

Impacts of Seismic Line Restoration on CO₂, CH₄, and Biomass

by

Megan Schmidt

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

Abstract

Oil and gas exploration has resulted in over 300,000 km of linear disturbances, known as seismic lines, throughout boreal peatlands across Canada. Sites are left with altered hydrologic and topographic conditions that prevent tree re-establishment. Restoration efforts have concentrated on tree recovery through mechanical mounding to re-create microtopography and support planted tree seedlings to block sightlines and deter predator use, but little is known about the impact of seismic line disturbance or restoration on peatland carbon cycling, vegetation, or biomass. This study looked at two mounding treatments: hummock transfer (HT), which transferred naturally formed hummocks from just off the seismic line onto the line, and inline mounding (IM), in which hummocks were formed by scooping peat from on the line and placing it nearby. We compared vegetation cover and composition, above- and belowground biomass, and carbon dioxide (CO₂) and methane (CH₄) fluxes on the treatments to untreated lines and natural reference areas in the first two years post-restoration.

There were few significant differences in understory percent cover or biomass across treatments, but forb and graminoid cover increased, low shrub cover decreased, and bryophyte distribution across microforms differed on untreated seismic lines from natural reference areas. Both mounding treatments increased forb cover but reduced graminoid, shrub, and bryophyte cover from untreated and natural areas. Belowground root biomass did not significantly change between treatments, and we found that only IM significantly reduced understory biomass. The absence of trees and mid-story shrubs on all three seismic line treatments resulted in a loss of $\sim 720 \text{ g m}^{-2}$, and the loss of a yearly uptake of $\sim 50 \text{ g C m}^{-2} \text{ y}^{-1}$. We found no significant differences in net ecosystem CO₂ exchange, but untreated seismic lines were slightly more productive than natural reference areas and mounding treatments. Both restoration treatments increased ecosystem respiration, decreased net productivity by $6 - 21 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, and created areas of increased CH₄ emissions, including an increase in the contribution of ebullition, of up to $2000 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$. Although further research on this site to assess the longer-term impacts of restoration, as well as application on other sites with varied conditions, is required to determine if these methods are effective, our study suggests that HT may provide the best option to improve the outcome of multiple ecosystem functions.

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Chapter 1: Introduction

Peatlands cover over 4 million km² worldwide (Holden 2005), including over 134,000 km² in northern Alberta, Canada alone (AEP 2018), a region rich in natural resources such as oil and gas, timber, and horticultural peat. These areas are not only economically important, but also serve many natural functions, including storing large amounts of carbon (C) and providing essential habitat for both flora and fauna (Filicetti et al. 2019). Exploration and extraction of oil and gas resources in the boreal region impact many peatlands, leading to degradation, loss, and long-term changes to these important ecosystems. One of the main concerns of these impacts is on the production and emissions of greenhouse gases (GHG) such as carbon dioxide (CO₂) and methane (CH₄). Given the extent of human disturbance across the boreal region, restoration of peatlands is of high importance. Peatland restoration and reclamation is a relatively new practice, and tricky due to peatlands' slow development, typically over decades, and often remote locations.

Northern peatlands develop due to the interactions between climate and landscape position over time. Cool mean annual temperatures, short growing seasons, and poor drainage create complex processes and feedbacks that slow litter decomposition and lead to gradual accumulation of organic matter (Clymo 1984; Yu et al. 2000). Slight changes in conditions such as groundwater connectivity, pH, nutrient concentrations, water table depth and fluctuation, and vegetation composition interact to form a spectrum of peatland types (Strack et al. 2006a; Waddington et al. 2009). The two main types of peatlands are bogs and fens. Bogs are disconnected from groundwater, ombrotrophic (receiving all water and nutrients from rain), acidic, dominated by *Sphagnum* spp., and have water tables that are generally below surface. Fens are connected to groundwater, minerotrophic (receiving nutrients and water from ground and surface water), near neutral pH, dominated by brown mosses and have water tables that are near or above surface (Vitt 1994, 2006).

Peatland development is largely driven by internal feedbacks between water table and vegetation. As vegetation dies at the surface it begins to decompose and mass continues to accumulate (Clymo 1984; Clymo et al. 1998). Peatlands form heterogenous landscapes, creating complexes of varying peatland types over large areas and within-peatland microtopography. Microforms are small variances in surface elevations (≤ 1 m) and are an integral feature of peatlands with both biogeochemical and physical impacts (Waddington et al. 2010). Microforms are classified by elevational position from the average and infer relationship to water table. Hummocks are elevated mounds with the deepest water

table, in Boreal peatlands dominated by *Sphagnum fuscum* (Schimp.) H. Klinggr., *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Larix laricina* (Du Roi) K. Koch, and *Picea mariana* (Miller) Britton in bogs, and *Tomentypnum nitens* (Hedw.) Loeske, *Aulacomnium palustre* (Hedw.) Schwaegr., *Carex* spp., *Betula* and *Salix* spp., *P. mariana*, and *L. laricina* in fens (Nungesser 2003; McCarter and Price 2012). Lawns and hollows exist as flat areas between or around hummocks and very near the water table; lawns are typically just above and hollows just below (Nungesser 2003). Lawns and hollows are dominated by more hydrophilic species such as *Sphagnum magellanicum* Brid., *Calliergon giganteum* (Schimp.) Kindb., *Drepanocladus aduncus* (Hedw.) Warnst., *Carex* spp., and *Salix* spp. (McCarter and Price 2012). Microform formation and persistence is linked to both internal feedbacks, such as decomposition and vegetation (Pouliot et al. 2011), and external factors such as fire (Waddington et al. 2010) and hydrologic regime (Benscoter et al. 2015).

Peatlands are adapted to natural disturbances, but anthropogenic disturbances are placing increasing pressure on these systems, especially in the face of ongoing climate change. Harvesting, forestry, agriculture, and oil and gas exploration and extraction create a variety of disturbances throughout northern peatlands. Historically, it was believed that many disturbances would recover without human influence (Lee and Boutin 2006), but that view is changing. Restoration practices for large scale disturbances such as horticultural peat extraction and oil sands exploration (OSE) well pads have been progressing (e.g., Quinty et al. 2020; Murray et al. 2021), but little has been done for linear disturbances such as seismic lines. Seismic lines are used to map underground oil and gas deposits and require clearing grids of long, linear corridors across the landscape, most of which remain for decades (Lee and Boutin 2006) (Figure 1.1). Seismic lines, though narrow, contribute to the cumulative impact of linear features on the landscape; the density of seismic lines on the landscape average 10 km km⁻² (Lee and Boutin 2006) and reach up to 40 km km⁻² in some areas (Schneider 2002). It has been estimated that over 345,000 km of seismic lines currently run through Alberta peatlands, an approximate area of 1900 km² (Strack et al. 2019).



Figure 1.1 Examples of seismic lines through peatlands.

Vegetation removal and surface changes that occur during seismic line construction start a domino effect on other physical and biogeochemical factors, from hydrology to peat properties and carbon exchange. Not only are hummocks physically removed in preparation for seismic surveying, but repeated passes of heavy machinery further compress the peat surface (Dabros et al. 2018; Strack et al. 2019), resulting in rutting from machinery and an increase in hollow coverage (Lovitt et al. 2018; Stevenson et al. 2019). Any microforms that do persist on seismic lines tend to be highly suppressed, varying only a few centimeters from mean elevation, compared to up to a meter in natural conditions (Caners and Lieffers 2014). Microform development in disturbed peatlands has been shown to be resistant to natural formation processes such as *Sphagnum* growth and fire (van Rensen et al. 2015; McCarter et al. 2021), likely due to shallow water tables.

Disturbance from seismic lines results in a shallower water table and increased surface water pooling, often creating sustained flooded conditions through the growing season (Caners and Lieffers 2014; Dabros et al. 2018). In addition, loss of surface vegetation, particularly trees and shrubs, reduces water uptake, further altering hydrology on and adjacent to the line (Stevenson et al. 2019). Given the density of seismic lines in northern Alberta, this potentially has a much farther-reaching effect on local or even watershed hydrology (Williams et al. 2013). Seismic line creation removes all woody vegetation, and even hydrophilic species such as *Salix* spp., *Betula* spp., *Picea mariana*, and *Larix laricina* struggle to re-establish (Lee and Boutin 2006; Filicetti et al. 2019). Loss of microtopography, specifically hummocks, and subsequent flooding reduces suitable seeding sites and

shifts lines towards more *Carex*, and other sedge and reed, dominated communities (Lee and Boutin 2006, van Rensen et al. 2015; Strack et al. 2018). Pouliot et al. (2011) found bryophyte cover was reduced on lines and exhibited slower growth overall, potentially due to increased light levels, while Caners and Lieffers (2014) and van Rensen et al. (2015) found hummock forming *Sphagnum* species had to compete with other species, resulting in slowed succession that often stalls in early stages. Edge effects may also explain some of the lack of recovery on seismic lines; increased peat temperatures and light at edges may inhibit bryophyte growth (Dabros et al. 2017) or, alternatively, increased tree and shrub growth along edges may shade out bryophyte species (Pouliot et al. 2011).

Long-term changes in vegetation communities in turn influence CO₂ and CH₄ balances in multiple ways: some species take up more CO₂ than others and can increase productivity, while others cannot tolerate wetter or drier conditions and die out, decreasing productivity. Additionally, some species, such as *Carex* spp., act as vents to the atmosphere for CH₄ produced in the rhizosphere and increase surface fluxes (Dabros et al. 2017; Dieleman et al. 2017; Pypker 2013). Graminoids and other vascular plant groups also produce more labile organic matter, resulting in faster C turnover and less accumulation (Yavitt and Williams 1997). Higher peat temperatures (Dabros et al. 2017; Strack et al. 2018) further contribute to increased CO₂ and CH₄ production, while increasingly wet conditions contribute to C loss as dissolved organic and inorganic carbon. These cumulative changes have the potential to shift peatland seismic lines from C sinks to sources (Strack et al. 2018).

As one of the main factors that prevent tree recovery in peatlands is the loss of microtopography, particularly hummocks, a restoration process called mounding has been developing over recent years (Figure 1.2). Mounding takes soil from one spot and places it nearby to create hummocks while leaving a hollow behind (Pyper et al. 2014). Mounding, until recently, has typically been applied at high densities with large mounds that are inverted, burying upper peat layers and vegetation, and exposing bare, deep peat and mineral soil (Echiverri et al. 2019; Murray et al. 2021). Mounding has been found to increase tree seedling recruitment (Filicetti et al. 2019) and foster survival of planted seedlings (Lieffers et al. 2017), but bryophyte and vascular cover are likely to be reduced (Echiverri et al. 2019) and recovery can be quite slow (Murray et al. 2021). The effects of mounding on water table, vegetation communities, and peat properties are not yet well known (e.g., Davidson et al. 2020), although raised microtopography in restored harvested peatlands has been found to increase soil temperatures and decrease soil moisture (Price et al. 1998). Even less known is the impact of seismic lines and seismic line restoration on carbon stocks and fluxes; Strack et al. (2018) found

increased CO₂ uptake and CH₄ emissions on winter roads (created similarly to seismic lines), and Murray et al. (2021) found flooded hollows from mounding OSE sites had high potential to become CH₄ emission hotspots. There is much uncertainty as to the long-term effects of mounding on carbon processes.

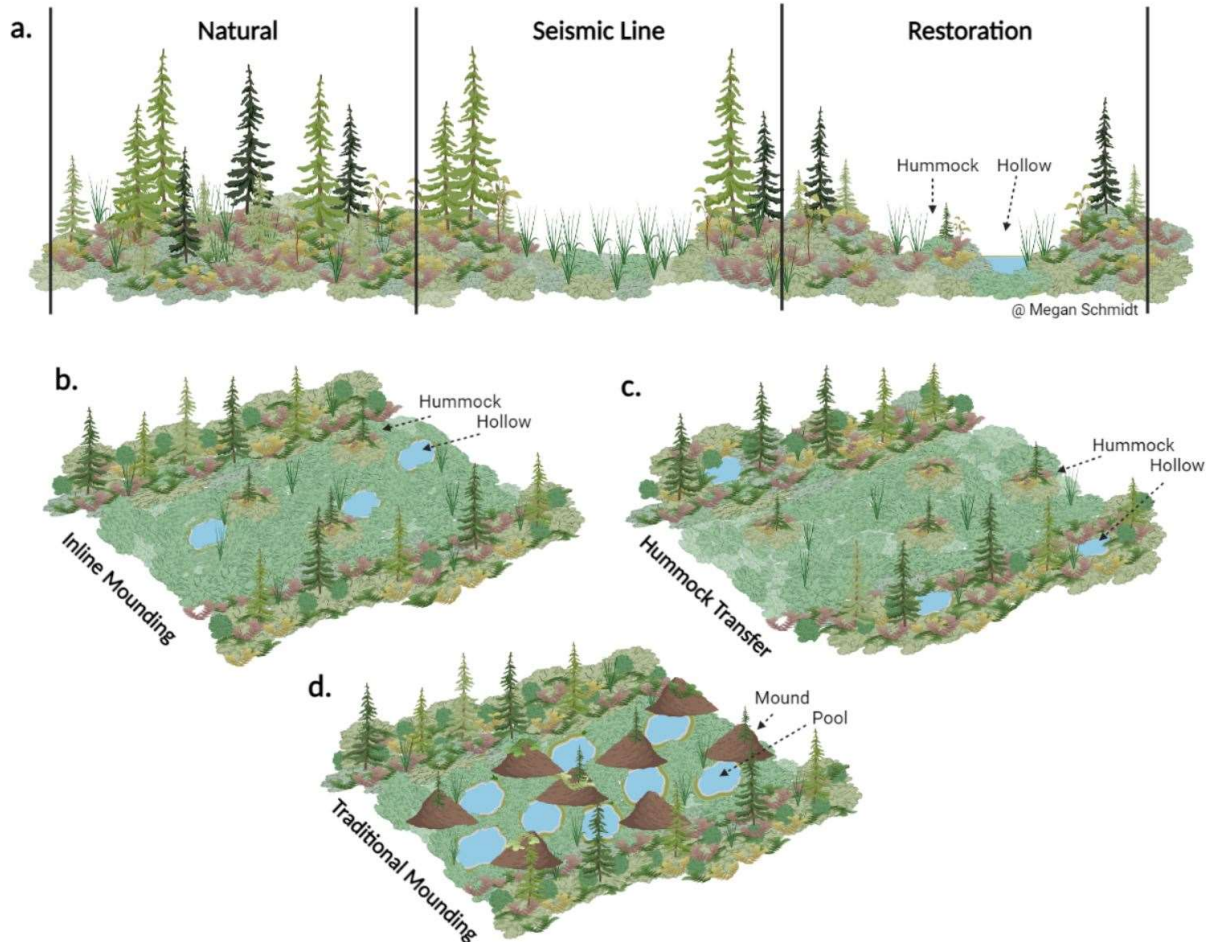


Figure 1.2 Schematic diagram of seismic line restoration. 2a. shows the difference in microtopography and vegetation from natural to unrestored seismic lines and restored seismic lines. 2b. shows the Inline Mounding method, in which peat from on the seismic line is used to create microtopography. 2c. shows the Hummock Transfer method, in which naturally formed hummocks just outside the edge of the seismic line are targeted and moved onto the line. 2d. shows the traditional method of mounding, also called mechanical mounding, in which large scoops of peat are taken from on the seismic line and inverted to create large mounds.

1.1 Objectives

Restoration of seismic lines has been largely ignored due to the assumption that such narrow disturbances will recover naturally with time. What little has been done has been with a focus on

functional restoration: to reduce sightlines and access by predators and humans in hopes of reducing the impact on endangered woodland caribou herds (Filicetti et al. 2019). Mitigation of the impacts of seismic lines requires a shift in this focus to restoration of ecological functions and return to successional peatland pathways. Few studies have looked at the impact of seismic lines and other similar, linear disturbances on CO₂ (Strack et al. 2018; Davidson et al. 2021) and CH₄ emissions have been estimated (Strack et al. 2019), but no study to date has looked at the restoration of seismic lines and the impact on C cycling. Additionally, there has been little study of the effects of restoration on understory vegetation composition or biomass (Echiverri et al. 2020, Murray et al. 2021). Therefore, the objectives of this research were to:

1. Determine if species composition differs between mounding treatments, untreated lines, and natural reference peatlands.
2. Determine if above- (vascular plants, bryophytes, shrubs, and trees) and belowground (roots) biomass differs between treatments.
3. Quantify CO₂ and CH₄ fluxes of two types of mounding treatments and compare to untreated lines and adjacent undisturbed reference peatlands.
4. Determine environmental relationships contributing to variation in CO₂ and CH₄ fluxes.

1.2 Thesis Structure

This thesis is written in manuscript format and as such some of the information within chapters may have been stated previously. Chapter 2 addresses objectives 1 and 2: species composition and biomass. Chapter 3 addresses objectives 3 and 4: CO₂ and CH₄ fluxes on untreated and treated seismic lines and has been submitted to *Wetlands Ecology and Management* (preprint doi: 10.21203/rs.3.rs-759056/v1). The concluding chapter includes a summary of the results of both chapters, insights learned from this study, and future work to be considered.

Chapter 2: Response of plant community composition and biomass to peatland seismic line restoration.

2.1 Introduction

Northern peatlands are estimated to contain $\sim 415 \pm 150$ Pg carbon (C) (Hugelius et al. 2020) – approximately one third of the global terrestrial C pool (Gorham 1991; Yu 2012). Cool, wet conditions slow decomposition of organic matter, resulting in productivity outweighing decomposition and the accumulation of peat over time (Loisel et al. 2014). Peatlands are resilient to many types of natural disturbances (Waddington et al. 2015), but anthropogenic disturbances such as forestry, mining, peat extraction, and oil and gas exploration, including linear features like seismic lines, contribute to the loss of vegetation and peat and can have lasting effects on ecosystem vegetation structure, hydrology, and C stores (Lee and Boutin 2006; Strack et al. 2018). Removal of trees and shrubs on seismic lines results in loss of canopy biomass, and studies have found changes to understory vegetation that persist over time (Caners and Lieffers 2014; van Rensen et al. 2015); however, the effects of these structural changes on ecosystem system C stocks, such as biomass, remain understudied. As interest in restoring seismic lines has increased, the focus has been primarily on tree recovery and ecosystem structure to return habitat suitability, particularly for woodland caribou (Dabros et al., 2018); the impacts of seismic line disturbance on landscape C are not well known, nor are the effects of restoration on plant species composition, particularly for peatlands. Thus, the aim of this study is to investigate the changes to plant species composition and biomass in peatlands in response to disturbance from seismic lines and seismic line restoration.

Peatlands form complex, heterogenous landscapes of varying types across large areas. Peatlands in the boreal regions of Canada are primarily bogs and fens (Vitt et al. 2000). Disconnected from groundwater, bogs are acidic and low in nutrients, receiving most of their water from precipitation, and are dominated by *Sphagnum* spp. Fens retain the connection to the water table and as such are minerotrophic, often wetter, and dominated by sedges, grasses, and bryophytes other than *Sphagnum* (Gorham 1991). Fens are further classified on a gradient of alkalinity from rich fens at the high end to poor fens at the low (Vitt et al. 2000). Local variation within peatlands is driven by external factors such as hydrologic regime (Benscoter et al. 2011) and fire (Waddington et al. 2010), and internal feedbacks such as decomposition and vegetation productivity (Pouliot et al. 2011). Within-peatland microtopography (microforms) plays an important role in C dynamics as it provides microsites with

varying conditions suitable for different plant species to thrive. Microform classification is determined by the elevational position relative to the average surface and infers the relationship to water table. Hummocks are mounds elevated above the surface and thus have the deepest water tables (Nungesser 2003). In Alberta, hummocks are often dominated by *Sphagnum fuscum* (Schimp.) H. Klinggr., vascular species such as *Rhododendron groenlandicum* (Oeder) Kron & Judd, and tree species such as *Larix laricina* (Du Roi) K. Koch. and *Picea mariana* (Miller) Britton (McCarter and Price 2012). Hollows are low points approximately at the water table (Nungesser 2003) and are dominated by more hydrophilic species such as *Sphagnum magellanicum* Brid. in bogs and *Carex* spp., *Salix* spp., water-loving *Sphagnum* spp., and brown moss species such as *Aulacomnium palustre* (Hedw.) Schwaeger and *Drepanocladus* spp. in fens (e.g., McCarter and Price 2012; Vitt 2014; ESRD 2015).

Species with similar effects on ecosystem processes, such as capacity to take up or release C (Dieleman 2017), are placed together as functional groups (Lavorel and Garnier 2002). Plant functional groups are a key component in C storage and peat formation as different forms have different rates of productivity and decomposition (Del Giudice and Lindo 2017). It is generally agreed that graminoids and herbaceous species contribute more easily decomposable litter while bryophytes, particularly *Sphagnum* species, are highly recalcitrant (Dieleman et al. 2017) but it is uncertain which groups are most important for peat accumulation in fens, despite many studies of fen peat (Graf and Rochefort 2009). In studying peat cores across North America, Vitt (2000) found *Sphagnum* and brown bryophytes to be the main component of poor and rich fens, respectively, and layers in which vascular plants dominated decomposed more easily and create less peat overall. Others, however, found vascular species and bryophytes to be of equal importance in peat formation (e.g., Nicholson and Vitt 1990; Lavoie and Richard 2000), or that vascular species made up the majority of fen peat (e.g., Warner, Tolonen and Tolonen 1991; Hu and Davis 1995). When Ward et al. (2009) selectively removed dominant plant functional groups from peatland plots to assess the role of the groups on short-term C cycling, removal of ericoid dwarf-shrubs significantly increased the rates of both respiration and photosynthesis of graminoids, but there was no significant effect on net ecosystem CO₂ flux after removal of any of the functional groups. Although Ward et al. (2009) did not measure effects on biomass, they also found changes to C turnover rates, which were longer in slow-growing dwarf-shrubs than in short-lived graminoids indicating that the dominant plant functional group influences rates of production and decomposition and long-term C sequestration.

Carbon storage in biomass is partitioned into two parts: aboveground, including all parts of vascular graminoids, forbs, shrubs, and trees that rise above the peat surface and the living portion of non-vascular species (i.e., bryophytes, lichens, and liverworts); and belowground, the live roots of all vascular plants (Vitt et al. 2000). Like different functional groups, different parts of plants decompose at different rates. Although large amounts of foliar litter are produced each year, fen peat is often primarily composed of vascular plant roots and rhizomes (Hinze et al. 2021). Belowground biomass may even be equal to or greater than aboveground biomass in peatlands (Murphy et al. 2009).

The northern half of the province of Alberta, Canada, is covered with over 134,000 km² of boreal peatlands (AEP 2018) and is underlain by globally significant oil and gas formations (Alberta Energy). The exploration and mapping of these deposits requires the creation of grids of linear clearings, called seismic lines, which remain on the landscape for decades (Lee and Boutin 2006). Recent estimates by Strack et al. (2019) indicate that over 345,000 km of seismic lines currently run through Alberta's peatlands, covering approximately 1900 km². The density of these lines on the landscape averages up to 10 km/km² (Lee and Boutin 2006) and can reach up to 40 km/km² (Schneider 2002). Seismic lines range in width from 1.5 – 10 m, and are cleared of trees, shrubs, and forbs at surface level to provide access for seismic equipment (Bliss and Wein 1972; Dabros et al. 2018). Seismic line creation and usage across peatlands results in long-term, if not permanent, alteration of conditions that slow the recovery of trees and shrubs. In particular, compression and flattening of microtopography create shallower water tables and increase surface pooling, often resulting in sustained flooded conditions throughout the growing season (Caners and Lieffers 2014). In addition, the loss of surface vegetation and canopy layers reduces water uptake (Stevenson et al. 2019), and vegetation shifts towards more *Carex* dominated communities that often stall in early successional stages (van Rensen et al. 2015).

In an attempt to restore seismic lines, methods are being developed to create artificial mounds that replace hummocks and create drier microsites for trees to establish (Lieffers et al. 2017; Filicetti et al. 2019). In mounding, soil is scooped from one spot and placed nearby to mimic hummocks and leave hollows behind (Pyper et al. 2014). Mounding has been used to restore peatland oil sands exploration (OSE) well sites, but these mounds are typically large and inverted, burying upper peat layers and vegetation, and exposing deep peat and/or mineral soil (Echiverri et al. 2020; Murray et al. 2021). Mounded OSE pads left to natural regeneration have been observed to shift from *Carex* dominated to co-dominance with woody species (Caners et al. 2019) and foster good survival of tree seedlings

(Lieffers et al. 2017). Similar results were found on mounded seismic lines by Echiverri et al. (2019), and others have seen success in planting tree seedlings on mounds on both OSE pads and seismic lines (Filicetti et al. 2019; Murray et al. 2021). Although the vegetation communities on unrestored seismic lines may differ from those of the surrounding peatlands, the species present may still contribute to peat formation, but to what extent is unknown, and it remains unclear whether highly productive graminoid and forb species compensate for the lack of woody species and trees. Therefore, shifts in plant species composition and resulting biomass production will have impacts on C stocks and peat accumulation potential. Given the changes in vegetation on seismic lines, and the unknown changes stemming from restoration, the objectives of this study were to determine: (1) if species composition and biomass differs between untreated seismic lines and natural reference fens, and (2) if mounding treatments for restoration further change species composition and biomass to resemble undisturbed peatlands more closely. We hypothesized that untreated seismic lines would have shifted to higher graminoid and lower bryophyte cover, resulting in lower biomass, and that mounding treatment using peat from the seismic line (i.e., inline mounding) would be similar. Creation of mounds using peat from the adjacent peatland (i.e., hummock transfer) would have an increased number of species and higher cover and biomass of bryophytes, particularly *Sphagnum* spp., and low shrubs.

2.2 Methods

2.2.1 Study site

The study area is in central Alberta, Canada approximately 11 km southwest of Brazeau Dam (52.889326, -115.549173; Figure 1). The region is classified as Boreal Plains Ecozone (Environment Canada 2001) and Central Mixedwood Natural Subregion (AEP 2006). Average temperatures range from 14 – 17 °C in June, July, and August to -15 – -12 °C in December, January, and February with an average of 97 frost free days per year (ECCC 2021). The area receives an average 462 mm precipitation per year, with most occurring during the growing season (May to August) (ECCC 2021). Wetlands comprise a large portion of the region, dominated by wooded and shrubby fens, in a mosaic of aspen and spruce upland (AEP 2006). The study site consists of ~3 km of peatland seismic line running north-south and east-west that are 3 m and 5.5 m wide, respectively (Fig. 2.1). Although the precise date of creation is unknown, satellite images show seismic lines present as far back as 1982. At time of restoration groundwork in March 2019 the line edges were still clearly visible, with little

regeneration of woody vegetation or trees. A hydrological gradient exists longitudinally, becoming drier as the center point is approached from both north and south ends. This corresponds to a gradient in vegetation and fen type, transitioning from rich fen at both north and south ends to poor fen in the center that extends the length of the east-west line. To capture these differences the site was divided into three subsites: north from the center point, south from the center point, and the entire east-west section. For this study only the north and central sections were chosen to equally represent the poor and rich fen sections (Fig. 2.1) and were combined into one data set.

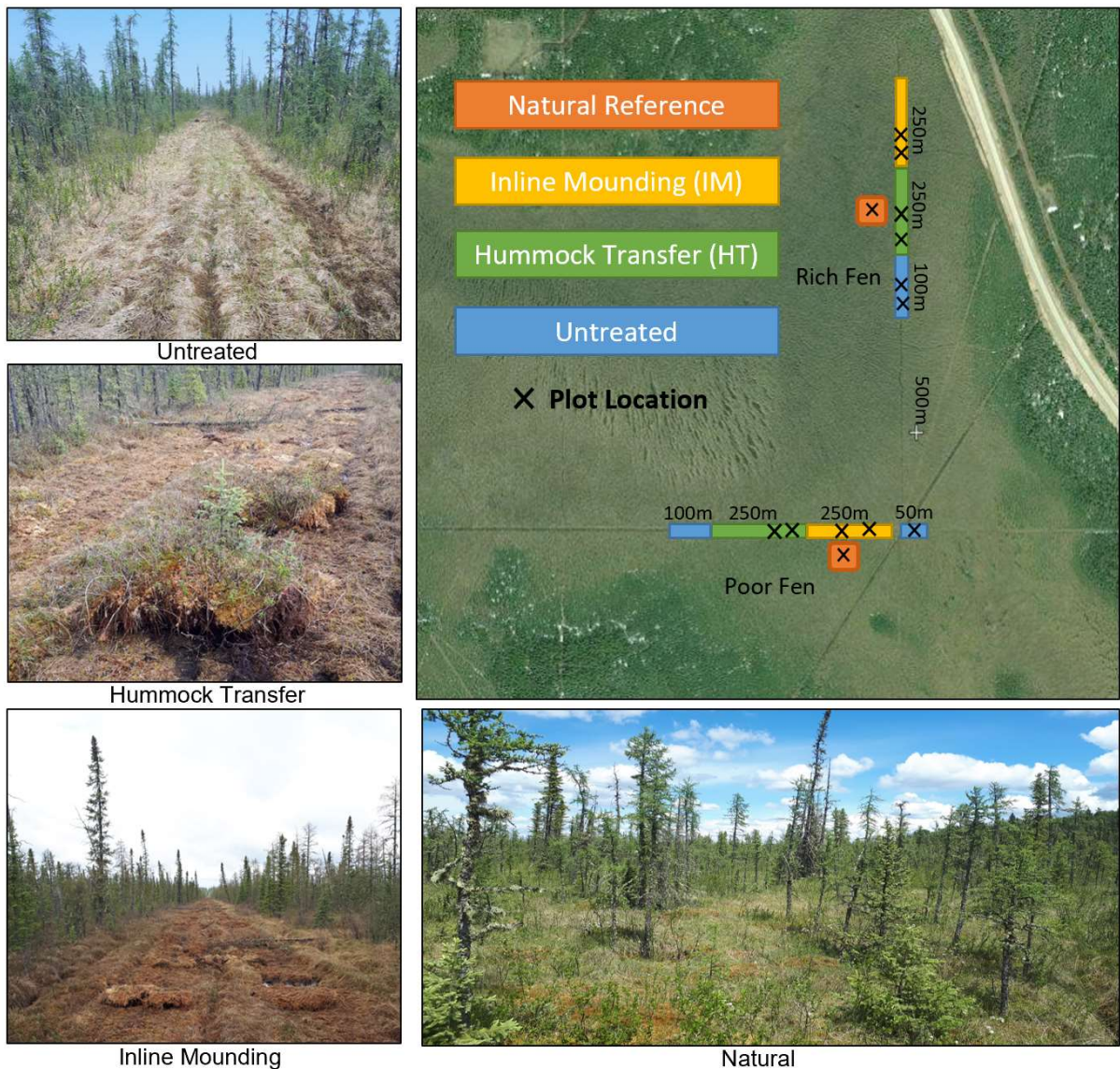


Figure 2.1 Study site with treatments, locations of sample plots, and photographs of the four treatments.

2.2.2 Restoration groundwork and project design

Restoration groundwork was carried out in March 2019 on frozen ground. Two different mounding techniques were investigated in this study: inline mounding (IM) and hummock transfer (HT). Mounding was done by a backhoe with toothed digging bucket, moving an intact scoop of soil from within the seismic line and placing it nearby in the same orientation (i.e., vegetated side up) for IM, and targeting naturally formed hummocks just off the line and moving them onto the line for HT, at an approximate density of 155 mounds/ha (Fig 2.1). Some of the transferred hummocks included woody shrubs and small trees (Fig 2.1). Hummocks for both treatments averaged a height of 20 cm, while hollows were an average depth of 19 cm in IM and 10 cm in HT. Single trees from the edges were randomly pulled down onto the line (often referred to as stem-bending) to provide block travel and provide seed input. Treatments were replicated on both poor fen and rich fen sections with some length of line left untreated as controls, and a natural reference site was selected for each section approximately 20 m away from the seismic line Fig. 2.1).

2.2.3 Vegetation surveys

Vegetation surveys were conducted in July and August of 2020. Two hummocks and two hollows were surveyed in each treatment in both fen sections, for a total of four replicates per microform per treatment, due to Covid-19, which the authors acknowledge is low repetition with limited statistical power. Surveys were done on the existing 60 cm x 60 cm plots installed for greenhouse gas measurements (Chapter 3; Fig 2.2). Each plot was visually surveyed for percent cover of species, which were later combined to functional groups (graminoids, vascular forbs, shrubs, *Sphagnum* spp., other bryophytes) and recorded to the nearest percent. Species nomenclature followed the USDA online plants database (<http://plants.usda.gov>). Species that were identified in only one or two plots at very low (< 1 – 2 %) cover were removed on the assumption of human error during field identification.

Average water table depths were obtained from data collected during greenhouse gas flux sampling at the plots. Water depth was measured approximately weekly in standpipes installed adjacent to each sample plot throughout the season (July – August).

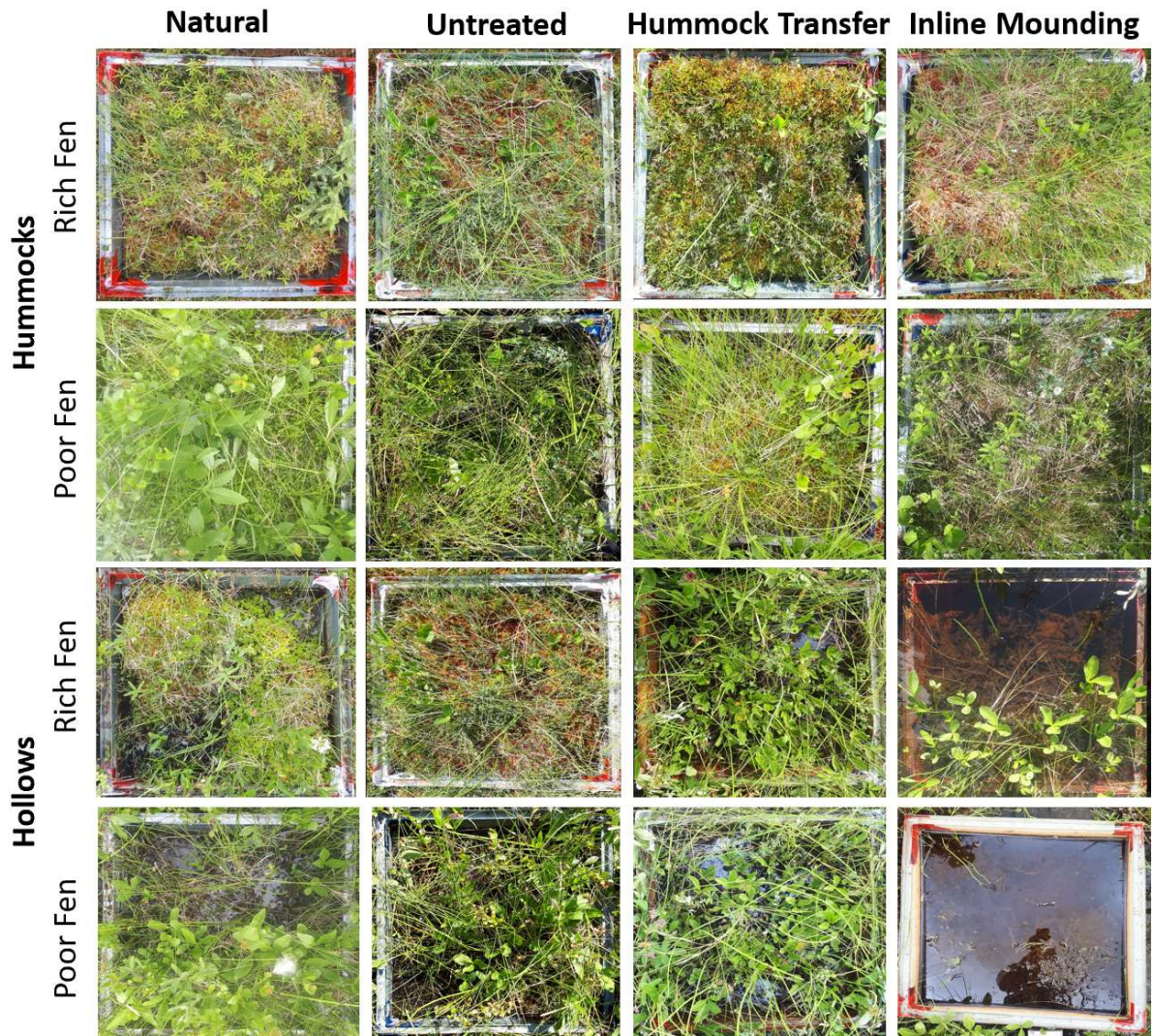


Fig. 2.2 Photographs of 16 of 32 survey plots in July 2020.

2.2.4 Biomass

Biomass sampling took place in July 2020, at the peak of plant productivity (Davidson et al. 2021). The vascular plant understory was sampled at two hummocks and two hollows per treatment (in both fens) by clipping all vegetation at the bryophyte surface from a 50 x 50 cm quadrat. Low shrubs and woody species such as *Rhododendron groenlandicum*, *Vaccinium oxycoccos* (L.) MacMill, *Andromeda polifolia* L., and *Vaccinium vitis-idaea* L. were collected as part of the understory. Bryophytes were collected via cores of 10 cm diameter and 10 cm depth. Vegetation was stored in plastic zipper bags at 4 °C until they were shipped to University of Waterloo for processing. In the

laboratory, samples were dried at 80 °C for 24 hours and weighed to obtain mass. For bryophytes, cores were dried intact at 80 °C for 24 hours and weighed; bulk density was calculated as dry mass divided by volume (Lewis et al. 2012). As there is no clear division between living and dead material for bryophytes (Clymo 1970), based on visual observations of colour change we assumed that the top 2 cm of bryophytes were live, and biomass of bryophytes was calculated as: surface area of the core (cm²) x 2 cm x bulk density (g cm⁻³).

Belowground biomass (roots) was measured to a depth of 50 cm. Peat cores of 10 cm diameter were collected using PVC pipe from hummocks and hollows adjacent to the aboveground sampling plots. Two cores per were collected from untreated, 2 from IM hummocks, and two per microform (hummock and hollow) from natural in each fen type, for a total of 16. Pipe was carefully inserted into the surface to limit compression and then hammered into 50 cm depth. The bottom was cut from the peat, the core lifted from the ground, sealed on both ends, and stored at 4 °C until shipping and processing. Storage and timing issues related to SARS-COVID-19 resulted in cores being drained before being separated into 10 cm sections (0-10, 10-20, 20-30, 30-40, 40-50 cm) from the surface, which may have caused some collapse of peat in the column; half of each section was used for root collection. Due to delays from SARS-COVID-19, samples were then dried for storage to prevent decomposition and only 8 were processed (one per each fen type). Upon processing, all living roots (identified by colour and firmness) of 0.5 mm diameter and larger were removed with tweezers, dried again at 60 °C for 12 hours, and weighed (Moore et al. 2002).

Aboveground biomass of trees can be estimated using allometric equations derived from regressions of dry biomass and tree height or diameter at breast height (DBH; 1.4 m) (Murray et al. 2021). Six 10 x 10 m plots were laid out in the natural fen along the length of the seismic lines (three in rich fen, three in poor fen) and all individual trees were identified and counted. Trees were categorized as either tall (> 1.4 m) and measured for DBH, or short (< 1.4 m) and measured for height. We estimated aboveground biomass of short *Picea mariana* with the allometric equation by Munir et al. (2014) where biomass = 0.0085(tree height)^{2.2088} (g); the biomass of tall *Picea mariana* were calculated as biomass = 0.153(DBH)^{2.248} (g) (Grigal and Kernick 1984). Aboveground biomass of tall *Larix laricina* were calculated as biomass = 0.1359(DBH)^{2.298} (g) (Carpenter 1983) and short *Larix laricina* as biomass = 0.3572e^{0.0532(tree height)} (g) (Murray et al. 2021). Midstory shrubs consisted of *Salix* spp. and *Betula* spp. Every individual in a 1 x 1 m plot within the 10 x 10 m tree plots was identified and counted, and we measured the diameter of each stem within 3 cm of where it emerged

from the peat (basal diameter: BD). Allometric equations from He et al. (2018) were used to estimate aboveground biomass of *Salix* and *Betula* where biomass = $55.85(\text{BD})^{2.325}$ (g) and biomass = $49.52(\text{BD})^{2.251}$ (g), respectively.

2.2.5 Statistical analysis

All analysis was done in the statistical analysis program R (R Core Team 2013). Species richness, functional group cover, and biomass between treatments and microforms were assessed with the `lm` function and anova outputs, and Tukey pairwise comparisons via the `lsmeans` function were used to identify differences between groups. Linear regressions, via the `lm` function, were used to explore relationships of water table on cover and biomass. For all analyses, differences in anova outputs were considered statistically significant when $p < 0.05$.

2.3 Results

2.3.1 Vegetation composition

The study area had a diverse plant community with substantial cover of forbs, graminoids and shrubs in most plots. Bryophytes cover most of the surface across all plots aside from those in the hollows created by both mounding treatments. Total percent cover of vascular plants was not significantly different across treatments ($F_{3,24} = 0.9406$, $p = 0.4365$), although hummocks had significantly higher cover than hollows ($F_{1,24} = 11.0176$, $p = 0.0028$), a pattern consistent across all treatments, resulting in no significant interaction between treatment and microform ($F_{3,24} = 0.9725$, $p = 0.4219$). Graminoid cover was higher on hummocks ($F_{1,24} = 7.5881$, $p = 0.0110$) in IM and HT ($F_{3,24} = 3.0803$, $p = 0.0465$), and HT hollows had significantly less graminoid cover than natural hollows or IM hummocks ($F_{3,24} = 3.1606$, $p = 0.0430$; Table 2.1). Cover of forbs was not significantly different across the site, and shrub cover only differed between microforms ($F_{1,24} = 6.6851$, $p = 0.0162$), regardless of treatment. Total bryophyte cover was much more variable between treatments ($F_{3,24} = 21.337$, $p < 0.0001$), microforms ($F_{1,24} = 156.167$, $p < 0.0001$), and with their interactions ($F_{3,24} = 21.920$, $p < 0.0001$). Hummocks had greater bryophyte cover, but the difference between microforms was only significant in some treatments. HT and IM hollows were significantly different from all other microforms, as were natural hollows; untreated hollows and all hummocks were not significantly different from each other. Overall, natural areas were significantly different from untreated, and HT and IM were significantly different from both. While *Sphagnum* cover did not differ across the site, cover of other

bryophytes was higher on hummocks than hollows regardless of treatment ($F_{1,24}=5.1590$, $p=0.0323$; Table 2.1).

Differences between treatments and microforms were link to local water table position. Although shallower water tables had a significant negative impact on total vascular plant cover across the site ($F_{1,30}=5.2821$, $p=0.0286$; Fig 2.2), the response varied depending on functional group. Water table significantly explained variation for shrub cover ($F_{1,30}=4.1406$, $p=0.0507$) but not for graminoids ($F_{1,30}= 0.9648$, $p=0.3338$) or forbs ($F_{1,30}= 0.9207$, $p=0.345$), and had no significant relationship to total bryophyte cover ($F_{1,30}=0.7638$, $p=0.3891$), *Sphagnum* ($F_{1,30}=2.1532$, $p=0.1527$), or other bryophytes ($F_{1,30}=0.4034$, $p=0.5302$; Fig 2.2).

Table 2.1 Average percent cover (%) of functional groups across treatments and microforms.

	Graminoids	Forbs	Low Shrubs	Sphagnum	Other Bryophytes
Natural	17	20	29	98	17
Hummock	18	29	45	98	27
Hollow	15	11	12	97	7
Untreated	21	30	18	98	14
Hummock	21	28	16	99	15
Hollow	20	32	19	96	13
Hummock Transfer	10	30	13	43	9
Hummock	14	22	23	85	17
Hollow	5	37	2	0	0
Inline Mounding	14	23	18	46	8
Hummock	22	23	34	95	14
Hollow	5	23	2	0	1

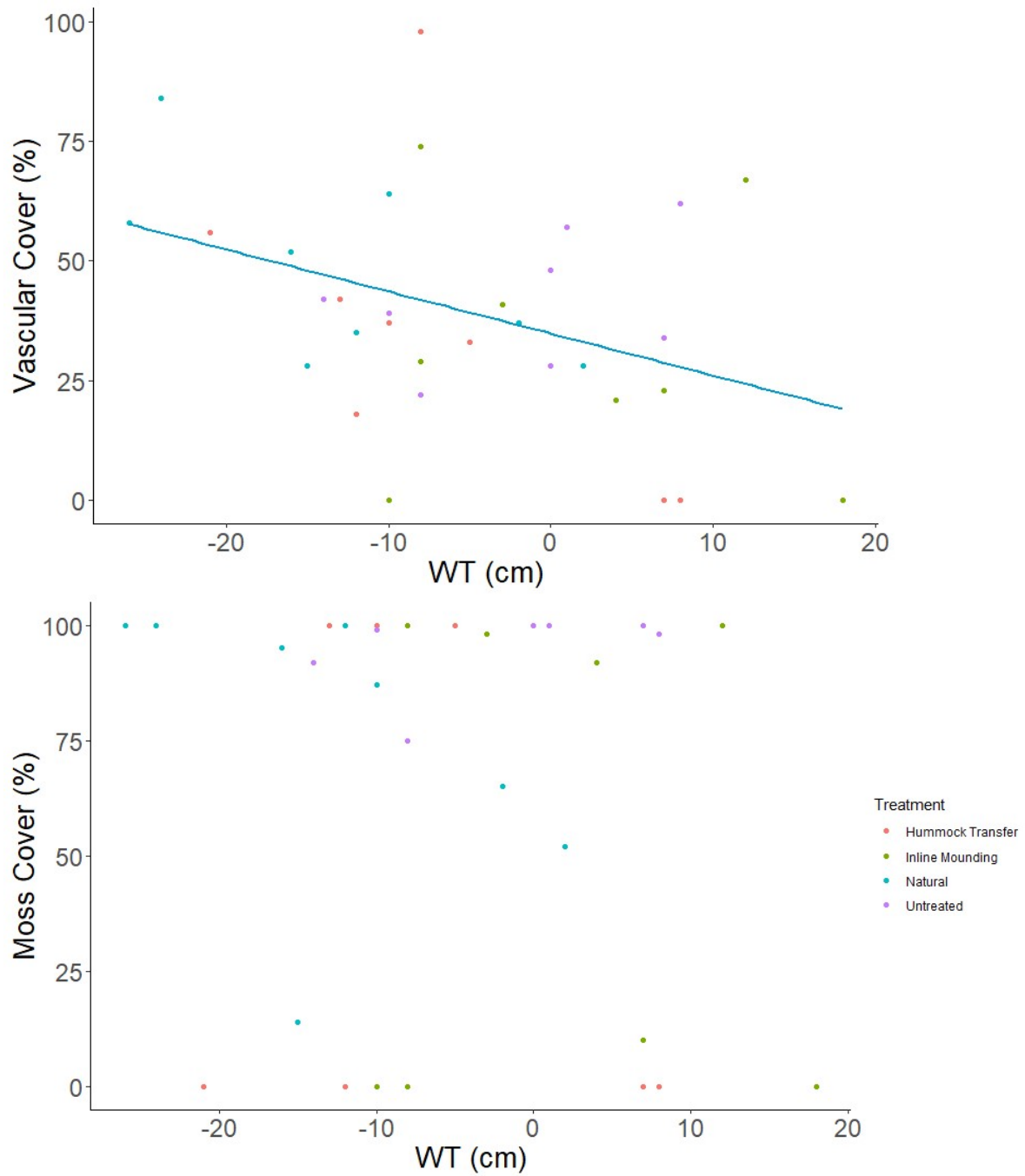


Figure 2.3 Relationship between water table (cm) and vascular plant and bryophyte cover (%). Total percent vascular cover decreased with increasing water levels. There was no significant relationship between total percent bryophyte cover and increasing water levels.

Table 2.2 ANOVA results of LME models for treatment, microform, water table, and interactions.

	Effect	DF	F-value	p-value
Total Vascular Cover	Treatment	3,24	0.9406	0.4365
	Microform	1,24	11.0176	0.0028
	Treatment:Microform	3,24	0.9725	0.4219
	WT	1,30	5.2821	0.0286
Graminoid	Treatment	3,24	3.0803	0.0465
	Microform	1,24	7.5881	0.0110
	Treatment:Microform	3,24	3.1606	0.0430
	WT	1,30	0.9648	0.3338
Forb	Treatment	3,24	0.3857	0.7643
	Microform	1,24	1.0932	0.3062
	Treatment:Microform	3,24	0.0554	0.9824
	WT	1,30	0.9207	0.345
Low Shrub	Treatment	3,24	0.4715	0.7049
	Microform	1,24	6.6851	0.0162
	Treatment:Microform	3,24	0.8664	0.4720
	WT	1,30	4.1406	0.0507
Total Bryophyte Cover	Treatment	3,24	21.3370	<0.0001
	Microform	1,24	156.1670	<0.0001
	Treatment:Microform	3,24	21.9200	<0.0001
	WT	1,30	0.7638	0.3891
Sphagnum	Treatment	3,24	0.6914	0.5662
	Microform	1,24	2.5111	0.1261
	Treatment:Microform	3,24	0.4768	0.7014
	WT	1,30	2.1532	0.1527
Other Bryophytes	Treatment	3,24	0.3825	0.7665
	Microform	1,24	5.1590	0.0323
	Treatment:Microform	3,24	0.5872	0.6292
	WT	1,30	0.4034	0.5302
Total Species Richness	Treatment	3,24	3.2509	0.0393
	Microform	1,24	12.7286	0.0015
	Treatment:Microform	3,24	5.8689	0.0037
Graminoid	Treatment	3,24	2.5147	0.0824
	Microform	1,24	4.4118	0.0463
	Treatment:Microform	3,24	1.5294	0.2324
Forb	Treatment	3,24	1.0933	0.3710
	Microform	1,24	13.5200	0.0011
	Treatment:Microform	3,24	6.2133	0.0028
Low Shrub	Treatment	3,24	4.2581	0.0151
	Microform	1,24	0.7742	0.3876

	Treatment:Microform	3,24	0.6452	0.5935
Bryophyte	Treatment	3,24	9.3871	0.0002
	Microform	1,24	11.7097	0.0022
	Treatment:Microform	3,24	9.6452	0.0002
Total Biomass	Treatment	3,24	1.8076	0.2237
	Microform	1,24	0.0426	0.8417
	Treatment:Microform	3,24	5.1055	0.0290
Bryophyte	Treatment	3,21	2.7405	0.0689
	Microform	1,21	4.9817	0.0366
	WT	1,13	8.7491	0.0111
	Treatment:Microform	3,21	3.5510	0.0319
	WT:Treatment	1,13	2.3022	0.1531
Vascular	Treatment	3,24	6.9100	0.0016
	Microform	1,24	14.9540	0.0007
	WT	1,16	20.2095	0.0003
	Treatment:Microform	3,24	1.3960	0.2682
	WT:Treatment	3,16	1.1370	0.3640
Root	Treatment	3,8	1.9458	0.2008
	Microform	1,8	0.0302	0.8664
	Treatment:Microform	3,8	5.8975	0.0200

Total species present (richness) varied significantly between treatments ($F_{3,24}=3.2509$, $p=0.0393$), microforms ($F_{1,24}= 12.7286$, $p=0.0015$), and as a result of interactions between them ($F_{3,24}= 5.8689$, $p=0.0037$). HT and IM hollows had significantly fewer species than any other microform at only 10 species on average (Table 2.3). Hummocks in natural, HT, and IM averaged 19 species while natural and untreated hollows averaged 23. Hummocks had significantly more ($F_{1,24}=4.4118$, $p=0.0463$) graminoid species than hollows, regardless of treatment, while the richness of forbs on microforms ($F_{1,24}=13.52$, $p=0.0011$) depended on interactions with treatment ($F_{3,24}=6.2133$, $p=0.0028$). The number of graminoid and forb species were both significantly different between HT and IM hollows and hummocks, with natural and untreated falling between. Species richness of low shrubs depended on treatment ($F_{3,24}=4.2581$, $p=0.0151$) and was significantly higher in natural than any other treatment. The number of bryophyte species varied significantly between treatments ($F_{3,24}=9.3871$, $p=0.0002$), microforms ($F_{1,24}= 11.7097$, $p=0.0022$), and with their interaction ($F_{3,24}= 9.6452$, $p=0.0002$). HT and IM had significantly fewer species than natural and untreated, and HT and IM hollows had very few species, resulting in these areas having significantly fewer species than any other microform (Table 2.3).

Of 33 species identified on the site, 14 were found across all four treatments, including *Calliergon giganteum*, *Sphagnum warnstorffii* Russ., *C. chordorrhiza* Ehrh. Ex L.f., *Menyanthes trifoliata* L., and *Andromeda polifolia* L. (Table 2.3). Several species found in natural were missing from untreated, including *Aulacomnium palustre*, *S. fuscum*, and *Rhododendron groenlandicum* (Table 2.3). *Drepanocladus aduncus* (Hedw.) Warnst., *Meesia triquetra* (Richt.) Ångstr, *Sphagnum angustifolium* (Russ.) C.Jens., and *Eriophorum angustifolium* L. were present in natural and untreated but not HT or IM (Table 2.3). Others, such as *S. warnstorffii* and *Vaccinium oxycoccos* (L.) MacMill, increased or decreased based on microform (Table 2.3).

Table 2.3 Species found on site across treatments and microforms and their percent cover (%). Species marked with * were found across all treatments. The number of species present in each treatment and microform is shown in the grey bars.

	Natural		Untreated		Hummock Transfer		Inline Mounding	
	Hummock	Hollow	Hummock	Hollow	Hummock	Hollow	Hummock	Hollow
Bryophytes	6	6	5	5	5	0	4	1
<i>Aulacomnium palustre</i> *	5	2	0	0	17	0	5	10
<i>Calliergon giganteum</i> *	95	0	91	65	80	0	94	0
<i>Drepanocladus aduncus</i>	85	0	2	18	0	0	2	0
<i>Meesia triquetra</i>	1	31	15	10	0	0	0	0
<i>Polytrichum strictum</i>	0	0	0	0	20	0	0	0
<i>Ptychostomum pseudotriquetrum</i>	1	2	0	0	0	0	0	0
<i>Tomenthypnum nitens</i>	0	15	0	0	0	0	0	0
<i>Sphagnum angustifolium</i>	0	45	1	2	0	0	0	0
<i>Sphagnum fuscum</i>	98	0	0	0	80	0	0	0
<i>Sphagnum warnstorffii</i> *	0	52	98	94	90	0	95	0
Graminoids	5	6	9	8	6	3	6	3
<i>Calamagrostis canadensis</i>	0	0	0	0	0	0	3	1
<i>Carex aquatilis</i> *	5	6	3	3	3	0	5	0
<i>Carex chordorrhiza</i> *	9	5	2	5	4	2	7	3
<i>Carex diandra</i> *	1	1	1	1	2	1	4	1
<i>Carex interior</i>	0	0	1	1	0	0	0	0
<i>Carex lasiocarpa</i> *	2	1	2	1	0	2	1	0
<i>Carex limosa</i>	0	1	1	1	2	0	0	0
<i>Eleocharis palustris</i>	0	0	9	7	1	0	0	0
<i>Eriophorum angustifolium</i>	0	1	1	1	0	0	0	0
<i>Triglochin maritima</i> *	1	0	1	0	2	0	2	0
Forbs	2	4	5	6	4	4	5	3
<i>Comarum palustre</i> *	0	3	1	1	0	5	6	2
<i>Drosera rotundifolia</i>	0	0	0	0	5	0	0	0
<i>Equisetum fluviatile</i> *	1	1	2	2	1	3	2	2
<i>Galium labradoricum</i>	0	0	1	2	2	1	1	0
<i>Menyanthes trifoliata</i> *	28	6	22	15	14	28	11	19
<i>Pedicularis vulgaris</i>	0	0	2	10	0	0	3	0
<i>Utricularia macrorrhiza</i>	0	1	0	2	0	0	0	0
Low Shrubs	3	2	2	2	2	1	2	2
<i>Andromeda polifolia</i> *	17	10	15	17	12	2	22	1
<i>Rhododendron groenlandicum</i>	23	2	0	0	1	0	0	0
<i>Vaccinium oxycoccos</i> *	5	0	1	2	11	0	12	0
Canopy Shrubs	3	3	2	3	2	2	1	1
<i>Betula glandulosa</i>	7	14	0	5	6	2	0	0
<i>Salix candida</i>	3	1	13	4	0	0	0	0
<i>Salix pedicellaris</i> *	1	4	2	4	4	12	9	2

2.3.2 Biomass

Total vascular plant biomass was significantly different between IM at 420 g m⁻² and untreated and natural at 655 g m⁻² ($F_{3,24}=6.910$, $p=0.00162$), and significantly higher on hummocks than in hollows ($F_{1,24}=14.954$, $p=0.0007$; Fig 2.3). At 533 g m⁻², HT biomass was intermediate. Vascular plant biomass was lower under shallower water tables/inundation ($F_{1,16}=20.2095$, $p=0.0003$) regardless of treatment, and was influenced by the interaction of water table with microform, although this was not significant ($F_{1,16}=4.3988$, $p=0.0522$; Fig 2.3).

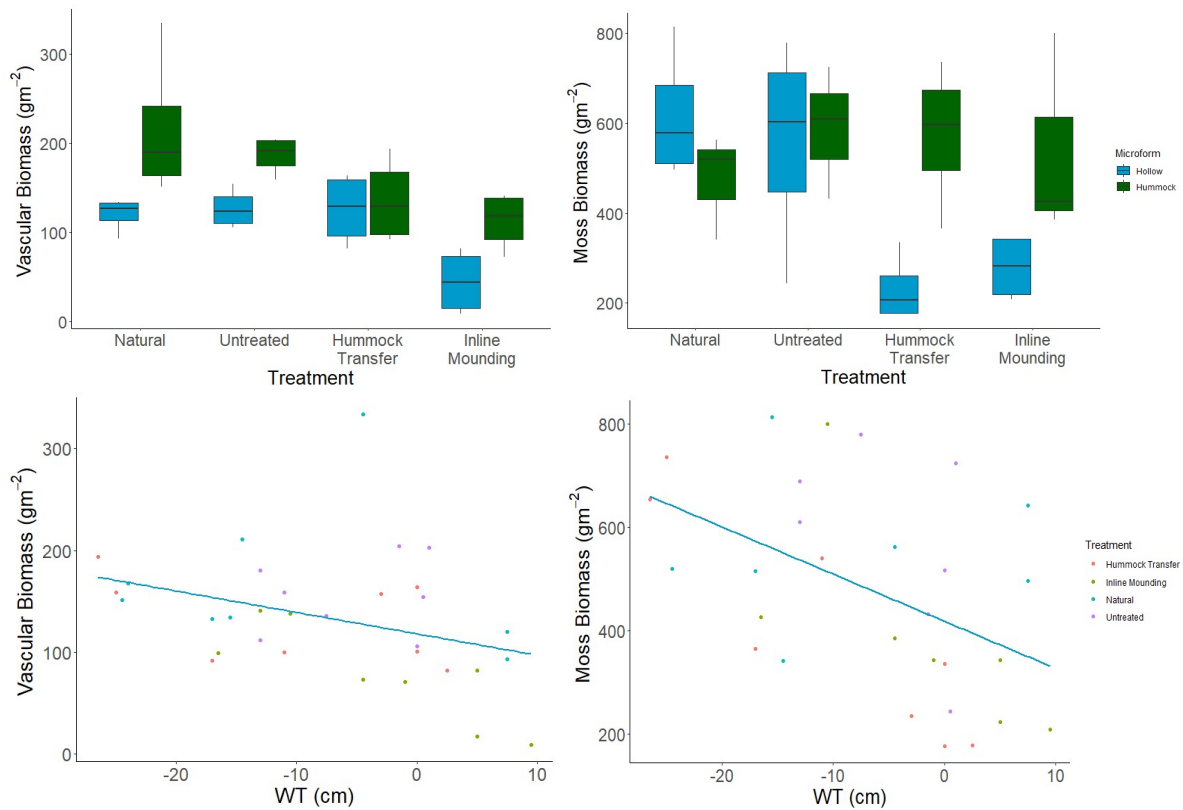


Figure 2.4 Vascular plant and bryophyte biomass (g m⁻²) by treatment and microform (top). Relationship between water table (cm) and vascular and bryophyte biomass (g m⁻²) (bottom).

Bryophyte biomass was not significantly different between treatments ($F_{3,21}=2.7405$, $p=0.0689$) and was higher on hummocks in HT and IM, but not necessarily in natural or untreated (microform $F_{1,21}=4.9817$, $p=0.0366$; treatment:microform $F_{3,21}=3.5510$, $p=0.0319$); only HT and natural hollows were significantly different from other microforms at 0 g m⁻² and 96 g m⁻², respectively (Fig 2.3). Average total bryophyte biomass in natural was 555 g m⁻², untreated was 570 g m⁻², and HT and IM were 401 and 390 g m⁻², respectively. Water table was a significant factor in predicting variation in

bryophyte biomass across all plots ($F_{1,13}=8.7491$, $p=0.0111$) regardless of treatment or microform (Fig 2.3).

At a total average of 1543 g m^{-2} in untreated followed by 1653 g m^{-2} in HT, 2073 g m^{-2} in IM, and 2562 g m^{-2} in natural, root biomass was not significantly different across treatments ($F_{3,8}= 1.9458$, $p=0.20084$) or microforms ($F_{1,8}= 0.0302$, $p=0.8664$) but the interaction between microform and treatment was significant ($F_{3,8}=5.8975$, $p=0.0200$). Natural hollows had double the biomass of natural hummocks while belowground biomass was similar between microforms for untreated lines and both mounding treatments (Table 2.4). Although root biomass generally decreased with shallower water tables, the relationship was not significant ($F_{1,14}= 0.0005$, $p=0.9826$).

Combining above- and belowground biomass, total biomass was not significantly different between treatments ($F_{3,8}= 1.8076$, $p=0.2237$) or microforms ($F_{1,8}=0.0426$, $p=0.8417$) alone but there was a significant interaction ($F_{3,8}= 5.1055$, $p=0.0290$). Natural hollows had higher biomass than natural hummocks. Across all other treatment, total biomass was higher in hummocks than hollows.

Estimated biomass of overstory trees and midstory shrubs in the natural areas added an additional $420 - 950$ (average 720) g m^{-2} . Of this, an average of 10.5 g m^{-2} ($5.6 - 22.8 \text{ gm}^{-2}$) were from mid-story shrubs, *Betula* spp. and *Salix* spp., with the majority of biomass coming from *P. mariana* and *L. laricina* trees.

Table 2.4 Average biomass of aboveground vascular species, bryophyte, belowground roots, and trees and shrubs by treatment and microform (g m^{-2}).

	Vascular	Bryophyte	Root	Tree	Total
Natural	168	546	2562	721	3997
Hummock	216	474	1609		2299
Hollow	120	617	3515		4252
Untreated	157	573	1543		2273
Hummock	187	588	1753		2528
Hollow	127	557	1333		2017
Hummock Transfer	131	403	1653		2187
Hummock	136	575	1701		2412
Hollow	126	231	1605		1962
Inline Mounding	9	408	2199		2686
Hummock	113	537	2294		2944
Hollow	45	279	2103		2427

2.4 Discussion

2.4.1 Shifts in species richness and cover

The presence and persistence of seismic lines through peatlands is known to alter vegetation composition; presence of trees and mid-story shrubs is nearly eliminated, and wetter conditions often lead to a shift towards domination by sedges. However, little is known about how restoration via mounding affect vegetation composition. In our study fen, the number of species present (richness) did not differ between the poor and rich fens on our site. In contrast, natural areas and untreated seismic lines had 5 – 10 more species than either HT or IM mounding treatments (Table 2.3). Unsurprisingly, this difference came primarily from hollows in the mounding treatments that had slightly less than half the number of species than those of natural and untreated areas. Species have preferential positions in relation to the mean water table level, causing a stratification across wetter and drier microforms (Caners and Lieffers 2014). Removal of the top layers of peat and vegetation to create hummocks left bare peat and open water in the hollows. Therefore, any species present had to come from the seed bank, encroach from the edges, or be brought in by wind or water. The hollows in HT and IM are deeper, and thus wetter, than the surrounding hollows, further reducing the number of potential species to those that are hydrophilic. This stratification across microforms and mean water table depth plays a part in determining the dominant plant species and composition within peatlands and following restoration.

In addition to the absence of most trees and shrubs, species on the untreated lines were those more suited to the higher water tables caused by depression of the surface and flattening of hummocks (Lovitt et al. 2018; Stevenson et al. 2019). Wetter conditions on the line allowed floating and emergent bryophytes, such as *C. giganteum* and *D. aduncus*, to spread across both hollows and hummocks but also limited slightly less tolerant lawn species like *M. triquetra* (Table 2.3). In the poor fen, *C. chordorrhiza* had the highest percent cover of the sedge species in natural plots but was replaced in the untreated plots by *C. aquatilis*, a species typically found in natural hollows and lawns (Douglas et al. 2001). Although total graminoid cover was not significantly higher in untreated than natural plots it did increase, and species richness was higher in both hollows and hummocks of untreated (Table 2.3). Higher graminoid cover and dominance by graminoid species on untreated seismic lines was also found by Echiverri et al. (2021) and Davidson et al. (2021). Greater numbers of graminoid species found on untreated lines suggests that, although microforms are highly depressed, small microsites likely still exist (Stevenson et al. 2019) with conditions for a wider range of species

than in undisturbed peatlands, and increased access to space and light. Additionally, species on the untreated lines were still those typical to peatlands, as were species found by Echiverri et al. (2021).

Plant cover retained by not inverting the mounds during restoration resulted in no significant differences in total vascular cover between treatments despite some reduction in total cover of vascular plants compared to natural and untreated for both mounding treatments. Percent cover of forbs was lower on IM and HT hummocks than natural and untreated at 23% and 29%, respectively but higher than reported in other peatland mounding studies. For example, three years after inverted mounding, Echiverri et al. (2019) found only ~15% cover of forbs on mounds. Similarly, in the present study, graminoid cover on hummocks was similar across all treatments at 14 – 22%, while graminoid cover on inverted mounds was only ~5% (Echiverri et al. 2019). The biggest difference between our vegetated hummocks and the inverted mounds was in bryophyte cover. At three years post-mounding, bryophyte cover on inverted mounds was < 25% (Echiverri et al. 2019) while both IM and HT hummocks were > 100% only two years after mounding. Although retaining vegetation on the hummocks has many benefits, such as reducing erosion and net greenhouse gas emissions while continuing to contribute to soil processes, it may increase competition for establishing tree seedlings - one of the main goals of restoration. While maintaining good cover, HT hummocks had approximately 20% less total vascular cover than IM hummocks, which could reduce competitive stress from tree seedlings while still providing benefits such as warmer microclimates and protection from the elements (Pouliot et al. 2011; Table 2.1). Small sample size may also have contributed to the full variation of cover not being captured across the site. Research on tree survival and growth on various mounding techniques is required to evaluate this.

Though hummocks had good cover, hollows in both IM and HT were near zero cover of graminoids and bryophytes. Cover of forbs, however, was higher than in natural hollows at 11%; forb cover in IM was double at 23% while HT hollows were over three times higher at 37%. Most of this difference was due to large increases in *M. trifoliata* from 6% in natural hollows to 28% and 19% in HT and IM, respectively (Table 2.3). As a shallow aquatic species, increased water levels and light from the removal of vegetation and undecomposed surface litter likely spurred its growth. Deep rhizomes would have remained at hollows following mounding, and potentially seeds, providing the source material for colonization.

Species found in HT were typically drier species located on the hummocks that were transferred from off the line, including bryophytes and other species such as *Andromeda polifolia* and *B.*

glandulosa (Table 2.3). Although percent cover was often less than half that on natural hummocks, it does support that species can be reintroduced to the lines via transfer and hummock creation and that mounding creates drier microsites (Murray et al. 2021). Interestingly, we found some species typically found in natural hollows were present in HT hummocks, including *Salix pedicellaris* and *Sphagnum warnstorffii* (Table 2.3). Although not investigated in this study, seismic lines have been found to have edge effects that affect understory vegetation composition into the adjacent peatland (MacFarlane 2003; Dabros et al. 2017); because hummocks were targeted from just outside of the seismic line edge this may have influenced species composition before being transferred. *S. warnstorffii*, typically a species of hollows and intermediate spots, was found across untreated sections and on hummocks in HT and IM (Table 2.3), suggesting that, although drier than untreated areas, the mounds in our treatments were not as dry as those in the natural fen. Hollow bryophyte species beginning to encroach onto the dry microsites after transfer may modify water transport, resulting in wetter conditions than natural hummocks. Contrary to this, despite preferring wetter positions, *Meesia triquetra* and *Sphagnum angustifolium* were present in natural hollows and untreated but not in HT or IM (Table 2.3); hollows were avoided during HT, but not during IM.

Similar to untreated areas, many drier hummock species in IM were replaced with more water-tolerant hollow species; however, raising the vegetation above the water table of the line via mounding resulted in a decrease in some wet-loving species and an increase in some drier species on the hummocks. For example, percent cover of *M. trifoliata* on hummocks, though still higher than on natural hummocks, was half as much as untreated hummocks (Table 2.3); as *M. trifoliata* is a semi-aquatic species (Douglas et al. 1999), lower water tables in hummocks reduce the ideal conditions needed to thrive. *S. pedicellaris*, on the other hand, prefers an aerobic zone around its roots, resulting in higher cover on IM hummocks compared to both natural and untreated (Table 2.3).

2.4.2 Changes in biomass

Vascular plant biomass followed similar patterns as vascular cover. In fact, the relationship between these two variables was significant ($F_{1,30}=8.0925$, $p=0.0079$, $R^2=0.2124$). Shallower water tables had a negative relationship with total vascular biomass as many forb and woody species were flooded out and water-tolerant graminoids and bryophytes took over (Fig 2.3). IM, in particular, had much lower vascular biomass than the other treatments (Fig 2.3), mostly as a result of the removal of vegetation from the hollows, most of which had only a few graminoids present. Despite this, IM had the highest root biomass of the line treatments in both hummocks and hollows (Table 2.4), suggesting that

vascular roots and rhizomes are indeed the primary input for fen peat formation, as was found by Hinzke et al. (2021) and Murphy et al. (2009). Potentially, the live plants on the hummocks were able to rapidly increase their root systems within the drier upper layer and then may have been able to extend downward to the water table below. Although bryophyte biomass did not change significantly between treatments, it dropped from $\sim 560 \text{ g m}^{-2}$ in natural and untreated to 403 g m^{-2} and 408 g m^{-2} in HT and IM, respectively (Table 2.4). Most of this difference came from hollows where the vegetation layer was removed and bryophytes were present only near the edges. Depending on hydrologic conditions over the next few years, filling of hollows could be quite slow; although bryophytes, particularly certain *Sphagnum* spp. and pool species of brown mosses, can create floating mats on open water, if inundation extent varies across years, resulting in repeated flooding of hollows, bryophyte growth can be delayed or lost (Caners and Lieffers 2014).

Natural areas had the highest vascular, root, and total understory biomass (i.e., without trees and mid-story shrubs; Table 2.4), but despite shifts in species and functional group cover, total understory biomass in IM and HT were not significantly different from natural. This suggests that despite seismic line disturbance and subsequent ground disturbance from restoration, careful restoration methods that avoid burying the established vegetation can maintain biomass in peatlands.

By far the greatest difference in biomass was the absence of trees and mid-story shrubs on the seismic lines, regardless of treatment; these represented an additional $\sim 720 \text{ g m}^{-2}$, with mid-story shrubs alone accounting for over 10 g m^{-2} (Table 2.4). Studies have found the presence of shrubs and trees in peatlands can help with the development of hummocks as they provide microsites for other species and support for bryophytes, particularly *Sphagnum* spp., to grow upwards (Pouliet et al. 2014). This is a substantial portion of peatland biomass missing from the lines which indicates a long-term shift in C stocks that will likely take decades to recover, even if mounding treatments are successful in establishing woody species on the lines. As we did not measure net primary productivity of trees and shrubs in this study, it is unclear whether increased productivity of the understory on the lines will compensate for the loss of trees, but studies of peatlands used as a source of donor vegetation for restoration suggest not (Murray et al. 2017). In this regard, the rapid reintroduction of woody vegetation via HT may have the potential to quickly restore mid-layer biomass accumulation and compensate for loss of trees on the lines.

2.4.3 Implications for management

The results of our study support previous research that found that the vegetation community composition on seismic lines was different than that of the surrounding peatlands. Additionally, we showed that maintaining existing vegetation on the hummocks, whether from on or off the line, has a positive impact on vegetation recovery. Despite changes to species composition and cover, both mounding treatments were able to produce at least similar total biomass to untreated lines and show potential for continued recovery of shrubs, and potentially trees, as hummocks mature and conditions improve over time.

Although HT and IM had fewer, and some different, species than untreated and natural areas, they provided the conditions needed for the species present to grow and increase production of biomass. Because the hummocks in both treatments were not inverted, total bryophyte and vascular cover were similar or higher in the second year after mounding than inverted mounds after three to six years. For example, inverted mounds on OSE well pads had only 19% bryophyte and 21% vascular cover on hummocks (Murray et al. 2021), and seismic lines had 20% vascular and < 25% bryophyte cover (Echiverri et al. 2019). On our site, vascular cover on HT and IM hummocks was 60% and 80%, respectively, and the lowest bryophyte cover was over 100%. After five years, hollows on the well pad had only reached 15% total vascular cover (Murray et al. 2021), whereas even our IM hollows averaged 16% in the second year, likely due to their shallow depth.

As we studied plant community and biomass in only the second growing season post-mounding, further data will need to be collected in the coming years to determine if these positive shifts continue and whether biomass on the mounded treatments continues to increase towards that of natural reference areas. These restoration techniques will also need to be studied across more peatlands with different hydrological and chemical conditions to develop best management practices, especially as different peatland types naturally begin with different species composition and proportions. Ideally, these practices will initiate successional pathways that restore species richness and diversity to the lines, helping to improve habitat and carbon sequestration.

Chapter 3: CO₂ uptake decreased and CH₄ emissions increased in first two years of peatland seismic line restoration

3.1 Introduction

The northern half of the province of Alberta, Canada is known for its vast underground oil and gas reserves and is covered by over 134,000 km² of boreal peatlands (AEP 2018). Extraction and exploration of oil and gas deposits has left a network of linear clearings, known as seismic lines, crisscrossing the boreal region even decades after their creation (Lee and Boutin 2006). Recent estimates put the total length of seismic lines through Alberta peatlands at over 345,000 km covering an estimated area of 1900 km² (Strack et al. 2019), reaching a mean density of up to 10 km/km² (Lee and Boutin 2006) or as high as 40 km/km² (Schneider 2002). Historically, seismic lines were created using heavy machinery during summer months, removing trees and vegetation, as well as roots and surface soil layers, to a width of 5 - 10 m (Bliss and Wein 1972); these are often referred to as “legacy lines”. Over time clearing began to take place over winter months and bulldozer blades were raised to reduce disturbance of the peat (Bliss and Wein 1972). Through the 1990s, line width was reduced to approximately 5 m and by the 2000s, low impact seismic (LIS) lines of 1.5 – 5.5 m, cleared with light-weight equipment, had become the preferred method (Dabros, Pyper, and Castilla 2018). Undisturbed, peatlands sequester large amounts of carbon (C) (e.g., Loisel et al. 2014) and provide important habitat for species such as the threatened woodland caribou (Filicetti, Cody, and Nielsen 2019). Alteration of hydrologic and topographic conditions on seismic lines prevents the re-establishment of trees, contributing to habitat fragmentation and increased predation of caribou, which has spurred efforts to restore them. The focus of restoration has, until recently, been on tree recovery, but little is known about the effects of linear disturbances and restoration of these features on peatland C exchange; thus, this is the goal of this study.

The accumulation and slow decomposition of organic matter in peatlands locks C in place, creating long-term sinks for atmospheric carbon dioxide (CO₂), and sources of methane (CH₄) (Blodau 2002). CO₂ is taken up by vegetation during photosynthesis (gross ecosystem productivity: GEP) and incorporated into plant tissues (Chapin et al. 2006), however, some C is re-released as CO₂ through respiration by roots, mycorrhizae, and microbes (Ryan and Law 2005). The net exchange of C between the atmosphere and an ecosystem is measured as net ecosystem exchange (NEE) (Chapin et al. 2006). Decomposition under saturated, anoxic conditions results in production of CH₄. Principle controls on C cycling in peatlands have been identified as water table position, soil temperature, and

plant community structure (e.g., Blodau 2002; Murray et al. 2021). Many studies have been carried out on the effects of water table draw down on peatlands (e.g., Gazovic et al. 2013; Pypker 2013) and have found that typically CO₂ production (respiration) increases and CH₄ production decreases. However, interactions with other factors, such as increased peat temperatures (e.g., Pypker 2013), may increase CH₄ production and release even under drying conditions. Rising water tables have been found to have the opposite effect: CO₂ production decreases and CH₄ production increases with flooding (Chimner et al. 2016; Strack et al. 2018). Soil temperature directly influences microbial community activity (Yavitt and Williams 1997), and higher soil temperatures may also increase the productivity and respiration of vegetation (e.g., Strack et al. 2007).

Peatlands form heterogenous landscapes at several scales, creating complexes with varying peatland types over large areas and within-peatland microtopography. Microforms are small variances in surface elevations (≤ 1 m) and are an integral feature of peatlands, with effects on both biogeochemical and physical ecosystem function (e.g., Waddington et al. 2010). Microforms are classified by elevational position from the average and infer relationship to water table. Hummocks are elevated mounds with the deepest water table (Nungesser 2003), dominated in Alberta by *Sphagnum fuscum* (Schimp.) H. Klinggr., vascular species such as *Rhododendron groenlandicum* (Oeder) Kron & Judd, and tree species such as *Larix laricina* (Du Roi) K.Koch. and *Picea mariana* (Miller) Britton (McCarter and Price 2012). Hollows exist between and around hummocks, are just above or below water table (Nungesser 2003) and are dominated by more hydrophilic species such as *Sphagnum magellanicum* Brid., *Carex* spp., and *Salix* spp. (e.g., McCarter and Price 2012). Microform formation and persistence is linked to both internal feedbacks, such as nutrient cycling (Eppinga et al. 2010), decomposition, and vegetation (Pouliot et al. 2011), and external factors such as fire and hydrologic regime (e.g., Waddington et al. 2010; Benscoter et al. 2015). Graminoids and herbaceous species take up large amounts of CO₂, but also respire at higher rates than mosses, particularly *Sphagnum* species (Dieleman et al. 2017). Dominance of *Sphagnum* species therefore contributes to growth and lower GHG production of peatland hummocks, while dominance of graminoids in hollows increases GHG production (Strack et al. 2016).

The complexity of peatland systems makes them especially vulnerable to disturbance and prone to long, slow recovery, if they recover at all. Vegetation removal and surface alteration during seismic line construction likely start a domino effect on other biogeochemical factors, from hydrology to peat properties and C cycling. Not only are hummock tops physically removed in preparation for seismic

surveying, but repeated passes of heavy machinery further compress the peat surface (e.g., Stevenson et al. 2019; Strack et al. 2019), resulting in rutting from machinery and an increase in hollow coverage (Lovitt et al. 2018; Stevenson et al. 2019). Any microforms that do persist on seismic lines tend to be highly suppressed, varying only a few centimeters from mean elevation, compared to up to a meter in natural conditions (e.g., Caners and Lieffers 2014). Microform development in disturbed peatlands has been shown to be resistant to natural formation processes such as *Sphagnum* growth and fire (e.g., van Rensen et al. 2015; Stevenson et al. 2019), likely due to shallow water tables and increasing surface water pooling that often sustains flooded conditions through the growing season (e.g., Caners and Lieffers 2014). This reduces suitable sites for tree establishment and shifts seismic lines towards more *Carex* dominated communities (e.g., Lee and Boutin 2006, van Rensen et al. 2015; Strack et al. 2018). Moss cover may be lower on lines and exhibits slower growth overall, potentially due to increased light levels (e.g., Pouliot et al. 2011), while hummock forming *Sphagnum* species must compete with other species, resulting in slowed succession that often stalls in early stages (e.g., Caners and Lieffers 2014; van Rensen et al. 2015). Loss of hummocks removes oxic zones that support higher rates of GEP and CH₄ oxidation, and in turn creates conditions that favour CH₄ production (Chimner et al. 2016; Strack et al. 2018). The net C uptake of the new plant community will determine the C balance on the line; how it compares to the adjacent forested peatland will depend on the ability of a more productive understory to compensate for the loss of C uptake by trees and increased CH₄ emissions.

Restoration of disturbed peatlands has the potential to return them to C sinks, as has been seen in peatlands used for horticultural peat extraction (e.g., Strack et al. 2016; Nugent et al. 2018). Until recently, restoration of seismic lines has been largely ignored due to the assumption that such linear disturbances would recover naturally with time. What has been done has focused mainly on structural restoration related to caribou habitat, such as reducing sightlines and access by predators (e.g., Filicetti et al. 2019); full mitigation of the impacts of seismic lines requires a shift in this focus to include restoration of ecological functions for a return to successional peatland pathways. As previous restoration has been targeted at tree recovery, the focus has been on creating artificial mounds to replace microtopography, namely hummocks, lost during construction and the use of these elevated microsites for tree establishment (e.g., Lieffers et al. 2017; Filicetti et al. 2019). Mounding is a mechanical process that scoops soil from one spot and places it nearby to create raised areas (hummocks) and leave low areas (hollows) that mimic natural microforms (Dabros et al. 2018). Studies on mounding have been ongoing for some time to restore peatland oil sands exploration well

sites, and mounds on these sites are often large, high, and inverted to expose deeper peat and/or mineral soil (Echiverri et al. 2020; Murray et al. 2021). Not only does inversion eliminate any potential uptake of CO₂ by buried vegetation, but peat surfaces are also exposed to erosion (Shuttleworth et al. 2014) and increased decomposition (Smolander and Heiskanen 2007; Lieffers et al. 2017). Meanwhile, large, flooded hollows have the potential to become CH₄ emission hotspots (Murray et al. 2021). While mounding on seismic lines has become more common (Echiverri et al. 2020; Murray et al. 2021), knowledge of impacts on GHG production and emissions remains limited; this paper is the first to capture detailed, plot-scale CO₂ and CH₄ fluxes on unrestored and restored seismic lines.

In this study, CO₂ and CH₄ fluxes were collected in the first two summers immediately following restoration work. The objectives of this study were to: (1) quantify CO₂ and CH₄ fluxes of two types of mounding - inline mounding (IM), in which mounds and hollows were created on the seismic line and not inverted, and hummock transfer (HT), in which established natural hummocks just off the edges of the line were targeted and placed vegetated side up on the line, leaving the associated hollow in the bordering undisturbed peatland. These treatments were compared to untreated lines and adjacent undisturbed peatland, and (2) determine environmental relationships contributing to CO₂ and CH₄ fluxes.

3.2 Methods

3.2.1 Study site

The study area is located in central Alberta, Canada approximately 11 km southwest of Brazeau Dam (52.889326, -115.549173; Figure 3.1). The region is classified as Boreal Plains Ecozone (Environment Canada 2001) and Central Mixedwood Natural Subregion (AEP 2006). Average temperatures range from 14 - 17°C in June, July, and August to -15 - -12°C in December, January, and February with an average of 97 frost free days per year (ECCC 2021). The area receives an average 462 mm precipitation per year, with most occurring during the growing season, May to August (ECCC 2021). Wetlands comprise a large portion of the region, dominated by wooded and shrubby fens, in a mosaic of aspen and spruce upland (AEP 2006). The study site consists of ~3 km of peatland seismic line running north-south and east-west. Although the precise date of creation is unknown, satellite images show seismic lines present as far back as 1982. At time of groundwork in March 2019 the line edges were still clearly visible, with little regeneration of woody vegetation or

trees. A hydrological gradient exists longitudinally, becoming drier as the center point is approached from both north and south ends. This corresponds to a gradient in vegetation and fen type, transitioning from rich fen at both north and south ends to poor fen in the center that extends the length of the east-west line. Dominant vegetation in the rich fen consists of *Larix laricina*, *Picea mariana*, *Betula* spp., *Carex* spp., *Menyanthes trifoliata* L., and *Polytrichum* spp. Dominant vegetation in the poor fen consists of *Picea mariana*, *Larix laricina*, *Rhododendron groenlandicum*, *Salix* spp., *Menyanthes trifoliata*, *Vaccinium oxycoccos* (L.) MacMill, *Sphagnum fuscum*, and *Sphagnum magellanicum*. To capture these differences the site was divided into three subsites: north from the center point, south from the center point, and the entire east-west section. For this study only the north and central sections were chosen to create an equal number of sampling points in the poor and rich fen sections.

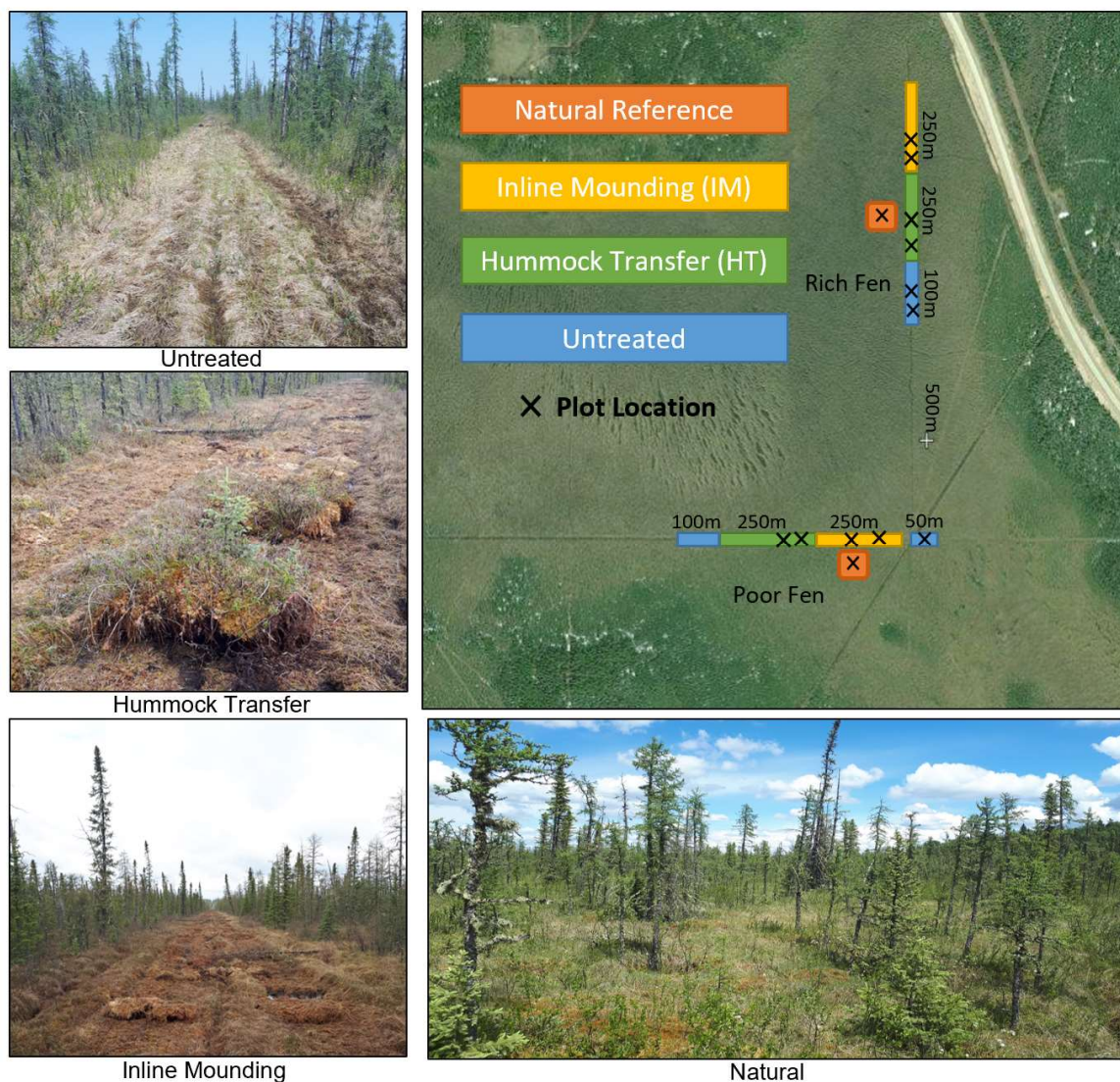


Figure 3.1 Study site with treatments, locations of collars, and photographs of the four treatments.

3.2.2 Groundwork and project design

Groundwork was carried out in March 2019 on frozen ground, installation of research equipment took place in May 2019, and data collection began June 2019. Mounding was done by a backhoe with toothed digging bucket, moving an intact scoop of soil from within the seismic line and placing it nearby in the same orientation (i.e., vegetated side up) for IM, and targeting naturally formed hummocks just off the line for HT. Hummocks with established woody shrubs and small trees were intentionally targeted (Figure 3.1). Hummocks for both treatments averaged a height of 20 cm, while hollows were an average depth of 10 cm in HT and 19 cm in IM. Single trees from the edges were

randomly pulled down onto the line (often referred to as stem-bending) to provide additional microsites. Treatments were replicated on both poor fen and rich fen sections with some length of line left untreated as controls, and a natural site was selected for each section approximately 20 m away from the seismic line.

3.2.3 Carbon dioxide (CO₂) flux

We collected CO₂ fluxes via the closed chamber method (Griffis et al. 2000), in which plexiglass chambers are placed onto metal collars installed in the peat. Pairs of 60 × 60 cm steel collars were permanently installed at each sample plot in corresponding hummocks and hollows. Two pairs were installed in each treatment in both sections, resulting in four replicate plots per microform per treatment. A clear acrylic chamber measuring 60 × 60 × 30 cm was set into a groove along the top of the collars that created a seal when filled with water. Air in the chamber was continuously circulated with a small battery-operated fan. CO₂ concentration in the chamber was measured at 15 second intervals for 105 - 120 seconds (~ 2 minutes) using a portable infrared gas analyzer (EGM-4, PP Systems, Massachusetts, USA), along with air temperature, relative humidity, and photosynthetically active radiation (PAR) within the chamber. An opaque tarp was used to create fully dark conditions, enabling ecosystem respiration (ER) to be measured. Order of sampling plots was changed daily to account for different light levels and solar angles throughout the day.

Net ecosystem exchange (NEE) is the overall exchange and direction of C movement between the atmosphere and an ecosystem, measured under full sun. Fluxes under dark condition capture ecosystem respiration (ER), and gross ecosystem productivity (GEP) is calculated as the difference between NEE and ER (Chapin et al. 2006). In this study, we use the sign conventions that C uptake from the atmosphere is negative and emission to the atmosphere is positive (Ryan and Law 2005). Raw data were inspected for linearity of fluxes, controlling for fit of $R^2 > 0.75$, except for fluxes that were relatively unchanging, representing a flux close to zero. Processing resulted in a data loss of 43% (due to issues with collar sealing in the newly formed hummocks) in 2019 and 0.5% in 2020.

3.2.4 Methane (CH₄) flux

We collected CH₄ fluxes from the same paired collars used for CO₂ with an opaque chamber and fans to maintain circulation and reduce chamber heating. In 2019 we collected CH₄ by extracting 20 ml gas samples from the chamber via syringe at 5, 10, 15, and 25 minutes post-closure that were injected into pre-evacuated Exetainers (Labco) and analyzed via gas chromatography on a flame ionization

detector (Shimadzu GC2014, Mandel Scientific) at the University of Waterloo. Atmospheric samples were collected via syringe and exetainer two to three times throughout each sampling day to provide CH₄ concentration at time zero. Fluxes were inspected for linearity and outlying points associated with potential ebullition were removed to control for $R^2 > 0.75$, resulting in a 6% loss of fluxes.

We changed methods in 2020 to continuous measurement every second for 300 seconds (5 minutes) with a CH₄/CO₂/H₂O Trace Gas Analyzer (LI-7810, LI-COR, Nebraska, USA). Per-second measurements allowed for ebullition (bubble) events to be parsed from diffusive fluxes; however, to capture total CH₄ contribution more accurately from the site, ebullitive fluxes were included in the data presented here. Fluxes were inspected for linearity following the same rules as CO₂ and ebullition events identified when concentration change was $>15\text{ppb s}^{-1}$ for minimum 3 seconds. Diffusive fluxes were calculated from the average of the linear changes before and after ebullition events (Goodrich et al. 2011); when more than one ebullitive event was present during the chamber closure, the linear slope between all ebullition events were averaged. By subtracting the diffusive flux slope from ebullitive slope we determined the additional CH₄ contribution of the ebullition events. The sum of the diffusive and ebullitive fluxes were used as the total flux; diffusive flux slopes were controlled for $R^2 > 0.75$ and in cases with an ebullition event(s) and no acceptable diffusive flux present, the ebullitive flux was used as the total flux. These processes resulted in only 1% loss of flux data.

We performed a cross-comparison between the two methods by collecting seven fluxes via the periodic sample extraction method immediately before measuring the same collar with the LI-COR. Cross-comparison found that, on average, flux determined by the extraction method was 1.3 times higher than the LI-COR but well within the range of fluxes from the research area. In addition to the small sample size, differences could be due to longer chamber closure times (15-20 mins vs 5 mins) increasing chances of capturing ebullition events. No correction was applied to calculated fluxes from either method as we did not directly compare between years.

3.2.5 Vegetation community and environmental conditions

Additional environmental factors were measured every time C fluxes were measured. Soil moisture was measured with a ML3 ThetaProbe Soil Moisture Sensor (Delta-T Devices) at five points in the hummock or hollow to achieve an average for the feature. A soil temperature probe was used to establish a temperature profile at -2, -5, -10, -15, -20, -25, and -30 cm. Water table was measured in a standpipe installed adjacent to each plot.

Vegetation surveys were conducted once in July of each summer. Each collar was assessed visually for percent cover of functional groups: *Sphagnum* spp., all other mosses (e.g., brown and feathermoss), graminoids (i.e., sedges, reeds, rushes, grasses), forbs, shrubs, and trees. Analysis showed similar relationships between C flux and individual vascular or moss plant functional groups so final analysis was based on data combined into two groups: all mosses and all vascular species.

To understand how shifts in environmental conditions between treatments influence productivity, we looked at the relationships of 2019 and 2020 data combined.

3.2.6 Data analysis

All data analysis was done in the statistical analysis program R (R Core Team 2013). As the main focus of this study was the impact of treatments on CO₂ and CH₄ exchange, we investigated the effect of treatment, microform, and their interaction as fixed effects in a separate linear mixed effects model for each flux component in the package nlme (Pinheiro et al. 2014). To account for repeated measures, plot was included as the random factor in each model. We used these models to assess treatment and microform impacts on GEP, ER, NEE, and CH₄ in each of 2019 and 2020, separately. Differences were considered statistically significantly when $p < 0.05$ using the anova output command for each model. CH₄ data was log transformed to improve normality of the residuals and a value of 1.6 added prior to transformation to adjust for negative values.

To understand how shifts in environmental conditions between treatments influence productivity, we created additional linear mixed effects models using combined 2019 and 2020 data with either water table or soil temperature as fixed effects along with treatment and interaction with treatment to evaluate whether response to environmental variables differed between treatments; plot was included as a random effect. We also investigated whether vegetation cover explained variation in C flux components. As vegetation was measured only once in July of each study season, C flux components were expressed as a seasonal average for each plot. Linear regressions, using the lm function were used to evaluate the effect of vascular or moss cover on variation in C fluxes.

3.3 Results

3.3.1 Environmental conditions

In general, average water table in the rich fen section was higher than the poor fen section at 0 cm and -10 cm, respectively. Although the difference was significant ($F_{1,44}=62.2$, $p<0.0001$), we were mainly

interested in the overall treatment effects and how they affected ecosystem function across the range of hydrological variation across the entire fen and therefore focused on treatment and microform effects (Table 3.1). Across the fen, microform alone significantly impacted water table (2019: $F_{1,20}=47.7$, $p<0.0001$; 2020: $F_{1,24}=20.6$, $p<0.0001$); treatment and the interaction with treatment were not significant. Water table followed the surface elevation gradient of microforms from hummocks to hollows, with the largest difference between HT hummocks (highest surface, deepest water table) and IM hollows (lowest surface, often inundated). Microform was also the only significant factor explaining variation in soil temperature at 10 cm below surface in both 2019 and 2020 (2019: $F_{1,20}=11.9$, $p=0.0025$; 2020: $F_{1,24}=25.7$, $p<0.0001$). Soils were warmest in hummocks and coolest in hollows, but differences were minimal aside from HT and IM, where hummocks were on average 3 °C warmer than hollows in both years (Table 3.1).

Table 3.1 Mean (SE) environmental conditions and vascular/moss cover for each treatment across both hummocks and hollows. Factors are significantly different if they do not share letters. Capital letters refer to the significance of treatments overall; lower case letters refer to differences between microforms.

Treatment	Soil temp 10 cm (C)		Water table (cm)		Moss cover (%)		Vascular cover (%)	
	2019	2020	2019	2020	2019	2020	2019	2020
Natural	15 (0.8)	18(0.4)	-3 (5.5)	-11 (4.5)	66 (18.3)	77 (11)	64 (7.3)	60 (6.9)
Hummock	15 (0.7)	18 (0.6)	-11 (4.3)	-17 (4.7)	100 (0)	96 (3.1)	80 (2.9)	69 (8.3)
Hollow	14 (1.5)	17 (0.3)	6 (7.7)	-4 (6.9)	32 (22.4)	58 (17.8)	45 (3.3)	52 (10.2)
Untreated	15 (0.6)	19 (0.4)	-3 (2.7)	-6 (2.2)	91 (5.5)	96 (3.1)	71 (8.4)	47 (5.5)
Hummock	15 (1.1)	19 (0.2)	-8 (2.5)	-6 (3.5)	88 (11.7)	99 (0.5)	53 (4.4)	51 (9.3)
Hollow	15 (0.9)	18 (0.6)	1 (3.3)	-5 (3.2)	93 (3.3)	92 (5.9)	89 (3.8)	43 (6.8)
Hummock Transfer	16 (0.6)	18 (0.4)	-5 (4.8)	-10 (4.1)	45 (16.7)	51 (18.7)	33 (10.4)	56 (13.2)
Hummock	17 (0.5)	19 (0.2)	-16 (3.7)	-20 (3.6)	89 (6.6)	100 (0)	35 (7.0)	64 (20.7)
Hollow	14 (0.5)	17 (0.3)	6.5 (2.7)	0 (1.1)	2 (1.2)	1 (1.3)	31 (21.4)	48 (18.2)
Inline Mounding	14 (0.9)	17 (0.7)	1 (4.8)	-3 (3.4)	46 (16.7)	51 (17.7)	31 (7.6)	42 (10.4)
Hummock	16 (0)	19 (0.6)	-11 (2.1)	-11 (2.5)	90 (3.5)	98 (1.8)	46 (5.9)	62 (14.4)
Hollow	13 (1.2)	16 (0.8)	13 (3.6)	5 (2.1)	2 (1.9)	4 (2.5)	15 (8.5)	23 (6.1)

Moss cover was higher in natural and untreated sections than IM and HT, and both treatment (2019: $F_{3,20}=13.181$, $p<0.0001$; 2020: $F_{3,24}=20.463$, $p<0.0001$), and microform (2019: $F_{1,20}=121.612$, $p<0.0001$; 2020: $F_{1,24}=151.932$, $p<0.0001$) were significant factors. Moss cover on natural and untreated hummocks ranged from 88 – 100 % and remained at 89 – 100 % in HT and IM (Table 3.1). In hollows, moss cover dropped from 32 – 93 % in natural and untreated to 1 – 4 % in HT and IM

resulting in a significant treatment-microform interaction (2019: $F_{3,20}=13.431$, $p<0.0001$; 2020: $F_{3,24}=21.086$, $p<0.0001$). Similarly, vascular cover was higher in natural and untreated areas (Table 3.1); treatment was significant in 2019 immediately following restoration, but not in 2020 (2019: $F_{3,20}=7.7636$, $p=0.0012$; 2020: $F_{3,24}=0.8002$, $p=0.5059$). Conversely, microform was not significant in 2019 but was in 2020 (2019 $F_{1,20}=1.4743$, $p=0.2388$; 2020 $F_{1,24}=5.0104$, $p=0.0347$) with higher cover on hummocks. The difference in vascular plant cover between microforms varied with treatment, with greater differences in HT and IM, but the interaction of treatment and microform was significant in 2019 only (2019: $F_{3,20}=4.1292$, $p=0.0197$; 2020: $F_{3,24}=0.5492$, $p=0.6535$). Vascular cover dropped from 51 – 80 % on natural and untreated hummocks to 35 – 64 % on HT and IM hummocks. In hollows vascular cover dropped from 43 – 89 % in natural and untreated to 15 – 48 % in HT and IM.

Soil temperature (2019 $F_{1,20}=9.82$, $p=0.0052$; 2020 $F_{1,24}=43.9$, $p<.0001$) and water table (2019 $F_{1,20}=123.0$, $p<.0001$; 2020 $F_{1,24}=67.2$, $p<.0001$) both had significant effects on moss cover in both years. Overall, moss cover decreased with shallower water tables (i.e., water closer to, or above, surface) and increased with warmer soil temperatures. These relationships were steepest in HT, followed by IM, natural, and untreated (WT:treatment 2019: $F_{3,20}=1.5379$, $p=0.2356$; 2020: $F_{3,24}=5.2071$, $p=0.0065$; soil temperature:treatment 2019: $F_{3,20}=3.3907$, $p=0.0381$; 2020: $F_{3,24}=3.4126$, $p=0.0336$). Treatment alone was significant ($F_{3,20}=6.0789$, $p=0.0041$) for explaining variation in vascular plant cover in 2019. In 2020, water table ($F_{1,24}=16.0$, $p=0.0005$) and soil temperature ($F_{1,24}=5.15$, $p=0.032$) were significant, regardless of treatment. As with moss cover, vascular cover decreased with shallower water tables and increased with warmer soils.

3.3.2 Carbon exchange

Average values for all C fluxes in each sampling year are given in the Supplementary Material (Table S1). After processing, 84 CO₂ fluxes were included for 2019. Average productivity across the study plots was significantly reduced (i.e., less negative GEP) in the two restoration treatments (HT - 16.9 g CO₂ m⁻² d⁻¹; IM -10.8 g CO₂ m⁻² d⁻¹) compared to natural (-24.8 g CO₂ m⁻² d⁻¹) and untreated (-36.2 g CO₂ m⁻² d⁻¹) sections. Generally, hummocks were more productive than hollows; however, this difference was only significant in HT (Table 3.2, Figure 3.2). Respiration did not differ significantly between any treatments or microforms (Table 3.2) although it ranged from 9.9 g CO₂ m⁻² d⁻¹ in natural to 16.4 g CO₂ m⁻² d⁻¹ in untreated. Respiration rates in hollows were roughly half that of hummocks except in untreated, where hollow ER was slightly higher than hummocks. On average across the study plots, NEE was positive (i.e., release to atmosphere) in IM and did not significantly differ from

HT (IM 0.9 g CO₂ m⁻² d⁻¹; HT -4.8 g CO₂ m⁻² d⁻¹); similarly, natural and untreated did not significantly differ (natural -14.9 g CO₂ m⁻² d⁻¹; untreated -19.8 g CO₂ m⁻² d⁻¹). Both IM hummocks and hollows acted as sources while natural, untreated, and HT acted as sinks (Figure 3.2).

Table 3.2 Results from the linear mixed effects models describing effects of treatment, microform, and interactions on CO₂ and CH₄ flux.

Flux Component	2019				2020			
	Effect	DF	F-value	p-value	Effect	DF	F-value	p-value
GEP	Intercept	1,54	126.06811	<.0001	Intercept	1,215	384.1633	<.0001
	Treatment	3,22	7.99214	0.0009	Treatment	3,24	5.7657	0.0041
	Microform	1,22	1.35438	0.257	Microform	1,24	9.7409	0.0046
	Treatment: Microform	3,22	3.38481	0.0362	Treatment: Microform	3,24	4.8673	0.0088
ER	Intercept	1,54	225.86548	<.0001	Intercept	1,215	739.8414	<.0001
	Treatment	3,22	1.53525	0.2334	Treatment	3,24	1.5581	0.2254
	Microform	1,22	5.89527	0.0238	Microform	1,24	52.755	<.0001
	Treatment: Microform	3,22	1.32057	0.293	Treatment: Microform	3,24	8.2871	0.0006
NEE	Intercept	1,54	31.343547	<.0001	Intercept	1,215	144.99811	<.0001
	Treatment	3,22	9.474923	0.0003	Treatment	3,24	6.02659	0.0033
	Microform	1,22	0.003486	0.9535	Microform	1,24	0.39921	0.5335
	Treatment: Microform	3,22	3.039399	0.0505	Treatment: Microform	3,24	2.49192	0.0844
CH ₄	Intercept	1,80	1342.0344	<.0001	Intercept	1,270	5218.587	<.0001
	Treatment	3,22	1.0722	0.3812	Treatment	3,28	2.94	0.0503
	Microform	1,22	4.3954	0.0478	Microform	1,270	2.848	0.0926
	Treatment: Microform	3,22	1.625	0.2123	Treatment: Microform	3,270	1.936	0.1241

In 2020, 247 CO₂ fluxes were included in the dataset. Productivity was significantly lower in IM (-20.5 g CO₂ m⁻² d⁻¹) than untreated (-38.4 g CO₂ m⁻² d⁻¹). Natural and HT were intermediate and did not significantly differ at -34.9 g CO₂ m⁻² d⁻¹ and -28.9 g CO₂ m⁻² d⁻¹, respectively. Microform had no significant effect on GEP (Table 3.2), except for IM hollows, which were much less productive (i.e., less negative GEP) than any other microform or treatment (Figure 3.2). Although treatments did not significantly differ in ER (Table 3.2), hummocks generally respired more than hollows. Respiration from IM and HT hollows (6.0 g CO₂ m⁻² d⁻¹; 9.5 g CO₂ m⁻² d⁻¹) was significantly lower than from natural and untreated hollows (13.6 g CO₂ m⁻² d⁻¹; 15.4 g CO₂ m⁻² d⁻¹) and similarly higher from IM and HT hummocks (20.4 g CO₂ m⁻² d⁻¹; 22.2 g CO₂ m⁻² d⁻¹) than natural and untreated (17.8 g CO₂ m⁻² d⁻¹; 17.6 g CO₂ m⁻² d⁻¹). NEE was significantly lower (i.e., less negative, less uptake) in IM (-7.4 g CO₂ m⁻² d⁻¹) than natural (-19.3 g CO₂ m⁻² d⁻¹) or untreated (-21.0 g CO₂ m⁻² d⁻¹), while HT (-13.0 g

CO₂ m⁻² d⁻¹) remained lower than natural and untreated but higher than IM. Only IM hollows had significantly lower uptake among all microform-treatment combinations, following a similar pattern to 2019 (Figure 3.2).

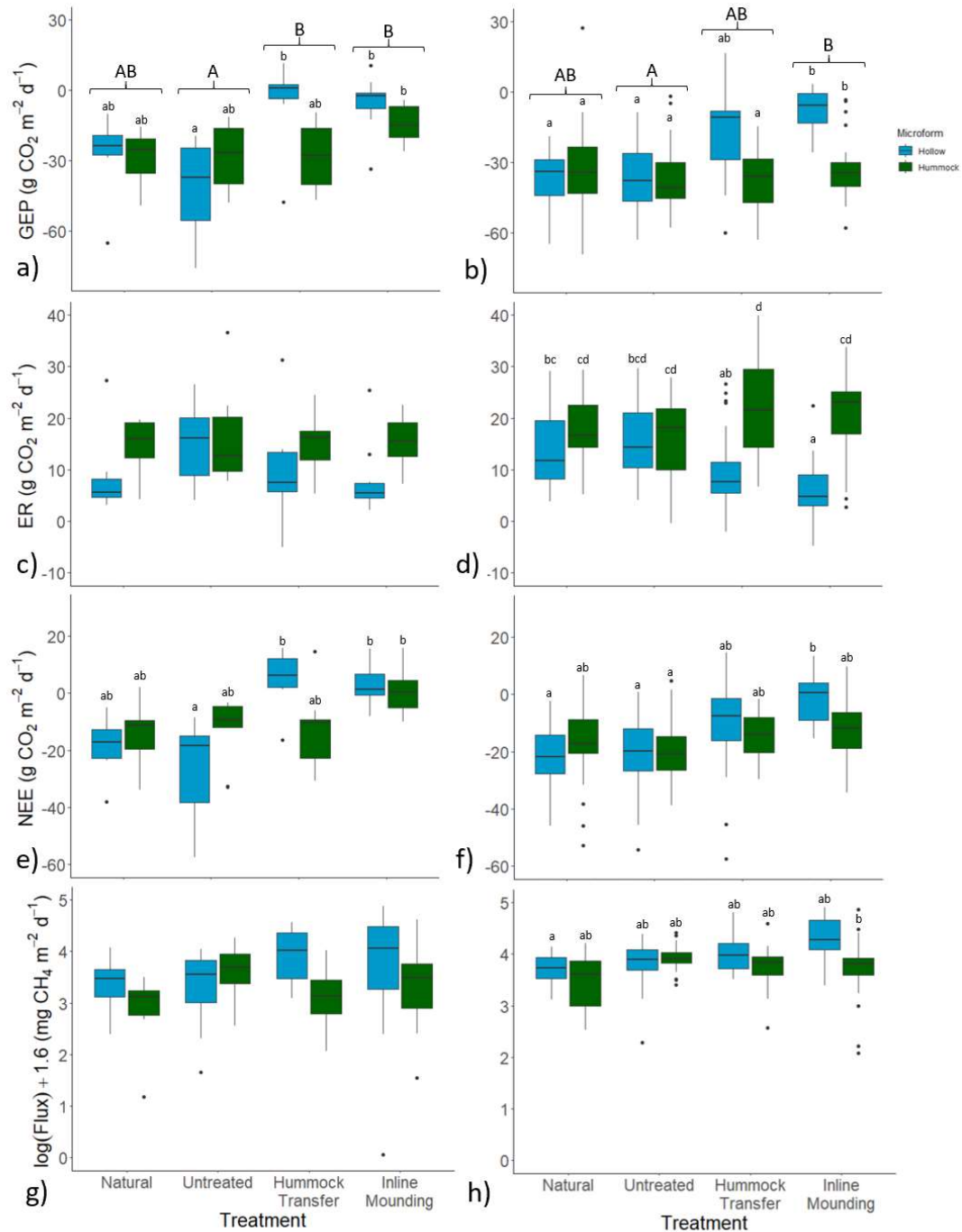


Figure 3.2 Fluxes of carbon dioxide (CO_2 ; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) (NEE = net ecosystem exchange, ER = ecosystem respiration, GEP = gross ecosystem productivity) and methane (CH_4 ; $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) from restoration treatments in 2019 and 2020 across both hummocks and hollows. Factors are significantly different if they do not share letters. Capital letters refer to the significance of treatments overall; lower case letters refer to differences between microforms.

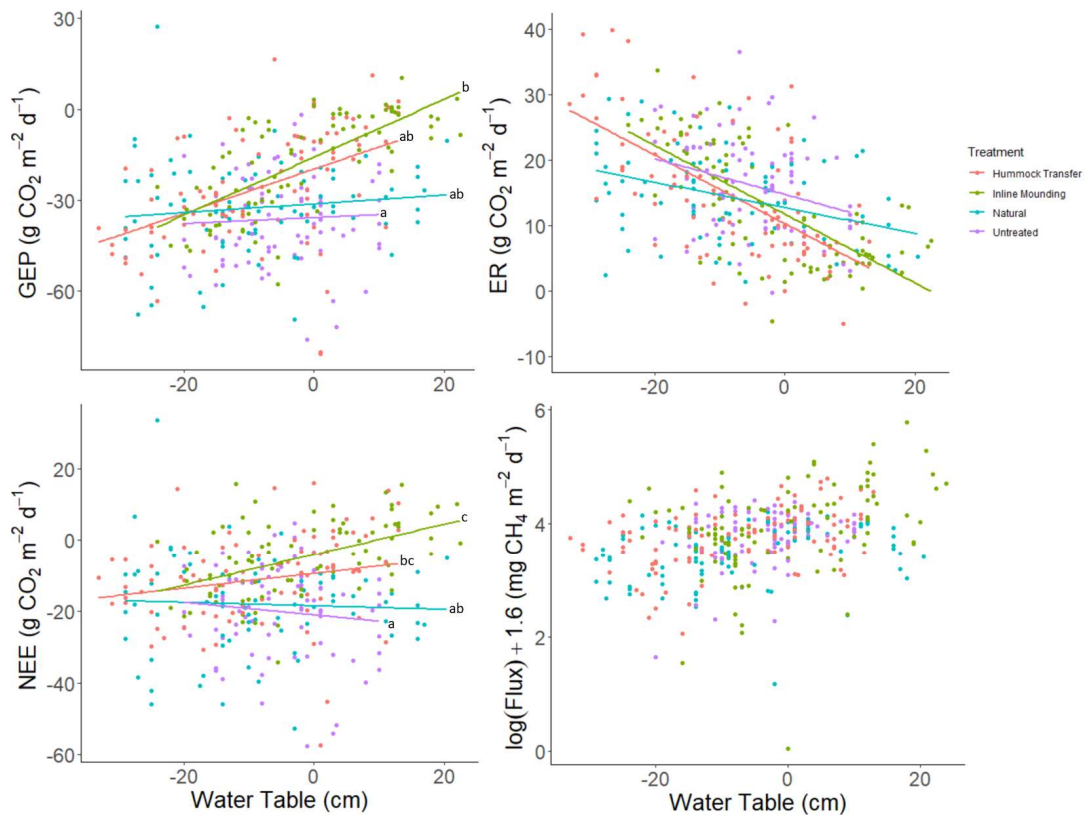


Figure 3.3 Relationship between water table (cm) and CO₂ and CH₄ across both hummocks and hollows. Increasing water tables resulted in decreasing (i.e., more positive) productivity, decreasing (i.e., lower) respiration, increasing (i.e., more positive, release) net exchange in HT and IM, and decreasing (i.e., more negative, uptake) net exchange in natural and untreated. Although CH₄ emission generally increased, there was no significant relationship with water table.

A total of 110 CH₄ fluxes passed quality control and were included for 2019. Fluxes ranged from 65.8 mg CH₄ m⁻² d⁻¹ in natural to 775.7 mg CH₄ m⁻² d⁻¹ in IM and were generally higher from hollows than hummocks (Figure 3.2). However, CH₄ flux was not significantly different between treatments or microforms and there was no significant treatment and microform interaction (Table 3.2). In the 2020 dataset, 306 CH₄ fluxes were included in the analysis. There was no significant effect from treatment and across all microform-treatment combinations only natural hummocks (122.2 mg CH₄ m⁻² d⁻¹) and IM hollows (1282.2 mg CH₄ m⁻² d⁻¹) were significantly different. Ebullition was captured in 23 flux measurements (Table S2): 2 in untreated, 1 HT hummocks, 5 HT hollows, 1 IM hummocks, and 14 IM hollows. Average ebullitive flux was 337.9 mg CH₄ m⁻² d⁻¹ in untreated, 349.0 mg CH₄ m⁻² d⁻¹ in HT, and 1752.2 mg CH₄ m⁻² d⁻¹ in IM, with no measured ebullition at natural plots.

Across the full 2019-20 dataset, higher productivity (i.e., more negative GEP) was significantly related to deeper water tables both alone ($F_{1,293}=34.0217$, $p<0.0001$) and in interaction with treatment ($F_{3,293}=3.4811$, $p=0.0163$). There were no significant differences in slope between HT and IM, which had the steepest slopes and were significantly less productive than untreated and natural when water tables were above -20 cm (Figure 3.3). Ecosystem respiration significantly decreased with shallower water tables ($F_{1,293}=96.6286$, $p<0.0001$) and although treatment did not have a significant effect on respiration, the interaction with treatment did ($F_{3,293}=4.6875$, $p=0.0033$), resulting in similar, steeper slopes for HT and IM, followed by untreated and natural (Figure 3.3). Overall, the effect of water table ($F_{1,293}=4.4572$, $p=0.0356$) on NEE was significant, resulted in increasing net CO₂ uptake (i.e., more negative) in natural and untreated with shallower water table, and decreasing net productivity in HT and IM. Slopes were very shallow and only untreated and IM were significantly different (Figure 3.3). Water table position did not significantly predict CH₄ flux, but flux did generally increase with shallower water table ($F_{1,378}=2.812$, $p=0.0944$); there was also no significant interaction between treatment and water table ($F_{3,378}=0.745$, $p=0.5258$).

Productivity was significantly greater (i.e., became more negative) with warmer 10 cm soil temperature ($F_{1,269}=28.4466$, $p<0.0001$) but there was no significant interaction with treatment ($F_{3,269}=2.5238$, $p=0.0581$). Soil temperature alone ($F_{1,269}=36.5174$, $p<0.0001$) also had a significant effect on ER, leading to higher respiration with warmer soils. The overall impact of soil temperature on NEE was significant ($F_{1,269}=8.5322$, $p=0.0038$) with greater net uptake from warmer soils, and there was no significant interaction with treatment ($F_{3,269}=1.8506$, $p=0.1383$). Higher soil temperatures also resulted in significantly higher CH₄ fluxes ($F_{1,349}=12.239$, $p=0.0005$) with no significant treatment interaction.

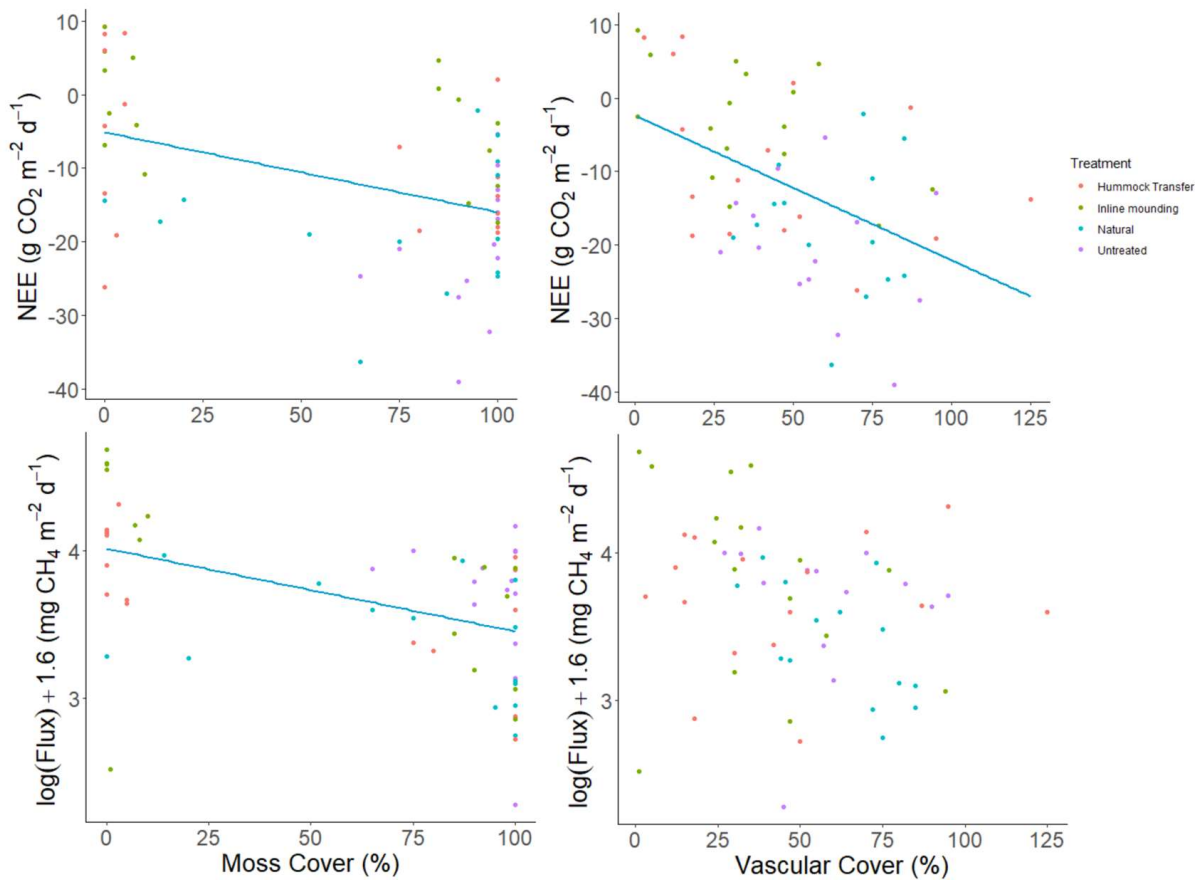


Figure 3.4 Relationships between moss and vascular percent cover on net ecosystem exchange (NEE) and CH_4 . Increasing moss cover resulted in increasing (i.e., more negative, uptake) NEE and decreasing CH_4 emissions. Increasing vascular cover resulted in increasing (i.e., more negative, uptake) NEE and had no significant relationship with CH_4 emission.

Both moss and vascular plant cover significantly explained variation in C fluxes (Figure 3.4), with no significant interactions with treatment in any case. GEP significantly increased (i.e., became more negative; $F_{1,52}=36.3839$, $p<0.0001$) with higher cover of mosses and increasing vascular plant cover ($F_{1,52}=28.6311$, $p<0.0001$). Respiration significantly increased with both increasing moss ($F_{1,52}=52.5004$, $p<0.0001$) and vascular ($F_{1,52}=19.4628$, $p<0.0001$) cover. NEE also significantly increased with increasing moss ($F_{1,52}=15.4873$, $p=0.0002$) and vascular ($F_{1,52}=21.1376$, $p<0.0001$) cover. Across all treatments, CH_4 fluxes decreased with increasing moss cover ($F_{1,52}=16.0536$, $p=0.0001$; Fig 3.4). Emission of CH_4 generally decreased with increasing vascular cover although there were no significant effects.

3.4 Discussion

3.4.1 Environmental conditions

The creation of seismic lines through our study site altered water tables, vegetation composition, CO₂ production and uptake, and CH₄ emission. Though not significantly different, average water tables in untreated sections were approximately 5 cm closer to the surface than in the undisturbed fen, leading to wetter conditions overall (Table 3.1). This was as expected as previous studies have shown depression in elevation and flattening of hummocks on lines (Stevenson et al. 2019) and concurrent rise in water table (e.g., Lovitt et al., 2018). Additionally, the study area received more than the average total annual precipitation from May 01 to August 31 in both years (551 mm and 510 mm for 2019 and 2020 respectively; ACIS 2020). These wet conditions were most noticeable in 2019, when water levels were near or above surface much of the season. Both mounding treatments increased the difference in water table between hummocks and hollows compared to untreated, as was intended. Surprisingly, there was very little difference among treatments in soil temperature at 10 cm below surface in both years, contrary to what was found by Strack et al. (2018) who reported warmer soils on seismic lines than the adjacent forested peatlands. The wet conditions and surface water flow through the fen likely limited the development of local temperature differences.

Moss cover was higher than vascular plant cover in both years, and although not significant, was higher on the untreated lines than in natural. Moss cover had a significant negative relationship with increasing water tables, and flooding has been shown to negatively impact some moss species (Granath et al. 2010), likely explaining the increase of moss cover in 2020 vs 2019, especially in natural hollows where water table dropped from 6 cm above surface to 4 cm below. Contrary to previous findings (Strack et al. 2018; Davidson et al. 2021), vascular plant cover was not significantly higher on the lines than the surrounding natural fen (Table 3.1), except for low spots on untreated lines in 2019, when they were wetter than hummocks in both untreated and natural but drier than natural hollows. This may be a result of differences in peatland types across studies, highlighting the need for further trials of these techniques. Murray et al. (2021) also found an increase in vascular plant cover versus natural peatland conditions at wet, unmounded controls on oil sands exploration (OSE) well pads but not on drier sites. Lower vascular plant cover can partially be attributed to the lack of woody vegetation, primarily shrubs, on the line, although increased light availability typically leads to higher cover of herbaceous species (Caners and Lieffers 2014; Strack et al. 2018; Murray et al. 2021). An increase on the line of primarily graminoids (e.g., *Carex* spp. and *Juncus* spp.) that have

small stem diameter and lack large, spreading leaves (e.g., *Menyanthes trifoliata*, *Caltha palustris*), may explain some of the decrease in cover, as may the difference in precipitation and water levels between the two years. As water levels drop hummocks become drier, and the deepest water tables may not be accessible for some plants, while hollows become less flooded, allowing for more water-intolerant species to flourish while still sustaining water-loving species with shallow water tables. In natural areas, this maintains a steady cover, though it fluctuates over time; on untreated lines, however, consistently shallow water tables may prevent water-intolerant species survival even in drier years.

Moss cover did not significantly change from natural and untreated areas on hummocks in either mounding treatment, but both increased from 2019 to 2020 (Table 3.1). While vascular plant cover was approximately half that of natural plots in 2019, it had recovered to similar levels as natural and untreated by 2020. Both the decrease and recovery can be attributed to our restoration techniques; disturbance during restoration work caused the loss of some vegetation, while not inverting the mounds maintained much of the existing vegetation, roots, and seedbank, allowing for better growth the following year. This contrasts with previous mounding techniques that invert the mounds and leave bare peat and/or mineral soil exposed. Murray et al. (2021) found only 19 % moss and 21 % vascular plant cover on inverted mounds five and six years following mounding. Moss cover was near zero in hollows in both years, but approximately one third the vascular plant cover of natural was maintained in IM hollows and two thirds in HT hollows in the first year. By 2020, vascular cover in HT hollows was similar to natural and untreated areas; after five years vascular cover was still only 15 % in Murray et al.'s (2021) hollows. The shallow depth of our hollows, particularly in HT where the natural hummock accounted for most of the height of the removed peat, not only left shallower pools of water, but also left some roots, rhizomes, and seedbank in place for recovery to begin immediately.

3.4.2 Changes in carbon exchange on untreated seismic lines

Carbon dioxide fluxes were not significantly different on the untreated lines compared to natural reference plots in either year (Table 3.2), but there was generally greater productivity and net CO₂ uptake on the line (Figure 3.2). Higher GEP (i.e., more negative) on the lines could be due to the lack of microtopography and resulting water tables; following high precipitation flooding was shallower in untreated sections than natural hollows, and during drier periods water table was not as far below ground. The difference in water table depths between years on untreated lines was also much less than

in natural, leading to a steadier water supply for plants; removal of trees and shrubs likely removes some of the competition for water on the lines as well. Moreover, removal of tree and shrub cover increases solar radiation reaching the peat surface on the seismic line and higher temperature and longer growing seasons have been shown to increase GEP (Lund et al. 2010). Davidson et al. (2021, preprint) found that peatland seismic lines greened up earlier and had higher GEP than natural reference sites. Although ER was higher from untreated lines, there was no significant difference from the undisturbed fen in either year, or between microforms. ER decreased as water levels rose and increased with warmer temperature; an increase in soil temperature of as little as 1° C has been shown to increase respiration (Walker et al. 2016). Warmer soils on the line spurs photosynthesis, the associated autotrophic respiration from roots and mycorrhizae (Ryan and Law 2005) and heterotrophic respiration of microbial and enzyme communities (Pendall et al. 2004). Rising water levels slow microbial growth and activity, leading to a decrease in respiration, as in natural hollows in 2019 (Figure 3.3). ER rates in hummocks also increase as CH₄ diffuses through the acrotelm and is converted to CO₂ by methanotrophs (Robroek et al. 2015). Overall, this site is consistent with results from Strack et al. (2018) and Davidson et al. (2021) who both found significantly higher productivity and NEE on seismic lines with increased total vascular cover; however, as total vascular cover was not significantly different from natural, species composition or functional groups may be a larger component than was studied here

Although neither soil temperature nor distance of water table from surface were significantly different in natural or untreated areas, warmer, wetter soils on the untreated lines favoured the production of CH₄ as methanogenic microbial activity increased under anoxic conditions. In addition to reaching the atmosphere via diffusion, some plants, including many sedge and rush species, including *Eriophorum vaginatum* L. found on the site, mediate the movement of CH₄ directly from peat to atmosphere (Carmichael et al. 2014), bypassing much of the potential oxidation in the peat profile. Ebullition events have also been shown to increase with rising soil temperatures (Fechner-Levy and Hemond 1996) and shallower water table depths (Lai 2009) but were only captured in 2/82 (2.4 %) fluxes of untreated lines and never from natural areas. Shallower water tables on the untreated lines reduced the depth or presence of an oxic layer, likely increasing methanogen activity and production of CH₄, while the lack of woody roots and organic matter led to a change in peat composition or density that allows for increased diffusion of CH₄ to the atmosphere. These results reflect those of Strack et al. (2018), who found GEP and NEE improved, ER varied little, and CH₄

increased on a winter road versus the adjacent natural wooded fen, although with more significant differences than on our site.

3.4.3 Impacts of restoration treatments on CO₂ and CH₄ exchange

There were few significant differences between IM and HT or between HT and natural and untreated areas in either year, although GEP approximately doubled from 2019 to 2020 in both mounding treatments (Figure 3.2), mirroring the recovery of vascular plant cover (Table 3.1). Low productivity on IM hummocks was largely the result of disturbance during restoration and root systems that were adapted to saturated conditions suddenly being moved above the ground surface, resulting in water level differences of ~10 cm. Hummocks may not have yet fully integrated and connected with the underlying surface, preventing water from rising up the peat column to the rooting zone. Removal of vegetation in HT hollows was the leading factor in low GEP; however, because we targeted established natural hummocks to transfer, resulting hollows were much shallower, with water levels and soil temperatures in line with those of natural hollows. Many roots, small plants, and some mosses were left behind, and both mosses and vascular species were able to move in from the edges. ER was not significantly different in IM or HT than natural or untreated, and only differed significantly between microforms in 2020. Hollows in IM and HT had decreased vegetation cover and water levels at or above surface both years, which favours CH₄ production (Chimner et al. 2016; Strack et al. 2018). ER from hummocks in IM and HT, however, was higher than natural and untreated in both years (Figure 3.2), likely due to a thicker oxic layer in the rooting zone (Pypker 2013) that resulted in increasing microbial activity and organic matter decomposition. Overall, decreased NEE (i.e., less negative) in the two mounding treatments is due to the loss and disturbance of vegetation and surface peat soils, shown by lower productivity and increased respiration.

While CH₄ emissions in both treatments were not significantly different than natural or untreated plots in either year, mounding increased CH₄ emission overall (Figure 3.2). At 585 mg CH₄ m⁻²d⁻¹ in 2019 and 775 mg CH₄ m⁻²d⁻¹, emissions were five to eight times higher in IM than natural. Presumably, some of the increase came from diffusion and plant mediated transport; however, ebullition events were much more frequent, occurring in 15/70 (21 %) of IM fluxes in 2020, predominantly from hollows. In contrast, only 6/79 (7.6 %) HT fluxes contained ebullition events, possibly due to the shallower hollows formed in this treatment.

3.4.4 Implications for management

When considering C fluxes measured in the study plots, these results include only CO₂ and CH₄ fluxes from the hummocks and hollows created during the treatment, but not the entire treatment area. By assessing the density and area of hummocks and hollows and using the values from untreated areas to represent the flat (i.e., untreated) parts of HT and IM areas, mean treatment CO₂ and CH₄ fluxes can be estimated (Table 3.3). Total treatment NEE increased in all four areas from 2019 to 2020, and untreated had the highest net CO₂ uptake in both years at 20 and 21 g CO₂ m⁻²d⁻¹. In 2019, natural, HT, and IM all averaged 15 g CO₂ m⁻²d⁻¹, and in 2020 natural was only slightly higher than HT and IM at 19, 18, and 17 g CO₂ m⁻²d⁻¹, respectively. CH₄ emission was also higher across treatments in 2020 than 2019 despite it being a drier year. Both years followed the same pattern, with natural emitting the least CH₄ (64 and 139 mg CH₄ m⁻²d⁻¹), followed by untreated (135 and 234 mg CH₄ m⁻²d⁻¹), HT (169 and 260 mg CH₄ m⁻²d⁻¹), and IM (280 and 438 mg CH₄ m⁻²d⁻¹). This is in line with Strack et al.'s (2019) modeling of increased CH₄ emissions on seismic lines due to shallower water tables.

Notably, we did not look at the contribution of trees to C emissions and uptake, which could potentially shift fluxes, although some tree and shrub roots inevitably contributed to ER of natural collars and of HT hollows, which were located outside of the defined edges of the lines. Nor did we look at the potential influences of tree seedlings planted across the site; however, planting avoided any features with collars, so they did not interfere either. Taking tree and shrub cover into account, the natural peatlands actually have a higher NEE than measured; Murray et al. (2021) estimated trees and shrubs in a wooded moderately rich fen captured an additional 50 g C m⁻²y⁻¹ through total above and belowground productivity.

Table 3.3 Proportion of treatment areas covered by hummocks, hollows, and flat, estimated net ecosystem exchange^a (g CO₂ m⁻²d⁻¹), and estimated total methane flux (mg CH₄ m⁻²d⁻¹).

Treatment	Proportion of treatment area (%)			Estimated Total NEE ^a	Estimated Total CH ₄
	Hummocks	Hollows	Flat		
Natural	50.0	50.0		-19.3	138.8
Untreated			100.0	-21.1	234.3
Hummock Transfer	1.3	2.4	96.3	-20.7	237.1
Inline Mounding	0.6	1.6	97.8	-20.7	252.8

^aNet ecosystem exchange represents full sun conditions and includes only understory plant community. It should not be interpreted as a growing season rate.

These results indicate that mounding results in a decline in CO₂ uptake and increase in CH₄ emission, at least in the first two years post-restoration, largely due to loss of productivity and high CH₄ in the created hollows. However, given the low density of mounds applied in these treatments, changes across the entire treatment area were small. Restoration of seismic lines and exploration well pads has, until this point, typically involved inverted mounds at very high densities of 1000 – 1200 mounds/ha (e.g., Golder 2015; Murray et al. 2021). In comparison, our mounds were not inverted and were applied at a density of 155 mounds/ha. It is important that lower mounding densities are considered going forward to maintain untreated surfaces and manage not only production of CO₂ and CH₄, but also maintain uptake of CO₂ from the plant community established on the lines, although the best density is as yet uncertain and may vary between peatland types. Over time C uptake through the re-establishment and growth of trees and woody species on the line may compensate for increased ER and CH₄, but the time needed for this transition remains unclear largely due to the young age of most restoration projects. Therefore, regardless of tree establishment, increased CH₄ emissions from hollows are likely to persist for years. For example, Murray et al. (2021) measured CH₄ fluxes of 14.3 g CH₄ m⁻²y⁻¹ (39.2 mg CH₄ m⁻²d⁻¹) from hollows 9 years after restoration, compared to 1.4 g CH₄ m⁻²y⁻¹ (3.8 mg CH₄ m⁻²d⁻¹) from natural and 6.2 g CH₄ m⁻²y⁻¹ (16.8 mg CH₄ m⁻²d⁻¹) from untreated.

The results from our study confirm the need for further data on C exchange on peatland seismic lines and potential outcomes of restoration. As this is the first study of its kind, measurements will need to be collected in the coming years to determine the long-term impacts on C emissions from the restoration treatments and which method results in the best outcomes for tree establishment and growth as well as ecosystem C and greenhouse gas exchange. Although untreated areas had the highest NEE (i.e., most negative) both years, by the second year post-restoration the difference

between untreated, natural, and HT had declined, suggesting that with time treated areas may have the same or greater C sink strength as untreated and natural areas. The treatments will also need to be applied and studied across more peatlands of differing hydrologic conditions and vegetation types to develop best management practices across a range of peatland conditions. This may help satisfy the goals of restoration from multiple angles, including reduced time and cost for industry, restoration of habitat and connectiveness for conservation, and reduction of GHG production. Ideally, these practices would put restored seismic lines on pathways to improved function, ultimately helping to mitigate climate change while protecting biodiversity.

Chapter 4: Conclusion

4.1 Summary

Though narrow, seismic lines contribute to the cumulative disturbance of boreal peatlands, many of the impacts are not fully understood. Although there are currently no requirements for restoration, interest has grown as peatlands are important habitat for many species, including the endangered Woodland Caribou. Mounding of peatland seismic lines has been deemed a restoration success by facilitating the re-establishment of trees, but other ecological functions have been overlooked, particularly the impacts on carbon cycling and greenhouse gas exchange. Research reported in this thesis begins to fill this gap.

Untreated seismic lines lacked the distinct hummock-hollow topography of undisturbed peatlands, and this resulted in shallower water tables across the line and a significant reduction in the water table variance between hummocks and hollows. This led to a shift from species that prefer drier conditions to more water-loving species. Overall, though, percent cover of functional groups did not significantly change. However, despite aboveground understory biomass being similar, root biomass on the untreated lines was nearly half that of natural area, a loss of $\sim 1000 \text{ g m}^{-2}$. An increase of sunlight and reduction of competition from removing trees and shrubs on the lines likely contributed to increased uptake of CO_2 as warmer soil temperatures and increased sunlight promote earlier green up and higher GEP (Lund et al. 2010; Davidson et al. 2021). Cumulatively, these changes resulted in slightly higher net CO_2 uptake by the understory plant community on the untreated lines than in natural. Conversely, warmer, wetter conditions on the lines, coupled with plant mediated transport, resulted in a $\sim 75\%$ increase in CH_4 emissions and a slight increase in captured ebullition events. The lack of trees and shrubs on the lines not only vastly reduced standing biomass by $\sim 720 \text{ g}$ but also a yearly uptake of $\sim 50 \text{ g C m}^{-2} \text{ y}^{-1}$ (Murray et al. 2021).

Hummocks transferred onto the line from the adjacent natural peatland brought with them associated species, including *S. fuscum*, and had an increase in the presence of species typically found in natural hollows. Neither total percent cover of vascular plants or bryophytes changed between hummocks on the line and in natural areas, but in hollows vascular cover fell by a third while bryophyte cover more than doubled. Compared to untreated sections, both vascular and bryophyte cover were higher on hummocks, while vascular cover decreased and bryophyte cover increased in hollows. These changes in vascular and bryophyte cover were reflected in the biomass for each

microform and ultimately evened out. Root biomass, however, was much higher in natural, particularly hollows, resulting in $\sim 1000 \text{ g m}^{-2}$ less total biomass in hummock transfer (HT). Biomass between HT and untreated were very similar, with only $\sim 100 \text{ g m}^{-2}$ more total biomass in HT. Generally, CO_2 fluxes were negative (i.e., CO_2 removed from the atmosphere) although lower than both natural and untreated plots. Ebullition events were more frequent in HT hollows than in natural or untreated but ebullitive fluxes (concentration*time) were no different than those of untreated. Though diffusive fluxes were higher in HT than both natural and untreated sections, there were no significant differences.

Overall, inline mounding (IM) had fewer species than the other treatments and maintained many of the wetter species found on untreated sections. Forb cover was significantly lower, resulting in total vascular cover of approximately one third of the other treatments, and vascular plant biomass was much lower overall. Despite this, IM had amongst the highest root biomass, below only natural. Net CO_2 exchange was the lowest in IM at half that of HT and less than half of natural and untreated. In the first year IM acted as a small source of CO_2 to the atmosphere, though by the second year it became a slight sink. There were no significant differences in total CH_4 flux from the other treatments, but fluxes from IM hollows were greater than natural hummocks by a factor of ten. At these hollows, ebullition events were most frequent and had the highest flux values, resulting in a total estimated CH_4 nearly double that of natural areas.

4.2 Insights

As traditional inverted mounds are reduced to bare soil and rely on dispersal of seed and propagules for plant recruitment, vegetation establishment is likely to be slow and the potential for the invasion of unwanted species is higher. Our study demonstrated how retaining plant cover can change outcomes immediately: two years after mounding, our site had 48 % and 111 % total vascular plant and 15 % and 31 % total bryophyte cover on IM and HT hummocks, respectively, compared to inverted mounds in a moderate-rich fen that, after three years, had only ~ 35 % percent total vascular cover and ~ 20 % total bryophyte cover (Echiverri et al. 2021). Not only does this loss of plant cover eliminate any uptake of CO_2 but it also increases potential respiration from the formerly anoxic peat. CO_2 and CH_4 exchange have not been measured on inverted mounding seismic lines before but has been reported from oilsands exploration well pads (Murray et al. 2021). By the second year, IM hummocks on our site had a flux of $-3.7 \text{ g C (CO}_2\text{) m}^{-2} \text{ d}^{-1}$ and $0.4 \text{ g C (CH}_4\text{) m}^{-2} \text{ d}^{-1}$, and fluxes at HT hummocks were $-3.9 \text{ g C (CO}_2\text{) m}^{-2} \text{ d}^{-1}$ and $0.15 \text{ g C (CH}_4\text{) m}^{-2} \text{ d}^{-1}$. With 21 % total vascular cover and

22 % bryophyte cover 7 years post-mounding, inverted mounds on OSE sites had a flux of ~ 3 g C (CO₂) m⁻² d⁻¹ and ~ 0.02 g C (CH₄) m⁻² d⁻¹ (Murray et al. 2021). This shows the importance of maintaining vegetation on the lines not only for cover, diversity, and richness, but also for other processes such as CO₂ uptake and carbon storage through biomass production.

Traditionally, mounding of seismic lines has been applied at high densities (1000 – 1200 mounds/ha; Murray et al. 2021) and create large mounds and deep pools. Not only does this disturb almost the entire site anew, but any functions of the unmounded spaces between are lost. Although untreated lines had lower biomass and released more CH₄ than natural, they still provide a significant source of plant species to fill hollows and take up a significant amount of CO₂. Nine years after restoration, pools on mounded well pads released 0.03 g C (CH₄) m⁻² d⁻¹ (Murray et al. 2021), while on our site, IM pools released 1 g C (CH₄) m⁻² d⁻¹ and HT pools released 0.3 g C (CH₄) m⁻² d⁻¹. Even at those lower rates, the dense application of mounds, and in turn hollows, on traditionally mounded sites quickly accumulates. Applying mounding at lower densities, like our 155 mounds/ha, helps to moderate changes across the entire treatment. Additionally, smaller mounds leave smaller, shallower hollows that are more conducive to regeneration from the seed bank and encroachment of the surrounding vegetation and will likely fill in sooner, further reducing CH₄ production as those hotspots shrink. However, smaller mounds are also closer to the water table and could reduce tree growth. Further research on tree survival and regeneration on IM and HT, particularly on these smaller sized hummocks is needed.

4.3 Conclusion

As this study is the first to look at plot-scale above- and belowground biomass, CO₂ and CH₄ fluxes on unrestored and restored seismic lines, and use new methods of mounding, further study is required. This should include application and study of these methods over time across a range of peatlands with differing hydrologic conditions and vegetation types, and an in-depth study of traditional inverted mounding for comparison. The different types of seismic lines requiring restoration should also be considered, i.e., wide legacy lines versus low impact, as the methods used during creation and the width of the lines may impact passive restoration and the outcomes of mounding. Finally, as tree recovery remains an important piece of biomass and carbon cycling, outcomes of natural regeneration and planting on restored lines should be studied. By understanding these components, integrated policies and procedures that support multiple facets of peatland seismic line restoration can be created.

Although the same process, our two mounding treatments differed in where the mounds came from and consequently where hollows were created. While there were differences in species composition, cover, and fluxes between the two treatments and between microforms, overall, biomass, net CO₂ flux, and total CH₄ flux were similar. Compared to natural and untreated, however, IM was much less productive, had much higher CH₄ fluxes, and a substantial increase in ebullition events and concentrations. Much of the difference came from IM hollows which were deeper, wetter, and had less vegetation than HT hollows on average, all conditions that are linked to the changes in CO₂ and CH₄ exchange. Given this, HT seems to be the better option on our site, at least in the first two years.

As this study did not include C processes of the canopy and was limited to the first two years post-restoration, there is no clear answer as to whether restoration of seismic lines is necessary or viable from an ecosystem C uptake perspective at this point. Based on the results of understory C fluxes, restoration is likely not needed but remains important for improving habitat; thus, if our methods can improve the outcome for multiple ecosystem functions, they should be considered. While the continued use of low impact seismic lines will reduce future peatland disturbance, there are many legacy lines left on the landscape that require restoration. Traditional mounding methods, though successful in re-establishing trees, negate much of the natural progression of ecosystem recovery already taking place on the untreated lines, leading to decreases in vegetation cover and productivity and creating CH₄ hotspots in the pools. By transitioning to the HT technique, woody vegetation is rapidly introduced to the line, vegetation and productivity remains, and fewer, shallower hollows reduce the number of CH₄ hotspots and the length of time they are active. Cumulatively, this will reduce the impacts of disturbing to restore, as well as reduce the costs of restoration, hopefully leading to best practices and meaningful policy changes.

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Appendix 1. Average CO₂ and CH₄ at each plot.

Collar	Treatment	Microform	NEE (g CO ₂ m ⁻² d ⁻¹)		ER (g CO ₂ m ⁻² d ⁻¹)		GEP (g CO ₂ m ⁻² d ⁻¹)		CH ₄ (mg CH ₄ m ⁻² d ⁻¹)	
			2019	2020	2019	2020	2019	2020	2019	2020
12U1a	Untreated	Hummock	-5.4	-32.3	13.5	17	-18.9	-49.3	45.5	148.2
12U1b	Untreated	Hollow	-12.9	-22.3	13	21.6	-25.8	-43.8	141.3	77.8
12U2a	Untreated	Hummock	-9.5	-20.3	19.4	19.6	-29	-39.9	8.3	198.8
12U2b	Untreated	Hollow		-25.4		15.4		-40.8		223.5
13U1a	Untreated	Hummock	-24.7	-14.3	10.6	15.4	-35.3	-29.7	259.6	259.3
13U1b	Untreated	Hollow	-27.5	-16.1	23.5	13.1	-51	-29.2	144.1	376.5
13U2a	Untreated	Hummock		-16.9		18.3		-35.1		260.9
13U2b	Untreated	Hollow	-39	-21	18.4	11.6	-57.3	-39.8	168.9	281.2
14N1a	Natural	Hummock	-10.9	-27	11.2	15.3	-22.1	-42.3	37.7	228.5
14N1b	Natural	Hollow	-14.3	-19	4.7	7.4	-18.5	-26.4	52.1	163.2
14N2a	Natural	Hummock		-9.1		20.6		-29.7		165.9
14N2b	Natural	Hollow	-14.3	-17.2	4.8	17.5	-19.1	-34.7	98.2	240.2
15N1a	Natural	Hummock	-5.4	-2.2	14.5	14	-20	-16.2	26	25.6
15N1b	Natural	Hollow	-19.9	-36.3	11.3	14.8	-31.2	-51.1	134.7	113
15N2a	Natural	Hummock	-24.7	-24.1	12.9	21.2	-37.6	-44.3	42.1	41.4
15N2b	Natural	Hollow		-19.6		15		-34.6		102.6
1I1a	Inline Mounding	Hummock	0.8	-14.7	15.7	23.1	-14.8	-37.9	317.5	218.1
1I1b	Inline Mounding	Hollow	9.2	6	6.5	6.2	2.8	-0.2	2158.7	1833.2
1I2a	Inline Mounding	Hummock	-0.6	-7.7	10.5	18.1	-11.1	-25.7	52.4	137.4
1I2b	Inline Mounding	Hollow	3.3	-6.8	5.7	7.1	-2.4	-13.9	1147.3	2250.8
2H1a	Hummock Transfer	Hummock	-18.5	-11.1	13.6	15.5	-32.1	-26.7	74.1	237
2H1b	Hummock Transfer	Hollow	8.4	-4.3	6.9	7.8	1.5	-12.1	153.5	444.6
2H2a	Hummock Transfer	Hummock	-7.1	-16.1	7.3	21.4	-14.4	-37.5	97.7	278.8
2H2b	Hummock Transfer	Hollow	6	-13.4	8.1	10.9	-2.1	-24.3	435.1	458.6
6H1a	Hummock Transfer	Hummock	2	-13.8	20.8	24.1	-18.8	-37.9	24	111.2
6H1b	Hummock Transfer	Hollow	8.3	-1.3	1.2	5.4	7	-6.7	184.4	113.3
6H2a	Hummock Transfer	Hummock	-18.7	-18	19.6	27.9	-38.3	-45.9	20.3	117.7
6H2b	Hummock Transfer	Hollow	-19.1	-26.2	19	14.1	-38.1	-40.3	570.6	386.2
7I1a	Inline Mounding	Hummock	4.7	-17.4	17.8	23.1	-13.1	-40.5	88.4	223.1
7I1b	Inline Mounding	Hollow	-4.1	-10.9	13.8	4.5	-17.9	-15.4	597.4	556.1
7I2a	Inline Mounding	Hummock	-3.9	-12.4	8.7	17.2	-22.6	-29.6	353.2	56.9
7I2b	Inline Mounding	Hollow	-2.5	5.1	4.9	6.3	-7.4	-1.2	41.3	590

Appendix 2. Ebullition events and contribution to CH₄ in 2020.

Treatment	Fluxes with Ebullition # (%)	Mean Diffusive Flux (mg CH ₄ m ⁻² d ⁻¹)	Mean Ebullitive Flux (g CO ₂ m ⁻² d ⁻¹)
Natural	0		
Hummock	0		
Hollow	0		
Untreated	2 (0.7)		337.9
Hummock	0		
Hollow	2 (2.4)	299.7	337.9
Hummock			
Transfer	6 (2)		349
Hummock	1 (1.3)	156.1	68
Hollow	5 (6.3)	324.4	629.9
Inline Mounding	15 (4.9)		1752.2
Hummock	1 (1.4)	418.7	217.8
Hollow	14 (20)	1043.1	3286.6