

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

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Research Article

Keywords: Peatland restoration, seismic lines, mounding, carbon dioxide, methane

Posted Date: August 13th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-759056/v1>

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Version of Record: A version of this preprint was published at Wetlands Ecology and Management on February 1st, 2022. See the published version at <https://doi.org/10.1007/s11273-022-09858-4>.

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. This study looked at two mounding treatments and compared carbon dioxide and methane fluxes to untreated lines and natural reference areas in the first two years post-restoration. 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 gCO₂m⁻²d⁻¹, and created areas of increased methane emissions, including an increase in the contribution of ebullition, of up to 2000 mgCH₄m⁻²d⁻¹. Further research on this site to assess the longer-term impacts of restoration, as well as application on other sites with varied conditions, will help determine if these restoration practices are effective.

Declarations

Acknowledgements: The authors would like to thank Bin Xu for leading restoration planning and groundwork on the site and Felix Nwaishi for input on study design. We would also like to thank Taylor Vodopija and Miranda Hunter for their help in the field and Blake Haskell for laboratory help.

This study took place on the unceded territories of the peoples of the Treaty 6 region and Métis Nation of Alberta, Region 4, and the authors live and work on the unceded traditional territory of the Attawandaron (Neutral), Anishinaabeg and Haudenosaunee peoples.

Funding: This work was supported by the Government of Canada Environmental Damages Fund, project number EDF-AB-2018c009. Research support was also provided via a Canada Research Chair to Maria Strack.

Conflicts of interest/competing interests: The authors declare no conflicts of interest.

Availability of data and material: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability: Not applicable

Authors' contributions: All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Megan Schmidt. The first draft of the manuscript was written by Megan Schmidt and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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, criss-crossing 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 heterogeneous 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; Benschoter 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 carbon 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.

2. Methods

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 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.

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. Some of the transferred hummocks included woody shrubs and small trees (Figure 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.

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.

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 R²>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 more accurately capture total CH₄ contribution 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 >15ppb 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 R²>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.

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.

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 significant 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. Results

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 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 1).

Table 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 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 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.

3.2 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 gCO₂ m⁻² d⁻¹; IM -10.8 gCO₂ m⁻²d⁻¹) compared to natural (-24.8 gCO₂ m⁻²d⁻¹) and untreated (-36.2 gCO₂ m⁻²d⁻¹) sections. Generally, hummocks were more productive than hollows; however, this difference was only significant in HT (Table 2, Figure 2). Respiration did not differ significantly between any treatments or microforms (Table 2) although it ranged from 9.9 gCO₂ m⁻² d⁻¹ in natural to 16.4 gCO₂ 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 gCO₂ m⁻² d⁻¹; HT -4.8 gCO₂ m⁻² d⁻¹); similarly, natural and untreated did not significantly differ (natural -14.9 gCO₂ m⁻² d⁻¹; untreated -19.8 gCO₂ m⁻² d⁻¹). Both IM hummocks and hollows acted as sources while natural, untreated, and HT acted as sinks (Figure 2).

Table 2. Results from the linear mixed effects models describing effects of treatment, microform, and interactions on CO₂ and CH₄ flux.

In 2020, 247 CO₂ fluxes were included in the dataset. Productivity was significantly lower in IM (-20.5 gCO₂ m⁻² d⁻¹) than untreated (-38.4 gCO₂ m⁻² d⁻¹). Natural and HT were intermediate and did not significantly differ at -34.9 gCO₂ m⁻² d⁻¹ and -28.9 gCO₂ m⁻² d⁻¹, respectively. Microform had no significant effect on GEP (Table 2),

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

with the exception of IM hollows, which were much less productive (i.e., less negative GEP) than any other microform or treatment (Figure 2). Although treatments did not significantly differ in ER (Table 2), hummocks generally respired more than hollows. Respiration from IM and HT hollows ($6.0 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$; $9.5 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$) was significantly lower than from natural and untreated hollows ($13.6 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$; $15.4 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and similarly higher from IM and HT hummocks ($20.4 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$; $22.2 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$) than natural and untreated ($17.8 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$; $17.6 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$). NEE was significantly lower (i.e., less negative, less uptake) in IM ($-7.4 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$) than natural ($-19.3 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$) or untreated ($-21.0 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$), while HT ($-13.0 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$) 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 2).

A total of 110 CH₄ fluxes passed quality control and were included for 2019. Fluxes ranged from $65.8 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ in natural to $775.7 \text{ mgCH}_4 \text{ m}^{-2} \text{ d}^{-1}$ in IM and were generally higher from hollows than hummocks

(Figure 2). However, CH₄ flux was not significantly different between treatments or microforms and there was no significant treatment and microform interaction (Table 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 mgCH₄ m⁻² d⁻¹) and IM hollows (1282.2 mgCH₄ 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 mgCH₄ m⁻² d⁻¹ in untreated, 349.0 mgCH₄ m⁻² d⁻¹ in HT, and 1752.2 mgCH₄ 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). 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). 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). 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 ($F_{1,269}=28.4466$, $p<.0001$) 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.

Both moss and vascular plant cover significantly explained variation in C fluxes (Figure 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, CH₄ fluxes decreased with increasing moss cover ($F_{1,52}=16.0536$, $p=0.0001$) (**Fig x**). Emission of CH₄ generally decreased with increasing vascular cover although there were no significant effects.

4. Discussion

4.1 Environmental Conditions

The creation of seismic lines through our study site altered water tables, vegetation composition, and CO₂ and CH₄ production and 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 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 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. 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 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.

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 2), but there was generally greater productivity and net CO₂ uptake on the line (Figure 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). ER rates in hummocks also increase as CH₄ diffuses through the acrotelm and is converted to CO₂ by methanotrophs (Robroek et al. 2015). Overall, increased NEE on the lines is due to the changes in plant community, as productivity increases with increasing vascular cover. This 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.

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.

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 2), mirroring the recovery of vascular plant cover (Table 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 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 2). At 585 mgCH₄ m⁻²d⁻¹ in 2019 and 775 mgCH₄ 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.

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). 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 gCO₂ m⁻² d⁻¹. In 2019, natural, HT, and IM all averaged 15 gCO₂ m⁻² d⁻¹, and in 2020 natural was only slightly higher than HT and IM at 19, 18, and 17 gCO₂ m⁻² d⁻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 mgCH₄ m⁻² d⁻¹), followed by untreated (135 and 234 mgCH₄ m⁻² d⁻¹), HT (169 and 260 mgCH₄ m⁻² d⁻¹), and IM (280 and 438 mgCH₄ m⁻² d⁻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 gC m⁻² y⁻¹ through total above and belowground productivity.

Table 3. Proportion of treatment areas covered by hummocks, hollows, and flat, estimated net ecosystem exchange^a (gCO₂ m⁻²d⁻¹), and estimated total methane flux (mgCH₄ 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. 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 gCH₄ m⁻²y⁻¹ (39.2 mgCH₄ m⁻²d⁻¹) from hollows 9 years after restoration, compared to 1.4 gCH₄m⁻²y⁻¹ (3.8 mgCH₄m⁻²d⁻¹) from natural and 6.2 gCH₄m⁻²y⁻¹ (16.8 mgCH₄m⁻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.

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Figures

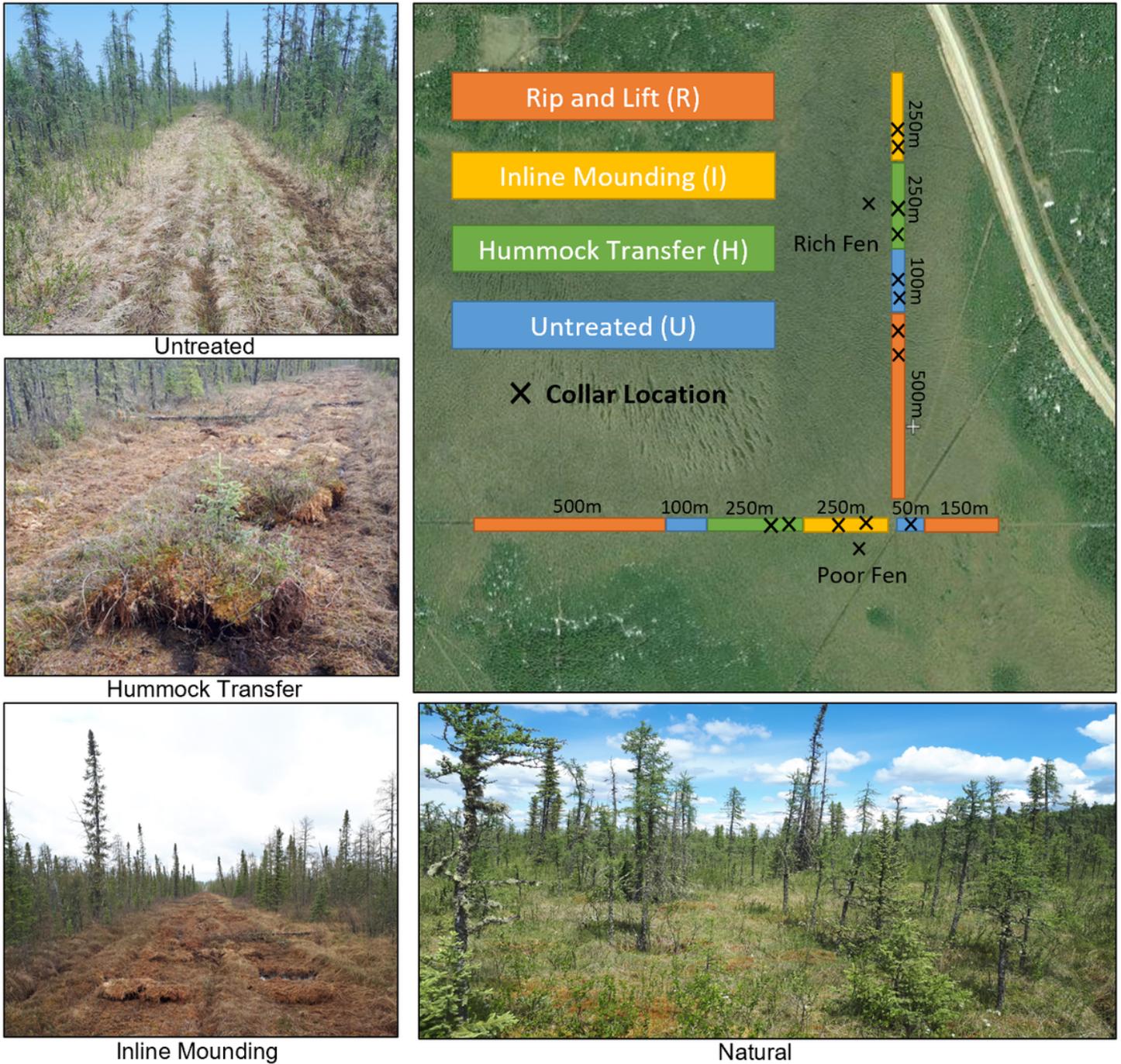


Figure 1

Study site with treatments, locations of collars, and photographs of the four treatments. Rip and lift restoration method was not measured in this study.

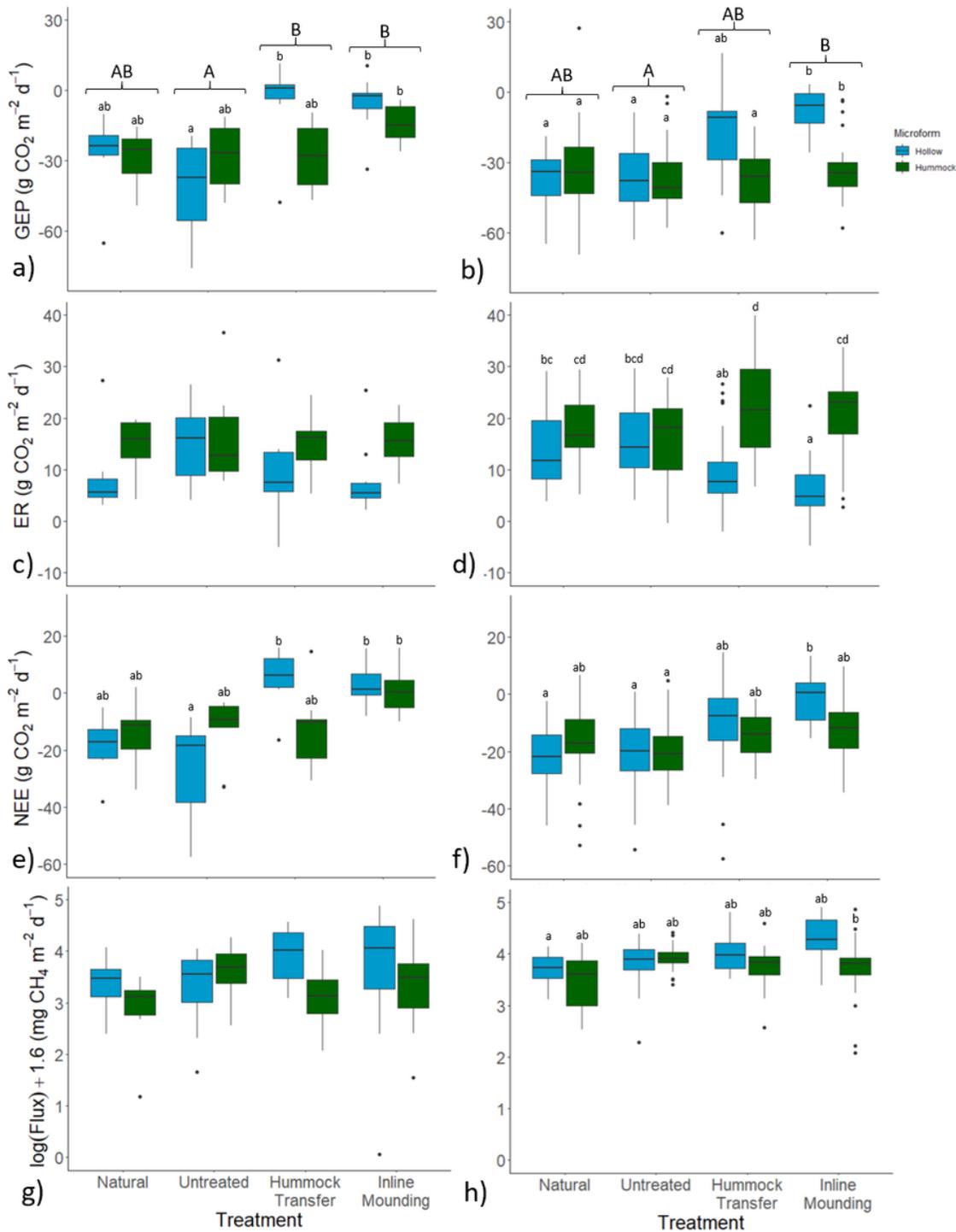


Figure 2

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.

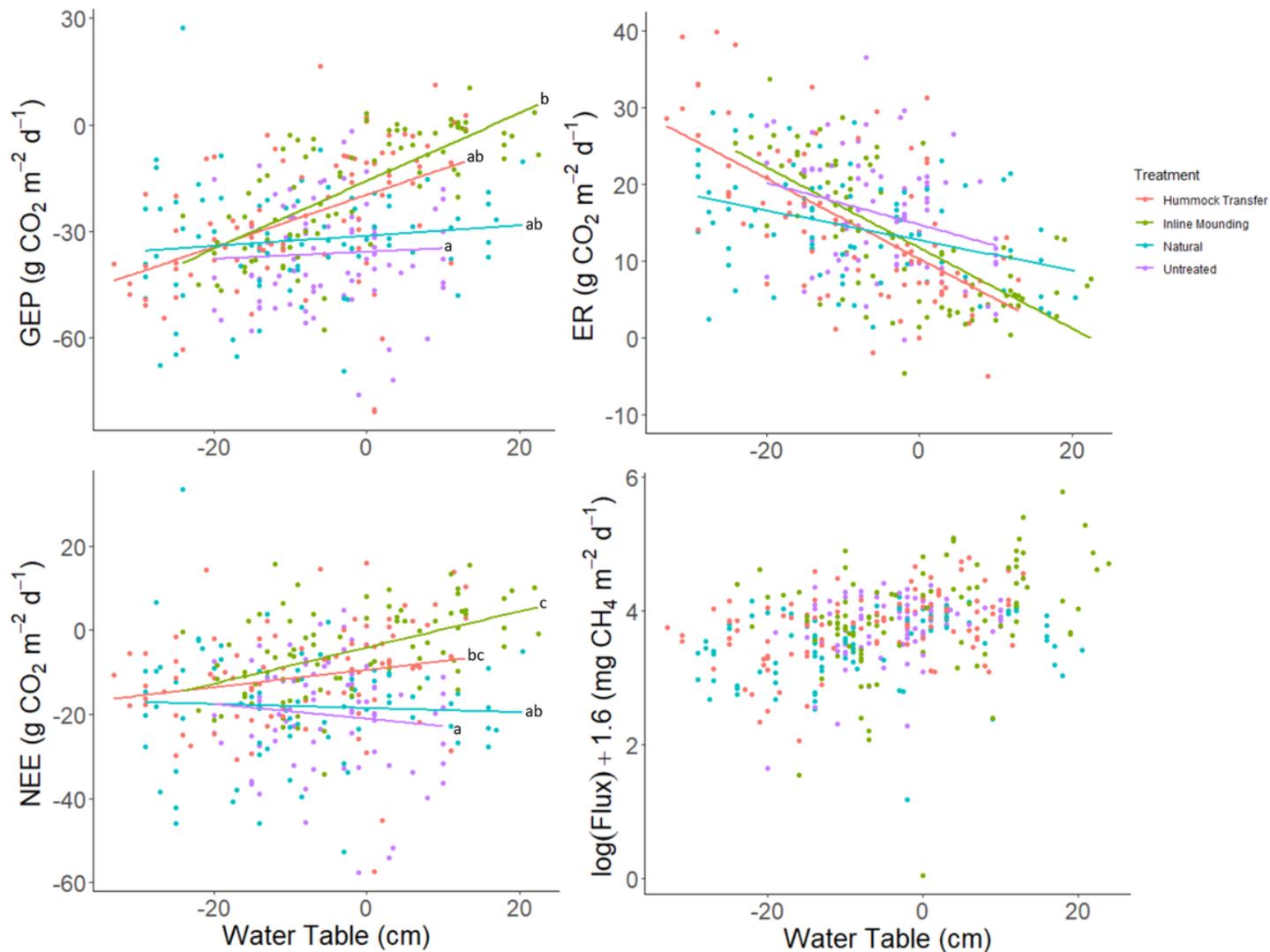


Figure 3

Relationship between water table (cm) and CO₂ and CH₄- across both hummocks and hollows.

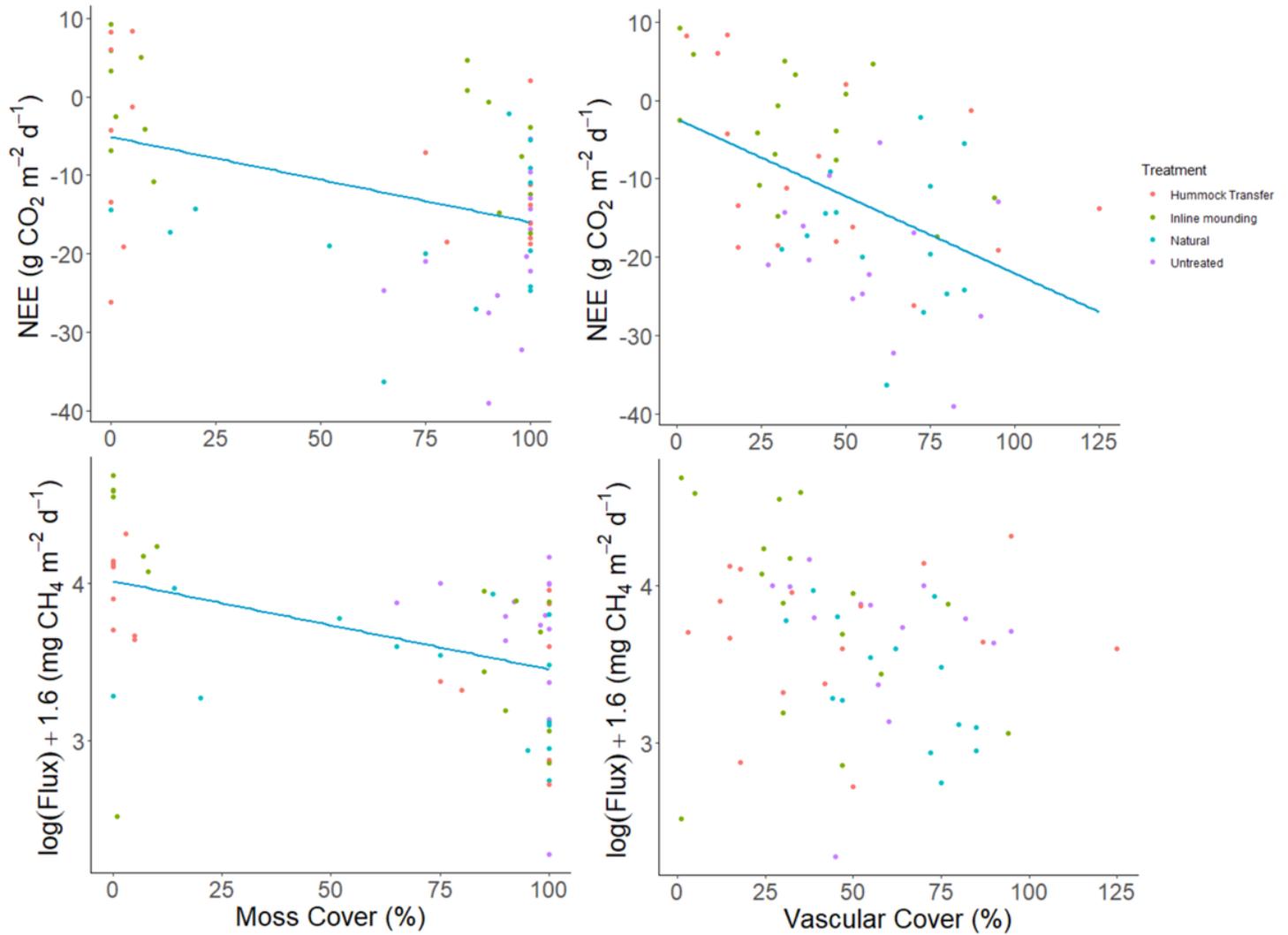


Figure 4

Relationships between moss and vascular percent cover on net ecosystem exchange (NEE) and CH₄.

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