Quantifying carbon pools and fluxes in Southern Ontario temperate swamps

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SUMMARY

Swamps are treed wetlands, which account for the highest areal extent of wetland types in Southern Ontario due to the difficulties of conversion for development and agriculture. However, little is known about the environmental factors and processes that influence carbon (C) dynamics or the resulting C stocks and fluxes therein. We studied 12 swamps across Southern Ontario for 12 consecutive months to measure the exchange of carbon dioxide (CO_2) and methane (CH_4) between soil and atmosphere and estimate current C stocks in soil and biomass. We found mean growing season soil respiration of CO_2 and CH_4 across the swamps ranged from 11 g m^{-2} d^{-1} to 49 g m^{-2} d^{-1} and -3 mg m^{-2} d^{-1} to 44 mg m^{-2} d^{-1}, respectively, with a water table threshold at about -20 cm where fluxes changed substantially. Biomass stored 7.92–37.0 kg m^{-2} of C across the sites, and soil stored 11.6–35.5 kg m^{-2}. Over the study year, the swamps functioned as C sinks and followed similar patterns of relationships to environmental conditions as bogs and fens, with little difference between hydrogeomorphic settings or canopy types.

KEY WORDS: carbon dioxide, forested peatland, methane, synoptic, wetland

INTRODUCTION

Swamps are forested wetlands that account for an important portion of wetland cover in Canada (Riley 1994, Tarnocai 2006, Byun *et al*. 2018, Amani *et al.* 2019). Despite their prevalence and potential as natural climate solutions, swamps are typically either combined with other wetland types (Kuhn *et al.* 2021, Olefeldt *et al.* 2021) or absent as a specific category (Bona *et al.* 2018, Webster *et al.* 2018, Pontone *et al.* 2024) from current models of peatland storage and carbon (C) cycling; thus, their contribution to C stocks and greenhouse gases are not fully considered in management decisions (Jenkins *et al*. 2006). Although some classification systems identify swamps as purely mineral wetlands, swamps can also contain mineral soils with thin organic layers or > 40 cm of organic soil, meeting the definition of peatlands (Joosten & Clarke 2002). This may may result in potentially large C soil stocks being missed, and creates variability in calculating the potential C stocks contained within the soil if the actual soil composition is not known (Byun *et al.* 2018, Dazé *et al.* 2022). The lack of field data makes identifying, mapping and parameterising models for swamps difficult (Yu *et al.* 2010, Bona *et al.* 2018). While a growing number of studies of subtropical and tropical swamps have been completed in recent years, data on temperate and boreal swamp C stocks and fluxes remain scarce (Davidson *et al.* 2022). This study aims to fill this knowledge gap by measuring across 12 swamp study sites in Southern Ontario.

Regardless of soil type and depth, swamps are typically defined by having hydric mineral or organic soils with seasonal or persistent surface water and over 20–30 % cover by trees greater than 5 m in height (NWWG 1997, MNRF 2022). In the USA, Scrub-Shrub Wetlands have > 30 % cover by shrubs and young trees < 6 m (20 feet) tall, including tree species that are stunted by adverse environmental conditions, while Forested Wetlands are those with > 30 % cover of trees at least 6 m (20 feet) in height (FGDC 2013). The Ramsar Convention on Wetlands classifies swamps as shrub-dominated, tree-dominated or forested wetlands or peatlands (Ramsar 2016). Two main characteristics are used to classify swamps in Canada: hydrogeomorphic setting and canopy type (NWWG 1997). Hydrogeomorphic setting describes the position of a swamp within the landscape in terms of proximity to the regional groundwater table and surface water bodies such as lakes and rivers, via elevation (Trettin & Jurgensen 2003). Canopies in swamps are dominated by either trees or tall shrubs, with tree cover further divided into broad-leaved, needle-leaved or mixedwood (NWWG 1997).

In Canada and the United States (US), high organic matter content and bulk density in swamp soils results in high soil C stocks in the top 0–90 cm across all four canopy types (Davidson *et al*. 2022). Below the canopy, understorey and ground layer vegetation may vary from sparse to fully covered, highlighting a wide range in possible cover and biomass (Bona *et al.* 2018, Davidson *et al*. 2022).

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Higher aboveground biomass has been found in swamps than in treed bogs and fens or marshes (Bona *et al.* 2018) and biomass in swamps is comparable to the range of mature forests across the US and Canada (Zhu *et al.* 2018), while soil C stocks are 4–5 times greater than in forest soils across the US (Domke *et al.* 2017). Carbon stocks in peat are 4–25 times higher than in the trees of boreal black spruce forested peatlands (Magnan *et al.* 2020, Beaulne *et al.* 2021). Few studies on soil CO_2 (n = 7) and CH_4 (n = 15) respiration from swamps exist, with a bias toward mixedwood and needle-leaved sites, respectively (Davidson *et al.* 2022). Measured fluxes of both gases in North America generally decrease toward the north (Davidson *et al.* 2022), and CH_4 fluxes are comparable to those in Canadian bogs and fens (Webster *et al.* 2018).

Given that biomass C stocks in swamps are similar to those in other forest types and soil C stocks are much greater, protection of these ecosystems from land-use change would provide greater conservation of land-based carbon stocks than protecting the same area of upland forest. Due to the historical conversion of other wetland types to agricultural and developmental use, swamps are now the dominant wetland type in Southern Ontario (Byun *et al.* 2018), making it even more important to understand their C dynamics such as net CO_2 exchange and CH_4 emissions, especially under a changing climate. This study provides data on temperate swamps in Southern Ontario, Canada to aid in more accurate carbon accounting and climate modelling. The objectives of this study were to:

(1) provide estimates of the current carbon stocks in soil and biomass, and net exchange of CO_2 and CH_4, between soil and atmosphere for 12 swamps in Southern Ontario;

(2) determine the effect of hydrogeomorphic setting and canopy type on soil CO_2 and CH_4 fluxes; and

(3) assess whether it is possible to estimate soil CO_2 and CH_4 across a range of swamp types with minimal information.

METHODS

Study sites

All 12 sites are located in Southern Ontario, between 42–44 °N and 80–82 °W (Figure 1, Table 1), and were identified and classified using the Canadian Wetland Classification System (NWWG 1997). Sites were chosen to cover a large portion of Southern Ontario and by the availability of access permission. All sites are owned by the *rare* Research Reserve, conservation authorities or the University of Waterloo. The swamps are situated in four hydrogeomorphic settings, include all four canopy types, and have organic or mineral-organic soils (Table 1). Basin swamps (n = 4) are well defined by the sides of the basin and occur in glacial deposits (e.g., kettle holes) or bedrock (NWWG 1997). Sifton and Spongy Lake are both kettle-hole peatlands with perimeter swamps; Sifton is ~23 ha in area and up to 11–14 m in depth (City of London 2009) and Spongy Lake is ~18 ha and up to 5–6 m (Dempster *et al.* 2006). Both receive water inputs from precipitation and surface runoff, and water loss is primarily through evapotranspiration with very low amounts moving vertically to recharge regional groundwater (Dempster *et al.* 2006, City of London 2009). Spongy Lake has a large, shallow open water expanse in the centre of the basin where water level can drop considerably in dry years. The centre of Sifton is domed, raising the local water table and feeding and/or moderating the water table in the edge swamps (City of London 2009). Ancient Woods is not a kettle hole but, rather, a clay-lined depression within a larger low-lying area without steep delineated edges. The depression itself has an estimated area of 0.3 ha and its deepest point is ~1 m below the edges with no apparent connection to groundwater (personal observation). The depression fills with surface runoff after precipitation events and appears to spill over the south edge until the water level drops below this height. Unconfined flat swamps (n = 6) lack clear topographical boundaries or banks and often occur in glacial lake beds or outwash (NWWG 1997). Riparian swamps occur along the edges of rivers, streams and lakes, and are directly influenced by the water body; riverine swamps in particular (n = 2) are situated along the banks of rivers and streams and often experience flooding when water levels are high (NWWG 1997). Canopies are dominantly broad-leaved (hardwood species that lose their leaves in the autumn, e.g., *Acer* spp., *Betula* spp.; n = 3), needle-leaved (softwood species with leaves modified as needles or scales, e.g., *Picea* spp., *Thuja* spp.; n = 3), mixedwood (neither needle-leaved nor broad-leaved species dominate; n = 5), or tall shrubs (multi-stemmed woody species < 3 m at maturity, e.g., *Rhamnus* spp., *Cornus* spp., *Alnus* spp.; n = 1).

The region is within the humid continental climate zone, characterised by mild summers and no significant precipitation differences between seasons. The coldest month averages below 0 °C, with all months averaging below 22 °C and at least four months with average temperatures greater than or equal to 10 °C (CEC 2021). Average growing season in the study area is 188 days. Average total

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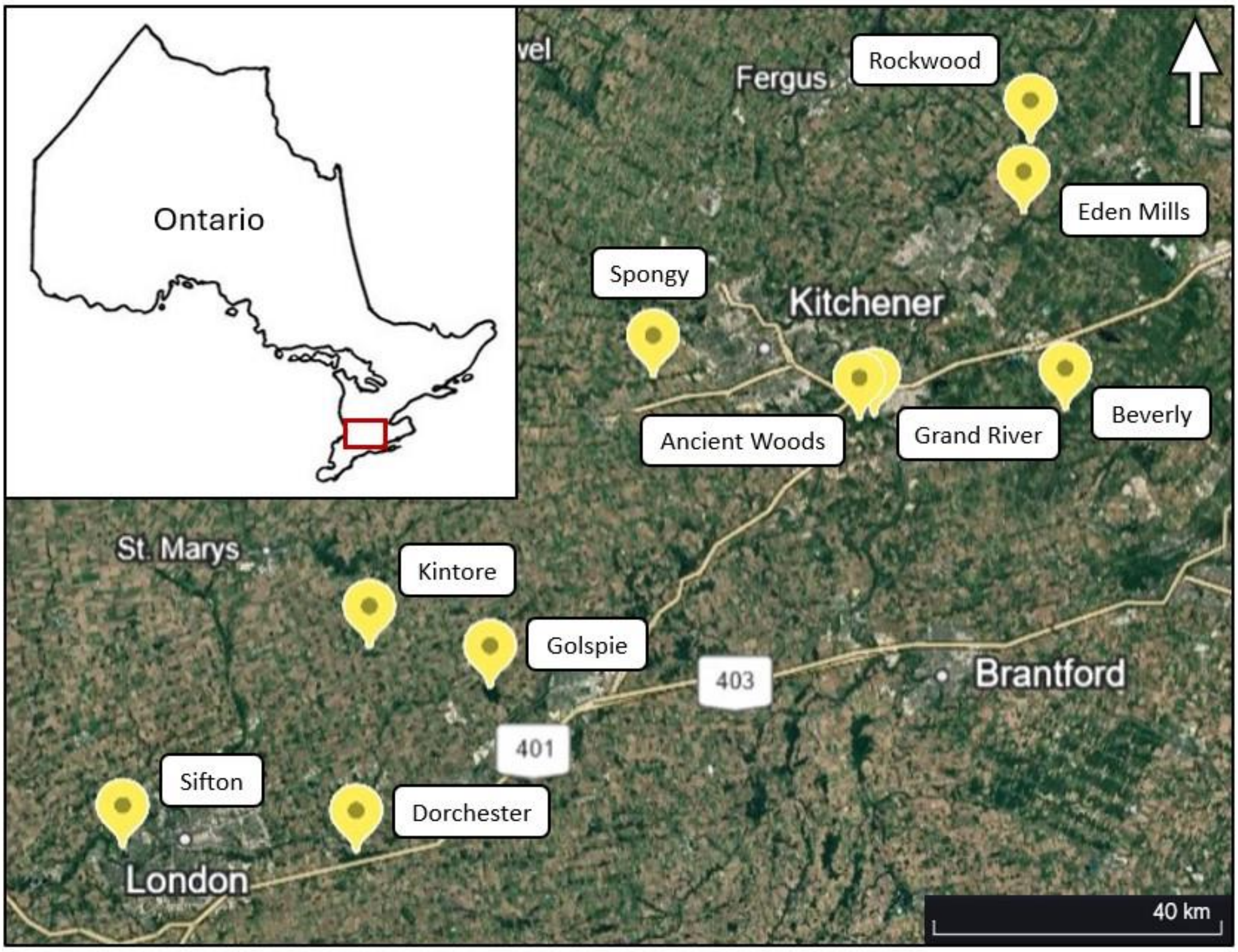

Figure 1. Map of site locations within the study area and Ontario (inset). Imagery from Google Earth (01 Jan 2025; accessed 18 Sep 2025).

Table 1. Summary of sites.

Site	Hydrogeomorphic setting	Canopy type	Soil type	Location (degrees) latitude longitude
Ancient Woods (AW)	Basin	Broad-leaved	Mineral	43.375982, -80.369919
Spongy Lake (SL)	Basin (kettle)	Broad-leaved	Organic	43.415068, -80.636090
Sifton B (SB)	Basin (kettle)	Needle-leaved	Organic	42.970822, -81.322589
Sifton A (SA)	Basin (kettle)	Shrub	Organic	42.970822, -81.322589
Grand River (GR)	Flat	Broad-leaved	Mineral	43.380983, -80.356012
Dorchester B (DB)	Flat	Broad-leaved	Mineral-organic	42.970488, -81.025187
Golspie (G)	Flat	Broad-leaved	Mineral-organic	43.121270, -80.845430
Beverly (B)	Flat	Broad-leaved	Organic	43.384143, -80.105097
Kintore (K)	Flat	Broad-leaved	Organic	43.161492, -81.005090
Dorchester A (DA)	Flat	Mixedwood	Organic	42.970488, -81.025187
Eden Mills (EM)	Riverine	Needle-leaved	Organic	43.570650, -80.152270
Rockwood (R)	Riverine	Needle-leaved	Organic	43.643069, -80.136263

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precipitation is 900–1000 mm with the rainiest months in spring and autumn; however, the main growing season of this study (2022) was hot and dry, with only 600–700 mm (Government of Canada 2024a). Southern Ontario is densely populated with 5–1000 people per square kilometre (outside of the Greater Toronto Area) (CEC 2020b) and is predominantly cropland with remnants of Carolinian and temperate continental forest (CEC 2020a, 2022). All sites are affected by some level of human activity but were chosen so as not to have any active clearing of the canopy within the past 100 years; therefore, disturbance is not considered specifically as an effect in this study.

Soil CH_4 and CO_2 fluxes

We measured understorey CO_2 and CH_4 fluxes simultaneously with a CH_4/CO_2/H_2O Trace Gas Analyzer (LI-7810, LI-COR, Nebraska, USA) approximately once per month from June 2022 to May 2023 via the closed chamber method (Griffis *et al.* 2000). At each location, acrylic collars (20 cm diameter, 10 cm tall) were permanently installed in the ground. Three locations were chosen within each site to characterise wet, dry and intermediate hydrological conditions, and contained forbs, grasses, mosses and seedlings < 24 cm in height. An acrylic chamber set into a corresponding groove in the collar created a seal over soil and vegetation and a small battery-operated fan continuously circulated the air within. Concentration of CO_2 was continuously measured every second with a transparent chamber (20 cm diameter × 40 cm tall, enclosing all vegetation within the collar) over a 3-minute closure, along with temperature and humidity within the chamber, resulting in a measure of understorey net ecosystem exchange (NEE_u). NEE_u is the overall exchange of CO_2 between the ecosystem and atmosphere, including respiration from the soil and uptake by understorey vegetation. Similarly, an opaque chamber (20 cm diameter × 24 cm tall) allowed for ecosystem respiration (ER; CO_2 released from soil and understorey plants) and CH_4 flux to be measured. By subtracting ER from NEE_u, gross ecosystem productivity of the understorey (GEP_u; CO_2 taken up by understorey vegetation) was calculated. We use the sign convention such that C emission to the atmosphere is positive and uptake from the atmosphere is negative (Ryan & Law 2005). A tablet computer connected to the LI-7810 enabled observation of fluxes in real time, allowing for adjustments to ensure chambers were well sealed to obtain a clear linear change in concentration over time. Fluxes were calculated from the slope of the linear change in concentration within the chamber over time, adjusted for chamber volume and the temperature within the chamber. The order of plots was changed each visit to account for diurnal light and temperature changes. For every flux measurement, soil temperature (ST) profiles from -5 to -30 cm were measured with a thermocouple soil temperature probe (Digi-sense) and reader (Omega HH200A) and water table position (WT) was measured as depth below ground surface in a dipwell (internal diameter 10 cm) adjacent to each collar.

Further inspection for linearity and slope of concentration vs. time relationships was done using the processing tool PEDRO (Newton 2023). Fluxes were accepted if $r^2 > 0.7$ (clear slope) or < 0.3 (flux nearly zero). After processing, 379 CO_2 (18 % data loss) and 382 CH_4 (8 % data loss) soil fluxes were included in the further analysis. Annual NEE_u and CH_4 flux were estimated by multiplying the mean of all fluxes from each month by the number of days in the month, then adding the monthly totals together. For months without data due to access issues or data loss during quality control, the mean flux of the preceding and following months was used.

Biomass and soil carbon

Tree and understorey vegetation surveys were conducted at all 12 sites in late July through early August 2022. Trees were measured in three 20 m × 20 m plots at each site. Every individual ≥ 3 m tall was identified to genus, and to species if possible, and its diameter at breast height (DBH) was measured. Allometric equations were used to estimate biomass carbon (C) of trees (kg m^{-2}; Ung *et al*. 2008). Quadrats (size 1 m × 1 m) were used to record % cover of understorey and overhanging vegetation (see Table A1 in the Appendix), as well as for biomass collection, with three replicates per collar (n = 9 per site); branches of young trees and shrubs ≤ 3 m tall that hung over the quadrat were included in biomass collection. All live plant material within the quadrat was clipped to soil level, and branches cut at the point where they crossed into the quadrat. Four litter traps (0.5 × 0.5 m) per site were installed between 15th and 30th August 2022 to catch leaves and twigs that fell from the canopy (adapted from Bernier *et al*. 2008). Litter from each trap was collected biweekly to monthly from September to November, then for a final time in May 2023 to include anything that fell over the winter and spring; this mass was added to the site total (Bernier *et al*. 2008). Biomass clippings and litter were stored in zip-top bags at 4 °C for a maximum of 48 hours before being dried at 60 °C until they reached a stable weight. The mass of litter from each trap was averaged for each site and then added over time to calculate total annual production.

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Dry mass was measured in g m^{-2}, and all biomass was converted to an estimated C stock using total C values from the bulk understorey of each site (39–45 %). Total C values were measured through combustion conversion of sample to gas in a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer.

A soil core to the confining layer or to a maximum depth of 50 cm (whichever was shallower) was collected within 2 m of each collar (n = 3 per site) across the 12 sites in 2022, using a Russian auger. Nine of the sites had a confining layer deeper than 50 cm. Cores were divided into 10 cm increments in the field, sealed in plastic zip-top bags, and returned to the laboratory. Samples were stored at 4 °C for 3–10 days before drying at 80 °C until they reached a stable weight; dry bulk density was calculated as dry mass per initial sample volume (g cm^{-3}). Half of the 10 cm increments, cut vertically, were analysed for organic matter content (OM, %) via loss on ignition. Approximately 3 g of soil was measured into a pre-weighed ceramic crucible, placed in a muffle furnace, and burned at 550 °C for four hours to ignite any organic material within (Heiri *et al*. 2001). Organic matter content was calculated as the weight lost as a percentage of initial mass, and organic C content as 50 % of OM (Kennedy & Woods 2013). The samples were then burned for two hours at 950 °C to ignite inorganic C (i.e., $CaCO_3$; Heiri *et al*. 2001)). Inorganic C content of the original sample was calculated as additional weight lost as a percentage of initial sample dry weight. Total C (kg m^{-2}) per core was calculated as the sum of all increments, and soil C per site as the average of all cores (n = 3).

Statistical analysis

All data analysis and visualisations were done using the statistical analysis program R (R Core Team 2013). Growing season (GS; 15 Apr – 20 Oct) was determined to begin when mean daily temperature was greater than or equal to 5 °C for five consecutive days after 01 Mar, ending when minimum daily temperature was less than -2 °C after 01 Aug (Mackey *et al.* 1996, Rafat *et al*. 2022). As it is well known that environmental conditions differ significantly between the GS and the non-growing season (NGS), we did not include season in the analyses. GEP_u and NEE_u were analysed for GS only as photosynthesis is minimal during the NGS. Not all combinations of settings and canopies were represented; therefore, interactions between site, setting and canopy could not be evaluated. Site, hydrogeomorphic setting, canopy, WT and soil temperature (ST) were used as fixed effects in separate linear mixed effects models for each flux component using the package *nlme* (Pinheiro *et al.* 2025). Collar was included as the random factor in each model to account for repeated measures. Differences were considered statistically significant when $p < 0.05$ in the *anova* output. Post-hoc Tukey tests (*emmeans* package, Lenth 2025) were performed for pairwise comparisons when an effect was significant. A value of 18 was added to CH_4 data to adjust for negative values before being log transformed to improve normality of residuals. Linear mixed effects models were created with ST or WT as fixed effects with interactions with hydrogeomorphic setting or canopy to evaluate whether response to environmental variables differed between settings or canopy types; site was included as a random effect. Due to the similarities between ST at 10 and 30 cm below surface, only 10 cm is presented in the results; data for ST at 30 cm can be found in Figure A1 in the Appendix. As biomass and soil C were measured only once, stored organic C amounts were expressed as annual averages per plot. Linear mixed effects models were used to evaluate C stocks against site, setting or canopy as fixed effects and plot as random effect.

RESULTS

Environmental conditions

The 2022 precipitation total for Southern Ontario was lower than the 30-year average resulting in dry conditions and deep WT through most of the growing season (GS); April 2023 saw higher than average precipitation while May 2023 was drier (Table A2). Mean WT during GS was shallower in basin sites than in flat or riverine sites ($F_{2,33} = 6.7453$, $p = 0.0035$; Table 2) and was driven by Sifton, where mean WT was shallower than at the other two basin sites ($F_{11,24} = 7.0285$, $p = < 0.0001$; Table 2). Similarly, WT was shallowest at shrub and needle-leaved sites, which include the two Sifton subsites ($F_{3,32} = 7.5167$, $p = 0.0006$). Mean WT in the non-growing season ranged from -53 cm to -1 cm among sites ($F_{11,24} = 8.2408$, $p = < 0.0001$; Table 2) and remained shallowest at basin sites. WT fell below the bottoms of the dipwells at Golspie (bottom = -100 cm, -85 cm, -85 cm; 6 days, n = 16), Grand River (bottom = -62 cm, -48 cm, -97 cm; 4 days, n = 10), and Rockwood (bottom = -82 cm, -69 cm, -54 cm; 3 days, n = 5). Samples with dry dipwell were removed from the analysis for gases × WT; therefore, minimum and mean WT are probably lower than shown (Table 2).

Mean GS ST at 10 cm (ST10) below surface was 14–17 °C, varying among sites (Table 2) with no notable differences between settings or canopies. Mean GS ST at 30 cm (ST30) was 12–16 °C (Table 2), lower at riverine and needle-leaved sites and increased with the presence of broad-leaved trees. Mean NGS ST10 cm varied from 4 °C to 8 °C across sites (Table 2), being coolest with shrub cover and warmer at broad-leaved sites. Mean NGS ST30 cm was 5–10 °C (Table 2) with no notable differences among settings or canopy cover types.

Carbon fluxes

Mean CH_4 fluxes during the GS ranged from -3 mg m^{-2} d^{-1} to 1,605 mg m^{-2} d^{-1} (Figure 2, Table A3). However, strong evidence indicated that only Kintore, Rockwood, Sifton A and Sifton B differed ($F_{11,24}$ = 23.9844, p = < 0.0001); fluxes from Sifton A and Sifton B were higher than from other sites by factors of 10 and 1,000 times, respectively. There was strong evidence that mean efflux from basin sites was higher than from flat sites which, along with efflux from riverine sites, was near zero ($F_{2,33}$ = 6.0997, p = 0.0056). Similarly, high CH_4 fluxes were observed at sites with needle-leaved and shrub canopies, which included Sifton B and Sifton A ($F_{3,32}$ = 3.4062, p = 0.0293). Mean NGS fluxes were predominantly near zero except for Sifton B at 228 mg m^{-2} d^{-1} ($F_{11,24}$ = 26.519, p = < 0.0001; Figure 3D). Methane efflux increased as water tables rose throughout the year with the exception of Sifton A and Sifton B (Figures 2B and 3E). In both seasons, CH_4 efflux increased substantially when WT reached approximately -20 cm. Warmer soils at both ST10 and ST30 corresponded with lower CH_4 flux for all sites except Sifton A and Sifton B (Figures 2C and 3F).

Mean understorey gross ecosystem productivity (GEP_u; uptake of CO_2 by understorey plants and soil organisms) during the GS ranged from -36 to -6 g m^{-2} d^{-1} (Figure 4A, Table A3), but strong evidence showed only Eden Mills and Grand River were different from Spongy Lake ($F_{11,24}$ = 3.432, p = 0.0056). Understorey productivity was highest (most uptake) in both flat and riverine sites, and in mixedwood sites. Generally, the understorey was more productive with wetter soils ($F_{1,166}$ = 18.6469, p = < 0.0001; Figure 4B) and as soils warmed, with the exception of Ancient Woods and Dorchester A at 10 cm ($F_{1,167}$ = 14.1687, p = 0.0002; Figure 4C) and Beverly, Eden Mills and Dorchester A at 30 cm ($F_{1,167}$ = 7.1529, p = 0.0082).

Mean ground layer respiration of CO_2 from the soil and understorey (ER; includes root respiration) during the GS ranged from 11 g m^{-2} d^{-1} to 49 g m^{-2} d^{-1}

Table 2. Descriptive statistics for seasonal water table (WT) and soil temperature (ST). Positive WT values indicate flooded conditions with WT above the ground surface. The water table fell below the bottoms of the dipwells at Golspie on six sampling days (n = 16), at Grand River on four sampling days (n = 10) and at Rockwood on three sampling days (n = 5). These values were removed from the analysis of WT, therefore the true minimum and mean water table levels at sites marked with asterisks (*) were probably deeper than shown.

Site	Growing Season						Non-Growing Season					
	WT (cm)				Mean ST (°C)		WT (cm)				Mean ST (°C)	
	Min	Max	Mean	Range	10 cm	30 cm	Min	Max	Mean	Range	10 cm	30 cm
Ancient Woods	-94	0	-45.6	94	15.1	14.2	-91	5	-44.3	96	6.0	6.8
Beverly	-54	0	-31.7	54	16.3	15.0	-34	14	-10.2	48	3.8	5.9
Dorchester A	-60	-28	-48.3	32	16.7	15.6	-49	-12	-28.1	37	5.0	6.5
Dorchester B	-59	-24	-43.7	35	16.7	15.6	-44	1	-21.7	45	4.8	6.1
Eden Mills	-61	-10	-33.6	51	15.0	13.6	-51	-7	-33.1	44	3.7	5.4
Golspie*	-74	7	-41.7	81	15.9	15	-74	-2	-52.8	72	5.9	7.4
Grand River*	-76	7	-32.5	83	14.9	14.3	-67	15	-36.7	82	5.7	6.9
Kintore	-59	-14	-40.8	45	15.6	14.7	-24	-2	-9.83	22	4.9	5.8
Rockwood*	-70	1	-37.2	71	13.9	12.3	-70	7	-20.7	77	4.1	5.8
Sifton A	-27	24	-4.25	51	16.8	15.9	-27	0	-12.1	27	3.9	5.7
Sifton B	-10	13	-0.25	23	15.2	14.4	-7	12	1.0	19	3.8	6.9
Spongy Lake	-53	-2	-28.1	51	14.7	13.5	-55	-24	-36.6	31	8.0	10.0

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($F_{11,24} = 4.84$, $p = 0.0006$) and was generally highest in flat sites and mixedwood canopies (Figure 5A, Table A3). Over the NGS, ER varied from 2 g m^{-2} d^{-1} to 23 g m^{-2} d^{-1} ($F_{11,24} = 1.45$, $p = 0.2129$) and was highest from needle-leaved and riverine sites (Figure 6D). Generally, ER decreased with deeper WT across both seasons, with the exception of Eden Mills and Dorchester A in the GS (Figure 5B) and Golspie and Sifton B in the NGS (Figure 6E). CO_2 efflux increased notably when WT reached approximately -20 cm and deeper. Warmer soils resulted in higher ER across sites and seasons, except for Kintore and Sifton B in NGS (Figure 6F) and Beverly and Eden Mills at 30 cm in GS (Figure 5C).

Mean net ecosystem respiration of the understorey (NEE_u; overall balance between GEP_u and ER in the understorey) during the GS ranged from 1 g m^{-2} d^{-1} to 24 g m^{-2} d^{-1} (Figure 7A, Table A3). The understoreys of all sites were a net source of CO_2, though only Sifton B differed from Kintore ($F_{11,24} = 3.047$, $p = 0.0109$). Mean NEE_u was highest (greatest efflux) from flat, broad-leaved and mixedwood sites. NEE_u

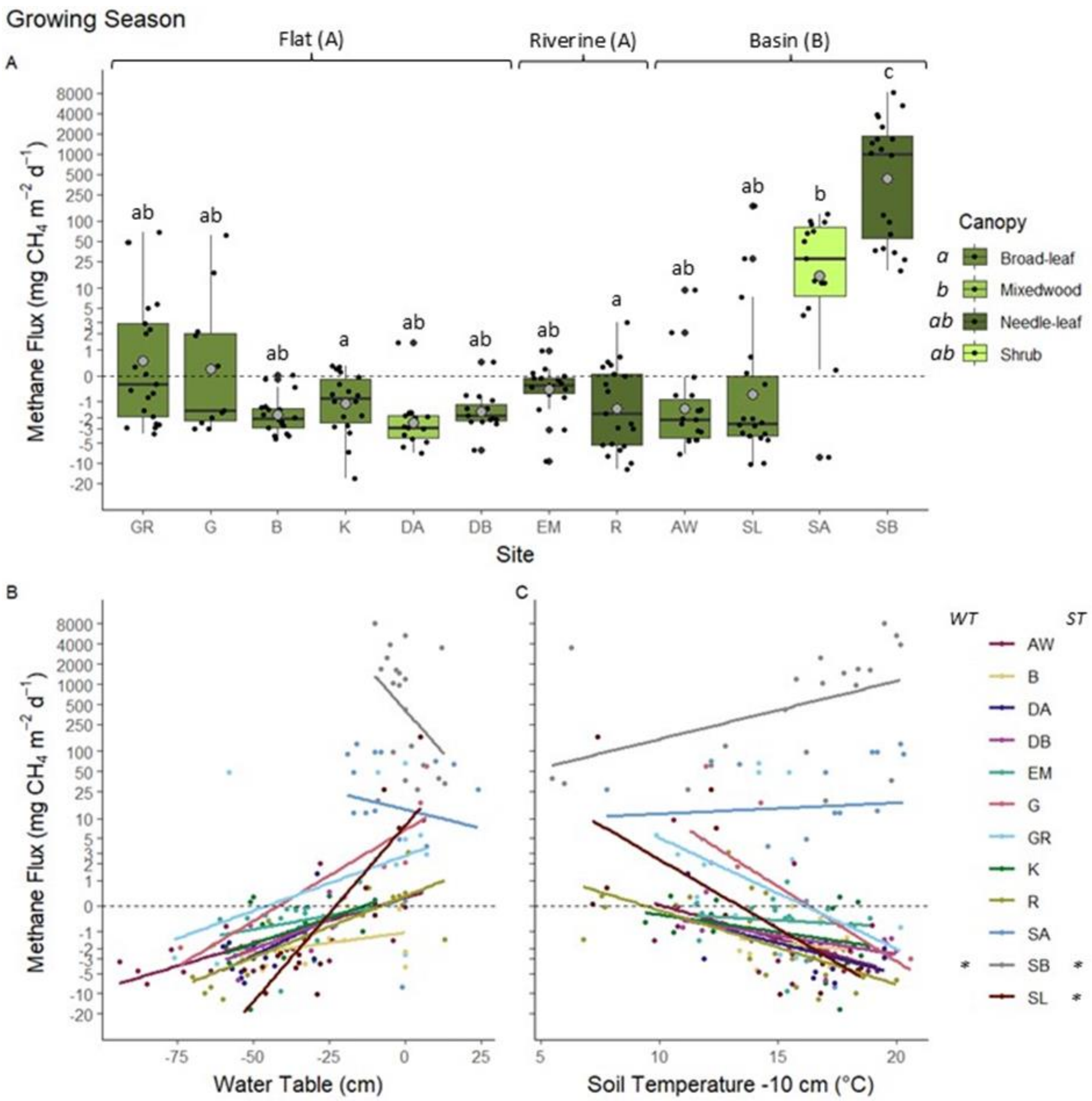

Figure 2. Growing season methane fluxes (mg m^{-2} d^{-1}). In (A), site, setting or canopy means are significantly different (based on post-hoc Tukey tests) if they do not share letters; lowercase letters refer to differences between sites, uppercase letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles within which 50 % of data points lie, and whiskers represent 1.5 times the interquartile range. Median is shown by a horizontal line within the box and mean by a grey circle. Significant relationships between CH_4 and (B) growing season water table or (C) soil temperature are denoted by *.

generally decreased (i.e., more uptake) as water tables neared the surface (Figure 7B) and increased as soils warmed, except in Sifton B (Figure 7C).

Carbon stocks and annual fluxes

Total estimated C stored in trees ranged from 7.92 kg m^{-2} to 37.0 kg m^{-2} across the sites (Table 3) and was highest in broad-leaved canopies (24.6 kg m^{-2}) followed by needle-leaved (20.2 kg m^{-2}) and mixedwood (20.0 kg m^{-2}), and shrub (7.92 kg m^{-2}). Tree litter collected ranged from 136 g m^{-2} under shrub canopy to 544 g m^{-2} under mixedwood, with no evidence for significant differences between settings or canopies. Generally, litterfall increased with broad-leaved presence but decreased as tree density increased, correlating with the high number of small diameter stems in the shrub site. Soil organic carbon (SOC) ranged from 11.6–35.5 kg m^{-2} (Table 3), regardless of understorey biomass. However, there was strong evidence that SOC depended on leaf litter ($F_{1,32} = 9.8338$, $p = 0.0037$), generally increasing with higher litter inputs.

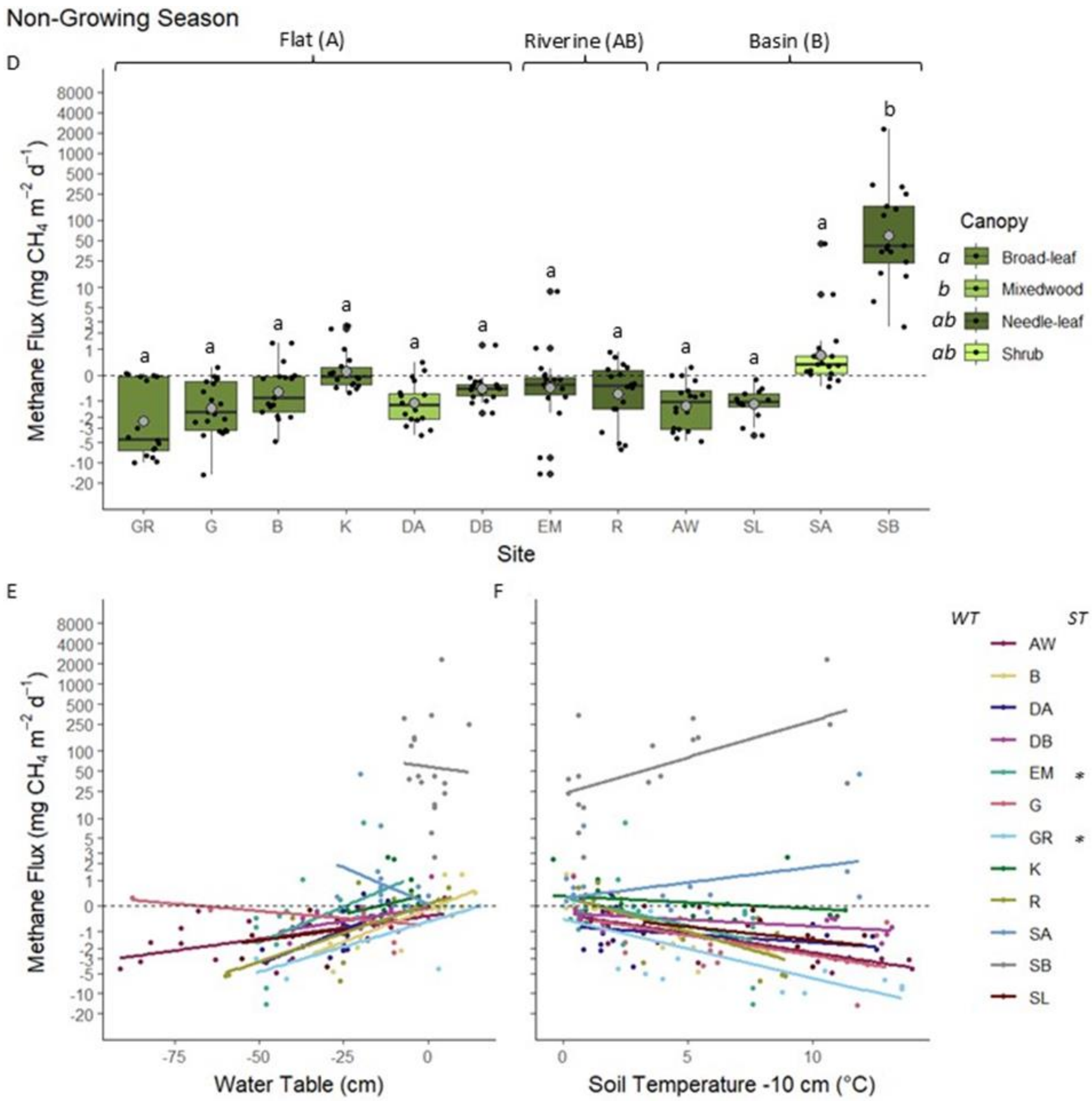

Figure 3. Non-growing season methane fluxes (mg m^{-2} d^{-1}). In (D), site, setting or canopy means are significantly different (based on post-hoc Tukey tests) if they do not share letters; lowercase letters refer to differences between sites, uppercase letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles within which 50 % of data points lie, and whiskers represent 1.5 times the interquartile range. Median is shown by a horizontal line within the box and mean by a grey circle. Significant relationships between CH_4 and (E) non-growing season water table or (F) soil temperature are denoted by *.

Across the sites, estimated cumulative net CO_2-C emissions from soil and understorey (NEE_u) over the period June 2022 to May 2023 ranged from 330.7 g m^{-2} yr^{-1} to 1331.4 g m^{-2} yr^{-1} (Table 3). Due to inaccessibility and poor data from Spongy Lake over the non-growing season, monthly NEE_u and CH_4 flux values were missing for January through April. Assuming that flux values do not vary greatly through the winter months, we used the December flux for January through March, then averaged March and May to estimate for April. We acknowledge that this method will have over-estimated some months and under-estimated others but believe the effect at the annual scale should be low. Highest NEE_u (most emission) was from riverine and mixedwood sites, followed by flat and basin, and broad-leaved, needle-leaved and shrub, respectively. Cumulative soil CH_4-C flux ranged from -0.488 (uptake) to 259 (emission) g m^{-2} yr^{-1} (Table 3) with uptake in flat and riverine sites. Mixedwood sites also took up a small amount

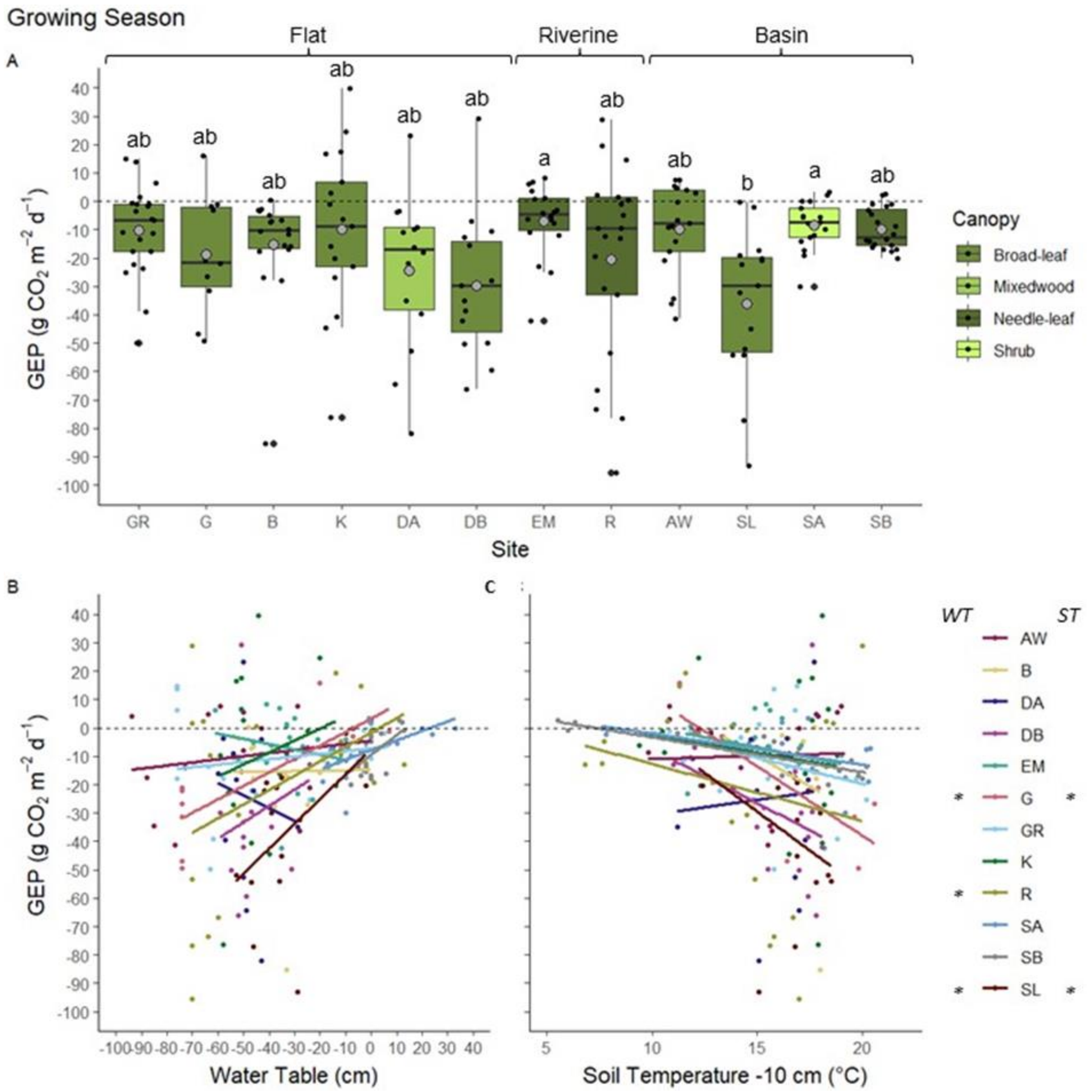

Figure 4. Growing season gross ecosystem productivity GEP_u (as CO_2; g m^{-2} d^{-1}). In (A), site, setting or canopy means are significantly different (based on post-hoc Tukey tests) if they do not share letters; lowercase letters refer to differences between sites, uppercase letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles within which 50 % of data points lie, and whiskers represent 1.5 times the interquartile range. Median is shown by a horizontal line within the box and mean by a grey circle. Significant relationships between GEP_u and (B) growing season water table or (C) soil temperature are denoted by *.

of CH_4, while broad-leaved sites were near zero and emission occurred in basin, shrub and needle-leaved sites. Given the much higher emissions from both Sifton sites, when data for this swamp was removed, all sites were net sinks for CH_4 except Grand River and Golspie, though they were also close to zero. Mean annual CH_4-C emission at basin sites dropped from 66.3 to 0.036 g m^{-2} yr^{-1}, and at needle-leaved sites from 86.0 to -0.351 g m^{-2} yr^{-1}; these estimates were not significantly different statistically from the other settings or canopies.

DISCUSSION

Mean GS soil respiration of CO_2 and CH_4 across the swamps ranged from 11 g m^{-2} d^{-1} to 49 g m^{-2} d^{-1} and -3 mg m^{-2} d^{-1} to 44 mg m^{-2} d^{-1}, respectively, falling well within the North American swamps range for CO_2 (0–50 g m^{-2} d^{-1}) and CH_4 (0–>150 mg m^{-2} d^{-1}) found by Davidson *et al.* (2022), with the exception of CH_4 at Sifton B at 1,605 mg m^{-2} d^{-1} (Table A3). In particular, our net CH_4 fluxes fall on the lower end of this range, with some sites even acting as small sinks.

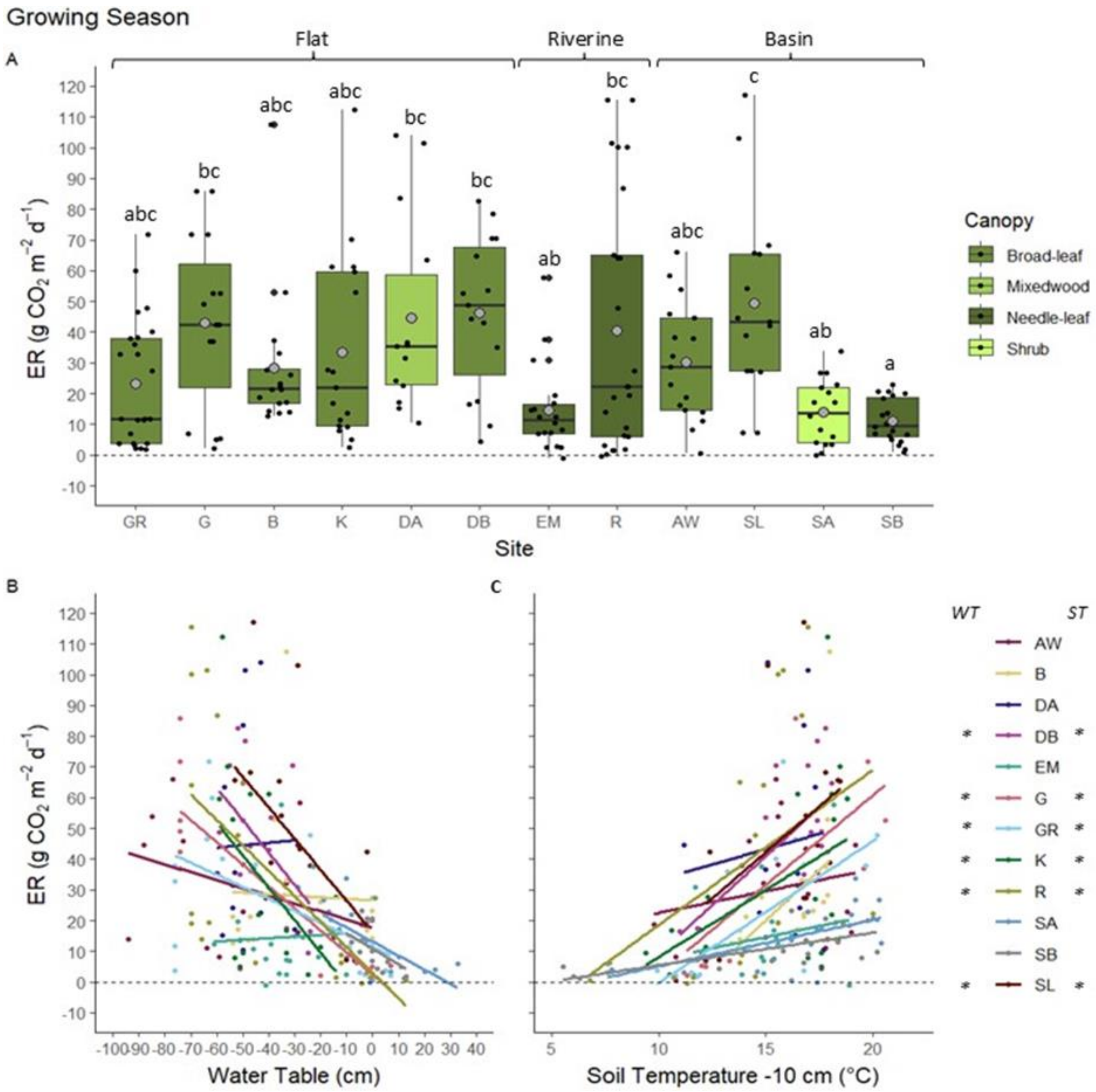

Figure 5. Growing season ecosystem respiration ER (as CO_2; g m^{-2} d^{-1}). In (A), site, setting or canopy means are significantly different (based on post-hoc Tukey tests) if they do not share letters; lowercase letters refer to differences between sites, uppercase letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles within which 50 % of data points lie, and whiskers represent 1.5 times the interquartile range. Median is shown by a horizontal line within the box and mean by a grey circle. Significant relationships between ER and (B) growing season water table or (C) soil temperature are denoted by *.

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Wetlands produce a large portion of all natural CH_4 released to the atmosphere (Saunois *et al.* 2025), but like most soils they also have the potential to take up CH_4 under certain conditions (e.g., Le Mer & Roger 2001, Liu *et al.* 2019, Gatica *et al.* 2020). As CH_4 production is an anaerobic process, CH_4 fluxes generally decrease with falling soil moisture and water tables and as the activity of methanotrophic microbes increases (Le Mer & Roger 2001). Annual precipitation from 2020 to 2022 was below the 30-year normal and during the study period the sites were dry, with WT well below surface for most of the growing season (except at Sifton), possibly explaining these low values. Several studies have shown a reversal from CH_4 source to sink during very dry and drought conditions in swamps, and that soils that experience repeated wet-dry cycles tend to have the highest CH_4 uptake when dry (Moore & Knowles 1980, Harriss *et al.* 1982, Nesbit & Breitenbeck 1992), as we found at our sites with rivers and streams that overflow their banks. Mean GS CH_4 of only the temperate swamps from Davidson *et al.*

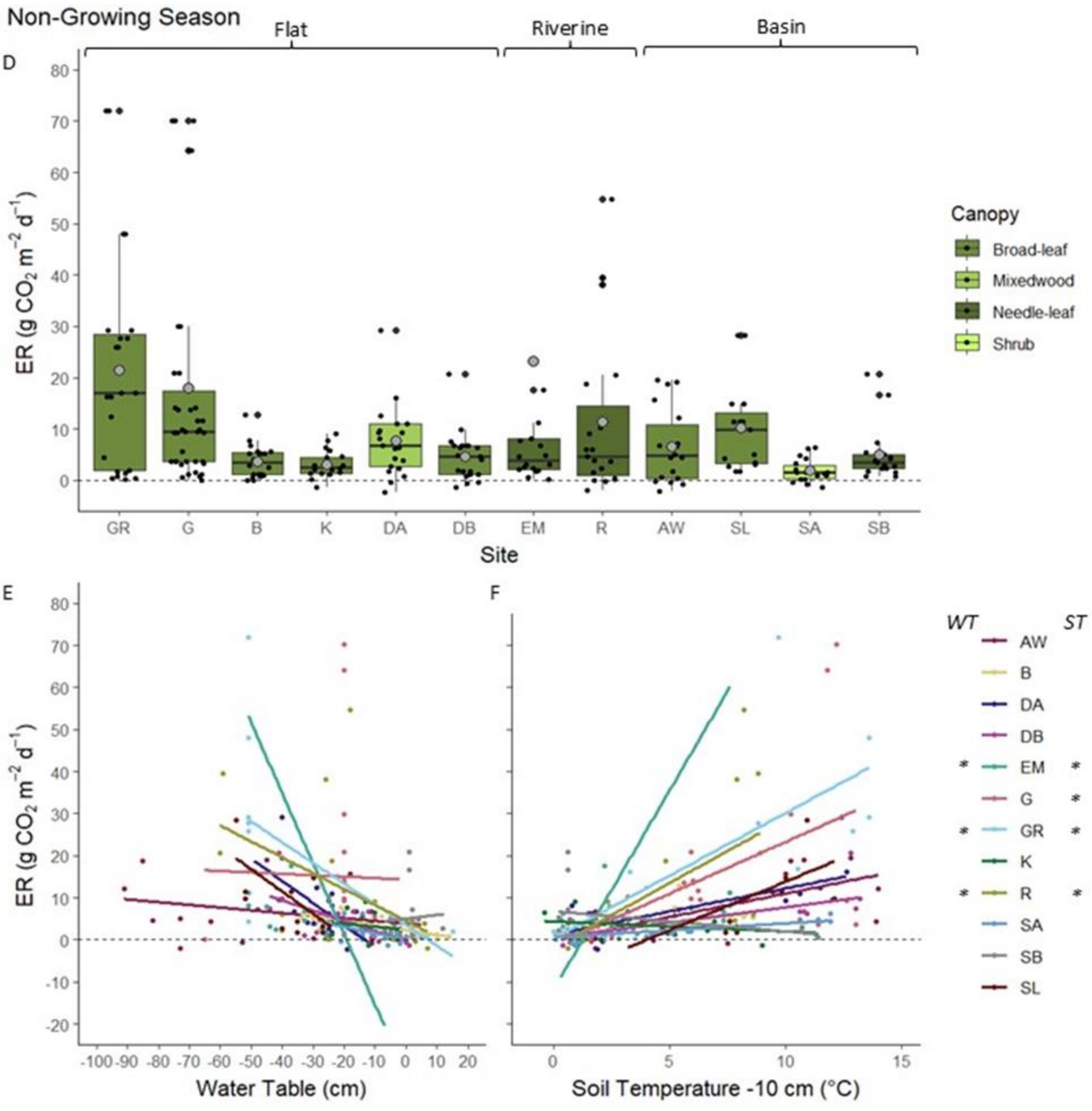

Figure 6. Non-growing season ecosystem respiration ER (as CO_2; g m^{-2} d^{-1}). In (D), site, setting or canopy means are significantly different (based on post-hoc Tukey tests) if they do not share letters; lowercase letters refer to differences between sites, uppercase letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles within which 50 % of data points lie, and whiskers represent 1.5 times the interquartile range. Median is shown by a horizontal line within the box and mean by a grey circle. Significant relationships between ER and (E) non-growing season water table or (F) soil temperature are denoted by *.

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(2022) ranged from -2 mg m^{-2} d^{-1} to 26.5 mg m^{-2} d^{-1}; Harriss *et al*. (1982) measured CH_4 fluxes of 1.3–19.7 mg $m^{-2}d^{-1}$ from saturated soils in the Great Dismal Swamp and up to 6 mg m^{-2} d^{-1} uptake during the following drought. Mean CH_4 fluxes from Canadian bogs and fens, which remain relatively wet year-round, have been estimated at ~35 and ~40 mg m^{-2} d^{-1} (Webster *et al.* 2018). In comparison, across worldwide upland forests, Gatica *et al.* (2020) found negative average CH_4 soil fluxes, with > 90 % of sites averaging < 0 kg ha^{-1} $year^{-1}$ (0 mg m^{-2} d^{-1}) and highest emission and uptake of +39 and -39 kg ha^{-1} $year^{-1}$ (106 and -106 mg m^{-2} d^{-1}), respectively, dependent on mean annual precipitation and temperature. Barring Sifton A and Sifton B, our swamps averaged -3–8.3 mg m^{-2} d^{-1}, with 7 of 10 showing uptake, aligning with patterns found in previous papers (e.g., Harriss, *et al*. 1982, Davidson *et al*. 2022). Climate change is expected to result in warmer temperatures and more prolonged dry periods in temperate regions (IPCC 2023), suggesting that in future temperate swamps may continue to act more like upland forests in regard

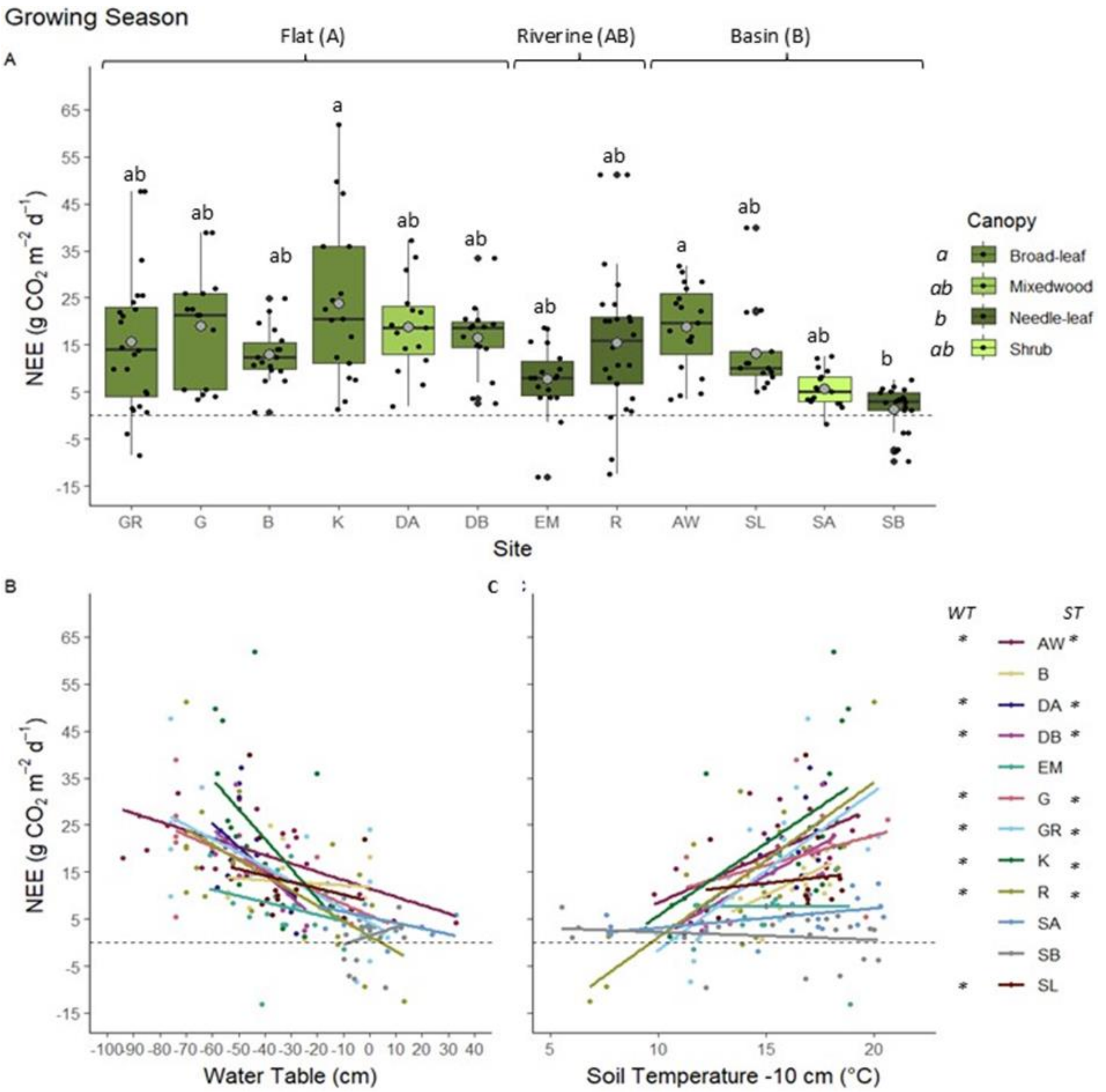

Figure 7. Growing season net ecosystem production NEE_u (as CO_2; g m^{-2} d^{-1}). In (A), site, setting or canopy means are significantly different (based on post-hoc Tukey tests) if they do not share letters; lowercase letters refer to differences between sites, uppercase letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles within which 50 % of data points lie, and whiskers represent 1.5 times the interquartile range. Median is shown by a horizontal line within the box and mean by a grey circle. Significant relationships between NEE_u and (B) growing season water table or (C) soil temperature are denoted by *.

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to CH_4 soil exchange, reducing overall gaseous CH_4 emissions.

During the growing season, mean CH_4 fluxes were much higher from basin sites than from either riverine or flat sites (Figure 2). High CH_4 effluxes at Sifton were likely to have been driven by shallow water tables. Throughout the growing season, mean WT at Sifton remained near the surface while the WT at all other sites was 30–40 cm deeper and remained at least 10 cm deeper during the non-growing season (Table 2). This difference included the other basin sites, Ancient Woods and Spongy Lake (Table 1). Spongy Lake's shallow open water depth allows the WT to drop significantly in drier years and this drop in water level is reflected in drying of the perimeter swamp. At Ancient Woods, the depression dried by evapotranspiration during the GS and our wells were dry to the underlying clay surface until late November when evapotranspiration decreased and rainfall increased, contributing to the low CH_4 emissions at this site. Sifton, however, is much deeper and domed, feeding water from the centre to the swamps, which is likely to contribute to the more consistent WT and higher CH_4 emissions at Sifton A and Sifton B. Lower CH_4 efflux at Sifton A than at Sifton B is likely to be due to deeper water tables and shallower peat depths caused by decreasing bottom slopes towards the outer edge of the kettle. Although variation in hydrology aligns with differences in measured CH_4 emissions among the basin sites, if Sifton is removed from the analyses there are no statistically significant differences in CH_4 flux between sites or settings (flat 0.853 mg m^{-2} d^{-1}, basin -1.85 mg m^{-2} d^{-1}, riverine -1.97 mg m^{-2} d^{-1}).

Although there were differences in CH_4 flux between canopy types, it is more likely they were linked to other factors such as water level and soil temperature than to canopy. Water tables, in particular, may be moderated by the setting and connectivity to ground and surface water features. Canopy type and structure do, however, influence understorey vegetation, as it changes the amount of light that reaches the ground. For example, needle-leaved canopies are typically thicker and remain

Table 3. Mean carbon stocks and annual fluxes across the study sites. SOC = Soil Organic Carbon, D = mean soil core depth. For annual NEE_u and CH_4, positive values indicate a release to the atmosphere and negative values indicate uptake from the atmosphere. Annual fluxes at Spongy Lake were estimated by gap-filling missing data for January through April; the December flux was used for January through March, then March and May were averaged for April. Soils were sampled to a maximum depth of 50 cm; depths of the soil layers at Dorchester A, Kintore, Sifton A, Sifton B and Spongy Lake exceeded 50 cm (i.e., confining layer was not reached) but the full depths are not known.

Site	Carbon stocks (kg m^{-2})			D (cm)	Carbon fluxes (g m^{-2} y^{-1})		
	Trees	Understorey vegetation	SOC		Tree litter	NEE_u	CH_4
Ancient Woods (mineral)	36.4	0.01	25.5	35	395	1155.1	-0.428
Beverly (organic)	31.0	0.08	33.3	47	304	733.2	-0.319
Dorchester A (organic)	19.9	0.03	34.6	50	544	1045.4	-0.488
Dorchester B (mineral-organic)	12.8	0.03	30.3	45	341	822.6	-0.261
Eden Mills (organic)	34.6	0.01	31.1	45	489	1330.4	-0.209
Golspie (mineral-organic)	28.2	0.05	28.8	33	500	1063.7	0.52
Grand River (mineral)	27.6	0.05	20.1	33	426	1313.8	0.088
Kintore (organic)	21.9	0.06	35.5	50	375	895.2	-0.168
Rockwood (organic)	13.0	0.08	24.0	30	302	1006.6	-0.493
Sifton A (organic)	6.8	0.11	21.9	50	142	330.7	6.468
Sifton B (organic)	10.6	0.02	11.6	50	136	401.3	258.8
Spongy Lake (organic)	14.1	0.01	19.1	50	390	979.3	0.5

consistent throughout the year, whereas broad-leaved canopies change through the seasons and often create more dappled shade. The amount of direct sunlight received by the understorey can influence productivity, soil temperature and, subsequently, microbial activity contributing to CH_4 cycling. We did find higher CH_4 efflux from needle-leaved sites, but conifers such as *Picea mariana* (Mill.) B.S.P., *Larix laracina* (Du Roi) K. Koch and *Thuja occidentalis* Linnaeus are typically more tolerant of wetter conditions and are thus more likely to be in low spots or along rivers (Burns & Honkala 1990). Only broad-leaved and needle-leaved were statistically significantly different, and when Sifton is removed there are no differences in CH_4 flux between canopy types (needle-leaved -2.0 mg m^{-2} d^{-1}). Davidson *et al.* (2022) reported higher mean CH_4 fluxes from broad-leaved swamps at 126.8 ± 33.9 mg m^{-2} d^{-1}, needle-leaved at 13.5 ± 10.3 mg m^{-2} d^{-1} and mixedwood at 31.7 ± 51.1 mg m^{-2} d^{-1}. However, the lower values found at our sites could be due to the very dry conditions over our study period and hydrological conditions specific to the swamps in the review.

Mean ER of CO_2 in the understorey was highest from our mixedwood sites (44.7 ± 31.3 g m^{-2} d^{-1}), followed by broad-leaved and needle-leaved at 34.4 ± 26.4 g m^{-2} d^{-1} and 20.3 ± 26.5 g m^{-2} d^{-1}, respectively. This pattern follows that found by Davidson *et al.* (2022) of 12.5 ± 16.5 g m^{-2} d^{-1} in mixedwood, 1.4 ± 0.8 g m^{-2} d^{-1} in broad-leaved, and 0.64 ± 0.1 g m^{-2} d^{-1} in needle-leaved swamps. In Nova Scotia (Canada), mean GS ER values of 1.4 g m^{-2} d^{-1} at a broad-leaved swamp and 0.63 g m^{-2} d^{-1} at two needle-leaved swamps were substantially lower than our measurements (Kendall *et al.* 2021). Our results could be higher in response to dry soil conditions, which also correlates with our lower CH_4 fluxes. Gross ecosystem productivity of the understorey (GEP_u; CO_2 taken up by plants via photosynthetic processes) was not reported in most other swamp studies, and understorey vegetation cover and species varied widely across and within our sites. Uptake was highest in mixedwood sites, followed by broad-leaved and needle-leaved, which is consistent with the notion that more light increases understorey vegetation and photosynthesis. The offset from GEP_u decreased mean net understorey CO_2 efflux (NEE_u) to 1–24 g m^{-2} d^{-1} across our sites, while NEE_u of temperate bogs and fens - mostly untreed systems - has been reported as -2 ± 2.3 g m^{-2} d^{-1} (Webster *et al.* 2018). Despite the effect on CO_2, the relative importance of understorey productivity (measured as biomass) was small, < 1 % of the biomass of the trees. Understorey NEE_u loss of C is partially offset by C additions from tree and understorey litter. Including these additions (Table 3) still results in losses of C from the understoreys of all swamps in the range 189–841 g m^{-2} d^{-1}. However, this would be further offset by the productivity of the trees themselves. Although we did not measure incremental growth of woody stocks in the trees, Davidson *et al.* (2022) reported aboveground net primary productivity uptake of CO_2 as 900–1600 g m^{-2} d^{-1}, more than offsetting the understorey C losses and suggesting that temperate swamps can act as net C sinks even in drought conditions.

Given the lack of data on swamps in general, C and greenhouse gas reporting and modelling for this wetland type has been limited by uncertainties about environmental drivers of fluxes and their relationships (Webster *et al.* 2018, Bona *et al.* 2020, Kuhn *et al.* 2021, Olefeldt *et al.* 2021). Overall, we observed that, as in other peatland types, CO_2 and CH_4 fluxes had an inverse relationship in which CO_2 increased and CH_4 decreased as soils dried, and vice versa. As soils warmed, CO_2 increased and CH_4 decreased. There was an observed shift in both CO_2 and CH_4 efflux when WT reached approximately -20 cm; WT below this level produced significantly higher CO_2 fluxes while anything above resulted in significantly higher CH_4. Such relationships with mean water table have been found across many wetland systems, both managed and natural, and critical depths where fluxes change can range broadly between wetland types (e.g., Evans *et al*. 2021, Li *et al*. 2023). Further identification of these WT thresholds, and determination of whether they hold true across many swamp types, could vastly improve C accounting and modelling capabilities and prediction of whether swamps are C sinks or sources. Nonetheless, our results indicate that relationships between CO_2 and CH_4 fluxes and environmental conditions such as WT and temperature developed in bogs and fens are likely also to predict patterns of swamp carbon cycling, with data from this study informing how the slopes of these relationships are likely to differ. While this study adds a large amount of data to understanding swamps, our study area represents a very small portion of total swamp extent in North America, and although we collected data over a full year, multi-year studies are needed to capture a range of conditions and climate trends. Given that mean NGS CH_4 fluxes were near zero (with the exception of Sifton B), and NGS ER was also low, winter data collection is likely to be less necessary than capturing GS fluxes across a range of swamp types and climatic conditions. However, the similarity of carbon fluxes across most of our sites suggests that location, setting and canopy may not be as important as other factors for C accounting and modelling purposes. Nevertheless, more research is needed to fully understand temperate swamp C balance. This study, as with most studies, has captured only some of the C dynamics of swamps; an accurate understanding requires quantification of C inputs and losses via water transport (DOC, DIC, etc.), decay and accretion rates, NPP of trees and above-canopy fluxes to capture the full ecosystem C exchange.

ACKNOWLEDGEMENTS

The authors acknowledge that we are settlers who live, work, and benefit from being on the traditional unceded lands of the Attawandaron (Neutral), Anishinaabeg, and Haudenosaunee peoples and that this research takes place across the territories of many more. The University of Waterloo is situated on the Haldimand Tract, the land promised to the Six Nations that includes ten kilometres on each side of the Grand River.

The harms of policies of expulsion and assimilation of Indigenous peoples during the time of settlement, Confederation and since are many and are still felt in Indigenous communities today. We have a responsibility to acknowledge and understand this history and the current experiences of First Nations, Inuit and Metis peoples, and for this understanding to inform the work that we do so that, first, we can stop perpetuating the damages of colonisation and, second, begin to repair them. Land acknowledgments are just one small, first step in this work.

The authors thank Dr Oluwabamise Afolabi and Dr Nicole Balliston for their invaluable field and lab support, as well as the rest of the GHG Lab PDFs, graduate and co-op students. Funding was provided by an NSERC Discovery Grant to Maria Strack, who also acknowledges support from the Canada Research Chairs program, and a NSERC PGS D scholarship and Ages Foundation Research Fellowship and Bursaries award from the *rare* Charitable Research Reserve to Megan Schmidt. We thank the *rare* Charitable Research Reserve, the University of Waterloo, the Upper Thames River Conservation Authority and the Hamilton Conservation Authority for allowing access to the sites.

AUTHOR CONTRIBUTIONS

MAS designed and planned the work, undertook field and lab work, wrote the first draft, and is the lead author. VS undertook field and lab work and the initial analysis of tree litter. SP and HK undertook field and lab work. MS helped design and plan the work and reviewed and edited manuscript drafts.

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Submitted 03 Oct 2025, revision 19 Nov 2025
Editor: Gerald Jurasinski

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Appendix

Table A1. Average vegetation survey results (% cover). At each site, three 1 m × 1 m quadrats were positioned within 5 m of each collar (n = 9 quadrats per site), primarily for biomass collection. Before the biomass collection, percent cover of each functional group was determined visually, including any branches of shrubs and trees < 3 m tall that overhung the quadrat. The data shown here are averages of all quadrat data per site.

Site	*Sphagnum*	Other mosses	Bare ground	Open water	Sedges	Grasses	Other monocots	Dicots	Shrubs	Trees
Ancient Woods (AW)	0	4	96	0	68	58	2	48	52	0
Spongy Lake (SL)	15	18	84	0	10	0	0	23	40	13
Sifton B (SB)	85	12	4	0	12	10	0	2	20	11
Sifton A (SA)	46	24	36	0	10	1	0	8	54	61
Grand River (GR)	0	4	96	0	68	58	2	48	52	0
Dorchester B (DB)	0	12	92	0	21	0	1	37	13	24
Golspie (G)	0	21	76	0	8	4	4	64	22	33
Beverly (B)	0	12	89	0	4	42	6	80	6	7
Kintore (K)	0	24	76	0	10	3	0	23	27	24
Dorchester A (DA)	0	17	87	0	1	1	0	40	14	27
Eden Mills (EM)	0	28	79	0	1	60	1	54	0	11
Rockwood (R)	0	41	59	0	20	27	10	62	8	12

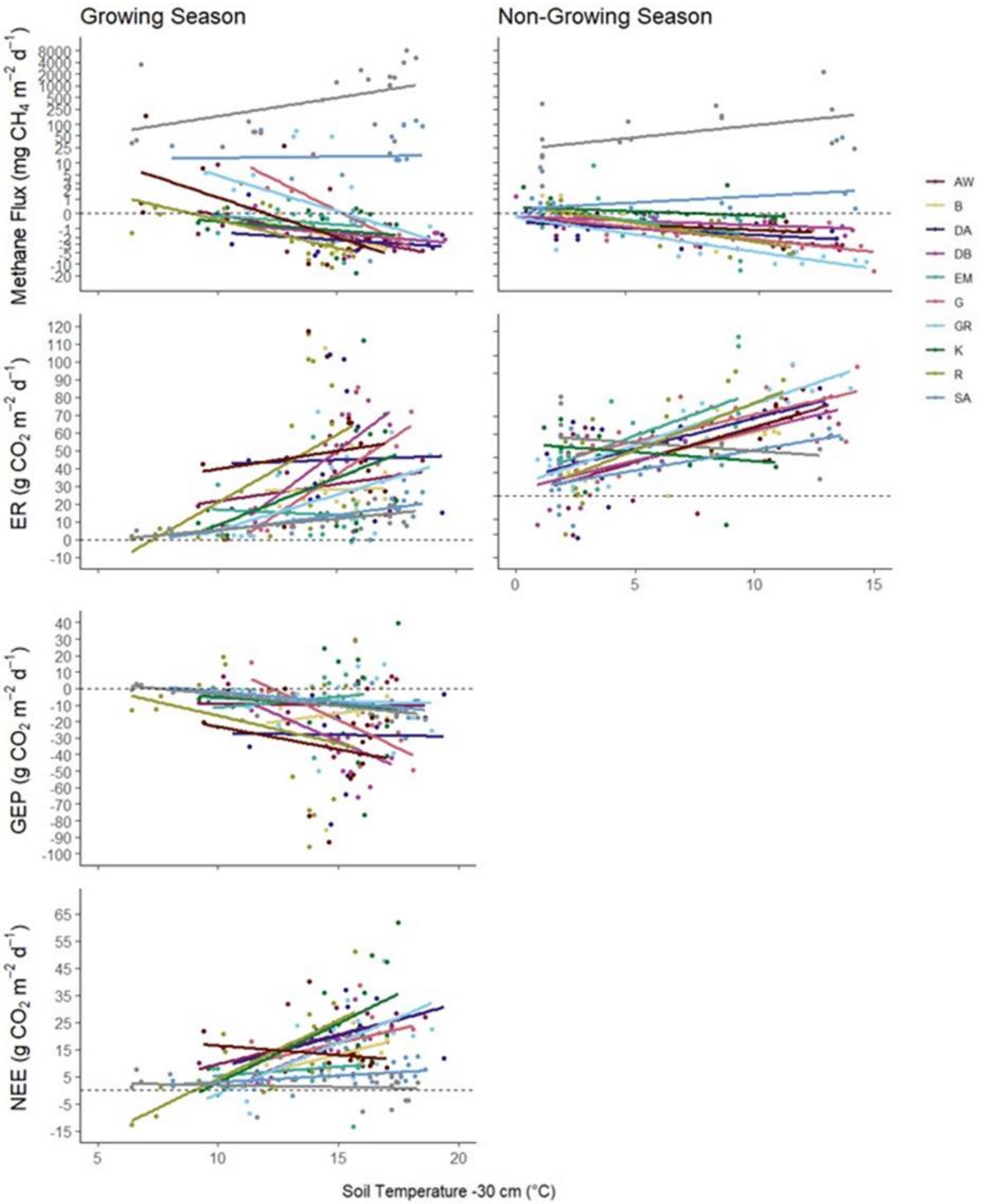

Figure A1. CH_4 and CO_2 flux responses to soil temperature at 30 cm below ground surface.

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Table A2. Monthly, annual and 30-year average precipitation (mm) for the study period, from five weather stations at locations chosen for proximity to one or more of the study sites (see bottom row). Green cells indicate months included in the growing season. Data from Government of Canada (2024b).

		Weather station name				
		Kitchener/ Waterloo	Hamilton A	Woodstock	Roseville	London A
30-year average (mm)		976.0	929.8	969.0	918.7	1011.5
Year	Month	Precipitation (mm)				
2022	Jan	15.4	37.3	24.0	53.0	33.3
	Feb	24.9	87.1	58.6	98.4	86.8
	Mar	42.4	60.4	35.3	66.7	50.4
	Apr	42.8	47.8	39.2	41.1	67.0
	May	60.6	50.8	37.5	64.5	49.1
	Jun	48.6	76.6	34.8	61.3	46.0
	Jul	18.7	56.9	12.9	19.4	44.3
	Aug	42.1	72.1	54.4	57.5	110.9
	Sep	22.2	47.2	39.0	26.8	43.4
	Oct	39.0	39.0	9.8	48.1	50.5
	Nov	28.3	39.7	11.0	37.7	30.3
	Dec	53.3	64.7	27.0	62.2	37.0
	Total	438.3	679.6	383.5	636.7	649
2023	Jan	49.4	75.5	22.5	80.6	60.7
	Feb	58.4	85.4	16.0	42.4	75.8
	Mar	69.9	117.2	55.5	114.7	38.4
	Apr	85.5	111.8	56.1	104.1	92.9
	May	47.0	39.1	8.3	45.3	4.1
	Jun	59.5	115.2	33.1	81.9	53.8
	Jul	166.4	123.8	52.0	160.0	151.5
	Aug	98.1	119.0	39.1	118.4	64.6
	Sep	21.2	25.9	24.2	23.5	49.2
	Oct	49.3	61.7	41.0	59.4	58.7
	Nov	41.1	44.2	37.6	57.4	43.7
	Dec	67.3	71.9	0.0	57.1	89.7
	Total	813.1	990.7	385.4	944.8	783.1
Sites represented		Grand River Eden Mills Rockwood	Beverly	Golspie Kintore Dorchester	Ancient Woods Spongy Lake	Sifton

Table A3. Average understorey fluxes of CH_4 and CO_2 (ER, GEP, NEE) for growing season and non-growing season by site, setting and canopy. Positive values indicate release to the atmosphere and negative values indicate uptake.

	Growing Season				Non-Growing Season	
	Mean CH_4 (mg m^{-2} d^{-1})	Mean ER (g m^{-2} d^{-1})	Mean GEP (g m^{-2} d^{-1})	Mean NEE (g m^{-2} d^{-1})	Mean CH_4 (mg m^{-2} d^{-1})	Mean ER (g m^{-2} d^{-1})
Site						
Ancient Woods	-1.90	18.00	-9.70	18.80	-1.67	6.59
Beverly	-2.10	28.20	-15.20	13.00	-0.84	3.73
Dorchester A	-3.00	22.50	-24.60	18.90	-1.39	7.66
Dorchester B	-1.90	46.10	-29.70	16.50	-0.51	4.62
Eden Mills	-0.90	14.60	-6.87	7.78	-1.05	23.30
Golspie	6.30	43.20	-18.70	17.10	-2.21	15.00
Grand River	7.70	23.20	-10.30	13.90	-4.11	16.20
Kintore	-2.20	33.50	-9.75	23.80	0.22	3.17
Rockwood	-2.90	40.60	-20.50	13.50	-1.31	11.70
Sifton A	44.30	14.00	-8.41	5.62	3.24	1.93
Sifton B	1605.00	11.00	-9.70	1.39	228.00	5.03
Spongy Lake	8.30	49.30	-36.00	13.30	-1.33	10.20
Setting						
Basin	463.00	24.80	-15.10	9.45	59.70	5.76
Flat	0.90	34.90	-17.60	17.59	-1.45	11.14
Riverine	-2.00	27.73	-17.45	12.28	-1.18	17.18
Canopy						
Broad-leaved	2.00	34.92	-17.63	17.08	-1.48	10.99
Mixedwood	-3.00	44.70	-27.88	18.92	-1.39	7.66
Needle-leaved	543.00	23.80	-15.00	8.71	72.20	13.36
Shrub	44.30	14.03	-8.41	5.62	3.00	1.93

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