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Key Points:

- Boreal conifer swamp wetlands are an underrepresented wetland class within wetland C cycling measurements and modeling
- These swamps store large volumes of organic C in their aboveground biomass but most importantly, in their soil organic carbon stock
- We also found that the ground-layer of this site is a net source of greenhouse gases during the growing season

Supporting Information:

Supporting Information may be found in the online version of this article.

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Carbon Stocks and Fluxes From a Boreal Conifer Swamp: Filling a Knowledge Gap for Understanding the Boreal C Cycle

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Abstract The carbon (C) dynamics of boreal coniferous swamps are a largely understudied component of wetland carbon cycling. We investigated the above- and below-ground carbon stocks and growing season carbon dioxide (CO_2) and methane (CH_4) fluxes from a representative boreal coniferous swamp in northern Alberta, Canada in 2022. Tree inventories, understory vegetation biomass and peat cores were collected across three sub-sites within the broader swamp, with gas flux collars placed in the dominant plant communities present. Alongside the C flux measurements, environmental variables such as water table depth, soil temperature and growing season understory green leaf phenology were measured. Our results show that these boreal coniferous swamps store large volumes of organic C in their biomass and soil (134 kg C m^{-2}), comparable with other wetland and forest types, although 95% of the total C stock at our site was within the soil organic carbon. We also found that understory CO_2 and CH_4 fluxes indicated that the ground layer of the site is a source of greenhouse gases (GHGs) to the atmosphere across the growing season. However, we did not measure litterfall input, tree GHG fluxes or net primary productivity of the overstory, therefore we are not able to say whether the site is an overall source of C to the atmosphere. This study provides a much-needed insight into the C dynamics of these under-valued wetland ecosystems, and we highlight the need for a coordinated effort across boreal regions to try to improve inventories of C stocks and fluxes.

Plain Language Summary Compared to other wetland types across Canada, boreal conifer swamps do not receive the same level of scientific attention and therefore our understanding of how much carbon they potentially store and release is limited. To fill this knowledge gap, our study measured how much carbon was stored both in the trees and within the soil itself, alongside measurements of carbon uptake and release within a representative conifer swamp wetland in Western Canada. We found that although these wetlands may function similarly to other wetland types, by ignoring them, we are missing out on large amounts of carbon being stored in these systems. We also found that at the ground layer, these sites are a source of carbon, that is, releasing more carbon than is being taken up by the understory moss and plant layer. However, we cannot say if the site overall is a source of carbon to the atmosphere as we were unable to measure other key components of a wetland carbon cycle including litterfall input and the productivity of the trees themselves. Our findings indicate that by not including these wetlands in modeling of carbon dynamics, we are missing a substantial component of boreal carbon cycling processes.

1. Introduction

Northern wetlands are an important component of the global carbon (C) cycle, storing a third of the soil C pool in less than 5% of the global land area (Gorham, 1991; UNEP, 2022; Xu et al., 2018). Their ability to store C on millennial timescales is increasingly being acknowledged as an important nature-based solution to climate change through protection and restoration efforts (Strack et al., 2022). However, wetlands, including peatlands, are also the largest natural source of methane (CH_4) to the atmosphere (Saunois et al., 2020), making it critical to quantify C storage and fluxes accurately for C accounting efforts globally.

Within northern wetland types, swamps pose a unique challenge when quantifying C dynamics due to their high tree cover and variable C stocks. Although they have variable definitions across the literature, swamps across

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northern regions are generally characterized by having at least 25% tree cover at >5 m height, a canopy cover that in many cases is comparable to adjacent uplands, leading to the potential for misclassification based on aerial surveys (Ducks Unlimited Canada, 2021; Locky et al., 2005; NWWG, 1997). Thus, they are not yet included in some wetland mapping studies (Pontone et al., 2024). Unlike other northern wetland types, such as bogs and fens, swamps can also be considered either mineral or peat-forming and therefore have a wide range of soil carbon masses per unit area in the literature (Byun et al., 2018; Davidson et al., 2022; Dazé et al., 2022; NWWG, 1997). However, if assumed to only be mineral wetlands, as some wetland classification schemes suggest, significant C stocks are being missed from wetland inventories. Further, the variability in hydrological conditions in swamps, ranging from being permanently flooded to seasonally indundated allow swamp trees to grow taller compared to other forested wetland types, and therefore have ability to store more aboveground biomass (Elmes et al., 2021; Locky et al., 2005). Although previous syntheses have highlighted that swamps as a general wetland class are understudied, it is also the case that boreal coniferous swamps are particularly neglected within this class (Davidson et al., 2022).

Accurately quantifying the role swamps play within northern wetland C dynamics also requires an understanding of how factors that control C cycling may differ from other wetland types. For example, the greater variability in hydrological conditions compared to other wetland types, ranging from being permanently flooded to seasonally inundated, allow swamp trees to grow taller compared to other forested wetland types, and therefore have the ability to store more aboveground biomass (Elmes et al., 2021; Locky et al., 2005). Higher tree cover, however, means that shading could influence understory vegetation productivity to a greater extent than other wetland types (Bisbee et al., 2001). Further, significant litter inputs from the overstory means that soil respiration is not necessarily driven solely by understory inputs (Webster et al., 2008), unlike many other wetland types (Philips et al., 2010). Davidson et al. (2022) found that aboveground biomasses in swamps (ranging from 4.0 to 21.5 kg m^{-2}) are significantly larger than those found in treed bogs and fens (1.2–2.3 kg m^{-2}), with swamps also having larger aboveground net primary productivity (NPP) values than the range for bogs and fens, at 0.92–1.57 and 0.2–0.4 kg m^{-2} yr^{-1}, respectively. Hydrologic variability also means that developing relationships between C dynamics and water table and soil temperature (ST) in swamps can be difficult, due to constantly changing redox conditions or lags/hysteresis, which is especially important for CH_4 production and emissions.

Despite key differences in the drivers of C cycling in swamps compared to other wetland types, there remains few studies in northern regions (Davidson et al., 2022). This is especially true for the Boreal Region of Canada, which holds approximately 60% of the 1.1 million km^2 of peatland area within the country, with a significant portion of this area potentially classified as swamp (Amani et al., 2019; Riley, 1994). These data gaps have led to their exclusion from national greenhouse gases (GHG) inventories and databases (e.g., IPCC, 2014; Kuhn et al., 2021), land cover mapping (Olefeldt et al., 2021), and modeling efforts (Bona et al., 2020) and there are few relevant process-based models that can be used to assess swamp ecosystem dynamics (Bona et al., 2020). Therefore, more empirical data is needed for the assessment of contemporary C stocks, GHG exchanges and environmental drivers in these understudied ecosystems.

In this study we aimed (a) to quantify the C stocks and fluxes at a representative boreal coniferous swamp located in boreal Canada and (b) investigate how different environmental factors are influencing the C dynamics.

2. Materials and Methods

2.1. Study Site

The study was undertaken in a boreal coniferous swamp (hereafter referred to as Heaven Swamp), approximately 30 km north of Fort McMurray, Alberta, Canada (56°57′28.0″N 111°33′24.0″W) (Figure 1). The mean annual temperature (1981–2010) in the region is 1°C, and mean annual precipitation is approximately 420 mm (Environment Canada, 2017). The study site is a 10 ha fragment of swamp and was classified using the Ducks Unlimited Canada Alberta Wetland Classification System (Ducks Unlimited Canada, 2021). The wider landscape is characterized by sand-dominated uplands (McPherson & Kathol, 1977) and a much larger (~200 ha) extreme-rich patterned fen peatland (Hartstock & Bremer, 2018) to the east. The hydrology of Heaven Swamp is hypothesized to be largely influenced by groundwater discharge from surrounding upland areas to the north and south.

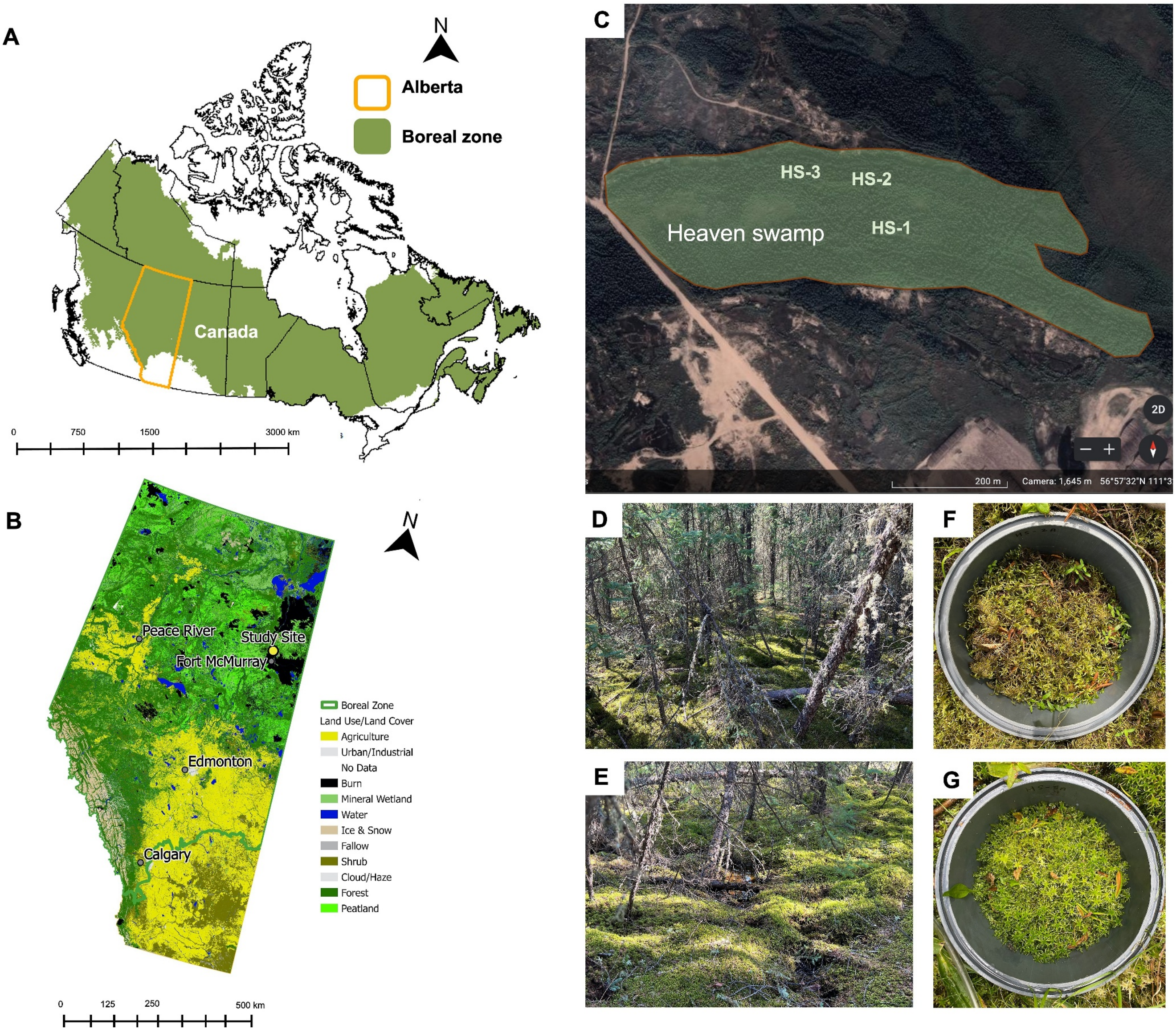

Figure 1. The location of the boreal zone (NRCan North American boreal zone layer; Brandt, 2009) and Alberta within Canada (a), the location of the study site within Alberta (data layer: Government of Alberta (2018)) (b), the location of the study area (Heaven Swamp: 56°57′28″N, 111°33′24″W) and the location of plots HS-1, HS-2, and HS-3 (base map: Google Earth: TerraMetrics (Accessed 25/06/2023)) (c) and photographs of the typical tree density (d), example of understory vegetation community (e), example of representative feather moss flux collar (f) and example of representative sphagnum flux collar (g). Map shown in panel (a) is adapted from Davidson et al. (2021).

However, due to its higher topographic position on the landscape, the swamp likely acts as a headwater system, and experiences greater water table variability relative to the extreme-rich patterned fen to the east.

This swamp is dominated by an overstory of *Picea mariana* (Mill,) *Larix laricina* (Du Roi) K. Koch, Britton, (L.) and an understory of typical shrubs such as *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Vaccinium oxycoccos* (L.) MacMill, and *Vaccinium vitis-idaea* L. as well as mosses such as *Sphagnum squarrosum* (Crome) and feather mosses, largely *Hylocomium splendens* (Hedw.) Schimp and *Ptilium crista-castrensis* (Hedw.) De Not. All vegetation was identified to the highest taxonomic resolution possible in the field, with nomenclature following the most recent records from the Integrated Taxonomic Information System (National Museum of Natural History, Smithsonian Institution, 2023). The peat depth within study locations at Heaven Swamp ranges between 2 and 3.5 m.

Table 1
Allometric Equations Used to Estimate Above and Belowground Biomass of Trees at Heaven Swamp

Species	Equation	Units		Reference
Larix laricina (>1.6 m)	$AG = 0.1361*DBH^{2.298}$	kg	cm	Carpenter (1983)
L. laricina (<1.6 m)	$AG = 0.3572e^{0.0532*TH}$	g	cm	Murray et al. (2021)
Picea mariana (>1.6 m)	$AG = 0.153*DBH^{2.248}$	kg	cm	Grigal and Kernick (1984)
P. mariana (<1.6 m)	$AG = 0.0085*TH^{2.2088}$	g	cm	Munir et al. (2014)
Salix (>1.6 m)	$AG = 23.19*DBH^{2.84}$	g	cm	Berner et al. (2015)
Betula (>1.6 m)	$AG = 28.1*DBH^{2.97}$	g	cm	Berner et al. (2015)
Belowground (conifers)	$BG = 0.232*AG$	kg	kg	Kurz et al. (1996)

Note. AG: aboveground biomass, DBH: diameter at breast height (1.4 m), TH: tree height, and BG: belowground biomass.

2.2. Tree Inventory and Biomass

Aboveground and belowground biomass of trees was estimated using allometric equations derived from regressions of dry biomass and tree height or diameter at breast height (DBH, 1.4 m) (Murray et al., 2021). Three 10 × 10 m plots (HS-1, HS-2, and HS-3) were laid out within the swamp and all individual trees were identified and counted (see Figure S1 in Supporting Information S1). Trees were categorized as either tall (>1.6 m) and measured for DBH, or short (<1.6 m) and measured for height. Allometric equations used in this study are found in Table 1.

2.3. Peat Characteristics

One peat cores was collected near the southwest corner of each tree inventory plot to determine the soil C stocks of the uppermost 50 cm of peat (see Figure S1 in Supporting Information S1). A replicate core was taken at site three for a total of 4 cores. Bulk density (g cm^{-3}) was determined on 10 cm depth intervals for a total of 5 samples per core. Each sub-section was dried in the oven at 60°C for 2 days or until the sample reached constant weight. Organic matter (OM) content (%) was calculated using the loss on ignition method (Rowell, 1995). Approximately 2 g of each dried sample was weighed and then burned in a muffle furnace at 550°C for 3 hr. After burning the samples, they were left to cool overnight and weighed post ignition. OM is calculated as the difference between pre-ignition and post-ignition mass expressed as a percentage of pre-ignition mass. A 1 mg subsample was taken from each 10 cm depth interval for C and nitrogen (N) analysis. Each subsample was ground to a fine powder using a Retsch ball mill and analyzed for C and N content using a 4010-elemental analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer at the University of Waterloo, Canada. Soil organic carbon (SOC, kg m^2) content for each sub section was calculated by first multiplying the bulk density (converted to kg m^3) by the total C content, and then by 0.1 (in meters) to account for the depth of the sample. These values where then summed to estimate the total soil C stock within the upper 50 cm.

Total peat depths were measured at three points within each tree plot. If the basal depth was not reached due to an obstruction (e.g., large wood pieces) the furthest depth possible was recorded. The minimum depth was then used for each plot to estimate total C stocks using the forested peatland equation from Magnan et al. (2023):

$$SOC = 0.485*(\text{peat depth; cm}) + 13.532\ (\pm 17\%) \qquad (1)$$

2.4. Understory Vegetation

Percentage cover of plant functional type (bryophyte, graminoid, and dwarf shrub), as well as bare ground and standing water within each flux plot was estimated once during the peak growing season during the measurement period. A photograph was taken of each flux collar at each flux measurement, totaling 234 photographs. We calculated green chromatic coordinate (GCC) by extracting the red-blue-green data from each photograph, following methods shown in Davidson et al. (2021) and results of this can be seen in Figure S2 in Supporting Information S1.

Understory biomass sampling took place in July 2022, at the peak of plant productivity when the increase in GCC had leveled off (Figure S2 in Supporting Information S1). Three 25 × 25 cm quadrats were randomly placed within the 10 × 10 m tree inventory grid and all vegetation was clipped at the bryophyte surface. Low shrubs and woody species such as *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Vaccinium oxycoccos* (L.) MacMill, and *Vaccinium vitis-idaea* L. were collected as part of the understory. As it can be difficult to determine the separation between bryophyte biomass and the underlying peat due to gradual decomposition, we included bryophyte biomass in the soil carbon stock estimates as they were collected as part of soil coring. Vegetation was stored in plastic sample bags at ∼4°C until they were shipped to University of Waterloo for processing. In the laboratory, samples were dried at 80°C for 24 hr and weighed to obtain mass.

2.5. Carbon Dioxide (CO_2) Flux

Carbon dioxide (CO_2) fluxes were measured using the closed chamber method 12 times between 25 May and 16 August 2022 (representative of the growing season ranging from completely snow free to the beginning of plant senescence). Within the two dominant vegetation communities (feather moss and sphagnum), six PVC collars per community (co-located in groups of three collars, height 15 cm × diameter 20 cm) were installed to a depth of approximately 8 cm in May 2022. Collars were in place for 1 week before the first flux measurements were taken. To investigate soil only fluxes of CO_2 (and CH_4), six more collars were installed but the vegetation (originally feather moss) was clipped from within the collar at soil level, totaling 18 collars. The height of the collar was measured from the soil surface to give the correct chamber headspace volume for flux calculations.

CO_2 concentrations were measured in a clear acrylic chamber (20 cm diameter × 50 cm height) placed on each flux collar, with water poured around the collar edge to create an airtight seal. Measurements were collected at 15 s intervals for 105–120 s using a portable infrared gas analyzer (EGM-4, PP Systems, Massachusetts, USA). A battery powered fan was used to mix the chamber headspace. A thermocouple located within the chamber, attached to a thermometer was used to measure air temperature during sampling. Relative humidity and photosynthetically active radiation were also measured within and on top of the chamber respectively with sensors connected to the EGM-4. A neoprene sleeve was used to create fully dark conditions, enabling ecosystem respiration (ER) to be measured. Order of sampling plots was randomized 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, here measured under full sun. Gross ecosystem productivity (GEP) is calculated as the difference between NEE and ER. In this study, we use the sign conventions that C uptake from the atmosphere is negative and emission to the atmosphere is positive. We subtracted CO_2 emissions from the clipped plots from the vegetated plots to represent autotrophic respiration. Raw data were inspected for linearity of fluxes, controlling for fit of $R^2 \geq 0.75$, except for fluxes that were relatively unchanging (<2 ppm over the closure period), representing a flux close to zero. Quality control resulted in a data loss of 12%.

2.6. Methane (CH_4) Flux

Methane (CH_4) flux was measured on the same collars during the same fieldwork period using a cylindrical opaque chamber (20 cm diameter × 50 cm height). A 20 mL syringe was used to collect gas samples at intervals of 5-, 10-, 15-, and 25-min following chamber closure and injected into 12 mL Exetainers (Labco, UK). Concentration of CH_4 in the samples was determined by injection in a DLT-100 Fast Methane Analyzer (Los Gatos Research) and comparison to standards of 1, 5, and 50 ppm. The CH_4 flux determined from the linear change in concentration over time, which includes corrections for temperature and volume of the chamber, controlling for fit of $R^2 \geq 0.75$. When concentration change over the closure period did not exceed 0.4 ppm (i.e., ±10% of atmospheric concentration and precision of concentration analysis accounting for injection in the vials, storage and then sample analysis) we assigned a zero-emission value to these flux measurements. After quality control, 14% of values were removed from further analysis.

2.7. Environmental Variables

A groundwater well made of PVC pipe (4 cm diameter × 100 cm long), slotted along the full length and covered in mesh, was installed adjacent to each set of three co-located collars to measure water table depth (WTD, relative to the ground surface). A ST profile was collected at each collar during each flux measurement at −30, −25, −20, −15, −10, −5, and −2 cm from ground surface using a handheld digital thermocouple thermometer and a type K

30 cm thermocouple probe (Omega, UK). The first two rounds of flux measurements did not have WTD, or ST data collected due to the ground still being frozen.

2.8. Statistical Analysis

All statistical analysis was undertaken in R version 3.6.1 (R Core Team, 2019), and all output and models were inspected for normality and homogeneity of residuals (Zuur et al., 2009), with statistical significance considered at $\alpha = 0.05$. The relationship between C and OM content in the upper 50 cm of the three peat profiles in this study was evaluated using the *lm* (linear regression) function in R. The linear fit was forced through the origin to evaluate the ratio between the two values.

Due to the C flux data being not normally distributed, an unpaired two-sample Wilcoxon test was used to evaluate significant differences in CO_2 and CH_4 fluxes between the Feather moss and Sphagnum plots.

A linear mixed effects (LME) model was used to evaluate the effect of water table, ST at 10 cm depth, and GCC on NEE, ER, and GEP using the *nlme* package (Pinheiro et al., 2018). Collar ID was included as a random factor to account for repeated measures. We calculated the amount of variance described by the model as R^2_{GLMM} (Nakagawa & Schielzeth, 2013), using the package *MuMIn* (Bartoń, 2019). Another LME was used to evaluate the effect of WTD and ST at 30 cm depth on CH_4 emissions.

3. Results

3.1. Above- and Belowground C Stocks

Aboveground C stocks at Heaven Swamp were predominately influenced by extent of tree cover and the presence of moss and ericaceous shrubs. HS-1 had the greatest tree above and belowground biomass with both *L. laricina* and *P. mariana* having DBH values greater than 6 cm and the largest basal area of the three sites (Figure 2 and Table 2). Lower tree basal area was related to greater understory biomass, which mainly came from increased shrub and bryophyte cover (Table 1). The highest ericaceous shrub cover, which was predominantly *Rhododendron groenlandicum* and *Vaccinium vitis-idaea*, was found at HS-3 that was also characterized by many small conifers (<1.6 m) contributing to the aboveground biomass (Table 3). The increase in shrub and small conifer biomass did not compensate for the differences in larger tree biomass between subsites, and therefore HS-2 and HS-3 had lower total aboveground C stocks than HS-1 (Figure 2). Combining the three study plots, mean understory, overstory and total aboveground C stocks at Heaven Swamp were 0.024, 4.9, and 5.0 kg C m^{-2}, respectively. Estimated belowground tree biomass C stocks were 1.1 kg C m^{-2}.

Estimated soil C stocks were 14–28 times higher than aboveground and belowground tree C stocks at all subsites, with all peat depths greater than 2 m (Figure 2). Variations in the upper 50 cm of each peat profile were the result of varying peat properties and vegetation cover. HS-1 and HS-2 had fibrous peat in the uppermost 10 cm of the peat profile and became mesic below that depth. This shift was also associated with a reduction in C:N ratio and an increase in bulk density (Figure 3). HS-3 had the lowest SOC (in the upper 50 cm) of the three sites and had a thicker fibric peat layer (0–20 cm) compared to the two other subsites (Figure 3). Within the fibric layers, HS-3 was also a mixture of feather moss and sphagnum, while HS-1 and HS-2 only had feather moss present within the peat profile. The proportion of C within the OM of the upper 50 cm across all profiles was 0.502 (Figure 3).

3.2. CO_2 and CH_4 Fluxes and Associated Environmental Drivers

For the measurement period, WTD ranged from approximately 24–2 cm below the ground surface, with a mean (±SD) of 8.5 (2.7) cm (Table 3). Soil temperatures at 10 cm depth ranged from 1.9°C to 22.2°C across the measurement period, with a mean (±SD) of 11 (3.6)°C (Table 4).

Despite having productive vegetation in the flux collars (Figure S2 in Supporting Information S1), understory NEE was largely positive across the measurement period (Figures 4c and 5c), indicating that for the 2022 growing season, the understory was a net source of CO_2 to the atmosphere, due to larger losses of CO_2 via ER than uptake via GEP. Although the mean CO_2 fluxes were higher in the sphagnum plots than in the feather moss plots (Table 4), no significant difference in GEP (Wilcoxon signed rank test; $z = -1.81$, $p = 0.07$), ER (Wilcoxon signed rank test; $z = -0.47$, $p = 0.63$) or NEE (Wilcoxon signed rank test; $z = -0.011$, $p = 0.9$) was found. Likewise, although mean CH_4 flux were higher in the sphagnum plots (49.9 mg CH_4 m^{-2} d^{-1}) compared to the

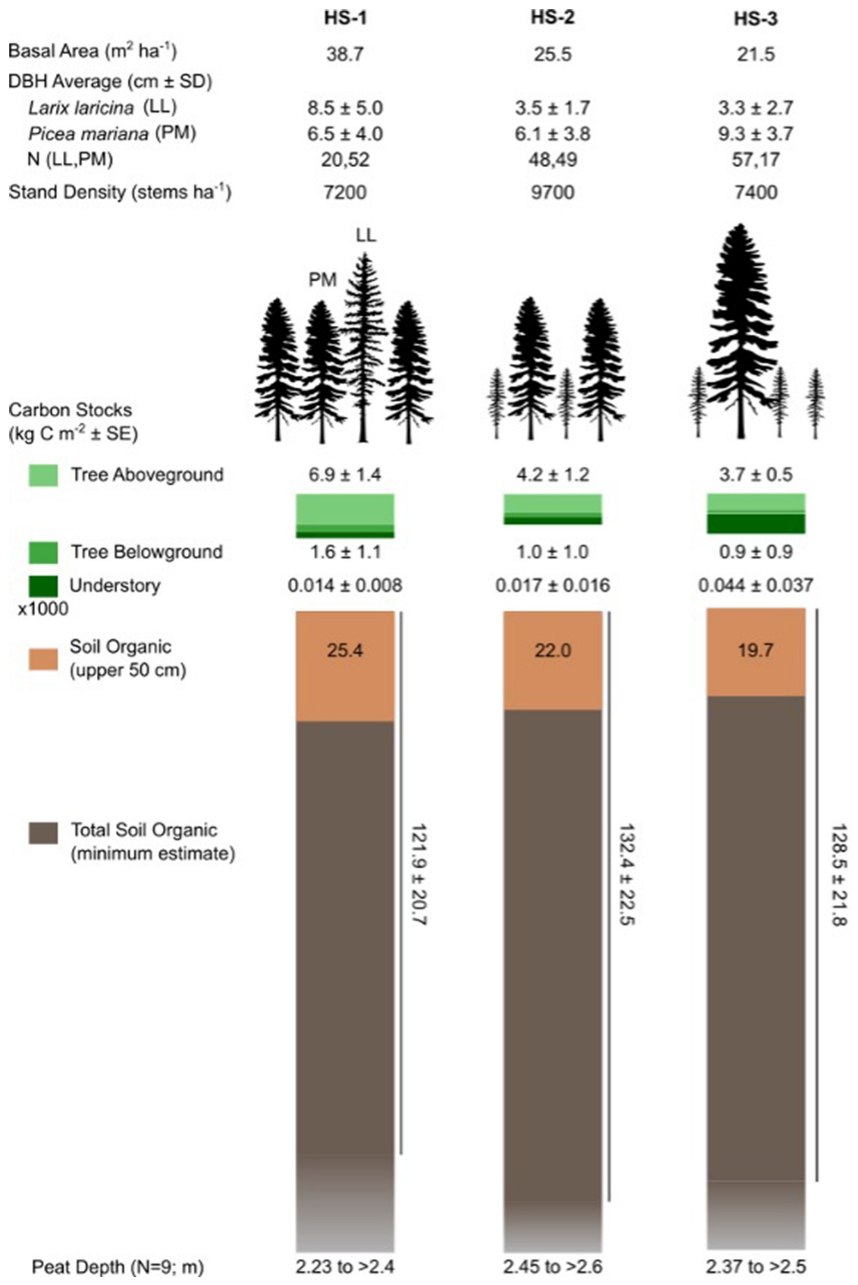

Figure 2. Schematic representation of the characteristics of the three sub-sites within Heaven Swamp. Aboveground tree biomass is shown in pale green. The biomass of the dominant understory vegetation is shown in dark green. The relative depth of the upper 50 cm soil organic layer and the estimated total soil organic layer are shown in light and dark brown, respectively (shading gray toward mineral layer at depth). Trees are not to scale but are representative of the variation in canopy openness and species (LL = *Larix laricina* and PM = *Picea mariana*). Tree counting was performed within a 10 × 10 m plot at each site. Standard errors are shown by ±values.

feather moss plots (30.6 mg CH_4 m^{-2} d^{-1}) the difference was not significant (Wilcoxon signed rank test; $z = -1.27$, $p = 0.21$) (Figure 5d). Clipped vegetation plots had much smaller fluxes than vegetated counterparts, with a mean (±SD) soil CO_2 flux of 6.9 (4.6) g CO_2 m^{-2} d^{-1} and mean (±SD) soil CH_4 flux of 5.3 (11.9) mg CH_4 m^{-2} d^{-1} (Figure S3 in Supporting Information S1). The difference in ER between clipped and unclipped plots (4.3 g CO_2 m^{-2} d^{-1}) indicates that understory plant respiration accounted for 44%–48% of understory ER.

Table 2
Total Tree Above and Belowground Biomass and Tree Height for Trees < 1.6 m for the Three Subplots at Heaven Swamp

	HS-1	HS-2	HS-3
A. Trees > 1.6 m			
		Total mass (kg C m^{-2} ± SE)	
Aboveground biomass	6.86 (1.37)	4.16 (1.18)	3.67 (0.48)
Picea mariana (Miller) Britton	4.08 (1.20)	3.36 (1.13)	2.33 (0.39)
Larix laricina (Du Roi) K. Koch	2.78 (0.17)	0.80 (0.05)	1.34 (0.08)
Betula glandulosa Michaux	–	–	0.00 (0.00)
Salix sp.	0.00 (0.00)	–	–
Belowground biomass (conifers)	1.59 (1.09)	0.96 (1.05)	0.85 (0.88)
B. Trees (<1.6 m)			
		Total mass (kg C m^{-2})	
Aboveground biomass	0.0198	0.0216	0.0309
Picea mariana (Miller) Britton	0.0198	0.0100	0.0163
Larix laricina (Du Roi) K. Koch	–	0.0116	0.0146
Acer sp.	–	–	0.0
		Tree height (cm ± SD)	
Picea mariana (Miller) Britton	89.4 (41.5)	87.2 (37.2)	70.76 (31.3)
Larix laricina (Du Roi) K. Koch	–	104.6 (42.0)	78.0 (37.1)

Note. Value in brackets is the standard deviation of the estimate from the allometric equation converted as appropriate using error propagation rules.

A significant relationship was found between NEE and WTD (LME, $F_{1,72} = 7.2$, $p = 0.0089$; Figure 6a) but not for GEP and ER. A significant relationship was also found between NEE and ST at 10 cm depth (LME, $F_{1,72} = 45.3$, $p < 0.001$) and ER and ST at 10 cm depth (LME, $F_{1,72} = 55.9$, $p < 0.001$; Figure 6b). The LME models explained 65% and 57% of the variance in NEE and ER, respectively. The model only explained 12% of

Table 3
Total Understory Biomass for the Three Subplots at Heaven Swamp

	Total Mass (g C m^{-2} ± SE)		
Vegetation group or species	HS-1	HS-2	HS-3
Ericaceae	5.2 (2.9)	15.8 (14.9)	43.2 (36.2)
Pyrola minor L.	4.0 (1.8)	–	1.3 (1.2)
Rhododendron groenlandicum (Oeder) Kron & Judd	1.2 (1.2)	3.9 (3.9)	14.4 (12.8)
Vaccinium oxycoccos L.	–	–	2.0 (1.6)
Vaccinium vitis-idaea L.	–	11.9 (11.0)	25.4 (20.7)
Cyperaceae (*Carex* sp.)	5.3 (2.9)	0.1 (0.1)	1.1 (0.7)
Other Vascular	1.8 (1.0)	0.6 (0.6)	–
Equisetum fluviatile L.	–	0.6 (0.6)	–
Equisetum scirpoides Michaux	0.9 (0.6)	–	–
Mitella nuda L.	0.7 (0.2)	–	–
Rubus pubescens Rafinesque	0.2 (0.2)	–	–
Liverwort (*Lophozia ventricosa* (Dicks.) Durmort.)	1.2 (1.0)	–	–
Bryophytes	14.5 (12.8)	205.9 (94.8)	173.3 (118.5)
TOTAL	28.1 (20.5)	222.4 (110.4)	217.6 (155.3)

Note. Triplicates were performed at each subplot ($N = 3$). Value in brackets is the standard error of the mean.

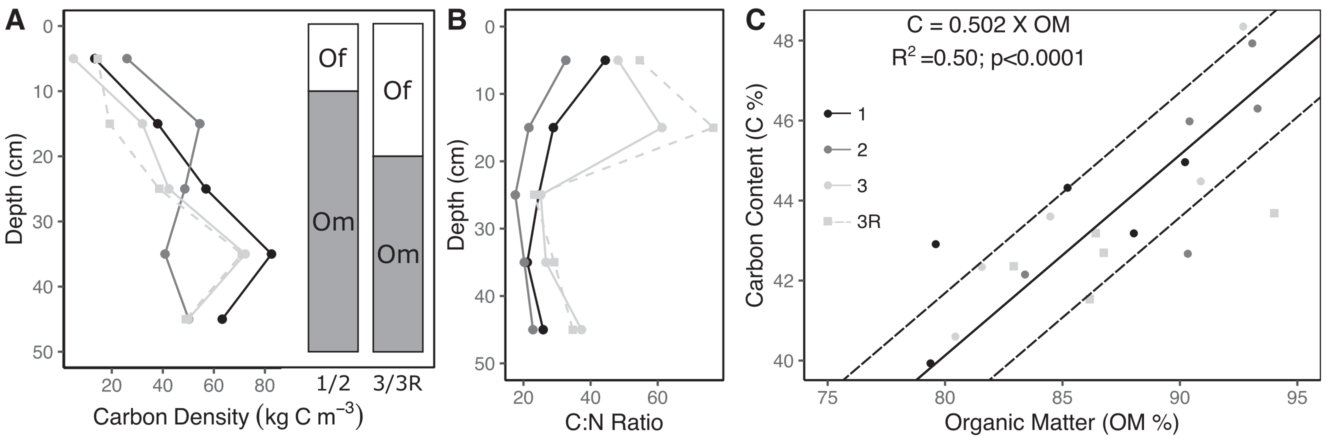

Figure 3. Belowground C density and soil classification (a), C:N ratio (b), and the relationship between C and organic matter content (c) for the upper 50 cm peat profile from three plots at Heaven Swamp. Linear regression in panel (c) was forced through (0,0) prior to fitting and dashed lines are the residual standard error. Soil classification after Agriculture and Agri-food Canada (1998). Of: organic-fibric and Om: organic-mesic.

the variance in GEP. No significant relationship was found between GEP and ST (LME, $F_{1,68} = 0.004$, $p = 0.9$), however there was a significant relationship found between GEP and GCC (LME, $F_{1,68} = 8.01$, $p = 0.0061$; Figure 6c), unlike NEE and ER. Finally, no significant relationship was found between CH_4 emissions and either WTD (Figure 6d) or ST at 30 cm depth (LME, $F_{1,23} = 0.01$, $p = 0.9$ and LME, $F_{1,23} = 1.8$, $p = 0.2$, respectively).

4. Discussion

This study investigated C stocks and growing season C fluxes in a representative boreal conifer swamp from Western Canada. As far as we know, this is the first study to measure plot-scale CO_2 and CH_4 fluxes from this type of swamp across boreal Canada (Davidson et al., 2022). Here, we contextualize our results by comparing them with other wetland studies. Additionally, we discuss the drivers of C and GHG exchange. Finally, we consider the implications of our work.

4.1. Above- and Belowground C Stocks

Overall, all plots contained sizable stocks of C with an overall mean of 134 kg C m^{-2}. Mean aboveground biomass was 5 kg C m^{-2}, which is low compared to the mean of all needle-leaved swamps of 22 kg C m^{-2} (Davidson et al., 2022). However, most of the biomass measurements synthesized by Davidson et al. (2022) are from south of 40°N, and therefore their value is likely to be unrepresentative of biomass C stocks in cool temperate and boreal swamps. Our value for aboveground C is the same as mean estimates of aboveground C biomass for boreal forest in the same region (Banfield et al., 2002), suggesting little difference between swamp and upland forest C stocks in this region (Table S1 in Supporting Information S1). The forest understory made a negligible contribution to total aboveground C stocks. In contrast, approximately 95% of total C stocks were found as SOC. This was due to a combination of deep peat (>2 m) and high C content; 50% of soil OM was C, in keeping with synthesized data for northern herbaceous and woody peat (Loisel et al., 2014). As such, our results are similar to those from

Table 4
Summary (Mean ± SD) of the C Flux (Gross Ecosystem Productivity, Ecosystem Respiration, Net Ecosystem Exchange, Methane (CH_4), Soil Temperature, and Water Table Depth at Both Vegetation Flux Collar Types at Heaven Swamp)

	GEP	ER	NEE	CH_4	ST at 10 cm depth	ST at 30 cm depth	Water table depth
Plot type		$g\ CO_2\ m^{-2}\ d^{-1}$		$mg\ CH_4\ m^{-2}\ d^{-1}$		°C	cm bgs
Feather moss	−1.8 (4.0)	12.6 (9.1)	10.5 (8.6)	30.6 (46.0)	11.9 (3.6)	8.5 (2.7)	12.2 (6.7)
Sphagnum	−2.6 (3.6)	13.6 (9.7)	11.1 (10.5)	49.9 (74.7)	11.3 (3.9)	8.4 (2.9)	11.3 (5.7)
Clipped	–	6.9[a] (4.6)	–	5.3[a,b] (11.9)	12.0 (3.2)	7.9 (2.8)	8.3 (11.1)

[a] Soil only flux. [b] CH_4 flux measurements for only May–June.

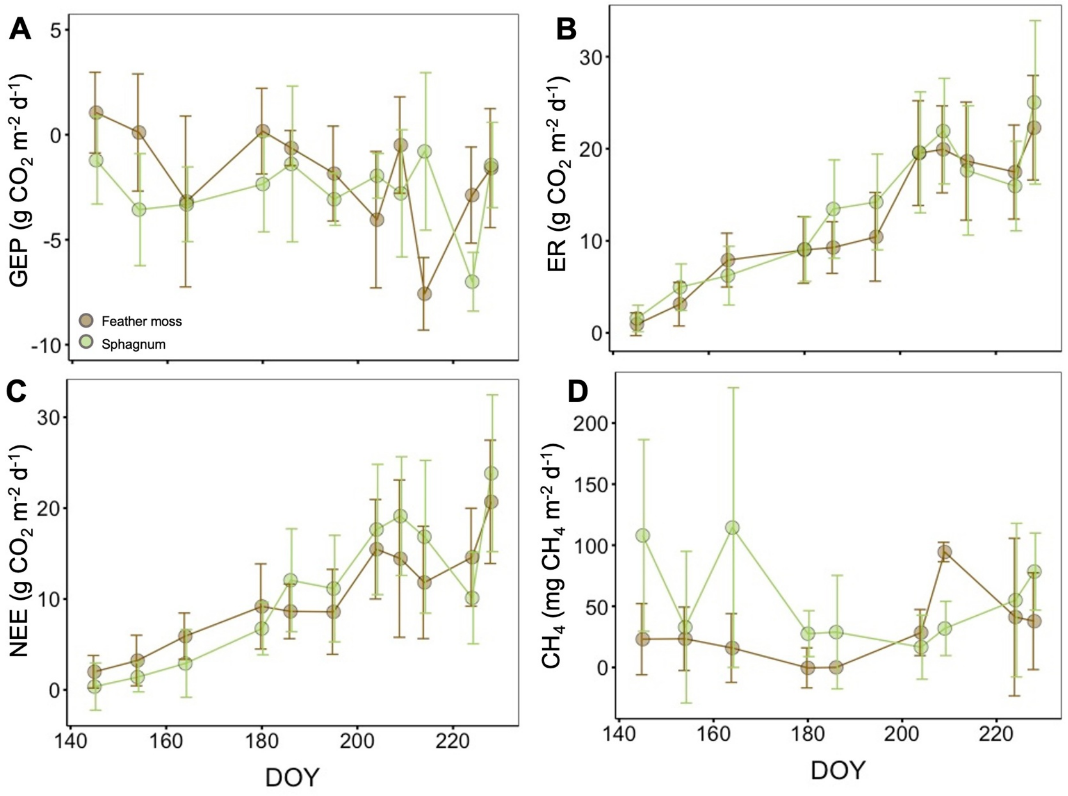

Figure 4. Time series plots of gross ecosystem productivity (g CO_2 m^{-2} d^{-1}) (a), ecosystem respiration (g CO_2 m^{-2} d^{-1}) (b), net ecosystem exchange (g CO_2 m^{-2} d^{-1}) (c), and CH_4 flux (mg CH_4 m^{-2} d^{-1}) (d) measurements for both Feather moss ($n = 6$) and Sphagnum ($n = 6$) collars at Heaven Swamp.

forested peatlands in eastern Canada, where C stored as tree biomass (1.5–5.7 kg C m^{-2}) was considerably less than SOC (23–170 kg C m^{-2}) (Beaulne et al., 2021; Magnan et al., 2020). SOC stocks reported by Beaulne et al. (2021) and Magnan et al. (2020) are smaller than ours (~130 kg C m^{-2}) because their peat depths were only 0.4–1 m. Our SOC stock estimate at the same depths is higher than those reported for upland boreal forests (ranging between 8 and 16 kg C m^{-2} (Banfield et al., 2002; Marty et al., 2015).

4.2. CO_2 and CH_4 Fluxes and Associated Environmental Drivers

Despite large belowground C stocks, over the course of the growing season the understory/soil of Heaven Swamp was a source of both CO_2 and CH_4. There was no significant difference in CO_2 or CH_4 fluxes between feather moss and sphagnum collars. This result is at odds with work suggesting differences in photosynthetic properties between these 2 moss groups (Kangas et al., 2014) but may simply arise due to the low number of collar replicates. For CO_2, overall mean GEP was −2.6 g CO_2 m^{-2} d^{-1}, whilst ER was 13.1 g CO_2 m^{-2} d^{-1}, resulting in a net efflux of CO_2. ER correlated positively with ST, reflecting the well-understood response of microbial respiration to warmer conditions (Lloyd & Taylor, 1994; Silvola et al., 1996). A similar result to Davidson et al. (2021) was found in relation to increasing vegetation greenness (GCC) and GEP, showing that more productive vegetation (i.e., greater CO_2 uptake) is related to green leaf phenology. In general, there is a lack of measurements of swamp CO_2 fluxes, and those that do exist overwhelmingly focus on soil fluxes only (Davidson et al., 2022). Nevertheless, our ER fluxes are comparable to those from northern swamps (beyond 40°N) for which the collated mean is 14.7 g CO_2 m^{-2} d^{-1} (Davidson et al., 2022). Despite measured net emission measured for understory NEE, our data do not necessarily suggest that Heaven Swamp is a net source of C to the atmosphere.

In northern swamps, litterfall inputs of C can be particularly high (e.g., 540 g m^{-2}) and outweigh gaseous C losses (Kendall et al., 2021). Similarly, NPP of trees could also offset gaseous C losses (J. Laine et al., 1996), with estimates of NPP in black spruce stands ranging from 44 g dry mass m^{-2} yr^{-1} in a moderate rich fen in Alberta

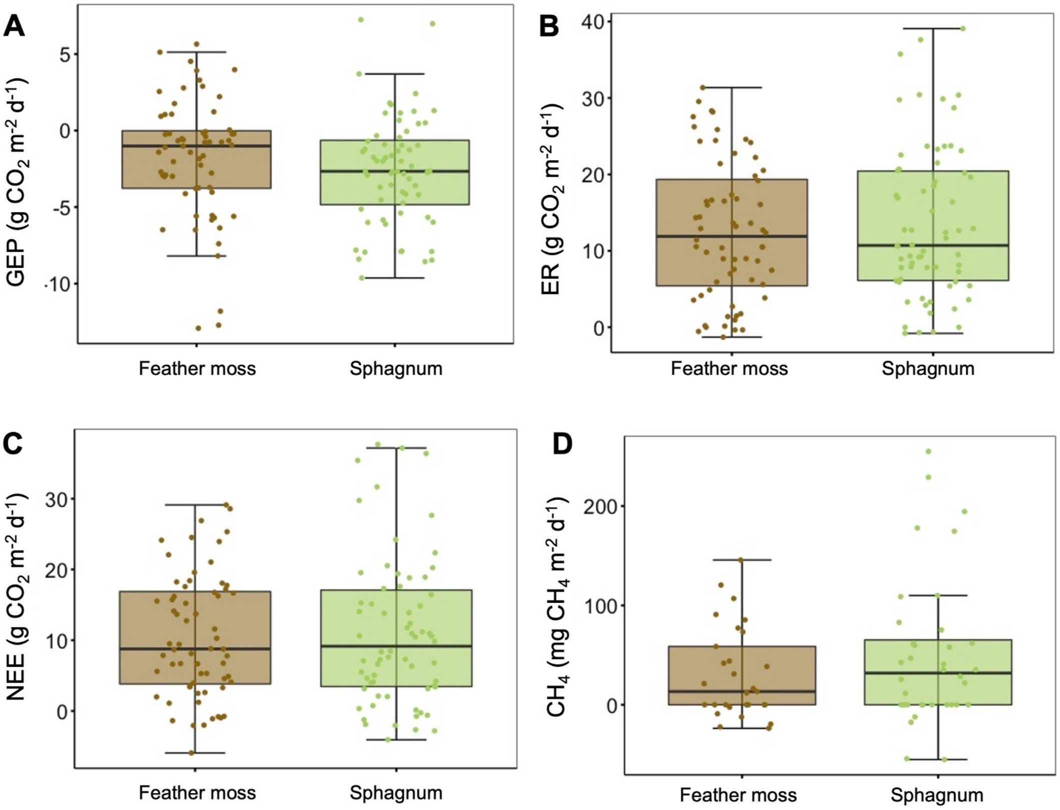

Figure 5. Gross ecosystem productivity (g CO_2 m^{-2} d^{-1}) (a), ecosystem respiration (g CO_2 m^{-2} d^{-1}) (b), net ecosystem exchange (g CO_2 m^{-2} d^{-1}) (c), and CH_4 flux (mg CH_4 m^{-2} d^{-1}) (d) measurements for both Feather moss ($n = 6$) and Sphagnum ($n = 6$) collars at Heaven Swamp.

(Szumigalski & Bayley, 1996) to 144 g C m^{-2} yr^{-1} in a black spruce stand with a 20–30 cm organic layer over mineral soil in Saskatchewan (Gower et al., 1997). Given we did not measure belowground biomass and NPP directly, there is potential that we are underestimating this component. In colder, wetter soils, *P. mariana* has been shown to allocate relatively more NPP belowground (Gower et al., 2001; Vogel et al., 2008), as well as more to fine roots compared deciduous species (Gower et al., 2001). This could mean that fine root turnover is likely contributing a significantly greater input to soil organic carbon in these boreal conifer compared to temperate deciduous swamps. Without measuring or modeling all CO_2 pathways in Heaven Swamp, no firm conclusions can be drawn.

Overall mean CH_4 flux from feather moss and sphagnum collars was ~40 mg m^{-2} d^{-1}, which is similar to the synthesis value for swamps given by Turetsky et al. (2014). The mean emission from collars where vegetation was clipped was lower, at 5.3 mg m^{-2} d^{-1}. Methane measurements from clipped collars only took place for 2 months, and thus are not directly comparable with vegetated collars. However, we can estimate that understory autotrophic respiration was 4.3 g CO_2 m^{-2} d^{-1}, substantially lower than the ER measured (~13 g CO_2 m^{-2} d^{-1}), a similar pattern shown by Munir et al. (2017) in a drained black spruce bog. The lack of a relationship between CH_4 flux and WTD is perhaps surprising, considering how WT is often viewed as a dominant control on peatland CH_4 emission (e.g., Evans et al., 2021; Turetsky et al., 2014). However, this relationship is frequently only apparent at large spatial/multi-site scales and/or over longer time periods (Treat et al., 2007), and many studies do not find WTD as an overriding control (e.g., Green et al., 2018; A. Laine et al., 2007; Levy et al., 2012; Wen et al., 2020), including in swamps (Koskinen et al., 2016). Within individual sites, WTD is not always an effective proxy for zones of CH_4 production, because peat soils can be highly heterogeneous with oxic areas below the water table and anoxic areas above it, over very small (cm^2) scales (Askaer et al., 2010). Additionally, at our site WTD varied across a comparatively small range, 2–24 cm below the peat surface. Other studies have suggested that WTD acts

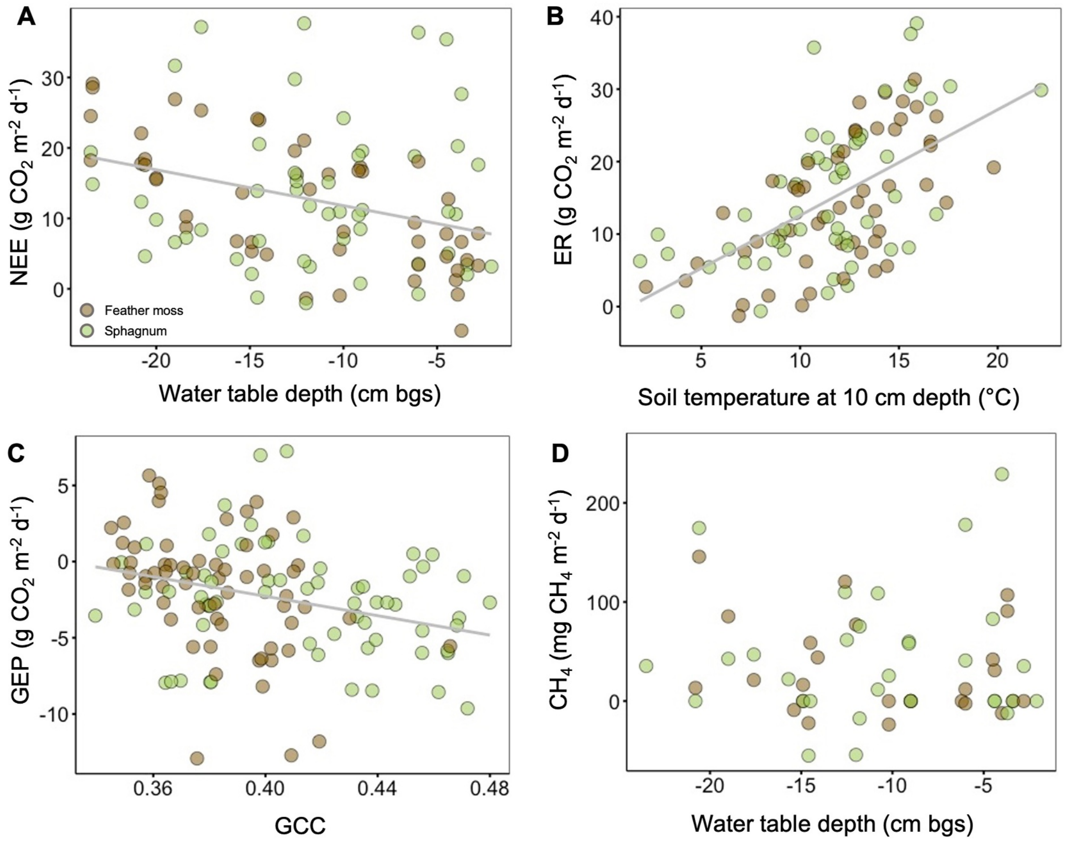

Figure 6. Relationship between water table depth (below ground surface (bgs)) and net ecosystem exchange (g CO_2 m^{-2} d^{-1}) (a), soil temperature at 10 cm depth (°C) and ecosystem respiration (g CO_2 m^{-2} d^{-1}) (b), green chromatic coordinate and gross ecosystem productivity (g CO_2 m^{-2} d^{-1}) (c) and water table depth (bgs) and methane emissions (mg CH_4 m^{-2} d^{-1}) for both vegetation plot types at Heaven Swamp.

as a “cut-off” for CH_4 production, with emissions increasing rapidly as WTD becomes shallower than 20–30 cm (Couwenberg & Fritz, 2012; Evans et al., 2021; Hondula, DeVries, et al., 2021; Levy et al., 2012).

Furthermore, and in contrast to both bogs and fens, swamps have a broad range of WTDs where large CH_4 emissions can occur (Turetsky et al., 2014). Other studies of forested peatlands have observed large variation in CH_4 fluxes over small scales (e.g., 15 m, Korkiakoski et al., 2017). Thus, we assume in our study that WTD was conducive to maintain CH_4 emissions throughout the measurement period, and other factors (temperature, vegetation, soil structure, nutrients, etc.) were implicated in driving higher/lower emissions from day-to-day. A second possibility is that WTD and CH_4 were related, but that this relationship was obscured due to hysteresis (e.g., A. Laine et al., 2007; Moore & Dalva, 1993).

4.3. Implications

Our results show that Heaven Swamp has sequestered large volumes of organic C in biomass and soil and continues to play an active role in ecosystem-scale gaseous C cycling. SOC stocks at Heaven Swamp (~130 kg C m^{-2}) are approximately the same as those in other Canadian peatlands (50–220 kg C m^{-2}, Akumu & McLaughlin, 2013; Beilman et al., 2008) which, on face value, suggests that boreal swamps are not “special cases” that require additional scrutiny and should be included in estimates of boreal peatland area. However, this is only half of the story; this site is classified as upland in the Alberta Biodiversity Monitoring Institute's Wetland Inventory (DeLancey et al., 2020) and therefore soil C stocks would potentially not be fully accounted for. The landscape-scale importance of northern swamps as “cryptic wetlands” has long been recognized for aquatic C exports (Creed et al., 2003), but the unmapped “cryptic carbon” these swamps hold is only now being properly considered. Emerging research in the United States suggests that forested wetlands contain vast stores of previously unaccounted C (Stewart et al., 2024). Similarly, although many forested wetlands are small (such as Heaven Swamp), their potentially abundant natures means that their cumulative CH_4 emissions can influence landscape-scale budgets (Hondula, Jones, & Palmer, 2021). Thus, there is a clear need to accurately map these swamps, their hydrology, and their C stocks and fluxes, to properly inform regional, national, and global budgets.

Furthermore, a timely accounting of the role these swamps play in C and GHG cycling is also necessary to define a baseline from which future global change can be evaluated. This is particularly relevant because boreal forests are predicted to experience the largest temperature increase of any forest biome (Gauthier et al., 2015). Additionally, climate driven changes in drought, fire regimes and biotic disturbance (e.g., bark beetle) all threaten to alter the stability of boreal forests, and their associated carbon stocks and fluxes (Anderegg et al., 2020). The magnitude and direction of future changes in the various components of swamp C and GHG balances is hard to predict, due to non-linear responses and feedbacks (Bonan, 2008). However, for *P. mariana* (the dominant tree species at our site), a combination of elevated air temperatures with increased soil water availability during spring will likely prolong the growth season length through a shift in key photosynthetic parameters. Together, these changes have the potential to significantly increase net annual C uptake (Jensen et al., 2015). Furthermore, there is potential for a shift in vegetation communities toward species more competitive in warmer environments, with some locations becoming dominated by deciduous species such as *Salix* spp. and *Alnus* spp. Balanced against this, research from northern peatlands shows that rising temperatures could lead to increased peatland CH_4 production, or this might be outweighed by reduced CH_4 production and greater CH_4 oxidation due to changes in water storage (Roulet et al., 1992).

Like other northern wetlands, swamps are complex ecosystems with a disproportionately large role in terrestrial carbon storage and flux. However, their distribution on the landscape, importance to biogeochemical cycling, and potential response to climate and other global changes remains poorly understood. For these reasons, and because of a current lack of data and biogeochemical understanding, we call for the establishment of a coordinated swamp observatory throughout the northern hemisphere. Measurements should include above and belowground carbon stocks; C and GHG fluxes from soils and vegetation, including tall tower eddy covariance to measure landscape-scale exchange (e.g., Deshmukh et al., 2021), and high-frequency water table data. Such measurement efforts need to be concerted and long-term. This approach would help bring these long underappreciated northern wetlands into the same spotlight occupied by bogs and fens.

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Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data available via the Dryad Digital Repository: Davidson (2024) Boreal conifer swamp carbon stocks and fluxes, Alberta, Canada. Dryad, https://doi.org/10.5061/dryad.dv41ns267.

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