia Handel, Christine Duke, and Dr. Caroline Franklin. Thank you so much for your patience, hardwork, and enthusiasm in the field. For assistance with site selection and logistics, I would like to thank Dr. Federico Riva, Dr. Angelo Filicetti, and Ashley Hillman. I would also like to thank Dr. Julia Linke of the Boreal Ecosystem Recovery and Assessment research team for sharing valuable site data. I am also grateful to Dr. Jennifer Klutsch for guiding me through the process of seed sterilization and to Dr. Nadir Erbilgin for kindly allowing me to use his laboratory space.

To Varina Crisfield, Dr. Jacqueline Dennett, and Ryan James, thank you for your help in plant identification and for sharing your *Salix*, *Carex,* and graminoid love. A huge thank you to Teri Hill, Dr. Richard Caners, Dr. René Belland, and Ruth Errington for guiding me through peatland sampling and bryophyte identification. Thank you to Anna Duke, Renae Shewan, Kristin Schafer, Anabel Dombro, and Claire Merkosky for generously volunteering their time to assist in

Table of Contents

List of Tables

List of Figures

Figure 2.4: Edge effects from seismic lines in in poor treed fens. Mean values for: (A) total understory cover, (B) forb cover, and (C) graminoid cover at each distance from the seismic line into the interior fen for the three treatment types. Error bars represent standard error of the mean. The horizontal dashed line represents the average value for the interior treed fens, with the standard error represented by the shaded grey area. Filled symbols indicate significant magnitude of edge influence (MEI, α = 0.1) and the horizontal solid line at the bottom indicates the distances over which there was significant depth of edge influence, color coded by treatment (see also Appendices 2.8 and 2.9). Asterisks represent a significant difference between the multiple

List of Appendices

Chapter 1: Introduction

Fragmentation is one of the leading causes of global biodiversity loss (Haddad et al. 2015; Newbold et al. 2015) and it is only set to increase with the continued rise of anthropogenic disturbances. Fragmentation compromises biodiversity by decreasing patch size and connectivity and increasing edge density (Fletcher et al. 2018). In the boreal forests of western Canada, seismic lines—narrow, deforested corridors used to locate fossil fuel reserves—are one of the primary drivers of forest fragmentation (Pattison et al. 2016). These narrow, linear disturbances have been shown to alter conditions in the adjacent forest and tend to persist in the landscape (MacFarlane 2003; Lee and Boutin 2006; van Rensen et al. 2015; Dabros et al. 2017). To inform conservation and restoration efforts, I examine the edge influence of seismic lines and assess the impacts of restoration efforts on understory communities.

1.1 Edge influence

In forest ecosystems, edge influence, or edge effect, is the set of abiotic and biotic changes which occur at the interface of a forest and the adjacent non-forested area. Edge influence is a major driver of forest structure and one of the important environmental consequences of forest fragmentation (Fahrig 2003; Laurance et al. 2007). In fragmented forest stands, edge influence can further reduce the area of "interior" forest habitat, as disturbance-related changes from the non-forested patch extend into the adjacent forest (Laurance et al. 2011). With continued forest fragmentation on the rise (Haddad et al. 2015), understanding the impacts of edge influence becomes increasingly important to determine species distributions across fragmented stands and to assess the cumulative impacts of forest fragmentation (Ries et al. 2017).

Edge influence is described by its magnitude and depth: 1) the magnitude of edge influence (MEI) describes how much a parameter differs between the edge and the interior forest and 2) the distance or depth of edge influence (DEI) describes how the edge influence extends into the adjacent forest (Harper et al. 2005). The DEI is particularly important for identifying the size of the remaining "interior forest" in a fragmented landscape (Ries et al. 2017). Several factors shape the MEI and DEI, including the degree of contrast between the edge and the adjacent forest (i.e. patch contrast), edge orientation, edge type, landscape context, and the response variables of interest (Gehlhausen et al. 2000; Laurance et al. 2011; Harper et al. 2015; Esseen et al. 2016; Franklin et al. 2021b).

Flow of energy and materials between the non-forested and forested patch is one of the main drivers of edge influence and edges with steeper gradients are likely to have a stronger edge influence (Ries et al. 2004; Harper et al. 2005; Esseen et al. 2016). Thus, edges with higher patch contrast, or greater differences in vegetation height, density, or composition, tend to have a stronger edge influence, e.g., larger MEI (Harper et al. 2005; Ries et al. 2017). For example, in the boreal forest, edge influence is generally less extensive than in temperate or tropical forests; this has been partially attributed to a shorter canopy height, i.e., reduced patch contrast, than the more productive forests of temperate and tropical biomes (Harper et al. 2015). As the non-forested patch regenerates, patch contrast can decline over time and edge influence can also weaken (Harper et al. 2015, 2016)—but see Dupuch and Fortin (2013) for strengthening edge influence over time. Edge orientation can also affect the energy exchange at the edge, leading to varied edge influence responses between edge aspects. In the northern hemisphere, south-facing and west-facing edges tend to have stronger edge influence than north-facing and east-facing edges (Gehlhausen et al. 2000; Hylander 2005; Franklin et al. 2021a).

Edge influence will also vary with edge type and landscape context. Natural edges tend to have a more gradual and extensive edge influence than anthropogenic edges, which are more abrupt (Harper et al. 2004, 2015). However, most studies on edge influence in the boreal have focused on large disturbances, such as fires and harvesting, and additional studies on narrow disturbances, like seismic lines, are needed (but see MacFarlane 2003; Dabros et al. 2017; Franklin et al. 2021a). The landscape context can also shape edge influence (Ries et al. 2004). For example, the relatively weaker edge influence in the boreal forest has also been attributed to the relatively high frequency of natural disturbances and the ubiquity of natural inherent edges, such as wetlands and lake edges (Harper et al. 2015). Due to this inherent landscape heterogeneity, edge-adapted species or species adapted to a wider range of micro-environmental conditions are common in the boreal forest, leading to weaker responses to edges (Harper et al. 2015). Despite this, understanding edge influence in the boreal forest is still important for conservation, as edge influence can jeopardize disturbance-sensitive species that are limited to "interior" forest conditions. For example, bryophytes are more sensitive to the altered micro-environmental conditions found at edges and usually exhibit a strong, negative response to edges (Hylander 2005; Harper et al. 2015). Landscape context includes the degree of habitat fragmentation as edge influence can change when multiple edges are in close proximity (Harper et al. 2007; Porensky and Young 2013; Ries et al. 2017). Understanding how edge influence changes with proximity to other edges becomes increasingly important, with the rise of high-density linear disturbances in the boreal forest.

Though studies on edge influence are on the rise, various knowledge gaps persist, including a limited understanding of how edge influence from multiple edges interact and of the mechanisms underlying the patterns of edge influence (Porensky and Young 2013; Ries et al.

2017). Most studies on edge influence focus on the effects from a singular edge (Porensky and Young 2013); however, edges rarely occur alone. To accurately assess the cumulative impacts of edges in fragmented stands, and to extrapolate their effects at a landscape scale, we need to understand how edge influence interacts. Additionally, most studies have focused on identifying patterns of edge influence. However to predict and mitigate edge influence, a better understanding of the mechanisms driving edge influence is essential (Murcia 1995; Ruffell and Didham 2016). In this thesis, I address these knowledge gaps by examining the edge influence of linear disturbances on the understory vegetation in the boreal forest—a biome where studies on these topics are particularly sparse (but see Harper et al. 2007).

1.2 Seismic lines

In western Canada, forest dissection by linear disturbances, such as seismic lines, is ubiquitous and only expected to increase (Schneider et al. 2003; Pattison et al. 2016; Riva and Nielsen 2021). Seismic lines are narrow, deforested corridors used to locate oil and gas reserves. Though seismic lines are relatively narrow disturbances (ranging from 2 m to 10 m wide), they are a concern because of their length, widespread distribution, and persistence in the landscape (Schneider et al. 2003; Lee and Boutin 2006; van Rensen et al. 2015; Pattison et al. 2016). For example, in southwestern Alberta, Pattison et al. (2016) found that seismic lines accounted for approximately 80% of all anthropogenic linear edges, and they dissected the forested landscape more than any other anthropogenic linear disturbance, such as roads, and power lines.

Seismic lines are created by clearing strips of forests, using either bulldozers or lightweight mulchers. Explosive devices are then placed on the seismic lines and the seismic waves from the detonation are tracked. Changes in seismic wave frequency indicate the presence of fossil fuels (Dabros et al. 2018). There are two types of seismic lines: conventional seismic

lines that are straight, approximately 5 -10 m wide, and created by bulldozers, and low-impact seismic lines which are winding, 2 – 4 m wide, and created with lightweight equipment to minimize soil disturbance and compaction (Dabros et al. 2018). To mitigate the environmental impacts of seismic line creation, operations are conducted in the winter and low-impact seismic lines are increasingly being used (Dabros et al. 2018). Historically, seismic lines were spaced 300- 500 m apart; however, locating unconventional oil reserves, such as oil sands (bitumen deposits), now requires seismic lines be placed at closer intervals (30-100 m apart) (Pattison et al. 2016).

Both types of seismic lines impact vegetation (MacFarlane 2003; Dabros et al. 2017; Finnegan et al. 2018; Abib et al. 2019), micro-environmental conditions (Stern et al. 2018; Stevenson et al. 2019; Franklin et al. 2021a), and wildlife (Bayne and Dale 2011; Dickie et al. 2017b; DeMars and Boutin 2018). In addition, edge influence from seismic lines causes vegetation shifts and altered micro-environmental conditions in the adjacent interior forest (MacFarlane 2003; Dabros et al. 2017; Abib et al. 2019; Franklin et al. 2021a). Previous studies have focused on the effects of a singular seismic line but seismic lines are very often found in dense grids. To explore the cumulative impacts of having multiple, closely spaced seismic lines, I assess how edge influence from multiple seismic lines interact and affect the understory vegetation in treed peatlands. In addition, while patterns of edge influence have been identified, little is known about the mechanisms driving the edge influence of seismic lines on understory vegetation. In this thesis, I explore the mechanisms driving edge influence on understory plants, by examining the performance of an herbaceous annual on seismic lines, at the edge of seismic lines, and in adjacent interior forest.

Seismic lines have also been shown to persist in the landscape (Lee and Boutin 2006; van Rensen et al. 2015). They tend to be depressed relative to the surrounding area (Stevenson et al. 2019) and are characterized by wetter conditions (Dabros et al. 2017). This can hinder tree regeneration, especially in wetter ecosites, such as treed peatlands (van Rensen et al. 2015; Kansas et al. 2015). The persistent presence of deforested linear corridors is of particular concern in relation to the woodland caribou, *Rangifer tarandus*—a threatened species that is sensitive to the effects of landscape dissection (Committee on the Status of Endangered Wildlife in Canada 2014). Seismic lines provide easier predator access to treed peatlands, an ecosite characterized by difficult terrain and typically used as predator refugia by woodland caribou (Dickie et al. 2017b; DeMars and Boutin 2018). The increased predation risk created by seismic lines on the already threatened caribou has motivated widespread active restoration efforts of seismic lines in Alberta.

The primary goal of restoration efforts is to increase tree regeneration, especially in treed peatlands, and one of the tools used to accomplish this is mounding (Pyper et al. 2014; Government of Alberta 2017). Mounding is a site-preparation technique used in forestry to create micro-topography on disturbed sites. With mounding, soil is excavated to create a hole and the excavated soil is piled on the adjacent ground to create a mound (Sutton 1993). Mounding can create suitable micro-habitat for tree growth and establishment, as it can expose mineral soil, reduce competing vegetation, and create an aerated rooting zone in flooded sites (Pyper et al. 2014). In treed peatlands, this technique attempts to re-create the hummock-hollow topography characteristic of peatlands. While mounding has shown some success in encouraging tree establishment on seismic lines and wellpads (Lieffers et al. 2017; Filicetti et al. 2019) and promoting understory recovery on wellpads (Caners et al. 2019), little is known about the

impacts of mounding of seismic lines on the recovery of understory vegetation. In this thesis, I address this knowledge gap and assess the impacts of mounding on the recovery of both the vascular and non-vascular understory vegetation in treed fens.

1.3 Understory vegetation

Though the understory vegetation comprises only a small portion of the forest's biomass, it is an essential component of forested ecosystems (Gilliam 2007). In the boreal forest, the understory vegetation accounts for most of the plant diversity (De Grandpre et al. 2003) and provides food and habitat for wildlife (Deal 2001). The understory also influences the regeneration of overstory trees and shapes overstory composition (Malmer et al. 1994; Nilsson and Wardle 2005; Gilliam 2007). For example, in treed peatlands, *Sphagnum* creates a moist environment that facilitates germination of trees; however, tree saplings must grow faster or at the same rate as *Sphagnum* to avoid being buried (Rydin and Jeglum 2006). Nutrient cycling is also shaped by the understory vegetation (Nilsson and Wardle 2005). For example, *Sphagnum*'s ability to translocate nutrients from senescing parts and the slow decay rate of its litter contribute to the nutrient-poor conditions of treed peatlands (Malmer et al. 1994); additionally, the slow decomposition rate of bryophytes is the primary driver of peat accumulation (i.e., carbon sequestration) in peatlands. Thus, understanding the impacts of seismic lines on the understory vegetation will not only help inform efforts to restore and conserve wildlife habitat, but will also inform efforts to maintain other ecosystem functions.

1.4 Research Objectives

The overall objective of this thesis is to quantify the edge influence from seismic lines and recovery following restoration treatments of seismic lines, with a focus on the understory vegetation. In chapter 2, I assess how edge influence from multiple seismic lines interact and

affect the understory vegetation in treed fens. The results of this study can provide a better understanding of the cumulative effects of the dense, networks of seismic lines on vegetation. In chapter 3, I explore the mechanisms driving edge influence on the understory vegetation by examining the performance of an herbaceous annual in xeric, pine-dominated stands and exploring the abiotic and biotic factors that affect it. In chapter 4 and 5, I assess the efficacy of mounding as a restoration technique on the vascular (chapter 4) and non-vascular (chapter 5) understory communities in treed fens. The results of these chapters can inform efforts to restore seismic lines in treed peatlands. The subsequent chapters are formatted in manuscript form, with citations in the style of the Canadian Journal of Forest Research.

Chapter 2: Neighboring edges: evidence of edge interaction of linear disturbances on vegetation in treed fens

2.1 Abstract

Edge influence is the set of ecological changes that occur at the interface of a forested and non-forested patch. It is an important environmental effect associated with habitat fragmentation, as edge effects can further reduce the remaining 'interior' habitat for species, including the understory plant community. However, extrapolating the influence of edges across the broader landscape has been hampered by knowledge gaps, such as how to collectively quantify impacts of multiple edges in close proximity, where edge effects might interact. To address this, I examined the interaction of edge effects for multiple edges from a dense network of narrow (3-8 m wide) linear disturbances called 'seismic lines'. Seismic lines are created during oil and gas exploration and are responsible for severe dissection of boreal forests in western Canada. The objectives were to: (1) compare the edge influence of "wide" (~8 m) and "narrow" (~3 m) seismic lines on vegetation abundance and diversity; and (2) to determine whether edges in close proximity show interaction of edge influences, i.e., do multiple narrow seismic lines have a stronger or weaker edge influence than a single narrow seismic line. We sampled vegetation along transects perpendicular to seismic lines in treed moderate-rich and poor fens. We used randomization tests of edge influence to calculate the magnitude and distance of edge effects. In moderate-rich fens, we found a positive edge influence on understory diversity from both wide and narrow seismic lines. We also found a weakening edge interaction on diversity, i.e., single narrow seismic lines had a stronger edge influence on diversity than multiple narrow seismic lines. In treed poor fens, multiple narrow seismic lines had a negative

edge effect on tree density, understory abundance, richness, and composition. In addition, we found strengthening edge interactions in treed poor fens on tree density, graminoid cover, and understory composition. Our results show the importance of assessing the edge influence of multiple disturbances in order to capture the cumulative effects of habitat fragmentation.

2.2 Introduction

Edge influences, also called edge effects, are the ecological changes that occur at the interface of a forest patch and the adjacent non-forested area. They can be a major driver of changes in forest structure (e.g., increased sapling density and plant diversity at the edge) and are associated with forest fragmentation (Fahrig 2003). For example, in western Canada's boreal forests, seismic lines—linear corridors of cleared forests (approx. 3-8 m wide) used for oil and gas exploration (Lee and Boutin 2006; Dabros et al. 2018)—are one of the main causes of forest dissection and can be found at densities, as high as 40 km/km^2 in some areas (Pattison et al. 2016). Edge effects from these linear disturbances are estimated to dominate the region despite seismic line footprints making up only 6% of the region (Riva and Nielsen 2020).

Edge influence can be quantified using two components: magnitude of edge influence (MEI) and distance of edge influence (DEI). Magnitude of edge influence (MEI) describes how much a parameter at the edge differs from values at the interior forest, while distance of edge influence (DEI) describes how far a significant difference between edge and interior forest extends from the edge into the forest (Harper et al. 2005). In the boreal forest, the extent of edge influence on vegetation is typically less than in temperate and tropical forests (Harper et al. 2015). This has been attributed to the shorter canopy height, inherent heterogeneity of forest types and canopy cover in the landscape, and frequent natural disturbances (Harper et al. 2015).

Though edge effects are well-studied, extrapolating their influence across landscapes has been limited by knowledge gaps in edge ecology, including a paucity of studies on how multiple edges interact (Ries et al. 2004, 2017; Porensky and Young 2013). In the boreal forest, Harper et al. (2007) examined the interaction of edge influences of large openings—i.e., harvest blocks and lakes, but little else has been done. Here, I take advantage of the highly dissected boreal landscape in western Canada to examine interactions of edge influence from the dense network of seismic lines. I focus on the impacts on vegetation as it is an important component of forest biodiversity and because it plays several key ecological roles: e.g., nutrient cycling, hydrologic cycle, provision of habitat, and influences forest regeneration (Nilsson and Wardle 2005).

There are two types of seismic lines: conventional seismic lines and low-impact seismic lines. Historically, conventional seismic lines (approximately 4-12 m wide) were created by using bulldozers to clear vegetation and were spaced at approximately 300-500 m intervals (Dabros et al. 2018). These conventional seismic lines are now increasingly being replaced with low-impact seismic lines, to mitigate the environmental impacts of oil exploration in the boreal. Low-impact seismic lines are narrower, approximately 3 meters wide, and involve lighter equipment, thus resulting in less soil disturbance (Dabros et al. 2018). Despite being quite narrow, low-impact seismic lines have still been shown to exhibit edge influence on understory vegetation (MacFarlane 2003; Dabros et al. 2017). In addition, low-impact seismic lines are placed at a much higher density (50-100 m apart) than conventional lines (Dabros et al. 2018); this could lead to a larger overall impact on the remaining forest than conventional seismic lines which, although wider, are more spaced out. In this study, I explore how edge influence changes when two lines are in proximity to each other compared to situations of single edges that have been more commonly studied.

The first objective was to compare the edge influence of conventional seismic lines (hereafter referred to as "wide" seismic lines) versus the more recent low-impact seismic lines (hereafter referred to as "narrow" seismic lines). I focused on the edge influence on understory vegetation in treed peatlands, as seismic lines in these ecosites are particularly long-lasting (van Rensen et al. 2015) and peatlands dominate large parts of northern Alberta (~65% of the oil sands region). Wide seismic lines have stronger changes in abiotic conditions, e.g., higher light intensity and air temperatures, and a higher DEI on micro-climatic conditions than narrow seismic lines (Stern et al. 2018; Franklin et al. 2021a). I thus expected wide seismic lines to have a higher DEI on vegetation compared to narrow seismic lines. The second objective was to determine if there is an interaction of edge influence when two narrow seismic lines are in close proximity. There are three possible outcomes when multiple edges are present: i) no edge interaction; i.e., the presence of a second edge does not alter the edge influence of a single edge, ii) strengthening interaction, the presence of a second edge strengthens the edge influence of a single edge, and iii) weakening interaction, the presence of a second edge weakens the edge influence of a single edge (Harper et al. 2007; Porensky and Young 2013). I expected a strengthening interaction on vegetation abundance as increased light availability from the higher density of linear disturbances would promote an even stronger increase in vegetation abundance. However, I expected a weakening or no edge interaction on plant diversity. This is based on an expectation of higher species diversity at edges as disturbance-adapted species are able to establish near the edge as an added component to the existing "interior" community (Ries et al. 2017). I expected that a higher density of disturbances would change conditions to the point where they are no longer suitable for "interior" species, thus leading to losses in interior species. This would counter any increase in species diversity associated with the ingress of edge-adapted

12

species, leading to a weakening edge interaction on plant diversity (i.e., when there are multiple edges, diversity at the edge is similar to the interior fen).

2.3 Methods

2.3.1 Study area

This study was conducted in treed peatlands approximately 50 km south of Fort McMurray, Alberta, Canada (56°23'4.32"N, 111°35'13.52"W). Mean annual temperature in the region is 1°C with an average annual precipitation of 418.6 mm (Environment and Climate Change 2013); from nearby meteorological station: Fort McMurray). Overstory trees were dominated by black spruce (*Picea mariana (Mill.) B.S.P.*) or tamarack (*Larix laricina* (Du Roi) K. Koch) or a mixture of both.

2.3.2 Data collection

Using GIS layers of forest type and linear disturbances, I identified sites with single wide, single narrow, and a grid of narrow seismic lines in treed peatlands. Of these, I chose one grid of seismic lines (over an area of 32 km^2) to maintain similar disturbance history between line types. In the field, seismic lines and their adjacent fens were classified as poor fens, or moderate-rich fens based on the vegetation (Beckingham and Archibald 1996). Sampled seismic lines were created 12 (8 lines) or 17 years (5 lines) before sampling (in 2005 or 2000). The seismic lines still had not developed any overstory trees at the time of sampling. Seismic lines ranged in width from 4 to 12 m for conventional wide seismic lines and 1.5 to 3 m wide for low-impact narrow seismic lines. Sampling occurred from late June to mid-August 2017.

I established multiple transects from a seismic line into the adjacent treed peatland for each of three treatments: i) "single wide" seismic line into the adjacent treed peatland (n = 5 in moderate-rich fens, n = 7 in poor fens), ii) "single narrow" seismic line into the adjacent treed

13

peatland (n = 6 in moderate-rich fens, n = 5 in poor fens), and iii) "multiple narrow", from a narrow seismic line to the nearest parallel narrow seismic line (n = 14 for each peatland type) (Appendix 2.1). Since seismic lines extend over long distances (10's of kms), there were a limited number of available seismic lines in treed fens that were adjacent to undisturbed treed peatland, especially narrow seismic lines that are clustered. Thus, for all line types, a given seismic line may have multiple transects (Appendix 2.1), but all were at least 100 m apart. Transects were also established to be at least 100 m from any other large disturbance (i.e., other wide seismic lines, well pads, or roads). Sampled seismic lines were oriented either N-S or E-W. For the E-W seismic lines, transects always went north of the seismic line (i.e., edge aspect was south-facing), while transects on N-S seismic lines always went west of the seismic line (edge aspect was east-facing). Transect orientation was kept consistent to minimize variation in edge influence due to differences in edge direction (orientation). These orientations were selected based on what was available in the sampling area, i.e., narrow seismic lines in the sampling area were always south or west of the adjacent undisturbed treed peatland.

To characterize vegetation on the seismic lines, two sampling points were established 1.4 m apart on the line and to either side of the starting point of each transect, for all three treatments. For the single wide and single narrow treatments, sampling locations were established at 1 m, 2.5 m, 5 m, 10 m, 15 m, 20 m, 25 m, 35 m, 50 m, and 75 m from the edge of the seismic line into the forest, with plots centered on these locations (Appendix 2.2). For the multiple narrow treatment, sampling points were established at 1 m, 2.5 m, 5 m, 10 m, 15 m, 25 m from the edge of both the starting and ending seismic line (Appendix 2.2). Further distances were not considered since some seismic line spacing was only 50 m. In one multiple narrow

transect, the distance between the two seismic lines was too small to allow for even a 25 m sampling location.

At each sampling location, percent cover of each species of understory vascular plant was visually estimated in 1 m^2 circular plots (Appendix 2.2). Nomenclature follows Moss (1983; Appendix 2.3). Canopy cover was estimated at the center of each plot using a convex spherical densiometer; measurements were made in each of the four cardinal directions and values averaged (Lemmon 1956).

Tree density and tree basal area were measured in plots (2 m by 4 m in size), with the long axis of these plots perpendicular to the edge. For the single wide and single narrow treatments these tree plots were placed along the transect at 0-4 m, 4-8 m, 8-12 m, 13-17 m, 23-27 m, 33-37 m, 48-52 m, 73-77 m from the seismic line (Appendix 2.2). For the multiple narrow treatment, tree plots were placed along the transect at 0-4 m, 4-8 m, 8-12 m, 13-17 m, 23-27 m from each seismic line (Appendix 2.2). Thus the 1 m and 2.5 m sampling locations for vascular understory vegetation were located within the same tree plot. Within each tree plot, we recorded the diameter at breast height at 1.3 m height (DBH) and species of all trees (for trees with DBH >1 cm) and calculated tree basal area and tree density for each plot.

2.3.3 Statistical analysis

Understory response variables of interest were species richness, Shannon's diversity, Simpson's diversity, short shrub cover (< 1 m tall; excluding tree species), forb cover, graminoid cover, and community composition (see paragraph below). Hill's numbers were used for the diversity indices, as they are in units of effective number of species (Hill 1973; Jost 2006). Shannon's diversity was calculated as the exponent of Shannon's entropy, while Simpson's diversity was calculated as the inverse of the Gini-Simpson index (Hill 1973; Jost 2006).

Overstory response variables were total tree density and tree basal area. The two site types (poor fen, moderate-rich fen) were analyzed separately since preliminary analysis showed that they responded differently. To characterize seismic line conditions, I compared understory abundance, diversity, and composition on wide and narrow seismic lines to the reference "interior" conditions, using the randomization test of edge influence (RTEI) excel program by Harper and Macdonald (2011; $\alpha = 0.10$). For this analysis, I was primarily interested in the effect of seismic line width, thus the seismic line plots from both the single narrow and multiple narrow treatments were combined.

Distance and magnitude of edge influence (MEI) were determined by running the RTEI analyses for each treatment type separately. MEI was calculated as $(\bar{e} - \bar{i})/(\bar{e} + \bar{i})$, where $\bar{e}$ is the average value at a given distance from the edge and $\bar{i}$ is the average value for the interior reference sites (Harper and Macdonald 2011). For all analyses, the 75 m plots from the single narrow and single wide treatments were used as reference interior plots; thus, edge effects for each treatment were quantified using the same reference interior dataset. The 75 m plots were used as representative of "interior" treed fen conditions because it has been shown that edge influence on vegetation in Canadian boreal forests rarely extends past 20 m and the maximum observed DEI reached 60 m (Harper et al. 2015). In addition, it is difficult to ensure a consistent site type and avoid other disturbances beyond 75 m. Significant edge influence was indicated by two or more consecutive (or separated by one distance) significant MEIs ($\alpha = 0.10$). I chose this alpha level to minimize the risk of missing an edge influence due to our study's lower power after splitting transects out by peatland type. To test the edge influence on community composition, I first conducted non-metric multidimensional scaling (NMDS) ordinations. For the NMDS, species that occurred in less than 5% of the plots for a given site type were excluded. I

then ran the RTEI analyses on the NMDS coordinates (axes 1 and 2). Following on initial results for edge effects on diversity in the treed moderate-rich fen site type, I undertook additional analyses to explore edge influence on the cover of the eleven most dominant species: *Ledum groenlandicum* (Oeder), *Smilacina trifolia* (L.) Desfontaines, *Rubus chamaemorus* (L.), *Picea mariana* (< 1 m tall), *Betula pumila* (L.)(< 1 m tall), *Salix planifolia* (Pursh), *Vaccinium vitis-idaea* (L.), *Oxycoccus microcarpus* (Turczaninow ex Ruprecht), *Carex aquatilis* (Wahlenberg), *Salix pedicellaris* (Pursh), and *Larix laricina* (< 1 m tall). I did not test the edge interaction (see below) on the cover of dominant species as I only examined these variables to explain the diversity trends I found. Since there were no significant edge effects on diversity in treed poor fens, I did not test the edge influence on individual species cover in poor fens.

For variables exhibiting an edge influence in either the single narrow or multiple narrow treatments, I tested for the presence of an edge interaction by using Welch's t-test to compare the average values of a response variable at each distance between these two treatments ($\alpha = 0.05$). No significant differences between the two treatments indicated no edge interaction. I defined a strengthening edge interaction as when the difference between the multiple narrow treatment and interior reference sites was greater than the difference between the single narrow treatment and interior sites, e.g. if both treatments had a positive edge influence and the average value at a given distance was higher at the multiple narrow treatment than at the single narrow treatment. In contrast, a weakening edge interaction was when the difference between the multiple narrow treatment and interior reference sites was less than the difference between the single narrow treatment and reference sites. When necessary, data were $\log_{10}$-transformed to ensure normality prior to analysis by Welch's t-test (NMDS 1st axis and tree density). The graminoid cover data

17

could not be normalized; therefore, these data were $\log_{10}$-transformed, to ensure homogeneity of variance, and then analyzed using a Wilcoxon rank sum test.

2.4 Results

2.4.1 Vegetation characteristics of seismic lines

In both peatland types, wide seismic lines tended to differ more as compared to the reference interior than narrow seismic lines, although there were notable differences for both types of seismic lines (Table 2.1). For both poor fens and moderate-rich fens, canopy cover was, as expected, significantly lower on both the narrow and wide seismic lines than in the reference interior treed fen (Table 2.1). In addition, for both site types graminoid cover was significantly higher on the wide seismic lines compared to the reference interior but did not differ between narrow seismic lines and the reference (Table 2.1). In poor fens, short shrub cover on both wide and narrow seismic lines was significantly higher than in the interior treed fens (Table 2.1). Only wide seismic lines had higher short shrub cover than the reference fen, while narrow seismic lines did not differ from the reference in moderate-rich fens, (Table 2.1). In poor fens, species richness, Shannon's diversity, and Simpson's diversity were significantly higher on wide seismic lines compared to the reference fen, while narrow seismic lines did not differ from the reference (Table 2.1). In moderate-rich fens, both wide and narrow seismic lines had significantly higher species richness and Shannon's diversity than the reference fen (Table 2.1). In contrast, Simpson's diversity in moderate-rich fens was significantly higher on narrow seismic lines compared to the reference fen but did not differ between wide seismic lines and the interior fen (Table 2.1). Community composition on wide seismic lines was also significantly different from the interior treed fen for both peatland types (based on scores on axis 1 and/or 2 of the NMDS) but did not differ between narrow seismic lines and the interior fen (Table 2.1). In both peatland

18

types, total understory cover and forb cover did not differ between either wide or narrow seismic lines and the reference interior fen (Table 2.1).

2.4.2 Edge influence from wide and narrow seismic lines

As expected, edge effects were minimal for the single narrow seismic line treatment. In moderate-rich fens, the single narrow treatment had a significant positive edge influence on Shannon's diversity of understory species from the seismic line to 2.5 m from the edge and from 15 to 25 m from the edge (Figure 2.1B, Appendices 2.4, 2.5). The single narrow treatment also had a significant positive edge influence on Simpson's diversity from 15 m to 25 m from the edge (Figure 2.1C, Appendices 2.4, 2.5). Similarly, the single wide treatment in moderate-rich fens had a significant positive edge influence on species richness (depth of edge influence (DEI) = 5 m to 20 m), Shannon's diversity (DEI = 1 m to 50 m), and Simpson's diversity (DEI = 5 m to 35 m; Figure 2.1, Appendices 2.4, 2.5). There was no significant edge influence on species richness for single narrow seismic lines (Appendices 2.4, 2.5).

In moderate-rich fens, both the single narrow and single wide treatments had a significant positive edge influence on the cover of *Salix planifolia* (Figure 2.2, Appendices 2.6, 2.7). For the single narrow treatment, DEI was from 5 m to 20 m, while for the single wide treatment, DEI was from 2.5 m to 20 m (Figure 2.2, Appendices 2.6, 2.7). The single narrow treatment also had a significant positive edge influence on *Smilacina trifolia* (DEI = 1 m to 25 m) and a negative edge influence on *Rubus chamaemorus* (DEI = 1 to 5 m; Figure 2.2, Appendices 2.6, 2.7). There was no significant edge influence for either the single wide or single narrow treatments in moderate-rich fens for any other variables (Figure 2.2, Appendices 2.4, 2.6).

19

In poor fens, the only significant edge influence for the single narrow treatment was on community composition, with DEI from 25 m to 50 m (Appendices 2.8, 2.9). There was no significant edge influence for the single wide treatment for any variables (Appendix 2.8).

2.4.3 Interaction of edge influence

For multiple narrow lines in moderate-rich fens, we found a significant negative edge influence on the cover of *Salix pedicellaris* (DEI = 5 m to 15 m) and *Larix laricina* (< 1 m tall; DEI = 1 m to 25 m; Figure 2.2, Appendices 2.6, 2.7). The multiple narrow treatment did not have significant edge influence on any other variables (Appendices 2.4, 2.6). Because Shannon's and Simpson's diversity had a significant edge influence for the single narrow treatment, we tested for interaction of edge effects by comparing mean values between the single narrow and multiple narrow lines. We found a weakening edge interaction at 15 m for both Shannon's and Simpson's diversity, i.e., the average values for the single narrow treatment were higher than for the multiple narrow treatment, and for the reference site (Table 2.2, Figure 2.1).

In contrast, we found a strengthening edge interaction on both the overstory and understory in treed poor fens. The multiple narrow treatment had a significant positive edge influence on tree density, up to 27 m from the edge (Appendices 2.8, 2.9), with a significant strengthening edge interaction at 17 m and 27 m (Table 2.2, Figure 2.3). The multiple narrow treatment also had a significant edge influence on understory composition, from 1 m to 25 m from the edge (Appendices 2.8, 2.9). For understory composition, there was a significant strengthening edge interaction 5 m from the edge (Table 2.2). The multiple narrow treatment had a significant negative edge influence on species richness (DEI = 5 m to 25 m), understory cover (DEI = 2.5 to 15 m), forb cover (DEI = 2.5 to 25 m), and graminoid cover (DEI = 1 m to 25 m; Figures 2.3, 2.4, Appendices 2.8, 2.9). There was a strengthening edge interaction on graminoid

20

cover at 1 m, 5 m, and 15 m from the edge (Table 2.2). In contrast, understory cover, forb cover, and species richness did not show significant differences between the multiple narrow and single narrow treatments for any distance; this suggests there were no interactions of edge influence for those variables (Table 2.2). There was no significant edge influence on the other variables from the multiple narrow treatments (Appendix 2.8).

2.5 Discussion

Seismic lines were generally characterized by lower canopy cover, higher short shrub and graminoid cover, and higher vascular plant diversity compared to the interior treed fens. Both edge influence and edge interaction varied between the site types. In moderate-rich fens, wide seismic lines had a higher DEI on understory diversity than narrow seismic lines and there was a weakening edge interaction on understory diversity. In contrast, both seismic line types had limited edge influence on understory communities in poor fens and there was a strengthening edge interaction on vegetation abundance in poor fens.

2.5.1 Edge type

Between the wide and narrow seismic lines, I had expected that the wide seismic lines would have a higher DEI on vegetation due to their stronger effects on abiotic conditions (Stern et al. 2018; Franklin et al. 2021a). However, this hypothesis was only supported in the moderate-rich fens, as edge influence did not strongly differ between line types in poor fens. In moderate-rich fens, single seismic lines had a positive edge influence on richness and diversity, regardless of line width. Depth of edge influence was higher for single wide seismic lines, up to 50 m from the edge, compared to single narrow seismic lines, where edge influence was limited to 25 m from the edge. Despite the continued open conditions found on seismic lines 12-17 years after their creation, edge effects into adjacent fens in the poor fen type were quite limited, regardless

21

of line width (wide or narrow). We only observed edge influence on community composition for single narrow seismic lines in poor fens

In contrast to our results, Dabros et al. (2017) found that in upland, black spruce-lodgepole pine dominated stands, narrow seismic lines had a negative and shallower edge influence on herbaceous plant diversity (DEI = 15 m) and cover (DEI = 5 m). This contrast may be due to differences in site type and in time since disturbance: they sampled three years after seismic line creation whereas we sampled lines more than 10 years after seismic line creation that were still open.

In moderate-rich fens, the observed increased diversity was likely a response to increased resource availability from the seismic line opening (Ries et al. 2004, 2017). Specifically, the seismic line opening could increase abundance of edge-adapted species that would be favored by increased light (Dawe et al. 2017; Stern et al. 2018; Franklin et al. 2021a) or increased pollinators (Riva et al. 2018, 2020; Nelson et al. 2021), and likely seed dispersers. However, this could also lead to shade-tolerant or interior species being out-competed at the edge of the seismic line; we found evidence of this in that *Rubus chamaemorus* had lower abundance at the edge of the single narrow treatment. Thus, the highest species diversity was found ~5 m to 25 m from the edge of seismic lines, as this is most likely where both edge-associated and interior species currently co-exist. Our analysis of the dominant species showed *Salix planifolia* and *Smilacina trifolia*—generalist fen species—increased at the edges of seismic lines. Finnegan et al. (2018) also found higher *Salix* spp. abundance on wide seismic lines in wetlands in western Alberta's foothills boreal forests, while Dabros et al. (2017) also found that *Rubus chamaemorus* cover was lower at the edge of narrow seismic lines in upland black spruce-lodgepole pine dominated stands. The harsh, acidic growing conditions found in poor fens may have limited or prevented

the increase of edge-adapted species, thus the lack of a positive edge influence on diversity in poor fens.

The limited edge influence on overstory and understory abundance for both single narrow and single wide seismic lines in poor fens was unsurprising due to the narrow nature of seismic line openings, the low patch contrast between these opening and the adjacent forest, and the inherent heterogeneity in treed peatlands. Our findings support Harper et al.'s (2005) hypotheses that reduced patch contrast and a heterogeneous landscape will lead to lower magnitude and distance of edge influence. Treed peatlands are characterized by a shorter canopy height (~8-10 m) and sparser tree cover than upland forest types (Coops et al. 2016; Guo et al. 2017; Mao et al. 2019), which results in a low patch contrast between the seismic line and the adjacent undisturbed peatland. In addition, treed peatlands here are interspersed with graminoid- and shrub-dominated fens, which lack an overstory of trees. Thus, the seismic lines are similar to tree-less fens and the plant communities we studied are either adapted to both habitats or to canopy openings. In drier black spruce forest stands, Harper et al. (2016) found that edge influence from harvesting decreased over time, with edge influence on forest structure and understory composition only extending 5 m into the adjacent forest, 16 years after harvest (but see Dupuch and Fortin 2013 for edge expansion 60 years after harvest). Based on this, it is unsurprising that we found limited edge influence from a much smaller disturbance.

2.5.2 Edge interaction

As expected, edge interaction was evident in both site types and the direction of the interaction differed between response variables. I hypothesized there would be a weakening edge interaction on diversity, however this was only observed in moderate-rich fens, 15 m from the edge. This weakening edge interaction on understory diversity may be due to the loss of

23

'interior' species, as multiple narrow seismic lines also had a negative edge influence on *Salix pedicellaris* and *Larix laricina* abundance, up to 25 m from the edge. I also expected a strengthening edge interaction on abundance, which I only observed in poor fens. In poor fens, there was a strengthening edge interaction for tree density (i.e., compared to both the reference forest and the single narrow treatment, the multiple narrow had higher tree density) (from 13 m to 27 m from the edge), graminoid cover (1 m, 5 m and 15 m from the edge), and understory composition (5 m from the edge). Additionally, multiple narrow seismic lines had a positive edge influence on tree density, negative edge influence on total understory cover, forb, and graminoid cover, species richness and an edge influence on community composition in poor fens. Distance of edge influence on forb and graminoid cover, species richness, understory composition, and tree density extended up to 25 m from the edge, and to 15 m for total understory cover.

The increase in conifer tree density at the edge of the multiple narrow seismic lines in treed poor fens would have resulted in lower light availability than in the reference interior, which in turn might explain the observed negative edge influence on understory, forb, and graminoid cover, species richness and the edge influence on community composition. Similarly, in upland coniferous stands, Dabros et al. (2017) found light availability was lowest 5 m from a single narrow seismic line and herbaceous cover was reduced 2-5 m from the seismic line; they attributed this to observed (but unquantified) increased tree canopy cover at the edge of the seismic line. However, we found multiple narrow seismic lines had a greater distance of edge influence on understory cover (DEI to 15 m), forb and graminoid cover, species richness, and composition (DEI to 25 m) in treed poor fens compared to Dabros's findings for single narrow seismic lines in upland stands.

We hypothesize that the increase in tree density at the edge is due to increased layering by the surrounding black spruce trees. Studies on regeneration following strip clear-cutting have found increased production of black spruce layers post-harvest, driven by increased soil temperature and reduced competition from shrubs and parent trees (Pothier 2011; Prévost and Dumais 2018). We may be seeing the same effect in seismic lines, which have been shown to have higher soil and air temperatures than in adjacent forests (Dabros et al. 2017; Franklin et al. 2021a). It is possible that the removal of trees and increase in resource availability associated with construction of a single narrow seismic line failed to trigger a strong response in vegetative growth, but proximity to multiple seismic lines stimulated a significant increase in black spruce layering.

It is also possible that the area between multiple narrow seismic lines may be experiencing a surface drying effect, which the single seismic lines may not have; this could explain the strengthening edge interaction on tree density in poor fens. This drying effect, coupled with increased light availability at the edge, may create abiotic conditions suitable for increased tree growth or increased layering, similar to that observed by Dabros et al. (2017) and MacFarlane (2003) at the edges of wide and narrow seismic lines in upland stands. We believe this surface drying between multiple narrow seismic lines could be contributing to the edge interactions observed in moderate-rich fens. As hypothesized, we found that single seismic lines had a positive edge influence on diversity in moderate-rich fens, but multiple narrow seismic lines did not have an edge influence on diversity. This weakened edge influence on plant diversity for multiple narrow seismic line edges could be due to surface drying causing a general loss of species with wetter habitat preferences and limiting any increase in edge-associated fen species. This is evident in the decline in species such as *S. pedicellaris* and *L. laricina* at the

edges of the multiple narrow treatment, with no accompanying increase in cover of *S. planifolia* and *S. trifolia*, as was observed at the edges of the single seismic lines. Future studies should verify this by examining how multiple seismic lines affect peatland hydrology (see Braverman and Quinton 2016 for the hydrological impacts of seismic lines in a zone of discontinuous permafrost). Our study is focused on one region of narrow seismic lines and has relatively low sample sizes. Additional research should build on these results by exploring these effects for other narrow seismic lines in various site types.

In general, Dabros et al. (2017) found edge influence from a single narrow seismic line did not extend past 15 m from the seismic line. We found deeper edge influence: single wide seismic lines had a DEI of up to 50 m in moderate-rich fens, single narrow seismic lines had a DEI of 25 m in moderate-rich fens and between 25 to 50 m in poor fens, and multiple narrow seismic lines had a DEI of at least 25 m from the seismic line in both poor and moderate-rich fens. Interestingly, these distances of edge influence are also larger than that of edges from harvesting, a much larger disturbance (Harper et al. 2016), and may be due to treed peatlands being more sensitive to disturbances compared to upland forests. Since edge influence can change over time (Ries et al. 2004; Dupuch and Fortin 2013; Harper et al. 2016), additional research is needed to explore how these distances of edge influence and evidence of edge interaction may change over time, in particular as the vegetation on the seismic line changes.

As previous studies have noted, extrapolating edge influences to landscape scales requires a better understanding of edge interactions (Porensky and Young 2013; Ries et al. 2017). Our study shows that though smaller (narrower) disturbances may not have an edge influence when they occur singly, the edge interaction from multiple small disturbances results in a much larger edge influence. This highlights the need for more studies on edge interaction. Our

results address another piece of the puzzle on the cumulative effects of landscape dissection from oil and gas extraction in the boreal forest. Although total forest conversion is low in the region (~6% loss), it is the dissection of habitats by linear disturbances that has the largest potential effect on the region's biodiversity when considering their edge effects (Riva and Nielsen 2020). And although low-impact seismic lines were designed to mitigate the negative environmental impacts of conventional seismic lines, placing them at high densities that occur in areas of concentrated oil sands developments may detract from their benefits.

Table 2.1: Comparisons of vegetation variables (means and in parentheses standard errors) on narrow and wide seismic lines against the reference "interior" treed fen sites for poor and moderate-rich fens. Significant differences between the seismic line and the reference (as determined by a significant magnitude of edge influence) is indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$.

Response variable	Poor fens			Moderate-rich fens		
	Wide SL	Narrow SL	Reference	Wide SL	Narrow SL	Reference
Canopy cover	***23.0***	***32.5***	61.4	***24.1***	***34.1***	58.8
	(3.2)	***(2.3)***	(5.3)	***(4.3)***	***(2.8)***	(6.1)
Understory cover	34.0	33.7	29.3	38.4	34.5	29.0
	(2.0)	(3.0)	(3.0)	(2.4)	(2.2)	(5.7)
Forb cover	14.0	12.2	12.9	14.6	14.7	13.7
	(0.9)	(1.1)	(2.1)	(1.8)	(1.4)	(3.7)
Graminoid cover	***3.0***	0.7	0.6	***5.1***	2.9	1.9
	(0.5)	(0.2)	(0.2)	***(0.6)***	(0.6)	(0.6)
Short shrub cover	**15.9**	***20.0***	10.3	***18.3***	15.9	10.9
	(2.3)	***(3.3)***	(1.5)	***(1.6)***	(2.2)	(2.1)
Species richness	***14.1***	8.3	8.5	***16.5***	**12.2**	9.8
	(0.7)	(0.4)	(1.0)	***(1.4)***	**(0.8)**	(1.0)
Shannon's diversity	***7.9***	4.5	4.9	***8.2***	**7.4**	5.6
	(1.0)	(0.4)	(0.7)	***(0.6)***	**(0.6)**	(0.5)
Simpson's diversity	**5.9**	3.5	3.8	5.3	**5.7**	4.3
	(0.9)	(0.3)	(0.6)	(0.4)	**(0.5)**	(0.4)
NMDS 1	***-0.6***	-0.1	-0.2	***-0.6***	-0.1	0.1
	(0.1)	(0.1)	(0.2)	***(0.1)***	(0.1)	(0.2)
NMDS 2	-0.1	0.0	-0.1	***-0.2***	-0.1	0.2
	(0.2)	(0.1)	(0.1)	***(0.1)***	(0.1)	(0.1)

Table 2.2: Results of edge interaction tests. Edge interaction was evaluated by comparing average values at a given distance between the single narrow and multiple narrow treatments ($\alpha = 0.05$) for the following variables (based on significant edge effects for either treatment – see Appendices 2.4 and 2.8): (A) Shannon's and Simpson's diversity in moderate-rich fens, (B) community composition (NMDS axes), understory cover, forb cover, graminoid cover, species richness in poor fens, and (C) tree density in poor fens. For moderate-rich fens, single narrow treatments had a positive edge influence on diversity and multiple narrow treatments had no edge influence on diversity; thus, significant differences between the two treatments would indicate a weakening edge interaction (i.e., the difference between the multiple narrow treatment and interior reference sites is less than the difference between the single narrow treatment and reference sites). In contrast, in poor fens, multiple narrow treatments had a negative edge influence on these variables and there was no edge influence from single narrow treatments; thus, significant differences between the two treatments would indicate a strengthening edge interaction (i.e., the multiple narrow treatment was more different from the reference than the single narrow was). Bolded values indicate significant differences between the two narrow treatments ($\alpha = 0.05$).

(A) Understory in moderate-rich fens		Distance from the edge of the seismic line					
		1 m	2.5 m	5 m	10 m	15 m	25 m
Shannon's diversity	t-statistic	1.33	1.78			**3.05**	1.32
	df	13.26	7.69			**14.54**	15.03
	P value	0.21	0.11			**0.008**	0.207
Simpson's diversity	t-statistic					**2.86**	1.05
	df					**12.87**	13.24
	P value					**0.014**	0.31

(B) Understory in poor fens							
NMDS 1st axis	t-statistic		-0.77	-1.02*	-1.04	-0.051	-1.53
	df		6.16	4.40	6.27	4.76	5.86
	P value		0.47	0.36	0.34	0.96	0.18
NMDS 2nd axis	t-statistic	-1.92	-1.23	**-2.78**			
	df	7.16	5.72	**8.78**			
	P value	0.10	0.27	**0.02**			
Understory cover (%)	t-statistic		1.29	1.41		1.06	
	df		4.43	4.37		5.39	
	P value		0.26	0.23		0.33	
Forb cover (%)	t-statistic		1.22	1.70	1.22	0.66	1.12
	df		5.31	5.46	4.17	6.67	4.11
	P value		0.27	0.14	0.29	0.53	0.32
Graminoid cover (%)	W statistic[+]	**54***	43*	**60***	46*	**52***	50*
	P value	**0.0547**	0.40	**0.008**	0.17	**0.047**	0.12

29

Species richness	t-statistic				1.16	1.20		1.58
(no. of species/m²)	df				4.71	5.68		6.53
	P value				0.30	0.28		0.16

| (C) Overstory in poor fens | | Distance from the edge of the seismic line | | | | |
		4 m	8 m	12 m	17 m	27 m
Tree density	t-statistic	-2.21*	-1.36*	-1.72	**-2.48**	**-3.07**
(No. of trees/ha)	df	5.99	8.47	9.64	**10.21**	**16.98**
	P value	0.07	0.21	0.12	**0.03**	**0.007**

*Log$_{10}$-transformation was applied to ensure conformation to the assumption of normality.

+ The data could not be normalized so a Wilcoxon test was used to compare the two treatments and log$_{10}$-transformation was applied to ensure homogeneity of variances.
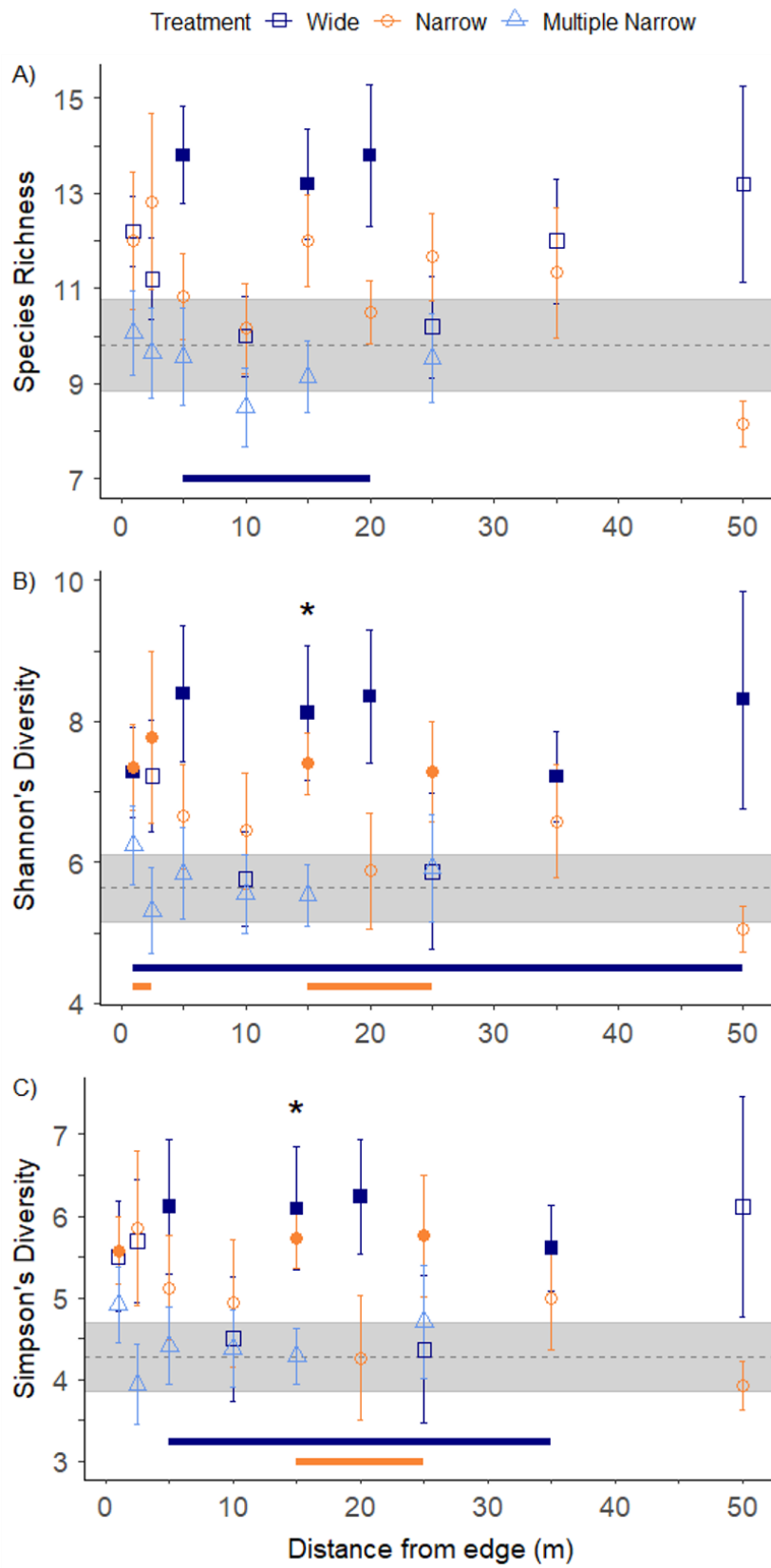
Figure 2.1: Edge effects from seismic lines in moderate-rich treed fens. Mean values for: (A) Species richness (no. of species / m^2), (B) Shannon's diversity, and (C) Simpson's diversity at each distance from the seismic line into the interior fen for each of the three treatments. Error bars represent standard error of the mean. The horizontal dashed line represents the average value for the interior treed fens, with the standard error represented by the shaded grey area. Filled symbols indicate significant magnitude of edge influence (MEI; $\alpha = 0.1$) and the solid horizontal line at the bottom indicates the distances over which there was a significant distance of edge influence (color coded by treatment). (See also Appendices 2.4 and 2.5). Asterisks represent a significant difference between the multiple narrow and single narrow treatments for that distance, indicating a significant edge interaction (see Table 2.2).
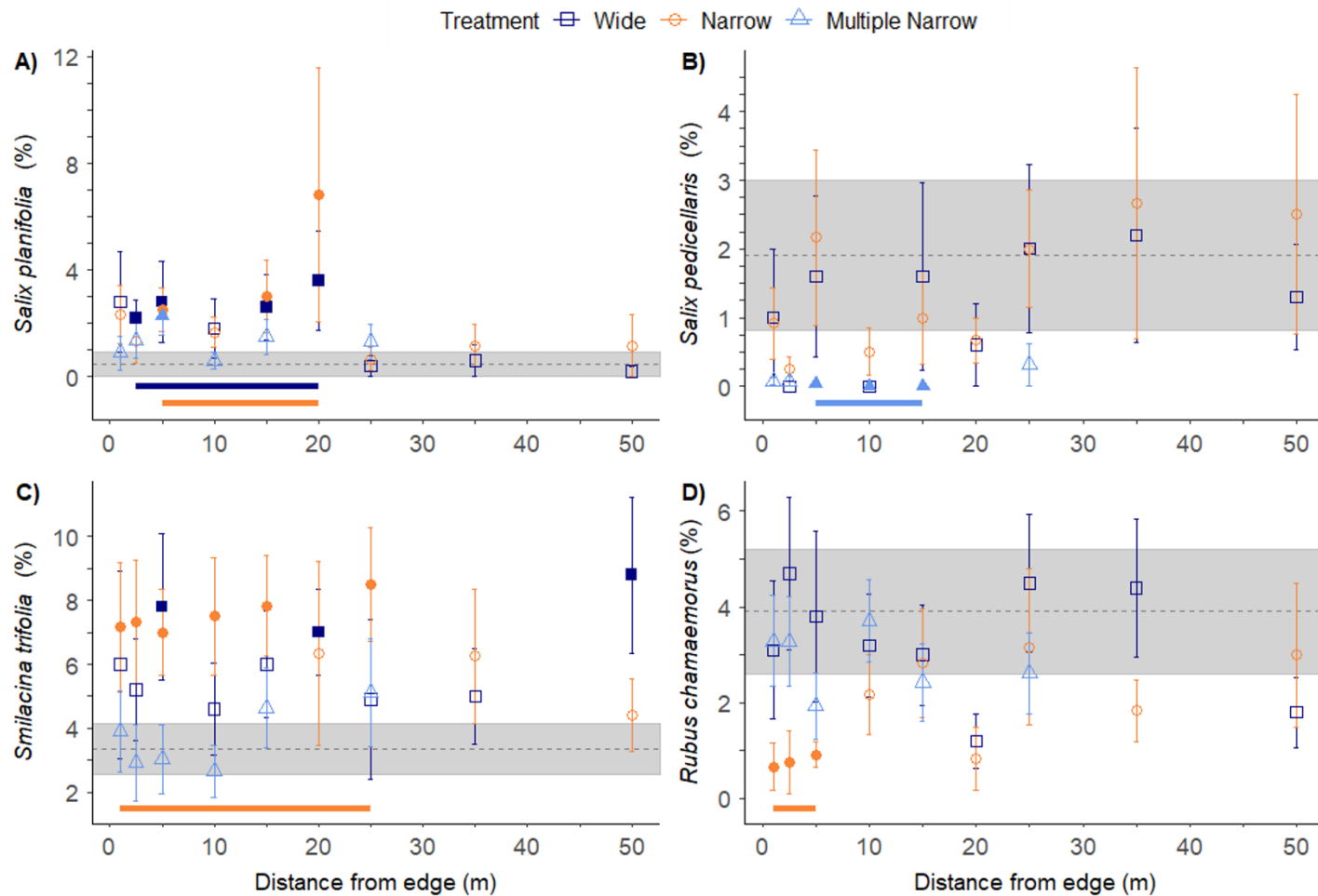
Figure 2.2: Edge effects from seismic lines in moderate-rich treed fens. Mean cover values for: (A) *Salix planifolia*, (B) *Salix pedicellaris*, (C) *Smilacina trifolia*, and (D) *Rubus chamaemorus* at each distance from the seismic line into the interior fen for the three treatments. Error bars represent standard error of the mean. The horizontal dashed line represents the average value for the interior treed fens, with the standard error represented by the shaded grey area. Filled symbols indicate significant magnitude of edge influence (MEI; $\alpha = 0.1$) and the solid horizontal line at the bottom indicates the distances over which there was a significant distance of edge influence (color coded by treatment). (See also Appendices 2.6 and 2.7).
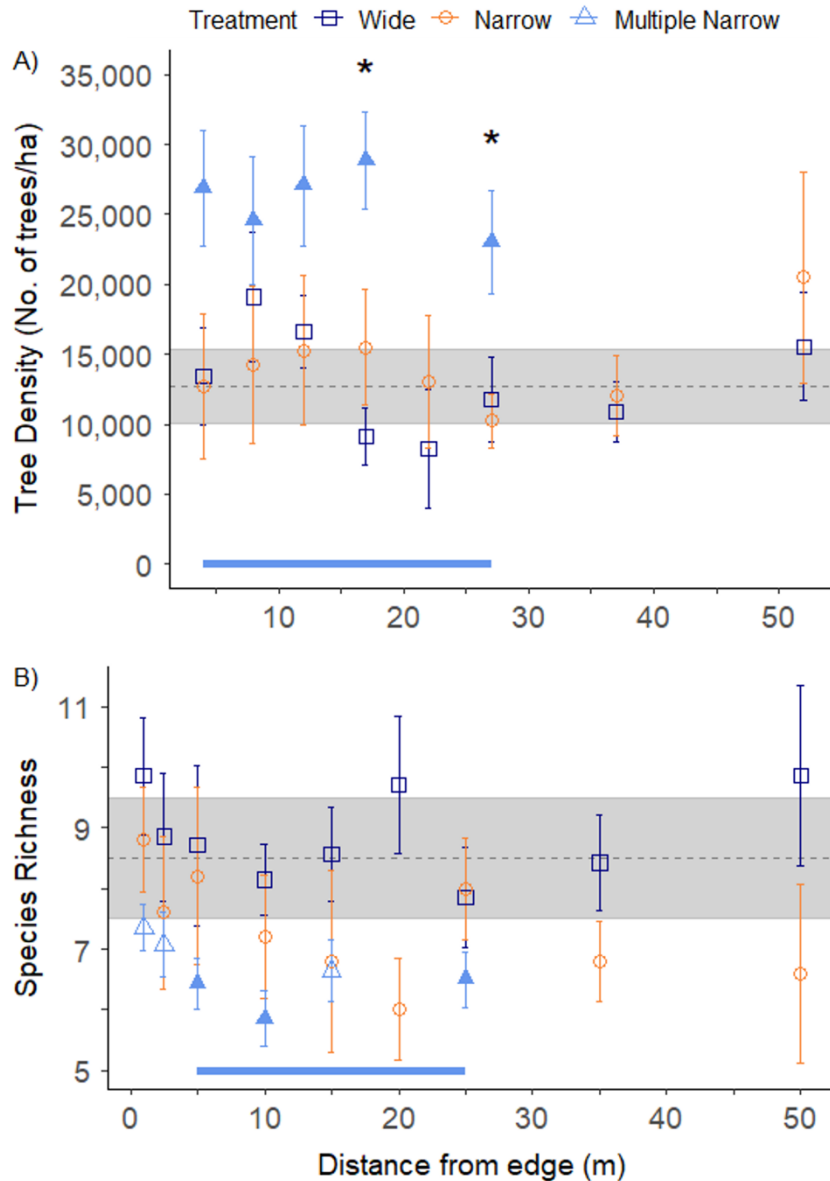
Figure 2.3: Edge effects from seismic lines in poor treed fens. Mean values for: (A) tree density (no. of trees/ha) and (B) species richness (no. of species/m^2) at each distance from the seismic line into the interior fen for the three treatment types. Error bars represent standard error of the mean. The horizontal dashed line represents the average value for the interior treed fens, with the standard error represented by the shaded grey area. Filled symbols indicate significant magnitude of edge influence (MEI, $\alpha = 0.1$) and the horizontal solid line at the bottom indicates the distances over which there was significant depth of edge influence, color coded by treatment (see also Appendices 2.8 and 2.9). Asterisks represent a significant difference between the multiple narrow and single narrow treatments for that distance, indicating a significant edge interaction (see Table 2.2).

Figure 2.4: Edge effects from seismic lines in in poor treed fens. Mean values for: (A) total understory cover, (B) forb cover, and (C) graminoid cover at each distance from the seismic line into the interior fen for the three treatment types. Error bars represent standard error of the mean. The horizontal dashed line represents the average value for the interior treed fens, with the standard error represented by the shaded grey area. Filled symbols indicate significant magnitude of edge influence (MEI, $\alpha = 0.1$) and the horizontal solid line at the bottom indicates the distances over which there was significant depth of edge influence, color coded by treatment (see also Appendices 2.8 and 2.9). Asterisks represent a significant difference between the multiple narrow and single narrow treatments for that distance, indicating a significant edge interaction (see Table 2.2).

Appendix 2.1: Location of the seismic lines sampled in Alberta, Canada. Shown are the sampling plots by treatment and ecosite (MRF = moderate-rich fen, PF = poor fen). Basemap accessed Feb. 24, 2021 (source: ESRI). Inset map shows the location of the study area in Canada (Alberta is highlighted in green).
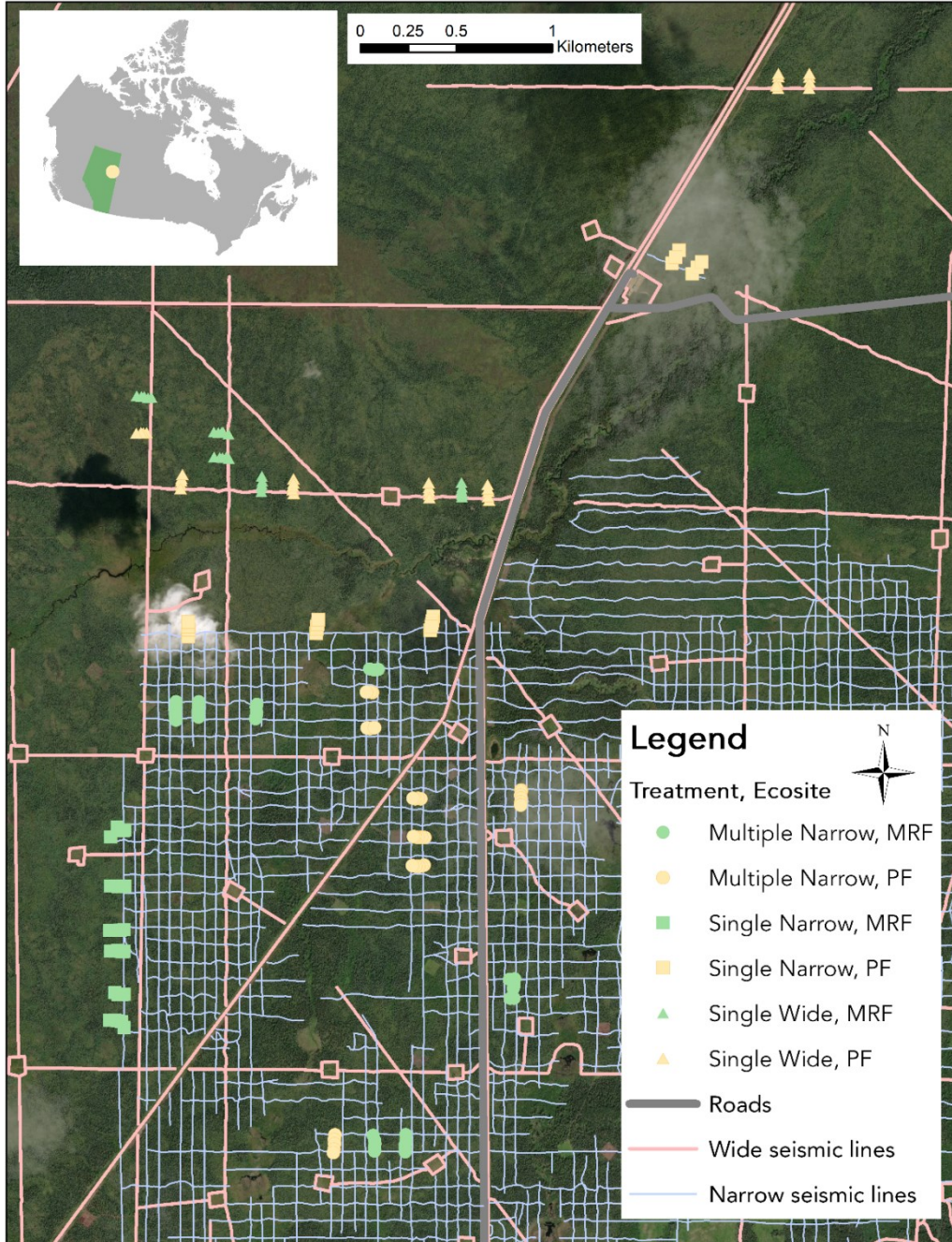
Appendix 2.2: Layout of the transects for the single wide, single narrow, and the multiple narrow treatments with the location of sampling for understory vegetation noted. The sampling location 75 m from the seismic line for the single narrow and single wide treatments were used as the reference interior treed fens. Inset illustrates the 1 m^2 circular plots (blue circles) placed on the seismic line and at each sampling distance to sample understory vegetation and the tree plot (2 m by 4 m; blue rectangle) surrounding each circular plot. The 1 m and 2.5 m circular plots were located within the same tree plot.
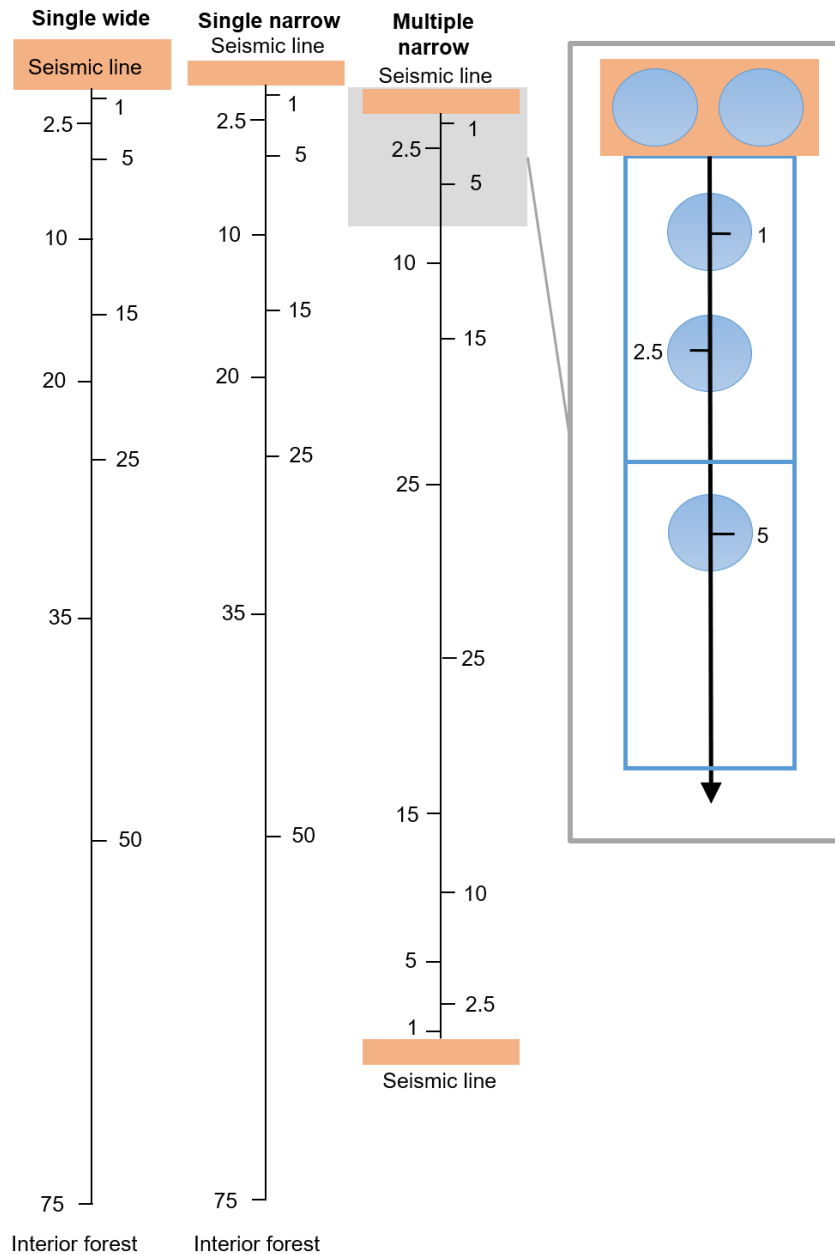
Appendix 2.3: List of species found in sites. Nomenclature follows (Moss 1983).

Scientific name	Scientific name	Scientific name
Agrostis scabris	*Equisetum palustre*	*Pyrola secunda*
Alnus rugosa	*Equisetum pratense*	*Ranunculus lapponicus*
Andromeda polifolia	*Equisetum scirpoides*	*Ribes hudsonianum*
Aster puniceus	*Equisetum species*	*Rubus acaulis*
Betula papyrifera	*Equisetum sylvaticum*	*Rubus chamaemorus*
Betula pumila	*Eriophorum species*	*Salix athabescensis*
Calamagrostis canadensis	*Eriophorum vaginatum*	*Salix bebbiana*
Calamgrostis species	*Gallium species*	*Salix discolor*
Caltha palustris	*Gaultheria hispidula*	*Salix maccalliana*
Carex aquatilis	*Geocaulon lividum*	*Salix myrtillifolia*
Carex brunnescens	*Habenaria hyperborea*	*Salix pedicellaris*
Carex canescens	*Hippuris vulgaris*	*Salix planifolia*
Carex chordorrhiza	*Kalmia polifolia*	*Salix pseudomyrsinites*
Carex deflexa	*Larix laricina*	*Salix pyrifolia*
Carex diandra	*Ledum groenlandicum*	*Salix serissima*
Carex disperma	*Linnaea borealis*	*Salix species*
Carex gynocrates	*Listera cordata*	*Smilacina trifolia*
Carex leptalea	*Lonicera villosa*	*Spiranthes rommanzoffiana*
Carex magellanica	*Luzula parviflora*	*Stellaria longifolia*
Carex species	*Lycopodium annotinum*	*Stellaria species*
Carex tenuiflora	*Menyanthes trifoliata*	*Trientalis borealis*
Carex vaginata	*Mitella nuda*	*Vaccinium caespitosum*
Chamaedaphne calyculata	*Moneses uniflora*	*Vaccinium myrtilloides*
Corallorhiza trifida	*Oxycoccus microcarpus*	*Vaccinium vitis-idaea*
Cornus canadensis	*Parnassia palustris*	*Viola nephrophylla*
Drosera rotundifolia	*Pedicularis labradorica*	
Empetrum nigrum	*Pedicularis parviflora*	
Epilobium angustifolium	*Petasites palmatus*	
Epilobium leptophyllum	*Petasites sagittatus*	
Epilobium palustre	*Picea mariana*	
Equisetum arvense	*Potentilla palustris*	
Equisetum fluviatile	*Pyrola asarifolia*	

Appendix 2.4: Magnitude of edge influence (MEI) values for (A) understory and (B) overstory response variables in treed moderate-rich fens. Results are given by treatment and distance from the seismic line influence (see Appendix 2.5 for mean and standard error values). Significant magnitudes of edge influence are indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$. Grey-shaded cells indicate the distances over which there was significant depth of edge.

(A) Understory variables in moderate-rich fens — Distance from edge of seismic line

Response variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m
Canopy cover	Single Wide	-0.095	0.022	0.047	0.076	-0.063	**-0.201**	0.014	-0.015	-0.047
	Single Narrow	-0.137	-0.134	-0.045	0.026	-0.048	-0.121	-0.100	-0.057	-0.006
	Multiple Narrow	-0.048	-0.064	0.024	0.050	0.017		-0.008		
Total understory cover	Single Wide	0.025	-0.048	0.018	-0.012	0.083	0.000	0.209	-0.010	0.003
	Single Narrow	-0.011	-0.066	-0.008	-0.042	0.047	0.015	0.058	0.027	-0.094
	Multiple Narrow	0.015	-0.003	-0.054	-0.127	-0.040		-0.108		
Forb cover	Single Wide	-0.015	-0.046	0.082	-0.105	0.002	-0.062	0.009	0.037	0.060
	Single Narrow	-0.084	-0.091	-0.121	-0.060	0.044	-0.161	0.044	-0.060	-0.216
	Multiple Narrow	-0.043	-0.053	-0.172	-0.146	-0.028		-0.052		
Graminoid cover	Single Wide	0.219	-0.031	0.090	0.068	-0.060	**0.351**	0.250	0.131	0.317
	Single Narrow	0.079	0.206	-0.070	-0.045	-0.045	0.192	0.020	0.147	-0.022
	Multiple Narrow	-0.099	-0.134	-0.035	***-0.437***	-0.184		-0.029		
Short shrub cover	Single Wide	0.102	-0.033	-0.023	0.131	0.047	0.022	-0.141	-0.038	-0.129
	Single Narrow	0.115	-0.069	0.103	0.033	0.093	0.213	0.071	0.135	0.081
	Multiple Narrow	0.032	-0.007	-0.045	-0.199	-0.069		-0.177		
Species richness	Single Wide	0.108	0.065	***0.168***	0.009	**0.146**	***0.168***	0.019	0.1	0.146
	Single Narrow	0.1	0.133	0.049	0.017	0.1	0.033	0.086	0.071	-0.091
	Multiple Narrow	0.012	-0.009	-0.012	-0.071	-0.035		-0.014		
Shannon's diversity	Single Wide	**0.127**	0.123	***0.196***	0.011	***0.180***	***0.194***	0.020	**0.122**	**0.191**
	Single Narrow	***0.132***	***0.159***	0.082	0.067	***0.135***	0.020	**0.127**	0.077	-0.053
	Multiple Narrow	0.051	-0.029	0.018	-0.007	-0.009		0.024		
Simpson's diversity	Single Wide	0.125	0.142	***0.176***	0.025	***0.174***	***0.186***	0.010	**0.134**	0.177
	Single Narrow	**0.131**	0.155	0.089	0.071	***0.145***	-0.001	**0.147**	0.077	-0.042
	Multiple Narrow	0.070	-0.041	0.016	0.011	0.000		0.047		
NMDS 1*	Single Wide	2.293	8.471	1.480	-0.071	2.145	1.598	0.404	***25.568***	1.569

	Single Narrow	1.724	1.911	2.220	-4.154	2.060	*1.385*	1.577	3.074	0.521
	Multiple Narrow	0.522	0.603	0.608	**0.733**	0.602		0.566		
NMDS 2*	Single Wide	-1.158	-1.009	-3.832	-1.135	-5.812	-0.380	***-33.184***	9.442	-0.311
	Single Narrow	-0.038	0.014	0.203	0.220	-0.380	0.286	0.289	-0.308	0.394
	Multiple Narrow	***55.362***	-0.888	-2.472	-9.622	-1.943		-4.220		

(B) Overstory variables in moderate-rich fens		Distance from edge of seismic line							
Response variable	**Treatment**	**4 m**	**8 m**	**12 m**	**17 m**	**22 m**	**27 m**	**37 m**	**52 m**
Tree basal area (m²/ha)	Single Wide	-0.084	0.117	0.265	0.137	0.075	0.101	0.150	0.047
	Single Narrow	0.153	0.040	-0.034	-0.093	-0.254	-0.133	0.006	0.107
	Multiple Narrow	0.026	-0.038	**0.271**	0.189		0.032		
Tree density (no. of trees/ha)	Single Wide	-0.142	0.031	0.1	-0.038	-0.254	-0.131	0.063	-0.088
	Single Narrow	-0.012	0.016	0.160	0.009	-0.241	-0.102	0.056	0.009
	Multiple Narrow	0.052	0.097	0.071	0.105		0.110		

* Due to the negative values of some NMDS coordinates, MEI can be more than 1 and less than -1.

Appendix 2.5: Mean (and standard error) values for (A) understory and (B) overstory response variables for sites in treed moderate-rich fens. Mean values are given for each treatment and distance combination. Reference sites represent interior treed fen conditions. Significant magnitudes of edge influence are indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$. Grey-shaded cells indicate the distances over which there was significant depth of edge influence.

(A) Understory		Distance from edge of seismic line									
Variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	Reference
Canopy cover	Single Wide	48.5 (5.5)	61.5 (7.0)	64.7 (2.8)	68.5 (6.2)	51.8 (10.1)	**39.1** **(9.4)**	60.6 (6.6)	57.1 (10.0)	53.5 (13.8)	58.8 (6.1)
	Single Narrow	44.6 (10)	44.9 (14.0)	53.7 (10)	62.0 (8.5)	53.4 (6.4)	46.1 (13.8)	48.0 (9.7)	52.5 (10.0)	58.1 (11.3)	
	Multiple Narrow	53.4 (4.7)	51.7 (6.1)	61.8 (6.8)	65.0 (5.9)	60.9 (5.3)		57.8 (6.1)			
Understory cover	Single Wide	30.5 (4.6)	26.3 (2.5)	30.1 (2.0)	28.3 (2.5)	34.3 (4.9)	29.0 (3.2)	44.4 (16.9)	28.4 (3.2)	29.2 (3.1)	29.0 (5.7)
	Single Narrow	28.3 (4.7)	25.4 (4.5)	28.5 (1.8)	26.7 (2.8)	31.9 (1.0)	29.9 (3.6)	32.6 (5.5)	30.7 (4.9)	24.0 (2.4)	
	Multiple Narrow	29.9 (3.1)	28.8 (3.0)	26.0 (4.4)	22.4 (2.3)	26.8 (2.4)		23.3 (2.3)			
Forb cover	Single Wide	13.3 (2.9)	12.5 (1.2)	16.2 (1.3)	11.1 (1.6)	13.8 (1.4)	12.1 (2.1)	14.0 (2.6)	14.8 (1.4)	15.5 (3.4)	13.7 (3.7)
	Single Narrow	11.6 (1.9)	11.4 (2.6)	10.8 (1.7)	12.2 (2.8)	15.0 (1.4)	9.9 (3.3)	15.0 (2.8)	12.2 (2.9)	8.8 (1.8)	
	Multiple Narrow	12.6 (2.1)	12.3 (2.5)	9.7 (2.1)	10.2 (1.3)	13.0 (1.6)		12.4 (2)			
Graminoid cover	Single Wide	3.0 (0.8)	1.8 (0.1)	2.3 (0.3)	2.2 (0.8)	1.7 (0.3)	**4.0** **(1.2)**	3.2 (0.8)	2.5 (0.9)	3.7 (0.9)	1.9 (0.6)
	Single Narrow	2.3 (0.5)	2.9 (1.1)	1.7 (0.5)	1.8 (0.6)	1.8 (0.5)	2.8 (0.5)	2.0 (0.3)	2.6 (1.3)	1.8 (0.8)	

(A) Understory		Distance from edge of seismic line									
Variable	**Treatment**	**1 m**	**2.5 m**	**5 m**	**10 m**	**15 m**	**20 m**	**25 m**	**35 m**	**50 m**	**Reference**
	Multiple Narrow	1.6 (0.5)	1.5 (0.5)	1.8 (0.5)	***0.8 (0.2)***	1.3 (0.3)		1.8 (0.7)			
Short shrub cover	Single Wide	13.4 (3.4)	10.2 (2.3)	10.4 (1.4)	14.2 (1.9)	12.0 (2.2)	11.4 (2.5)	8.2 (3.6)	10.1 (2.1)	8.4 (1.9)	10.9 (2.1)
	Single Narrow	13.8 (2.9)	9.5 (1.9)	13.4 (2.0)	11.7 (1.6)	13.2 (0.7)	16.8 (3.7)	12.6 (2.5)	14.3 (3.4)	12.8 (2.0)	
	Multiple Narrow	11.6 (2.3)	10.8 (1.5)	10.0 (1.4)	7.3 (0.9)	9.5 (1.6)		7.6 (1.0)			
Species richness	Single Wide	12.2 (0.7)	11.2 (0.9)	***13.8 (1.0)***	10.0 (0.8)	***13.2 (1.2)***	***13.8 (1.5)***	10.2 (1.1)	12.0 (1.3)	13.2 (2.1)	9.8 (1.0)
	Single Narrow	12.0 (1.4)	12.8 (1.9)	10.8 (0.9)	10.2 (1.0)	12.0 (1.0)	10.5 (0.7)	11.7 (0.9)	11.3 (1.4)	8.2 (0.5)	
	Multiple Narrow	10.1 (0.9)	9.6 (0.9)	9.6 (1.0)	8.5 (0.8)	9.1 (0.8)		9.5 (0.9)			
Shannon's diversity	Single Wide	**7.3 (0.6)**	7.2 (0.8)	***8.4 (0.9)***	5.8 (0.7)	***8.1 (1.0)***	***8.4 (0.9)***	5.9 (1.1)	**7.2 (0.7)**	**8.3 (1.5)**	5.6 (0.5)
	Single Narrow	***7.4 (0.6)***	**7.8 (1.2)**	6.7 (0.7)	6.5 (0.8)	***7.4 (0.4)***	5.9 (0.8)	**7.3 (0.7)**	6.6 (0.8)	5.1 (0.3)	
	Multiple Narrow	6.3 (0.6)	5.3 (0.6)	5.9 (0.6)	5.6 (0.6)	5.5 (0.4)		5.9 (0.8)			
Simpson's diversity	Single Wide	5.5 (0.7)	5.7 (0.8)	***6.1 (0.8)***	4.5 (0.8)	***6.1 (0.8)***	***6.2 (0.7)***	4.4 (0.9)	**5.6 (0.5)**	6.1 (1.4)	4.3 (0.4)
	Single Narrow	**5.6 (0.4)**	5.9 (1.0)	5.1 (0.6)	4.9 (0.8)	***5.7 (0.4)***	4.3 (0.8)	**5.8 (0.7)**	5.0 (0.6)	3.9 (0.3)	
	Multiple Narrow	4.9 (0.5)	3.9 (0.5)	4.4 (0.5)	4.4 (0.5)	4.3 (0.3)		4.7 (0.7)			

(A) Understory — Distance from edge of seismic line

Variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	Reference
NMDS 1	Single Wide	-0.18 (0.13)	-0.09 (0.12)	-0.36 (0.19)	0.06 (0.13)	-0.19 (0.14)	-0.30 (0.09)	0.16 (0.25)	*-0.07 (0.23)*	-0.31 (0.20)	0.07 (0.15)
	Single Narrow	-0.26 (0.17)	-0.22 (0.19)	-0.18 (0.14)	-0.04 (0.14)	-0.20 (0.13)	*-0.43 (0.14)*	-0.31 (0.13)	-0.14 (0.21)	0.22 (0.14)	
	Multiple Narrow	0.22 (0.12)	0.28 (0.17)	0.28 (0.17)	**0.45 (0.13)**	0.28 (0.10)		0.25 (0.16)			
NMDS 2	Single Wide	-0.01 (0.11)	0.00 (0.12)	-0.09 (0.10)	-0.01 (0.18)	-0.11 (0.11)	0.07 (0.17)	*-0.15 (0.15)*	-0.20 (0.13)	0.08 (0.13)	0.16 (0.12)
	Single Narrow	0.15 (0.12)	0.16 (0.12)	0.24 (0.06)	0.25 (0.07)	0.07 (0.07)	0.29 (0.13)	0.29 (0.11)	0.08 (0.09)	0.37 (0.09	
	Multiple Narrow	*-0.17 (0.10)*	0.01 (0.11)	-0.07 (0.10)	-0.13 (0.09)	-0.05 (0.12)		-0.10 (0.09)			

(B) Overstory — Distance from edge of seismic line

Variable	Treatment	4 m	8 m	12 m	17 m	22 m	27 m	37 m	52 m	Reference
Tree basal area (m2/ha)	Single wide	15.3 (5.2)	23.0 (7.5)	31.2 (8.5)	23.9 (14.2)	21.1 (9.8)	22.3 (7.7)	24.6 (6.3)	19.9 (8.2)	18.1 (4.8)
	Single narrow	24.7 (10.0)	19.7 (6.4)	16.9 (3.3)	15.0 (3.9)	10.8 (5.7)	13.9 (6.4)	18.4 (8.1)	22.5 (6.8)	
	Multiple narrow	19.1 (2.6)	16.8 (3.1)	**31.6 (4.5)**	26.6 (5.0)		19.4 (3.8)			
Tree density (No. of trees/ha)	Single wide	10750.0 (2423.8)	15250.0 (1075.3)	17500.0 (2404.4)	13250.0 (5208.2)	8500.0 (3072.1)	11000.0 (4209.4)	16250.0 (7664.9)	12000.0 (3482.1)	14318.2 (2740.5)
	Single narrow	13958.3 (4010.6)	14791.7 (2198.9)	19791.7 (6033.0)	14583.3 (4228.7)	8750.0 (2602.1)	11666.7 (1728.0)	16041.7 (3958.3)	14583.3 (2450.9)	

| Multiple narrow | 15892.9 (3146.0) | 17410.7 (4622.5) | 16517.9 (2601.6) | 17678.6 (3319.8) | 17884.6 (3879.7) |

Appendix 2.6: Magnitude of edge influence (MEI) values for cover of the eleven most dominant understory species in treed moderate-rich fens. Results are given by treatment and distance from the seismic line influence (see Appendix 2.7 for mean and standard error values). Significant magnitudes of edge influence are indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$. Grey-shaded cells indicate the distances over which there was significant depth of edge.

Species	Treatment	Distance from the seismic line edge (m)								
		1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m
Betula pumila	Single wide	0.056	-0.197	-0.146	-0.197	-0.197	0.185	-0.253	-0.224	-0.146
	Single narrow	0.235	0.302	0.096	-0.069	0.187	0.217	0.317	0.235	-0.035
	Multiple narrow	-0.377	-0.377	-0.579	-0.649	-0.705		-0.520		
Carex aquatilis	Single wide	0.484	0.008	0.207	0.301	0.085	**0.544**	0.461	0.340	0.435
	Single narrow	0.328	0.495	0.119	0.328	0.216	**0.529**	0.257	0.358	0.358
	Multiple narrow	0.163	0.163	0.163	-0.405	0.014		0.257	-0.405	
Larix laricina	Single wide	-0.130	-0.610	-0.389	-0.639	0.138	-0.290	0.898	-0.389	-0.639
	Single narrow	-0.290	-0.290	-1.000	-0.832	-0.444	-0.569	0.294	-0.290	-1.000
	Multiple narrow	**-1.000**	**-1.000**	-0.841	**-1.000**	**-1.000**		**-1.000**		
Ledum groenlandicum	Single wide	0.044	-0.025	-0.309	0.293	-0.064	-0.372	-0.150	-0.044	-0.251
	Single narrow	-0.064	-0.335	-0.016	0.067	-0.047	-0.154	-0.361	0.027	0.074
	Multiple narrow	0.209	0.161	0.075	0.015	0.094		-0.060		
Oxycoccus microcarpus	Single wide	0.375	0.158	0.158	-0.019	0.245	-0.019	-0.096	0.048	**0.467**
	Single narrow	0.232	-0.272	0.232	0.322	0.322	0.232	0.413	0.232	-0.185
	Multiple narrow	0.158	0.336	0.102	-0.090	0.015		-0.185		
Picea mariana	Single wide	-0.869	0.017	-0.318	-0.441	0.567	-0.205	0.128	-0.427	-0.049
	Single narrow	-0.722	-0.176	0.266	-0.214	0.038	**-0.878**	-0.074	-0.176	-0.511
	Multiple narrow	0.457	0.467	0.486	0.439	0.309		-0.002		
Rubus chamaemorus	Single wide	-0.115	0.092	-0.014	-0.100	-0.132	-0.530	0.070	0.059	-0.369
	Single narrow	**-0.709**	**-0.678**	**-0.620**	-0.287	-0.160	-0.649	-0.105	-0.361	-0.132
	Multiple narrow	-0.087	-0.087	-0.339	-0.026	-0.234		-0.198		
Salix pedicellaris	Single wide	-0.313	-1.000	-0.088	-1.000	-0.088	-0.522	0.023	0.071	-0.190
	Single narrow	-0.351	-0.768	0.063	-0.585	-0.313	-0.482	0.023	0.166	0.134
	Multiple narrow	-0.928	-0.928	**-0.963**	**-1.000**	**-1.000**		-0.722		
Salix planifolia	Single wide	0.721	**0.658**	*0.721*	0.597	**0.702**	**0.776**	-0.064	0.138	-0.389

46

	Single narrow	0.674	0.492	**0.692**	0.571	**0.737**	**0.875**	0.189	0.439	0.439
	Multiple narrow	0.325	0.498	**0.664**	0.144	0.535		0.484		
Smilacina trifolia	Single wide	0.282	0.214	**0.397**	0.155	0.282	*0.351*	0.186	0.196	*0.447*
	Single narrow	**0.361**	**0.371**	*0.351*	*0.381*	*0.399*	0.306	*0.433*	0.300	0.135
	Multiple narrow	0.073	-0.069	-0.051	-0.120	0.160		0.207		
Vaccinium vitis-idaea	Single wide	0.231	-0.111	-0.111	0.355	0.310	-0.176	0.429	0.333	-0.250
	Single narrow	-0.091	-0.091	-0.412	-0.412	0.226	-0.333	-0.500	0.200	-0.200
	Multiple narrow	0.282	0.317	0.273	0.125	0.411		0.297		

Appendix 2.7: Mean (and standard error) values for cover of the eleven most dominant understory species for sites in treed moderate-rich fens. Mean values are given for each treatment and distance combination. Reference sites represent interior treed fen conditions. Significant magnitudes of edge influence are indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$. Grey-shaded cells indicate the distances over which there was significant depth of edge influence.

Species	Treatment	Distance to seismic line edge (m)									Reference
		1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	Reference
Betula pumila	Single wide	3.00 (1.14)	1.80 (1.2)	2.00 (1.05)	1.80 (0.96)	1.80 (1.56)	3.90 (1.96)	1.60 (0.75)	1.70 (1.58)	2.00 (1.26)	2.68 (1.77)
	Single narrow	4.33 (1.2)	5.00 (1.21)	3.25 (1.46)	2.33 (0.71)	3.92 (1.33)	4.17 (1.6)	5.17 (1.05)	4.33 (1.43)	2.50 (0.72)	
	Multiple narrow	1.21 (0.48)	1.21 (0.59)	0.71 (0.41)	0.57 (0.25)	0.46 (0.2)		0.85 (0.41)			
Carex aquatilis	Single wide	1.70 (0.62)	0.60 (0.19)	0.90 (0.33)	1.10 (0.75)	0.70 (0.2)	**2.00 (0.82)**	1.60 (0.51)	1.20 (0.72)	1.50 (0.32)	0.59 (0.30)
	Single narrow	1.17 (0.46)	1.75 (0.96)	0.75 (0.31)	1.17 (0.46)	0.92 (0.44)	**1.92 (0.71)**	1.00 (0.26)	1.25 (0.96)	1.25 (0.73)	
	Multiple narrow	0.82 (0.37)	0.82 (0.36)	0.82 (0.4)	0.25 (0.11)	0.61 (0.27)		1.00 (0.55)			
Larix laricina	Single wide	0.70 (0.58)	0.22 (0.2)	0.40 (0.24)	0.20 (0.2)	1.20 (0.8)	0.50 (0.39)	17.00 (17)	0.40 (0.4)	0.20 (0.2)	0.91 (0.55)
	Single narrow	0.50 (0.34)	0.50 (0.22)	0 (0)	0.08 (0.08)	0.35 (0.33)	0.25 (0.17)	1.67 (0.84)	0.50 (0.34)	0 (0)	
	Multiple narrow	**0 (0)**	**0 (0)**	0.08 (0.07)	**0 (0)**	**0 (0)**		**0 (0)**			
Ledum groenlandicum	Single wide	6.20 (2.62)	5.40 (1.21)	3.00 (1.14)	10.40 (2.2)	5.00 (1.3)	2.60 (1.08)	4.20 (1.74)	5.20 (1.62)	3.40 (0.68)	5.68 (1.59)
	Single narrow	5.00 (1.03)	2.83 (0.6)	5.50 (0.85)	6.50 (1.34)	5.17 (0.75)	4.17 (1.47)	2.67 (1.05)	6.00 (2.31)	6.58 (2.01)	
	Multiple narrow	8.68 (1.99)	7.86 (1.57)	6.61 (0.77)	5.86 (0.74)	6.86 (1.25)		5.04 (0.86)			
Oxycoccus microcarpus	Single wide	1.60 (0.66)	1.00 (0.5)	1.00 (0.27)	0.70 (0.37)	1.20 (0.72)	0.70 (0.12)	0.60 (0.24)	0.80 (0.34)	**2.00 (0.71)**	0.73 (0.30)

48

		Distance to seismic line edge (m)									Reference
Species	**Treatment**	**1 m**	**2.5 m**	**5 m**	**10 m**	**15 m**	**20 m**	**25 m**	**35 m**	**50 m**	**Reference**
	Single narrow	1.17 (0.64)	0.42 (0.08)	1.17 (0.59)	1.42 (0.57)	1.42 (0.45)	1.17 (0.59)	1.75 (0.93)	1.17 (0.6)	0.50 (0.18)	
	Multiple narrow	1.00 (0.49)	1.46 (0.72)	0.89 (0.33)	0.61 (0.24)	0.75 (0.27)		0.50 (0.16)			
Picea mariana	Single wide	0.11 (0.11)	1.60 (0.75)	0.80 (0.58)	0.60 (0.4)	5.60 (3.76)	1.02 (0.77)	2.00 (1.55)	0.62 (0.6)	1.40 (1.17)	1.55 (0.68)
	Single narrow	0.25 (0.17)	1.08 (0.47)	2.67 (1.98)	1.00 (0.52)	1.67 (0.99)	0.10 (0.08)	**1.33 (0.8)**	1.08 (0.49)	0.50 (0.22)	
	Multiple narrow	4.14 (1.36)	4.25 (2.12)	4.46 (2.82)	3.96 (1.51)	2.93 (1.01)		1.54 (0.58)			
Rubus chamaemorus	Single wide	3.10 (1.44)	4.70 (1.59)	3.80 (1.77)	3.20 (1.07)	3.00 (1.05)	1.20 (0.56)	4.50 (1.43)	4.40 (1.44)	1.80 (0.73)	3.91 (1.30)
	Single narrow	**0.67 (0.49)**	**0.75 (0.66)**	**0.92 (0.27)**	2.17 (0.83)	2.83 (1.14)	0.83 (0.65)	3.17 (1.62)	1.83 (0.65)	3.00 (1.51)	
	Multiple narrow	3.29 (0.95)	3.29 (0.94)	1.93 (0.69)	3.71 (0.86)	2.43 (0.81)		2.62 (0.84)			
Salix pedicellaris	Single wide	1.00 (1)	0 (0)	1.60 (1.17)	0 (0)	1.60 (1.36)	0.60 (0.6)	2.00 (1.22)	2.20 (1.56)	1.30 (0.77)	1.91 (1.09)
	Single narrow	0.92 (0.52)	0.25 (0.17)	2.17 (1.28)	0.50 (0.34)	1.00 (0.68)	0.67 (0.33)	2.00 (0.86)	2.67 (1.98)	2.50 (1.75)	
	Multiple narrow	0.07 (0.05)	0.07 (0.07)	**0.04 (0.04)**	**0 (0)**	**0 (0)**		0.31 (0.31)			
Salix planifolia	Single wide	2.80 (1.88)	**2.20 (0.66)**	***2.80 (1.52)***	1.80 (1.11)	**2.60 (1.21)**	**3.60 (1.86)**	0.40 (0.4)	0.60 (0.6)	0.20 (0.2)	0.45 (0.45)
	Single narrow	2.33 (1.09)	1.33 (0.8)	**2.50 (0.81)**	1.67 (0.56)	**3.00 (1.37)**	**6.83 (4.76)**	0.67 (0.42)	1.17 (0.79)	1.17 (1.17)	
	Multiple narrow	0.89 (0.64)	1.36 (0.65)	**2.25 (0.7)**	0.61 (0.32)	1.50 (0.67)		1.31 (0.66)			
Smilacina trifolia	Single wide	6.00 (2.93)	5.20 (1.59)	**7.80 (2.29)**	4.60 (1.44)	6.00 (1.67)	***7.00 (1.34)***	4.90 (2.51)	5.00 (1.48)	***8.80 (2.44)***	3.36 (0.80)

		Distance to seismic line edge (m)									
Species	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	Reference
	Single narrow	**7.17 (2.02)**	**7.33 (1.94)**	*7.00 (1.34)*	*7.50 (1.84)*	*7.83 (1.58)*	6.33 (2.87)	*8.50 (1.77)*	6.25 (2.1)	4.42 (1.14)	
	Multiple narrow	3.89 (1.28)	2.93 (1.2)	3.04 (1.09)	2.64 (0.81)	4.64 (1.25)		5.12 (1.67)			
Vaccinium vitis-idaea	Single wide	1.60 (0.91)	0.80 (0.56)	0.80 (0.56)	2.10 (1.27)	1.90 (1.07)	0.70 (0.34)	2.50 (1.47)	2.00 (0.84)	0.60 (0.4)	1.00 (0.34
	Single narrow	0.83 (0.46)	0.83 (0.44)	0.42 (0.15)	0.42 (0.15)	1.58 (0.58)	0.50 (0.22)	0.33 (0.11)	1.50 (1.11)	0.67 (0.28)	
	Multiple narrow	1.79 (0.54)	1.93 (0.73)	1.75 (0.76)	1.29 (0.36)	2.39 (0.67)		1.85 (0.46)	1.75 (0.56)		

Appendix 2.8: Magnitude of edge influence (MEI) values for (A) understory and (B) overstory response variables in treed poor fens. Results are given by treatment and distance from the seismic line (see Appendix 2.9 mean values of each response variable at each distance by treatment). Significant magnitudes of edge influence are indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$. Grey-shaded cells indicate the distances over which there was significant depth of edge influence.

(A) Understory variables in poor fens		Distance from edge of seismic line								
Response variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m
Canopy cover	Single Wide	*-0.180*	-0.143	-0.056	-0.026	-0.083	-0.100	0.006	-0.002	-0.066
	Single Narrow	-0.141	-0.123	-0.013	-0.011	-0.082	-0.041	-0.021	-0.006	-0.016
	Multiple Narrow	-0.043	0.018	0.008	0.023	-0.020		-0.056		
Total understory cover	Single Wide	0.049	0.070	0.159	0.064	0.083	-0.005	0.043	0.081	0.069
	Single Narrow	0.164	0.069	0.018	-0.010	-0.059	-0.103	0.051	-0.131	0.047
	Multiple Narrow	0.064	*-0.156*	*-0.174*	-0.104	*-0.153*		-0.058		
Forb cover	Single Wide	0.016	-0.044	-0.165	-0.118	0.021	-0.020	-0.072	-0.108	0.002
	Single Narrow	-0.074	-0.161	-0.120	0.019	-0.251	-0.204	0.157	-0.251	-0.239
	Multiple Narrow	-0.050	*-0.366*	*-0.382*	*-0.343*	*-0.329*		*-0.259*		
Graminoid cover	Single Wide	0.048	-0.152	-0.240	0.048	-0.010	0.294	-0.152	-0.240	0.147
	Single Narrow	0.090	0.090	0.345	-0.186	-0.186	-0.320	0.014	-0.489	-0.076
	Multiple Narrow	*-0.462*	*-0.606*	*-0.689*	*-0.781*	*-0.781*		*-0.606*		
Short shrub cover	Single Wide	0.194	0.185	*0.352*	0.229	0.142	-0.041	0.231	**0.292**	-0.057
	Single Narrow	*0.413*	0.339	0.233	0.078	0.197	0.114	-0.161	0.012	**0.381**
	Multiple Narrow	0.273	0.096	-0.053	0.140	-0.037		0.194		
Species richness	Single Wide	0.073	0.020	0.012	-0.021	0.004	0.066	-0.039	-0.004	0.073
	Single Narrow	0.017	-0.055	-0.017	-0.082	-0.111	-0.172	-0.030	-0.111	-0.125
	Multiple Narrow	-0.072	-0.091	**-0.138**	*-0.184*	-0.122		**-0.133**		
Shannon's diversity	Single Wide	0.067	-0.028	0.022	-0.063	0.024	0.091	-0.005	-0.103	0.077
	Single Narrow	-0.060	-0.051	0.026	-0.051	-0.061	-0.185	0.024	-0.056	-0.197
	Multiple Narrow	-0.038	-0.065	-0.071	-0.138	-0.055		-0.132		
Simpson's diversity	Single Wide	0.050	-0.079	0.033	-0.079	0.039	0.085	0.004	-0.117	0.086
	Single Narrow	-0.071	-0.021	0.032	-0.031	-0.024	-0.193	0.059	-0.053	-0.214
	Multiple Narrow	-0.025	-0.053	-0.049	-0.119	-0.028		-0.129		
NMDS 1*	Single Wide	0.144	-0.176	-0.998	0.001	-0.402	-0.006	-1.375	-0.033	0.191

(A) Understory variables in poor fens		Distance from edge of seismic line								
Response variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m
	Single Narrow	-0.284	-1.154	-2.243	-4.612	9.446	9.191	-0.248	-3.587	5.163
	Multiple Narrow	-1.765	*266.478*	*5.020*	*3.362*	*7.017*		*18.433*		
NMDS 2*	Single Wide	-1.089	-0.475	-1.398	-0.300	-0.174	-0.832	-0.605	-0.002	-0.910
	Single Narrow	0.126	-0.382	0.224	0.360	0.251	-0.896	*87.213*	*19.809*	*479.262*
	Multiple Narrow	*5142.991*	*8.290*	*229.136*	-18.800	-0.671		-0.678		

(B) Overstory variables in poor fens		Distance from edge of seismic line							
Response variable	Treatment	4 m	8 m	12 m	17 m	22 m	27 m	37 m	52 m
Tree basal area	Single Wide	-0.124	0.038	0.017	-0.248	-0.235	-0.043	-0.314	-0.150
(m^2/ha)	Single Narrow	-0.167	0.124	0.127	-0.022	-0.483	-0.268	-0.226	0.205
	Multiple Narrow	-0.061	-0.144	-0.001	-0.159		-0.132		
Tree density	Single Wide	0.026	0.201	0.132	-0.165	-0.214	-0.037	-0.076	0.100
(no. of trees/ha)	Single Narrow	0.001	0.057	0.090	0.098	0.011	-0.107	-0.028	0.234
	Multiple Narrow	*0.357*	*0.317*	*0.360*	*0.388*		*0.288*		

* Due to the negative values of some NMDS coordinates, MEI can be more than 1 and less than -1

Appendix 2.9: Mean (and standard error) values for (A) understory and (B) overstory response variables for sites in treed poor fens. Mean values are given for each treatment and distance combination. Reference sites represent interior treed fen conditions. Significant magnitudes of edge influence are indicated in bold for $P < 0.1$ or in bold and italicized for $P < 0.05$.   Grey-shaded cells indicate the distances over which there was significant depth of edge influence.

(A) Understory		Distance from edge of seismic line									
Variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	Reference
Canopy cover	Single wide	*42.7* *(4.6)*	46.0 (8.3)	54.8 (8.1)	58.2 (7.2)	51.9 (6.2)	50.2 (9.7)	62.2 (4.4)	61.1 (5.8)	53.8 (5.8)	61.4 (5.3)
	Single narrow	46.2 (7.9)	47.9 (4.5)	59.7 (11.6)	60.0 (10.4)	52.1 (5.0)	56.5 (12.9)	58.8 (7.96)	60.6 (13.6)	59.4 (7.7)	
	Multiple narrow	56.3 (4.7)	63.7 (4.7)	62.4 (4.5)	64.4 (4.3)	58.9 (4.6)		54.8 (4.1)			
Understory cover	Single wide	32.4 (2.6)	33.7 (4.8)	40.4 (9.2)	33.4 (6.9)	34.7 (4.8)	29.0 (2.9)	31.9 (5.0)	34.5 (5.0)	33.6 (5.7)	29.3 (3.0)
	Single narrow	40.8 (9.3)	33.7 (9.4)	30.4 (6.8)	28.7 (6.6)	26.0 (3.9)	23.8 (3.6)	32.5 (9.0)	22.5 (3.4)	32.2 (7.9)	
	Multiple narrow	33.3 (6.2)	*21.4* *(2.1)*	*20.6* *(1.5)*	23.8 (3.3)	*21.5* *(1.6)*		26.1 (3.5)			
Forb cover	Single wide	13.3 (1.1)	11.8 (3.5)	9.2 (2.6)	10.1 (3.3)	13.4 (3.0)	12.4 (1.9)	11.1 (1.8)	10.4 (3.2)	12.9 (2.4)	12.9 (2.1)
	Single narrow	11.1 (2.0)	9.3 (2.5)	10.1 (2.4)	13.4 (5.8)	7.7 (1.6)	8.5 (3.8)	17.7 (9.0)	7.7 (2.4)	7.9 (3.1)	
	Multiple narrow	11.6 (1.9)	*6.0* *(1.0)*	*5.8* *(1.0)*	*6.3* *(0.8)*	*6.5* *(0.9)*		*7.6* *(1.1)*			
Graminoid cover	Single wide	0.6 (0.2)	0.4 (0.1)	0.4 (0.2)	0.6 (0.2)	0.6 (0.3)	1.1 (0.3)	0.4 (0.2)	0.4 (0.1)	0.8 (0.3)	0.6 (0.2)
	Single narrow	0.7 (0.3)	0.7 (0.5)	1.2 (0.6)	0.4 (0.2)	0.4 (0.2)	0.3 (0.2)	0.6 (0.3)	0.2 (0.1)	0.5 (0.3)	

(A) Understory		Distance from edge of seismic line									
Variable	Treatment	1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	Reference
	Multiple narrow	**0.2 (0.1)**	*0.1 (0.1)*	*0.1 (0.1)*	*0.1 (0.1)*	*0.1 (0.1)*		*0.1 (0.1)*			
Short shrub cover	Single wide	15.2 (3.3)	14.9 (3.7)	*21.4 (5.0)*	16.4 (5.6)	13.6 (3.0)	9.4 (1.9)	16.4 (6.7)	**18.7 (5.4)**	9.1 (1.4)	10.3 (1.5)
	Single narrow	*24.7 (10.2)*	20.8 (10.9)	16.5 (7.2)	12.0 (6.8)	15.3 (4.3)	12.9 (3.1)	7.4 (2.1)	10.5 (2.4)	**22.9 (7.5)**	
	Multiple narrow	18.0 (5.2)	12.4 (2.1)	9.2 (1.1)	13.6 (3.6)	9.5 (0.8)		15.2 (3.2)			
Species richness	Single wide	9.9 (1.0)	8.9 (1.1)	8.7 (1.3)	8.1 (0.6)	8.6 (0.8)	9.7 (1.1)	7.9 (0.8)	8.4 (0.8)	9.9 (1.5)	8.5 (1.0)
	Single narrow	8.8 (0.9)	7.6 (1.3)	8.2 (1.5)	7.2 (1.0)	6.8 (1.5)	6.0 (0.8)	8.0 (0.8)	6.8 (0.7)	6.6 (1.5)	
	Multiple narrow	7.4 (0.4)	7.1 (0.5)	**6.4 (0.4)**	*5.9 (0.5)*	6.6 (0.5)		**6.5 (0.5)**			
Shannon's diversity	Single wide	5.6 (0.7)	4.6 (0.7)	5.1 (1.0)	4.3 (0.6)	5.1 (0.7)	5.9 (0.7)	4.8 (0.7)	4.0 (0.7)	5.7 (1.0)	4.9 (0.7)
	Single narrow	4.3 (0.8)	4.4 (1.2)	5.1 (1.1)	4.4 (0.7)	4.3 (1.1)	3.4 (0.7)	5.1 (1.1)	4.4 (0.5)	3.3 (0.7)	
	Multiple narrow	4.5 (0.4)	4.3 (0.5)	4.2 (0.3)	3.7 (0.4)	4.4 (0.3)		3.7 (0.3)			
Simpson's diversity	Single wide	4.2 (0.6)	3.2 (0.5)	4.0 (0.8)	3.2 (0.5)	4.1 (0.6)	4.5 (0.6)	3.8 (0.6)	3.0 (0.5)	4.5 (0.8)	3.8 (0.6)
	Single narrow	3.3 (0.7)	3.6 (1.0)	4.0 (0.9)	3.5 (0.6)	3.6 (1.0)	2.6 (0.6)	4.3 (1.0)	3.4 (0.4)	2.4 (0.6)	
	Multiple narrow	3.6 (0.3)	3.4 (0.4)	3.4 (0.3)	3.0 (0.3)	3.6 (0.3)		2.9 (0.2)			

54

(A) Understory

Variable	Treatment	Distance from edge of seismic line									Reference
		1 m	2.5 m	5 m	10 m	15 m	20 m	25 m	35 m	50 m	
NMDS 1	Single wide	-0.25 (0.11)	-0.13 (0.15)	0.00 (0.21)	-0.18 (0.13)	-0.08 (0.12)	-0.18 (0.18)	0.03 (0.13)	-0.17 (0.14)	-0.27 (0.16)	-0.18 (0.16)
	Single narrow	-0.10 (0.16)	0.01 (0.20)	0.07 (0.25)	0.12 (0.19)	0.23 (0.33)	0.23 (0.21)	-0.11 (0.19)	0.10 (0.13)	0.27 (0.22)	
	Multiple narrow	0.05 (0.10)	*0.18 (0.10)*	*0.27 (0.08)*	*0.34 (0.10)*	*0.24 (0.10)*		*0.20 (0.09)*			
NMDS 2	Single wide	0.01 (0.16)	-0.05 (0.15)	0.02 (0.15)	-0.08 (0.16)	-0.10 (0.19)	-0.01 (0.26)	-0.04 (0.18)	-0.14 (0.15)	-0.01 (0.15)	-0.14 (0.11)
	Single narrow	-0.18 (0.15)	-0.06 (0.18)	-0.23 (0.11)	-0.30 (0.11)	-0.24 (0.11)	-0.01 (0.14)	*0.15 (0.06)*	**0.16 (0.16)**	*0.14 (0.15)*	
	Multiple narrow	*0.14 (0.09)*	*0.18 (0.08)*	*0.14 (0.08)*	0.13 (0.06)	-0.03 (0.09)		-0.03 (0.08)			

(C) Overstory

Variable	Treatment	Distance from edge of seismic line								Reference
		4 m	8 m	12 m	17 m	22 m	27 m	37 m	52 m	
Tree basal area (m2/ha)	Single wide	22.8 (7.1)	31.6 (13.6)	30.3 (11.4)	17.6 (5.2)	18.1 (6.0)	26.9 (5.5)	15.3 (2.9)	21.6 (6.1)	29.3 (9.7)
	Single narrow	20.9 (3.3)	37.6 (13.7)	37.8 (17.8)	28.0 (10.8)	10.2 (4.2)	16.9 (9.0)	18.5 (3.9)	44.4 (20.4)	
	Multiple narrow	25.9 (3.7)	21.9 (3.7)	29.2 (4.9)	21.2 (3.8)		22.4 (5.0)			
Tree density (No. of trees/ha)	Single wide	13392.9 (3458.0)	19107.1 (4586.4)	16607.1 (2598.0)	9107.1 (1999.2)	8214.3 (4224.5)	11785.7 (3011.1)	10892.9 (2142.9)	15535.7 (3875.5)	12708.3 (2633.0)
	Single narrow	12750.0 (5175.1)	14250.0 (5570.6)	15250.0 (5353.2)	15500.0 (4100.3)	13000.0 (4736.8)	10250.0 (1952.6)	12000.0 (2866.8)	20500.0 (7537.4)	
	Multiple narrow	*26875.0 (4151.5)*	*24553.6 (4621.0)*	*27053.6 (4315.5)*	*28839.3 (3480.4)*		*23035.7 (3677.7)*			

Chapter 3: Local vegetation shapes the performance of an herbaceous annual, *Melampyrum lineare*, in fragmented boreal forest

3.1 Abstract

Edge influence is a critical by-product of forest fragmentation; as disturbance-related changes in biotic interactions or abiotic conditions extend into the adjacent forested patch, the amount of "interior" forest habitat is reduced. While there is an abundance of research characterizing edge influence patterns, far less research has explored the mechanisms underlying these edge effects. In this study, I examine the performance of cow-wheat (*Melampyrum lineare*), an herbaceous annual, and explore the mechanisms driving edge influence on understory plants. The objectives of this study are to: 1) determine the edge influence of linear disturbances on the abundance and performance of cow-wheat 2) determine the edge influence on vegetation structure, and 3) explore the mechanisms driving edge influence on cow-wheat abundance. We expected reduced vegetative competition on the seismic line would lead to higher cow-wheat population density and taller cow-wheat individuals. We also expected higher fruit production and seed set on seismic lines, due to higher pollinator abundance on seismic lines. We measured cow-wheat height, reproductive success, and abundance in three treatments: on the seismic line, at the edge of the seismic line and in the interior forest. As expected, cow-wheat population density and seed production per fruit was highest on the seismic lines, however cow-wheat height and reproductive success did not differ between treatments. While we also found differences in vegetation at the edge and on the seismic lines, as compared to the interior forest, these were not related to the differences in cow-wheat population density between treatments. In contrast, at the individual level, understory vegetation abundance surrounding individuals were directly related

to cow-wheat height and reproductive success. Our study shows that at the population level, cow-wheat abundance is influenced by fragmentation, but at the individual level, cow-wheat fitness is primarily influenced by competition with the understory vegetation and losses due to herbivory.

3.2 Introduction

Edge influence is a critical by-product of forest fragmentation; as disturbance-related changes in biotic interactions or abiotic conditions extend into the adjacent forested patch, the amount of "interior" forest habitat is reduced. Edge influence or edge effects are the ecological changes found at the interface of non-forested and forested patches. While there is an abundance of research characterizing edge influence patterns on understory communities, far less research has explored the mechanisms underlying these edge effects. As forest fragmentation increases, understanding the mechanisms driving edge influence is essential for predicting, and then mitigating, the effects of edge creation (Murcia 1995; Ries et al. 2004; Ruffell and Didham 2016). In this study, I explore the mechanisms driving edge influence on an herbaceous annual in the boreal forest—where mechanistic studies of edge influence are particularly sparse.

Edge influence on plant populations can be driven by biotic interactions such as changes in competition (Lienert 2004), pollinator availability (Burgess et al. 2006), and seed dispersal or predation (Jules and Rathcke 1999). Micro-habitat conditions can also explain responses of plant populations at forest edges, with altered micro-climatic conditions affecting population processes (Honnay et al. 2005), such as germination and seedling recruitment rates (Tomimatsu and Ohara 2004). Local vegetation structure shapes the micro-climatic conditions, as vegetation cover can limit light availability, modulate temperature fluctuations, and influence soil moisture (Giuggiola et al. 2018; Stickley and Fraterrigo 2021). Studies have shown how vegetation structure can

mediate the edge influence on animal populations (Ruffell et al. 2014). We can expect that vegetation structure would have an even stronger effect on plant populations, as neighboring plants would not only shape the micro-climate, but also act as competitors (Giuggiola et al. 2018). Herein, I examine the edge influence of linear disturbances on vegetation structure and explore how this affects population-level and individual performance of an herbaceous annual.

In the boreal forest of western Canada, seismic lines are a major source of forest fragmentation (Schneider et al. 2003). Seismic lines are linear corridors of cleared forests created to locate fossil fuel reserves. Although seismic lines are relatively narrow disturbances (~1.5-8 m wide), they extend for kilometers and can be found at high densities (Lee and Boutin 2006). Despite their narrow nature, studies have found seismic lines affect the understory vegetation communities up to 15 m into the adjacent forest (MacFarlane 2003; Dabros et al. 2017). As compositional shifts are driven by changes within individual plant populations, identifying the drivers of individual plant performance can provide insights into the mechanisms behind changes in understory vegetation observed at edges. In this study, I build on these broader community-based studies and explore the edge influence of seismic lines on *Melampyrum lineare* (Desr.), hereafter referred to as cow-wheat, at a population and individual level. I chose to focus on cow-wheat because it is an annual—a relatively under-studied life history in fragmentation studies (Aguilar et al. 2006) and an uncommon life history in the boreal forest.

My objectives were to: 1) determine the edge influence on cow-wheat abundance and fitness, 2) determine the edge influence on vegetation structure, and 3) explore the mechanisms driving edge influence on cow-wheat abundance and fitness. At the population level, I expected the reduced vegetative competition on the seismic line would lead to higher cow-wheat population density on the seismic lines. In addition, I expected increased overstory and

understory abundance at the edge in response to the increased light availability associated with reduced canopy cover along the seismic line. At the individual level, I expected the reduced vegetation cover to lead to taller cow-wheat plants and higher fecundity on the seismic lines. The latter is based on studies that have found higher pollinator abundance on seismic lines (Riva et al. 2018; Nelson et al. 2021), which can further promote higher fruit production and seed set on seismic lines (Dawe et al. 2017).

3.3 Methods

3.3.1 Study species

Melampyrum lineare (Desr.), cow-wheat, is an understory forest forb that is a facultative hemi-parasite found across continental Canada and the United States on well-drained sandy soils; its range extends as far south as Virginia's Appalachian Mountains (Cantlon et al. 1963; Oldham and Weeks 2017). It is an annual that is capable of self-fertilization, though host attachment is usually needed for flowering and seed production (Cantlon et al. 1963)**.** It has a variety of hosts including *Vaccinium angustifolium* (Aiton)*,* and *Pinus* and *Populus* species, such as jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) (Cantlon et al. 1963; Nave et al. 2018)**.** Cow-wheat uses haustoria to attach and obtain water, phosphorus, and carbon from its hosts (Cantlon et al. 1963; Nave et al. 2018). Its fruit is a capsule that usually contains four seeds; the seeds are ejected upon maturity (Cantlon et al. 1963) and are attached to an elaiosome, which attract ants—known dispersal agents for *M. lineare* (Cantlon et al. 1963).

3.3.2 Study area

Sampling occurred in xeric forest stands dominated by *Pinus banksiana*, north of Lac La Biche, Alberta (55° 1′48″N, 112° 1′4.44″W) and near Franchere, Alberta (54° 18′15.84″N , 110° 55′4.44″W) in western Canada. Kinnikinnick (*Arctostaphylos uva-ursi* (Linnaeus)

Sprengel), velvetleaf blueberry (*Vaccinium myrtilloides* Michaux), and lingonberry (*Vaccinium vitis-idaea* L.) dominated the understory layer. Average daily temperature in the region is 1.6° C, with an average annual precipitation of 478.6 mm (from nearby meteorological station St. Lina, Alberta, Canada);(Environment and Climate Change 2013).

Using GIS layers of forest types, linear disturbances, and cow-wheat (*Melampyrum lineare*) observations, I identified sites with older seismic lines (approx. 6-8 m wide, ~20 years old) located in pine-dominated stands with nearby cow-wheat observations. In the field, I then searched these sites for cow-wheat on the seismic lines, at the edge of the line, and 50 m into the forest. I conducted population sampling at 18 sites where I found cow-wheat (*Melampyrum lineare*) populations in at least one of these locations. A subset of these sites had cow-wheat populations on the seismic line, at the edge of the line, and in the forest; ten of these were selected for sampling of seed production and individual cow-wheat performance.

Despite their age, seismic lines in the study area have limited tree regeneration, due to repeated use by all-terrain vehicles (ATVs). While I avoided sampling seismic lines that were highly disturbed by ATVs, all sampled lines continued to be open with limited to no tree regeneration. Sampling occurred mid-July to mid-August 2019.

3.3.3 Population sampling

At each of the 18 sampling sites, I established a 1 m by 30 m belt transect along the seismic line, a parallel transect at the edge of the seismic line (3 m from the seismic line plot into the adjacent forest), and another parallel transect in the interior forest (50 m from the seismic line plot into the adjacent forest; Figure 3.1). Hereafter, site refers to a set of seismic line, edge, and interior forest transects. The three locations of these belt transects are hereafter referred to as "treatments": seismic line, edge, and interior forest. For each transect the long axis of the belt

60

transect was parallel to the edge. The seismic line belt transect was placed at the edge of the

seismic line to avoid the frequently disturbed area, due to motorized vehicle use, often found at

the center of the seismic line.

Within the belt transect, I counted the number of cow-wheat individuals and the number

of flowering cow-wheat individuals (July 11 to July 31, 2019; Figure 3.1). I also visually

estimated litter cover and abundance of understory vegetation by growth form—short shrub

(woody species < 1 m tall, including tree species), forb (including dwarf shrub species, e.g.,

Linnaea borealis, Vaccinium vitis-idaea, and *Arctostaphylos uva-ursi*), and graminoid—in three

1 m^2 quadrats placed at the 5 m, 15 m and the 25 m point of the belt transect (Figure 3.1). At the

center of each vegetation quadrat, I measured litter depth and soil moisture, and estimated

canopy cover using a convex spherical densiometer (Lemmon 1956). Soil moisture was

measured as the volumetric water content, using a time domain reflectometer (HydroSense II,

Campbell Scientific). Data from the three quadrats per transect were then averaged for the

analysis. For a population level measure of seed production, in a subset of ten sites (described

below), I collected 10 fully developed, but not yet mature, cow-wheat fruits from 10 cow-wheat

individuals in each treatment and later counted the number of seeds per fruit. I also established a

larger 2 x 50 m belt transect, centered on the smaller belt transect. In this larger belt transect, I

counted all tree saplings (> 1.3 m height; diameter at 1.3m height (DBH) < 5 cm) and trees

(DBH ≥ 5 cm) to species (Figure 3.1).

3.3.4 Individual sampling

At a subset (n = 10) of the sites sampled for cow-wheat populations I tracked cow-wheat

growth and reproduction at the individual plant level. These sites had cow-wheat populations in

all three treatments: on the seismic line, at the edge, and in the interior forest. Random numbers

were generated and the cow-wheat individuals closest to those distances within the belt transect were used as focal cow-wheat individuals (n = 10 per treatment; total of 30 individuals per site). However, when there were fewer than 10 cow-wheat individuals available within the belt transect, I selected all cow-wheats within the transect as focal individuals and then selected the nearest cow-wheat individuals outside the belt transect, as necessary, to end up with 10 focal individuals. Focal individuals were marked with a bamboo skewer and aluminum tag and were visited twice during the growing season in 2019.

In the first visit (between July 15 to July 27, 2019) I recorded the following for each focal individual: extent of herbivory, plant height, number of flowers, and number of fruits. The second visit was approximately two weeks after the first visit (July 29 to August 10); at that time I recorded the same variables as well as the number of branches. Extent of herbivory was classified on a scale from 0 to 5: 0 = no evidence of herbivory, 1 = one or two leaves show evidence of light herbivory and all leaves are intact, 2 = three or more leaves have been browsed but all branches are intact, may be missing one or two leaves, 3 = a side branch is missing, or half of the leaves have been browsed and missing a few leaves, 4 = main stem or multiple side branches have been browsed with only a few leaves remaining but the individual is still alive, and 5 = the individual is dead, the main stem is clipped almost to the ground, and all leaves are missing. For six sites, these variables were re-measured a third time (August 9-12) because the 2nd sampling visit was too early to capture maximum cow-wheat fruiting. The other four sites were only visited twice, as their second visits had been later in the growing season and many focal individuals were already senescing by the time we could complete a third visit. To describe the understory vegetation surrounding each focal individual, I visually estimated the abundance of understory vegetation by species in a 0.5 m^2 hoop centered on each cow-wheat focal

individual. I also estimated canopy cover above each focal individual using a convex spherical densiometer. Lastly, I measured each focal individual's distance to the nearest tree (DBH > 5 cm), as a measure of host availability.

3.3.5 Statistical analysis

To examine the effects of treatment on the cow-wheat response variables and covariates, I used generalized linear mixed-effects models with treatment as the fixed effect. Response variables at the population-level were: cow-wheat population density, proportion of flowering individuals, and number of seeds per fruit (seed production from a subset of 10 sites). Population covariates included: canopy cover, live tree and sapling density, average understory cover [total (sum of short shrub, forb, and graminoid cover), and separately for short shrubs, forbs, and graminoids], litter cover, litter depth and soil moisture. For canopy cover, total understory cover, understory cover by growth form, litter cover, litter depth, and soil moisture, I used the average of the three 1 m^2 quadrats from each transect.

At the population level, I included site as a random effect. Cow-wheat population density was modelled with a negative binomial distribution and a log link function. Proportion of flowering cow-wheat individuals was modelled with a beta distribution and logit link function. Since proportion of flowering individuals included the values 0 and 1, I applied the following transformation $\frac{y*(n-1)+0.5}{n}$, where n is the sample size (Cribari-Neto and Zeileis 2010). Live tree and sapling density, and short shrub and litter cover at the population level were modelled with a Poisson distribution and a log link function. For number of seeds per fruit, in addition to having site as a random effect, I also used transect nested within site as a random effect. Canopy cover, total understory cover, forb cover, graminoid cover, litter depth and soil moisture were modelled with a normal distribution. Graminoid cover was $\log_{10}$-transformed to improve model fit.

Response variables at the individual-level were: maximum height (hereafter referred to as height), maximum number of flowers (hereafter referred to as number of flowers), and maximum number of fruits (hereafter referred to as number of fruits). For all, this was the larger(est) value from the two or three visits. Individual covariates were: treatment, maximum herbivory (hereafter referred to as herbivory), inverse distance to nearest host tree (as a measure of overstory host availability), total understory cover (the sum of short shrub, forb and graminoid cover), canopy cover, and understory host availability around each focal individual. Understory host availability was the sum of the understory cover for known *M. lineare* hosts, including: *Pinus banksiana*, *Populus* spp., *Betula* spp. seedlings, *Carex* spp., *Amelanchier alnifolia, Rubus idaeus, Vaccinium vitis-idaea, Vaccinium myrtillifolia, Arctostaphylos uva-ursi,* and *M. lineare* (Piehl 1962; Cantlon et al. 1963; Oldham and Weeks 2017). We included *Arctostaphylos uva-ursi* as studies suggest that most ericaceous shrubs are *M. lineare* hosts (Oldham and Weeks 2017).

To account for the nested sampling design at the individual level, I included site and transect within site as random effects. Individual cow-wheat height was modelled with a Poisson distribution and a log link function. Number of flowers and fruits per individual, total understory cover, and understory host availability around each focal individual were modelled with a negative binomial distribution and a log link function. Canopy cover around each focal individual and inverse distance to nearest host tree were modelled with a normal distribution. Two individuals lacked distance to nearest host tree values and were excluded from the distance to nearest host tree analysis. Finally, ordinal logistic regression was used for herbivory on cow-wheat, with extent of herbivory treated as ordinal categorical variables.

Mixed models with normal distributions were done using the lme4 package (Bates et al. 2015) and generalized linear mixed models were done using the glmmTMB package (Brooks et al. 2017) in the R statistics programming environment (version 3.5.2; R Core Team 2018). Residuals were examined using the DHARMA package (Hartig 2020) to ensure the appropriate distributions were used. When treatment was significant ($\alpha = 0.05$), post hoc analyses were completed using the emmeans package, with P values adjusted using the Tukey HSD method (Lenth 2020). Ordinal logistic regression was done using the ordinal package (Christensen 2019). The package ggplot2 was used to create graphs (Wickham 2016).

3.3.6 Structural Equation Models

I used structural equation models to further explore the relationships between treatment, the cow-wheat response variables, and the vegetation covariates. At the population level, I created a structural equation model (SEM) to explore the direct and indirect relationships between treatment, vegetation cover and litter depth at each treatment, and population density (Appendix 3.1). Cow-wheat population density was $\log_{10}$-transformed for this analysis. Site was used as a random effect.

At the level of the focal individual, I used a second structural equation model to explore the direct and indirect relationships between treatment, vegetation cover around each focal individual, herbivory, and cow-wheat height, flower, and fruit production (Appendix 3.2). Understory cover, cow-wheat height, and flower and fruit production were $\log_{10}$-transformed. Site and transect were used as nested random effects.

I expected treatment to affect vegetation growth, i.e., canopy cover, understory abundance, and cow-wheat abundance, growth, and fecundity. In turn, I expected the canopy to compete with the understory and limit understory establishment and growth, thereby influencing

understory abundance and cow-wheat abundance, growth, and fecundity. Understory vegetation could then compete with cow-wheat and limit cow-wheat establishment, growth, and fecundity. Alternatively, understory vegetation could also act as cow-wheat hosts and promote cow-wheat establishment, growth and fecundity. Thus, I expected a relationship between understory vegetation and cow-wheat population density, cow-wheat height, and flower and fruit production. At the population level, I also expected treatment to affect litter depth, which could influence cow-wheat seed germination or cow-wheat establishment; thus, I expected a relationship between litter depth and cow-wheat population density. At the individual level, I expected herbivory to limit cow-wheat growth and fecundity, and thus expected relationships between herbivory and cow-wheat height, flower and fruit production.

I started with a global model of hypothesized relationships (Appendices 3.3 and 3.4). Non-significant relationships were then removed, and a parsimonious final model was created. I used the package 'piecewiseSEM'(Lefcheck 2016) to fit each component model of our SEM individually and allow for a mixed-modelling approach, which best suited our sampling design. Global model fit was evaluated using Fisher's C statistic (P > 0.05) as derived from Shipley's test of d-separation, which determines whether paths are missing from the model. A P value greater than 0.05 indicates good fit, with the model not significantly differing from the data. Non-normal response variables were log-transformed to conform to the normality assumptions of SEMs.

3.4 Results

3.4.1 Population level

Cow-wheat population density and number of seeds per fruit were significantly different among the three treatments (seismic line, edge, forest) (Table 3.1; Figure 3.2). Population density

was higher on the seismic line than in the interior forest; the edge was intermediate and did not differ from either (Table 3.1; Figure 3.2a). A higher number of seeds per fruit was more likely on the seismic line than in the forest; the edge was intermediate and did not significantly differ from either (Table 3.1; Figure 3.2b). Proportion of flowering cow-wheat individuals was high for all treatments (over 80% on average) and did not significantly differ between treatments (Table 3.1).

At the population level, treatment was significant for canopy cover, tree and sapling density, short shrub cover, and litter cover and depth, but had no effect on total understory, forb, and graminoid cover, and soil moisture (Table 3.1, Figure 3.3). Canopy cover and litter cover were significantly lower at the seismic line than at the edge and the interior forest, which did not differ from one another (Figures 3.3a, 3e). Tree density at the edge was significantly higher than in the interior forest and the interior forest had significantly higher tree density than on seismic lines (Figure 3.3b). Sapling density was also significantly higher at the edge than in the interior forest or on the seismic lines, which did not differ from one another (Figure 3.3c). Short shrub cover was significantly lower in the interior forest than at the edge or on the seismic line, which did not differ from one another (Figure 3.3d). Litter depth at the seismic line was significantly lower than at the edge; the forest did not differ from either the seismic line or the edge (Figure 3.3f).

The final, simplified SEM at the population level showed that treatment (seismic line, edge, forest) affected canopy cover, litter depth, and cow-wheat population density (Table 3.2, Figure 3.4). Canopy cover was negatively related to understory cover (Table 3.2, Figure 3.4). Treatment was the only significant predictor for cow-wheat population density (Table 3.2, Figure 3.4, Appendix 3.3). The final, simplified SEM had a Fisher's C of 10.535 (P-value = 0.569, df = 12, see Table 3.2B for marginal and conditional R^2 values).

3.4.2 Individual level

Cow-wheat response variables at the individual level—maximum (individual) height, number of flowers, and number of fruits—did not differ between treatments (Table 3.1). Treatment was only significant for canopy cover at each focal individual and for inverse distance to nearest host tree; however, pairwise comparisons of distance to nearest host tree did not show differences between treatments (Table 3.1). Canopy cover around each focal individual was highest at the edge and lowest at the seismic line; canopy cover at the forest was in between these two treatments, and differed from both of them (Table 3.1, Figure 3.5). Total understory cover and understory host availability around each focal individual and herbivory on focal cow-wheat individuals did not differ between treatments (Table 3.1).

The results of the final, simplified SEM aligned with the mixed effects models with treatment only significant for canopy around each focal individual (Table 3.3, Figure 3.6). Understory cover around each focal individual was significantly positively related to cow-wheat height, but negatively related to flower and fruit production (Table 3.3). Cow-wheat height was positively related to flower and fruit production (Table 3.3). Lastly, flower and fruit production were positively related, and herbivory was negatively related to fruit production (Table 3.3). The final, simplified SEM had a Fisher's C of 17.475 (P-value = 0.622, df = 20, see Table 3.3B for marginal and conditional R^2 values).

Based on the global structural equation model (SEM), canopy cover around each focal individual was not related to understory cover around each focal individual, cow-wheat height, or flower or fruit production (Appendix 3.4). Treatment was not significant for total understory cover around each focal individual (Appendix 3.4). Treatment and herbivory were also not significant for cow-wheat height and flower production (Appendix 3.4).

68

3.5 Discussion

We found higher cow-wheat population density on the seismic lines than in the interior forest; however, at the individual level cow-wheat height and reproductive success did not differ between treatments. In addition, we found that cow-wheat on seismic lines were more likely to have a higher number of seeds per fruit than those in the forest. While we also found differences in vegetation at the edge and on the seismic lines, as compared to the interior forest, these were not related to the differences in cow-wheat population density between treatments. In contrast, at the individual level, understory vegetation abundance surrounding each focal individual was directly related to cow-wheat height and reproductive success. Our study shows that at the population level, cow-wheat abundance was influenced by fragmentation, but at the individual level, cow-wheat fitness was primarily influenced by competition with the understory vegetation and losses due to herbivory.

More than 20 years after seismic line creation, seismic lines continued to be distinct from the interior forest, with lower litter and canopy cover. However, I also observed "edge sealing" (Harper et al. 2005) — increased vegetation growth at the edge in the open pine stands. We found an edge influence on woody plant abundance, with higher tree and sapling density at the edge compared to both the interior forest and seismic lines. Both the edge and seismic line also had higher short shrub cover than the interior forest. This "sealing" effect can moderate the micro-climatic changes associated with forest openings (Dovciak and Brown 2014) and limit the extent of the edge influence. In addition, competition with the overstory can limit understory abundance, as was evident in our SEM analysis at the population level, where canopy cover was negatively related to understory abundance.

69

Seismic lines were more likely to have a higher number of seeds per fruit than the forest. This may be due to higher light availability on the seismic lines, due to the lack of a canopy, or it may be due to increased pollinator abundance on seismic lines (Riva et al. 2018; Nelson et al. 2021). Dawe et al. (2017) observed similar trends for *Vaccinium myrtilloides*, with higher berry production on seismic lines compared to the interior forest. Similarly, Valdes and Garcia (2011) found higher fruit production of *Primula vulgaris* in areas with higher edge density—which could also indicate increased pollinator activity around edges. In turn, the likelihood of having higher number of seeds per fruit on the seismic lines may help explain the higher population density on the seismic lines. However, population density can also be driven by changes in seed dispersal, predation and germination rates—population processes that have been shown to be altered by edge effects (Jules and Rathcke 1999; Tomimatsu and Ohara 2004), thus future studies should monitor survival after seed production through dispersal and establishment.

In contrast to our findings at the population level, treatment had no effects on cow-wheat performance; instead, understory vegetation around each focal individual was a primary driver of cow-wheat performance. Understory cover had direct positive effects on cow-wheat height, and indirect positive effects on flower and fruit production. This could be due to a confounding factor positively influencing both understory cover and cow-wheat height and fecundity, such as higher nutrient availability. Alternatively, cow-wheat individuals may grow taller when more abundant vegetation surrounds them, to out-compete their neighbors. However, this growth would come at a cost to resources available for reproduction, thus we also see the negative direct effects of understory cover on both flower and fruit production (Karlsson and Méndez 2005). This trade-off would be more evident in an annual plant like cow-wheat, which does not have stored resources from previous years. Similarly, Ågren et al. (2008) found local conditions played an

important role in the reproduction of *Vincetoxicum hirundinaria*, an herbaceous perennial, with conspecific competition limiting flower production. Unsurprisingly, we also found that herbivory, which would represent a further resource loss, negatively affected fruit production. Similarly, Gibson and Good (1987) show that herbivory is an important driver of cow-wheat mortality in New Jersey's pine stands.

This is one of only a few studies that examine the mechanisms driving edge influence on plant populations and individuals in the boreal forest. We show how structural equation modelling can be used to develop a mechanistic understanding of edge influence, as recommended by Ruffell and Didham (2016). However, this is a case study of one species with a life history not commonly found in the boreal forest. Future studies can apply a similar methodology to examine the edge influence on species with other life histories, such as clonal or shade-intolerant species, or species that require management, such as endangered or invasive species. In addition, we focused on a single growing season and were unable to account for temporal variability in plant reproduction. However, plant reproduction and their drivers can vary between years (Valdes and Garcia 2011). Long-term studies can identify the temporal variation in reproduction, which may better explain the differences in population density at the different treatments.

Table 3.1: Results of the mixed-effects models for response variables and covariates as affected by treatment (seismic line (SL), edge, forest). Results are presented for data collected at (A) the population level: cow-wheat population density, proportion of flowering cow-wheat individuals, average number of seeds per cow-wheat fruit, canopy cover, litter depth, live tree density, and total understory cover; and (B) at the level of the focal cow-wheat individual: maximum cow-wheat height, maximum no. of cow-wheat flowers and fruits per individual, herbivory, and canopy and understory cover around each focal individual. For normally-distributed variables, the F- statistic for treatment is given and for non-normally distributed variables, the chi-square statistic is given. P value is given for treatment, with significant values in bold ($P < 0.05$). When treatment was significant, the estimated marginal mean (and standard error) for each treatment is given, with superscripted letters indicating differences between treatments. See also Figures 3.2, 3.3, and 3.5.

Response variable	Distribution	Treatment	P value	Forest	Edge	SL
(A) Population response						
Cow-wheat population density	Negative binomial	8.047	**0.0179**	1.4[a] (0.3)	2.3[ab] (0.5)	3.2[b] (0.6)
Proportion of flowering CW individuals	Beta regression	5.284	0.0712			
No. of seeds per fruit	Ordinal logistic regression	6.85*	**0.033**	0.5[a]	1.3 [ab]	2 [b]
Population covariates						
Canopy cover	Normal	28.855	**<0.001**	77.2[b] (2.5)	75.2[b] (2.5)	61.7[a] (2.5)
Live tree density (No. of trees/100 m^2)	Poisson	85.16	**<0.001**	5.8[b] (0.8)	9.1[c] (1.1)	1.4[a] (0.3)
Sapling density (No. of saplings/100 m^2)	Poisson	38.696	**<0.001**	5.0[a] (1.0)	9.9[b] (1.8)	6.2[a] (1.2)
Total understory cover	Normal	2.077	0.141			
Short shrub cover	Poisson	19.213	**<0.001**	3.0[a] (0.7)	4.5[b] (1.1)	5.5[b] (1.3)
Forb cover	Normal	0.472	0.628			
Graminoid cover[†]	Normal	2.637	0.086			
Litter cover	Poisson	106.21	**<0.001**	23.1[b] (4.7)	24.5[b] (5.0)	12.1[a] (2.5)
Litter depth (cm)	Normal	7.813	**0.002**	1.7[ab] (0.2)	2.2[b] (0.2)	1.3[a] (0.2)
Soil moisture (volumetric water content)	Normal	0.456	0.638			
(B) Individual response						
Cow-wheat height	Poisson	2.349	0.309			
Number of flowers	Negative binomial	1.100	0.577			

Number of fruits	Negative binomial	0.124	0.94			
Individual covariates						
Canopy cover	Normal	17.094	**<0.001**	72.6[b] (3.2)	75.9[c] (3.2)	62.8[a] (3.2)
Total understory cover	Negative binomial	2.243	0.326			
Herbivory	Ordinal logistic regression	0.031*	0.985			
Understory host availability	Negative binomial	2.263	0.323			
Inverse distance to nearest host tree	Normal	3.402	**0.048**	0.0053[a] (0.0006)	0.0057[a] (0.0006)	0.0037[a] (0.0006)

*Effect of treatment was tested using likelihood ratio tests; the likelihood ratio statistic is given. When treatment was significant, we include the odds ratio (exponent of β estimate) instead of the estimated marginal mean. For the edge and seismic line values, the forest treatment was used as reference, and for the forest treatment the seismic line treatment was used as the reference.

[†]log_{10}-transformation applied

Table 3.2: (A) Regression coefficients for the simplified structural equation model for the relationships between treatment, canopy cover, understory cover and litter depth at the population level, and cow-wheat population density. Standardized coefficients (scaled by standard deviations) for continuous variables are given. Significant relationships are in bold (P < 0.05). Cow-wheat population density was $\log_{10}$-transformed. (B) Coefficient of determination (R^2) values for the component models of the simplified structural equation model. Marginal R^2 is the variance explained solely by fixed effects, while conditional R^2 is the variance explained by both the fixed and random effects.

(A)

Response	Predictor	Estimate	SE	df	P Value	Std. Estimate
Canopy cover	**Location**	-	-	2	**<0.001**	
Canopy cover	Forest	77.233	2.498	17		
Canopy cover	Edge	75.245	2.498	17		
Canopy cover	SL	61.710	2.498	17		
Understory cover	**Canopy cover**	-0.498	0.165	35	**0.005**	**-0.325**
Litter depth	**Location**	-	-	2	**0.0004**	
Litter depth	Forest	1.722	0.217	17		
Litter depth	Edge	2.176	0.217	17		
Litter depth	SL	1.333	0.217	17		
Cow-wheat pop. density[†]	**Location**	-	-	2	**0.021**	
Cow-wheat pop. density	Forest	0.315	0.062	17		
Cow-wheat pop. density	Edge	0.437	0.062	17		
Cow-wheat pop. density	SL	0.557	0.062	17		

* Significance of treatment is tested with an ANOVA and the estimated marginal means (and standard error) for each treatment are given instead of the regression coefficient.

[†]$\log_{10}$-transformation applied

(B)

Response	Marginal R^2	Conditional R^2
Canopy cover	0.30	0.72
Understory cover	0.10	0.67
Litter depth	0.12	0.58
Cow-wheat pop. density	0.13	0.13

Table 3.3: (A) Regression coefficients for the simplified structural equation model for the relationships between treatment, canopy and understory cover around each focal individual, cow-wheat height, and maximum number of flowers and fruits per individual. Standardized coefficients (scaled by standard deviations) for continuous variables are given. Significant relationships are in bold ($P < 0.05$). Understory cover, cow-wheat height, number of flowers and fruits were $\log_{10}$-transformed. (B) Coefficient of determination (R^2) values for the component models of the simplified structural equation model. Marginal R^2 is the variance explained solely by fixed effects, while conditional R^2 is the variance explained by both the fixed and random effects.

(A)

Response	Predictor	Estimate	SE	df	P Value	Std. Estimate
Canopy Cover	**Treatment***			2	**<0.001**	
Canopy Cover	Forest	72.588	3.201	9		
Canopy Cover	Edge	75.912	3.201	9		
Canopy Cover	SL	62.824	3.201	9		
Cow-wheat height†	**Understory cover†**	0.085	0.026	269	**0.001**	**0.208**
No. of flowers†	**Understory cover**	-0.163	0.041	268	**<0.001**	**-0.194**
No. of flowers	**Cow-wheat height**	1.360	0.089	268	**<0.001**	**0.663**
No. of fruits†	**Understory cover**	-0.117	0.041	266	**0.004**	**-0.100**
No. of fruits	**Cow-wheat height**	1.462	0.122	266	**<0.001**	**0.511**
No. of fruits	**No. of flowers**	0.592	0.059	266	**<0.001**	**0.425**
No. of fruits	**Herbivory**	-0.025	0.008	266	**0.002**	**-0.094**

* Significance of treatment was tested with an ANOVA and the estimated marginal means (and standard error) for each treatment are given instead of the regression coefficient.

$^\dagger\log_{10}$-transformation applied

(B)

Response	Marginal R^2	Conditional R^2
Canopy cover	0.15	0.61
Cow-wheat height	0.04	0.25
No. of flowers	0.43	0.57
No. of fruits	0.72	0.75
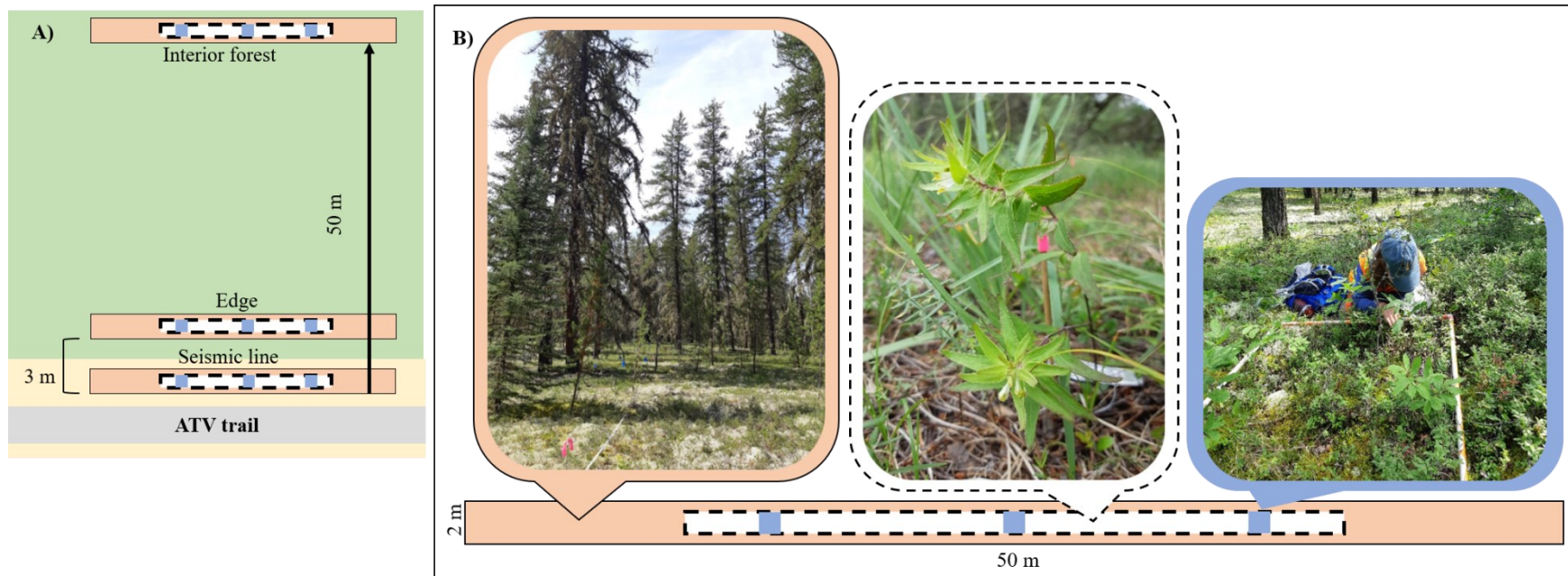
Figure 3.1: (A) Layout of belt transects at the seismic line, edge, and interior forest locations. (B) Tree and sapling density were measured in the 2 m x 50 m belt transect (tan rectangle with solid outline). Cow-wheat population density was measured within the 1 x 30 m belt transects (white rectangle with dashed outline), which were nested in the larger tree plot. Focal cow-wheat individuals were also selected within this plot (or near this plot). At the 5 m, 15 m, and 25 m points within the 1 x 30 m transect, abundance of short shrubs, forbs, and graminoids were visually estimated in 1 m^2 quadrats (blue squares).
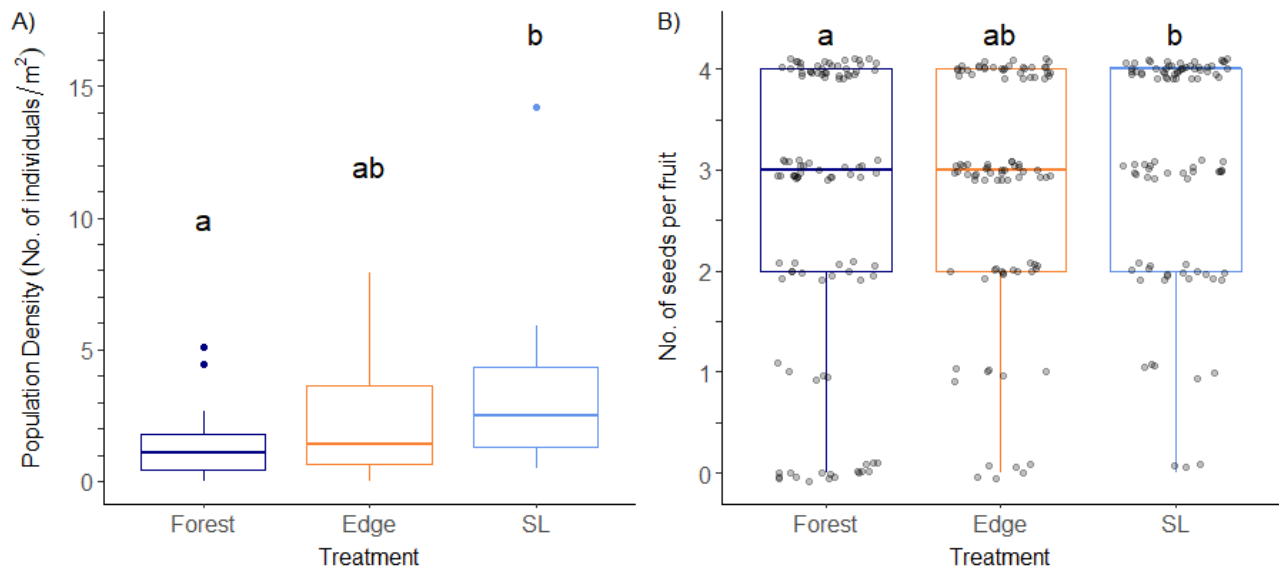
Figure 3.2: Boxplots (in Tukey style) of (A) cow-wheat population density (no. of individuals per m^2) and (B) no. of seeds per fruit for each treatment (forest, edge, or seismic line), with the raw data shown as grey circles. Generalized mixed effect models showed that treatment was significant for population density and average no. of seeds per capsule. Letters indicate significant differences between treatments based on pairwise comparisons of estimated marginal means (P < 0.05). The horizontal line within the boxplot represents the median; the lower and upper hinges represent the 25th and 75th percentiles, respectively. Whiskers represent the smallest and largest values within 1.5 times the interquartile range (IQR) and outliers (values greater than or less than 1.5 x IQR) are represented as dots outside the box and whiskers.
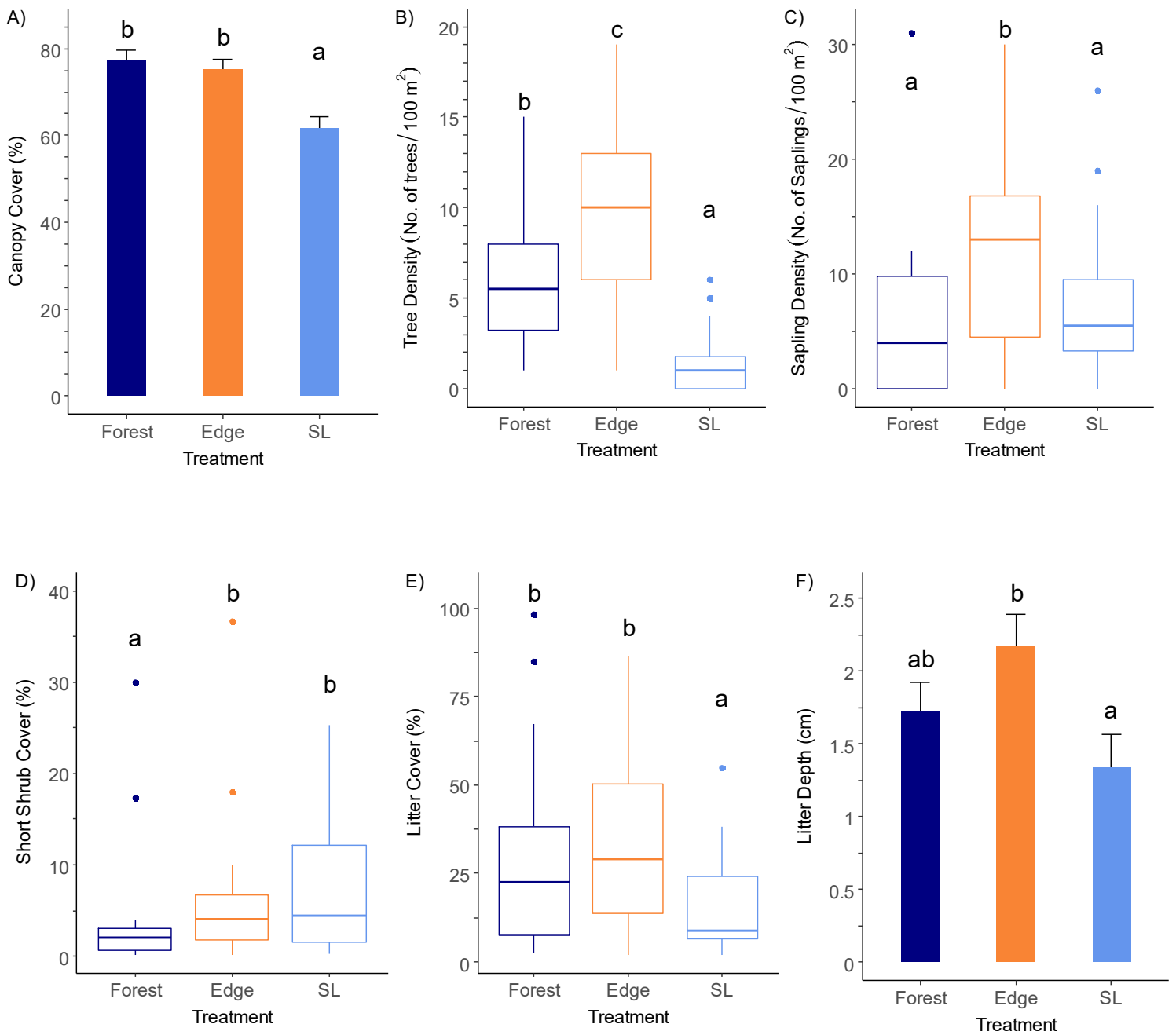
Figure 3.3: Canopy cover (A), tree density (B), sapling density (C), short shrub cover (D), litter cover (E), and litter depth (F) at the population level by treatment. (A) and (F) show means with standard errors; (B)-(E) shows boxplots (details as per Figure 3.1). Letters indicate significant differences between treatments based on pairwise comparisons of estimated marginal means (P < 0.05).
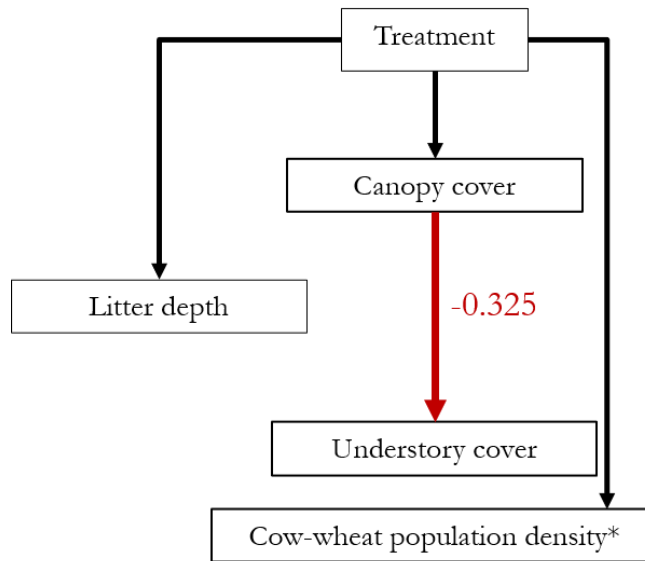
Figure 3.4: Final simplified structural equation model of direct effects on cow-wheat population density. Arrows indicate significant effects. Arrow width for significant continuous predictor variables is proportional to standardized effect sizes, which are included as arrow labels; red arrows represent negative effects, and black arrows represent treatment effect. Cow-wheat population density was $\log_{10}$-transformed. For unstandardized coefficients, see Table 3.2. See Appendix 3.3 for the results of the global structural equation model.
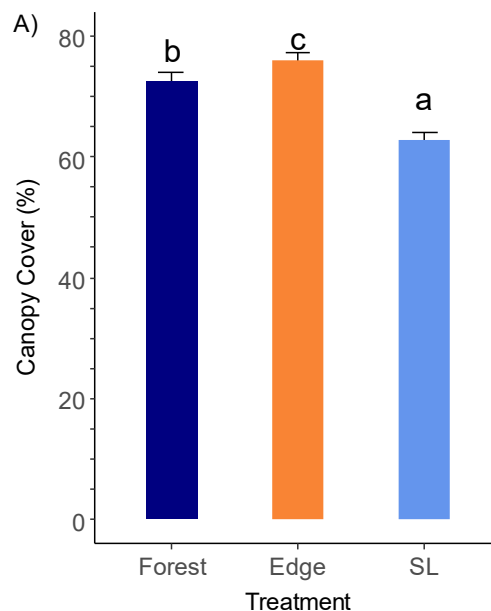
Figure 3.5: Average canopy cover around each focal cow-wheat individual in each treatment (forest, edge, or seismic line). Letters indicate significant differences between treatments based on pairwise comparisons of estimated marginal means ($P < 0.05$). Error bars represent standard error.
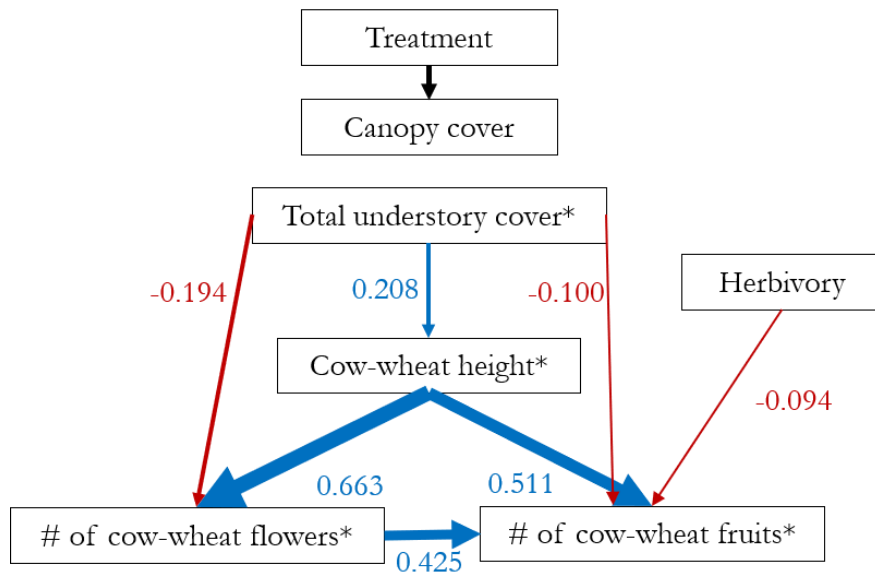
Figure 3.6: Final simplified structural equation model of direct and cascading effects on individual cow-wheat growth and fecundity (Fisher's C = 17.475, df = 20, P value = 0.622). Arrows indicate significant effects. Arrow width for significant continuous predictor variables is proportional to standardized effect sizes, which are included as arrow labels; blue arrows represent positive effects, red arrows represent negative effects, and black arrows represent treatment effect. Understory cover, cow-wheat height, maximum number of flowers and fruits were $\log_{10}$-transformed. For unstandardized coefficients, see Table 3.3. See Appendix 3.4 for the results of the global structural equation model.
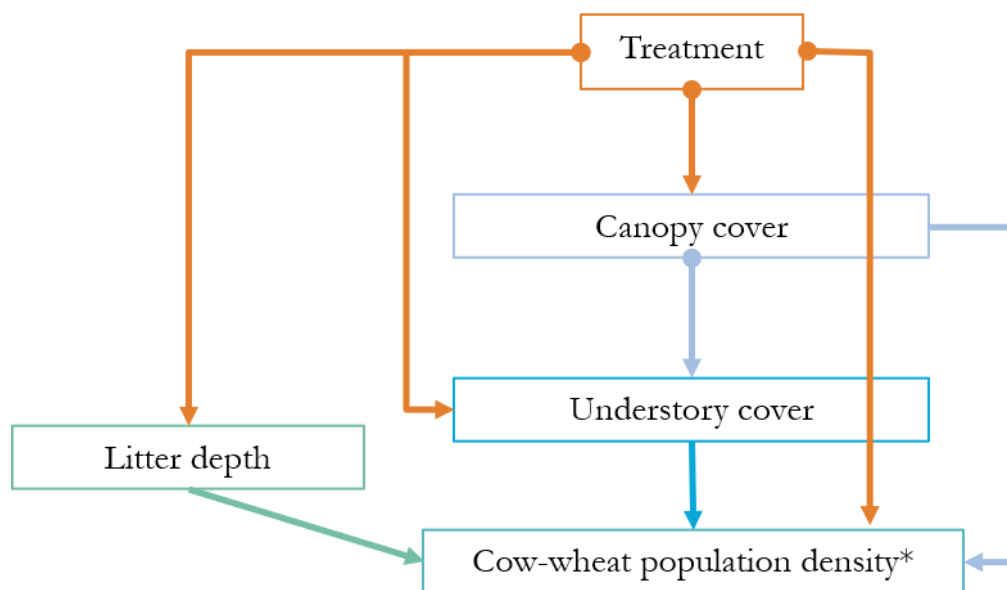
Appendix 3.1: Causal diagram of the global structural equation model at the population level. Shown are the expected relationships between treatment, canopy cover, understory cover, litter depth, and cow-wheat population density. Cow-wheat population density was $\log_{10}$-transformed.
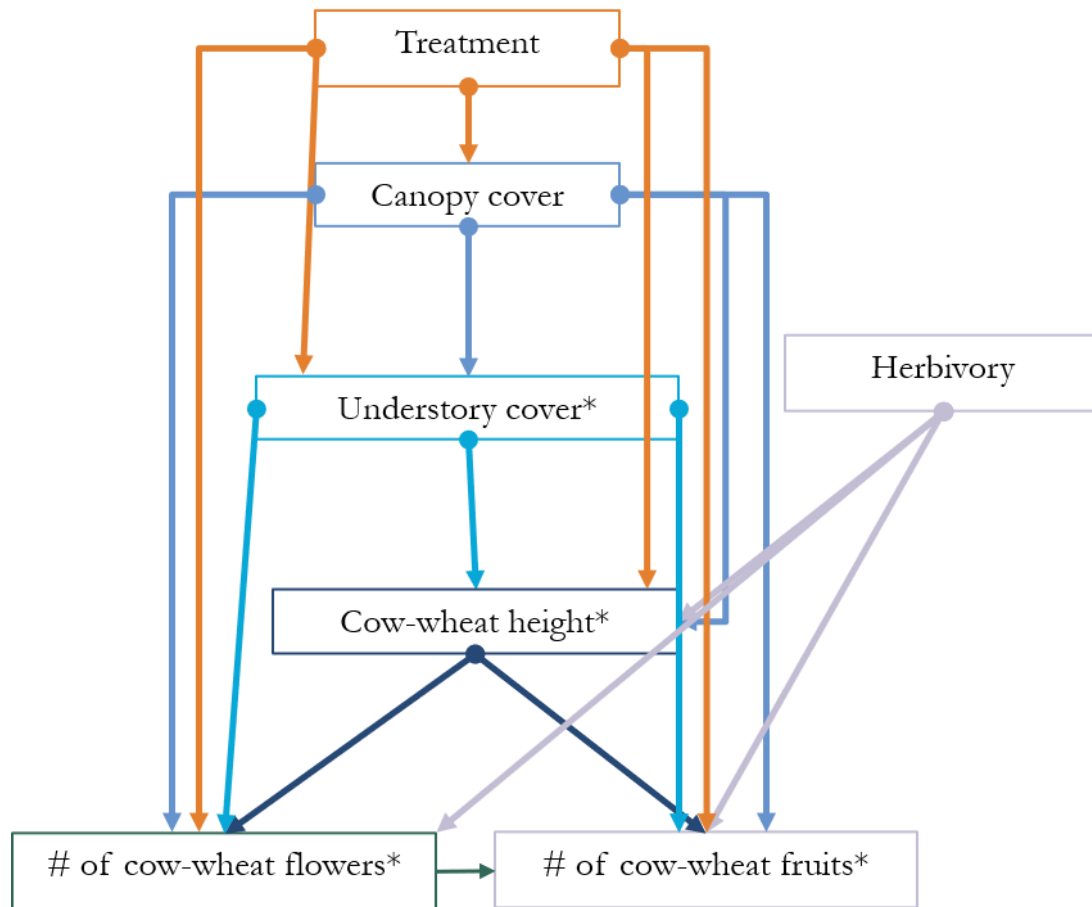
Appendix 3.2: Causal diagram of the global structural equation model at the individual level. Shown are the expected relationships between treatment, canopy and understory cover, herbivory, cow-wheat height, and flower and fruit production.

Appendix 3.3: (A) Regression coefficients for the global structural equation model for the relationships at the population level between treatment, canopy cover, understory cover, litter depth, and cow-wheat population density. Standardized coefficients (scaled by standard deviations) for continuous variables are given. Significant relationships are in bold ($P < 0.05$) and were included in the final, simplified structural equation model (Figure 3.4). Cow-wheat population density was $\log_{10}$-transformed. (B) Coefficient of determination (R^2) values for the component models of the global structural equation model. Marginal R^2 is the variance explained solely by fixed effects, while conditional R^2 is the variance explained by both the fixed and random effects.

(A)

Response	Predictor	Estimate	SE	df	Crit. value	P value	Std. Estimate
Canopy cover	**Location**	-	-	2	57.711	**<0.001**	
Canopy cover	Forest	77.233	2.498	17	30.925		
Canopy cover	Edge	75.245	2.498	17	30.129		
Canopy cover	SL	61.710	2.498	17	24.709		
Understory cover	**Canopy cover**	-0.597	0.244	33	-2.445	**0.02**	**-0.390**
Understory cover	Location	-	-	2	1.676	0.433	
Understory cover	Forest	24.908	4.715	17	5.283		
Understory cover	Edge	28.963	4.592	17	6.308		
Understory cover	SL	23.861	5.078	17	4.699		
Litter depth	**Location**	-	-	2	15.625	**0.0004**	
Litter depth	Forest	1.722	0.217	17	7.924		
Litter depth	Edge	2.176	0.217	17	10.012		
Litter depth	SL	1.333	0.217	17	6.135		
Cow-wheat pop. density[†]	Canopy cover	0.004	0.004	31	1.154	0.257	0.195
Cow-wheat pop. density	Understory cover	0.003	0.002	31	1.266	0.215	0.172
Cow-wheat pop. density	Litter depth	-0.043	0.042	31	-1.028	0.312	-0.151
Cow-wheat pop. density	**Location**	-	-	2	7.130	**0.028**	
Cow-wheat pop. density	Forest	0.301	0.065	17	4.603		
Cow-wheat pop. density	Edge	0.437	0.065	17	6.774		
Cow-wheat pop. density	SL	0.571	0.070	17	8.125		

* Significance of treatment is tested with an ANOVA and the estimated marginal means (and standard error) for each treatment are given instead of the regression coefficient.

[†]$\log_{10}$-transformation applied

(B)

Response	Marginal R^2	Conditional R^2
Canopy cover	0.30	0.72
Understory cover	0.12	0.69

Litter depth	0.12	0.58
Cow-wheat pop. density	0.17	0.17

Appendix 3.4: (A) Regression coefficients for the global structural equation model for the relationships between treatment, canopy and understory cover around each focal individual, cow-wheat height, and maximum number of flowers and fruits per individual. Standardized coefficients (scaled by standard deviations) for continuous variables are given. Significant relationships are in bold ($P < 0.05$) and were included in the final, simplified structural equation model (Figure 3.6). Understory cover, cow-wheat height, maximum number of flowers and fruits were $\log_{10}$-transformed. (B) Coefficient of determination (R^2) values for the component models of the global structural equation model. Marginal R^2 is the variance explained solely by fixed effects, while conditional R^2 is the variance explained by both the fixed and random effects.

(A)

Response	Predictor	Estimate	SE	df	P value	Std. Estimate
Canopy cover	**Treatment***			2	**<0.001**	
Canopy cover	Forest	72.588	3.201	9		
Canopy cover	Edge	75.912	3.201	9		
Canopy cover	SL	62.824	3.201	9		
Understory cover	Canopy cover	-0.002	0.002	269	0.116	-0.106
Understory cover	Treatment*			2	0.207	
Understory cover	Forest	1.397	0.074	9		
Understory cover	Edge	1.396	0.075	9		
Understory cover	SL	1.288	0.075	9		
Cowwheat height	Canopy cover	-0.001	0.001	267	0.507	-0.050
Cowwheat height	**Understory cover**	0.081	0.027	267	**0.003**	**0.199**
Cowwheat height	Herbivory	-0.002	0.005	267	0.697	-0.021
Cowwheat height	Treatment*			2	0.418	
Cowwheat height	Forest	1.155	0.023	9		
Cowwheat height	Edge	1.167	0.024	9		
Cowwheat height	SL	1.134	0.024	9		
No. of flowers	Canopy cover	0.000	0.001	266	0.872	-0.009
No. of flowers	**Understory cover**	-0.160	0.042	266	**<0.001**	**-0.191**
No. of flowers	**Cowwheat height**	1.361	0.090	266	**<0.001**	**0.664**
No. of flowers	Herbivory	0.001	0.008	266	0.931	0.004
No. of flowers	Treatment*			2	0.619	
No. of flowers	Forest	0.714	0.038	9		
No. of flowers	Edge	0.744	0.038	9		
No. of flowers	SL	0.747	0.039	9		
No. of fruits	Canopy cover	0.000	0.001	265	0.687	0.016
No. of fruits	**Understory cover**	-0.110	0.042	265	**0.008**	**-0.095**
No. of fruits	**Cowwheat height**	1.481	0.123	265	**<0.001**	**0.518**
No. of fruits	**No. of flowers**	0.589	0.059	265	**<0.001**	**0.423**
No. of fruits	**Herbivory**	-0.025	0.008	265	**0.003**	**-0.094**

No. of fruits	Treatment*			2	0.142
No. of fruits	Forest	0.976	0.027	9	
No. of fruits	Edge	0.952	0.028	9	
No. of fruits	SL	1.027	0.029	9	

* Significance of treatment is tested with an ANOVA and the estimated marginal means (and standard error) for each treatment are given instead of the regression coefficient.

(B)

Response	Marginal R^2	Conditional R^2
Canopy cover	0.15	0.61
Understory cover	0.02	0.47
Cow-wheat height	0.05	0.27
No. of flowers	0.43	0.57
No. of fruits	0.73	0.75

Chapter 4: Disturbing to restore? Effects of mounding on understory communities on seismic lines in treed peatlands

4.1 Abstract

In peatlands, micro-topography strongly affects understory plant communities. Disturbance can result in a loss of micro-topographic variation, primarily through the loss of hummocks. To address this, mounding treatments can be used to restore micro-topography. I examined the effects of mounding on the understory vegetation on seismic lines in wooded fens. Seismic lines are deforested linear corridors (~3-8 m wide), created for oil and gas exploration. The objectives were to compare the recovery of understory communities on unmounded and mounded seismic lines and determine how recovery varies with micro-topographic position. Recovery was evident in the unmounded seismic lines, with higher shrub and total understory cover at the 'tops' of the small, natural hummocks than at lower micro-topographic positions —much like the trends in adjacent treed fens. In contrast, mounding treatments that artificially created hummocks on seismic lines significantly changed understory communities. Mounded seismic lines had higher forb cover, much lower bryophyte cover, less variation along the micro-topographic gradient, and community composition less similar to the reference sites than were unmounded seismic lines, due to higher abundance of marsh-associated species. These results suggest mounding narrow seismic lines can be detrimental to the recovery of the understory communities in treed peatlands.

4.2 Introduction

Forests across the world are experiencing increases in the levels of human disturbance that are influencing their ecological function and biodiversity (Haddad et al. 2015). In regions with oil and gas reserves, seismic lines represent a major source of human-caused disturbance, where linear corridors of cleared forests are used to locate fossil fuel reserves (Dabros et al. 2018). There are two types of seismic lines: conventional seismic lines (approximately 4-12 m wide) and low-impact seismic lines (approximately 3 m wide). Conventional seismic lines are increasingly being replaced with low-impact seismic lines to mitigate the environmental impacts of oil exploration in the boreal. Low-impact seismic lines are created using lighter equipment and thus minimize the disturbance on the understory vegetation and underlying soil (Dabros et al. 2018). Although seismic lines are relatively narrow, they can extend for kilometers (Pattison et al. 2016) and can be locally dense (up to 40 km km^{-2}). In addition, vegetation on seismic lines can be slow to recover (Lee and Boutin 2006; van Rensen et al. 2015) leaving a lasting imprint. Seismic lines affect understory vegetation composition, both within the seismic line itself and into the adjacent forest due to edge effects (MacFarlane 2003; Dabros et al. 2017). Lastly, seismic lines also act as travel corridors for predators, such as wolves, by improving accessibility to previously difficult terrain (Dickie et al. 2017a; DeMars and Boutin 2018).

Due to the increased habitat fragmentation and predation risk to threatened species, such as caribou (Committee on the Status of Endangered Wildlife in Canada 2014), restoration of seismic lines, as measured by tree establishment and the limitation of predator movement, has become a priority. One restoration tool being used is "mounding" – the excavation and piling of soil to create "mounds" (Sutton 1993; Pyper et al. 2014). The purpose of mounding is to create suitable micro-habitats for successful tree establishment and to hinder human and predator use of

legacy seismic lines (Government of Alberta 2017). In this study, we focus on measuring the effectiveness of mounding to restore ground vegetation in wooded moderate-rich fens, where recovery of seismic lines has been shown to be particularly slow (Lee and Boutin 2006; van Rensen et al. 2015). While mounding has been shown to have promising effects on tree establishment in peatlands (Lieffers et al. 2017; Filicetti et al. 2019), the effects on other ecological aspects of peatlands—notably understory plant communities—requires further study. Since low-impact seismic lines have extensive coverage in areas of active exploration for oil sands resources, I will be focusing on the impact of mounding low-impact seismic lines on the understory vegetation.

Peatlands are known for their hummock-hollow topography, which creates a diversity of micro-habitats for peatland flora and fauna. Hummocks are mounds of elevated peatland vegetation, about 20-50 cm above the lowest surface level, while hollows are depressions or the lowest surface level. Understory communities are stratified along the hummock-hollow gradient based on their ability to tolerate anoxic conditions, or in the case of bryophytes, tolerate desiccation (Rydin and Jeglum 2006; Vitt and Wieder 2008). Some forbs and graminoids are adapted to survive the flooded conditions of hollows and lower micro-topographic positions (i.e., having aerenchyma), while woody plants are inhibited by saturated conditions (Pouliot et al. 2012). In contrast, distance from the water table limits bryophyte distribution based on their ability to avoid desiccation in the relatively drier hummock tops (Rydin and Jeglum 2006). In turn, development of hummock-hollow micro-topography is in large part a reflection of differences in net primary production and decomposition rates among bryophyte species and the role of vascular plants, especially shrubs, providing structural support for

upward-growth of bryophytes (Malmer et al. 1994; Rydin et al. 2006; Vitt and Wieder 2008; Pouliot et al. 2011; Turetsky et al. 2012).

Compaction of peat caused by machine traffic along seismic lines in peatlands results in them being depressed in elevation relative to the surrounding areas and exhibiting reduced micro-topographic complexity (Stevenson et al. 2019). The reduced elevation leads to wetter conditions on the seismic line than in the reference adjacent forest (Dabros et al. 2017); this can hinder establishment of woody vegetation. Mounding treatments result in an elevated micro-habitat, which increases habitat heterogeneity and allows vegetation to escape the saturated conditions common to compacted peatlands (Lieffers et al. 2017; Caners et al. 2019). For example, in wooded moderate-rich fens, Caners et al. (2019) found higher richness and cover of woody vegetation on mounded portions of abandoned, flooded wellpads. However, it is a delicate balance as conditions that are too dry or too far removed from the water table can inhibit bryophyte establishment. For example, Price et al. (1998) found that in drier, post-harvested peatlands (bog and poor fen complex), elevated micro-topographic positions had reduced *Sphagnum* colonization, due to a drier and warmer micro-climate. Thus, mounding may benefit vascular plants, but could also result in reduced bryophyte cover at the tops of artificial hummocks. This may benefit vascular plants since they would otherwise compete with bryophytes for nutrients and space (Malmer et al. 1994; Rydin and Jeglum 2006).

Here the objective was to compare the recovery of understory plant communities on mounded and unmounded seismic lines in wooded moderate-rich fens. We defined recovery as similarity to the adjacent reference wooded fen (hereafter referred to as reference sites). Since understory communities stratify along the hummock-hollow gradient, I compared the effects of mounding at three micro-topographic positions: top of hummock, slope or side of the hummock,

and the level ground adjacent to mounds. In the reference sites, I expected shrub cover and total vascular cover to be highest at the tops of the hummocks, as the anoxic conditions at lower micro-topographic positions will limit the establishment of vascular plants. Since some forb and graminoid species are adapted to anoxic conditions, I did not expect to see a strong influence of micro-topographic position on forb and graminoid cover. Hummocks are naturally created by bryophyte growth; thus, I expected higher bryophyte cover at the tops of the hummocks. In the mounding treatments, I expected the restoration of the aerated rooting zone to lead to higher total vascular plant cover and shrub cover at the 'top' of the mounds, much like in the reference sites. However, I expected the drier conditions at the 'top' of the mounds to limit bryophyte establishment and reduce bryophyte cover. Since unmounded seismic lines have limited micro-topography, I expected no difference in vascular plant and shrub cover between positions. In addition, I expected the wetter conditions of seismic lines would result in higher bryophyte cover and reduced shrub cover.

4.3 Methods

4.3.1 Data collection

This study was conducted in treed moderate-rich fens near Kirby Lake, Alberta, approximately 45 km south of Conklin, Alberta, Canada (55°21'57.51"N, 111°09'46.10"W). Sites were considered moderate-rich fens based on ground water pH values that ranged from 5.69 to 7.12 (μ = 6.46) and a moderate electrical conductivity (μ = 102.84 μs cm^{-1}). Reference wooded fens were dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) or tamarack (*Larix laricina* (Du Roi) K. Koch; Appendix 4.1)

and *Rhododendron groenlandicum* ((Oeder) Kron and Judd), *Maianthemum trifolium* ((L.) Sloboda), and *Sphagnum* spp. in the understory layer. Average daily temperature in the region is 2.1°C with an average annual precipitation of 421 mm (Environment and Climate Change 2013 from nearby meteorgological station: Cold Lake A).

Seismic lines in the area were created in 1998/2001 during exploration for bitumen (oil sands) reserves as part of a "3D" seismic program, which involves creation of narrow (~ 3 m width) lines in an intensive (50 to 100 m spacing) grid. These seismic lines were created in the winter, with lightweight equipment to minimize disturbance of soil and the understory. Travel by machinery on these lines has been limited since their creation. A sample of representative seismic lines were mounded in 2015 and sampling occurred three years later (late June to mid July 2018). Mounding was done with a construction excavator with a bucket attachment, which excavated and placed the inverted substrate adjacent to the newly created pit. Mounds were created to be 0.75 m wide, 1 m long, and 0.80 m tall and placed every 6 m along the seismic lines. For additional details on mounding specifications, see Filicetti et al. (2019).

I sampled seismic lines with mounding treatments (n = 8) and unmounded seismic lines (n = 9) (Appendix 4.2). For each of these I also sampled the adjacent wooded fen to represent the reference condition. Sampling for the reference wooded fen took place 25 to 50 m from the center of the seismic line, with the ecosite type kept consistent between the seismic line and reference wooded fen. Average mound height (± standard error) was 40.1± 4.0 cm on the mounded seismic lines, 32.1 ± 1.4 cm on the unmounded seismic lines, and 30.7 ± 2.2 cm in the reference sites (n = 5; C.M.A. Franklin unpublished data).

At each seismic line and paired reference wooded fen, I established a 20 m transect along the center of the seismic line and a parallel one in the adjacent reference wooded fen. Three

mounds were chosen and sampled along each transect, those closest to the 5 m, 15 m, and 20 m distances. For each selected mound, I used a 20 cm by 20 cm (400 cm^2) quadrat to assess vegetation at each of three micro-topographic positions: the top of the mound, the south-facing slope, and on the adjacent level ground (Appendix 4.3). To maintain consistency across the different positions sampled, I only sampled one quadrat for each slope position. To ensure that the effect of aspect was consistent across treatments, I standardized our sampling to the south-facing slope as I expected this aspect to have the strongest effect. Since hollows in our sites were predominantly pools of water with little to no vegetation, I excluded this micro-topographic position from the analysis, but note that the mounding treatment overall led to saturated hollows that had limited plant cover. In each quadrat, I visually estimated the cover of each understory vascular species and total bryophyte cover (we are exploring community-level responses of the bryophyte community in a separate paper). For unmounded seismic lines with no clear mounds present, quadrats were randomly placed with the same micro-topographic positions being maintained relative to each other—i.e., the level ground position was still placed at the lowest position, followed by slope, and top at the highest position.

Groundwater samples were collected from shallow, excavated wells at the 10 m midpoint transect distance using 500 mL Nalgene bottles. Samples were stored in 4°C for 48 hours prior to analysis by the Biogeochemical Analytical Service Laboratory (BASL) at the University of Alberta. Samples were analyzed for pH, electrical conductivity, alkalinity (mg/L CaCO$_3$), and base cation content (mg/L).

4.3.2 Statistical analysis

Response variables for vascular plants were species richness, Shannon's diversity, Simpson's diversity, total cover, and shrub, forb, graminoid, and bryophyte cover. To examine the effects of mounding treatment, micro-topographic position, and their interaction, I used linear mixed effects models with mounding treatment (mounded seismic line, unmounded seismic line, reference sites), microtopographic position, and their interactions as fixed effects, and seismic line as a random effect (the three mounds on a transect at a given sampling location were treated as sub-samples). For the model comparisons, the reference treatment and the 'level' position were used as reference categories. Vascular plant diversity indices and bryophyte cover used a gaussian distribution, while total vascular plant cover, shrub cover, forb cover, and graminoid cover were log-transformed and analyzed with a gaussian distribution. All analyses were done with the lme4 package (Bates et al. 2015) in the R statistics programming environment, version 3.5.2 (R Core Team 2018). Residuals were examined to ensure normality and homogeneity of variance. When the predictor variables were significant, post-hoc analyses were completed using the emmeans package, with p-values adjusted using the Tukey HSD method (Lenth 2020). When the interaction term was significant, I tested for differences between all micro-topographic positions within each treatment, and between treatments for each micro-topographic position.

Finally, the effects of treatment, micro-topographic position, and their interaction on vascular community composition were visualized using non-metric multidimensional scaling (NMDS) and tested using permutational multivariate analysis of variance (PERMANOVA), with 1000 permutations for tests of significance. A separate NMDS showed that the reference sites for unmounded seismic lines did not differ from the reference sites for mounded seismic lines [available from authors]. NMDS and PERMANOVA were done with the vegan package

(Oksanen et al. 2018). Indicator species for each treatment and micro-topographic position were identified using the indicspecies package (De Cáceres and Legendre 2009). For the indicator species analysis, rare species—species found in less than 5% of the sampled sites—were not included.

4.4 Results

4.4.1 Vascular plant diversity and cover

For vascular plant species richness, Shannon's and Simpson's diversity, forb cover, and graminoid cover, only the treatment effect of mounding was significant (Table 4.1). The reference sites had significantly lower (~35%) vascular plant richness, diversity (Shannon's and Simpson's), and graminoid cover (from an average of 1% in reference sites to approx. 5% in both seismic lines) than mounded or unmounded seismic lines, which did not differ from one another (Figures 4.1 and 4.2B). Graminoid cover in unmounded sites was composed primarily of *Carex* spp. Forb cover was slightly significantly higher on the mounded seismic lines than on unmounded seismic lines and in the reference sites, which did not differ from one another (Figure 4.2A).

Shrub cover was significantly affected by both mounding treatment and position, but not their interaction (Table 4.1, Figure 4.3). For all treatments, the top position had significantly higher shrub cover (~60%) than the slope or the level position; the latter two microtopographic positions did not differ (Figure 4.3A). Reference sites had significantly higher shrub cover than unmounded seismic lines, while mounded seismic lines were intermediate and did not differ from either (Figure 4.3B).

For total vascular plant cover, the interaction between treatment and position was significant (Table 4.1, Figure 4.4). In the reference sites, the 'top' microtopographic

95

position had significantly higher vascular cover (~50%) than the 'slope' position (Figure 4.4); values for the 'level' position were intermediate and did not differ from either (Figure 4.4). On the mounded seismic lines, there were no significant differences in vascular cover between the different micro-topographic positions (Figure 4.4). On the unmounded seismic lines, the 'top' position had significantly higher vascular cover (~60%) than the 'level' position (Figure 4.4); vascular cover on the 'slope' position was intermediate and did not differ from either (Figure 4.4). There were no significant differences in vascular cover between the treatments for any of the micro-topographic positions.

All three treatments were dominated by *Rhododendron groenlandicum, Maianthemum trifolium,* and *Betula pumila. M. trifolium* was most abundant at the level position for all three treatments (Appendix 4.4). For both unmounded seismic lines and reference sites, *Rhododendron groenlandicum* was most abundant at the top position, while in mounded sites, *R. groenlandicum* cover did not differ between positions. Both mounded seismic lines and reference sites were also dominated by *Rubus chamaemorus* and *Menyanthes trifoliata,* with *M. trifoliata* having the highest cover at the level position. *Equisetum fluviatile* was also a dominant species on mounded seismic lines. *Salix planifolia* and *Carex aquatilis* also dominated on unmounded seismic lines, with *S. planifolia* being most abundant at the top position.

4.4.2 Bryophyte cover

For bryophyte cover, the interaction between treatment and position was significant (Table 4.1, Figure 4.5). In the reference site, the 'level' position had significantly less (~30%) bryophyte cover than both the 'slope' or 'top' position, which did not differ from one another (Figure 4.5). In contrast, on mounded seismic lines the 'top' position had significantly lower

bryophyte cover (~70%) than both the 'level' and 'slope' positions, which did not differ from one another (Figure 4.5). On unmounded seismic lines, there were no significant differences in bryophyte cover between the positions (Figure 4.5).

Looking at bryophyte cover between treatments for each micro-topographic position separately, there were significant differences between all three treatments for the slope and top positions. In both cases the reference site had significantly higher (~30%) bryophyte cover than unmounded treatments, which had significantly higher cover (~50%) than mounded seismic lines (Figure 4.5). For the level position, there were no significant differences in bryophyte cover between treatments (Figure 4.5). For both unmounded and reference sites, *Sphagnum* spp. were the dominant bryophytes at the slope and top position.

4.4.3 Vascular community composition

Treatment, micro-topographic position, and their interaction were significant for vascular plant community composition (Table 4.2). In the reference sites, composition at the 'level' position was significantly different from both the 'slope' and 'top' positions, which did not differ from one another (Table 4.3). In both mounded and unmounded seismic lines, composition at the 'level' position significantly differed from the 'top' position; the 'slope' position did not differ from either the 'top' or the 'level' position (Table 4.3). There were significant differences between all three treatments for the 'slope' and 'top' position for vascular plant composition (Table 4.3). At the 'level' position, the reference sites had significantly different composition from both mounded and unmounded seismic lines, which did not differ from each other (Table 4.3).

97

The NMDS ordination (based on 3 dimensions with a final stress of 0.178) showed that the vascular plant community composition of the three micro-topographic positions were nested within each other in order of micro-topographic position: the 'top' position was nested within the 'slope' position, which was nested within the 'level' position (Figure 4.6A). *Caltha palustris, Comarum palustre,* and *Maianthemum trifolium* were associated with the 'level' position, while *Drosera rotundifolia, Vaccinium microcarpum, Salix* spp., *Populus tremuloides* seedlings and *Betula pumila* were associated with the 'top' position. The NMDS also showed some separation between the three treatments, with unmounded sites found in between the clusters of the reference sites and mounded sites (Figure 4.6B). In addition, unmounded sites strongly overlapped with the reference sites cluster (Figure 4.6B). *Populus tremuloides* seedlings, *Chamerion angustifolium, Calamagrostis* spp., *Caltha palustris*, *Equisetum* spp., and *Petasites frigidus* were associated with mounded seismic lines, while woody plants were associated with the reference wooded fens.

Based on the indicator analysis, *Rubus chamaemorus* and woody species, such as *Rhododendron groenlandicum, Vaccinium vitis-idaea,* and *Picea mariana,* were indicator species for the reference sites (Table 4.4). *Equisetum* spp. and *Stellaria* spp. were indicators for the mounded sites (Table 4.4). Finally, peatland-associated species, such as *Vaccinium microcarpum, Carex magellanica, Carex chordorrhiza*, and *Andromeda polifolia*, were indicators for the unmounded seismic lines (Table 4.4). There were no indicator species for the micro-topographic positions.

4.5 Discussion

Mounding of seismic lines changes the abundance (cover) of both vascular plants and bryophytes with the effects varying by micro-topographic position. As expected, shrub cover was

lower on the unmounded seismic lines than in the reference sites. In addition, shrub cover was higher at the 'top' position for both the mounded seismic lines and reference sites. However, contrary to our expectations, this gradient in shrub cover along the micro-topographic positions also occurred in unmounded seismic lines—where we expected micro-topography to be limited. In reference sites, we found total vascular cover was higher at the 'top' of hummocks. Unexpectedly, unmounded seismic lines also had higher vascular cover at the 'top' of the mounds, while total vascular cover did not differ with position in mounded seismic lines. In line with our hypotheses, the 'top' of hummocks had higher bryophyte cover than lower micro-topographic positions in the reference sites, while within mounded seismic lines, bryophyte cover was lower at the 'top' of the hummocks compared to lower micro-topographic positions. Lastly, as expected, forb and graminoid cover did not differ between micro-topographic positions.

Unmounded seismic lines reflected a recovering community. Though we expected limited micro-topographic variation on unmounded lines, we found total vascular plant cover and shrub cover followed similar trends across micro-topographic positions as in the reference treed fen. Although shrub cover was lower on the unmounded seismic lines than in the reference sites, it is interesting to note that the natural hummock development on unmounded seismic lines had reached a height which supports significantly higher shrub cover than the lower micro-topographic positions. This reflects the presence of an aerated rooting zone on hummocks, which is required for shrub growth and is one objective of the mounding treatments (Rydin and Jeglum 2006). The indicator species analysis further illustrates shrub recovery, with two shrub species (*Andromeda polifolia* and *Salix planifolia*) identified as indicators of unmounded seismic lines. A developing

shrub layer will help with continued hummock formation as shrubs provide structural support to

the upward-growth of bryophytes (Pouliot et al. 2012). Changes in total vascular plant cover and

the NMDS ordination further illustrates the recovery of the vascular community composition on

unmounded seismic lines as both show the similarity of unmounded seismic lines to reference

sites. Lastly, the indicator species associated with unmounded sites were predominantly species

common in peatlands, such as *Carex magellanica* and *Andromeda polifolia*; thus indicating a

trajectory of continued peatland development, rather than a shift towards a different ecosite. As

Graf (2009) suggests, recovery on legacy seismic lines may not be as nonexistent as the lack of

tree regeneration might be taken to indicate.

Understory recovery on the unmounded seismic lines was also reflected in the changes of

bryophyte cover, with unmounded seismic lines having significantly higher bryophyte cover than

in mounded seismic lines. The recovery of bryophyte cover on unmounded seismic lines reflects

their tolerance for the flooded conditions of seismic lines and their faster growth in wet

conditions, as mound height in unmounded seismic lines was comparable to those in the

reference sites. In their submergence experiments, Borkenhagen and Cooper (2018) found that

post-submergence, bryophytes species tolerant to flooding compensated in growth for the loss of

bryophytes that were more sensitive to flooding; thus, total bryophyte cover was resilient to

flooding. Experimental studies also show that growth of some *Sphagnum* spp., such as *S.

angustifolium,* is not hindered by shallow flooding and optimal bryophyte growth occurs when

the water level is close to the surface (Rochefort et al. 2002; Graf and Rochefort 2010).

In contrast to our reference treed fen sites, bryophyte cover on mounded seismic lines

was significantly reduced on the tops of the artificial hummocks. This is likely a result of

unsuitable micro-climatic conditions in the 'top' position of the artificial hummocks, as

bryophytes, especially *Sphagnum* spp., can have limited tolerance of extended periods of desiccation (Price et al. 1998; Turetsky et al. 2012). In peatlands, natural hummocks develop by the upward growth of bryophytes. As hummock height increases, bryophytes at the top of hummocks rely on capillary action to maintain access to the water table and avoid desiccation (Rydin and Jeglum 2006; Vitt and Wieder 2008). However, with mounding treatments, this connection to the water table is lost and could explain the limited bryophyte establishment on the 'tops' of the mounds, with a drier micro-climate. In post-harvested peatlands, Price et al. (1998) found increased soil temperatures and reduced soil moisture on raised micro-topographic positions, which proved to be unsuitable for colonization of *Sphagnum*. The presence of vascular plants or early-successional bryophytes on the hummocks could ameliorate the micro-climatic conditions (Groeneveld et al. 2007; Graf and Rochefort 2010), allowing for bryophyte abundance to increase with time. On the other hand, high levels of vascular plant cover could also be detrimental to bryophyte growth, since vascular plants can limit light available to bryophytes (Malmer et al. 1994; Graf and Rochefort 2010).

Thus, while mounding has been shown to improve tree establishment (Lieffers et al. 2017; Filicetti et al. 2019), we found it resulted in a loss of bryophyte cover. Bryophyte cover, however, is only one aspect of the bryophyte community. For example, Caners et al. (2019) found unmounded portions of a wellpad had higher cover, but lower richness, of true mosses (class: Bryopsida) than mounded portions. In general, the loss in bryophyte cover on mounded sites is concerning as bryophytes are primarily responsible for peat accumulation and play an important role in ecosystem functioning (Turetsky et al. 2012).

In addition to the loss of bryophyte cover, mounding seems to cause a shift in vascular community composition. In the NMDS ordination, mounded seismic lines are further away from the reference sites than the unmounded seismic lines (Figure 4.6), with higher abundance of marsh-associated species, such as *Equisetum fluviatile, Caltha palustris*, and *Petasites frigidus*, and disturbance-adapted species, such as *Chamerion angustifolium* and *Populus tremuloides.* This is further reflected in the indicator species analysis, where disturbance-adapted species, such as *Equisetum arvense* and *Stellaria* spp., are indicators of mounded seismic lines (Table 4.4). The shift in vascular community composition could be temporary, as we sampled only a few years after the application of mounding treatments. However, if bryophyte dominance and peat development are not re-established, mounded seismic lines could potentially develop into a different ecosite type.

Caners et al. (2019) studied the effects of mounding that occurred immediately after decommissioning of well pads in treed peatlands; they found that mounding improves recovery of the understory communities. However, in our study we not only found that recovery was well underway in unmounded seismic lines, but we also found that mounding could be detrimental to understory recovery. The difference between our findings could be due to the difference in disturbance severity between well pads and seismic lines. Well pads not only undergo repeated peat compression due to traffic from heavy machinery but are also intentionally compressed and additional water introduced to some pads in order to improve frost penetration (Caners et al. 2019). In contrast, compression of peat on seismic lines is a by-product of machine traffic, and as part of best management practices compression is minimized through the use of lightweight equipment (Dabros et al. 2018). The saturated conditions on seismic lines are due to this compression, with no additional water introduced to the system. Thus, we can expect the peat

compression and subsequent flooding in seismic lines to be relatively mild compared to the disturbance experienced on well pads; thus, recovery of these seismic lines may require minimal intervention. Another important difference between the Caners et al. (2019) study and ours is that in Caners et al. (2019) mounding was applied directly after the wellpads were disabled whereas in ours mounding was applied to the site approximately 15 years after seismic line creation. Restoration of older legacy seismic lines will always be delayed for several years after seismic line creation (Dabros et al. 2018). These results highlight the need for development of restoration treatments that are specific to different disturbance types.

More work is needed to examine bryophyte diversity and composition between the three treatments, as well as continued monitoring to determine whether: 1) bryophyte cover on the tops of the artificial hummocks will recover; 2) tree growth is faster on these artificial hummocks; and 3) the artificial hummocks will cause shifts in understory composition over time. Studies also need to explore differences in recovery along the bog-fen gradient (but see Filicetti et al. 2019). Lastly, further research should investigate the effects of mounding on other ecological measures, especially the effects on carbon cycling and hydrological flow, as peatlands play an important role in regulating these (Rydin and Jeglum 2006; Strack et al. 2019).

We found signs of recovery in the understory communities of unmounded low-impact seismic lines. This indicates that recovery may be slow, but not entirely lacking on narrow, linear disturbances in treed peatlands (Graf 2009). However, our study only examined low-impact seismic lines, which undergo minimal understory and soil disturbance. In addition, their narrow width allows for proximity to diaspores from the

adjacent reference treed fen, which can facilitate regeneration. Further research should examine the recovery of the understory in larger, conventional seismic lines since responses may differ from those reported here on low-impact seismic lines.

In addition, our study shows re-disturbing these linear footprints to apply a restoration treatment, could have detrimental effects on the understory. This is primarily shown through a significant reduction of bryophyte cover in mounded seismic lines. The loss in bryophyte cover may assist with tree regeneration, since bryophytes can limit tree growth through competition for nutrients and burial of seedlings (i.e., vascular plants must keep up with the growth of *Sphagnum*) (Malmer et al. 1994; Rydin and Jeglum 2006). However, bryophytes are also the drivers of peat accumulation and play an important role in overall peatland ecosystem functioning (Graf and Rochefort 2010). In fact, restoration efforts in harvested peatlands in eastern Canada often have the short term-objective of restoring *Sphagnum* or brown moss cover and the long-term objective of re-establishing "a functional peat-accumulating ecosystem" (Rochefort 2000; Rochefort et al. 2003). In Alberta, the current restoration objective for seismic lines in treed peatlands is primarily the recovery of caribou, rather than a return of peatland function, with restoration success defined by the presence and density of trees (Graf 2009; Government of Alberta 2017). However, if the treatments used to encourage tree establishment lead to a loss in bryophyte cover, the organisms responsible for peat accumulation and peatland functioning, we will need to explore less disruptive restoration options or re-assess our restoration objectives.

Table 4.1: Results of the mixed effects models for vascular species richness, Shannon's diversity, Simpson's diversity, total vascular plant cover, shrub cover, forb cover, graminoid cover, and bryophyte cover as affected by mounding treatment, microtopographic position, and their interaction; F-values, numerator degrees of freedom [df], and p-values [P] are shown.

Response variable	Treatment			Position			Treatment × position		
	F	df	P	F	df	P	F	df	P
Diversity									
Vascular plant richness	**82.31**	**2**	**<0.001**	0.32	2	0.727	0.41	4	0.801
Vascular Shannon's diversity	**76.29**	**2**	**<0.001**	0.54	2	0.583	0.78	4	0.541
Vascular Simpson's diversity	**54.98**	**2**	**<0.001**	0.65	2	0.524	0.766	4	0.548
Abundance (cover)									
Total vascular plant cover	0.47	2	0.625	**4.01**	**2**	**0.019**	**2.70**	**4**	**0.031**
Shrub cover	**3.54**	**2**	**0.030**	**9.28**	**2**	**<0.001**	1.81	4	0.127
Forb cover	**5.75**	**2**	**0.004**	0.65	2	0.521	0.62	4	0.652
Graminoid cover	**78.78**	**2**	**<0.001**	0.32	2	0.725	1.57	4	0.183
Bryophyte cover	**57.98**	**2**	**<0.001**	0.72	2	0.488	**11.30**	**4**	**<0.001**

Note: Bolded values indicate significance (α = 0.05). Total vascular plant cover, shrub cover,

forb cover, and graminoid cover were log-transformed for analysis.

Table 4.2: Results of PERMANOVA for vascular plant community composition as affected by mounding treatment, micro-topographic position, and their interaction.

	Treatment			Position			Treatment × position		
	F	df	P	F	df	P	F	df	P
Community composition	**10.984**	**2**	**0.001**	**3.147**	**2**	**0.001**	**1.547**	**4**	**0.008**

Table 4.3: PERMANOVA results showing the effect of micro-topographic position on vascular plant community composition within each treatment, and vice versa, and the pairwise tests within each treatment and micro-topographic position.

	Treatment			Position			Pairwise comparison (p-values)		
	F	df	P	F	df	P	Level-Slope	Level-Top	Slope-Top
Reference				**3.518**	**2**	**0.001**	**0.020**	**0.003**	0.051
Mounded				**1.619**	**2**	**0.001**	0.154	**0.003**	0.325
Unmounded				**1.394**	**2**	**0.001**	0.987	**0.012**	0.987
							Mounded vs. Reference	Reference vs. Unmounded	Unmounded vs. Mounded
Level	**2.592**	**2**	**0.001**				**0.012**	**0.003**	0.055
Slope	**4.915**	**2**	**0.001**				**0.003**	**0.003**	**0.003**
Top	**6.418**	**2**	**0.001**				**0.003**	**0.003**	**0.003**

Table 4.4: Results of Indicator Species Analysis for understory vascular plant communities in reference sites, mounded seismic lines, and unmounded seismic lines.

Treatment	Species	Component A	Component B	Indicator Value	P
Reference	*Rhododendron groenlandicum*	0.640	0.628	0.634	0.001
	Vaccinium vitis-idaea	0.544	0.392	0.462	0.002
	Rubus chamaemorus	0.577	0.366	0.459	0.004
	Picea mariana	0.847	0.137	0.341	0.028
Mounded	*Equisetum fluviatile*	0.766	0.764	0.765	0.001
	Stellaria spp.	0.905	0.292	0.514	0.001
	Equisetum palustre	0.638	0.389	0.498	0.001
	Carex spp.	0.829	0.236	0.442	0.001
	Salix spp.	0.762	0.181	0.371	0.001
	Equisetum arvense	0.803	0.167	0.366	0.001
	Equisetum scirpoides	0.628	0.153	0.310	0.022
Unmounded	*Carex aquatilis*	0.596	0.753	0.670	0.001
	Vaccinium microcarpum	0.589	0.556	0.572	0.001
	Calamagrostis spp.	0.576	0.469	0.520	0.004
	Carex disperma	0.740	0.333	0497	0.001
	Carex magellanica	0.838	0.284	0.488	0.001
	Carex chordorrhiza	0.504	0.444	0.473	0.002
	Andromeda polifolia	0.546	0.309	0.410	0.013
	Salix planifolia	0.749	0.136	0.319	0.003
	Carex gynocrates	0.652	0.111	0.269	0.026

Note: Component A represents the probability of a site belonging to a treatment based on the presence of the indicator species, while Component B represents the probability of encountering the indicator species in sites belonging to a treatment. The Indicator Value is the product of Component A and B (see De Caceres and Legendre 2009). The p-value [P] represents the significance of the association between the indicator species and its corresponding treatment, based on a permutation test of 1000 runs.
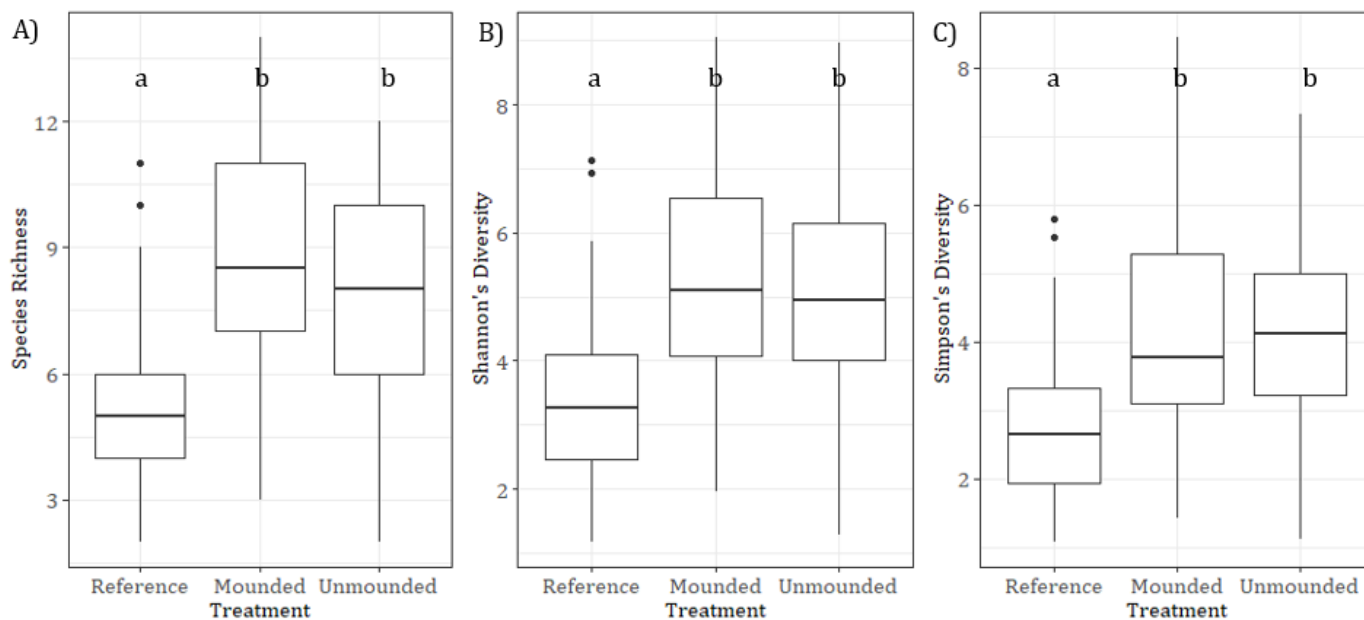
Figure 4.1: Boxplots (in Tukey style) of vascular plant richness (A; no. per 0.04 m^2), Shannon's diversity (B), and Simpson's diversity (C) by treatment (reference sites, mounded seismic line, and unmounded seismic line). Different letters indicate significant (P < 0.05) differences between treatments, based on pairwise comparison of estimated marginal means. There were no significant effects of micro-topographic position or interaction of position and mounding treatment (see Table 4.1). The thick horizontal line within the boxplot represent the median, the lower and upper hinges represent the 25th and 75th percentiles (respectively), the whiskers represent the smallest and largest value within 1.5 times the interquartile range (IQR), and the outliers (values greater than or less than 1.5*IQR) are represented as dots outside the box and whiskers.
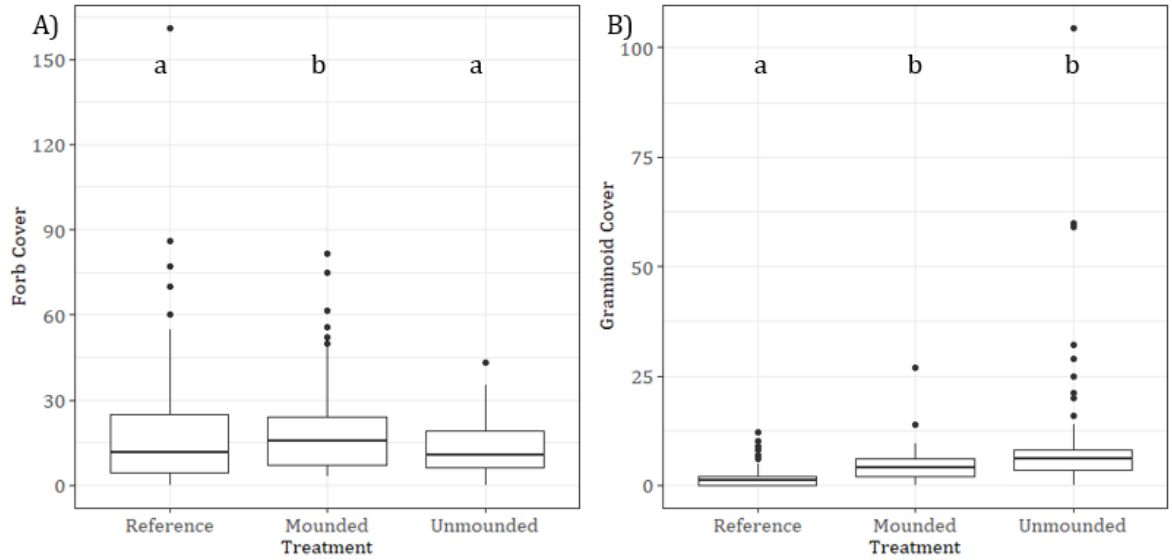
Figure 4.2: Boxplots (in Tukey style) of total forb (A) and graminoid cover (B) by treatment (reference sites, mounded seismic line, and unmounded seismic line). Different letters indicate significant ($P < 0.05$) differences between treatments, based on pairwise comparisons of estimated marginal means. There were no significant effects of micro-topographic position or interaction of position and mounding treatment (see Table 4.1). For the statistics used to create the boxplot see Figure 4.1.
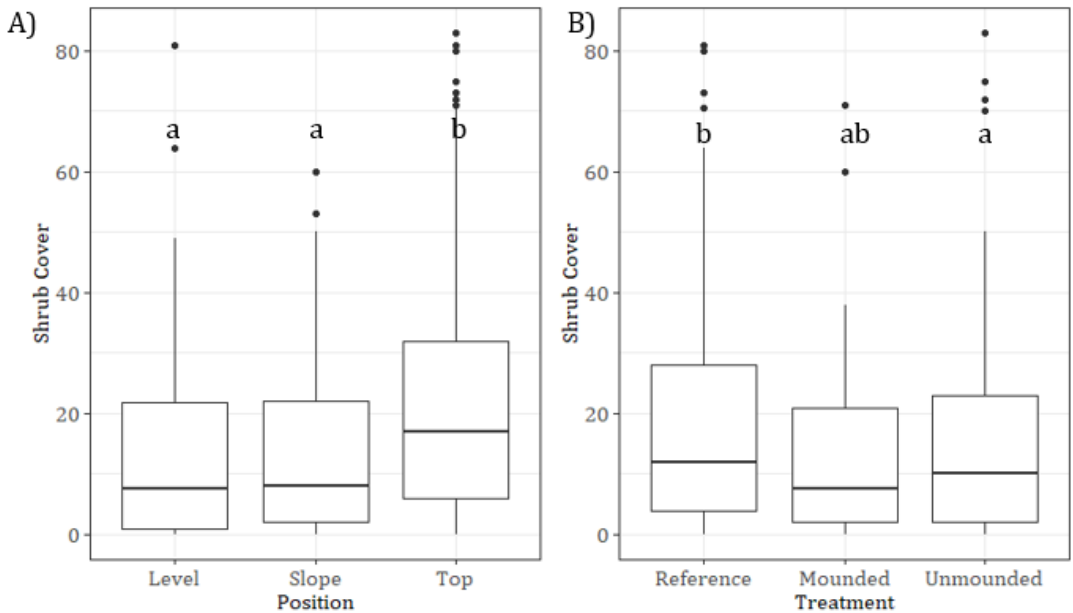
Figure 4.3: Boxplots (in Tukey style) of total shrub cover by position (A) and treatment (B). Different letters indicate significant ($P < 0.05$) differences between treatments or micro-topographic positions, based on pairwise comparisons of estimated marginal means of log-transformed shrub cover. For the statistics used to create the boxplot see Figure 4.1.
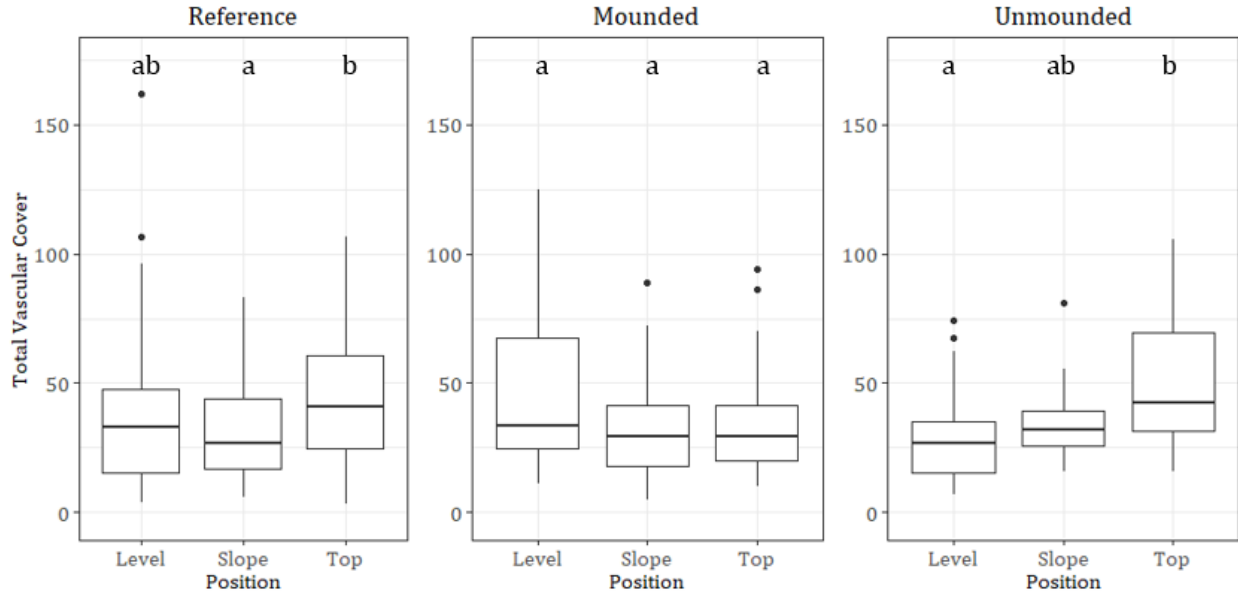
Figure 4.4: Boxplots (in Tukey style) of total vascular plant cover by treatment and micro-topographic position. Different letters indicate significant (P < 0.05) differences between micro-topographic positions within each treatment, based on pairwise comparisons of estimated marginal means. For the statistics used to create the boxplot see Figure 4.1.
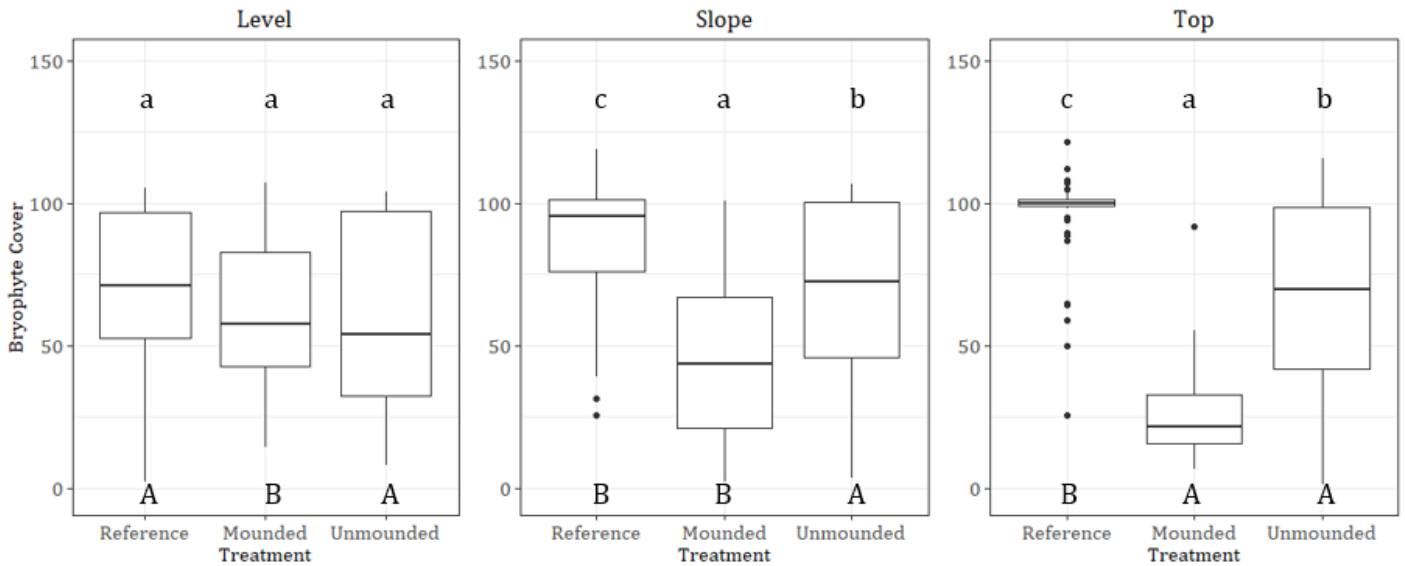
Figure 4.5: Boxplots in (Tukey style) of bryophyte cover by position in the reference sites, mounded seismic lines, and unmounded seismic lines. Different letters indicate significant (P < 0.05) differences between treatments within each position (lower-case letters), or between positions within each treatment (upper-case letters), based on pairwise comparisons of estimated marginal means. For the statistics used to create the boxplot see Figure 4.1.
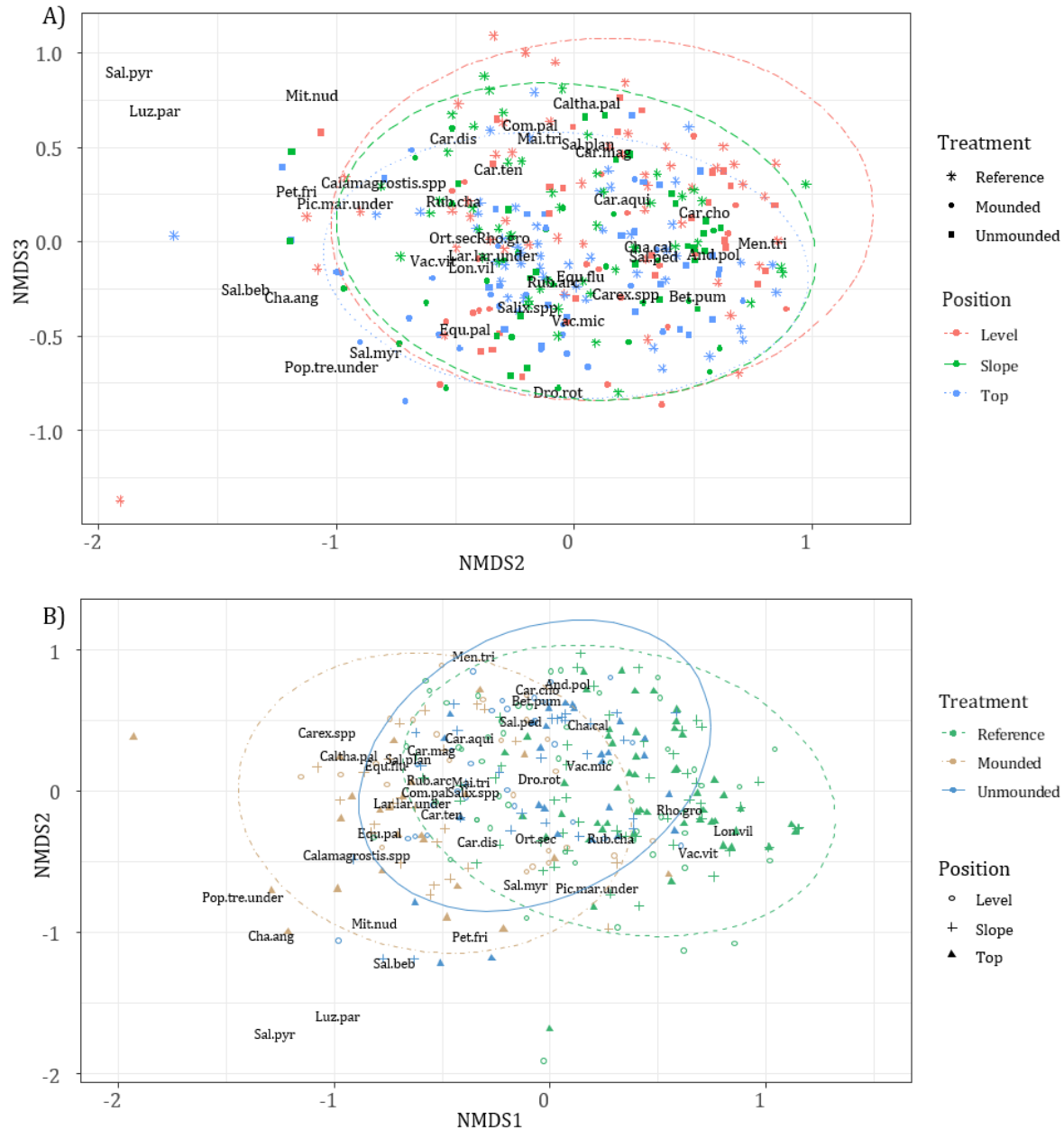
Figure 4.6: Results of a non-metric multidimensional scaling (NMDS), an unconstrained ordination, of understory vascular community composition in three micro-topographic positions (A)—level, slope, and top—and three treatments (B): reference sites, mounded and unmounded seismic lines. Points represent sampled sites, with color and shape representing treatment or position. Ellipses represent the 95% confidence intervals for each micro-topographic position or treatment centroid, with color and linetype representing treatment or position. The most abundant species are represented by six letter codes (first three letters of genus and species epithet; see Appendix 4.4). The optimal solution was three-dimensional and had a final stress of 0.178.

Appendix 4.1: Average (and standard error) tree density, basal area, and tree height by species, and water chemistry variables for the unmounded and mounded reference habitats. T-tests showed variables did not significantly differ between the two reference types (P > 0.05).

Variables	Unmounded Reference	Mounded Reference
Total tree density	8527.8 (579.5)	7500.0 (1187.7)
Larix laricina	888.9 (356.3)	625.0 (340.7)
Picea mariana	7638.89 (709.69)	6875.00 (1327.93)
Total basal area	550.81 (44.88)	486.84 (70.59)
Larix laricina	108.79 (38.40)	80.07 (46.17)
Picea mariana	442.02 (56.73)	406.77 (84.93)
Average tree height	5.20 (0.53)	6.25 (0.72)
Larix laricina*	1.02 (0.67)	3.4 (1.32)
Picea mariana	5.24 (0.53)	6.07 (0.76)
Water chemistry		
pH	6.36 (0.14)	6.65 (0.14)
Conductivity	73.91 (15.26)	126.24 (25.96)
Alkalinity	31.18 (8.37)	59.48 (13.23)
Seismic line width	4.11 (0.07)	4.25 (0.09)

*Due to limited samples, we were unable to test the statistical differences in *L. laricina* height between the two reference types.
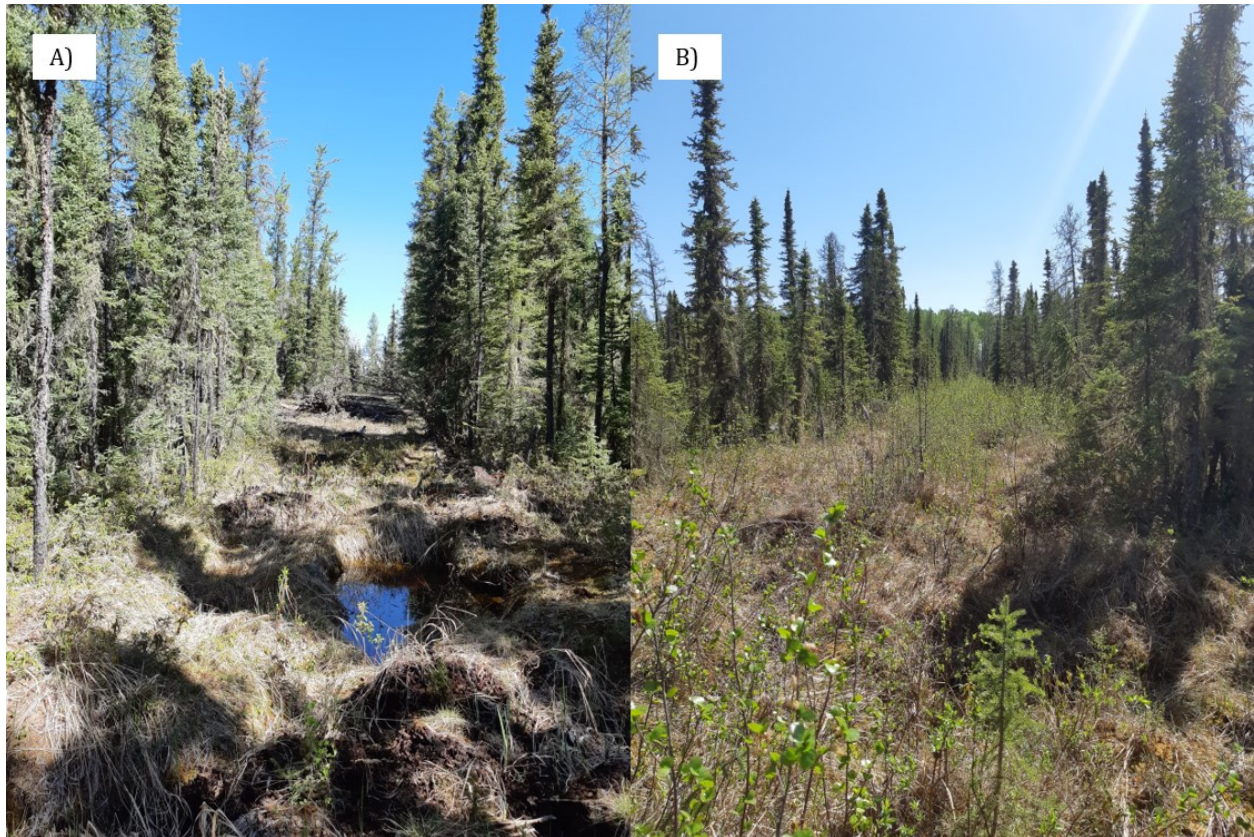
Appendix 4.2: Mounded seismic lines (A) and unmounded seismic lines (B) were sampled to examine the impacts of mounding on understory recovery. Mounding was applied by excavating and placing the inverted substrate adjacent to the newly created pit. A mound can be seen in the foreground of the mounded seismic line (A) and the "hollow" is the water-filled pit directly behind it. Images were taken in May 2018.
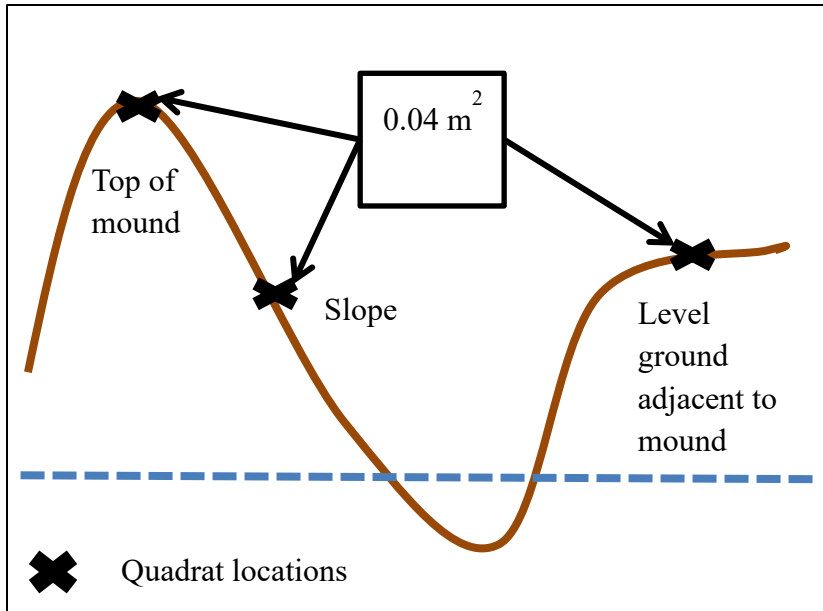
Appendix 4.3: 20 cm by 20 cm sampling quadrats were placed at three micro-topographic positions: top of the hummock, slope of the hummock (south facing), and the level ground adjacent to the mound. The dashed blue line represents the water table and the brown line represents the ground surface.

Appendix 4.4: Mean percent cover and standard error (in parentheses) and the species code (see Figure 4.6) for vascular plants found in each treatment (unmounded, mounded, and reference) and micro-topographic position (top, slope, and level). Nomenclature follows VASCAN (Brouillet et al. 2010).

Latin binomial	Unmounded			Mounded			Reference		
(species code)	Top	Slope	Level	Top	Slope	Level	Top	Slope	Level
Agrostis scabra (Agr.sca)	-	-	-	0.04 (0.04)	-	-	-	-	-
Andromeda polifolia (And.pol)	2.15 (0.60)	1.44 (0.55)	0.93 (0.35)	0.08 (0.08)	1.00 (0.66)	0.42 (0.17)	0.98 (0.31)	0.93 (0.59)	0.35 (0.17)
Betula papyrifera (Bet.pap)	-	-	-	0.13 (0.09)	-	1.46 (1.46)	-	-	-
Betula pumila (Bet.pum)	5.44 (2.88)	1.56 (0.65)	2.52 (1.25)	1.33 (0.93)	2.54 (2.50)	1.88 (1.04)	2.88 (1.43)	1.03 (0.61)	3.05 (1.28)
Calamagrostis spp.	3.13 (2.20)	1.11 (0.56)	1.02 (0.32)	1.52 (0.63)	1.13 (0.31)	0.65 (0.21)	0.17 (0.06)	0.24 (0.12)	0.18 (0.07)
Caltha palustris (Cal.pal)	-	-	0.74 (0.74)	0.08 (0.08)	-	1.50 (0.97)	0.29 (0.29)	0.08 (0.08)	2.26 (1.65)
Carex aquatilis (Car.aqu)	2.56 (0.73)	2.85 (0.53)	2.11 (0.39)	0.69 (0.23)	1.33 (0.35)	1.79 (0.39)	0.54 (0.17)	0.35 (0.12)	0.38 (0.13)
Carex canescens (Car.can)	-	0.07 (0.05)	0.11 (0.82)	0.08 (0.08)	-	0.04 (0.04)	-	-	-
Carex capillaris (Car.cap)	-	-	-	0.13 (0.13)	-	-	-	-	-
Carex chordorrhiza (Car.cho)	0.96 (0.26)	0.61 (0.14)	0.57 (0.14)	0.17 (0.10)	0.15 (0.07)	0.27 (0.11)	0.62 (0.21)	0.47 (0.15)	0.44 (0.10)
Carex diandra (Car.dia)	-	-	-	0.19 (0.13)	0.13 (0.13)	0.21 (0.15)	-	-	-
Carex disperma (Car.dis)	0.57 (0.22)	0.81 (0.32)	1.22 (0.92)	0.13 (0.09)	0.29 (0.17)	0.17 (0.10)	0.04 (0.02)	0.08 (0.04)	0.22 (0.16)
Carex gynocrates (Car.gyn)	0.15 (0.11)	0.19 (0.11)	0.17 (0.12)	-	-	0.04 (0.04)	0.03 (0.02)	0.06 (0.04)	0.14 (0.07)
Carex interior (Car.int)	-	-	-	-	0.04 (0.03)	-	-	-	-
Carex leptalea (Car.lep)	-	-	-	0.04 (0.03)	0.13 (0.13)	0.04 (0.04)	-	-	-
Carex limosa (Car.lim)	0.04 (0.04)	-	0.04 (0.04)	-	-	-	-	-	-
Carex magellanica (Car.mag)	1.52 (0.78)	2.37 (1.09)	1.63 (0.95)	-	0.06 (0.05)	0.46 (0.24)	0.01 (0.01)	0.12 (0.05)	0.42 (0.22)
Carex tenuiflora (Car.ten)	0.15 (0.07)	0.09 (0.05)	0.13 (0.08)	0.35 (0.19)	0.21 (0.09)	0.08 (0.08)	0.05 (0.04)	0.11 (0.05)	0.31 (0.20)
Carex vaginata (Car.vag)	0.15 (0.09)	0.37 (0.37)	0.19 (0.13)	0.08 (0.08)	-	0.04 (0.04)	0.01 (0.01)	-	0.29 (0.022)

Latin binomial	Unmounded			Mounded			Reference		
(species code)	Top	Slope	Level	Top	Slope	Level	Top	Slope	Level
Carex spp.	0.07 (0.07)	-	0.09 (0.07)	0.54 (0.44)	0.27 (0.15)	0.75 (0.24)	0.04 (0.04)	0.10 (0.08)	0.02 (0.01)
Chaemenerion angustifolium (Cha.ang)	-	0.19 (0.19)	-	1.63 (0.70)	0.17 (0.13)	0.13 (0.13)	-	-	-
Chamaedaphne calyculata (Cha.cal)	0.56 (0.29)	0.89 (0.40)	0.96 (0.35)	-	0.17 (0.17)	0.17 (0.13)	1.38 (0.50)	0.72 (0.35)	1.32 (0.43)
Chrysosplenium spp.	-	-	-	1.46 (1.25)	0.08 (0.08)	0.04 (0.04)	-	-	-
Comarum palustre (Com.pal)	0.93 (0.75)	1.15 (0.51)	1.04 (0.40)	0.21 (0.15)	1.88 (1.11)	1.54 (0.77)	0.06 (0.06)	1.06 (0.43)	0.43 (0.26)
Coptidium lapponicum (Cop.lap)	-	-	0.02 (0.02)	-	-	-	-	0.08 (0.08)	-
Cornus canadensis (Cor.can)	-	-	-	0.08 (0.08)	-	-	-	-	-
Corallorhiza trifida (Cor.tri)	-	-	-	-	-	-	-	-	0.01 (0.01)
Drosera rotundifolia (Dro.rot)	0.31 (0.13)	0.19 (0.09)	0.20 (0.09)	0.19 (0.09)	0.04 (0.03)	0.35 (0.18)	0.15 (0.07)	0.33 (0.15)	0.01 (0.01)
Epilobium ciliatum (Epi.cil)	-	-	-	0.19 (0.12)	0.35 (0.26)	0.88 (0.66)	-	-	-
Epilobium palustre (Epi.pal)	-	0.04 (0.04)	0.07 (0.07)	0.04 (0.04)	0.08 (0.06)	0.13 (0.13)	-	-	-
Epilobium spp.	0.04 (0.04)	-	-	0.06 (0.03)	0.06 (0.05)	0.04 (0.04)	-	-	-
Equisetum arvense (Equ.arv)	0.04 (0.04)	0.07 (0.07)	-	0.63 (0.42)	0.38 (0.19)	0.25 (0.14)	0.03 (0.02)	0.01 (0.01)	0.16 (0.09)
Equisetum fluviatile (Equ.flu)	0.28 (0.10)	0.44 (0.12)	0.31 (0.09)	1.90 (0.40)	2.71 (0.81)	2.25 (0.67)	0.17 (0.06)	0.40 (0.12)	0.49 (0.18)
Equisetum palustre (Equ.pal)	0.48 (0.23)	0.22 (0.11)	0.11 (0.06)	0.63 (0.21)	0.75 (0.25)	0.44 (0.19)	0.10 (0.04)	0.06 (0.03)	0.06 (0.03)
Equisetum scirpoides (Equ.sci)	0.13 (0.05)	0.04 (0.03)	0.07 (0.03)	0.17 (0.13)	0.27 (0.17)	0.17 (0.07)	-	0.04 (0.02)	0.08 (0.05)
Equisetum sylvaticum (Equ.syl)	0.22 (0.16)	0.28 (0.20)	0.04 (0.04)	0.30 (0.19)	0.38 (0.20)	0.17 (0.10)	0.01 (0.01)	0.06 (0.04)	0.20 (0.08)
Eriophorum gracile (Eri.gra)	-	-	-	-	-	0.04 (0.04)	-	-	-
Forb spp.	-	0.02 (0.02)	-	0.08 (0.05)	0.17 (0.07)	0.02 (0.02)	-	0.04 (0.04)	-

Latin binomial (species code)	Unmounded			Mounded			Reference		
	Top	Slope	Level	Top	Slope	Level	Top	Slope	Level
Fragaria virginiana (Fra.vir)	-	0.22 (0.22)	-	-	-	-	-	-	-
Galium spp.	-	-	-	-	0.08 (0.05)	0.10 (0.09)	0.01 (0.01)	0.01 (0.01)	0.03 (0.02)
Graminoid spp.	-	-	-	0.17 (0.17)	0.13 (0.09)	-	-	-	0.01 (0.01)
Larix laricina (Lar.lar)	-	1.11 (0.82)	0.15 (0.15)	0.42 (0.24)	0.19 (0.07)	0.04 (0.04)	0.04 (0.04)	0.03 (0.02)	0.16 (0.16)
Lonicera villosa (Lon.vil)	-	-	-	-	-	0.80 (0.80)	0.59 (0.59)	0.31 (0.31)	-
Luzula parviflora (Luz.par)	3.70 (3.70)	-	0.07 (0.07)	0.08 (0.08)	-	-	-	-	-
Lysimachia thyrsiflora (Lys.thy)	-	-	-	0.42 (0.42)	-	-	-	-	-
Maianthemum trifolium (Mai.tri)	2.91 (0.90)	3.85 (0.82)	4.48 (0.77)	3.75 (1.00)	5.79 (1.49)	8.08 (3.29)	2.92 (0.96)	5.00 (1.35)	9.43 (1.89)
Melampyrum lineare (Mel.lin)	-	-	-	0.08 (0.08)	-	-	-	-	-
Menyanthes trifoliata (Men.tri)	0.56 (0.39)	0.41 (0.27)	0.44 (0.23)	0.71 (0.63)	0.54 (0.43)	4.63 (2.80)	0.73 (0.54)	1.10 (0.81)	4.31 (1.53)
Mitella nuda (Mit.nud)	0.04 (0.04)	0.63 (0.56)	0.41 (0.24)	0.13 (0.09)	0.21 (0.21)	0.42 (0.42)	-	0.04 (0.04)	0.14 (0.14)
Orchid spp.	-	0.30 (0.21)	-	-	-	-	-	-	-
Orthilia secunda (Ort.sec)	0.07 (0.05)	0.17 (0.12)	0.02 (0.02)	0.67 (0.50)	0.10 (0.09)	0.13 (0.09)	0.47 (0.31)	0.06 (0.03)	0.10 (0.10)
Pedicularis spp.	0.07 (0.07)	0.004 (0.004)	-	-	0.08 (0.08)	0.04 (0.04)	-	-	-
Petasites frigidus (Pet.fri)	0.43 (0.30)	0.50 (0.44)	0.78 (0.56)	2.08 (2.08)	0.04 (0.04)	1.38 (0.96)	0.39 (0.39)	0.73 (0.42)	1.25 (1.00)
Picea mariana (Pic.mar)	0.04 (0.04)	0.07 (0.07)	-	0.69 (0.32)	0.15 (0.09)	-	2.24 (0.96)	1.18 (0.58)	1.81 (1.57)
Populus balsamifera (Pop.bal)	-	-	-	1.33 (0.88)	0.04 (0.04)	-	-	-	-
Populus spp.	-	-	-	0.92 (0.55)	0.13 (0.09)	-	-	-	-
Populus tremuloides (Pop.tre)	-	-	-	2.00 (0.78)	0.44 (0.22)	-	-	-	-
Rhododendron groenlandicum (Rho.gro)	5.35 (1.43)	2.19 (0.81)	1.30 (0.49)	1.50 (1.26)	1.08 (0.75)	2.83 (1.35)	11.24 (1.66)	8.73 (1.46)	5.38 (1.42)

Latin binomial (species code)	Unmounded			Mounded			Reference		
	Top	Slope	Level	Top	Slope	Level	Top	Slope	Level
Ribes oxyacanthoides (Rib.oxy)	-	-	0.74 (0.74)	-	-	-	-	-	-
Rubus arcticus (Rub.arc)	0.48 (0.26)	0.26 (0.16)	0.19 (0.13)	0.63 (0.51)	0.21 (0.21)	0.27 (0.25)	0.12 (0.12)	0.09 (0.09)	-
Rubus chamaemorus (Rub.cha)	2.89 (1.23)	2.41 (1.13)	0.89 (0.65)	0.54 (0.39)	3.46 (2.24)	1.04 (0.61)	7.80 (1.96)	4.53 (1.17)	2.96 (1.02)
Rubus idaeus (Rub.ida)	-	-	-	-	0.63 (0.63)	-	-	-	-
Salix bebbiana (Sal.beb)	-	-	0.11 (0.11)	1.04 (1.04)	0.17 (0.13)	-	0.49 (0.49)	-	-
Salix myrtillifolia (Sal.myr)	0.93 (0.93)	0.22 (0.22)	0.74 (0.51)	0.54 (0.46)	0.04 (0.04)	0.88 (0.62)	-	-	-
Salix pedicellaris (Sal.ped)	1.48 (0.86)	0.44 (0.31)	1.02 (0.40)	0.50 (0.35)	1.79 (1.03)	2.17 (0.92)	3.12 (1.46)	0.63 (0.31)	0.96 (0.36)
Salix planifolia (Sal.pla)	6.85 (3.89)	1.19 (0.94)	2.44 (1.32)	0.33 (0.33)	-	2.54 (1.39)	0.59 (0.59)	-	0.06 (0.06)
Salix pseudomyrsinites	-	-	-	-	-	0.75 (0.75)	-	-	-
Salix pyrifolia (Sal.pyr)	-	1.85 (1.85)	-	-	-	-	-	-	-
Salix spp.	0.26 (0.26)	-	0.15 (0.12)	0.63 (0.34)	1.38 (0.79)	0.06 (0.05)	0.14 (0.14)	0.04 (0.04)	0.06 (0.06)
Stellaria spp.	0.04 (0.03)	0.04 (0.04)	0.04 (0.04)	0.833 (0.26)	0.46 (0.15)	0.15 (0.07)	-	0.04 (0.03)	-
Vaccinium microcarpum (Vac.mic)	3.89 (0.70)	2.50 (0.68)	1.04 (0.38)	0.27 (0.17)	0.31 (0.15)	1.19 (0.56)	2.16 (0.35)	0.85 (0.27)	0.39 (0.16)
Vaccinium vitis-idaea (Vac.vit)	1.30 (0.72)	0.59 (0.41)	0.19 (0.13)	1.58 (1.26)	0.10 (0.09)	0.75 (0.48)	3.19 (0.72)	1.32 (0.36)	0.86 (0.26)
Viburnum edule (Vib.edu)	0.04 (0.04)	-	-	-	-	-	-	-	-

Chapter 5: Disturbing to restore? Mounding upends bryophyte communities on linear disturbances in treed peatlands[1]

5.1 Abstract

Treed peatlands are ecosystems dominated by bryophytes, which create the hummock-hollow topography typically found in them. This microtopographic variation, in turn, shapes the distribution of bryophyte communities. Disturbances can lead to a loss in this microtopographic variation. For example, in Alberta, seismic lines are widespread, deforested linear disturbances (~ 3 to 8 m wide) created for oil and gas exploration. Recovery of tree cover on seismic lines in treed peatlands tends to be slow, potentially due to the reduced microtopographic variation on these linear disturbances. To facilitate tree establishment, mounding is being applied to restore the microtopography. However, in the previous chapter, I found that understory communities were negatively impacted by mounding, with significant losses in bryophyte abundance. In this study, I build on these results and compare the recovery of bryophyte communities on unmounded and mounded seismic lines and evaluate how the recovery varies with microtopographic position (i.e., top of hummock, slope or side of the hummock, and level ground), with recovery defined as similarity to the adjacent reference treed fen. In 20 cm by 20 cm quadrats, I visually assessed bryophyte cover by species at each microtopographic position on mounded and unmounded seismic lines, and their adjacent fens and used mixed-effects models to assess the effects of treatment, position, and their interaction on bryophyte abundance and diversity. The results support the vascular plant community

---

[1] Most of the bryophyte identification for this chapter was done by Steve Joya.

findings: recovery on the unmounded seismic lines is well underway, while mounding acts as a more severe disturbance agent and winds back recovery on seismic lines. In unmounded seismic lines, *Sphagnum* cover was similar to that of reference treatments at all microtopographic positions, and pioneer true moss cover, species richness and Shannon's diversity only differed between the unmounded and reference treatments at the top position. In contrast, mounded seismic lines had lower *Sphagnum* cover and higher pioneer true moss cover, species richness and diversity than both the reference and unmounded treatments. Lastly, the lower microtopographic positions were quicker to recover than the higher positions in both unmounded and mounded treatments. Overall, these results show that mounding sets back the recovery of bryophyte communities—the very organisms responsible for the microtopographic variation we are trying to establish. Given these results, mounding and any additional anthropogenic disturbance to these recovering seismic lines should be avoided.

5.2 Introduction

Peatlands are ecosystems that provide essential ecological functions, such as habitat for wildlife, carbon storage, and water regulation (Rydin and Jeglum 2006). Peatlands are defined by the significant peat accumulation found within these ecosystems, which can take centuries to develop (Wieder 2006). Peat accumulation is driven by slow decomposition rates due to low temperatures and anoxic conditions (Wieder 2006; Vitt and Wieder 2008). In *Sphagnum*-dominated peatlands, *Sphagnum* contributes to this slow decomposition rate by creating cold, acidic conditions and producing litter that is high in carbon to nitrogen ratios and thus slow to decay (van Breemen 1995; Rochefort 2000; Rydin et al. 2006). *Sphagnum* can also raise the water table height by moving water through its hyaline cells, creating anaerobic conditions, and contributing to the slower decomposition (Vitt and Wieder 2008). In addition, bryophytes have a

much slower decomposition rate than vascular plants and make up most of the plant organic matter that becomes peat, with brown mosses dominating in fens and *Sphagnum* dominating in bogs (Vitt and Wieder 2008). Since bryophytes play an important role in peatland ecosystems, understanding how bryophyte communities respond to disturbances and restoration efforts can inform efforts to conserve and maintain peatlands.

The hummock-hollow topography, which is characteristic of peatlands, results in a diversity of micro-habitats that influence peatland flora. This micro-topography is in large part due to the understory plant community (Malmer et al. 1994; Rydin and Jeglum 2006). Differences in net primary production and decomposition rates between moss species help drive the creation of hummock-hollow topography (Turetsky et al. 2008). For example, *Sphagnum* hummock species, such as *Sphagnum fuscum,* have slower decay rates than hollow species, thus allowing for increased peat accumulation on hummocks (Turetsky et al. 2008). In addition, vascular plants, especially shrubs, provide structural support to *Sphagnum* in the hummock development and create suitable micro-climatic conditions for *Sphagnum* growth (Pouliot et al. 2011).

While bryophytes help create the hummock-hollow micro-topography, their distribution is, in turn, shaped by the microtopography they create. Bryophytes are positioned along the hummock-hollow gradient based on their desiccation avoidance strategies and their competitive growth rates. Hummock species have drought avoidant morphology but have lower growth rates than species of lower microtopographic positions (Rydin et al. 2006). For example, *Tomenthypnum nitens* is found on hummocks in fens and its growth form, tomentum, and canopy structure optimize water uptake and retention (Vitt and Wieder 2008). Similarly, *Sphagnum*'s unique morphology acts like a wick that optimizes water capillarity both within an individual

shoot, and between shoots. In addition, tightly packed shoots, as found in *S. fuscum's* dense hummocks, help reduce evaporative loss (Rydin et al. 2006). Lastly, poorly decomposed *Sphagnum* individuals—which have maintained their capillarity—act like a straw connecting the living *Sphagnum* layers to the water table. In contrast, species found at lower micro-topographic positions form looser carpets and are more drought tolerant than hummock species; thus, they are better adapted to the variable conditions near the water table, i.e., flooded conditions in the spring, and drier conditions in the summer. Species dominating lower micro-topographic positions tend to have faster growth rates and can outcompete hummock species in wetter micro-sites (Turetsky et al. 2008).

Peatlands in Alberta, Canada are dissected by linear corridors of cleared forests, called seismic lines, which are used to locate oil and gas reserves. While seismic lines are relatively narrow (1.5 – 12 m wide), low-severity disturbances, they can extend for kilometers and are found at high densities (Dabros et al. 2018). Seismic lines alter the understory communities, both on the seismic line and into the adjacent forest (MacFarlane 2003; Dabros et al. 2017; Echiverri et al. 2020). In addition, seismic lines in peatlands have reduced micro-topographic complexity and tend to be depressed relative to the adjacent forested peatland (Stevenson et al. 2019), which can lead to wetter conditions on the seismic lines (Dabros et al. 2017). While there is evidence of natural recovery of understory vascular plant communities and tree establishment on seismic lines (Filicetti et al. 2019; Echiverri et al. 2020), studies suggest that tree cover on seismic lines is slow to recover (Lee and Boutin 2006; van Rensen et al. 2015), potentially due to the wetter conditions.

Mounding is a site-preparation technique used in forestry to create micro-topographic variation on disturbed sites to promote tree establishment (Sutton 1993). It involves excavating

122

soil to create a hole (artificial "hollow") and the piling of the excavated soil on the adjacent ground to create a mound (artificial "hummock"). Specifically, it is meant to expose mineral soil, reduce competing vegetation and, more importantly, create an aerated rooting zone for trees in sites that are normally flooded (Sutton 1993; Pyper et al. 2014).

Seismic lines which were mounded and planted with trees had higher tree regeneration than untreated seismic lines (Filicetti et al. 2019). Similarly, mounded oil-sand exploration wellpads were found to have higher sapling density than unmounded wellpads (Lieffers et al. 2017). Mounded well pads have also been shown to have higher bryophyte diversity than unmounded well pads (Caners et al. 2019). However, mounding has also been shown to set back understory recovery and lead to a loss in bryophyte cover on seismic lines (Echiverri et al. 2020). This could be due to the micro-environmental conditions created by mounding. Similarly, in post-harvested peatlands, creating micro-topography with machine tracks inhibited *Sphagnum* establishment, with the higher micro-topographic positions proving to be too dry and hot for *Sphagnum* (Price et al. 1998).

In this study, I further explore the effects of mounding on bryophyte communities, by comparing the recovery of mounded and unmounded (i.e., lines left to recovery naturally) seismic lines. Since bryophyte communities stratify along the hummock-hollow gradient, I also compared the recovery between micro-topographic positions: top of hummock, slope or side of the hummock, and level ground (also referred to as carpets) adjacent to mounds. Recovery of the community was defined as similarity to the adjacent reference wooded fen (hereafter referred to as reference sites). Since the legacy seismic lines in our case had been left undisturbed for more than 10 years, mounding acted as a new disturbance on a recovering community. Similar to Caners et al. (2019), I expected the ingress of weedy, disturbance-adapted species would lead to

higher diversity on mounded seismic lines, compared to both reference sites and unmounded seismic lines. In a previous study, we found total bryophyte cover was most similar between reference sites and unmounded seismic lines, which was higher than on mounded seismic lines (Echiverri et al. 2020). I expected that successful *Sphagnum* establishment on unmounded seismic lines drove this similarity, thus, I also expected bryophyte composition and *Sphagnum* cover to be similar between the reference and unmounded seismic lines. Much like Price et al. (1998), I expected mounded seismic lines to have lower *Sphagnum* cover than the other treatments, with the top position having the least *Sphagnum* cover. Lastly, since hummocks are formed by the upward growth of bryophytes, I expected the top position to be the least recovered position in unmounded seismic lines.

5.3 Methods

I sampled in treed moderate-rich fens near Kirby Lake, approximately 45 km south of Conklin, Alberta, Canada (55°21'57.51"N, 111°09'46.10"W). Sites were classified as moderate-rich fens based on ground water pH values that ranged from 5.69 to 7.12 ($\mu = 6.46$) and a moderate electrical conductivity ($\mu = 102.84$ µs cm^{-1}). Reference wooded fens were dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) or tamarack (*Larix laricina* (Du Roi) K. Koch) with an understory layer characterized by *Rhododendron groenlandicum* ((Oeder) Kron and Judd), *Maianthemum trifolium* ((L.) Sloboda), and *Sphagnum* spp. Average daily temperature in the region is 2.1°C with an average annual precipitation of 421 mm (Environment and Climate Change Canada 2018; from nearby meteorological station: Cold Lake A).

Seismic lines in the area were created in 1998/2001 during exploration for bitumen (oil sands) reserves as part of a "3D" seismic program, which involves creation of narrow (~ 3 m width) lines in an intensive (50 to 100 m spacing) grid. To minimize disturbance of soil and the

understory, seismic lines were created in the winter, with lightweight equipment. Travel by machinery on these lines has been limited since their creation. A sample of representative seismic lines were mounded in 2015 as part of a restoration program and sampling occurred three years later (late June to mid July 2018). Mounding was done with a construction excavator with a bucket attachment, which excavated and placed the inverted substrate adjacent to the newly created pit. Mounds were created to be 0.75 m wide, 1 m long, and 0.80 m tall and placed every 6 m along the seismic lines. For additional details on mounding specifications, see Filicetti et al. (2019).

I sampled seismic lines with mounding treatments (n = 8) and unmounded seismic lines (n = 8) (Figure 5.1; see Echiverri et al. 2020 for additional details). For each of these I also sampled the adjacent wooded fen to represent the reference condition. Sampling for the reference wooded fen took place 25 to 50 m from the center of the seismic line, with the ecosite type kept consistent between the seismic line and reference wooded fen. Average mound height (± standard error) was 40.1 ± 4.0 cm on the mounded seismic lines, 32.1 ± 1.4 cm on the unmounded seismic lines, and 30.7 ± 2.2 cm in the reference sites (C.M.A. Franklin unpublished data).

At each seismic line and paired reference wooded fen, I established a 20 m transect along the center of the seismic line and a parallel one in the adjacent reference wooded fen. Three mounds were chosen and sampled along each transect, those closest to the 5 m, 15 m, and 20 m distances. For each selected mound, I used a 20 cm by 20 cm (400 cm^2) quadrat to assess vegetation at each of three micro-topographic positions: the top of the mound, the south-facing slope, and on the adjacent level ground. To maintain consistency across the different positions sampled, I only sampled one quadrat for each

slope position. Sampling was standardized to the south-facing slope to ensure the effect of aspect was consistent across treatments; I expected the south-facing aspect to have the strongest effect. For unmounded seismic lines with no clear mounds present, quadrats were randomly placed with the same micro-topographic positions being maintained relative to each other—i.e., the level ground position was still placed at the lowest position, followed by slope, and top at the highest position. Since the artificially-created hollows on the mounded seismic lines were predominantly deep pools of water with little to no vegetation, hollows were excluded from the analysis. In each quadrat, I visually estimated the cover of each bryophyte species (Appendix 5.1). Due to their relatively low abundance, liverworts were not identified to species.

Groundwater samples were collected from shallow, excavated wells at the 10 m midpoint transect distance using 500 mL Nalgene bottles. Samples were stored in 4°C for 48 hours prior to analysis by the Biogeochemical Analytical Service Laboratory (BASL) at the University of Alberta. Samples were analyzed for pH, electrical conductivity, alkalinity (mg/L $CaCO_3$), and base cation content (mg/L).

5.3.1 Statistical analysis

For each quadrat, I calculated species richness, Shannon's diversity, and bryophyte abundance by growth form—total pioneer true moss cover (i.e., Class Bryopsida; sensu Benscoter and Vitt 2008), total feather moss cover, and total *Sphagnum* cover. As per Caners et al. (2019), we also included species from Class Polytrichopsida in the total pioneer "true moss" growth form. While feather mosses (i.e., *Ptilium crista-castrensis, Hylocomium splendens,* and *Pleurozium schreberi*) are also in the Class Bryopsida, we placed them in a separate growth form as they are associated with undisturbed fens, as opposed to the disturbance-associated pioneer true mosses (Benscoter and Vitt 2008). Hill's number was used for Shannon's diversity, as it is

in units of effective number of species (Hill 1973; Jost 2006); Shannon's diversity was calculated as the exponent of Shannon's entropy. We also calculated and analyzed species richness by mound, i.e., the total number of species found in the top, slope, and level quadrats for each mound.

To examine the effects of mounding treatment, micro-topographic position, and their interaction, I used linear mixed effects models with mounding treatment (mounded seismic line, unmounded seismic line, reference sites), microtopographic position, and their interactions as fixed effects ($\alpha = 0.05$), and transect as a random effect (the three mounds on a transect at a given sampling location were treated as sub-samples). All response variables were analyzed with a gaussian distribution. True moss cover and Shannon's diversity were log_{10}-transformed to conform to model assumptions. Residuals were examined to ensure normality and homogeneity of variance. All analyses were done with the lme4 package (Bates et al. 2015) in the R statistics programming environment, version 3.5.2 (R Core Team 2018). When the predictor variables were significant, post-hoc analyses were completed using the emmeans package, with P values adjusted using the Tukey HSD method (Lenth 2020). When the interaction term was significant, I evaluated differences between treatments for each micro-topographic position, and between micro-topographic positions within each treatment.

Indicator species for each treatment were identified using the indicspecies package (De Cáceres and Legendre 2009); all species were included in the indicator species analysis. Due to differences in the multivariate dispersion between treatments, I was unable to test the overall effects of treatment, micro-topographic position, and their interaction on bryophyte community composition. Instead, I separately tested the effects

127

of treatment on bryophyte composition for each micro-topographic position. This was done using the permutational multivariate analysis of variance (PERMANOVA), with 1000 permutations for tests of significance and transect as a random effect. To visualize these differences in composition among treatments, NMDS analyses were completed for each micro-topographic position; all species were included for these PERMANOVA and NMDS analyses. NMDS and PERMANOVA were done with the vegan package (Oksanen et al. 2018). A separate NMDS and PERMANOVA analysis showed that the reference sites for unmounded seismic lines did not differ from the reference sites for mounded seismic lines [available from authors]. Figures were created using the ggplot package (Wickham 2016).

5.4 Results

5.4.1 Bryophyte abundance and diversity

For all univariate response variables (pioneer true moss cover, feather moss cover, *Sphagnum* cover, species richness, and Shannon's diversity), treatment and the interaction between treatment and position were significant (Table 5.1). Pioneer true moss cover was higher on the mounded seismic lines than in both the unmounded and reference treatments at all micro-topographic positions (Figure 5.2). At the top position, the unmounded treatment had significantly higher pioneer true moss cover than the reference treatment; at the level and slope position the unmounded and reference treatments did not differ in pioneer true moss cover. Within the reference treatment, the level position had significantly higher pioneer true moss cover than the slope and top positions. Pioneer true moss cover did not differ between positions in the unmounded and mounded treatments.

For feather moss cover, the reference treatment had significantly higher feather moss cover than the unmounded treatment at the level position; the mounded treatment was

128

intermediate and did not differ from either (Figure 5.3). At the slope and top positions, the reference treatment had significantly higher feather moss cover than both the unmounded and mounded seismic lines, which did not differ from one another. Within the reference treatment, the top position had significantly higher feather moss cover than both the slope and level positions. Feather moss cover did not differ between positions in the unmounded and mounded treatments.

For *Sphagnum* cover, the mounded treatment had significantly lower *Sphagnum* cover than both the unmounded and reference treatments at the slope and top positions, with most mounded sites having very low (~0) *Sphagnum* cover (Figure 5.4). The unmounded and reference treatments did not differ from one another, in *Sphagnum* cover, at the slope and top positions. There was no difference in *Sphagnum* cover between the three treatments at the level position.

Looking at *Sphagnum* cover between positions at each treatment, *Sphagnum* cover significantly differed between positions for both the mounded and reference treatment; *Sphagnum* cover did not differ between positions in the unmounded treatment (Figure 5.4). In the mounded treatment, the level position had significantly higher *Sphagnum* cover than the top position; the slope position was intermediate and did not differ from either. In the reference treatment, the slope position had significantly higher *Sphagnum* cover than both the top and level position, which did not differ from one another.

At all positions, the mounded treatment had significantly higher species richness and Shannon's diversity than both the reference and unmounded treatments (Figures 5.5, 5.6). At the top position, the unmounded treatment had significantly higher species richness and Shannon's

diversity than the reference treatment. For the slope and level positions, richness and diversity did not differ between the unmounded and reference treatments. These trends were also reflected in the species richness at the mound-level (treatment F-value = 26.544, df = 2, P value < 0.001; Figure 5.7). At the mound-level, species richness was significantly higher in the mounded treatments than in the reference and unmounded treatments, which did not differ from one another (Figure 5.7).

Looking at differences between micro-topographic positions at each treatment, both richness and diversity only differed between positions in the reference treatment (Figures 5.5, 5.6). In the reference treatment, the level position had significantly higher Shannon's diversity and species richness than the top position; the slope position was intermediate and did not differ from either.

5.4.2 Indicator species and community composition

Common boreal feather mosses—*Pleurozium schreberi, Hylocomium splendens, and Ptillium crista-castrensis*—and *Sphagnum fuscum* were the indicator species for reference sites (Table 5.2). Feather mosses were mostly restricted to reference sites, however not all reference sites had feather mosses (Table 5.2). Common hummock fen *Sphagnum* species (e.g., *S. angustifolium* and *S. warnstorfii*) and *Straminergon straminergon* were the indicator species for the unmounded treatment (Table 5.2). In contrast, disturbance-associated true mosses were primarily the indicator species for the mounded treatment, including *Ceratodon purpureus, Funaria hygrometrica, Leptobryum pyriforme* (Table 5.2). In addition, *C. purpureus, F. hygrometrica, L. pyriforme, F. hygrometrica, Polytrichum commune,* and *Meesia ulignosa* were only found on mounded seismic lines (Table 5.2). There were no indicator species found for micro-topographic positions.

Bryophyte composition only differed between treatments at the slope and top positions, for which there were significant differences in composition among all three treatments (Table 5.3). Despite significant treatment effect for the level position, post-hoc comparisons showed that bryophyte composition did not differ between treatments (Table 5.3).

The NMDS ordination for the top position (based on 2 dimensions, final stress of 0.142) showed strong separation between the three treatments along the first axis, with some overlap between the unmounded and reference treatment (Figure 5.8A). Much like the results of the indicator species analysis, *Ceratodon purpureus* was associated with mounded seismic lines. Feather mosses and *S. fuscum* were associated with the reference treatment. *S. warnstorfii, S. angustifolium, T. nitens, T. falcifolium,* and *A. palustre* were associated with both reference and unmounded treatments. In contrast, in the NMDS ordination for the slope position (based on 2 dimensions, final stress of 0.166; Figure 5.8B), the unmounded treatment had considerable overlap with the reference treatment, while the mounded treatment was slightly separated from the other two treatments on the second axis (Figure 5.8B). *L. pyriforme, P. creberrimum, C. purpureus* were associated with mounded treatments, while S. *warnstorfii, S. angustifolium, and Pleurozium schreberi* were associated with both the unmounded and reference treatments. Lastly, the NMDS for the level position showed both the mounded and unmounded treatments were nested within the reference treatment (based on 2 dimensions, with a final stress of 0.161; Figure 5.8C).

5.5 Discussion

The results of this study support the conclusions from the previous chapter on vascular plants (Echiverri et al. 2020): vegetation communities on unmounded seismic lines are recovering and are dominated by peatland species, while mounding treatments that have further

disturbed the vegetation for forest restoration have initially led to communities dominated by disturbance-associated species. As expected, *Sphagnum* cover did not differ between the unmounded and reference treatments; pioneer true moss cover, species richness and Shannon's diversity only differed between the unmounded and reference treatments at the top of mounds. In contrast, mounded seismic lines had lower *Sphagnum* cover and higher pioneer true moss cover, species richness, and diversity than both the reference and unmounded treatments. In addition, bryophyte composition of the unmounded and reference treatments showed considerable overlap, while the mounded treatment was often separated from the reference treatment. Unmounded and reference treatments were associated with *Sphagnum* species, while mounded treatments were characterized by cosmopolitan, disturbance-associated species. Lastly, in concordance with our hypothesis, we found that the bryophyte communities at the level position did not differ between the three treatments, while the communities at the top position showed the strongest differences among treatments.

5.5.1 Recovery by micro-topographic position

On both mounded and unmounded seismic lines, the level position was most similar to the reference sites, while the top position was the least recovered. This aligns with results for recovery of the vascular plant community, for which the level position also showed the least differences in composition between treatments (Echiverri et al. 2020). On mounded seismic lines, the level position was the relatively untouched portions of the mounded seismic lines—the areas between the artificially-created mounds and their accompanying hollows; this likely explains why the level position on mounded seismic lines was least affected by mounding. In both mounded and unmounded seismic lines, the level position was most similar to the pre-disturbance proximity to the water table; it stands to reason, therefore, that bryophyte species

adapted to this micro-topographic position were able to quickly colonize and establish. The wet conditions found at this position would allow for *Sphagnum* colonization on both types of seismic lines, as can be seen in *Sphagnum* cover not differing between treatments at the level position. Similarly, studies have found increased *Sphagnum* cover and regeneration of common fen bryophytes in micro-sites with high water levels (Campeau and Rochefort 1996; Cobbaert et al. 2004; Benscoter 2006; Graf and Rochefort 2010; Borkenhagen and Cooper 2016). Bryophyte species tolerant of flooding are capable of compensating in growth for the loss of bryophytes that are more sensitive to flooding (Borkenhagen and Cooper 2018), leading to higher resilience in overall bryophyte abundance at the level position.

In undisturbed peatlands, hummocks are formed by the upward growth of hummock-forming bryophytes, such as *S. fuscum* and *S. warnstorfii* (Rydin and Jeglum 2006). Thus, it is unsurprising that the top position of unmounded seismic lines was the slowest to recover—it will take time for enough peat accumulation to achieve the hummock height above the water table found in the reference sites. However, it is promising that *Sphagnum* cover at the tops of unmounded seismic lines was similar to that of reference sites. In addition, the indicator species associated with unmounded seismic lines include *Sphagnum warnstorfii*—a hummock-forming species in moderately-rich fens. Over time, we can expect *S. warnstorfii* to continue hummock expansion and development. On the mounded seismic lines, the harsh micro-climatic conditions (warm and dry) on the tops of the artificially-created mounds could hinder the establishment of *Sphagnum* species (Campeau and Rochefort 1996; Price et al. 1998). The presence of *Polytrichum* spp. and other vascular plants may help mitigate the temperature extremes and maintain humid conditions, facilitating *Sphagnum* establishment (Groeneveld et al. 2007; Graf

and Rochefort 2010; Borkenhagen and Cooper 2016); however, once dominant, vascular plants could also outcompete bryophytes and prevent bryophyte establishment (Malmer et al. 1994).

5.5.2 Recovery by treatment

The results show that approximately 18 years after seismic line creation, recovery in unmounded seismic lines was similar to the second phase of the post-fire bryophyte recovery in bogs as described by Benscoter and Vitt (2008): unmounded seismic lines had high *Sphagnum* abundance—comparable to the reference sites—and less pioneer true moss cover than mounded seismic lines. In addition, the indicator species for the unmounded seismic lines are species commonly found in moderately-rich fens. This aligns with the vascular plant community results, suggesting a trajectory of continued fen development on unmounded seismic lines (Echiverri et al. 2020). Since fen bryophytes are tolerant of some degree of flooding (Borkenhagen and Cooper 2018), it is unsurprising that bryophyte communities were able to recover in the flooded conditions of unmounded seismic lines. In addition, the seismic lines we studied are a low-severity, narrow disturbance, with soil disturbance mitigated with the use of lightweight equipment (Dabros et al. 2018). The narrow nature of this disturbance could allow for hummock expansion from the adjacent treed fens to extend into a portion of the seismic lines, which could help accelerate recovery. These results are encouraging, as they show that bryophyte recovery on unmounded seismic lines is well underway and may not require the further intervention or intensive site-preparation that is often needed for restoration following more severe disturbances, like peat harvesting (Rochefort and Lode 2006).

In contrast, mounding wound back recovery. Three years after mounding treatments were applied, higher micro-topographic positions of mounded seismic lines matched the first phase of the post-fire recovery trajectory observed by Benscoter and Vitt (2008). The slope and tops of

mounded seismic lines were similar to post-fire recovery in bogs, primarily characterized by pioneer mosses, such as *Polytrichum strictum,* at lower overall cover (Benscoter and Vitt 2008). Indicator species associated with the mounded seismic lines included ruderal bryophytes such as, *Leptobryum pyriforme, Ceratodon purpureus, Polytrichum* spp., and bryophytes not commonly found in fens, such as *Funaria hygrometrica.* Similarly, these ruderal bryophytes were also found on mounded well pads (Caners et al. 2019) and reclaimed fens (Borkenhagen and Cooper 2016). As expected, the ingress of ruderal species led to higher bryophyte richness and diversity on mounded seismic lines than on unmounded seismic lines and reference sites. Though mounded seismic lines had higher diversity, the opportunistic species found on mounded seismic lines were found at low abundance, resulting in overall lower total bryophyte cover on mounded seismic lines (Echiverri et al. 2020).

Although mounding may improve tree establishment (Lieffers et al. 2017; Filicetti et al. 2019), it may negatively affect other aspects of peatland vegetation. If these micro-sites follow the post-fire trajectory described by Benscoter and Vitt (2008), true mosses may gradually be replaced by *Sphagnum* in the next 10 to 20 years, which is 10 to 20 years behind the recovery of the unmounded seismic lines. Alternatively, the harsh micro-climatic conditions on the tops of the mounds and the altered position of the peat layers due to mounding, may hinder fen bryophyte establishment and lead to the development of a different ecosite. For example, the indicator species for the vascular plants on mounded seismic lines were marsh-associated species (Echiverri et al. 2020). Our results suggest that mounding acts as a relatively severe disturbance on a recovering bryophyte community, creating micro-site conditions similar to those found after more severe disturbance such as fire (Benscoter and Vitt 2008) or even peat harvesting (Price et al. 1998). Ironically, mounding done to create conditions to ensure tree establishment and growth

on seismic lines, not only sets back the recovery of the ground layer, but it also jeopardizes the establishment of hummock-forming bryophytes—the very organisms that create microsites for tree growth in undisturbed fens. Since the problem with seismic lines is not the severity of the disturbance, but their ubiquity, it begs the question: as a restoration tool, is mounding in treed peatlands doing more harm than good?

Another issue associated with mounding of seismic lines is the creation of deep, wide pools along the seismic lines (~ 0.75 m wide, 1 m long, and 0.80 m tall). At our study site, artificial mounds were established every 6 m along the seismic line, each one accompanied by a deep pool of water, i.e., an artificial "hollow". While peatlands are known to have occasional pools of water, in western Canada, they are not usually found at this frequency (Vitt and Wieder 2008), where most fens are covered by lawns and carpets (such as the "slope" and "level" positions). We were unable to analyze the vegetation for these pools of water since the pools on mounded seismic lines had little to no vegetation present (both vascular plants and bryophytes), while unmounded seismic lines and reference hollows were often vegetated. We expect the recovery of these artificial hollows will likely take a long time, as bryophytes must first colonize the pools before significant plant material can accumulate and fill up the pools. Though these pools of water do not help with vegetation recovery, they might be effective in discouraging human or predator travel along seismic lines and associated effects on wildlife; this is worthy of further investigation.

Future studies should also examine the impacts of mounding on carbon storage (see Schmidt et al. 2020) and hydrology. Since production and decomposition rates vary between species, the changes in bryophyte composition could lead to altered rates of peat accumulation (Benscoter and Vitt 2008), with consequences for carbon storage in these ecosystems. This is of

particular concern in the face of climate change, with peatlands playing an essential role in global carbon storage. In addition, other peatland types should be examined as recovery can vary between bogs and fens.

5.5.3 Management implications

To address the slow recovery of the canopy layer on seismic lines in peatlands, mounding is being applied to seismic lines, years after their creation. Since peatlands are nutrient-poor and harsh environments for tree growth, it is unsurprising that canopy height on seismic lines is slow to develop. However, attempts to restore existing seismic lines and accelerate tree regeneration may do more harm than good. For the understory and ground layer vegetation, mounding only acts as a more severe disturbance on recovering vegetation communities. In addition, recovery of vegetation communities on unmounded seismic lines is very promising, with hummock-forming *Sphagnum* species associated with unmounded lines and hummocks already tall enough to support woody growth (Echiverri et al. 2020). In fact, untreated seismic lines within peatlands with little to no human activity showed substantial tree recruitment (Filicetti et al. 2019). Instead of mounding, I recommend minimizing further human activity on seismic lines, as this will prevent any additional disturbance that could further delay plant community recovery. I also recommend prevention: minimize the creation of linear disturbances using zero-impact seismic lines. Zero-impact seismic lines are created by a relatively recent technology that eliminates the need for deforested linear corridors. While zero-impact seismic lines may be initially more costly, they reduce the costs associated with restoration and more importantly they can potentially reduce the negative impacts of oil and gas exploration on peatlands.

Table 5.1: Results of the mixed effects models for *Sphagnum* cover, true moss cover, bryophyte richness and Shannon's diversity for each quadrat as affected by mounding treatment, micro-topographic position, and their interaction; F-values, numerator degrees of freedom (df), and p-values (P) are shown. Bolded values indicate significance ($\alpha= 0.05$); see Appendix 5.1.

Response variable	Treatment			Position			Treatment x Position		
	F	df	P	F	df	P	F	df	P
Abundance (cover)									
Pioneer true moss	**16.953**	**2**	**<0.001**	**4.406**	**2**	**0.013**	**5.175**	4	**<0.001**
Feather moss	**20.050**	**2**	**<0.001**	2.394	2	0.093	**3.373**	**4**	**0.010**
Sphagnum	**12.852**	**2**	**<0.001**	2.660	2	0.072	**4.502**	**4**	**0.002**
Diversity									
Species richness	**22.203**	**2**	**<0.001**	0.868	2	0.421	**2.532**	**4**	**0.041**
Shannon's diversity*	**30.447**	**2**	**<0.001**	0.0078	2	0.992	**3.598**	**4**	**0.007**

*$\log_{10}$-transformed

Table 5.2: Results of Indicator Species Analysis for bryophyte communities in reference sites, mounded seismic lines, and unmounded seismic lines, irrespective of micro-topographic position.

Treatment	Species	Component A[*]	Component B[†]	Indicator value	P value
Reference	*Pleurozium schreberi*	0.937	0.625	0.765	0.001
	Hylocomium splendens	0.990	0.215	0.432	0.001
	Sphagnum fuscum	0.543	0.222	0.347	0.047
	Ptillium crista-castrensis	0.991	0.118	0.342	0.005
Unmounded	*Sphagnum angustifolium*	0.554	0.750	0.645	0.001
	Sphagnum warnstorfii	0.468	0.667	0.559	0.002
	Straminergon straminergon	0.692	0.208	0.380	0.005
	Sphagnum Sect. Cuspidata	0.760	0.097	0.272	0.004
Mounded	*Ceratodon purpureus*	1	0.563	0.751	0.001
	Ptychostomum creberrimum	1	0.451	0.671	0.001
	Leptobryum pyriforme	1	0.423	0.650	0.001
	Aulacomnium palustre	0.516	0.775	0.632	0.014
	Polytrichum strictum	0.749	0.521	0.625	0.001
	Funaria hygrometrica	1	0.352	0.593	0.001
	Ptychostomum pseudotriquetrum	0.618	0.394	0.493	0.001
	Liverwort	0.760	0.254	0.439	0.001
	Plagiomnium ellipticum	0.473	0.380	0.424	0.008
	Polytrichum commune	1	0.155	0.394	0.001
	Pohlia nutans	0.794	0.183	0.381	0.041
	Ptychostomum spp.	0.995	0.085	0.29	0.001
	Drepanocladus aduncus	0.703	0.113	0.282	0.023
	Meesia uliginosa	1	0.056	0.237	0.007
	Meesia triquetra	0.924	0.056	0.228	0.02

Note: Component A represents the probability of a site belonging to a treatment based on the presence of the indicator species; component B represents the probability of encountering the indicator species in sites belonging to a treatment; indicator value is the product of component A and component B (see De Caceres and Legendre 2009). The P value represents the significance of the association between the indicator species and its corresponding treatment, based on a permutation test of 1000 runs.

Table 5.3: Results of PERMANOVA for bryophyte community composition at each micro-topographic position as affected by treatment. Bolded values indicate significance (α= 0.05).

Position	Treatment			Mounded vs. Reference	Reference vs. Unmounded	Unmounded vs. Mounded
	F	df	P			
Level	**1.546**	**2**	**0.047**	0.170	0.170	0.170
Slope	**5.015**	**2**	**<0.001**	**0.003**	**0.045**	**0.003**
Top	**9.952**	**2**	**<0.001**	**0.003**	**0.003**	**0.003**

Figure 5.1: A) Unmounded seismic line and B) mounded seismic line in May 2018. C) Slope of a hummock on an unmounded seismic line, with a 20 x 20 cm quadrat, taken in June 2018. D) Exposed peat at the top of a "mound" on a mounded seismic line in May 2018.
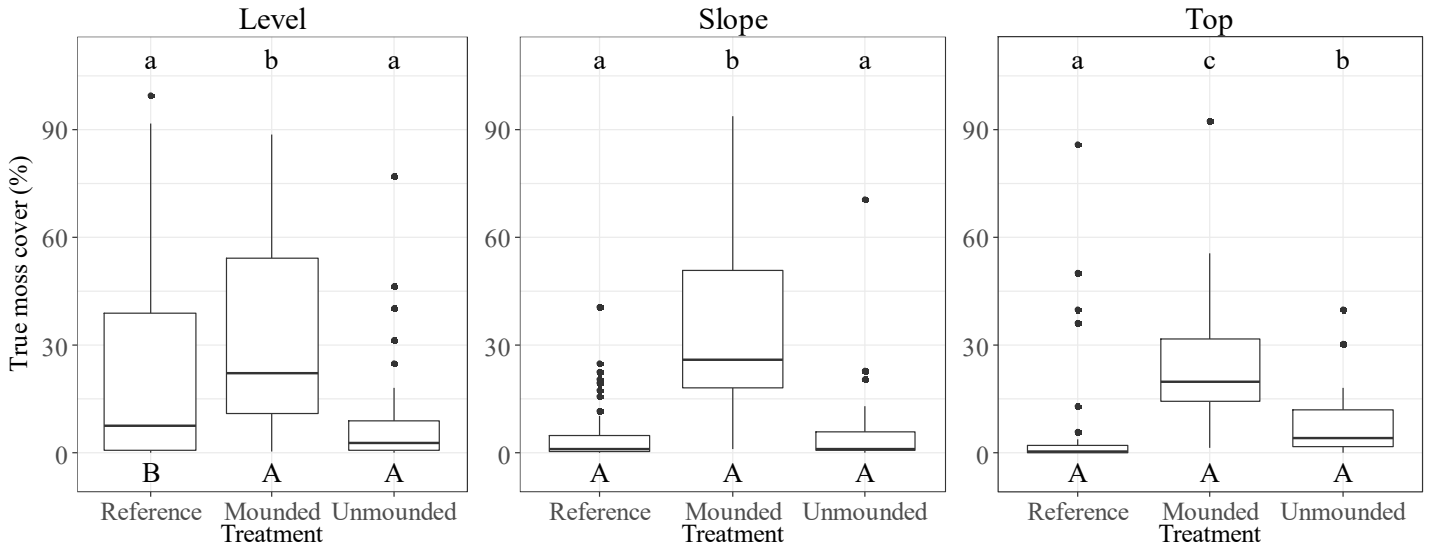
Figure 5.2: Boxplots (in Tukey style) of "pioneer" true moss cover (sans feather moss cover, see Appendix 5.1) by treatment (reference sites, mounded seismic lines, and unmounded seismic lines) and microtopographic position. Different letters indicate significant ($\alpha = 0.05$) differences between treatments within each position (lower-case letters), or between positions within each treatment (upper-case letters), based on pairwise comparison of estimated marginal means. (Analysis done on log-transformed data, See also Table 5.1). The horizontal line within the boxplot represents the median, the lower and upper hinges represent the 25th and 75th percentiles (respectively), the whiskers represent the smallest and largest value within 1.5 times the interquartile range (IQR), and the outliers (values greater than or less than 1.5*IQR) are represented as dots outside the box and whiskers.
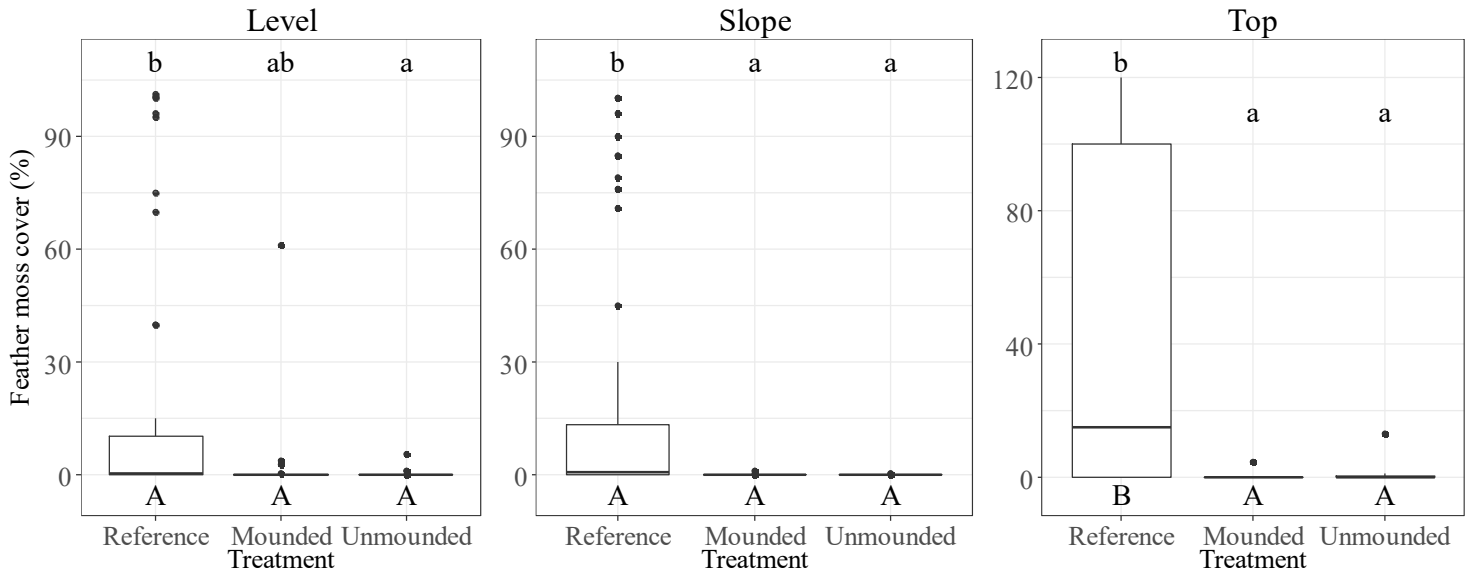
Figure 5.3: Boxplots (in Tukey style) of feather moss cover (see Appendix 5.1) by treatment (reference sites, mounded seismic line, and unmounded seismic lines) and microtopographic position. Different letters indicate significant ($\alpha = 0.05$) differences between treatments within each position (lower-case letters), or between positions within each treatment (upper-case letters), based on pairwise comparisons of estimated marginal means. See also Table 5.1. For the statistics used to create the boxplot see Figure 5.2.
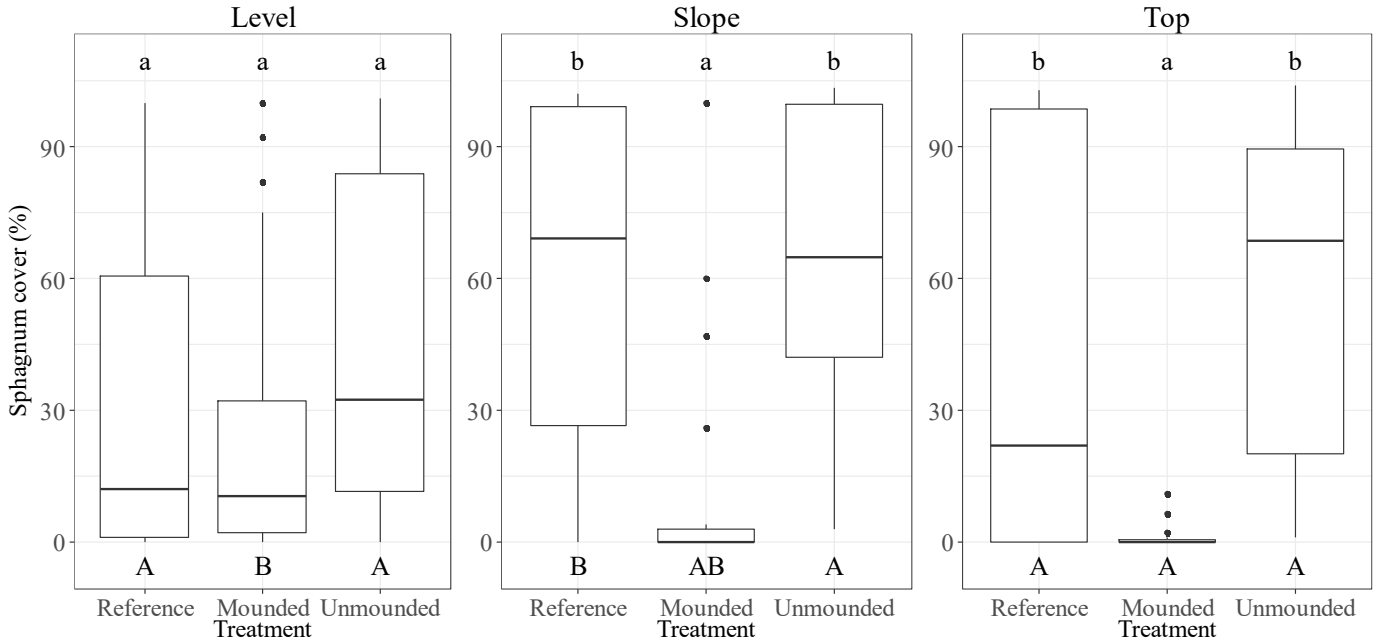
Figure 5.4: Boxplots (in Tukey style) of *Sphagnum* cover by treatment (reference sites, mounded seismic line, and unmounded seismic lines) and microtopographic position. Different letters indicate significant ($\alpha = 0.05$) differences between treatments within each position (lower-case letters), or between positions within each treatment (upper-case letters), based on pairwise comparisons of estimated marginal means. See also Table 5.1. For the statistics used to create the boxplot see Figure 5.2.
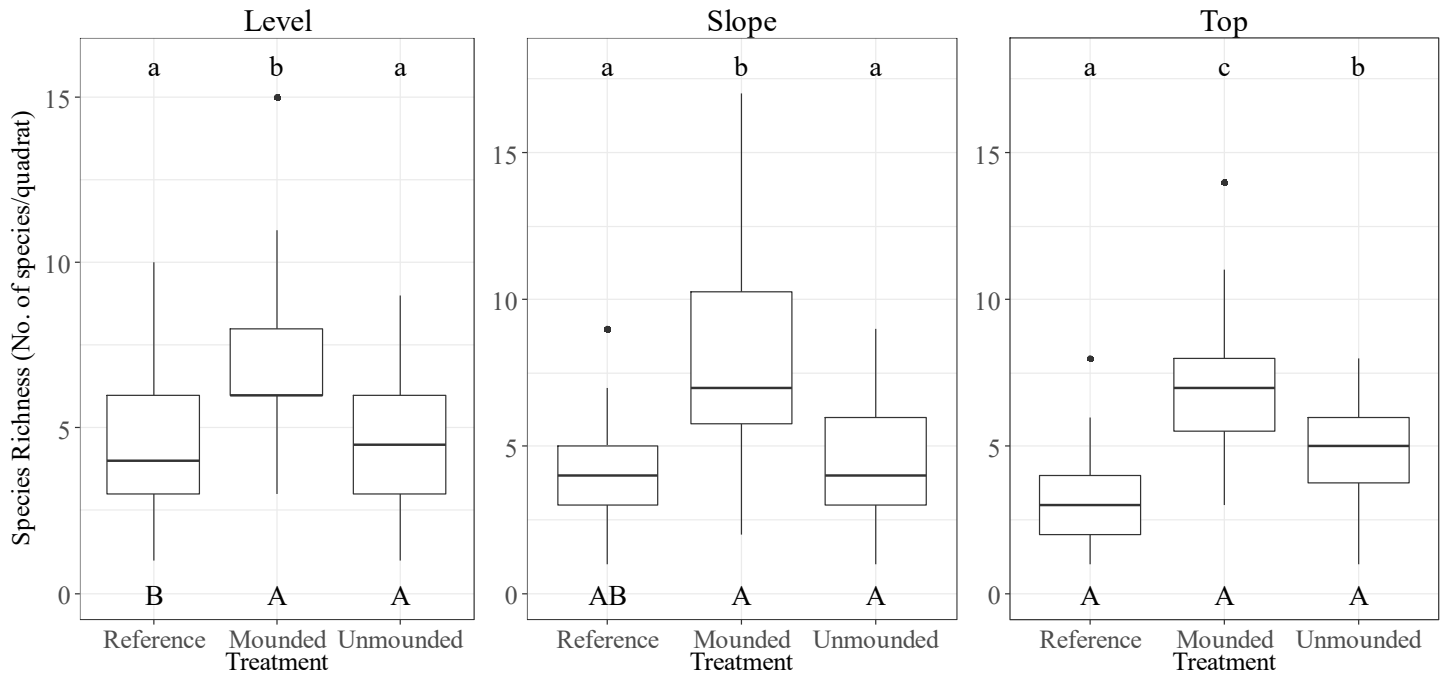
Figure 5.5: Boxplots (in Tukey style) of species richness per quadrat by treatment (reference sites, mounded seismic line, and unmounded seismic lines) and microtopographic position. Different letters indicate significant ($\alpha = 0.05$) differences between treatments within each position (lower-case letters), or between positions within each treatment (upper-case letters), based on pairwise comparisons of estimated marginal means. See also Table 5.1. For the statistics used to create the boxplot see Figure 5.2.
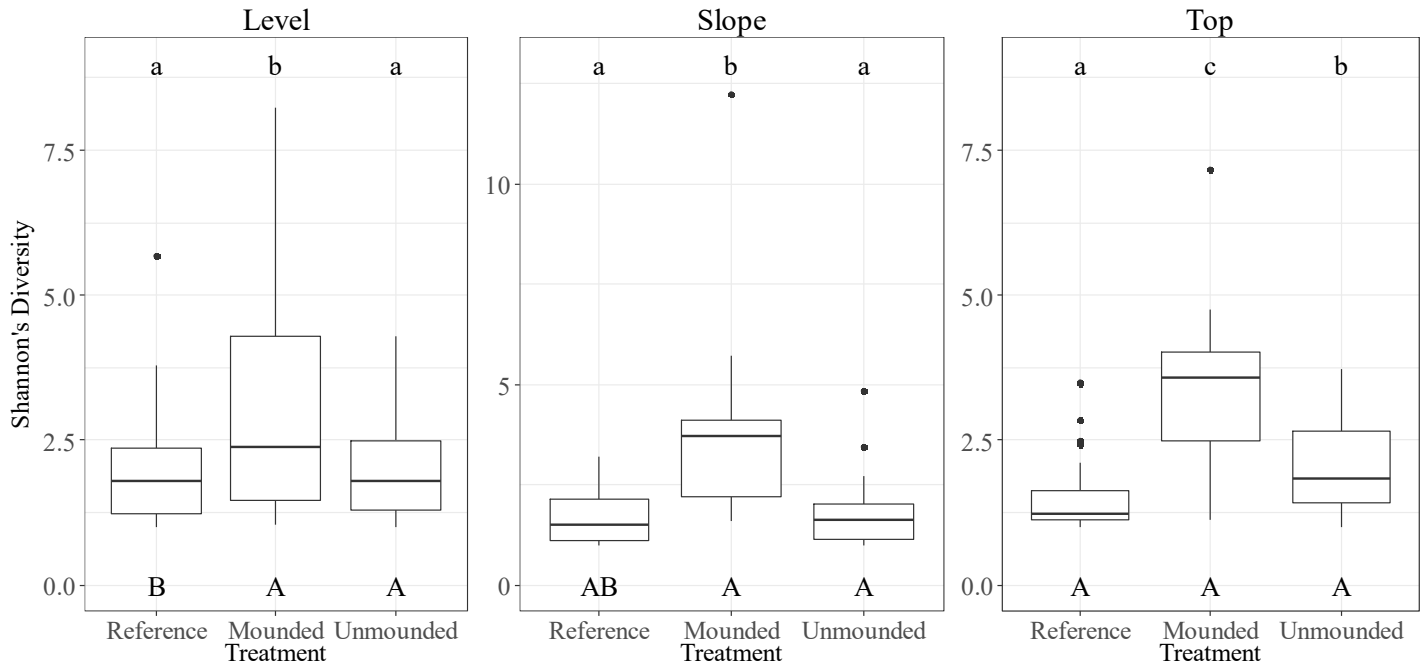
Figure 5.6: Boxplots (in Tukey style) of Shannon's diversity by treatment (reference sites, mounded seismic line, and unmounded seismic lines) and microtopographic position. Different letters indicate significant ($\alpha = 0.05$) differences between treatments within each position (lower-case letters), or between positions within each treatment (upper-case letters), based on pairwise comparisons of estimated marginal means. (Analysis done on log-transformed data, See also Table 5.1). For the statistics used to create the boxplot see Figure 5.2.
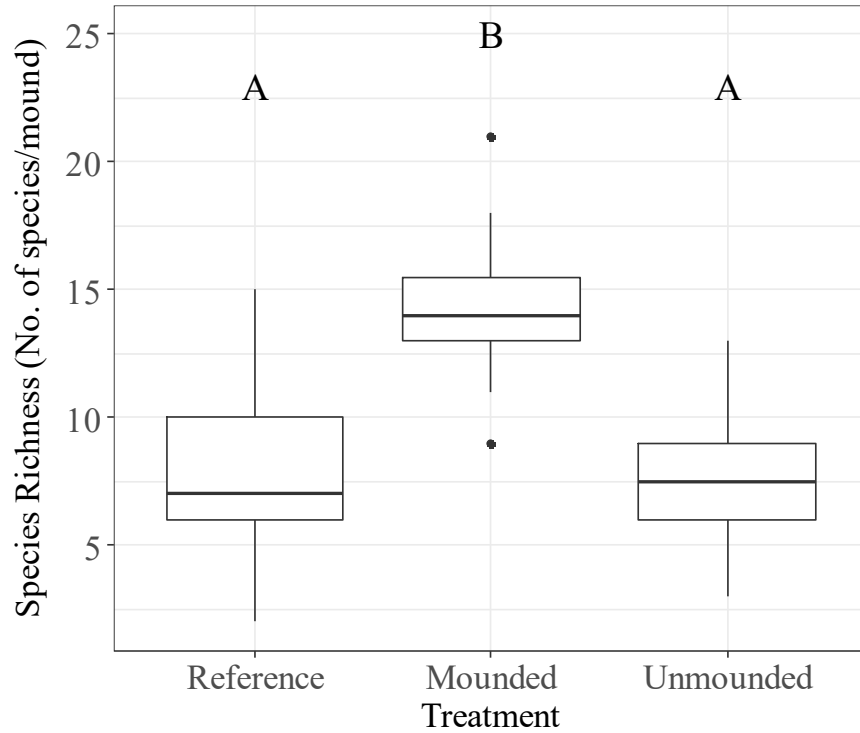
Figure 5.7: Boxplots (in Tukey style) of species richness per mound (the three microtopographic positions combined) by treatment (reference sites, mounded seismic lines, and unmounded seismic lines). Different letters indicate significant ($\alpha = 0.05$) differences between treatments, based on pairwise comparison of estimated marginal means. For the statistics used to create the boxplot see Figure 5.2.
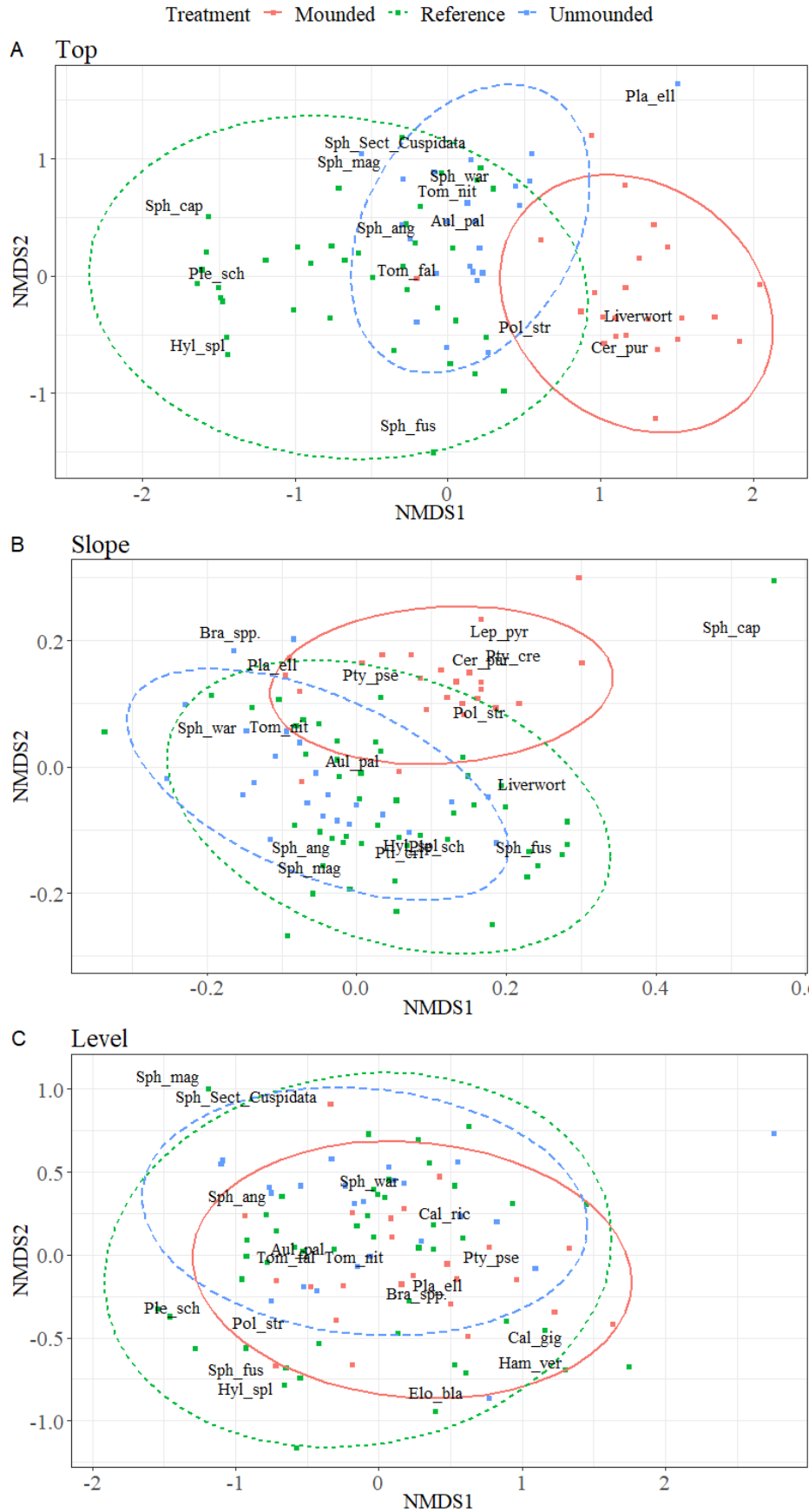
**Figure 5.8:** Results of a non-metric multidimensional scaling (NMDS), an unconstrained ordination, of bryophyte community composition by treatment (reference sites, mounded seismic lines, and unmounded seismic lines) at each micro-topographic position: A) top, B) slope, and C) level. Points represent sampled sites, with color representing treatment. Ellipses represent the 95% confidence intervals for the treatment centroid, with color and linetype representing treatment. The most abundant species are represented by six letter codes (first three letters of genus and species epithet; see Appendix 5.1). To better visualize the differences between treatments at the slope position, we removed one outlier quadrat, which was from the unmounded treatment.

Appendix 5.1: List of species found in sample quadrats with their corresponding codes (See Figure 5.8). Nomenclature follows Flora of North America Editorial Committee (2007, 2014).

Species code	Latin name	Family	Growth form
Aul_pal	*Aulacomnium palustre*	Aulacomniaceae	True moss
Bra_spp.	*Brachythecium spp.*	Brachytheciaceae	True moss
Bry_rec	*Bryoerythrophyllum recurvirostrum*	Pottiaceae	True moss
Cal_gig	*Calliergon giganteum*	Calliergonaceae	True moss
Cal_ric	*Calliergon richardsonii*	Calliergonaceae	True moss
Cam_chr	*Campyliadelphus chrysophyllus*	Amblystegiaceae	True moss
Cam_ste	*Campylium stellatum*	Amblystegiaceae	True moss
Cer_pur	*Ceratodon purpureus*	Ditrichaceae	True moss
Clim_den	*Climacium dendroides*	Climaciaceae	True moss
Dic_het	*Dicranella heteromalla*	Dicranaceae	True moss
Dic_pol	*Dicranum polysetum*	Dicranaceae	True moss
Dic_sco	*Dicranum scoparium*	Dicranaceae	True moss
Dic_und	*Dicranum undulatum*	Dicranaceae	True moss
Dre_adu	*Drepanocladus aduncus*	Amblystegiaceae	True moss
Elo_bla	*Elodium blandowii*	Helodiaceae	True moss
Fun_hyg	*Funaria hygrometrica*	Funariaceae	True moss
Ham_ver	*Hamatocaulis vernicosus*	Calliergonaceae	True moss
Hyl_spl	*Hylocomium splendens*	Hylocomiaceae	Feather moss
Hyp_lin	*Hypnum lindbergii*	Hypnaceae	True moss
Hyp_pra	*Hypnum pratense*	Hypnaceae	True moss
Iso_pul	*Isopterygiopsis pulchella*	Hypnaceae	True moss
Lep_pyr	*Leptobryum pyriforme*	Meesiaceae	True moss
Liverwort	*Liverwort*		Liverwort
Mee_lon	*Meesia longiseta*	Meesiaceae	True moss
Mee_tri	*Meesia triquetra*	Meesiaceae	True moss
Mee_uli	*Meesia uliginosa*	Meesiaceae	True moss
Pla_cil	*Plagiomnium ciliare*	Mniaceae	True moss
Pla_ell	*Plagiomnium ellipticum*	Mniaceae	True moss
Pla_spp.	*Plagiomnium spp.*	Mniaceae	True moss
Ple_sch	*Pleurozium schreberi*	Hylocomiaceae	Feather moss
Poh_nut	*Pohlia nutans*	Mielichhoferiaceae	True moss
Pol_com	*Polytrichum commune*	Polytrichaceae	True moss
Pol_jun	*Polytrichum juniperinum*	Polytrichaceae	True moss
Pol_pil	*Polytrichum piliferum*	Polytrichaceae	True moss
Pol_str	*Polytrichum strictum*	Polytrichaceae	True moss
Pti_cri	*Ptilium crista-castrensis*	Hypnaceae	Feather moss
Pty_pse	*Ptychostomum pseudotriquetrum*	Bryaceae	True moss
Pty_cre	*Ptychostomum creberrimum*	Bryaceae	True moss
Pty_spp.	*Ptychostomum spp.*	Bryaceae	True moss
Rhi_gra	*Rhizomnium gracile*	Mniaceae	True moss
San_uni	*Sanionia uncinata*	Amblystegiaceae	True moss

Species code	Latin name	Family	Growth form
Sar_exa	*Sarmentypnum exannulatum*	Calliergonaceae	True moss
Sph_ang	*Sphagnum angustifolium*	Sphagnaceae	Sphagnum
Sph_cap	*Sphagnum capillifolium*	Sphagnaceae	Sphagnum
Sph_cen	*Sphagnum centrale*	Sphagnaceae	Sphagnum
Sph_fus	*Sphagnum fuscum*	Sphagnaceae	Sphagnum
Sph_mag	*Sphagnum magellanicum*	Sphagnaceae	Sphagnum
Sph_Sect_Acutifolia	*Sphagnum sp. Section Acutifolia*	Sphagnaceae	Sphagnum
Sph_Sect_Cuspidata	*Sphagnum sp. Section Cuspidata*	Sphagnaceae	Sphagnum
Sph_spp.	*Sphagnum spp.*	Sphagnaceae	Sphagnum
Sph_squ	*Sphagnum squarrosum*	Sphagnaceae	Sphagnum
Sph_sub	*Sphagnum subsecundum*	Sphagnaceae	Sphagnum
Sph_ter	*Sphagnum teres*	Sphagnaceae	Sphagnum
Sph_war	*Sphagnum warnstorfii*	Sphagnaceae	Sphagnum
Str_str	*Straminergon stramineum*	Calliergonaceae	True moss
Tom_fal	*Tomentypnum falcifolium*	Amblystegiaceae	True moss
Tom_nit	*Tomentypnum nitens*	Amblystegiaceae	True moss
UnkMoss1	Unknown Moss1		True moss
UnkMoss3	Unknown Moss3		True moss
UnkMoss4	Unknown Moss4		True moss

Chapter 6: Conclusion

In this thesis, I assessed the edge influence associated with seismic lines and the efficacy of treatments designed to restore seismic lines, with a focus on the understory vegetation in treed peatlands and xeric, pine-dominated stands. Despite their narrow nature, I found that seismic lines had a significant edge influence on the understory vegetation in treed peatlands. In addition, there was evidence of edge interaction when multiple seismic lines were in proximity. In xeric, pine-dominated stands, there was a sealing effect at the edges of wider and older seismic lines, with woody vegetation increasing in abundance at the edge. In addition, I found that the population-level performance of an herbaceous annual was shaped by the presence of seismic lines, while at the individual-level, performance was primarily shaped by the vegetation surrounding each individual. Finally, attempts to re-create micro-sites for tree establishment on seismic lines only set back the recovery of understory communities in treed peatlands; while seismic lines left to recover naturally showed promising results, with the re-establishment of a peat-accumulating understory community.

In the first chapter, I examined how edge influence on understory communities differed between seismic line types (narrow vs. wide) and whether edge influence from multiple narrow seismic lines interacted. In moderate-rich fens, wide seismic lines had a higher DEI (up to 50 m from the seismic line) than narrow seismic lines (up to 25 m from the seismic line). There was also evidence of interacting edge influence from multiple seismic lines, with the direction of edge interaction varying with fen type. In moderate-rich fens, there was a weakening edge interaction on understory diversity. Both wide and narrow singular seismic lines had higher understory diversity at edges, due to the increase of opportunistic species. In contrast, there was

no edge influence on diversity from multiple, narrow seismic lines. This weakening edge interaction on diversity was due to the ingress of opportunistic species being countered by the loss of wet associated and specialist species. In poor fens, there was a strengthening edge interaction on vegetation abundance. Multiple narrow seismic lines resulted in increased tree density at edges, which led to a reduction in understory abundance; in contrast, there was minimal to no edge influence from singular seismic lines, either wide or narrow. These results add to the growing evidence that edge influence can vary when multiple edges are in close proximity (Fletcher 2005; Harper et al. 2007; Porensky and Young 2013) and highlight the need for incorporating landscape context when examining edge influence (Porensky and Young 2013; Ries et al. 2017).

While the direction of edge interaction differed between fen types, both results suggest a drying of the area between seismic lines. Since seismic lines tend to be depressed in elevation and thus wetter than the adjacent fens (Dabros et al. 2017; Stevenson et al. 2019), it is possible that groundwater within the peat is being drawn towards the seismic line, gradually drying out the surface in the adjacent fens. This drying effect would explain the loss of species with an affinity for wetter sites in moderate-rich fens and the increased tree density in the poor fens—as tree establishment and growth in peatlands is in part limited by the flooded, anaerobic conditions. Overall, this highlights the importance of assessing the cumulative impacts of seismic lines, as their impacts can clearly extend beyond their narrow boundaries (Schneider et al. 2003; Pattison et al. 2016). However, in this study I only examined one grid of seismic lines over an area of approximately 14 km^2 to maintain similar disturbance history. Future studies should verify these trends in other site types and disturbance histories (other grids of seismic lines). These results also show that edge influence should be kept in mind when designing studies examining the

impacts of seismic lines, e.g., researchers should consider placing reference sites outside the grids of seismic lines.

In the second chapter, I explored the mechanisms driving edge influence on understory vegetation in upland pine forests, by examining the edge influence on the performance of the herbaceous annual plant, cow-wheat (*Melampyrum lineare*). At the population level, I found increased abundance of woody vegetation at the edges of wide seismic lines, resulting in a "sealing effect". I also found that population density and seed production of cow-wheat was higher on the seismic line than at the edge or in the interior of the adjacent forest. At the individual level, I found vegetation was associated with cow-wheat performance and individual performance did not differ between the seismic line, edge, or interior forest. While I was unable to determine the mechanism(s) driving edge influence on cow-wheat population density, this chapter showed the importance of examining edge influence at both the population and individual level, as the drivers of plant performance can vary with scale. Future research should explore edge influence on other population-level processes, such as seed dispersion, predation, and germination rates, as differences in these processes might explain the differences in population density between the seismic line, edge, and interior forest.

Finally, in the third and fourth chapters, I assessed the impacts of mounding on the understory communities on seismic lines in treed fens—an ecosite attributed to having particularly slow recovery (Lee and Boutin 2006; van Rensen et al. 2015; Kansas et al. 2015). Mounding is a restoration technique that is intended to create micro-sites for tree establishment. In both studies, I found that mounding acted as another subsequent disturbance to the initial seimic line disturbance and set back the recovery of the understory communities. In contrast, I found promising evidence of understory recovery on the seismic lines that were left to recover

naturally, i.e., unmounded seismic lines. Hummock-forming *Sphagnum* species successfully established on unmounded lines and hummock height was tall enough to provide aerated rooting conditions for woody growth. While unmounded seismic lines were associated with typical fen species, mounded seismic lines were associated with disturbance-associated species, some of which were not typically found in fens. The bryophyte communities were particularly sensitive to the effects of mounding, with mounded seismic lines having significantly lower *Sphagnum* and total bryophyte cover than both unmounded seismic lines and reference fens. This is concerning as bryophytes are the primary drivers of peat accumulation (i.e., carbon storage) and hummock development in treed peatlands. Given the widespread presence and impact of seismic lines within Alberta, it is encouraging that the local government and industries are eager to restore the existing legacy seismic lines. However, these results highlight the importance of assessing the impacts of restoration techniques prior to their widespread implementation. As bryophyte composition shapes the rate of peat accumulation, future research should explore the impact of mounding on carbon storage. In addition, future research should assess how woodland caribou respond to restoration treatments.

6.1 Management Implications

As previous studies have found (Lee and Boutin 2006; van Rensen et al. 2015; Kansas et al. 2015), treed peatlands seem to be sensitive to the presence of seismic lines. The results of my first chapter support this with seismic lines altering the vegetation at least 25 m into the adjacent fen—a comparable distance to the DEI of larger disturbances in upland stands. More alarmingly, the vegetation changes within the grid of dense, narrow seismic lines, suggest a gradual draining of the treed peatlands. Studies and restoration efforts are primarily focused on the impacts of

155

seismic lines on wildlife, especially the threatened woodland caribou, *Rangifer tarandus*. However, if this draining effect is truly happening, there could be substantive impacts on carbon storage and water regulation at a landscape level. Thus, these effects should be examined further, as peatlands play an important role in these functions. The impact on carbon storage is especially of concern in the face of climate change.

Unfortunately, the current focus on restoring seismic lines for woodland caribou may only be hampering the recovery of treed peatlands. Currently the primary focus of restoration efforts is to rapidly establish trees on seismic lines (Pyper et al. 2014; Government of Alberta 2017), even in treed peatlands where tree density is low and growth is known to be slow due to harsh growing conditions (Rydin and Jeglum 2006). The hope is that by re-establishing trees in the deforested seismic lines, peatlands can once again provide refuge from predators for woodland caribou. However, in treed peatlands, the emphasis on tree establishment and growth seems to come at a cost to the understory communities—ironically, the very organisms responsible for creating the micro-sites for tree establishment and growth. Specifically, I found mounding degraded any recovery already underway and created micro-sites that are unsuitable for bryophyte establishment. This is consequential as bryophytes play an important role in peatland ecosystem functions and we can expect subsequent changes to carbon storage and water regulation as a result of the shifts in bryophyte composition (Schmidt et al. 2020). In fact, bryophytes play such an integral role in peatland functioning that most peatland restoration efforts have the short-term objective of restoring bryophyte cover, in order to meet the long-term objective of re-establishing "a functional peat-accumulating ecosystem" (Rochefort 2000; Rochefort et al. 2003; Rochefort and Lode 2006). While peatlands can exist without trees, the

peat accumulation that defines the peatland ecosystem does not occur without bryophytes (Rydin and Jeglum 2006).

In light of these results, I recommend 1) preventing any additional creation of conventional and/or low impact seismic lines and 2) minimizing or preventing any additional disturbance on existing seismic lines. Considering the slow recovery of existing seismic lines and their cumulative impacts on the landscape, preventing any additional seismic line creation is imperative. Fortunately, this is now possible with "zero-impact" seismic lines—a recently developed technology that eliminates the need for clearing linear corridors of forest. "Zero-impact" seismic lines can further reduce the disturbance footprint associated with oil and gas exploration. Though zero-impact seismic lines are initially costly, they reduce restoration costs, and more importantly mitigate the environmental consequences of disturbing sensitive ecosystems, like treed peatlands.

Since the understory communities on seismic lines are already showing signs of recovery and additional restoration efforts may only act as a secondary disturbance, preventing any additional disturbance on existing seismic lines may be the best way to facilitate the recovery of seismic lines, in both xeric, pine-dominated stands and treed peatlands. Preventing anthropogenic travel on seismic lines is important, as studies have shown anthropogenic use of seismic lines can hinder seismic line recovery (van Rensen et al. 2015). In addition, existing research on tree recovery in peatlands for both treated and untreated seismic lines suggests that at least some areas without human activity on lines recover at tree densities that are above some thresholds for recovery and are similar to adjacent reference conditions (Filicetti et al. 2019). Preventing seismic line use can be done by blocking access to seismic lines with coarse woody debris,

especially in areas near major roads or settlements. Fortunately, this is one of the restoration techniques already being implemented in Alberta.

Lastly, I propose a re-examination of the current restoration goals. Given the increasing threat of climate change and the important role of peatlands in carbon storage, are peatlands only valuable because they provide habitat for a threatened mammal? Should this be the ecosystem function we prioritize when creating restoration objectives? Should we prioritize the short-term objective of tree establishment over the long-term objective of re-establishing a peat-accumulating ecosystem, even when a peat-accumulating community naturally establishes post-disturbance? Additionally, will woodland caribou truly benefit from the re-establishment of trees if overall peatland functioning continues to be sub-optimal? Clearly, peatlands are complex ecosystems, but in terms of seismic line recovery, perhaps the best way forward is to simply let them be.

Literature Cited

Abib, T.H., Chasmer, L., Hopkinson, C., Mahoney, C., and Rodriguez, L.C.E. 2019. Seismic line impacts on proximal boreal forest and wetland environments in Alberta. Sci. Total Environ. **658**: 1601–1613. Elsevier, Amsterdam. doi:10.1016/j.scitotenv.2018.12.244.

Ågren, J., Ehrlén, J., and Solbreck, C. 2008. Spatio-temporal variation in fruit production and seed predation in a perennial herb influenced by habitat quality and population size. Journal of Ecology **96**(2): 334–345. doi:https://doi.org/10.1111/j.1365-2745.2007.01334.x.

Aguilar, R., Ashworth, L., Galetto, L., and Aizen, M.A. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol. Lett. **9**(8): 968–980. Wiley, Hoboken. doi:10.1111/j.1461-0248.2006.00927.x.

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Bayne, E.M., and Dale, B.C. 2011. Effects of Energy Development on Songbirds. *In* Energy Development and Wildlife Conservation in Western North America. *Edited by* D.E. Naugle. Island Press/Center for Resource Economics, Washington, DC. pp. 95–114. doi:10.5822/978-1-61091-022-4_6.

Beckingham, J.D., and Archibald, J.H. 1996. Field Guide to Ecosites of Northern Alberta. UBC Press, Vancouver, British Columbia.

Benscoter, B.W. 2006. Post-fire bryophyte establishment in a continental bog. Journal of Vegetation Science **17**(5): 647–652. John Wiley & Sons, Ltd (10.1111). doi:10.1111/j.1654-1103.2006.tb02488.x.

Benscoter, B.W., and Vitt, D.H. 2008. Spatial Patterns and Temporal Trajectories of the Bog Ground Layer Along a Post-Fire Chronosequence. Ecosystems **11**(7): 1054–1064. doi:10.1007/s10021-008-9178-4.

Borkenhagen, A., and Cooper, D.J. 2016. Creating fen initiation conditions: a new approach for peatland reclamation in the oil sands region of Alberta. Journal of Applied Ecology **53**(2): 550–558. John Wiley & Sons, Ltd (10.1111). doi:10.1111/1365-2664.12555.

Borkenhagen, A., and Cooper, D.J. 2018. Tolerance of fen mosses to submergence, and the influence on moss community composition and ecosystem resilience. Journal of Vegetation Science **29**(2): 127–135. doi:10.1111/jvs.12610.

Braverman, M., and Quinton, W.L. 2016. Hydrological impacts of seismic lines in the wetland-dominated zone of thawing, discontinuous permafrost, Northwest Territories, Canada. Hydrological Processes **30**(15): 2617–2627. doi:https://doi.org/10.1002/hyp.10695.

van Breemen, N. 1995. How Sphagnum bogs down other plants. Trends in Ecology & Evolution **10**(7): 270–275. Elsevier Current Trends. doi:10.1016/0169-5347(95)90007-1.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., and Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal **9**(2): 378–400. Technische Universitaet Wien. doi:10.3929/ethz-b-000240890.

Brouillet, L., Desmet, P., Coursol, F., Meades, S.J., Favreau, M., Anions, M., Bélisle, P., Gendreau, C., Shorthouse, D., and contributors. 2010. Database of Vascular Plants of Canada (VASCAN). Available from https://data.canadensys.net/vascan [accessed 19 July 2021].

Burgess, V.J., Kelly, D., Robertson, A.W., and Ladley, J.J. 2006. Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of Peraxilla tetrapetala (Loranthaceae). N. Z. J. Ecol. **30**(2): 179–190. New Zealand Ecol Soc, Christchurch.

Campeau, S., and Rochefort, L. 1996. Sphagnum Regeneration on Bare Peat Surfaces: Field and Greenhouse Experiments. The Journal of Applied Ecology **33**(3): 599–608. doi:10.2307/2404988.

Caners, R.T., Crisfield, V., and Lieffers, V.J. 2019. Habitat heterogeneity stimulates regeneration of bryophytes and vascular plants on disturbed minerotrophic peatlands. Can. J. For. Res. **49**(3): 281–295. NRC Research Press. doi:10.1139/cjfr-2018-0426.

Cantlon, J.E., Curtis, E.J.C., and Malcolm, W.M. 1963. Studies of Melampyrum lineare. Ecology **44**(3): 466–474. Ecological Society of America. doi:10.2307/1932525.

Christensen, R.H.B. 2019. ordinal- Regression Models for Ordinal Data. R package version 2019.12-10. https://CRAN.R-project.org/package=ordinal. Available from https://CRAN.R-project.org/package=ordinal.

Cobbaert, D., Rochefort, L., and Price, J.S. 2004. Experimental restoration of a fen plant community after peat mining. Applied Vegetation Science **7**(2): 209–220. John Wiley & Sons, Ltd (10.1111). doi:10.1111/j.1654-109X.2004.tb00612.x.

Committee on the Status of Endangered Wildlife in Canada. 2014. COSEWIC assessment and status report on the caribou, Rangifer tarandus: Newfoundland population, Atlantic-Gaspésie population, boreal population, in Canada.

Coops, N.C., Tompaski, P., Nijland, W., Rickbeil, G.J.M., Nielsen, S.E., Bater, C.W., and Stadt, J.J. 2016. A forest structure habitat index based on airborne laser scanning data. Ecological Indicators **67**: 346–357. doi:10.1016/j.ecolind.2016.02.057.

Cribari-Neto, F., and Zeileis, A. 2010. Beta Regression in R. Journal of Statistical Software **34**(1): 1–24. doi:10.18637/jss.v034.i02.

Dabros, A., James Hammond, H.E., Pinzon, J., Pinno, B., and Langor, D. 2017. Edge influence of low-impact seismic lines for oil exploration on upland forest vegetation in northern Alberta (Canada). Forest Ecology and Management **400**: 278–288. doi:10.1016/j.foreco.2017.06.030.

Dabros, A., Pyper, M., and Castilla, G. 2018. Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. Environmental Reviews. NRC Research Press. doi:10.1139/er-2017-0080.

Dawe, C.A., Filicetti, A.T., and Nielsen, S.E. 2017. Effects of Linear Disturbances and Fire Severity on Velvet Leaf Blueberry Abundance, Vigor, and Berry Production in Recently Burned Jack Pine Forests. Forests **8**(10): 398. Multidisciplinary Digital Publishing Institute. doi:10.3390/f8100398.

De Cáceres, M., and Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology **90**(12): 3566–3574. doi:10.1890/08-1823.1.

De Grandpre, L., Bergeron, Y., Nguyen, T., Boudreault, C., and Grondin, P. 2003. Understory vegetation in the boreal forests of Quebec. *In* The Herbaceous Layer in Forests of Eastern North America, 1st edition. Oxford University Press, New York, New York. pp. 238–261.

Deal, R.L. 2001. The effects of partial cutting on forest plant communities of western hemlock – Sitka spruce stands in southeast Alaska. Can. J. For. Res. **31**(12): 2067–2079. NRC Research Press. doi:10.1139/x01-143.

DeMars, C.A., and Boutin, S. 2018. Nowhere to hide: Effects of linear features on predator-prey dynamics in a large mammal system. Journal of Animal Ecology **87**(1): 274–284. John Wiley & Sons, Ltd (10.1111). doi:10.1111/1365-2656.12760.

Dickie, M., Serrouya, R., DeMars, C., Cranston, J., and Boutin, S. 2017a. Evaluating functional recovery of habitat for threatened woodland caribou. Ecosphere **8**(9): e01936–e01936. Wiley-Blackwell. doi:10.1002/ecs2.1936.

Dickie, M., Serrouya, R., McNay, R.S., and Boutin, S. 2017b. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology **54**(1): 253–263. John Wiley & Sons, Ltd (10.1111). doi:10.1111/1365-2664.12732.

Dovciak, M., and Brown, J. 2014. Secondary edge effects in regenerating forest landscapes: vegetation and microclimate patterns and their implications for management and conservation. New For. **45**(5): 733–744. Springer, Dordrecht. doi:10.1007/s11056-014-9419-7.

Dupuch, A., and Fortin, D. 2013. The extent of edge effects increases during post-harvesting forest succession. Biol. Conserv. **162**: 9–16. Elsevier Sci Ltd, Oxford. doi:10.1016/j.biocon.2013.03.023.

Echiverri, L.F.I., Macdonald, S.E., and Nielsen, S.E. 2020. Disturbing to restore? Effects of mounding on understory communities on seismic lines in treed peatlands. Can. J. For. Res. **50**(12): 1340–1351. NRC Research Press. doi:10.1139/cjfr-2020-0092.

Environment and Climate Change. 2013, September 25. Canadian Climate Normals 1981-2010 Station Data - Climate - Environment and Climate Change Canada. Available from https://climate.weather.gc.ca/climate_normals/index_e.html [accessed 26 February 2021].

Esseen, P.-A., Hedstrom Ringvall, A., Harper, K.A., Christensen, P., and Svensson, J. 2016. Factors driving structure of natural and anthropogenic forest edges from temperate to boreal ecosystems. J. Veg. Sci. **27**(3): 482–492. Wiley, Hoboken. doi:10.1111/jvs.12387.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**: 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419.

Filicetti, A., Cody, M., Nielsen, S., Filicetti, A.T., Cody, M., and Nielsen, S.E. 2019. Caribou Conservation: Restoring Trees on Seismic Lines in Alberta, Canada. Forests **10**(2): 185–185. Multidisciplinary Digital Publishing Institute. doi:10.3390/f10020185.

Finnegan, L., MacNearney, D., and Pigeon, K.E. 2018. Divergent patterns of understory forage growth after seismic line exploration: Implications for caribou habitat restoration. Forest Ecology and Management **409**: 634–652. doi:10.1016/j.foreco.2017.12.010.

Fletcher, R.J. 2005. Multiple edge effects and their implications in fragmented landscapes. Journal of Animal Ecology **74**(2): 342–352. John Wiley & Sons, Ltd (10.1111). doi:10.1111/j.1365-2656.2005.00930.x.

Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tscharntke, T., Laurance, W.F., Lovejoy, T., and Haddad, N.M. 2018. Is habitat fragmentation good for biodiversity? Biological Conservation **226**: 9–15. doi:10.1016/j.biocon.2018.07.022.

Flora of North America Editorial Committee. 2007. Flora of North America north of Mexico. Oxford University Press, New York.

Flora of North America Editorial Committee. 2014. Flora of North America north of Mexico. Oxford University Press, New York.

Franklin, C.M.A., Filicetti, A., and Nielsen, S.E. 2021a. Seismic line width and orientation influence micro-climatic forest edge gradients and tree regeneration. Forest Ecology and Management.

Franklin, C.M.A., Harper, K.A., and Clarke, M.J. 2021b. Trends in studies of edge influence on vegetation at human-created and natural forest edges across time and space. Can. J. For. Res. **51**(2): 274–282. NRC Research Press. doi:10.1139/cjfr-2020-0308.

Gehlhausen, S.M., Schwartz, M.W., and Augspurger, C.K. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology **147**(1): 21–35. doi:10.1023/A:1009846507652.

Gibson, D.J., and Good, R.E. 1987. The Seedling Habitat of Pinus echinata and Melampyrum lineare in Oak-Pine Forest of the New Jersey Pinelands. Oikos **49**(1): 91–91. WileyNordic Society Oikos. doi:10.2307/3565558.

Gilliam, F.S. 2007. The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. BioScience **57**(10): 845–858. doi:10.1641/B571007.

Giuggiola, A., Zweifel, R., Feichtinger, L.M., Vollenweider, P., Bugmann, H., Haeni, M., and Rigling, A. 2018. Competition for water in a xeric forest ecosystem – Effects of understory removal on soil micro-climate, growth and physiology of dominant Scots pine trees. Forest Ecology and Management **409**: 241–249. doi:10.1016/j.foreco.2017.11.002.

Government of Alberta. 2017. Restoration and Establishment Framework. Prepared for Alberta Environment and Parks, Land and Environment Planning Branch, Edmonton, Alberta.

Graf, M.D. 2009. Literature review on the Restoration of Alberta's Boreal Wetlands Affected By Oil, Gas and In Situ Oil Sands Development Prepared for Ducks Unlimited Canada.

Graf, M.D., and Rochefort, L. 2010. Moss Regeneration for Fen Restoration: Field and Greenhouse Experiments. Restoration Ecology **18**(1): 121–130. John Wiley & Sons, Ltd (10.1111). doi:10.1111/j.1526-100X.2008.00437.x.

Groeneveld, E.V.G., Massé, A., and Rochefort, L. 2007. Polytrichum strictum as a Nurse-Plant in Peatland Restoration. Restoration Ecology **15**(4): 709–719. John Wiley & Sons, Ltd (10.1111). doi:10.1111/j.1526-100X.2007.00283.x.

Guo, X., Coops, N.C., Tompalski, P., Nielsen, S.E., Bater, C.W., and John Stadt, J. 2017. Regional mapping of vegetation structure for biodiversity monitoring using airborne lidar data. Ecological Informatics **38**: 50–61. doi:10.1016/j.ecoinf.2017.01.005.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., and Townshend, J.R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1**(2): e1500052–e1500052. American Association for the Advancement of Science. doi:10.1126/sciadv.1500052.

Harper, K.A., Drapeau, P., Lesieur, D., and Bergeron, Y. 2016. Negligible structural development and edge influence on the understorey at 16–17-yr-old clear-cut edges in black spruce forest. Applied Vegetation Science **19**(3): 462–473. doi:https://doi.org/10.1111/avsc.12226.

Harper, K.A., Lesieur, D., Bergeron, Y., and Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. Can. J. For. Res. **34**(2): 289–302. Canadian Science Publishing, Ottawa. doi:10.1139/X03-279.

Harper, K.A., and Macdonald, S.E. 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. Ecosphere **2**(8): 94. Wiley, Hoboken. doi:10.1890/ES11-00146.1.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., and Esseen, P.A. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. **19**(3): 768–782. Wiley, Hoboken. doi:10.1111/j.1523-1739.2005.00045.x.

Harper, K.A., Macdonald, S.E., Mayerhofer, M.S., Biswas, S.R., Esseen, P.-A., Hylander, K., Stewart, K.J., Mallik, A.U., Drapeau, P., Jonsson, B.-G., Lesieur, D., Kouki, J., and Bergeron, Y. 2015. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. J. Ecol. **103**(3): 550–562. Wiley, Hoboken. doi:10.1111/1365-2745.12398.

Harper, K.A., Mascarua-Lopez, L., Macdonald, S.E., and Drapeau, P. 2007. Interaction of edge influence from multiple edges: examples from narrow corridors. Plant Ecol. **192**(1): 71–84. Springer, Dordrecht. doi:10.1007/s11258-006-9227-z.

Hartig, F. 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /Mixed) Regression Models. R package version 0.3.2.0. https://CRAN.R-project.org/package=DHARMa. Available from http://florianhartig.github.io/DHARMa/.

Hill, M.O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology **54**(2): 427–432. doi:https://doi.org/10.2307/1934352.

Honnay, O., Jacquemyn, H., Bossuyt, B., and Hermy, M. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytol. **166**(3): 723–736. Wiley, Hoboken. doi:10.1111/j.1469-8137.2005.01352.x.

Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. J. Appl. Ecol. **42**(3): 518–525. Wiley, Hoboken. doi:10.1111/j.1365-2664.2005.01033.x.

Jost, L. 2006. Entropy and diversity. Oikos **113**(2): 363–375. doi:https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Jules, E.S., and Rathcke, B.J. 1999. Mechanisms of reduced Trillium recruitment along edges of old-growth forest fragments. Conserv. Biol. **13**(4): 784–793. Blackwell Science Inc, Malden. doi:10.1046/j.1523-1739.1999.97435.x.

Kansas, J.L., Charlebois, M.L., and Skatter, H.G. 2015. Vegetation Recovery on Low Impact Seismic Lines in Alberta's Oil Sands and Visual Obstruction of Wolves (Canis lupus)

and Woodland Caribou (Rangifer tarandus caribou). Canadian Wildlife Biology and Management **4**(2): 137–149.

Karlsson, P.S., and Méndez, M. 2005. The Resource Economy of Plant Reproduction. *In* Reproductive allocation in plants. Elsevier Academic Press Inc. pp. 1–49. [accessed 6 June 2021].

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H.L., Van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., and Lovejoy, T.E. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**(1): 56–67. doi:10.1016/j.biocon.2010.09.021.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizão, R.C.C., and Ribeiro, J.E. 2007. Habitat Fragmentation, Variable Edge Effects, and the Landscape-Divergence Hypothesis. PLoS ONE **2**(10): e1017–e1017. Public Library of Science. doi:10.1371/journal.pone.0001017.

Lee, P., and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management **78**(3): 240–250. doi:10.1016/j.jenvman.2005.03.016.

Lefcheck, J.S. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution **7**(5): 573–579. doi:https://doi.org/10.1111/2041-210X.12512.

Lemmon, P.E. 1956. A Spherical Densiometer For Estimating Forest Overstory Density. Forest Science **2**(4): 314–320. doi:10.1093/forestscience/2.4.314.

Lenth, R. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.0. https://CRAN.R-project.org/package=emmeans. Available from https://CRAN.R-project.org/package=emmeans.

Lieffers, V.J., Caners, R.T., and Ge, H. 2017. Re-establishment of hummock topography promotes tree regeneration on highly disturbed moderate-rich fens. Journal of Environmental Management **197**: 258–264. Academic Press. doi:10.1016/J.JENVMAN.2017.04.002.

Lienert, J. 2004. Habitat fragmentation effects of fitness of plant populations - A review. Journal for Nature Conservation. doi:10.1016/j.jnc.2003.07.002.

MacFarlane, A.K. 2003. Vegetation response to seismic lines: edge effects and on-line succession.

Malmer, N., Svensson, B.M., and Wallén, B. 1994. Interactions between Sphagnum mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobotanica et Phytotaxonomica. doi:10.1007/BF02883146.

Mao, L., Bater, C.W., Stadt, J.J., White, B., Tompalski, P., Coops, N.C., and Nielsen, S.E. 2019. Environmental landscape determinants of maximum forest canopy height of boreal forests. Journal of Plant Ecology **12**(1): 96–102. doi:10.1093/jpe/rtx071.

Moss, E.H. 1983. Flora of Alberta. *In* 2nd edition. University of Toronto Press, Canada.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution. doi:10.1016/S0169-5347(00)88977-6.

Nave, L., Heckman, K., Muñoz, A., and Swanston, C.W. 2018. Radiocarbon Suggests the Hemiparasitic Annual Melampyrum Lineare Desr. May Acquire Carbon from Stressed Hosts. Radiocarbon **60**(01): 269–281. doi:10.1017/RDC.2017.97.

Nelson, C.J., Frost, C.M., and Nielsen, S.E. 2021. Narrow anthropogenic linear corridors increase the abundance, diversity, and movement of bees in boreal forests. Forest Ecology and Management **489**: 119044. doi:10.1016/j.foreco.2021.119044.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., and Purvis, A. 2015. Global effects of land use on local terrestrial biodiversity. Nature **520**(7545): 45–50. doi:10.1038/nature14324.

Nilsson, M.-C., and Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment **3**(8): 421–428. doi:10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.

Oksanen, J., Blanchet, G.B., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H.

167

2018. vegan: Community Ecology Package. R package version 2.5-3. https://CRAN.R-project.org/package=vegan.

Oldham, K.A., and Weeks, A. 2017. Varieties of Melampyrum lineare (Orobanchaceae) Revisited. Rhodora **119**(979): 224–259. Allen Press. doi:10.3119/16-13.

Pattison, C.A., Quinn, M.S., Dale, P., and Catterall, C.P. 2016. The Landscape Impact of Linear Seismic Clearings for Oil and Gas Development in Boreal Forest. Northwest Sci. **90**(3): 340–354. Northwest Scientific Assoc, Seattle. doi:10.3955/046.090.0312.

Piehl, M.A. 1962. The parasitic behavior of Melampyrum lineare and a note on its seed color. Rhodora **64**(757): 15–23. New England Botanical Club, Inc.

Porensky, L.M., and Young, T.P. 2013. Edge-Effect Interactions in Fragmented and Patchy Landscapes. Conservation Biology **27**(3): 509–519. Wiley/Blackwell (10.1111). doi:10.1111/cobi.12042.

Pothier, D. 2011. Ten-year results of strip clear-cutting in Quebec black spruce stands. Canadian Journal of Forest Research. NRC Research Press Ottawa, Canada. doi:10.1139/x99-189.

Pouliot, R., Rochefort, L., and Karofeld, E. 2011. Initiation of microtopography in revegetated cutover peatlands. Applied Vegetation Science **14**(2): 158–171. Wiley/Blackwell (10.1111). doi:10.1111/j.1654-109X.2010.01118.x.

Pouliot, R., Rochefort, L., and Karofeld, E. 2012. Initiation of microtopography in re-vegetated cutover peatlands: Evolution of plant species composition. Applied Vegetation Science **15**: 369–382. doi:10.1111/j.1654-109X.2011.01164.x.

Prévost, M., and Dumais, D. 2018. Long-term growth response of black spruce advance regeneration (layers), natural seedlings and planted seedlings to scarification: 25th year update. Scandinavian Journal of Forest Research **33**(6): 583–593. Taylor & Francis. doi:10.1080/02827581.2018.1430250.

Price, J., Rochefort, L., and Quinty, F. 1998. Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and Sphagnum regeneration. Ecological Engineering **10**(4): 293–312. Elsevier. doi:10.1016/S0925-8574(98)00046-9.

Pyper, M., Nishi, J., and McNeil, L. 2014. Linear Feature Restoration in Caribou Habitat: A summary of current practices and a roadmap for future programs.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/ [accessed 22 March 2021].

van Rensen, C.K., Nielsen, S.E., White, B., Vinge, T., and Lieffers, V.J. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. Biological Conservation **184**: 127–135. Elsevier. doi:10.1016/J.BIOCON.2015.01.020.

Ries, L., Fletcher, R.J., Battin, J., and Sisk, T.D. 2004. Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. Annual Review of Ecology, Evolution, and Systematics **35**(1): 491–522. Annual Reviews. doi:10.1146/annurev.ecolsys.35.112202.130148.

Ries, L., Murphy, S.M., Wimp, G.M., and Fletcher, R.J. 2017. Closing Persistent Gaps in Knowledge About Edge Ecology. Curr Landscape Ecol Rep **2**(1): 30–41. doi:10.1007/s40823-017-0022-4.

Riva, F., Acorn, J.H., and Nielsen, S.E. 2018. Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests. Biological Conservation **217**: 173–180. doi:10.1016/j.biocon.2017.10.022.

Riva, F., and Nielsen, S.E. 2020. A functional perspective on the analysis of land use and land cover data in ecology. Ambio. doi:10.1007/s13280-020-01434-5.

Riva, F., and Nielsen, S.E. 2021. A functional perspective on the analysis of land use and land cover data in ecology. Ambio **50**(5): 1089–1100. doi:10.1007/s13280-020-01434-5.

Riva, F., Pinzon, J., Acorn, J.H., and Nielsen, S.E. 2020. Composite Effects of Cutlines and Wildfire Result in Fire Refuges for Plants and Butterflies in Boreal Treed Peatlands. Ecosystems **23**(3): 485–497. doi:10.1007/s10021-019-00417-2.

Rochefort, L. 2000. Sphagnum—A Keystone Genus in Habitat Restoration. The Bryologist **103**(3): 503–508. American Bryological and Lichenological Society. doi:10.1639/0007-2745(2000)103[0503:SAKGIH]2.0.CO;2.

Rochefort, L., Campeau, S., and Bugnon, J.-L. 2002. Does prolonged flooding prevent or enhance regeneration and growth of Sphagnum? Aquatic Botany **74**(4): 327–341. Elsevier. doi:10.1016/S0304-3770(02)00147-X.

Rochefort, L., and Lode, E. 2006. Restoration of Degraded Boreal Peatlands. *In* Boreal Peatland Ecosystems. Springer, Germany. pp. 381–424.

Rochefort, L., Quinty, F., Campeau, S., Johnson, K., and Malterer, T. 2003. North American approach to the restoration of Sphagnum dominated peatlands. Wetlands Ecology and Management **11**(1/2): 3–20. Kluwer Academic Publishers. doi:10.1023/A:1022011027946.

Ruffell, J., and Didham, R.K. 2016. Towards a better mechanistic understanding of edge effects. Landscape Ecol **31**(10): 2205–2213. doi:10.1007/s10980-016-0397-3.

Ruffell, J., Didham, R.K., Barrett, P., Gorman, N., Pike, R., Hickey-Elliott, A., Sievwright, K., and Armstrong, D.P. 2014. Discriminating the Drivers of Edge Effects on Nest Predation: Forest Edges Reduce Capture Rates of Ship Rats (Rattus rattus), a Globally Invasive Nest Predator, by Altering Vegetation Structure. PLOS ONE **9**(11): e113098. Public Library of Science. doi:10.1371/journal.pone.0113098.

Rydin, H., Gunnarsson, U., and Sundberg, S. 2006. The Role of Sphagnum in Peatland Development and Persistence. *In* Boreal Peatland Ecosystems. Springer, Germany. pp. 47–66.

Rydin, H., and Jeglum, J. 2006. The Biology of Peatlands. Oxford University Press, Oxford, UK.

Schmidt, M., Davidson, S.J., and Strack, M. 2020. Impact of peatland seismic line restoration on CO2 and CH4 fluxes. **2020**: EP042-02.

Schneider, R.R., Stelfox, J.B., Boutin, S., and Wasel, S. 2003. Managing the Cumulative Impacts of Land Uses in the Western Canadian Sedimentary Basin: A Modeling Approach. Conservation Ecology **7**(1). Resilience Alliance Inc. Available from https://www.jstor.org/stable/26271918 [accessed 7 June 2021].

Stern, E.R., Riva, F., and Nielsen, S.E. 2018. Effects of Narrow Linear Disturbances on Light and Wind Patterns in Fragmented Boreal Forests in Northeastern Alberta. Forests **9**(8): 486. Multidisciplinary Digital Publishing Institute. doi:10.3390/f9080486.

Stevenson, C.J., Filicetti, A.T., and Nielsen, S.E. 2019. High Precision Altimeter Demonstrates Simplification and Depression of Microtopography on Seismic Lines in Treed Peatlands. Forests **10**(4): 295. Multidisciplinary Digital Publishing Institute. doi:10.3390/f10040295.

Stickley, S.F., and Fraterrigo, J.M. 2021. Understory vegetation contributes to microclimatic buffering of near-surface temperatures in temperate deciduous forests. Landscape Ecol **36**(4): 1197–1213. doi:10.1007/s10980-021-01195-w.

Strack, M., Hayne, S., Lovitt, J., McDermid, G.J., Rahman, M.M., Saraswati, S., and Xu, B. 2019. Petroleum exploration increases methane emissions from northern peatlands. Nature Communications **10**(1): 1–8. Nature Publishing Group. doi:10.1038/s41467-019-10762-4.

Sutton, R.F. 1993. Mounding site preparation: A review of European and North American experience. New Forests **7**(2): 151–192. Kluwer Academic Publishers. doi:10.1007/BF00034198.

Tomimatsu, H., and Ohara, M. 2004. Edge effects on recruitment of Trillium camschatcense in small forest fragments. Biological Conservation **117**(5): 509–519. doi:10.1016/j.biocon.2003.08.010.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D., and Tuittila, E.S. 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytologist **196**(1): 49–67. John Wiley & Sons, Ltd. doi:10.1111/j.1469-8137.2012.04254.x.

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H., and Wieder, R.K. 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. Journal of Ecology **96**(6): 1297–1305. doi:10.1111/j.1365-2745.2008.01438.x.

Valdes, A., and Garcia, D. 2011. Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb. J. Appl. Ecol. **48**(6): 1422–1431. Wiley, Hoboken. doi:10.1111/j.1365-2664.2011.02047.x.

Vitt, D.H., and Wieder, K.R. 2008. The structure and function of bryophyte-dominated peatlands. *In* Bryophyte Biology, Second. Cambridge University Press. pp. 357–391.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York. Available from https://ggplot2.tidyverse.org.

Wieder, R.K. 2006. Primary Production in Boreal Peatlands. *In* Boreal Peatland Ecosystems. *Edited by* R.K. Wieder and D.H. Vitt. Springer-Verlag, Berlin, Heidelberg. pp. 145–164.