

RESEARCH ARTICLE

Environmental drivers of gaseous carbon fluxes in drained and rewetted Minnesota peatlands, U. S. A.

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Abstract

Introduction: Rewetting shows promise for mitigating carbon loss from drained peatlands. However, knowledge gaps remain in rewetting impacts on gaseous carbon fluxes and factors affecting rewetting success, especially in Minnesota and the Upper Midwest, United States, despite abundant degraded peatlands presenting restoration opportunities.

Objectives: This study fills knowledge gaps in carbon flux from partially drained and rewetted Minnesota peatlands and quantifies environmental drivers of gaseous carbon fluxes to better estimate peatland carbon flux throughout Minnesota and the region.

Methods: We paired chamber-based ecosystem respiration (R_{eco}), net ecosystem exchange (NEE), and methane (CH_4) flux measurements with measurements of environmental variables. We used a linear mixed-effects model comparison approach to identify important environmental drivers of gaseous carbon flux.

Results: Overall, R_{eco} and NEE were lower and CH_4 fluxes higher at the rewetted site versus the drained site (4.42 vs. 11.21 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, 2.57 versus 5.26 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and 18.69 versus 3.58 $\text{nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$, respectively). Open water produced extremely high CH_4 fluxes at both sites. Water table depth, sphagnum cover, grass/sedge cover, restoration status, and pH predicted CH_4 flux; sphagnum cover, soil temperature, and pH predicted R_{eco} ; and sphagnum cover, restoration status, and soil temperature predicted NEE.

Conclusions: The results add to a growing body of research demonstrating peatland rewetting effects on carbon fluxes, allowing comparison of Minnesota drainage-impacted peatland fluxes to global measurements. Additionally, strong associations identified between field-measured environmental characteristics and gaseous carbon fluxes may aid in scaling flux estimates.

Implications for Practice: This study significantly expands measurements of gaseous carbon fluxes in partially drained and rewetted Minnesota peatlands, which were previously poorly represented. Such measurements are essential to support efforts to promote implementation of protection and restoration. High open water methane (CH_4) flux measurements suggest that CH_4 flux reductions from eliminating drainage ditch open water during restoration could offset a substantial portion of rewetting-associated soil CH_4 flux and demonstrate the importance of restoration practices that limit open water areas. Quantitative relationships between environmental variables and peatland carbon fluxes allow for estimation of fluxes without direct measurement, potentially providing a tool for scaling estimates.

Key words: carbon dioxide, drainage ditch, ecosystem respiration, methane, peatland restoration, vegetation

Introduction

Recent research suggests that protecting intact peatlands and restoring degraded peatlands globally is important for mitigating climate change by preserving carbon stocks and potentially restoring carbon sequestration (Nugent et al. 2019; Günther et al. 2020). Globally, peatlands play a key role in the carbon cycle, accumulating dense soil carbon stocks over thousands of years as primary production outpaces microbial decomposition due to wet conditions and cool climates in northern latitudes. When undisturbed, peatlands can continue sequestering carbon (Strack et al. 2023), and globally, peatlands hold one third or more of global soil carbon (Yu et al. 2010; Hiederer & Köchy 2011; Strack et al. 2023) despite covering a small fraction of Earth's land area (2.84%) (Xu et al. 2018). However, peatland carbon cycling and stocks are sensitive to disturbances, such as drainage, which can cause rapid release of stored carbon.

Carbon storage and sequestration benefits depend heavily on geography, disturbance, and restoration context, so project prioritization, regulatory policy, and carbon financing to drive

Author contributions: KB led the project team; KB, CL, RK conceptualized the research; MF, KB, CL, RK, DD designed the study; MS managed the project; MF led study implementation, assisted by KB, CL, MS, DD; MF, AE analyzed data, created figures, and drafted the manuscript; all authors contributed to editing and revisions.

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doi: 10.1111/rec.70443

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70443/supinfo>

peatland protection and restoration require regionally specific peatland carbon flux estimates. However, accurately measuring carbon benefits of peatland restoration and protection is costly and logistically difficult due to the peatlands' often-remote location and highly heterogeneous nature, leaving large knowledge gaps around management impacts on regional-scale peatland carbon flux. Minnesota and the Upper Midwest, United States, host large peatland areas but lack data on altered peatland carbon fluxes. In addition to needs for more regionally specific data, improved quantification of factors driving net climate benefits from different peatland types, sites, and restoration methods is needed to assess restoration cost-effectiveness with respect to climate versus other co-benefits. Better quantification of drivers may also support the development of predictive carbon flux models from readily measured or remotely sensed biophysical data, providing tools for overcoming these challenges.

Drainage lowers water tables and increases the aerated soil volume, leading to accelerated microbial carbon mineralization often exceeding plant production, causing net carbon loss to the atmosphere as carbon dioxide (CO₂) (Landry & Rochefort 2012). More aerobic conditions tend to reduce soil methane (CH₄) emissions, but open water within drainage ditches often creates CH₄ emission hotspots (Gan et al. 2024). Peatland rewetting through ditch blocking or filling to restore near-surface water tables can slow or reverse carbon losses from drained peatlands (Schuster et al. 2024). Reduced CO₂ flux in rewetted peatlands may be accompanied by increased CH₄ emission, which impacts overall climate benefits of peatland rewetting (Abdalla et al. 2016; Wilson et al. 2016; Schuster et al. 2024). Understanding what drives the balance between CO₂ and CH₄ flux is important for assessing the benefits of and prioritizing restoration projects, and implementing rewetting techniques that maximize climate benefits (Zak & McInnes 2022). Despite broad agreement around the net climate benefits of peatland rewetting (Nugent et al. 2019; Günther et al. 2020), at least over longer time horizons (Frolking et al. 2006), many uncertainties remain, especially around restoration impacts on CH₄ emissions; evidence suggests different trajectories for CH₄ flux post-rewetting (Abdalla et al. 2016; Escobar et al. 2022; Darusman et al. 2023). Varying gaseous carbon flux estimates with peatland rewetting and growing interest in restoring Minnesota peatlands for carbon, water storage, water quality, and biodiversity benefits necessitate refined estimates of peatland gaseous carbon fluxes in the state.

Minnesota contains the largest peatland area in the contiguous United States; thousands of hectares of peatlands were drained for agriculture and forestry during the late nineteenth and early twentieth century (King 1980; Hanson 1987). Large areas of drained Minnesota peatlands are no longer used for agriculture or forestry, but drainage ditches continue to alter hydrology, ecosystem functioning, and carbon balance, causing estimated ongoing statewide carbon losses of 0.26–0.40 Mg C ha⁻¹ yr⁻¹, excluding lost carbon sequestration (Krause et al. 2021). Despite large drainage impacts in Minnesota, few studies of gaseous carbon flux under drainage and rewetting have been conducted; our understanding of peatland responses to drainage and rewetting relies largely on studies of Canadian and European peatlands extracted for horticulture or energy experiencing much different

types and levels of disturbance than the partially drained peatlands common in Minnesota, which often contain widely spaced ditches across entire landscapes and lack comparable restoration sites at the landscape scale.

Given needs for regionally relevant field-measured carbon flux data, the objectives of this study were to (1) fill gaps in gaseous carbon flux for drained and rewetted Minnesota peatlands and contextualize fluxes relative to published greenhouse gas emissions factors, and (2) quantify environmental drivers of gaseous carbon fluxes in partially drained and rewetted peatlands to better estimate peatland carbon flux throughout Minnesota and the region. We used chamber-based methods to measure CH₄ and CO₂ fluxes at a drained and a rewetted peatland in northern Minnesota and quantify their relationship with environmental variables, including water level, soil pH, soil temperature, and plant community composition.

Methods

Study Sites

We studied two peatland sites in southwestern Saint Louis County, Minnesota, United States, representing actively drained and recently rewetted peatlands. The climate is humid continental, with nearby National Oceanic and Atmospheric Administration (NOAA) weather stations (FLOODWOOD 3 NE, MN US USC00212842; COTTON, MN US USC00211840) recording mean annual temperature of approximately 3°C and mean annual precipitation of approximately 73 cm, characterized by cold winters (−12°C) and warm summers (17°C) (Palecki et al. 2021). These sites are both classified as Holocene peat (Hobbs & Goebel 1982) and lie within an area of extensive peatlands formed after the last glaciation, within the Tamarack Lowlands ecological subsection according to the Minnesota Department of Natural Resources (MN DNR) Ecological Classification System hierarchy (Minnesota Department of Natural Resources 2003), which is roughly defined by the former lakebeds of Glacial Lake Aitkin and Glacial Lake Upham. The rewetted site formed in the Glacial Lake Upham lakebed, and the drained site formed from a depression created in the Superior moraine (Olson et al. 1979).

Drained Site. The drained site (46.932100°, −92.680413°) is located on MN DNR Forestry land within the Arlberg bog, a large (approximately 4500 ha), partially drained ombrotrophic bog (Olson et al. 1979) with a network of public ditches constructed in 1917 (Judicial ditch 4) and spaced 0.8 (E–W) to 1.6 km (N–S) apart in a grid pattern. Site vegetation shows a gradient relative to the ditch, with high disturbance adjacent to the ditch. In minimally disturbed areas, vegetation consists of sparse stunted Black spruce (*Picea mariana*) and Tamarack (*Larix Laricina*), a shrub layer of Labrador tea (*Rhododendron groenlandicum*), Bog laurel (*Kalmia polifolia*), Bog rosemary (*Andromeda polifolia*), Leatherleaf (*Chamaedaphne calyculata*), and Bog cranberry (*Vaccinium oxycoccos*), grasses/sedges and forbs, including Cottongrass (*Eriophorum* sp.), Sundew (*Drosera* sp.), and Pitcher plant (*Sarracenia purpurea*), and near continuous cover of Sphagnum moss (*Sphagnum* spp.). Tree cover generally increases in height and

density closer to the ditch, while moss cover decreases. Near-ditch groundcover consists primarily of Blueberry (*V. angustifolium*), Blackberry (*Rubus* sp.), with some sedges. Soils are mapped as 60% Lobo, 35% Waskish, and 5% Greenwood, representing deep sphagnum-derived fibric to hemic peat soils typically associated with acidic bogs on previously glaciated landscapes (Soil Survey Staff [n.d.-a](#), [n.d.-b](#)).

Rewetted Site. The rewetted site (47.228843°, -92.577057°) is located within a wetland mitigation bank (approximately 9800 ha), which underwent phased restoration beginning in 2015. Prior to restoration, the site was covered with a drainage ditch network consisting of main ditches spaced approximately 1.6 km apart with a higher density of smaller lateral ditches running E–W on the western side of the site. Many larger ditches contain significant open water throughout the growing season. Vegetation shows a gradient with respect to the drainage ditches. Near-ditch plant communities consist of Canada bluejoint grass (*Calamagrostis canadensis*), sedges (*Carex* spp.), and Rattlesnake manna grass (*Glyceria canadensis*). Farther from the ditch, vegetation transitions into communities characterized by sparse cover of stunted Black spruce and Tamarack, a shrub layer of Bog rosemary, Leatherleaf, and Bog cranberry, unidentified grasses and sedges, and near continuous cover of Sphagnum moss. Bog birch (*Betula pumila*) is abundant within the transitional area. Soils are mapped as Greenwood, a deep, predominantly hemic peat soil associated with acidic bogs on previously glaciated landscapes (Soil Survey Staff [n.d.-a](#), [n.d.-b](#)).

Site Selection. We sought to identify drained and rewetted sites with likely similar characteristics prior to the extensive alteration caused by drainage and restoration. Despite current apparent differences in biology and soil properties, evidence suggests greater pre-disturbance similarity. While associated with different soil types, both sites are dominated by soil series associated with similar landscapes and genesis (Soil Survey Staff [n.d.-b](#)). For example, the soil series found at both sites are geographically associated; Greenwood and Lobo soils tend to form nearer the margins and Waskish near the center of acidic, nutrient-poor peatlands, and are associated with overlapping vegetation. Extensive pre-restoration site characterization suggested that despite currently elevated pH levels and significant extent of fen/marsh/wet meadow plant communities, prior to drainage, the rewetted site most likely formed under acidic ombrotrophic conditions, potentially containing extensive Waskish soils prevalent at the drained site (U.S. Army Corps of Engineers 2015).

Furthermore, the Marschner Map of pre-settlement plant communities based on survey notes collected from 1847 to 1907 (Marschner 1974) maps both sites as Conifer Bogs and Swamps. Additionally, the hydrogeomorphic wetland classification system identifies both sites as TEPTVR, suggesting similar landscape positions, water sources, and hydrology (TE, terrene landscape; PT, peatland landform; VR, vertical flowpath; Ulrich et al. 2019). Finally, all are predicted to be Acid Peatlands

Native Plant Community (NPC) by the Minnesota Department of Natural Resources potential NPC system classification model (Brown et al. 2013).

Gas Flux Monitoring

Gas flux collars constructed from 11.5 cm lengths of 20.3 cm diameter SDR35 polyvinyl chloride (PVC) pipe beveled on one edge were installed 6 June 2023 to 12 July 2023 and remained in place throughout the season. Measurements occurred biweekly to monthly, July–October 2023. Collars were driven into the ground until firmly seated often facilitated by cutting a shallow trench into which the collar was inserted. Sixteen and 10 collars were installed at the drained and rewetted sites, respectively, in transects extending from two to approximately 100–150 m from the edge of ditches (Fig. 1). Average collar height measured at four points was used as the collar offset for flux calculations.

We measured CH₄ and CO₂ flux with a LI-COR LI-7810 CH₄/CO₂/H₂O Trace Gas Analyzer (LI-COR Biosciences, Lincoln, NE, U.S.A.) connected to an 8200-01S Smart Chamber portable survey chamber (LI-COR Biosciences, Lincoln, NE, U.S.A.) or a custom transparent chamber. The transparent chamber consisted of a 20.3 cm diameter cylindrical chamber of 0.3 cm-thick clear acrylic. A small 5 cm diameter fan ensured complete headspace mixing. Weatherstripping and a truck tire inner tube segment allowed air-tight sealing with gas flux collars.

For each measurement, the chamber was sealed on the collar for 120 seconds, during which time concentrations were continuously measured. For analysis, a “deadband” (40 seconds for Smart Chamber, 20 seconds for clear chamber) allowing chamber gas concentrations to equilibrate was discarded for curve fitting. Between runs, the chamber was vented to achieve ambient gas concentrations. We collected all clear chamber measurements between 9:00 and 17:00 hours local time. We collected 101 opaque chamber measurements, 88 clear chamber measurements, and 23 floating chamber measurements throughout the season across all transects at both sites. We calculated all soil gas fluxes using Soil Flux Pro software (version 5.3.1; LI-COR Environmental Inc.) and visually inspected concentration versus time curves, removing one sample due to unrealistically high initial CO₂ concentrations associated with instrument error codes during run initiation.

We also measured CH₄ fluxes in drainage ditches by placing the custom chamber with an attached float directly on the water surface. Due to prevalent and large ebullition in open water (e.g. Fig. S1), fluxes were calculated from the slope between the initial and final point of the run.

Clear chamber CO₂ flux represents net ecosystem exchange (NEE) of sphagnum and other small-stature vegetation. Opaque chamber CO₂ flux represents ecosystem respiration (R_{eco}). Negative flux values represent net uptake and positive values represent net emission to the atmosphere.

Groundwater Monitoring

Two 5 cm diameter 10S schedule 40 PVC groundwater monitoring wells were installed at each site in a proximal (2 m from

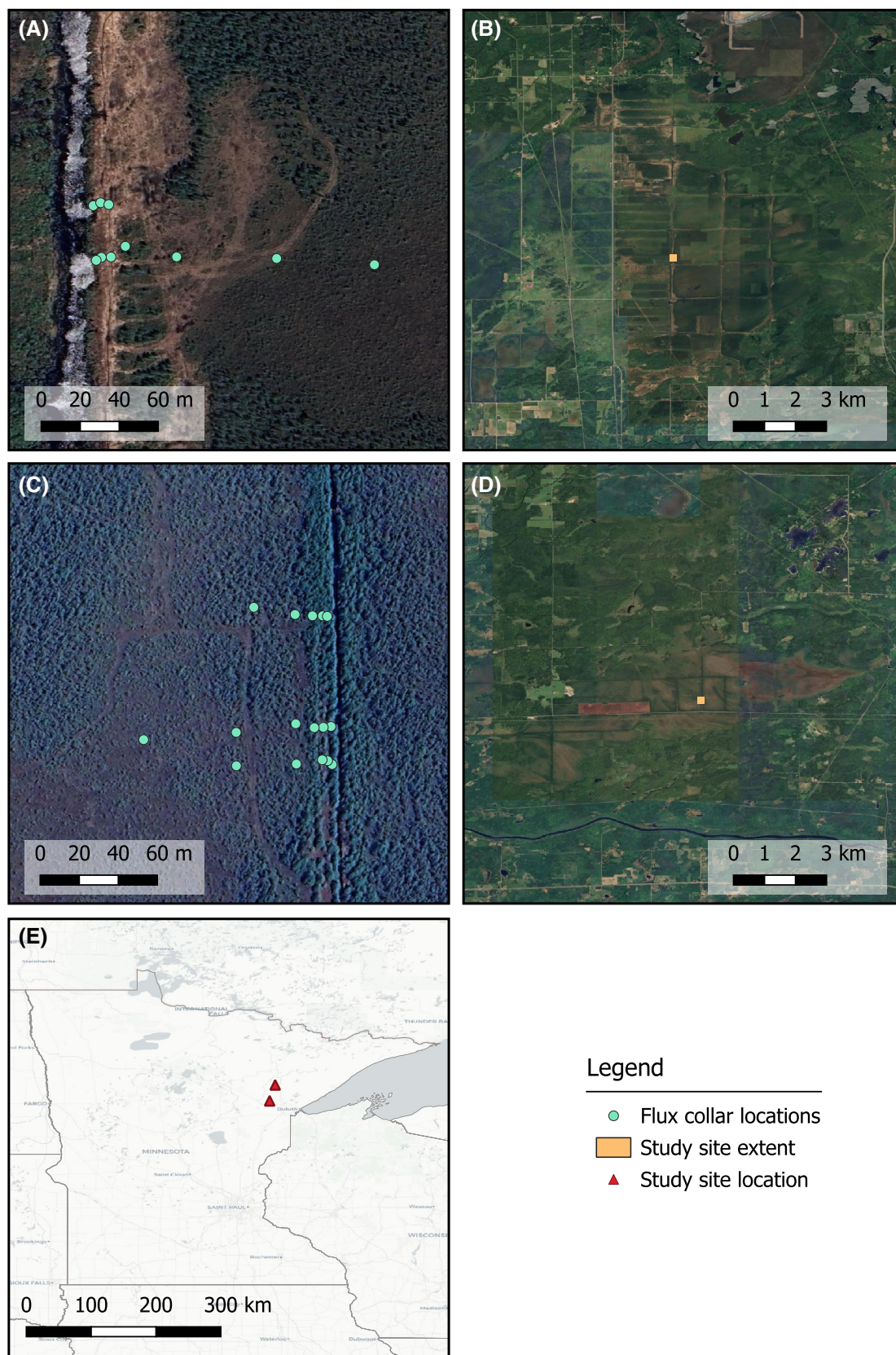


Figure 1. Overview of field monitoring sites, including gas flux collar locations at rewetted site (A) and drained site (C); extent of rewetted (B) and drained (D) monitoring sites; and site locations (E).

ditch bank) and distal location (50–75 m from ditch bank). Five foot well screens were wrapped in landscaping fabric and inserted into hand-augered holes. Each well was instrumented with a pressure transducer (3001 Levellogger Scout, Solinst Canada Ltd., Georgetown, Ontario, Canada). One well at each site was also instrumented with a barometric pressure logger (3001 Barologger 5, Solinst Canada Ltd., Georgetown, Ontario, Canada) to compensate Levellogger readings for barometric pressure. Pressure transducers and barometric pressure loggers began logging on 13 July 2023 and were retrieved on 17 October 2023 and 25 October 2023 from the rewetted and drained sites, respectively. Water levels are reported relative to the ground surface at the well location; negative numbers represent water levels belowground surface.

Soil pH

A monolith was cut with a bread knife, extracted by hand, and partitioned into 0–10, 10–20, and 20–30 cm subsamples. We homogenized subsamples by hand and packed approximately 5 mL into a graduated 30 mL plastic cup. We added 10 mL of deionized water to the peat, and thoroughly mixed the slurry. After sitting for 10 minutes, we measured samples with a portable pH probe (Hanna HI981030 GroLine Soil pH Tester, Hanna Instruments, Smithfield, RI, U.S.A.).

Plant Community Survey

We surveyed plant communities at each gas flux collar and several randomly placed monitoring points between the more widely spaced collars. Within a 0.5 m × 1.0 m quadrat centered over gas flux collars where present, we identified all plants to the species level or next higher taxonomic level and assigned an estimated percent cover. We summed the percent cover of grasses and sedges for use as explanatory variables in statistical modeling. We qualitatively observed tree cover near each quadrat.

Data Analysis

We conducted data analysis in RStudio (v2024.04.2 + 764) using R software (version 4.2.2) (R Core Team 2022).

We used linear mixed-effects models to assess environmental drivers of CH₄ flux, NEE, and R_{eco} using the lme4 package (v 1.1.33; Bates et al. 2015). Water table depth, soil temperature, soil pH, % grass/sedge cover, % sphagnum cover, and restoration status were included as fixed effects. Previous studies suggest these environmental variables are important controls on peatland gas flux (e.g. Couwenberg et al. 2011; Strack & Zuback 2013; Abdalla et al. 2016). Explanatory variables were scaled and centered by subtracting the mean and dividing by the standard deviation to improve model fitting and allow effect size comparison (Table S4). Sampling week and gas flux collar were included as intercept-only random effects accounting for temporal and spatial non-independence (i.e. measurements collected on the same date, repeated measures taken at the same site). Models were run using all combinations of fixed effects variables that included at least one predictor monitored

throughout the study period (water table depth and soil temperature). Models were initially screened using Akaike's Information Criterion for small sample sizes (AIC_c). Models with an AIC_c within 4 units of the minimum AIC_c (see Table S3 for statistics of all models where $AIC - AIC_{min} < 4$) were retained for comparison of marginal r^2 , based on the rule of thumb described by Burnham and Anderson (2002) where models with AIC more than 4 units above AIC_{min} are considered to have weaker support (Burnham & Anderson 2002). Of these, we selected the model with the highest marginal r^2 as the final model. While standardized predictors were used for model selection and comparison of predictor effect sizes, statistics for the selected models were also fit with non-standardized predictors to allow direct interpretation of predictor effects on gas flux (Table S5).

The following packages were used for data handling, cleaning, and visualization: tidyverse (Wickham et al. 2019), afex (Singmann et al. 2024), readxl (Wickham & Bryan 2023), openxlsx (Schauberger & Walker 2023), broom.mixed (Bolker & Robinson 2024), and MuMIn (Bartoń 2023).

Estimation of Open Water CH₄ Flux Contributions

To estimate potential changes in CH₄ flux between drained and rewetted peatlands, we modified the method of Roulet and Moore (1995; Equation 1), where $A_{rewetted}$, A_{ditch} , and $A_{drained}$ represent the areas of rewetted soil, ditch open water, and drainage-impacted soil, respectively; and $F_{rewetted}$, F_{ditch} , and $F_{drained}$ represent the average CH₄ flux measured in rewetted soil, ditch open water, and drainage-impacted soil, respectively.

$$\Delta F = A_{rewetted} \times F_{rewetted} - (A_{ditch} \times F_{ditch} + A_{drained} \times F_{drained}) \quad (1)$$

We assumed a 3 m ditch width, consistent with our drained study site, and a lateral drainage effect of 50 m, consistent with the distance where CH₄ fluxes at drained and rewetted sites converged. This estimate is for a hypothetical ideal restoration that eliminates all open water (see Table S8 for full calculations).

Results

Environmental Data

Soil pH. Overall, soil pH was lower at the drained site with mean pH of 3.65, 3.57, and 3.62 at 0–10, 10–20, and 20–30 cm, respectively, compared to 4.92, 4.83, and 4.95 at 0–10, 10–20, and 20–30 cm, respectively, at the rewetted site (Table S1). The rewetted site showed a pronounced pH gradient, with values at 0–10 cm depth decreasing with distance from the ditch. The gradient was more muted at 10–20 cm and absent at 20–30 cm depth. The drained site showed a weak trend of decreasing pH with distance from the ditch at 0–10 cm depth and no discernible trend at deeper depths.

Water Levels. Drained site mean water levels (from July 14 to October 17) were consistently lower proximal to the drainage ditch versus distal (−0.824 vs. −0.346 m at 2 and 50 m from the ditch, respectively). By contrast, rewetted site water levels were consistently higher adjacent (2 m) versus distal (74 m) to

the drainage ditch (-0.0607 vs. -0.531 m). At both drained site wells and the rewetted site distal well, water levels declined throughout the summer until rebounding in early September, then plateauing from late September through mid-October when we removed pressure transducers (Fig. S2). At the rewetted site proximal well, water levels increased until late August, then began to decline and showed a similar trajectory to the other wells through the remainder of the season. Overall, rewetted site water levels showed larger fluctuations.

Vegetation. A vegetation gradient was present at both sites with respect to the current and former drainage ditches (Table S2; Fig. S3). At the drained site, dense stands of Black spruce and Tamarack dominated near the drainage ditch, with minimal to no moss cover and sparse cover of sedges, forbs, and shrubs. Moving away from the ditch, Black spruce and Tamarack trees decreased in stature with a more open canopy. Ten meters from the ditch, sparse sphagnum and other mosses appeared, and sedges, Bog cranberry, Bog laurel, and Labrador tea were present. Beyond 10 m, sphagnum cover increased to near continuous, forming hummock and hollow microtopography. Understory vascular plants were dominated by Leatherleaf, Labrador tea, Bog laurel, Bog rosemary, Bog cranberry, and Cottongrass. A sparse tree canopy consisted of stunted Black spruce and some Tamarack.

Near-ditch vegetation at the rewetted site was representative of wet meadows, dominated by Canada bluejoint grass, sedges, and Rattlesnake manna grass. Moving away from the ditch, the vegetation transitioned into open rich peatland communities with significant moss cover, dominated by vascular plants, such as sedges, grasses, and Bog birch with some ericaceous shrubs, such as Leatherleaf. Locations farther from the ditch featured acid peatland plant communities with significant cover of hummock-forming Sphagnum mosses and ericaceous shrubs, such as Leatherleaf, Bog rosemary, and Bog cranberry, and a sparse canopy of stunted Black spruce and Tamarack.

Gas Flux

Mean CH_4 fluxes were higher and more variable at the rewetted (mean = $18.69 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$, standard deviation (SD) = $31.71 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$) versus drained site (mean = $3.58 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$, SD = $15.44 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$), both seasonally and spatially (Table 1). Drained site fluxes increased with distance from drainage ditch to a peak at 50 m before decreasing or leveling off at 100 m (Fig. 2). Rewetted site fluxes were highest and most variable at collars within 10 m from the ditch,

dropping significantly by 20 m and remaining relatively constant. Fluxes did not follow a consistent seasonal trend at either site.

Mean R_{eco} was higher and more variable at the drained site (mean = $11.21 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, SD = $12.48 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) versus rewetted site (mean = $4.42 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, SD = $2.43 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Table 1). Respiration showed some seasonality, peaking in August.

NEE was measured under varying light levels, but sample size and the range of light levels were insufficient for light response curves capable of normalizing measurements for direct comparison. Values here may be affected by light levels at the time of measurement and exclude CO_2 uptake by trees and other large-stature vegetation. Mean NEE was higher at the drained site (mean = $5.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, SD = $3.82 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than the rewetted site (mean = $2.57 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, SD = $2.82 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Table 1). At the drained site, negative NEE values were only observed on 3 October 2023, while the rewetted site included negative observations on all sampling dates.

Drivers of CO_2 and CH_4 Flux. The best fit (highest r^2) model for CH_4 flux was $F_{\text{CH}_4} \sim \text{Depth to water table} + \text{sphagnum cover} + \text{sedge/grass cover} + \text{rewetting status} + \text{pH} + (1|\text{week}) + (1|\text{flux collar})$ ($n = 55$, marginal $r^2 = 0.577$, conditional $r^2 = 0.711$; Table S3). Restoration status had the largest effect on CH_4 flux, with a rewetted state associated with lower CH_4 flux (Table S4; Fig. 3). pH had the largest positive effect on CH_4 flux, followed by sedge/grass cover, water table depth, and sphagnum cover. However, wide CIs for sphagnum cover and water table depth effects spanned zero. The lowest AIC_c model had only slightly lower marginal r^2 (0.575) than the selected model with similar structure but did not include sphagnum cover (Tables S3 and S6).

The best fit (highest r^2 , lowest AIC_c) model for R_{eco} was $R_{\text{eco}} \sim \text{sphagnum cover} + \text{soil temperature} + \text{pH} + (1|\text{week}) + (1|\text{flux collar})$ ($n = 55$, marginal $r^2 = 0.465$, conditional $r^2 = 0.733$; Table S3). Sphagnum cover had the largest effect on R_{eco} and along with soil pH negatively affected R_{eco} (Table S4; Fig. 3). Overall, soil temperature positively affected R_{eco} .

The best fit (highest r^2) model for NEE was $\text{NEE} \sim \text{depth to water table} + \text{sphagnum cover} + \text{rewetting status} + \text{soil temperature} + (1|\text{week}) + (1|\text{flux collar})$ ($n = 43$, marginal $r^2 = 0.524$, conditional $r^2 = 0.777$; Table S3). Restoration status had the largest effect on NEE, with lower NEE associated

Table 1. Carbon flux (NEE, CH_4 flux, R_{eco}) at drained and rewetted sites.

Site	Methane flux ($\text{nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$)				Ecosystem respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)				Net carbon exchange ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Drained	3.58	15.44	-17.30	88.34	11.21	12.48	-2.90	82.35	5.26	3.82	-3.05	13.40
Rewetted	18.69	31.71	-3.31	133.90	4.42	2.43	0.80	8.21	2.57	2.82	-1.17	10.15

Abbreviation: SD, standard deviation.

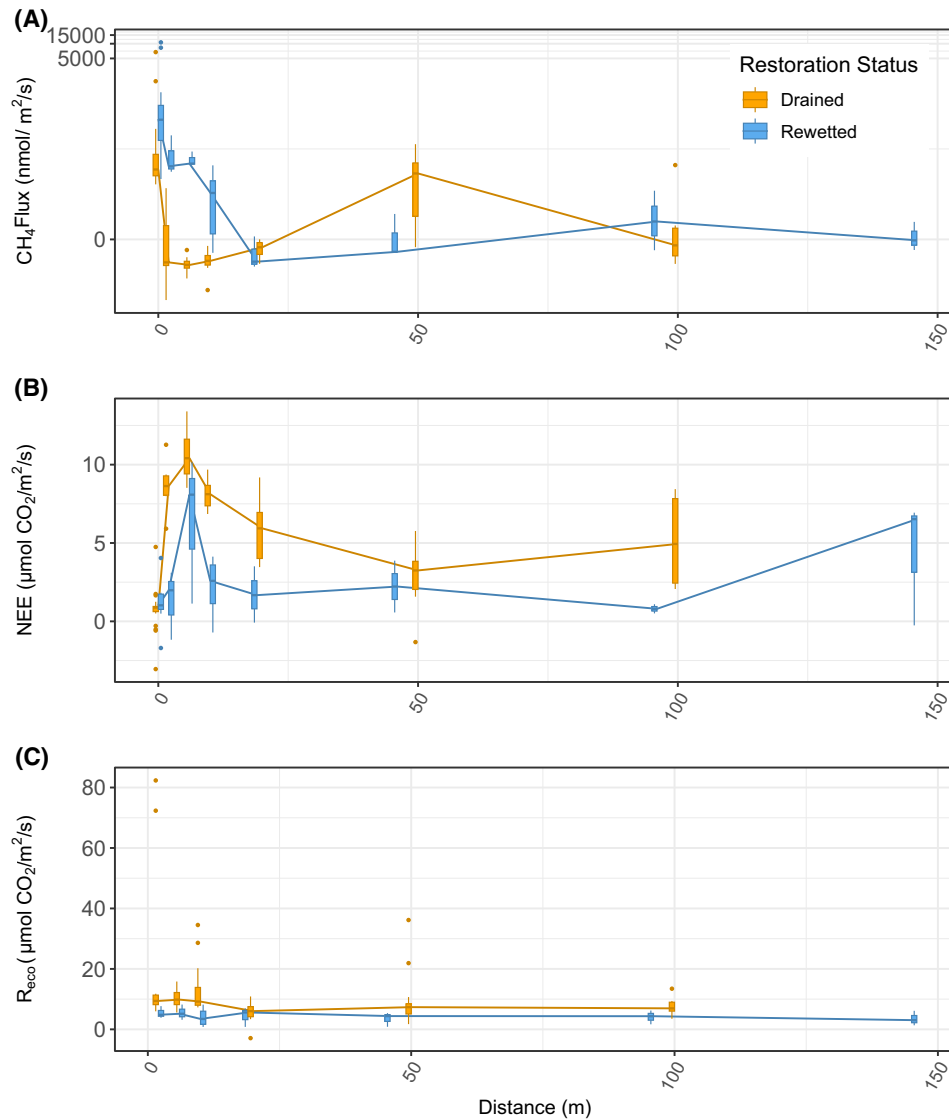


Figure 2. Spatial distribution of CH_4 flux (A), NEE (B), R_{eco} (C) along transects at drained and rewetted study sites. Lines show the median flux at each collar location. CH_4 flux is plotted on a pseudo-log scale.

with a rewetted state (Table S4; Fig. 3). However, the restoration status coefficient's large CIs spanned zero. Sphagnum cover and water table depth were negatively associated and soil temperature positively associated with NEE, but large CIs around water table depth and soil temperature coefficients spanned zero. The lowest AIC_c model had a slightly lower marginal r^2 (0.506) than the selected model, with similar structure, but excluding water table depth (Tables S3 and S7).

Open Water CH_4 Flux. Drainage ditch open water fluxes were very high (mean at drained site: $597 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$, rewetted: $3334 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$; Table 2) and variable, ranging from 13.3 to $6734 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ at the drained site and from 17.1 to $10,652 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ at the rewetted site.

Discussion

Gaseous Carbon Fluxes From Drained and Rewetted Peatlands

Mean CH_4 fluxes from both sites aligned with reported values from intact Minnesota ombrotrophic bogs, which range from 1.5 to $71.3 \text{ nmol m}^{-2} \text{ s}^{-1}$ (Crill et al. 1988; Dise et al. 1993; Zalman et al. 2018). Mean rewetted site R_{eco} was near the high end of R_{eco} observed in a forested and an open ombrotrophic Minnesota bog ($2\text{--}4 \text{ µmol m}^{-2} \text{ s}^{-1}$; estimated from Zalman et al. 2018), while drained site R_{eco} exceeded even R_{eco} reported for a restored Minnesota calcareous fen ($6\text{--}8 \text{ µmol m}^{-2} \text{ s}^{-1}$; estimated from Wille et al. 2023). Conversely, NEE measured at both the drained and rewetted sites exceeded published values for Minnesota peatlands (Olson et al. 2013; Griffiths et al. 2017). While the rewetted site more closely resembled Intergovernmental Panel on Climate Change (IPCC) tier 1 estimates of

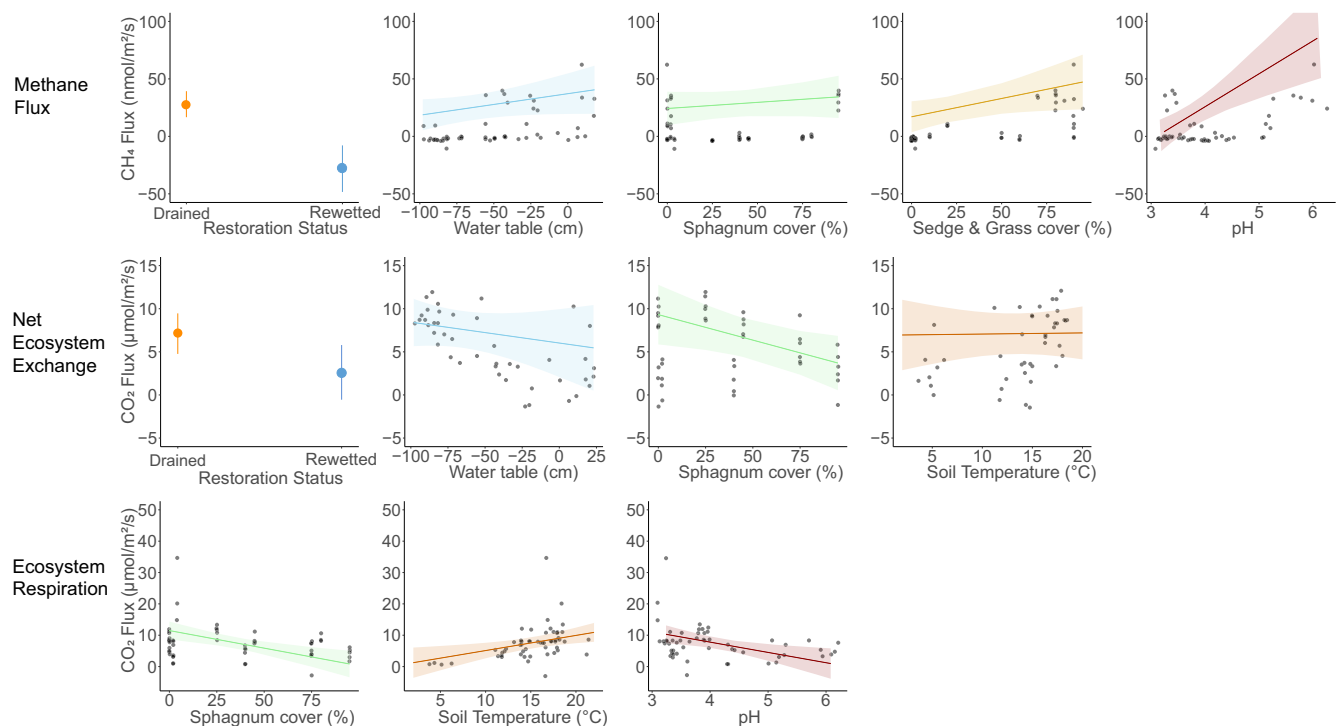


Figure 3. Modeled relationships between environmental variables and instantaneous carbon flux. Modeled relationships are based on the selected best fit model for each type of carbon flux.

$2.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ for drained boreal/temperate cropland, drained site NEE surpassed IPCC emission factors for temperate and boreal climates (Hiraishi et al. 2014).

Higher rewetted site NEE values may result partially from comparing individual point measurements from our study to integrated seasonal or annual values. Each month of the study except for September received below-average precipitation, and rewetted site water levels remained 20+ cm below the ground surface for much of the study, potentially too great to play a role in inhibiting microbial respiration or soil CO_2 flux (Sulman et al. 2009; Couwenberg et al. 2011).

While the mean fluxes we observed generally align with published values, measurements varied widely with distance from drainage ditches, showing ditching and restoration influences and reinforcing the value of point-based measurements in identifying drainage impact extent. Scaling estimates of gaseous carbon flux impacts of rewetting should account for gradients in gas flux occurring near drainage ditches, especially in Minnesota, where ditches are often spaced 800–1600 m apart, leaving large minimally impacted areas.

Table 2. Summary of open water CH_4 fluxes. *n* shows the number of samples collected across the study period.

Site	CH_4 flux ($\text{nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$)			Mean temp (°C)	n
	Mean	Min	Max		
Drained	597.33	13.27	6734.43	17.82	16
Rewetted	3333.99	17.09	10,651.93	16.53	7

Peatland drainage creates strong environmental gradients, primarily altered hydrology, with numerous secondary effects on soil characteristics (degree of decomposition, bulk density/hydraulic conductivity, nutrient availability, redox status) and plant communities. At the drained site, the lowest CH_4 fluxes and highest R_{eco} and NEE were observed at 2, 6, and 10 m from the drainage ditch, suggesting the zone of greatest drainage impact. High CH_4 fluxes were sometimes observed at 50 m, possibly related to site heterogeneity and locally high water tables, as standing water was periodically observed here but not at nearby locations. Drainage effects are a function of peatland characteristics, ditch characteristics, and climatic conditions (Landry & Rochefort 2012; Krause et al. 2021; Reagan 2023), and can therefore be site-specific. Studies summarized by Landry and Rochefort (2012) found drainage effects ranging from 30 to 200 m and 5 to 60 m in the upper active and deeper peat layers, respectively. Two studies from Minnesota suggested wider drainage impact zones of 333 ± 8.32 and 161 m based on subsidence (Krause et al. 2021; Reagan 2023). The cumulative impacts of decades of drainage on subsidence may provide more sensitivity than highly variable instantaneous flux data, such as ours, which may struggle to detect subtle differences in carbon balance near the edge of the lateral drainage effect zone. Rewetted site flux also showed distinct patterns with respect to the filled drainage ditch. At the rewetted site, CH_4 fluxes were highest at 2 and 6 m from the ditch, likely driven by the higher near-ditch water tables. Spatial trends in R_{eco} and NEE were less discernible. The rewetted site also displayed a significant

pH gradient, decreasing with distance from the ditch, which may result from altered hydrology.

Drivers of Gaseous Carbon Fluxes

The models fit with vegetation cover, restoration status, soil pH, soil temperature, and water table depth explained large portions of observed variation in carbon fluxes, suggesting these environmental variables may provide suitable time- and cost-efficient proxies for carbon flux measurements. Other studies have identified some of these factors as important drivers of peatland carbon flux able to predict and upscale fluxes (Dias et al. 2010; Couwenberg et al. 2011; Gray et al. 2013). However, published relationships between environmental drivers and carbon flux vary, especially between different geographies or contexts. Filling gaps in regionally specific carbon flux data is essential for developing predictive carbon flux models. We need to build on these models and incorporate data from multiple seasons, additional peatland sites, and other environmental parameters to test their broad applicability across the region.

Our measurements highlight the importance of restoration in affecting carbon flux. Restoration status strongly affected CH_4 flux and NEE, with lower CH_4 fluxes associated with rewetting. Although we measured higher mean CH_4 flux from the rewetted site, our model, which statistically accounted for contributions of site-specific factors (e.g. pH, water table, and soil temperature), predicted lower CH_4 flux under rewetting, suggesting the higher observed fluxes were driven by other environmental variables.

Restoration has been linked to changes in substrate availability and microbial communities that may affect CH_4 fluxes (Escobar et al. 2022). One study tied incomplete post-restoration recovery of CH_4 fluxes to lower methanogen abundance in forestry-drained peatlands (Juottonen et al. 2012). Another found post-rewetting recovery of methanogen abundance but continued low CH_4 production potential due to substrate limitation in bog and spruce swamp soils (Urbanová & Bárta 2020). Similarly, lower CH_4 fluxes in a restored cutover versus intact peatland were attributed to altered peat quality and substrate availability for methanogens (Nugent et al. 2021). NEE measured in our study was also lower in the rewetted site, consistent with evidence suggesting that peatland rewetting can reduce carbon loss (Wilson et al. 2016). While this is generally driven by higher water tables, it seems reasonable that the same alterations in peat quality and substrate availability impacting CH_4 production could also reduce aerobic carbon losses. Restoration status was not an important predictor of R_{eco} . However, carbon flux dynamics may continue to change, as peatlands may require decades to recover their pre-disturbance function (Escobar et al. 2022).

Despite efforts to select sites with similar genesis and pre-disturbance conditions (see Section 2), our study sites displayed some notable differences in characteristics, such as pH and vegetation, and site characteristics unrelated to restoration status may affect carbon fluxes and the broader applicability of restoration status-flux association. Further, these peatlands may not represent all comparably altered Minnesota peatlands. Though

our modeling approach statistically accounted for differences in important characteristics that affect carbon flux, site-specific differences could affect our interpretation of restoration effects on carbon flux. Given diverse peatland site types and restoration settings, building a solid evidence base for restoration effects requires inclusion of more varied sites, longer-term monitoring, and use of before-after-control-intervention design comparing carbon flux within the same peatlands, which could help more definitively isolate drivers associated with site disturbance.

Vegetation cover was another important predictor of carbon flux. Sedge/grass cover was significantly associated with higher CH_4 flux, consistent with studies showing many emergent grass and sedge species facilitate CH_4 transport from the subsurface through aerenchymous tissues, bypassing CH_4 -oxidizing microorganisms in overlying soils (Couwenberg et al. 2011; Korrensalo et al. 2022). Vascular plants have also been associated with higher substrate availability (Verhoeven & Toth 1995; Szumigalski & Bayley 1996), which could contribute to higher CH_4 flux. Sphagnum cover was included in our best fit model for CH_4 flux, but large uncertainty intervals reflect varying effects of sphagnum on CH_4 . Previous studies have linked sphagnum with lower CH_4 fluxes, as it does not facilitate transport of CH_4 (Greenup et al. 2000), harbors endophytic methanotrophs (Larmola et al. 2010; Kox et al. 2021), and produces low-quality litter (Verhoeven & Toth 1995; Szumigalski & Bayley 1996), providing less substrate for methanogenesis. Sphagnum cover was an important predictor of R_{eco} and NEE, negatively associated with both fluxes.

Previous studies have identified strong pH effects on CH_4 flux (Abdalla et al. 2016) consistent with our finding that pH was positively associated with CH_4 flux. In contrast, we found negative associations between pH and R_{eco} . Other studies have shown varying impacts of pH on peatland soil respiration (Moore & Dalva 1997; Fisk 2003; Myers et al. 2012).

The positive relationship we quantified between soil temperature and R_{eco} has been widely observed in peatlands and may be due to increased microbial activity with temperature (Strack & Zuback 2013; Ballantyne et al. 2014; Strack et al. 2014). However, soil temperature was only weakly positively correlated with NEE, with wide uncertainty. While partial coupling of the temperature response of the NEE components (R_{eco} and gross primary productivity [GPP]) can mute the effect on NEE (Bubier et al. 1998; Ballantyne et al. 2014), R_{eco} may be more sensitive than GPP. The positive relationship between NEE and soil temperature may have also resulted from dry conditions predominating during warmer months, which may have reduced plant GPP (Lund et al. 2012; Helfter et al. 2015), consistent with our field observations of dormant sphagnum during much of the season. Soil temperature was not included in the best model for CH_4 flux, although soil temperature measured at 10 cm (Kalhori et al. 2024) and 30 cm (Dise et al. 1993) has been identified as an important driver of peatland CH_4 flux. However, the 12.5 cm depth of our temperature measurements was often well above the water table at many collars and may not reflect saturated zone temperatures where CH_4 production is high. Chen et al. (2021) found that the temperature (5 cm depth) dependence of wetland CH_4 flux declined as water table depth increased.

Sitewide temperature differences may also confound the temperature-CH₄ flux relationship, since soil temperatures overall were warmer at the drained site where drier conditions were less conducive to CH₄ emissions. These differences are consistent with changes in soil physical properties causing generally higher temperatures in surface layers of drained peatland soils (Landry & Rochefort 2012).

Water level is often a primary driver of CH₄ and CO₂ flux, as water level controls soil redox status and peat volume accessible for methanogenesis versus aerobic respiration and CH₄ oxidation. While water level was a predictor in our CH₄ and NEE models, consistent with previous studies, the water level effect size was much smaller than other explanatory variables, such as restoration status, soil pH, and sphagnum cover, possibly because water levels were well below the ground surface through much of the study period, where studies have found poor correlations between water level and gas flux (Sulman et al. 2009; Couwenberg et al. 2011).

Open Water Fluxes

Although drainage ditches represent relatively small areas of drainage-impacted peatlands, high open water fluxes observed in this study suggest potentially significant contributions to site-wide CH₄ flux. High CH₄ fluxes from ditches compared to rewetted peatland soils highlight the importance of limiting open water during restoration. Estimates based on measurements from this study indicate that open water CH₄ fluxes within the ditch alone could approach soil-based CH₄ fluxes from an area of rewetted peat equivalent to the observed drainage-impacted zone. Accounting for CH₄ emitted by drained peat soils, rewetting would not be expected to increase overall CH₄ emissions across an entire drainage-impacted area. An accurate site-wide CH₄ budget requires more data, but our estimate demonstrates that despite relatively small areal coverage of drainage ditches, impacts can be significant and should be included in evaluations of restoration impacts on carbon budgets, as it can dramatically affect cost–benefit analyses of rewetting for carbon emissions reduction, and in fact, the IPCC Wetland Supplement advises including ditch CH₄ fluxes in estimating overall peatland emissions due to their potentially significant contribution (Hiraishi et al. 2014).

Measured mean open water fluxes were higher than IPCC tier 1 emission factors for boreal/temperate drainage ditches and those reported in meta-analyses of global peatland ditches (e.g. Peacock et al. 2021; Gan et al. 2024) and previous studies of harvested (Strack & Zuback 2013), and forestry-drained peatlands (Roulet & Moore 1995). Rewetted site ditch fluxes were similar to fluxes observed in ditches with no standing water in an actively extracted peatland (Hunter et al. 2024). Drained site ditch fluxes were more comparable to those observed in a drained minerotrophic fen (Minkinen & Laine 2006) and actively extracted peatland ditches with standing water (Hunter et al. 2024). Minkinen and Laine (2006) showed a similar pattern of higher fluxes in fen versus bog ditches and that ditch characteristics, particularly water movement, played an important role in regulating drainage ditch CH₄ flux.

This study adds to a growing body of research demonstrating the role of peatland restoration on carbon fluxes and provides field-measured estimates allowing comparison of Minnesota peatland fluxes to global measurements. Flux estimates from this study fill a critical data gap by including less-often measured ditch fluxes. Based on this study, relatively high open water CH₄ fluxes could dramatically affect the estimated tradeoffs between reduced CO₂ and increased CH₄ flux associated with rewetting peatlands, and are therefore important to include when determining rewetting benefits. Regression models, like those used here, represent a promising approach for scaling up estimation of regional peatland carbon fluxes and potential emissions reductions from peatland restoration, while overcoming challenges associated with direct peatland carbon flux measurements.

Acknowledgments

We thank M. Cornett for important initial contributions, leadership, and support; N. Hill and A. Kottkamp-Hoard for contributions in early stages; E. Lilleskov and R. Chimner for scientific advising related to experimental design and data interpretation. We thank Ecosystem Investment Partners and SEH Inc., especially D. Deuschle and E. Massa, for site access and data sharing, and the Minnesota Department of Natural Resources for access to conduct research on DNR-administered lands. Funding for this research was provided by the Bezos Earth Fund through The Nature Conservancy's Natural Climate Solutions Prototyping Network; the Cox Family Fund; the Patrick and Aimee Butler Family Foundation; and contributions from private donors. The authors declare no conflicts of interest. The data that support the findings of this study (Felice et al. 2025) are openly available in the Knowledge Network for Biocomplexity (KNB) repository, <https://doi.org/10.5063/F1DB80B4>, reference number urn:uuid:de9400c0-a766-4be4-98b5-65622a7595e5.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Soil pH data measured in the field using 2:1 water: soil ratio.

Table S2. Vegetation coverage measured within 0.5 × 1.0 m quadrats.

Table S3. Summary statistics for candidate models that fit selection criteria based on AIC_c (AIC_c – AIC_{c-min} < 4).

Table S4. Summary statistics for selected methane flux, net ecosystem exchange, and ecosystem, respiration linear mixed-effects model.

Table S5. Summary statistics for selected methane flux, net ecosystem exchange, and ecosystem, respiration linear mixed-effects model using non-standardized predictors.

Table S6. Summary statistics for selected methane flux mixed-effects model with lowest AIC_c for comparison to selected model.

Table S7. Summary statistics for net ecosystem exchange mixed-effects model with lowest AIC_c for comparison to selected model.

Table S8. Example calculation for the change in flux between drained and rewetted peatlands.

Figure S1. Example flux concentration versus time plot from open water CH₄ flux measurement taken on 1 August 2023.

Figure S2. Hydrographs proximal and distal to drainage ditches at drained and rewetted sites.

Figure S3. Coverage of plant functional groups along monitoring transects.

Coordinating Editor: Virginia Matzek

Received: 14 March, 2025; First decision: 16 May, 2025; Revised: 12 December, 2025; Accepted: 11 May, 2026