Carbon Cycling, Carbon Storage, and Greenhouse Gas Dynamics in Temperate Southern Ontario Swamps

by

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.
I understand that my thesis may be made electronically available to the public.

Statement of Contributions

Unlike the traditional thesis format, this submission has been compiled as a collection of written scholarly work (manuscripts). Three independent manuscripts to be submitted for publication are presented as chapters 2, 3, and 4 of this thesis. As a result, repeated information may be included.

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M. Schmidt designed and planned the work, undertook field and lab work, wrote the manuscript, 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. M. Strack helped design and plan the work and reviewed and edited manuscript drafts.

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Abstract

Swamps are treed wetlands and account for the highest areal extent of wetland types in Southern Ontario due to the conversion of other wetlands 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. Additionally, historically soils were considered the primary or only source of methane (CH_4) efflux from swamps, but recent studies have shown that tree stems contribute a significant amount of the total ecosystem CH_4 emissions. Swamps are relatively understudied in Canada, therefore uncertainties remain in the true extent of swamps nationally, that, combined with the lack of data, has limited their inclusion in C accounting, climate modelling, and policy.

A multi-year study of temperate swamps was conducted across southern Ontario to assess the exchange of C, carbon dioxide (CO_2) and CH_4 between soil, trees, and atmosphere, and estimate current C stocks in soil and biomass. To do so, we began with a synoptic study of 12 swamps over 12 months that looked at the effects of hydrogeomorphic setting and canopy type on measurable variables of water table and soil temperature and the subsequent effects on CH_4 and CO_2. We found mean growing season soil respiration of CO_2 and CH_4 across the swamps ranged from 11–49 g m^{-2} d^{-1} and -3–44 mg m^{-2} d^{-1}, respectively; 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.

To assess the contribution of tree stems to CH_4 flux, three common genera (*Acer*, *Betula*, and *Thuja*) within 3 of the previous 12 swamps were measured simultaneously with soil fluxes over 21 months. As most CH_4 emitted from tree stems in wetlands is produced within the soil and transported up the stem, we also measured soil CH_4 fluxes alongside environmental conditions such as water table and soil temperature. We found that stem CH_4 emissions varied substantially among species, sites, and seasons, and were influenced by soil temperature, water-table position, and soil CH_4 availability. However, the importance of these drivers differed among sites and tree species, indicating that methane transport through trees is controlled by interacting environmental and physiological processes rather than a single universal mechanism. The highest mean fluxes were from *Acer* at 0.23

– 20.82 mg CH_4 m^{-2} of stem yr^{-1}, followed by *Betula* at 0.09 – 0.89 mg CH_4 m^{-2} yr^{-1}, and *Thuja* at 0.12 – 0.63 mg CH_4 m^{-2} yr^{-1}.

Finally, these studies were combined to create estimates of the full current C stocks and fluxes for four of the swamps. We found that C storage was dominated by soils at 20 – 86 kg C m^{-2} of swamp, followed by living trees at 9.8 – 19.9 kg C m^{-2}. Woody debris contained 2.9 – 12.5 kg C m^{-2}, while the contribution from living understory vegetation was minimal at 0.1 kg C m^{-2} or less. Total C stored within the sites ranged from 45.6 to 108.3 kg C m^{-2}. Trees and understory vegetation took up 619 – 982 g C m^{-2} of swamp yr^{-1} but were offset by soil and tree fluxes of 898 – 1213 g C m^{-2} of swamp yr^{-1}, resulting in three swamps acting as C sources at 25 – 298 and one swamp acting as a C sink at -108 g C m^{-2} of swamp yr^{-1}.

In conclusion, temperate swamps in southern Ontario represent locally important stocks of both biomass and soil C, surpassing both upland forests and other wetland classes. Carbon dynamics in temperate swamps are driven by different controls across timescales, with long-term C storage determined by peat accumulation and climate, while short-term greenhouse gas fluxes are regulated by temperature-moisture interactions that respond to the changing seasons and annual weather. As a result, future warming may increase CH_4 emissions, particularly if conditions are able to sustain high water tables that support anaerobic processes. Conversely, increased prolonged dry periods may enhance CO_2 losses while limiting CH_4 emissions, potentially shifting the balance of GHG outputs, but could be offset by enhanced overstory productivity and litter inputs. Fragmentation, conversion, and drainage result in isolated remnants, and these remnant swamps still account for a large portion of wetland in southern Ontario. Both within and surrounding swamps, anthropogenic disturbances may create drier conditions, in turn increasing soil C oxidation and reducing C stores and peat accumulation ability. Incorporating these data into C accounting and modelling will help inform future policies of wetland conservation and restoration and management of swamps as natural climate solutions.

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Chapter 1
Introduction

Wetlands are among the most important ecosystems on the planet. Wetlands reduce the impact of waves on shorelines, provide a buffer for both floods and droughts, filter sediments and toxins from water, provide food and habitat for a disproportionately high number of species, provide food, energy, building material, and recreational areas for activities such as hunting, fishing, and birdwatching (Environment and Climate Change Canada 2025). Wetlands are an important and dynamic part of the climate system, acting as a persistent long-term sink of carbon dioxide (CO_2), while also being a major source of natural methane (CH_4) (Covey & Megonigal 2018; Saunois et al. 2019). Wetlands occupy only ~6% of earth's terrestrial surface, yet store >30% of global soil organic carbon (C) (Jackson et al. 2017; Poulter et al. 2021), with over half, about 415 ± 150 Gt of C, attributed to northern peatlands where bogs and fens dominate (Hugelius et al. 2020). Tropical peatlands, particularly throughout South America, Southeast Asia, and Central Africa, contain an additional 469 – 694 Gt of C in only 90 – 170 million ha (Gumbricht et al., 2017, Ribeiro et al. 2019). As of 2024, wetlands covered roughly 1.25 million km^2 in Canada, approximately 13% of the country's terrestrial and freshwater area, primarily concentrated across the boreal region (Environment and Climate Change Canada 2025). Swamps may account for up to 9% of Canada's wetlands (Tarnocai 2006, Amani et al. 2019), but due to the lack of data it is unclear how much C they contain. To date, most research has focused on boreal and tropical wetlands, leaving other regions and wetlands, including temperate and forested wetlands, comparatively understudied. Therefore, the goal of this thesis is to help fill these gaps by assessing C cycling and stores within temperate swamps in southern Ontario.

1.1 Swamps: an overlooked wetland type

Swamps, like all wetlands, are complex systems influenced by both internal and external variables and processes. Definitions of what constitutes a swamp vary as much as their distribution from the tropics to the subarctic, but swamps are generally agreed to have hydric mineral or organic soils with seasonal or persistent surface water and over 25% cover of trees or shrubs (Environment Canada, 1987; Federal Geographic Data Committee, 2013; Government of Ontario, 2014; National Wetlands Working Group, 1997). Within the literature, common terms for swamps include "treed peatlands", "treed wetlands", "forest swamps", "swamp forests", "forested wetlands", "riparian wetlands", "bottomlands", "floodplain forests", "peat swamps", "peat forests", "seasonally flooded forests", and "sloughs". The

Ramsar Convention on Wetlands classifies swamps as shrub-, tree-dominated, or forested wetlands or peatlands (2016). 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 (Federal Geographic Data Committee 2013). In Alberta, Canada, swamps are classified as mineral systems only (AEP 2018), while in Quebec organic treed wetlands that are not bogs or fens are defined as peatlands (Bazoge et al 2014). The dominance of trees in temperate swamps sets them apart from all other wetland types, including treed bogs and fens. Although shrubs may be present in marshes or open water wetlands, they are often restricted to shallower, drier perimeters; in fens and bogs shrubs may be more common but do not meet or exceed 30% cover (National Wetlands Working Group, 1997). Similarly, though Black Spruce and Tamarack may be present across fens and bogs, they do not exceed 30% cover (National Wetlands Working Group, 1997). Additionally, trees and shrubs in other wetlands remain small and stunted due to persistent poor conditions, whereas water table is deep enough in swamps to provide an aerobic rooting zone that enables many tree species to thrive (Zoltai and Vitt, 1995).

Although swamps may be difficult to define, they can account for a large proportion of wetland area. Swamps make up an estimated 49% of wetland extent in the conterminous United States, while in Alaska, shrub-dominated wetlands account for approximately 68% of wetlands, and only approximately 8% are forested wetlands (Hall et al. 1994). In Canada, swamps are estimated to represent up to 9% of national wetlands (Tarnocai 2006, Amani et al. 2019); in northern Ontario, conifer swamps make up an estimated 40–60% of peatlands (Riley 1994). Treed and shrub swamps, at approximately 76 and 11%, respectively, have become the most common wetland type in southern Ontario due to disproportionate loss of other wetland types to wetland drainage, conversion, and other anthropogenic disturbance (Byun et al. 2018).

In *The Canadian Wetland Classification System* (NWWG 1997), two main characteristics are used to classify swamps in Canada: hydrogeomorphic setting and canopy type. Hydrogeomorphic setting describes the position of a swamp within the landscape, proximity to regional groundwater tables, and surface water bodies such as lakes and rivers via elevation (Trettin & Jurgensen 2003); there are 8 forms and 21 subforms of swamps defined for Canada (NWWG 1997). Canopies in swamps are dominated by either trees or tall shrubs, with tree cover further divided into broad-leaved (mostly deciduous, hardwood), needle-leaved (mostly coniferous, evergreen, softwood), or mixedwood, where neither dominate (NWWG 1997). Temperate treed swamps commonly contain several species

of maple (*Acer*), ash (*Fraxinus*), elm (*Ulmus*), oak (*Quercus*), cedar (*Thuja*), spruce (*Picea*), tamarack (*Larix*), and birch (*Betula*), with willow (*Salix*), alder (*Alnus*), and dogwood (*Cornus*) the dominant species in shrub swamps (NWWG 1997). Swamps often occur as transitional systems between other wetlands and upland; drier treed swamps may grade into upland forest on mineral soil while the wettest grade into treed fen, and tall shrub swamps grade into treed fen or marsh (NWWG 1997). Nutrient regimes in swamps are highly variable due to the influence of minerotrophic groundwater, and pH ranges widely, from 4.5 or less to above 7.0 (NWWG 1997).

Despite their prevalence, 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 C cycling; thus, their contribution to C stocks and greenhouse gas (GHG) exchange are not fully considered in management decisions. The Canadian Model for Peatlands (CaMP, Bona et al. 2020), for example, includes 11 different peatland types but does not include swamps as there is insufficient data to calibrate the model for swamps. 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 miss potentially large soil C stocks 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). Swamps may be misclassified as uplands if surveyed during dry periods, or as treed bogs or fens if canopy cover is not accurately estimated (e.g., Locky et al. 2005, Amani et al. 2021). The lack of field data makes identifying, mapping, and parameterizing 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).

1.2. Carbon storage potential of swamps

Higher aboveground biomass has been found in swamps than in treed bogs and fens, or in marshes (Bona et al. 2018) and biomass in swamps is comparable to that of mature forests across Canada and the USA (Zhu et al. 2018, Davidson et al. 2022). Below the canopy, understory 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).

The high cover of trees and shrubs and relatively low cover of forbs and mosses in swamps result in typically well-decomposed woody peat (National Wetlands Working Group, 1997). Peat layers in swamps have been measured from as little as 10 or 20 cm to upwards of 4 m (Byun et al., 2018; Daze et al., 2022; Kendall et al., 2021; Riley, 1994). Peat in coniferous swamps (199 cm) tends to be thicker than in deciduous (101 cm) and shrub (181 cm) swamps (Davidson et al., 2022). Mixedwood swamps vary in the proportion of coniferous and deciduous species and have some of the deepest peat deposits of all swamps at a mean depth of 236 cm, yet they have some of the lowest bulk densities among swamps at a mean 0.14 g/cm^3 (Davidson et al., 2022). Coniferous swamps have the second lowest mean bulk density at 0.15 g/cm^3, followed by shrub at 0.16 g/cm^3 and deciduous at 0.2 g/cm^3 (Davidson et al., 2022). Combining bulk density, organic layer thickness and carbon content shows that swamps contain a significant pool of soil C, ranging from ~53 kg C/m^2 in coniferous, ~67 kg C /m^2 in mixedwood and shrub, and ~70 kg C/m^2 in deciduous swamps, with an overall mean of 64.5 kg C/m^2 (Davidson et al., 2022). This is comparable to moss-dominated bogs and fens that may have organic soil layers that are much deeper (mean depth 2.5 – 3.5 m) but are much less dense at 0.10 g/cm^3 (Chimner et al., 2014; Gorham, 1991; Gorham et al., 2003). Even forested bogs and fens have significantly lower bulk densities than treed swamps (Davidson et al., 2022). This also shows the importance of proper delineation and classification of swamps, as each type has the potential to store different amounts of C (Byun et al., 2018). In Canada and the USA, high organic matter contents and bulk densities in swamps result in high soil C stocks in the top 0–90 cm, regardless of canopy type (Davidson et al. 2022). Dense, woody peat in swamps contains up to 4–5 times more C than upland forest soils across the USA (Domke et al. 2017). Carbon stocks held in swamp peat are 4–25 times higher than that of the trees in boreal black spruce forested peatlands (Magnan et al. 2020; Beaulne et al. 2021).

Although peat layers are often the focus for C stock studies, mineral soils in swamps can also contain >30% organic matter across much of the soil profile, storing a significant amount of C. This C storage includes mineral layers beneath peat layers. Organic matter accumulates in mineral soils in the same ways as it does in peat, via the breakdown and incorporation of litter from the surface, through root growth and decay, dissolved organic carbon percolating downwards and being adsorbed under aerobic conditions, and via perturbation from animals and insects digging and burrowing (Kroestch et al., 2011). Although surface layers may have higher concentrations of soil organic C, the increased soil mass in deeper layers often results in higher soil organic C stocks with depth. Mineral soils across Canada have been estimated to contain a mean 68 ± 75 kg/m2 organic C in the upper 2 m (Sothe et al., 2022, and

references therein); of that, an estimated 20 kg C/m2 is stored in mineral forested wetlands (Trettin and Jurgensen, 2002).

Given that biomass C stocks in swamps are similar to other forest types and soil C stocks are much greater, conservation of these ecosystems from land-use change would provide greater protection of land-based carbon stocks than the same area of upland forest. Therefore, temperate swamps likely represent carbon storage hotspots on the landscape but remain poorly quantified with few studies in southern Ontario that quantify biomass and soil C stocks across a range of swamp conditions.

1.3 Carbon cycling within swamps

The C balance of an ecosystem, net ecosystem carbon balance (NECB) is the net sum of all C inputs (primarily through photosynthesis) and outputs (decomposition, fire, harvest, physical matter removal) over time (Randerson et al. 2002, Chapin et al. 2006). NECB accounts for all vertical and lateral C fluxes entering and leaving a defined 3D ecosystem boundary (Randerson et al. 2002, Chapin et al. 2006). A positive NECB indicates that the ecosystem is acting as a C sink (storing C), whereas a negative NECB indicates a C source (losing C). Ecosystem C stocks are commonly divided into five pools: aboveground biomass, belowground biomass, dead wood, litter, and soil organic C (IPCC 2003). C is continually transferred among these pools through processes such as photosynthesis, litterfall, root turnover, decomposition, and hydrologic transport (Chapin et al. 2006, Bridgham et al. 2013).

Swamp vegetation absorbs atmospheric CO_2 through photosynthesis and converts it into living plant biomass, and C is allocated to above- (stems, branches, leaves, etc.) and belowground (roots, rhizomes, and mycorrhizal fungi) biomass (Jackson et al. 1997, Clemmensen et al. 2013, Bona et al. 2018, Zhu et al. 2018). As plants die, C moves from biomass to the dead pool. Standing dead trees, fallen logs, branches, and coarse woody debris represent an intermediate C pool between living biomass and soil organic matter (SOM); decomposition transfers C from dead wood into soils while releasing CO_2 to the atmosphere (Harmon et al. 2004, Russell et al. 2015). Fruit and reproductive parts in the spring, leaves senescing each fall, and twigs, bark, and small branches falling throughout the year accumulate on the forest floor and form the litter layer. This pool provides the primary organic matter input to soil and supports decomposition and nutrient cycling (Prescott 2010, Berg and McClaugherty 2020). Finally, soil is the largest C pool in most wetlands (Domke et al. 2017, Magnan et al. 2020, Beaulne et al. 2021). Soil C includes both organic and inorganic carbon, although organic C dominates and consists of living

microorganisms, partially decomposed plant material, and stabilized organic matter that accumulates over years to millennia.

Carbon is transported within wetlands as dissolved and particulate organic and inorganic C by groundwater and surface water flow (Wei et al. 2024). Partially decomposed organic matter remains soluble (by definition DOC includes all molecules that pass through a 0.45 μM filter) and can be exported during periods of high discharge or groundwater movement; similarly, particulate organic C can be washed from the surface by overland flow and flooding (Li et al. 2025). Although smaller than the soil C pool, these exports represent important losses from wetland ecosystems and connect wetlands to downstream aquatic systems (Olefeldt et al. 2017, Chaplot and Mutema 2021). C can also be lost from the system by way of CO_2 and CH_4 release to the atmosphere (Davidson et al. 2022), increased aerobic decomposition due to drainage and water table lowering (Holden 2005), harvest (physical removal of trees or soil), fire (consumption and loss as smoke and particulates; Nelson et al. 2021), and land use change (clearing and restructuring for another use such as agriculture or development; Bridgham et al. 2006, Page et al. 2022).

Hydrology and temperature are likely the primary drivers of C cycling in swamps. Hydrologic changes in temperate swamps follow seasonal cycles driven by climate, i.e., less precipitation and higher temperatures in summer, increasing precipitation and decreasing temperatures in fall, freezing and snow accumulation in winter, and increasing temperatures, precipitation, and snowmelt in spring. Connections to streams or rivers that regularly flood may deposit or remove materials (Walling et al. 1998), while persistent saturation slows decomposition (Blodau, 2011). Although all temperate wetlands will experience some version of seasonal changes in temperature and precipitation, swamps are unique in the magnitude and length of their hydroperiods. While water levels in other wetlands generally experience small fluctuations and remain within a few centimeters above or below the soil surface, in swamps water levels can vary from tens of centimeters above to over a meter below the soil surface (Davidson et al., 2019; National Wetland Working Group, 1997). Depending on the site, surface water may persist for only a short while or well into the growing season in low elevation areas. Prolonged saturation slows microbial decomposition in the soil and, as organic matter accumulates faster than it decomposes, C-rich soils and peat develop over time (Joosten & Clarke 2002, Poulter et al. 2021). Additionally, temperature modulates nearly every component of C cycling, including photosynthesis, decomposition, respiration, methanogenesis, and CH_4 oxidation (Blodau 2002, Davidson & Janssens 2006, Chapin et al. 2011, Zhu et al. 2018). In forested wetlands its effects are closely coupled with hydrology as soil saturation controls

oxygen availability, altering soil redox conditions and regulating the dominant microbial pathways of C mineralization (Blodau 2002, Bridgham et al. 2013, Megonigal et al. 2014). Consequently, interactions between temperature and water table position often explain more variation in CO_2 and CH_4 fluxes than either variable alone (Moore & Dalva 1993). Although these processes are analogous to other wetlands and upland forests, their importance in swamps remains poorly resolved.

1.4 Greenhouse gas exchange

Greenhouse gases (GHG) are atmospheric gases that absorb and emit longwave (infrared) radiation, trapping heat within the lower atmosphere through the greenhouse effect (IPCC 2021). This process regulates Earth's energy balance and maintains a global average surface temperature suitable for life (IPCC 2021). However, increases in atmospheric GHG concentrations strengthen the greenhouse effect, resulting in global warming and climate change (Canadell et al. 2021, IPCC 2021). Water vapour, CO_2, CH_4, nitrous oxide (N_2O), and ozone (O_3) are the primary GHGs in the Earth's atmosphere (IPCC 2021). Of these, CO_2, CH_4, and N_2O are the three most important GHGs due to their strength and lifetime in the atmosphere (Canadell et al. 2021). While CO_2 has the longest lifetime, the global warming potential of CH_4 is 27 times greater over a 100-year time scale (IPCC 2021), and the global warming potential of N2O is 265 times greater with a lifespan of ~114 years (IPCC 2013). Anthropogenic activities account for ~60% of global annual CH_4 emissions and wetlands are the largest natural sources of CH_4 globally (Covey & Megonigal 2018, Machacova et al. 2021),

1.4.1 Soil CO_2 exchange

Ecosystem respiration (ER) is the primary source of CO_2 efflux in swamps and forested wetlands, combining autotrophic respiration by living plants, including roots, and heterotrophic respiration from fauna and microorganisms as they decompose organic matter (Hanson et al. 2000, Chapin et al. 2006). Temperature is one of the strongest controls of ER as microbial activity and plant growth generally increase with warming. However, heterotrophic respiration is often constrained by water table position as saturation reduces oxygen availability in the soil, limiting aerobic decomposition (Blodau 2002, Bridgham et al. 2006), whereas lowering water tables increases oxygen diffusion and can substantially increase decomposition and CO_2 emissions (Davidson & Janssens 2006, Bridgham et al. 2006). Therefore, interactions between temperature and hydrology largely determine seasonal and spatial variation in ER within wetlands (Blodau 2002, Chapin et al. 2002, Davidson & Jannsens 2006, Bridgham et al. 2013).

ER is closely linked to ecosystem productivity. Together with gross primary productivity (GPP), it determines net ecosystem productivity (NEP): NEP = GPP – ER. When GPP exceeds ER, the ecosystem functions as a CO_2 sink. Conversely, when respiration exceeds photosynthesis (GPP), the ecosystem becomes a net source of CO_2 to the atmosphere (Randerson et al. 2002, Chapin et al. 2006). To date, there have been relatively few studies on swamps, with a Web of Science search for swamp, carbon, CO_2, and CH_4 returning under 200 results. Additionally, current C exchange data in northern swamps is often based on the chamber method and limited to warmer months, missing important spatial and temporal variability and making it difficult to estimate an annual C budget when forest overstory C uptake is not includedv(Blais et al. 2005).

1.4.2 Soil CH_4

CH_4 is present at much lower atmospheric concentrations than CO_2 but is considerably more effective at warming (IPCC 2014). CH_4 is produced by methanogenesis under anaerobic conditions and emitted through diffusion, ebullition, ground layer vegetation (e.g., sedges and forbs), and tree stems (Bridgham et al. 2013, Covey & Megonigal 2018). High water tables create anoxic conditions that favor methanogenesis, while warmer temperatures increase methanogen metabolic activity, generally increasing CH_4 production (Conrad 2020). Conversely, drainage introduces oxygen into the soil, suppressing methanogenesis; CH_4 emissions generally change opposite to CO_2 (Serrano-Silva et al. 2014, Conrad 2020). Additionally, under aerobic conditions, specialized microorganisms known as methanotrophs consume CH_4, converting it primarily to CO_2 (Serrano-Silva et al. 2014, Guerrero-Cruz et al. 2021). Methanotrophy primarily occurs where both oxygen and CH_4 are available, often in the upper few centimeters of saturated soils, around plant roots, within moss layers, and near the water table between saturated and unsaturated soil layers (Serrano-Silva et al. 2014, Conrad 2020). Methanotrophs often intercept CH_4 produced deeper in the soil as it diffuses upwards, and excessive drying can reduce CH_4 production sufficiently that little remains for methanotrophs (Serrano-Silva et al. 2014, Conrad 2020, Guerrero-Cruz et al. 2021). Consequently, net CH_4 emissions from wetlands are determined by the balance between methanogenesis and methanotrophy, both of which are strongly regulated by interactions between water table position, oxygen availability, soil temperature, substrate availability, and vegetation (Whalen 2005, Turetsky et al. 2014, Määttä & Malhotra 2024). Depending on ecosystem type and hydrologic conditions, methane oxidation can consume 20–90% of CH_4 produced within wetland soils, although values vary considerably among sites and seasons (Le Mer & Roger 2001; Bridgham et al. 2013). Hydrologic variability in temperate swamps creates large

spatial and temporal variation, making it essential to understand these controls to predict CH_4 fluxes (Bridgham et al. 2013, Davidson et al. 2022).

1.4.3 Tree-mediated CH_4 emissions

Although the existence of high CH_4 concentrations within tree stems has been known for decades (Bushong 1907, Schutz 1991), the importance of emissions of CH_4 from tree stems has only recently been recognized (e.g., Barba et al. 2019, Covey and Megonigal 2019, Pangala et al. 2017) and this pathway is mostly missing from global CH_4 budgets (Bona et al. 2018, Saunois et al. 2019). Methanogenic communities have been identified within woody tissues, and this internal production may be the primary source of CH_4 from upland trees (Yip et al. 2019, Jeffrey et al. 2021, Putkinen et al. 2021, Smits et al. 2021, Feng et al. 2022, Jeffrey et al. 2023a). In wetlands, CH_4 emitted from tree stems has been shown to predominantly originate from the soil, being transported up the stem through both passive (diffusion) and active (transpiration and plant tissues) processes, particularly in wet conditions (Mander et al. 2021, Jeffrey et al. 2023a).

Passive diffusion is considered the most widespread mechanism of CH_4 transport in wetland trees. Methane produced in anoxic soils diffuses into roots and enters interconnected gas-filled spaces within the xylem, bark, and stem tissues (Barba et al., 2019; Covey and Megonigal, 2019). Driven by concentration gradients, CH_4 moves upward through the stem and diffuses through lenticels, bark fissures, or permeable bark into the atmosphere (Pangala et al., 2014; Megonigal et al., 2019). Because diffusion depends on CH_4 concentration gradients rather than plant physiological activity, emissions can continue even when transpiration is low, such as at night or during dormant seasons (Mander et al. 2022, Jeffrey et al. 2023). Strong relationships between soil porewater CH_4 concentrations and stem emissions and decreasing stem CH_4 fluxes with increasing sampling height (Pangala et al. 2013, Jeffrey et al. 2020, Sjögersten et al. 2020) provide evidence supporting diffusion as a pathway for CH_4 transport through trees. Wetland trees have been found to develop aerenchyma, enlarged gas spaces in roots and stems, in response to saturated soil conditions (Topa & McLeod 1986, Drew et al. 2000, Evans, 2004). These tissues faciliate rapid gas transport between soil and atmosphere to supply oxygen to roots in anoxic soils (Jackson & Armstrong 1999), as evidenced by the presence of oxidized rhizospheres (Armstrong 1697, Hook et al. 1972, Schroder 1989). Aerenchyma have not been observed in trees in well-drained, upland soils (Armstrong 1980).

Methane dissolved in soil water may be absorbed by roots and transported upward in the xylem with transpiration-driven sap flow. As water moves toward the canopy, decreasing pressure allows dissolved CH_4 to exsolve from solution and diffuse through stem tissues and bark to the atmosphere (Anttila et al. 2022). The amount of CH_4 transported in xylem sap has been shown to increase with sap flow velocity, increasing stem diameter, decreasing temperature, and increasing stem water content (Sorz & Hietz 2006, Norwood et al. 2021, Anttila et al. 2022).

Although soil pore water CH_4 appears to be the main source of tree stem CH_4 emissions in wetland trees, studies have shown that in-situ CH_4 production is the primary source within upland trees (e.g., Yip et al. 2019, Flanagan et al. 2021). Internal tree stem CH_4 concentrations have been linked to heartwood rot, water content, and saprotrophic fungi (Zeikus & Ward 1974, Covey et al. 2012, Lenhart et al. 2012, Wang et al. 2017). Additionally, methanogenic archaea have been identified within tree stems (Yip et al. 2018, Flanagan et al. 2021, Putkinen et al. 2021, Feng et al. 2022). Wang et al. (2016) found that wood incubations under anoxic conditions produced CH_4, but that emissions did not follow the vertical pattern of decreasing with stem height (Wang et al. 2016, Machacova et al. 2023). Internal production has not been correlated with soil properties or soil CH_4 fluxes and concentrations (Pitz & Megonigal 2017, Machacova et al. 2023) but has been strongly associated with tree properties such as wood moisture, stem diameter, and wood pH (Yip et al. 2018). The presence of internal CH_4 production does not exclude soil CH_4 transportation and vice versa; both processes have been detected simultaneously in both wetland and upland trees (Megonigal et al. 2020, Flanagan et al. 2021, Feng et al. 2022).

Tree stem CH_4 emissions seem to respond to the same main environmental controls as wetland soils: water table and soil temperature (Turetsky et al. 2014). Because CH_4 emitted from wetland trees is derived primarily from the soil, any factor that influences methanogenesis, CH_4 oxidation, or transport through the tree can affect stem emissions. Shallow water tables create anoxic soil conditions that increase methanogenesis and, as CH_4 concentrations increase in soil pore water, more CH_4 becomes available for root uptake and transport through tree stems (Covey & Megonigal 2018, Wu et al. 2024). Consequently, stem CH_4 emissions typically increase at the water table rises and decline as soils dry. Hydrology also influences transport by determining the extent of root inundation and hydrologic connectivity between the soil and root system (Barba et al. 2024, Wu et al. 2024). Soil temperature regulates stem emissions primarily through its effects on microbial activity. Warmer soils increase decomposition and methanogenesis, increasing CH_4 production as long as soils remain anoxic (Pangala et al. 2015, Pitz & Megonigal 2017, Pitz et al. 2018). Higher temperatures may also enhance

CH_4 transport by increasing diffusion rates and sap flow. In many forested wetlands, the largest stem CH_4 fluxes occur during the warm growing season when both methanogenesis and plant activity are highest (Maier et al. 2017, Pitz & Megonigal 2017). Historically, GHG soil fluxes in northern wetlands have often been assumed to be negligible during winter or omitted from annual budgets. However, a growing body of evidence demonstrates that snow-covered season CO_2 and CH_4 fluxes contribute substantially to annual greenhouse gas budgets, indicating that this assumption can lead to underestimation of annual emissions (Maljanen et al. 2007, Miao et al., 2012, Meyer et al. 2024).

Tree species identity is among the strongest biological controls of stem CH_4 emissions because species differ in traits that influence CH_4 transport, including wood anatomy, bark permeability, lenticel density and size, sap flow, root architecture, tolerance to flooding, and internal microbial communities (Pangala et al. 2015, 2017, Wang et al. 2016, 2017, Barba 2018, Pitz et al. 2018, Barba et al. 2019). These characteristics affect both the efficiency of CH_4 movement through the stem and the potential for internal CH_4 production or oxidation. Consequently, stem CH_4 emissions often vary among individuals of the same species or co-occurring species even under similar environmental conditions. Tree size has also been linked to stem emissions; however, relationships between stem diameter and CH_4 emission are inconsistent among studies and ecosystems, suggesting that tree size interacts with species identify and hydrological conditions. Both negative realationships, where stem CH_4 emissions decreased with increasing diameter (Pangala et al. 2015, 2017, Wu et al. 2024), and positive, where emissions increased with diameter (Pitz et al. 2018, Barba et al. 2021), have been found. Lower wood density contains more pore spaces for CH_4 diffusion or transportation (Pangala et al. 2015, Wang et al. 2017, Zhang et al. 2022), while greater lenticel density increases gas exchange capacity between the stem interior and the atmosphere (Pangala et al. 2014, Covey and Megonigal 2019, Barba et al. 2019, Zhang et al. 2022). CH_4 oxidizing bacteria have been found within tree stems and bark, potentially oxidizing a portion of CH_4 before it is emitted (Keppler et al. 2006, Covey & Megonigal 2019, Jeffrey et al. 2021). Net consumption of CH_4 has been found in upland trees (Sundqvist et al. 2012, Machacova et al. 2016, Pitz & Megonigal 2017, Warner et al. 2017), and occasionally in wetland trees (Machacova et al. 2016, Pitz et al. 2018).

Altogether, tree stem CH_4 emissions can be viewed as the product of three interacting processes: 1) CH_4 production – regulated primarily by water table position, soil temperature, substrate availability, and anaerobic microbial activity; 2) CH_4 transport – controlled by root uptake, diffusion, sap flow, stem anatomy, and species-specific traits; and 3) CH_4 consumption – influenced by

CH_4 oxidation in soils and potentially within bark and woody tissues before CH_4 reaches the atmosphere. As has been shown, rates of these processes are highly variable in space and time and likely extremely site- and species-specific and require further investigation. Additionally, almost no studies on tree stem CH_4 emissions exist for temperate swamps, where cold soils and freezing conditions likely affect emission rates, or for the tree species dominant in Ontario swamps.

1.5 Temperate swamp carbon stocks and GHG exchange: Remaining knowledge gaps

Despite the growing number of studies on swamp C cycling and GHGs, there is still a significant lack of data for temperate ecozones. For example:

- Swamp carbon stocks remain poorly quantified.
- Temperate swamps are underrepresented globally.
- Annual CO_2 and CH_4 budgets are rare.
- Carbon transfers among pools remain uncertain.
- Tree stem CH_4 is largely absent from temperate studies.
- Species-specific controls are poorly understood.
- Winter and freeze–thaw dynamics remain almost completely unknown.
- Differences in C stores and cycling between types of swamps (i.e., as classified by hydrogeomorphic setting + canopy) are unknown.

Due to these factors, existing C and climate models lack sufficient swamp-specific data to be included as a separate class even though distribution of C stocks between biomass and soil pools and rates of GHG exchange are likely different from other wetland types. Additionally, with their large above- and belowground C stocks, swamps are potential C "hotspots" on the landscape and candidates for conservation as a natural climate solutions.

1.6 Thesis objectives

This thesis is written in manuscript format and as such some of the information within chapters may be repeated.

Chapter 2 provides 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; determines the effect of hydrogeomorphic setting and canopy types on soil CO_2 and CH_4 fluxes, and; assesses if it is possible to estimate soil CO_2 and CH_4 across a range of swamp types with minimal information. This manuscript was published as:

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Chapter 3 assesses the annual C balance of 4 of the 12 swamps from Chapter 2. It estimates the current C stocks held within soil, dead wood, living trees, and understory vegetation; estimates the addition and losses of C to the ecosystem annually via growth and decay, and determines if the study swamps are sources or sinks of C.

Chapter 4 assesses tree stem CH_4 emissions of 3 of the 12 swamps from Chapter 2. Based on field measurements across 18 months, it quantifies stem CH_4 fluxes from three dominant genera (maple, birch, cedar), assesses environmental controls on tree stem CH_4 flux, and determines the relative contribution of tree stems and soils to temperate swamp CH_4 budgets.

Chapter 5 is a synthesis of temperate swamp C cycling. It integrates C stocks and GHG fluxes with environmental controls to update the state of the knowledge on temperate swamps and addresses the need for Canadian swamp C budgets in modeling and policy. This chapter also discusses the implications of the thesis findings for natural climate solutions and climate mitigation.

Chapter 2

Quantifying Carbon Pools and Fluxes in Southern Ontario Temperate Swamps

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2.1 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. 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 miss potentially large C soil stocks 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 parameterizing 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 height (NWWG 1997, Government of Ontario 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 (Federal Geographic Data Committee 2013). The Ramsar Convention on Wetlands

classifies swamps as shrub-, tree-dominated, or forested wetlands or peatlands (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, proximity to regional groundwater tables, 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, high organic matter contents and bulk densities in swamps results in high soil C stocks in the top 0–90 cm across all four canopy types (Davidson *et al*. 2022). Below the canopy, understory 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). 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 forest soils across the US (Domke *et al.* 2017). Carbon stocks in peat are 4–25 times higher than that of the trees in 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 Canadian bogs and fens (Webster *et al.* 2018).

Given that biomass C stocks in swamps are similar to other forest types and soil C stocks are much greater, conservation of these ecosystems from land-use change would provide greater protection of land-based carbon stocks than 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 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 types on soil CO_2 and CH_4 fluxes

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

2.2 Methods

2.2.1 Study sites

All 12 sites are located in southern Ontario, between 42–44°N and 80–82°W (Figure 2.1, Table 2.1), 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 access permission. All sites are owned by the *rare* Research Reserve, conservation authorities, or the University of Waterloo. The swamps fell into four hydrogeomorphic settings, including all four canopy types, and had organic or mineral-organic soils (Table 2.1). Basin swamps (n = 4) are well-defined by the sides of the basin and occur in glacial deposits (e.g., kettle) or bedrock (NWWG 1997). Sifton and Spongy Lake are both kettle peatlands with perimeter swamps; Sifton is ~23 ha and up to 11–14 m 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 groundwaters (Dempster *et al.* 2006, City of London 2009). Spongy Lake has a large, shallow open water expanse in the center of the basin where water level can drop considerably in dry years. The center 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 is ~1 m at the deepest point from 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 were dominantly broad-leaved (hardwood species that lose leaves in the fall, 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 or 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).

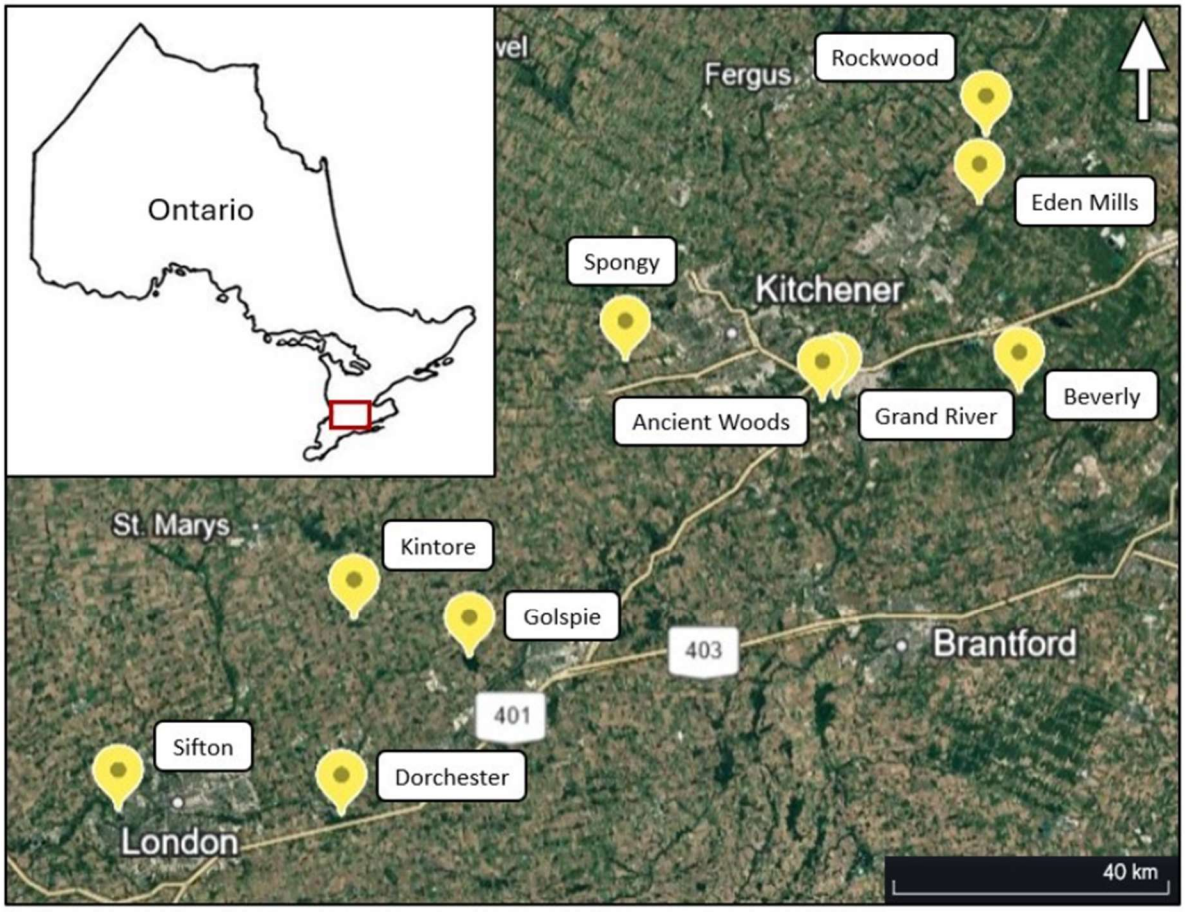


Figure 2.1 Map of site locations within study area and Ontario (inset). Imagery from Google Earth (01/01/2025). Accessed 18-Sept-2025.

Table 2.1 Summary of Sites.

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

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 4 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 precipitation is 900–1000 mm with the rainiest months in spring and fall; however, 2022, the main growing season of this study, was hot and dry, with only 600–700 mm (Government of Canada 2024). Southern Ontario is densely populated with 5–1000 people per square kilometer (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 impacted 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.

2.2.2 Soil CH_4 and CO_2 fluxes

We measured understory 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, 20 cm diameter, 10 cm tall acrylic collars were permanently installed in the ground. Three locations were chosen within each site to characterize wet, dry, and intermediate hydrologic conditions, and contained forbs, grasses, mosses, and seedlings <24

cm 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 x 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 understory 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 understory vegetation. Similarly, an opaque chamber (20 cm diameter x 24 cm tall) allowed for ecosystem respiration (ER; CO_2 released from soil and understory plants) and CH_4 flux to be measured. By subtracting ER from NEE_u, gross ecosystem productivity of the understory (GEP_u; CO_2 taken up by understory 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 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. 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 (WT) was measured as depth from surface in a standpipe adjacent to each collar.

Further inspection for linearity and slope of fluxes was calculated 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 for further analysis. Average values for all C fluxes are given in Supplementary Material Table S1.
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 months together. For months without data due to access issues or data loss during quality control, the mean of the preceding and following months was used as an estimate.

2.2.3 Biomass and soil carbon

Tree and understory vegetation surveys were conducted at all 12 sites in late July through early August 2022. Trees were measured in three 20 m x 20 m plots at each site. Every individual ≥ 3 m tall

was identified to genus, and to species if possible, and measured for diameter at breast height (DBH). Allometric equations were used to estimate biomass of trees (kg C m^{-2}; Ung et al. 2008). One by one meter quadrats were used for understory 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. See Supplementary Table S1 for vegetation survey summaries. Four litter traps (0.5 x 0.5 m) per site were installed between August 15–30, 2022 to catch leaves and twigs that fell from the canopy (adapted from Bernier *et al*. 2008). Each trap was collected biweekly to monthly from September to November and was collected a final time in May 2023 to include anything that fell over the winter and spring; this mass added to the site total (Bernier *et a*l. 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. 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 understory of each site (39 – 45%); total C values were measured through combustion conversion of sample to gas through 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 was collected within 2 m of each collar (n=3 per site) across the 12 sites in 2022 with a Russian auger to the confining layer or to a maximum depth of 50 cm, whichever was shallowest. 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 lab. Samples were stored at 4 °C for 3–10 days until being dried 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 analyzed for organic matter content (OM%) via loss on ignition. Approximately 3 g of soil was measured into a pre-weighed ceramic crucible, placed into a muffle furnace, and burned at 550 °C for 4 hours to ignite any organic material within. 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 2 hours at 950 °C to ignite inorganic C (i.e., $CaCO_3$). 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).

2.2.4 Statistical analysis

All data analysis and visualizations were done using the statistical analysis program R (R Core Team 2013). Growing season (GS; April 15–October 20) was determined to begin when mean daily temperature was greater than or equal to 5 °C for five consecutive days after March 1, ending when minimum daily temperature was less than -2 °C after August 1 (Mackey *et al.* 1996). As it is well known that environmental conditions differ significantly between the GS and non-growing season (NGS), we did not include season in the analyses. GEP_u and NEE_u were only analysed for GS as photosynthesis is minimal during the NGS. Not all combinations of settings and canopies (particularly shrub) were represented, therefore, interactions between site, setting, and canopy could not be evaluated. Caution should therefore be used in interpreting results from these models and differences between canopy types and hydrogeomorphic settings considered as only a preliminary assessment. Some groups contained only one site, therefore site-specific conditions could not be separated from specific canopy or setting effects. 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.* 2016). 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; figures for ST at 30 cm can be found in Supplementary Materials Figure S1. As biomass and soil were measured only once, stored organic C amounts were expressed as annual averages for each plot. Linear mixed effects models were used to evaluate C stocks against site, setting, or canopy as fixed effects and plot as random effect.

2.3 Results

2.3.1 Environmental Conditions

Precipitation in southern Ontario was lower in 2022 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 (Supplementary Table S2.2). Mean WT during GS was shallower in basin sites than 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 the other two basin sites ($F_{11,24}$=7.0285, p = <0.0001; Table 2.2). 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 -53–1 cm among sites ($F_{11,24}$= 8.2408, p = <0.0001; Table 2.2) and remained shallowest at basin sites. WT fell below the bottom of the well 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 where the well was dry were removed from the analysis for gases x WT; therefore, minimum and mean WT are likely lower than shown.

Mean GS ST at 10 cm (ST10) below surface varied from 14–17 ℃ among sites (Table 2.2) with no notable differences between settings or canopies. Mean GS ST at 30 cm (ST30) varied from 12–16 ℃ (Table 2.2), was cooler at riverine and needle-leaved sites and increased with the presence of broad-leaved trees. Mean NGS ST10 cm varied from 4–8 ℃ across sites (Table 2.2), being coldest with shrub cover, and warmer at broad-leaved sites. Mean NGS ST30 cm ranged from 5–10 ℃ (Table 2) with no notable differences among settings or canopy cover types.

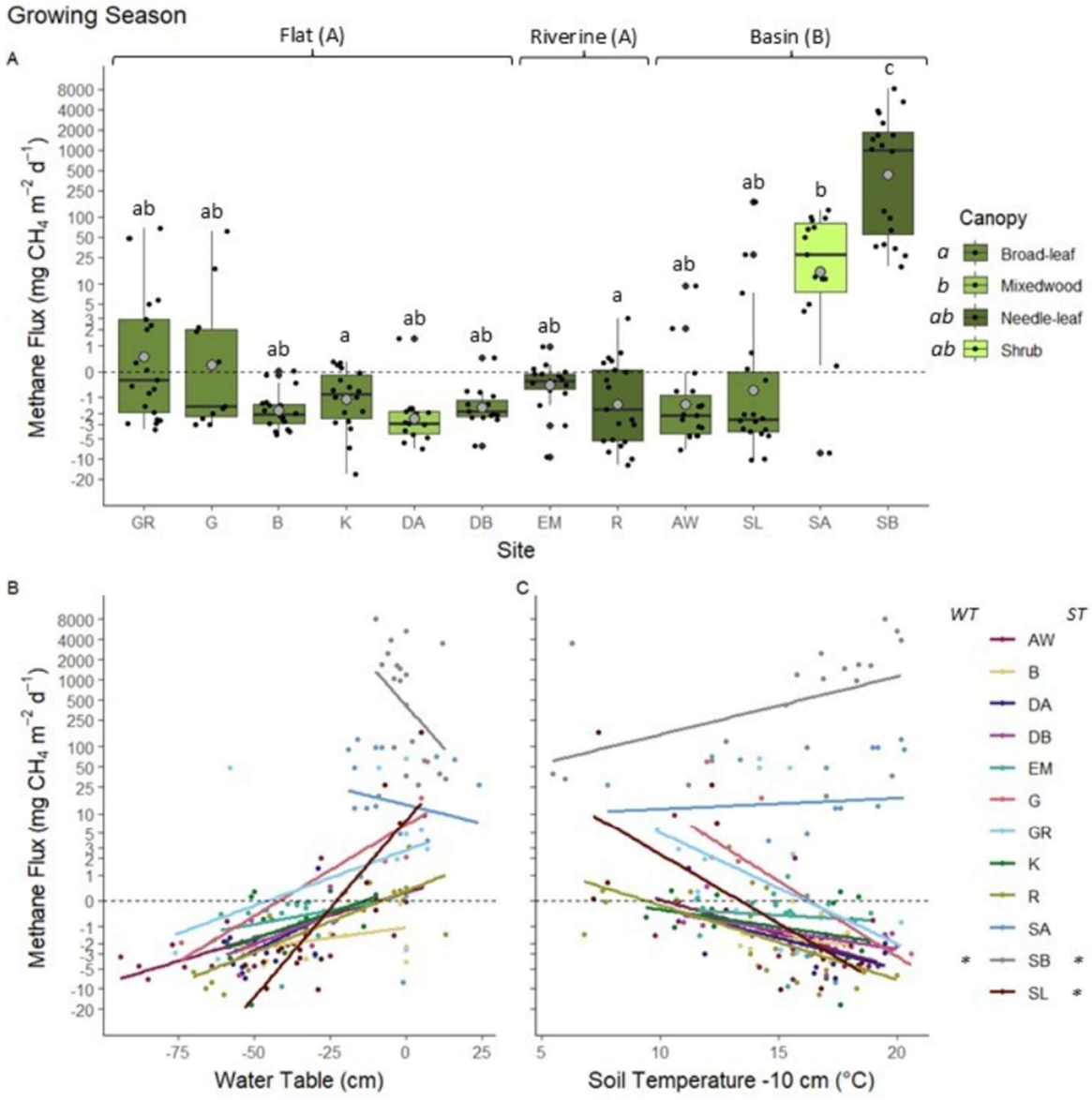
Table 2.2 Seasonal water table (WT) and soil temperature (ST) descriptive statistics. Positive WT values indicate flooded conditions where the water table was above the surface.

Site	Growing Season						Non-Growing Season					
	Min WT* (cm)	Max WT (cm)	Mean WT (cm)	Range (cm)	Mean ST 10 cm	Mean ST 30 cm	Min WT* (cm)	Max WT (cm)	Mean WT (cm)	Range (cm)	Mean ST 10 cm	Mean ST 30 cm
Ancient Woods	-94	0	-45.6	94	15.1	14.2	-91	5	-44.3	96	6	6.8
Beverly	-54	0	-31.7	54	16.3	15	-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	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	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	19	3.8	6.9
Spongy Lake	-53	-2	-28.1	51	14.7	13.5	-55	-24	-36.6	31	8	10

* WT fell below the bottom of the well at Golspie on 6 sampling days (n=16), Grand River 4 (n=10), and Rockwood 3 (n=5). These values were removed from analysis of WT, therefore minimum and mean water table levels were likely deeper than shown.

2.3.2 Carbon Fluxes

Mean CH_4 fluxes during the GS ranged from -3–1,605 mg m^{-2} d^{-1} (Figure 2.2A, Table S2.3), however strong evidence indicated that only Kintore, Rockwood, Sifton A, and Sifton B differed ($F_{11,24}$= 23.9844, p = < .0001); fluxes from Sifton A and Sifton B were a factor of 10 and 1,000 times, respectively, higher than other sites. There was strong evidence that mean efflux from basin sites was higher than flat sites that, along with riverine, were near zero ($F_{2,33}$= 6.0997, p = .0056). Similarly, high CH_4 fluxes were observed at needle-leaved and shrub canopies, which included Sifton B and Sifton A ($F_{3,32}$=3.4062, p = .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 = < .0001; Figure 2D). Methane efflux increased as water tables rose throughout the year with the exception of Sifton A and Sifton B (Figure 2.2B, E). 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 (Figure 2.2C, F).


Growing Season
Flat (A)
Riverine (A)
Basin (B)
A
Methane Flux (mg CH4 m-2 d-1)
Site
GR
G
B
K
DA
DB
EM
R
AW
SL
SA
SB
Canopy
a Broad-leaf
b Mixedwood
ab Needle-leaf
ab Shrub
B
Water Table (cm)
C
Soil Temperature -10 cm (°C)
WT
ST
AW
B
DA
DB
EM
G
GR
K
R
SA
SB
SL

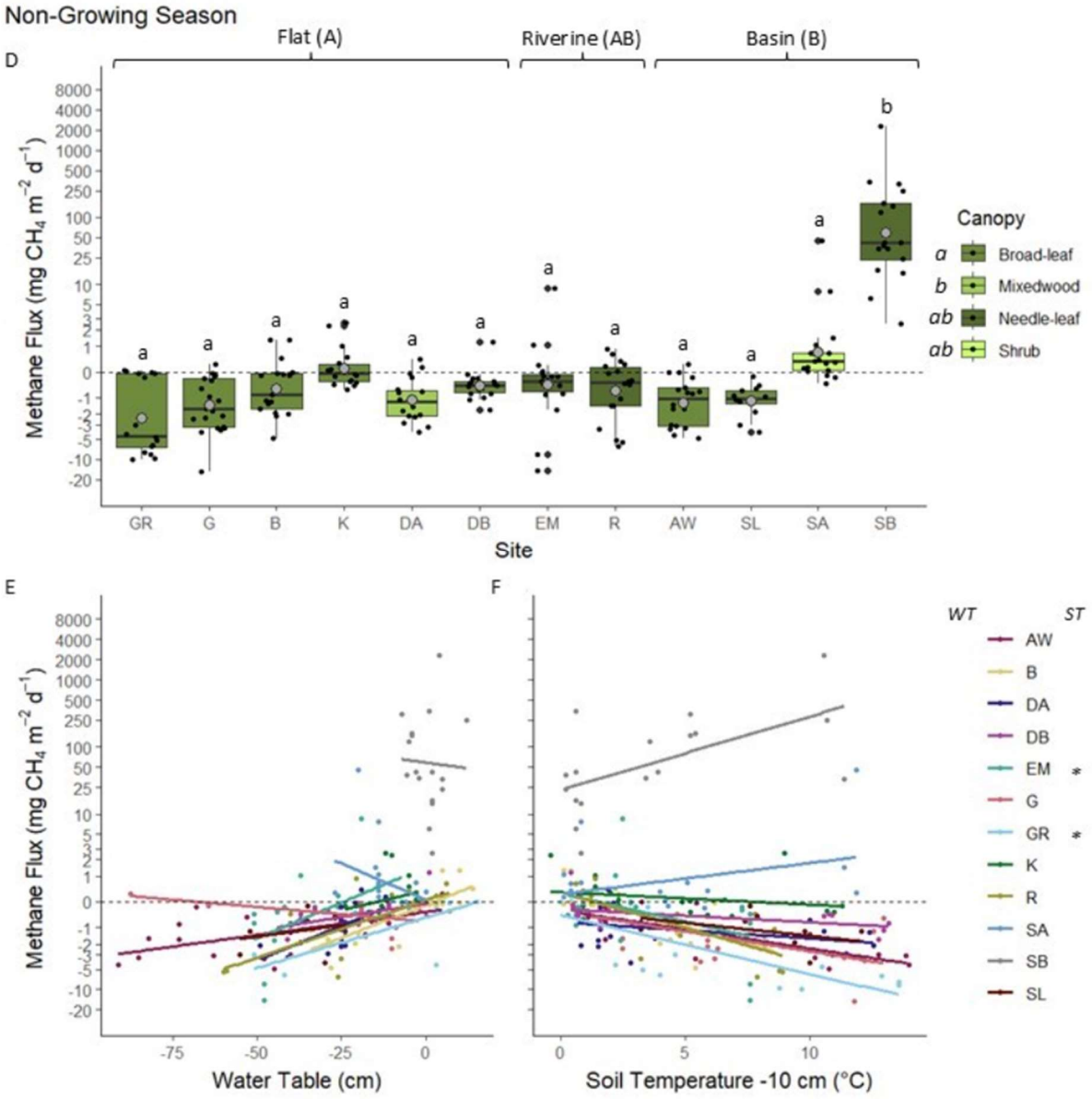


Figure 2.2 Growing season and non-growing season methane fluxes (mg CH_4 $m^{-2}d^{-1}$). (A, D) Site, setting, or canopy means are significantly different if they do not share letters, as per post-hoc Tukey tests. Lower case letters refer to differences between sites, capital letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles in 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. CH_4 relationship to growing season water table (B, E) and soil temperature (C, F); significant relationships are denoted by *.

Mean understory gross ecosystem productivity (GEP_u, uptake of CO_2 by understory plants and soil organisms) during the GS ranged from -36 to -6 g m^{-2} d^{-1} (Figure 2.3A, Table S2.1), but strong evidence showed only Eden Mills and Grand River were different from Spongy Lake ($F_{11,24} = 3.432$, $p = 0.0056$). Understory productivity was highest (most uptake) in both flat and riverine sites, and mixedwood sites. Generally, the understory was more productive with wetter soils ($F_{1,166} = 18.6469$, $p = <.0001$; Figure 2.3B) and as soils warmed, with the exception of Ancient Woods and Dorchester A at 10 cm ($F_{1,167} = 14.1687$, $p = .0002$; Figure 2.3C) and Beverly, Eden Mills, and Dorchester A at 30 cm ($F_{1,167} = 7.1529$, $p = .0082$).

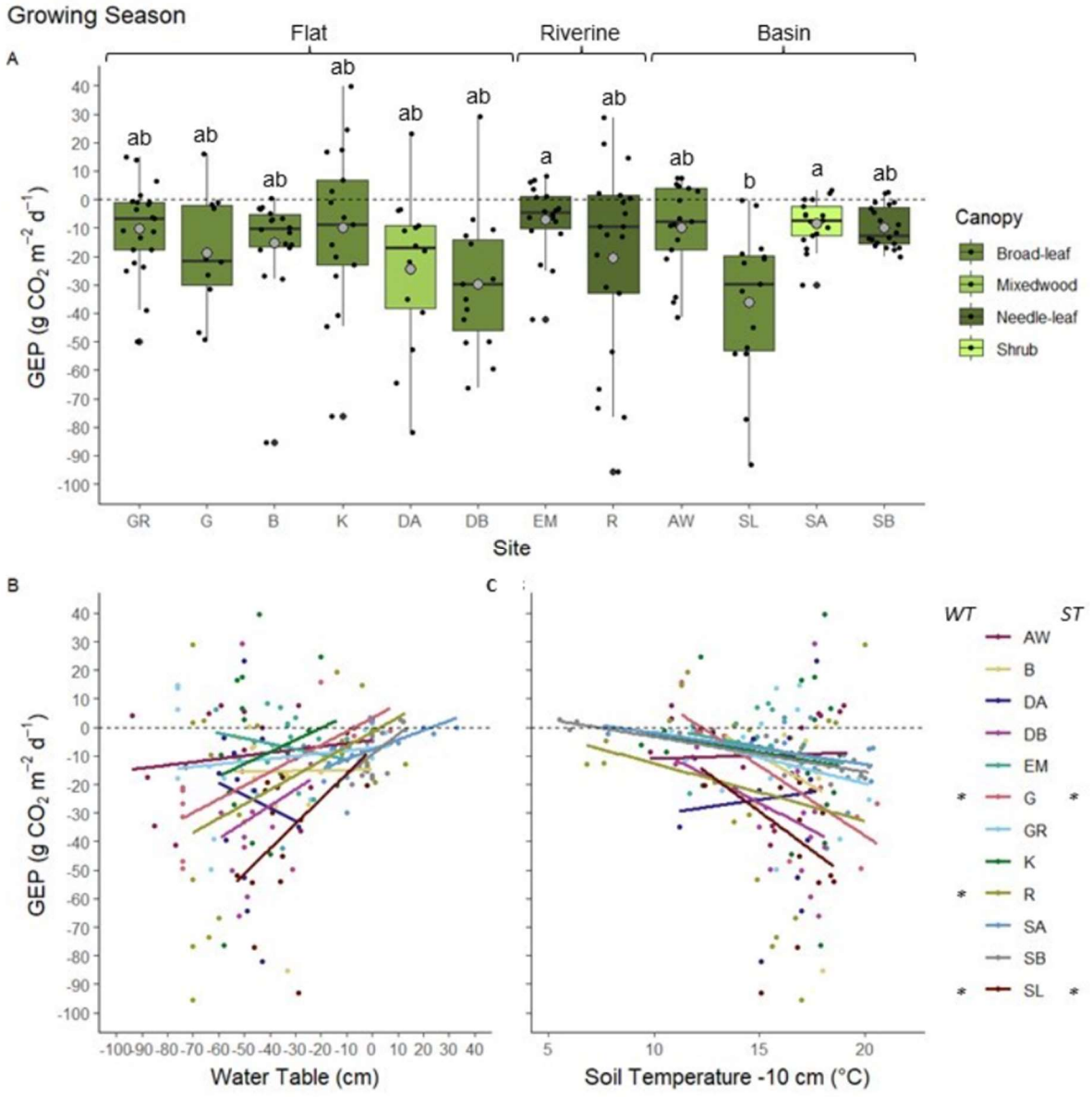
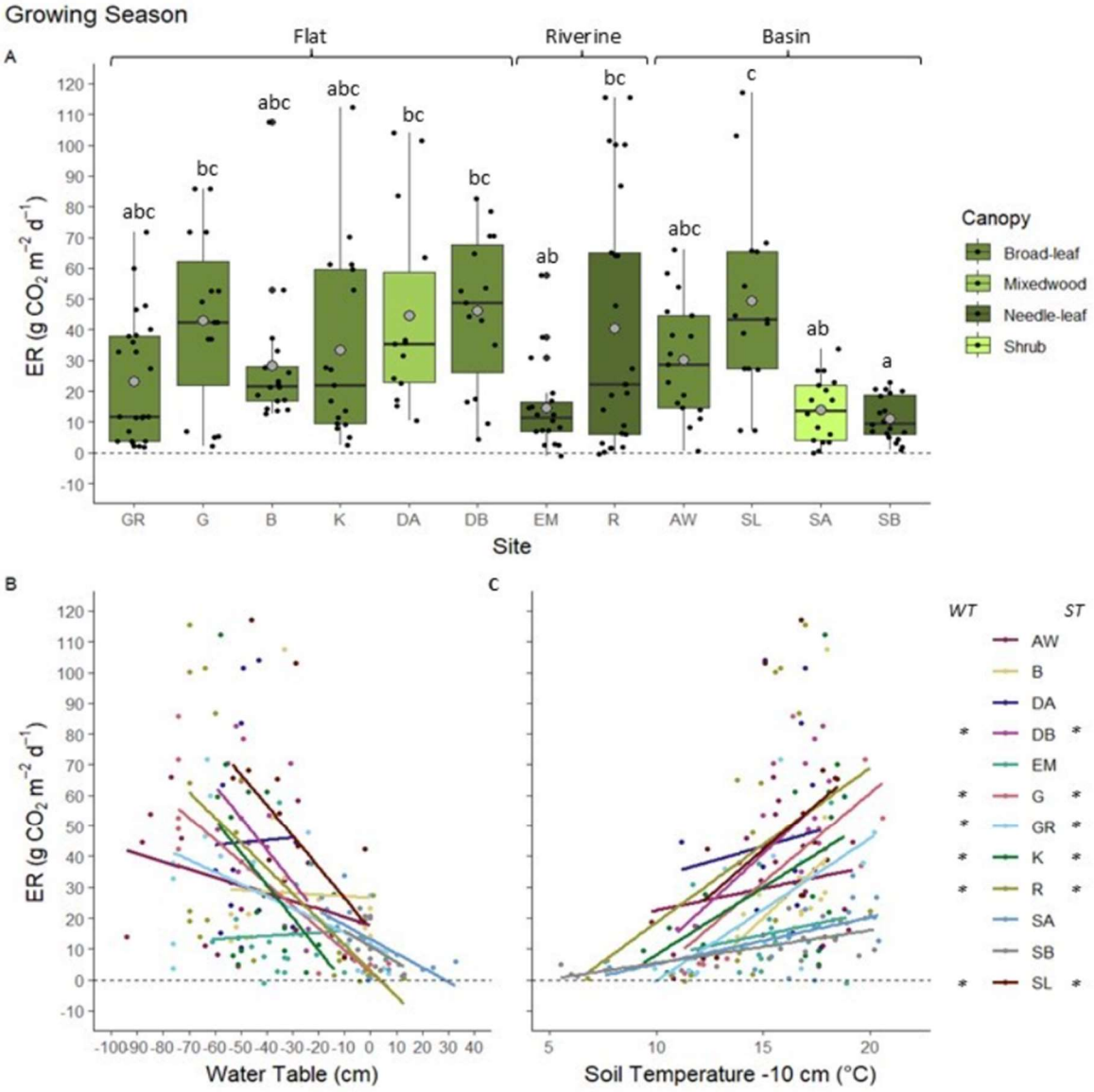


Figure 2.3 Growing season gross ecosystem productivity (GEP_u g CO_2 $m^{-2}d^{-1}$). (A) Site, setting, or canopy means are significantly different if they do not share letters, as per post-hoc Tukey tests. Lower case letters refer to differences between sites, capital l letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles in 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. GEP_u relationship to growing season water table (B) and soil temperature (C): significant relationships are denoted by *

Mean ground layer respiration of CO_2 from the soil and understory (ER; includes root respiration) during the GS ranged from 11–49 g m^{-2} d^{-1} ($F_{11,24}$ = 4.84, p = 0.0006) and was generally highest in flat sites and mixedwood canopies (Figure 2.4A, Table S1). Over the NGS, ER varied from 2–23 g $m^{-2}d^{-1}$ ($F_{11,24}$ = 1.45, p = 0.2129) and was highest from needle-leaved and riverine sites (Figure 2.4D). Generally, ER increased with deeper WT across both seasons, with the exception of Eden Mills and Dorchester A in the GS (Figure 2.4B) and Golspie and Sifton B in the NGS (Figure 2.4E). 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 2.4F) and Beverly and Eden Mills at 30 cm in GS (Figure 2.4C).


Growing Season
A
Flat
Riverine
Basin
ER (g CO2 m-2 d-1)
abc
bc
abc
abc
bc
bc
ab
bc
abc
c
ab
a
GR
G
B
K
DA
DB
EM
R
AW
SL
SA
SB
Site
Canopy
Broad-leaf
Mixedwood
Needle-leaf
Shrub
B
Water Table (cm)
C
Soil Temperature -10 cm (°C)
WT
ST
AW
B
DA
DB
EM
G
GR
K
R
SA
SB
SL

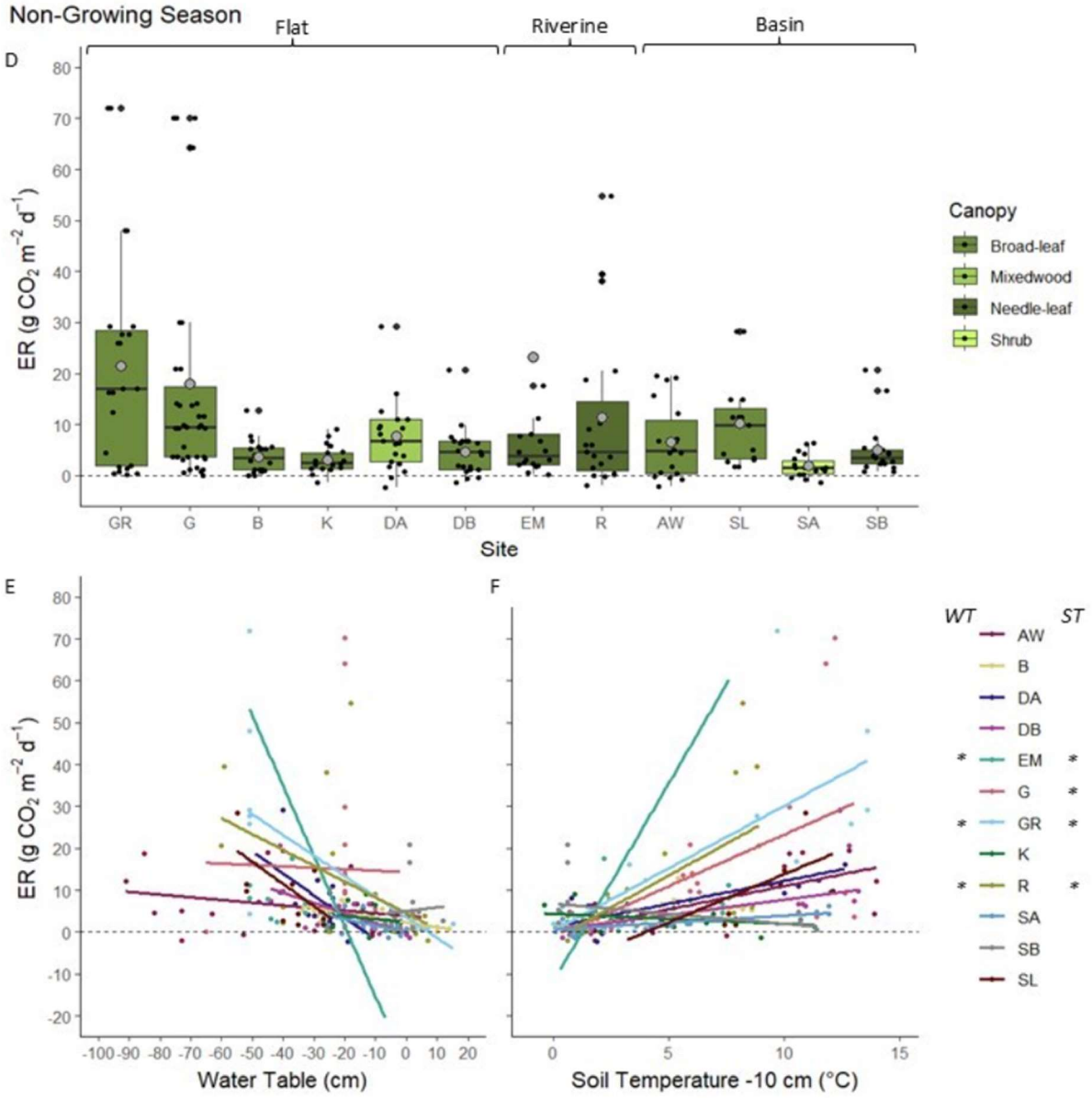


Figure 2.4 Growing season and non-growing season ecosystem respiration (ER g CO_2 $m^{-2}d^{-1}$). (A, D) Site, setting, or canopy means are significantly different if they do not share letters, as per post-hoc Tukey tests. Lower case letters refer to differences between sites, capital letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles in 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. ER relationship to growing season water table (B, E) and soil temperature (C, F): significant relationships are denoted by *.

Mean net ecosystem respiration of the understory (NEE_u: overall balance between GEP_u and ER in the understory) during the GS ranged from 1–24 g $m^{-2}d^{-1}$ (Figure 2.5A, Table S2.1). The understories of all sites were a net source of CO_2, though only Sifton B differed from Kintore ($F_{11,24}$= 3.047, p = .0109). Mean NEE_u was highest (greatest efflux) from flat, broad-leaved, and mixedwood sites. Generally NEE_u decreased (i.e., more uptake) as water tables neared the surface (Figure 2.5B) and increased as soils warmed, except in Sifton B (Figure 2.5C).

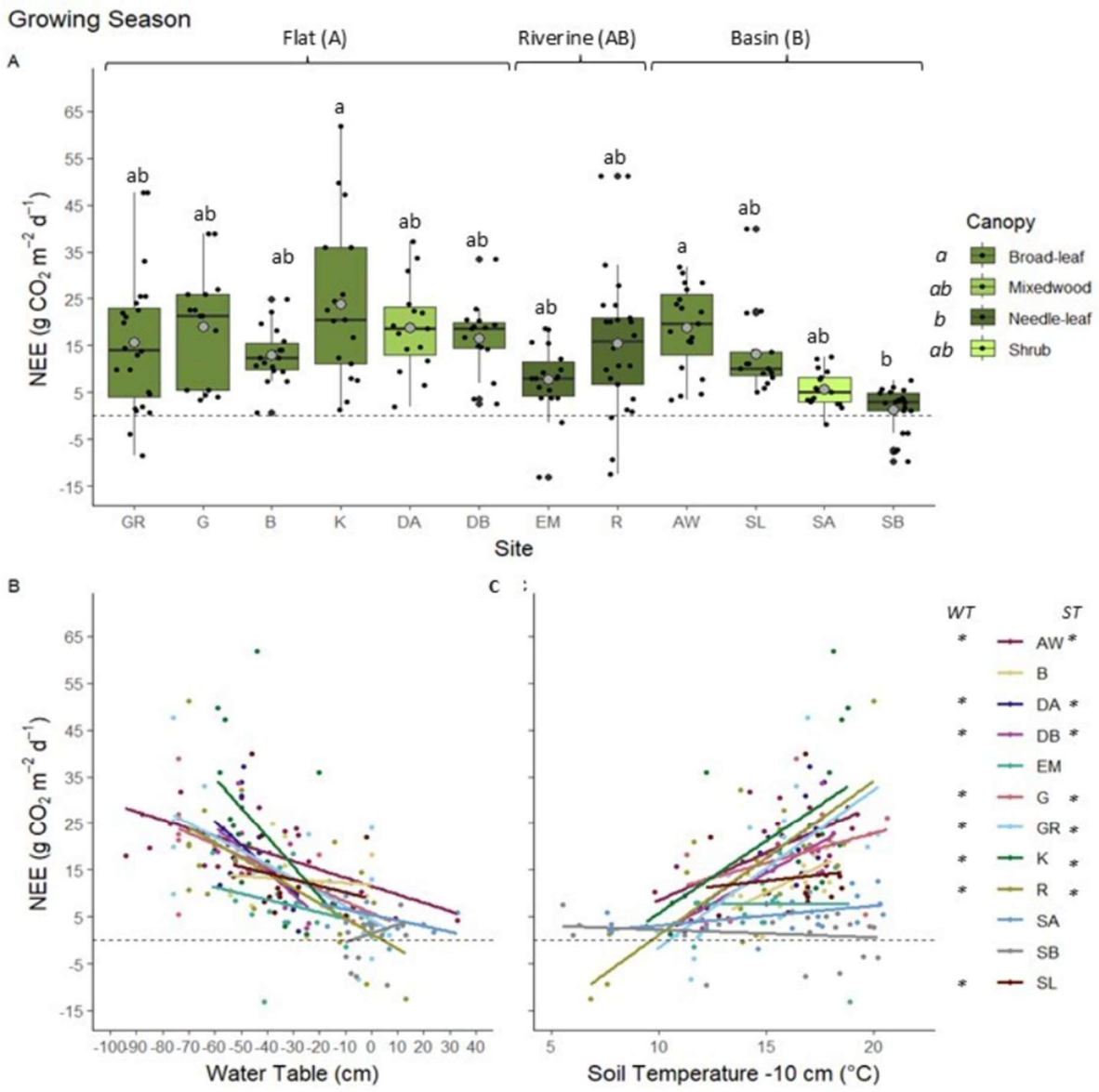


Figure 2.5 Growing season net ecosystem production (NEE_u g CO2 m-2d -1). (A) Site, setting, or canopy means are significantly different if they do not share letters, as per post-hoc Tukey tests. Lower case letters refer to differences between sites, capital letters settings, and italicised letters canopies. Boxes represent the upper and lower quartiles in 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 diamond. GEP_u relationship to growing season water table (B) and soil temperature (C): significant relationships are denoted by *.

2.3.3 Carbon Stocks and Annual Fluxes

Total estimated C stored in trees ranged from 7.92–37.0 kg m^{-2} across the sites (Table 2.4) 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 (Table 2.4). 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 2.4), regardless of understory 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.

Across the sites, estimated cumulative net CO_2-C emissions from soil and understory (NEE_u) over June 2022 to May 2023 ranged from 330.7–1331.4 g m^{-2} yr^{-1} (Table 2.3). Due to accessibility 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 highly through the winter months, we used the December flux for January through March, then averaged March and May to set an estimate for April. We acknowledge that this method will have over-estimated some months and under-estimated others but believe the impact 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 2.3) with uptake in flat and riverine sites. Mixedwood sites also took up a small amount 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 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 from basin sites dropped from 66.3 to 0.036 g m^{-2} yr^{-1}, and needle-leaved from 86.0 to -0.351 g m^{-2} yr^{-1}; these estimates were not statistically significantly different from the other settings or canopies.

Table 2.3 Mean carbon stocks and annual fluxes across study sites. For annual NEE_u and CH4, 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 only sampled to a maximum depth of 50 cm; soils at Dorchester A, Kintore, Sifton A, Sifton B, and Spongy Lake exceeded 50 cm (i.e., confining layer was not reached), but the full depth is not known.

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

*Soils were only sampled to a maximum depth of 50 cm; Dorchester A, Kintore, Sifton A, Sifton B, and Spongy Lake exceeded 50 cm.

2.4 Discussion

Mean GS soil respiration of CO_2 and CH_4 across the swamps ranged from 11–49 g m^{-2} d^{-1} and -3–44 CH_4 $m^{-2}d^{-1}$, 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 S1). In particular, our net CH_4 fluxes fall on the lower end of this range, with some even acting as small sinks.

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., Lui *et al.* 2019, Le Mar & Roger 2001, 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 for Sifton), possibly explaining these low values. Several studies have shown a reversal from CH4 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.* (2022) ranged from -2 – 26.5 mg CH_4 $m^{-2}d^{-1}$; Harriss, Sebacher & Day (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, Sebacher & Day 1982; Davidson et al. 2022). Climate change is expected to result in warmer temperatures and more prolonged dry periods in temperate regions (IPCC 2021), suggesting that in future temperate swamps may continue to act more like upland forests in regard 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 either riverine or flat sites (Figure 2.2). High CH_4 effluxes at Sifton were likely 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 2.2). This difference included the other basin sites, Ancient Woods and Spongy Lake (Table 2.1). 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 center to the swamps, likely 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 Sifton B is likely 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 $m^{-2}d^{-1}$); these differences should be interpreted with caution as some groups had only one site

Although there were differences in CH_4 flux between canopy types, they were more likely linked to other factors such as water level and soil temperature than canopy. Water tables, in particular, may be moderated by setting and connectivity to ground and surface water features. Canopy type and structure do, however, influence understory vegetation as it changes the amount of light that reaches the ground. For example, needle-leaved canopies are typically thicker and remain consistent throughout the year, whereas broad-leaved canopies change through seasons and often create more dappled shade. The amount of direct sunlight received by the understory 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 and 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 $m^{-2}d^{-1}$), although the uneven site design may mask specific canopy effects. Davidson *et al.* (2022) reported mean CH_4 from broad-leaved swamps at 126.8 ± 33.9 mg $m^{-2}d^{-1}$, needle-leaved 13.5 ± 10.3 mg $m^{-2}d^{-1}$, and mixedwood 31.7 ± 51.1 mg $m^{-2}d^{-1}$, quite a bit higher than our sites, however this could be due to the very dry conditions over our study period and hydrologic conditions specific to the swamps in the review.

Mean ER of CO_2 in the understory 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} broad-leaved, and 0.64 ± 0.1 g m^{-2} d^{-1} in needle-leaved swamps. In Nova Scotia, Canada, mean GS ER 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 understory (GEP_u; CO_2 taken up by plants via photosynthetic processes) was not reported in most other swamp studies, and understory vegetation cover and species varied widely across and within our sites. Uptake was highest in mixedwood sites, followed by broad-leaved and

needle-leaved, following that more light increases understory 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 impact on CO_2, the relative importance of understory productivity (measured as biomass) was small, < 1% of the biomass of the trees. Understory NEE_u loss of C is partially offset by C additions from tree and understory litter. Including these additions (Table 2.4) still results in a loss of C from the understory of all swamps in the range of 189 to 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.* reported aboveground net primary productivity uptake of CO_2 as 900 - 1600 g m^{-2} d^{-1}, more than offsetting these understory 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 modeling 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, like 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. These relationships with mean water tables 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 if they hold true across many swamp types could vastly improve C accounting and modeling 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 to also predict patterns of swamp carbon cycling, with data from this study informing how slopes 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 not as necessary as 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 only captured 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.

2.5 References

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2.6 Supplemental

Table S2.1 Average 1 m x 1 m vegetation survey results to functional group.

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

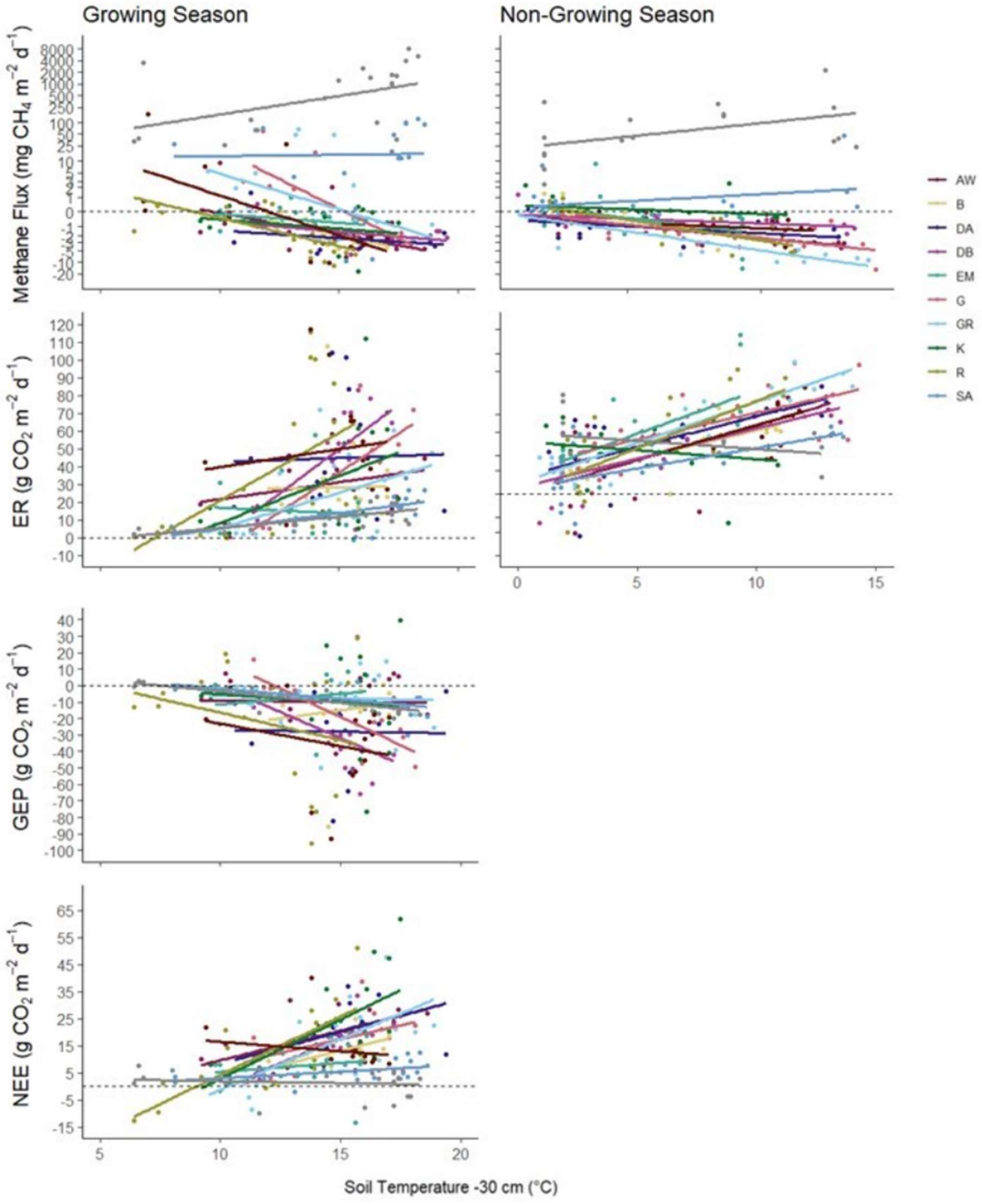


Figure S2.1 CH_4 and CO_2 flux response to soil temperature at 30 cm below surface.

Table S2.2 Historic monthly, annual, and 30-year average precipitation for study period. Green cells indicate months included in growing season. Data obtained from Government of Canada. Weather station location names: 1. Kitchener/Waterloo; 2. Hamilton A; 3. Woods tock; 4. Roseville; 5. London A.

	Precipitation (mm)				
Month	Grand River, Eden Mills, Rockwood[1]	Beverly[2]	Golspie, Kintore, Dorchester[3]	Ancient Woods, Spongy Lake[4]	Sifton[5]
22-Jan	15.4	37.3	24	53	33.3
22-Feb	24.9	87.1	58.6	98.4	86.8
22-Mar	42.4	60.4	35.3	66.7	50.4
22-Apr	42.8	47.8	39.2	41.1	67
22-May	60.6	50.8	37.5	64.5	49.1
22-Jun	48.6	76.6	34.8	61.3	46
22-Jul	18.7	56.9	12.9	19.4	44.3
22-Aug	42.1	72.1	54.4	57.5	110.9
22-Sep	22.2	47.2	39	26.8	43.4
22-Oct	39	39	9.8	48.1	50.5
22-Nov	28.3	39.7	11	37.7	30.3
22-Dec	53.3	64.7	27	62.2	37
2022 Total	438.3	679.6	383.5	636.7	649
23-Jan	49.4	75.5	22.5	80.6	60.7
23-Feb	58.4	85.4	16	42.4	75.8
23-Mar	69.9	117.2	55.5	114.7	38.4
23-Apr	85.5	111.8	56.1	104.1	92.9
23-May	47	39.1	8.3	45.3	4.1
23-Jun	59.5	115.2	33.1	81.9	53.8
23-Jul	166.4	123.8	52	160	151.5
23-Aug	98.1	119	39.1	118.4	64.6
23-Sep	21.2	25.9	24.2	23.5	49.2
23-Oct	49.3	61.7	41	59.4	58.7
23-Nov	41.1	44.2	37.6	57.4	43.7
23-Dec	67.3	71.9	0	57.1	89.7
2023 Total	813.1	990.7	385.4	944.8	783.1
30 yr avg.	976	929.8	969	918.7	1011.5

Table S2.3 Average fluxes for growing season and non-growing season by site, setting, and canopy (CH_4 mg m^{-2} d^{-1}; CO_2 g m^{-2} d^{-1}). Positive values indicate release to the atmosphere; negative values indicate uptake.

	Growing Season				Non-Growing Season	
	Mean CH_4[a]	Mean ER[b]	Mean GEP[b]	Mean NEE[b]	Mean CH_4[a]	Mean ER[b]
Site						
Ancient Woods	-1.9	18.00	-9.7	18.80	-1.67	6.59
Beverly	-2.1	28.20	-15.2	13.00	-0.84	3.73
Dorchester A	-3	22.50	-24.6	18.90	-1.39	7.66
Dorchester B	-1.9	46.10	-29.7	16.50	-0.51	4.62
Eden Mills	-0.9	14.60	-6.87	7.78	-1.05	23.30
Golspie	6.30	43.20	-18.7	17.10	-2.21	15.00
Grand River	7.70	23.20	-10.3	13.90	-4.11	16.20
Kintore	-2.20	33.50	-9.75	23.80	0.22	3.17
Rockwood	-2.90	40.60	-20.5	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

[a] mg $m^{-2}d^{-1}$ [b] g $m^{-2}d^{-1}$

Chapter 3

Tree stem CH_4 emissions vary between species and seasons in three southern Ontario swamps

3.1 Introduction

Methane (CH_4) is a potent greenhouse gas with a global warming potential 45 times greater than carbon dioxide (CO_2) over a 100-year time scale (IPCC 2014, Neubauer & Megonigal 2015, Masson-Delmotte et al. 2021). Anthropogenic activities account for ~60% of global annual CH_4 emissions and wetlands are the largest natural sources of CH_4 globally (Covey & Megonigal 2018, Machacova et al. 2021), but the global wetland CH_4 budget still contains large uncertainties and missing constraints (Saunois et al. 2019).

It has long been known that high CH_4 concentrations exist within tree stems (Bushong 1907, Schutz 1991); however, the importance of trees as CH_4 sources has only recently been realized (e.g., Barba et al. 2019, Covey and Megonigal 2019, Pangala et al. 2017) and is not currently fully included in global CH_4 budgets (Carmichael et al. 2014, Saunois et al. 2019). Previously, it was assumed that wetland soils and ground layer vegetation, such as sedges that contain aerenchymatous tissue, were the main pathways for CH_4 emission (Vroom et al. 2022, Guo et al. 2024). With advances in portable CH_4 sensors and the creation of tree stem chambers over the last decade, CH_4 emissions have been detected from woody stems, filling the gap between ecosystem scale (e.g., eddy covariance) and plot scale chamber measurements (e.g., field chamber) measurements (Pangala et al. 2017, Covey & Megonigal 2018). The contribution of tree stem fluxes to ecosystem CH_4 cycle varies widely across regions and ecosystem types. In the Tropics, stem CH_4 emissions contributed 30% of the total ecosystem flux in a forested peatland (Sjogersten et al. 2019), 26% in a mangrove forest (Jeffrey et al. 2019), and up to 87% in a forested wetland (Pangala et al. 2013). In upland forests, stem CH_4 emissions offset soil CH_4 uptake by anywhere from 1-6% in Maryland, USA (Pitz & Megonigal 2017), 13% in montane Czech Republic (Machacova et al. 2023), 63% in semi humid, warm-temperate continental Beijing (Wang et al. 2016), and up to 100% in southern Alberta, Canada (Flanagan et al. 2021). Given that forested wetlands account for ~60% of total global wetland extent (Matthews & Fung, 1987; Prigent et al., 2007), and wetland trees could account for 5-10% of global CH_4 emissions (Pangala et al. 2017, Covey

& Megonigal 2018), assessing wetland tree stem emissions is essential to improving CH_4 emission budgets.

Methanogenic communities have also been identified within woody tissues, and this internal production may be the primary source of CH_4 from upland trees (Yip et al. 2019, Jeffrey et al. 2021, Putkinen et al. 2021, Smits et al. 2021, Feng et al. 2022, Jeffrey et al. 2023a). In wetlands, methane emitted from tree stems has been shown to predominantly originate from the soil, being transported up the stem through both passive (diffusion) and active (transpiration and plant tissues) processes, particularly in wet conditions (Mander et al. 2021, Jeffrey et al. 2023a). Production of CH_4 in wetland soils is influenced by water table fluctuations, duration of inundation, soil temperature, substrate availability, and microbial presence and activity within the soil (Blodau 2002, Holden 2005, Jeffrey et al. 2019). Higher water tables and warmer temperatures have a positive relationship with both soil and tree stem CH_4 fluxes; even within upland forests, a warm, wet period can increase tree stem emissions while simultaneously reducing soil uptake capacity (Terazawa et al. 2015, Pitz & Megonigal 2017). As oxygen availability within the soil increases during dry periods, methanogenic microbes become less active. Methanotrophic microbes that consume CH_4 then dominate and reduce soil CH_4 concentrations; if soil concentrations fall below atmospheric concentrations, CH_4 diffuses into the soil, becoming a CH_4 sink (Wei et al. 2024).

Understanding tree stem CH_4 dynamics is further complicated by variation among traits of the trees (Moisan et al. 2024). Temperate swamps in southern Ontario consist of a long list of tree species and a wide range of community compositions. Multiple angiosperm species of maple (*Acer*), birch (*Betula*), oak (*Quercus*), and ash (*Fraxinus*) thrive in swamps, as do gymnosperms such as eastern white cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*) (Lee et al. 1998, Ontario Ministry of Natural Resources and Forestry 2022). Differences between species, including tissue density, microbial community, stem diameter, etc., influence transport of water and dissolved CH_4 up the stem and diffusion through the bark (Pangala et al. 2013, Barba et al. 2019, 2024, Covey and Megonigal 2019, Jeffrey et al. 2021, 2023). Additionally, the drivers of CH_4 production and emission may differ, which, combined with different transport processes, may create time lags between production and release, making it hard to identify the environmental controls behind measured CH_4 fluxes (Barba et al. 2024). Methane fluxes from tree stems have also been shown change with height, with the highest emissions coming from nearest the soil and tapering off higher up the stem (Jeffrey et al. 2020b, Sjogersten et al. 2020), requiring measurements at multiple heights to avoid over- or underestimating emissions.

Cool temperate systems experience freezing temperatures over the winter and, in southern Ontario, freeze-thaw cycles are not uncommon. There are currently no studies of the impact of these dynamics on tree stem CH_4 emissions. Nor have there been studies on CH_4 emissions from stems of silver, red, or Freeman maple, yellow or paper birch, or eastern white cedar, the species in this study. Due to conversion of other wetland types, swamps are the most common wetland type in southern Ontario today (Byun et al. 2018). Therefore, it is important to understand the impact of environmental conditions and species identity on tree stem emissions within these swamps to better constrain tree stem CH_4 emissions for more accurate C accounting, modelling, and policy within Canada and globally. Therefore, the goals of this study were to: (1) Quantify stem CH_4 fluxes from three dominant genera (*Acer* spp., *Betula* spp., and *Thuja occidentalis*) within three swamps in temperate southern Ontario, (2) Assess environmental controls (e.g., water table, soil temperature) on CH_4 flux, and (3) Determine the relative contribution of tree stems and soils to temperate swamp CH_4 budgets.

3.2 Methods

3.2.1 Study sites

Three of 12 sites from Schmidt et al. (2025) were selected to study tree stem CH_4 emissions. Sites were selected to represent a range of hydrogeomorphic settings and had our target tree genera present. All sites located in southern Ontario, between 42–44°N and 80–82°W (Figure 3.1). The swamps fall into two hydrogeomorphic settings with organic or mineral-organic soils (Table 3.1).

The study area is situated in a humid continental climate characterized by mild summers and relatively uniform precipitation throughout the year (CEC 2021). Mean temperatures fall below 0 °C in the coldest month, remain below 22 °C in every month, and reach or exceed 10 °C for at least four months annually (CEC 2021). The growing season lasts an average of 188 days, and annual precipitation typically ranges from 900 to 1000 mm, with the highest rainfall occurring during spring and fall (Government of Canada 2024). Beyond the Greater Toronto Area, southern Ontario supports population densities ranging from 5 to 1000 people per square kilometer (CEC 2020b). Land use is dominated by agriculture, particularly cropland, while remaining patches of Carolinian and temperate continental forest persist across the region (CEC 2020a, 2022). Human activities have influenced all study sites to some extent; however, site selection excluded areas that had undergone active canopy clearing during the preceding 100 years. As a result, disturbance was not directly assessed as an effect in this study.



Figure 3.1 Map of site locations within study area and Ontario (inset). Base imagery from Google Earth, accessed 24-July-2026.

Table 3.0.1 Summary of sites.

Site	Hydrogeo-morphic Setting	Canopy Type	Soil Type	Location	Peat Depth (m)
Ancient Woods (AW)	Basin	Broadleaf (mixed)	Mineral-Organic	43.3759, -80.3699	0.2 - 0.6
Beverly (B)	Flat	Broadleaf (mixed)	Organic	43.3841, -80.1050	0.3 - 1.5
Kintore (K)	Flat	Mixedwood	Organic	43.1614, -81.0050	1 - 2

Beverly Swamp is a mixedwood flat swamp (Fig 3.2). Unconfined flat swamps lack clear topographical boundaries or banks and often occur in glacial lake beds or outwash (Warner & Rubec 1997). The specific study area of Beverly Swamp used in this study had a predominantly broadleaf canopy, with peat soils (0.3–1.5 m) and a channelized stream running through it (Warren et al. 2001), indicating that it can also be classified as a riparian swamp. Dominant tree species included *Acer rubrum, Acer saccharinum*, and

their hybrid, *Acer x freemanii*, *Betula alleghaniensis*, *B. papyrifera*, *Thuja occidentalis*, and *Fraxinus* spp. Understory vegetation was predominantly broadleaf saplings, and the ground layer consists of ferns, graminoids, forbs, patchy bryophytes, and large areas of bare peat.

Ancient Woods swamp is a mixedwood, mineral-organic (0.2–0.6 m) basin swamp within which Bauman Creek originates from groundwater seepage (Fig 3.2). Dominant tree species included *Acer* spp., *Betula alleghaniensis*, and *Thuja occidentalis*. The understory included broadleaf saplings and tall shrubs such as *Sambucus canadensis* and *Cornus* spp.; *Symplocarpus foetidus* makes up most of the ground cover from early spring to its senescence in mid- to late-June, after which bare peat dominates with patches of ferns, forbs, and bryophytes.

Kintore Swamp is a mixedwood flat swamp with peat soils 1–2 m deep (Fig 3.2). Dominant tree species included *Tilia americana*, *Acer* spp., *Betula alleghaniensis*, and *Thuja occidentalis*. Understory species included *Lindera benzoin*, and *Cornus* spp.; the ground layer included large areas of *Symplocarpus foetidus* that transition to bare peat, and patchy forbs, graminoids, ferns, and bryophytes. A gravel road runs north to south through the swamp; plots were located on both sides to account for any potential effects on hydrology.



Figure 3.2 . From left: Kintore, Ancient Woods, Beverly; tree chamber in use at Kintore. Photographs by M. Schmidt.

3.2.2 Soil CH_4 Flux

Soil CH_4 fluxes were measured with a $CH_4/CO_2/H_2O$ Trace Gas Analyzer (LI-7810, LI-COR, Nebraska, USA) weekly March to November 2024, once per month January to April 2025, bi-weekly May to

August 2025, and monthly September to November 2025 via the closed chamber method (Griffis et al. 2000). No measurements were taken in December due to site access limitations during hunting season. Twelve acrylic collars (20 cm diameter x 10 cm height) were installed in 4 parallel transects with collars approximately 30 m equidistant to capture spatial and microtopographical variation. Fluxes were measured by placing an opaque acrylic chamber (20 cm diameter x 40 cm height) into a corresponding groove in the collars to create a closed system. A small battery-operated fan continuously circulated the air within. When water levels were >10 cm above surface a floating chamber secured above the collar was used. Concentrations of CH_4 were measured every second over a 3-minute closure, as were temperature and humidity within the chamber. We use the sign convention such that C emission to the atmosphere is positive (+) and uptake (-) from the atmosphere is negative (Ryan & Law 2005). Chamber headspace concentration was observed in real time via a tablet connected to the LI-7810 to monitor for leaks or issues with the chamber during the flux. Fluxes were calculated from the slope of the linear change in concentration within the chamber over time and adjusted for chamber volume and the temperature within the chamber. Plots were measured in a different order each visit to account for diurnal temperature changes. Further inspection for linearity and slope of the concentration change over the chamber closure was calculated using the processing tool PEDRO (Newton et al. 2025). Fluxes were accepted if visual inspection showed a clear slope with no signs of leakage, even when change is concentration over time was minimal, indicating a near 0 flux. After processing, 849 soil CH_4 and 866 tree stem CH_4 fluxes were retained in the analysis, representing a loss of ~2% of data points each.

Soil temperature (ST) profiles from -5 to -30 cm were measured with a thermocouple soil temperature probe (Digi-sense) and reader (Omega HH200A), soil moisture (SM) of the top 10 cm was calculated as the average of 4 points surrounding the collar via a Wet-2 Sensor and HH2 Moisture Meter (Delta-T Devices), and water table (WT) was measured as distance from surface in a dip well adjacent to each collar for every flux measurement. We use sign convention such that distance to WT below the surface is negative (-) and WT above the surface is positive (+).

3.2.3 Tree Stem CH_4

Tree stem CH_4 was measured simultaneously with soil fluxes Chapter 4 from March 2024 to November 2025 following the same general closed-chamber procedure as the soil fluxes with an adapted chamber system. The chamber was designed to be easily portable and quick to secure, as well as accommodate multiple stem diameters and differences in bark textures. Modified from Jeffrey et al.

(2020), a 13 cm x 13 cm x 10 cm chamber was made from a snap-lid food storage container and a buckle strap attached to opposite sides. To secure, putty was applied to the bottom edge of the chamber, then placed against the tree; once the strap was buckled and tightened, the putty could be molded to fill any gaps in the bark, creating an airtight seal (Fig. 3.3). Three species were targeted (*Acer rubrum*, *Betula alleghaniensis*, and *Thuja occidentalis*) but due to local forest composition we had to measure across two species of birch (B. alleghaniensis and *papyrifera*) and maples could not be easily identified due to frequent hybridization. Therefore, three individuals of *Acer* (*A. rubrum*, *A. saccharinum*, or their cross, *A x freemanii*), *Betula alleghaniensis* or *papyrifera*, and *Thuja occidentalis* were chosen at each site (total n = 9 per species). Nonetheless, although different genera were targeted, most individuals were of the same species and we will refer to species differences for the remainder of the paper. Measurements were taken from the same spot every time at 1 m above the root flare, marked with a painted right angle (Fig 3). This height was selected to account for variability in microtopography at the tree bases and deep flooding that occurred at some of the study sites. Fluxes were measured with the $CH_4/CO_2/H_2O$ Trace Gas Analyzer (LI-7810, LI-COR, Nebraska, USA) over a 3-minute closure and start and end temperature within the chamber was recorded. For every measurement taken, a temperature profile from –5 to –30 cm was taken near the base of the tree, and a SM averaged from 4 spots around the base. Water table measurements were taken from the associated soil flux measurement plot for each tree.

3.2.4 Upscaling to annual emissions

To upscale stem emissions from area of tree stem surface to stem emissions per area of swamp, measurements were taken at 0.30, 0.65, 1.05, and 1.35 m at two sides of the stem (e.g., north and west side, south and east, etc.) of each study tree in fall of 2025. No significant relationship was found between CH_4 flux and height of measurement for any species (all $p > 0.94$); species specific regression lines were nearly flat. Therefore, we used the equation of an open cylinder to estimate surface area of the tree stem and, as slopes were slight but not zero, we calculated stem emissions to a height of 2 m, estimating that most trees would have minimal or no flux by this height. Similar studies have truncated height at 1 – 5 m, with most at ≤ 2 m (Pangala et al. 2013, Sjogersten et al. 2019, Zhang et al. 2021, Jeffrey et al. 2020).

Annual emissions at the stem scale were estimated by first multiplying the average daily flux per site and study species by the number of days in each respective month, then summed to reach an annual flux per m^2 of stem. The flux values of deciduous trees other than maple and birch were assigned the mean

flux of maple and birch; any other coniferous species received the same value as cedar. Three 20 m x 20 m tree survey plots in which each stem was identified to genus and measured for circumference at breast height, as described in Chapter 2, were used for site composition and density. Fluxes were multiplied by the calculated surface area using measured circumference at breast height and summed per plot, then divided by plot area to reach a flux value per m2 of swamp. Plots were then averaged to estimate the site total.

3.2.5 Statistical Analysis

All analyses were conducted in the statistical analysis program R (R Core Team 2025). Methane fluxes were analysed using linear mixed-effects models (lme; Pinheiro *et al.* 2016) to account for hierarchical sampling and repeated measurements. To assess variation in tree and soil CH_4 fluxes among sites, genera and throughout the study period, a linear mixed effects model with site, genus and season (where each measurement was assigned to spring, summer, autumn or winter) was assessed with all two-way and three-way interactions included. Tree identity was included as a random intercept and CH_4 fluxes were log-transformed to improve normality and homoscedasticity. A variance structure based on site and species was applied to account for higher flux variation from maples in Ancient Woods. Significance of fixed effects was assessed using the anova function.

To assess environmental controls on tree stem CH_4 fluxes variation in fluxes were modelled as functions of site, genus, and environmental covariates, with tree identity included as random intercepts. As with the anova model, methane fluxes were log-transformed to improve normality and homoscedasticity and a variance structure based on site and species was applied. A global model was defined to include fixed effects of water table, 10 cm soil temperature, soil volumetric water content, soil CH_4 flux, site, genus and all two-way interactions between the environmental variables and site, all environmental variables and genus and then three-way interactions including site, genus and each environmental variable. We selected the top model based on Akaike Information Criterion (AIC) using the dredge function in the package MuMIn (Barton 2026). Models were fitted using maximum likelihood, and collinear predictors were evaluated separately when necessary. In all models, post-hoc comparisons were performed using estimated marginal means (emmeans; Lenth 2025) with Tukey adjustment. Model assumptions were assessed using residual diagnostics, and statistical significance was evaluated at $\alpha = 0.05$.

3.3 Results

3.3.1 Site, species, and seasonality

Total precipitation in 2024 at Ancient Woods and Beverly exceeded the 2025 total but were lower than the 30-year average; both were lower than the 30-year average in 2025. At Kintore, both years exceeded the 30-year average and 2024 was drier than 2025. On average, 2024 was approximately 1.5 - 2 °C warmer than 2025 (Environment and Climate Change Canada 2026, Zoomash Ltd. 2026). Monthly and yearly precipitation and temperature data are available in Supplementary Table S3.1. Median WT at each site ranged from -2 to –22.5 cm in 2024 and -18 to -25 cm in 2025. Median and mean WT was deepest at Beverly and shallowest at Ancient Woods in 2024, whereas in 2025, both were deepest at Kintore and shallowest at Beverly. Consequently, SM in both years was similar at Ancient Woods and Kintore, while at Beverly mean SM was ~10% higher in 2025. ST at 10 cm was 1 – 3.5 °C warmer across all sites in 2024 than 2025; differences between sites in 2024 were small with much overlap, while Kintore was up to 3 °C warmer than Ancient Woods and Beverly in 2025. Summary statistics for site-level environmental conditions are available in Supplementary Table S3.2.

Tree stems were generally sources of CH_4, with mean fluxes per sampled tree varying from 0.029 to 56.33 mg CH_4 m^{-2} d^{-1}. Species effects differed strongly among sites (Site × Species: $F_{4,18} = 11.83$, $p < 0.001$), reflecting the disproportionally higher CH_4 emissions of maple trees at Ancient Woods compared to the much smaller differences between species at Beverly and Kintore (Fig. 3.3). Models allowing residual variance to differ among site–species combinations (AIC = −2072) provided a substantially better fit than models assuming homogeneous variance (AIC = −471; ΔAIC = 1601). Ancient Woods maple trees exhibited much greater variability in stem CH_4 emissions than any other site–species combination, with some individual trees emitting substantially more CH_4 than others. However, exclusion of the highest-emitting tree (AW02) produced nearly identical model results, indicating that the observed patterns were not driven by a single individual. Across sites, maple generally exhibited higher stem CH_4 fluxes than birch or cedar, although the magnitude of these differences varied among sites.

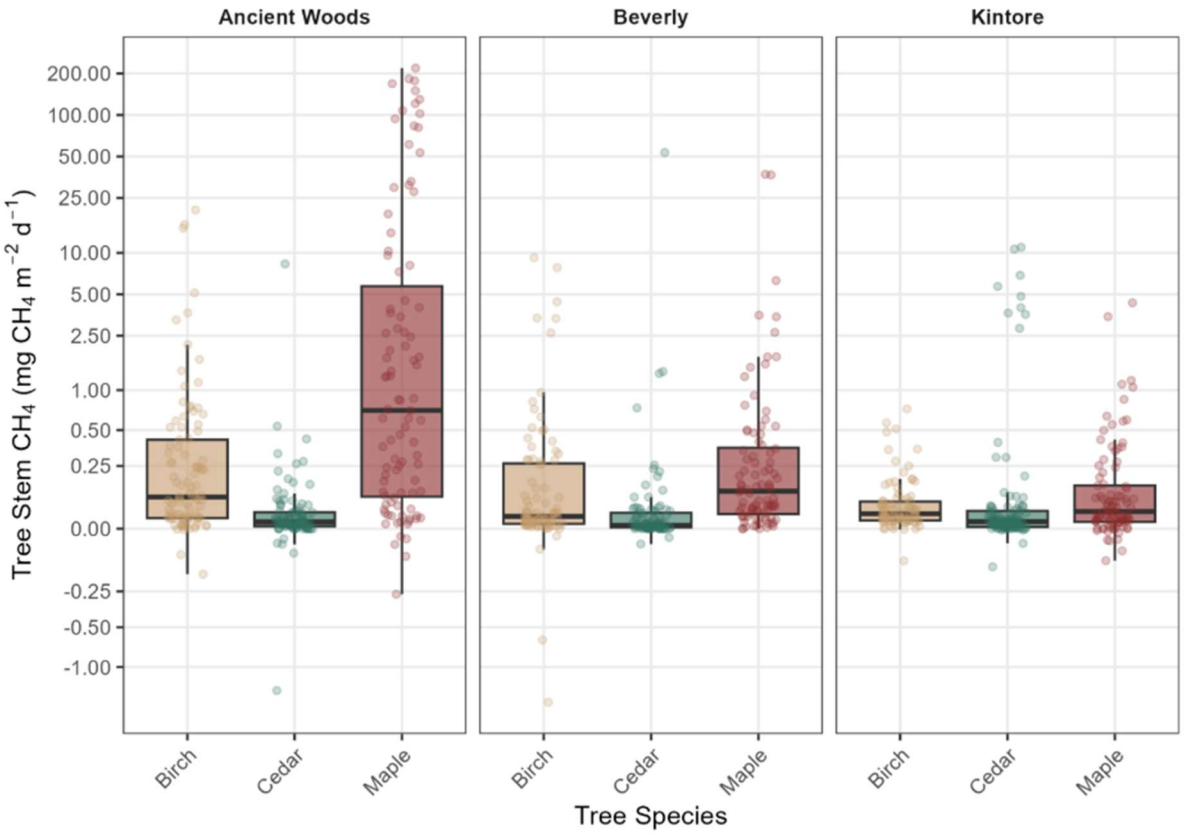


Figure 3.3 Tree stem methane (CH_4) fluxes by tree species and site. Boxplots show medians and interquartile ranges. Jittered points represent individual observations. Data points are in mg CH4 m-2 d-1 and are displayed on a pseudo-log scale to better visualize high and low points.

Tree stem CH_4 emissions exhibited clear seasonal patterns, with emissions generally peaking between May and July and reaching their lowest values between November and February. Seasons were divided into spring (March – May), summer (June – August), fall (September – November), and winter (December – February). A strong Site × Species × Season ($F_{12,794} = 2.28$, $p = 0.0076$) interaction indicated that seasonal patterns for specific genera differed among sites, therefore, seasonal patterns were assessed within each site separately (Fig. 3.4).

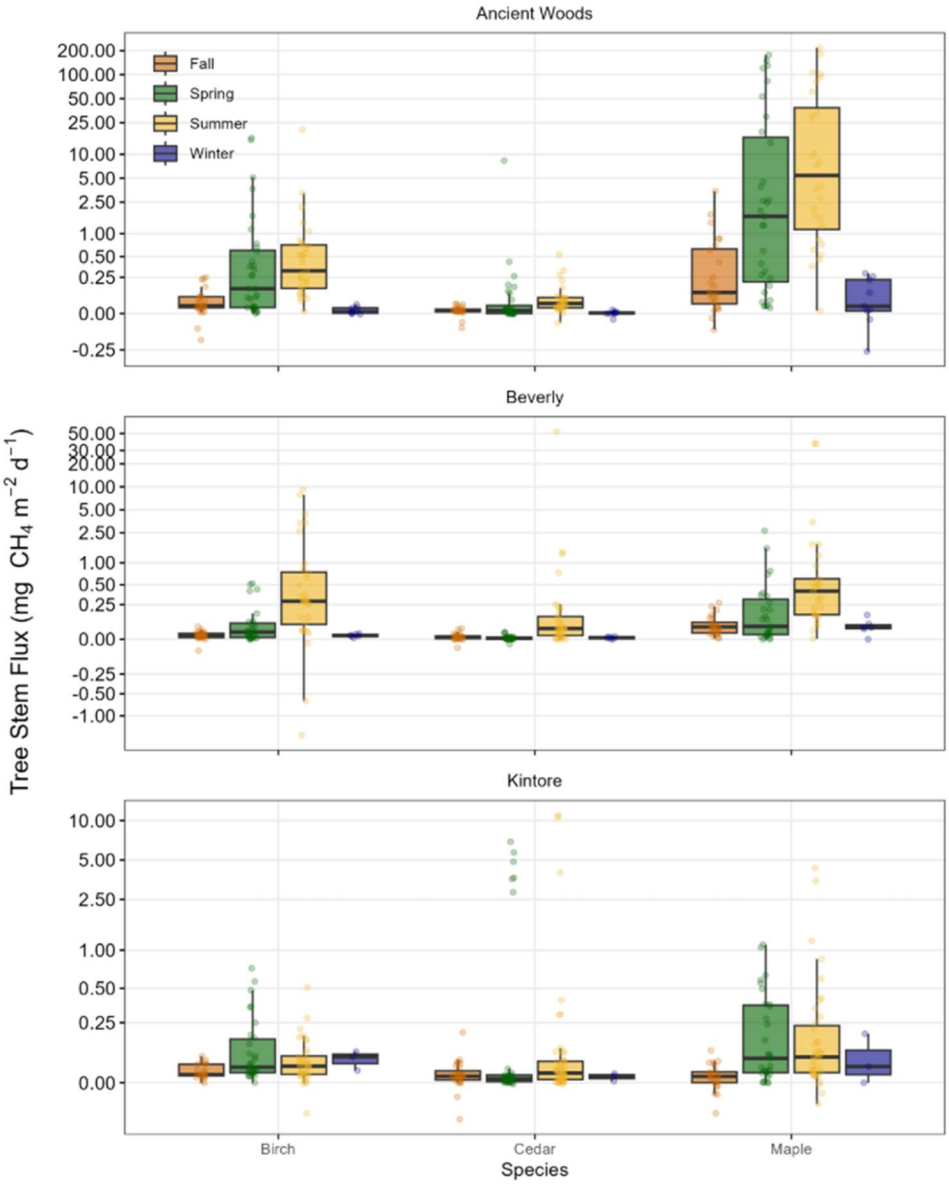


Figure 3.4 Seasonal emissions of tree stem CH_4 for birch, cedar, and maple during spring (March – May), summer (June – August), fall (September – November), and winter (December – February) at Ancient Woods, Beverly, and Kintore. Boxplots show medians and interquartile ranges. Jittered points represent individual observations. Data points are in mg CH_4 m^{-2} d^{-1} and are displayed on a pseudo-log scale to better visualize high and low points. Note that y-axes are different for each site.

At Ancient Woods (Fig 3.5), both species ($F_{2,6} = 29.41$, $p = 0.0008$) and season ($F_{3,266} = 2.87$, $p = 0.0371$) significantly affected stem CH_4 emissions, with a significant Species × Season interaction ($F_{6,266} = 4.73$, $p = 0.0001$). Maple emitted significantly more CH_4 than both birch and cedar during spring (both $p \leq 0.017$) and summer (both $p \leq 0.0025$), whereas species did not differ during fall or winter (Fig 5). Seasonal comparisons showed that maple emissions increased from fall to spring ($p = 0.0108$) and were highest during summer, exceeding both fall ($p = 0.0001$) and winter ($p = 0.0032$). In contrast, birch and cedar exhibited relatively little seasonal variation.

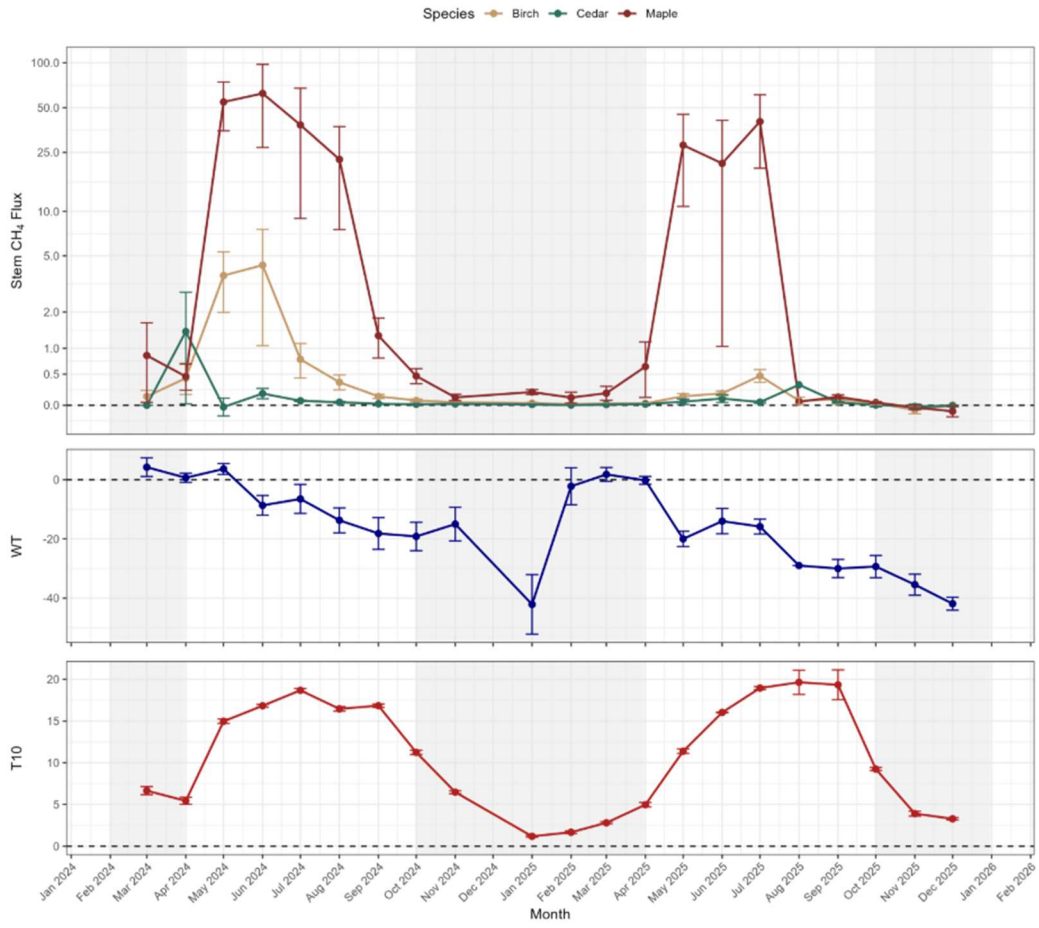


Figure 3.5 Monthly mean stem CH4 emissions in mg CH4 m-2 d-1 for each species, monthly mean WT (cm), and monthly mean soil temperature at 10 cm below surface (°C) at Ancient Woods over the entire study. Positive WT values denote WT height above the soil surface, while negative values indicate the depth below surface. Tree stem CH4 data are displayed on a pseudo-log scale to better visualize high and low points.

At Beverly (Fig 3.6), season significantly influenced stem CH_4 emissions ($F_{3,249} = 7.62$, $p = 0.0001$), whereas species ($F_{2,6} = 1.60$, $p = 0.277$) and the Species × Season interaction ($F_{6,249} = 0.32$, $p = 0.928$) were not significant. Stem CH_4 fluxes were not statistically significantly different among genera in any season. Seasonal differences were modest, with birch exhibiting lower emissions during summer than fall ($p = 0.0217$) and spring ($p = 0.0479$), while maple showed lower emissions in fall than summer ($p = 0.0285$) (Fig. 6). Cedar had no significant seasonal differences, although stem CH4 emissions were higher than normal in July 2025.

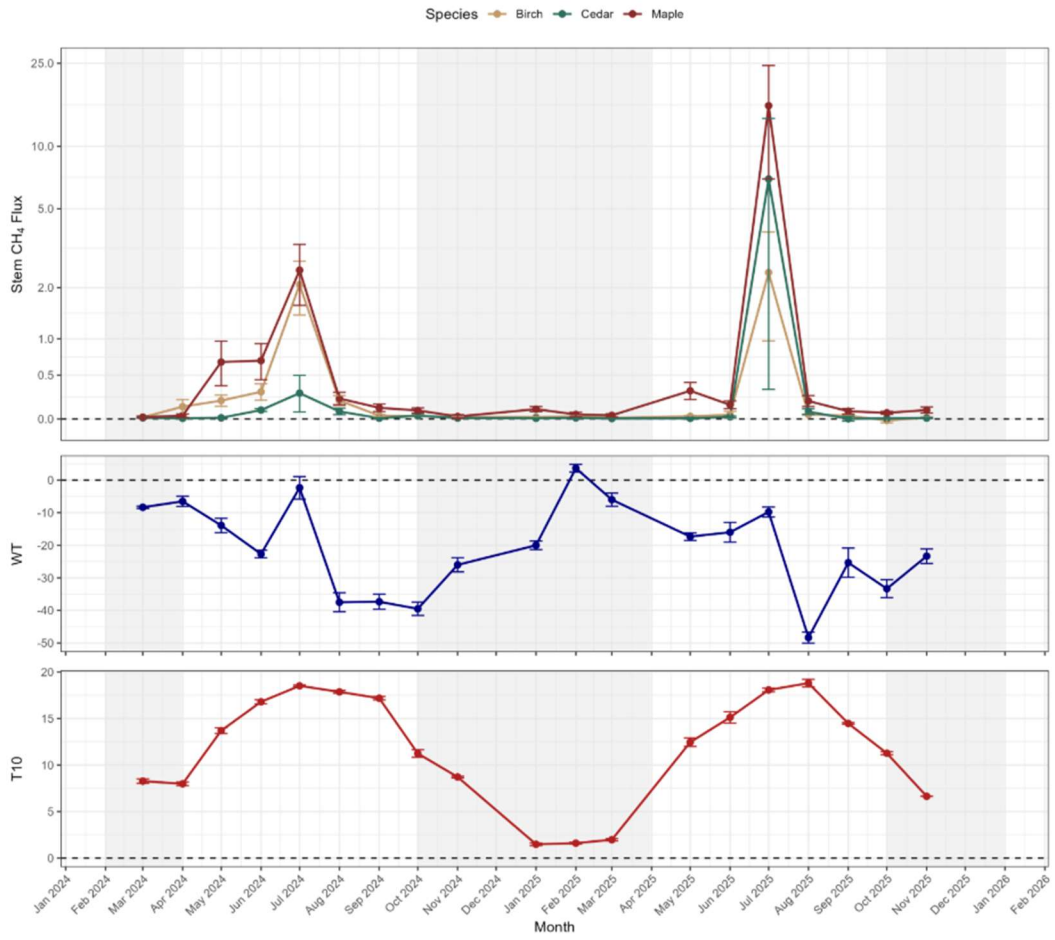


Figure 3.6 Monthly mean stem CH4 emissions in g CH_4 m^{-2} d^{-1} for each species, monthly mean WT (cm), and monthly mean soil temperature at 10 cm below surface (°C) at Beverly over the entire study. Positive WT values denote WT height above the soil surface, while negative values indicate the depth below surface. Tree stem CH_4 data are displayed on a pseudo-log scale to better visualize high and low points.

At Kintore (Fig 3.7), season significantly affected stem CH_4 emissions ($F_{1,287} = 10.37$, $p = 0.0014$), whereas neither species ($F_{2,6} = 2.16$, $p = 0.197$) nor the Species × Season interaction ($F_{2,287} = 2.19$, $p = 0.114$) were significant. Species did not differ for stem CH_4 fluxes within any season (Fig 7). Only birch exhibited a significant seasonal difference, with higher emissions in spring than fall ($p = 0.0256$), while cedar and maple showed no detectable seasonal variation. Similar to Beverly, cedar had higher emissions in summer 2025, but this was inconsistent between the study years, so was not statistically significant.

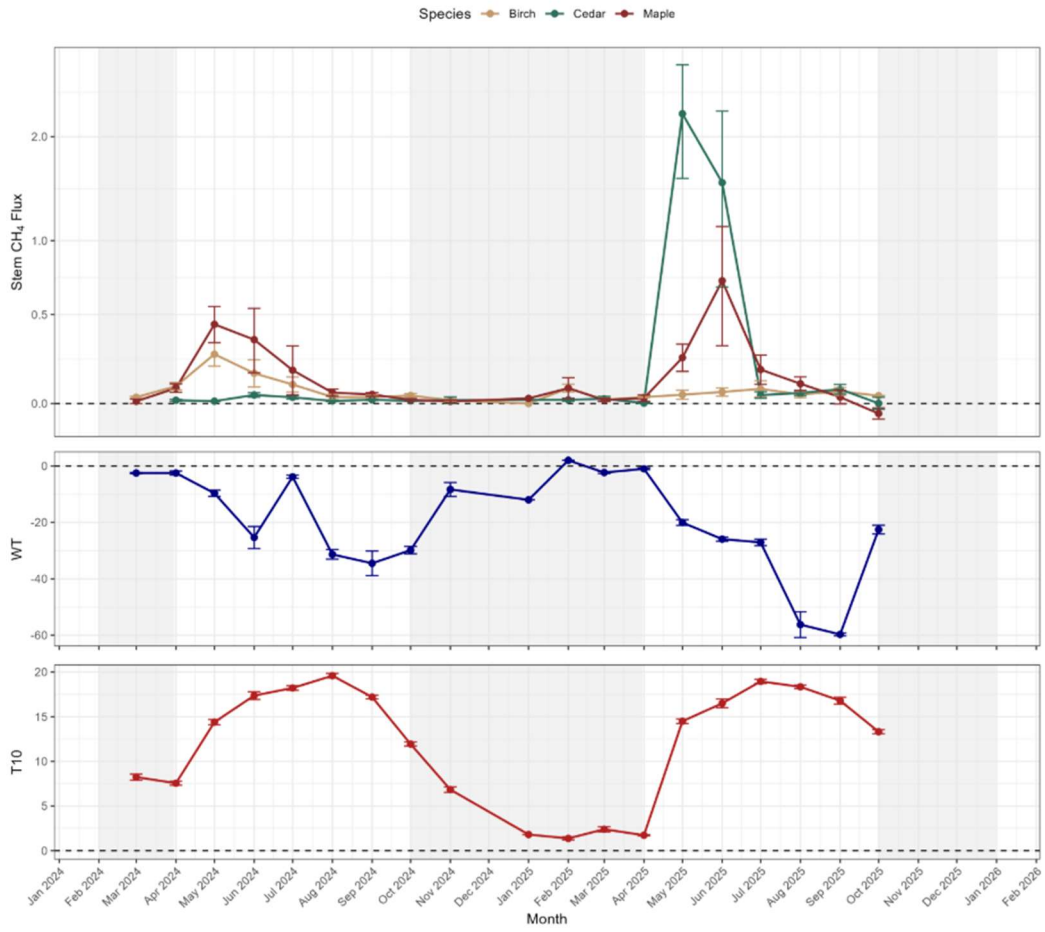


Figure 3.7 Monthly mean stem CH_4 emissions in mg CH_4 m^{-2} d^{-1} for each species, monthly mean WT (cm), and monthly mean soil temperature at 10 cm below surface (°C) at Kintore over the entire study. Positive WT values denote WT height above the soil surface, while negative values indicate the depth below surface. Tree stem CH_4 data are displayed on a pseudo-log scale to better visualize high and low points.

3.3.2 Environmental conditions

The model selected based on AIC included water table, soil temperature, soil moisture and soil CH_4 flux, alongside site and genus and several two-way and three-way interactions (Table 3.2). Total variation explained by the model remained modest with marginal R^2 of 0.16 accounting for the fixed effects.

Table 3.2 Final mixed-effects model results for environmental controls on tree stem CH_4 flux[a].

Effect	df	F	p
(Intercept)	1,785	13387.61	**< .0001**
Water table	1,785	8.31	**0.0040**
Site	2,18	2.40	0.12
Soil CH4	1,785	5.27	**0.022**
Species	2,18	6.66	**0.0068**
Soil temperature	1,785	21.62	**< .0001**
Soil moisture	1,785	6.13	**0.014**
Water table:Site	2,785	4.83	**0.0083**
Water table:Species	2,785	8.50	**0.0002**
Water table:Soil temperature	1,785	0.01	0.93
Site:Soil CH4	2,785	8.86	**0.0002**
Site:Species	4,18	14.48	**< .0001**
Site:Soil temperature	2,785	9.64	**0.0001**
Site:Soil moisture	2,785	4.31	**0.014**
Soil CH4:Species	2,785	1.16	0.32
Species:Soil temperature	2,785	7.91	**0.0004**
Water table:Site:Species	4,785	2.01	0.092

Water table:Site:Soil temperature	2,785	2.11	0.12
Water table:Species:Soil temperature	2,785	2.91	0.055
Site:Soil CH4:Species	4,785	5.23	**0.0004**
Site:Species:Soil temperature	4,785	7.45	**< .0001**
Water table:Site:Species:Soil temperature	4,785	2.25	0.062

a. Values in bold represent significant differences at $\alpha = 0.05$. $R^2m=0.16$, $R^2c=0.16$

The relationship between WT position and tree stem CH_4 flux differed among sites and tree species (Table 3.2). At all three sites, stem CH_4 increased as the WT became shallower for all three species (Fig 3.8). Water table slopes did not differ between Ancient Woods and Beverly ($p = 0.971$), whereas WT slopes were significantly weaker at Kintore than both (AW: $p = 0.0059$; B: $p = 0.0028$) (See Table S3.3 for model summary output). Across all sites, cedar exhibited a significantly weaker WT response than maple ($p = 0.0098$), while birch did not differ significantly from either species (cedar $p = 0.0564$, maple $p = 0.2728$). Therefore, rising WTs were associated with a stronger increase in stem CH_4 for birch than cedar, and maple and birch did not have statistically distinguishable WT slopes. These results indicate that wetter conditions were generally associated with greater stem CH_4 emissions, but the magnitude of this response depended on both site and species. This is supported by the relationship with soil moisture, where, although not as significant as WT, higher soil moisture resulted in higher CH_4 flux.

Soil temperature effects on tree stem CH_4 varied jointly among sites and species, as indicated by the significant Site × Species × Soil temperature (ST) interaction (Table 3.2, Fig 3.8). At Ancient Woods, maple exhibited a stronger positive response to increasing ST than both birch ($p = <.0001$) and cedar ($p = <.0001$), while birch and cedar slopes did not differ significantly ($p = 0.596$). The maple temperature slope was significantly greater than those of both birch and cedar (0.035, 0.002, -0.0008, respectively), indicating that the species interaction at Ancient Woods was driven primarily by maple. At Beverly, stem CH_4 increased significantly with ST for birch and maple, while the positive cedar response was not statistically significant. Temperature slopes did not differ among species at Beverly (all $p > 0.05$). At Kintore, none of the species exhibited a significant temperature response, and ST slopes did not differ among species (all $p > 0.05$).

Temperature sensitivity also varied within species between sites (Table 2). Birch showed a stronger positive ST response at Beverly than at Kintore ($p = 0.0371$). Maple temperature sensitivity was significantly greater at Ancient Woods than both Kintore ($p = <.0001$) and Beverly ($p = 0.0028$), while the difference between Kintore and Beverly was marginal ($p = 0.0835$). No significant site differences were detected for cedar. Overall, the results indicate that warming enhanced stem CH_4 emissions only for particular site–species combinations. Soil temperature and WT position were both associated with tree stem CH_4 flux, but there was no evidence that their effects depended directly on one another (Table 3.2). Instead, ST and WT responses varied independently among sites and species. Thus, warmer soils and shallower water tables may each favour greater stem CH_4 emissions, but the temperature response did not consistently strengthen or weaken as WT position changed.

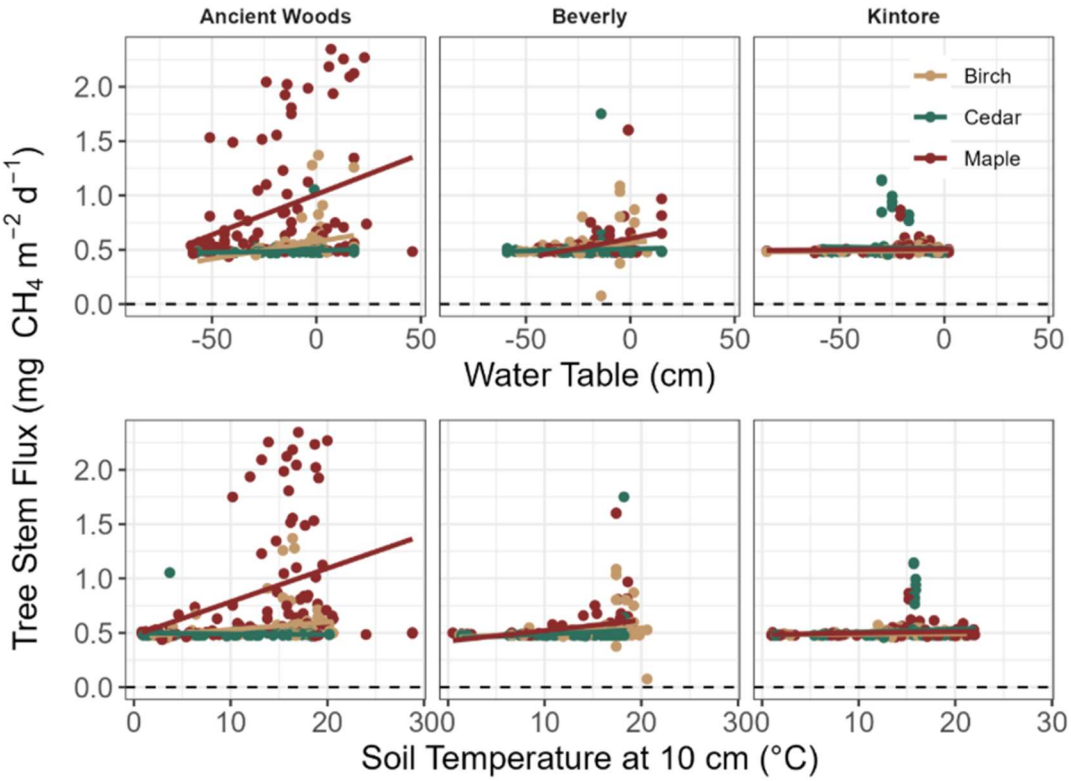


Figure 3.8 Relationships of tree stem CH_4 flux and water table and soil temperature at 10 cm belowground by Site and Species. Points represent individual observations and lines represent the relationship trend.

The relationship between soil CH_4 flux and tree stem CH_4 flux differed among both sites and species, as indicated by the significant Site × Species × Soil CH_4 interaction (Table 3.2). At Ancient Woods, maple exhibited a significant positive relationship between soil and stem CH_4, whereas the slopes for birch and cedar were not significantly different from zero (Fig 3.8). Maple had a steeper soil CH_4 response slope than cedar ($p = 0.0304$), while birch did not differ from either species (cedar 0.8324, maple 0.3146). At Beverly, none of the species exhibited significant soil CH_4 slopes, and no differences among species were detected (Fig 3.8). In contrast, at Kintore, cedar was the only species with a significant positive relationship between soil and stem CH_4, and its slope was steeper than those of both birch and maple (Fig 3.8). Comparisons among sites revealed no significant differences in soil CH_4 responses for birch or cedar, however, maple exhibited a significantly stronger soil CH_4 response at Ancient Woods than at Kintore ($p = 0.0052$). Collectively, these results indicate that the coupling between soil and stem CH_4 fluxes was highly dependent on site–species combinations rather than following a consistent pattern across all studied swamps. Average tree stem CH_4 emissions by site and species are available in supplementary Table S3.3.

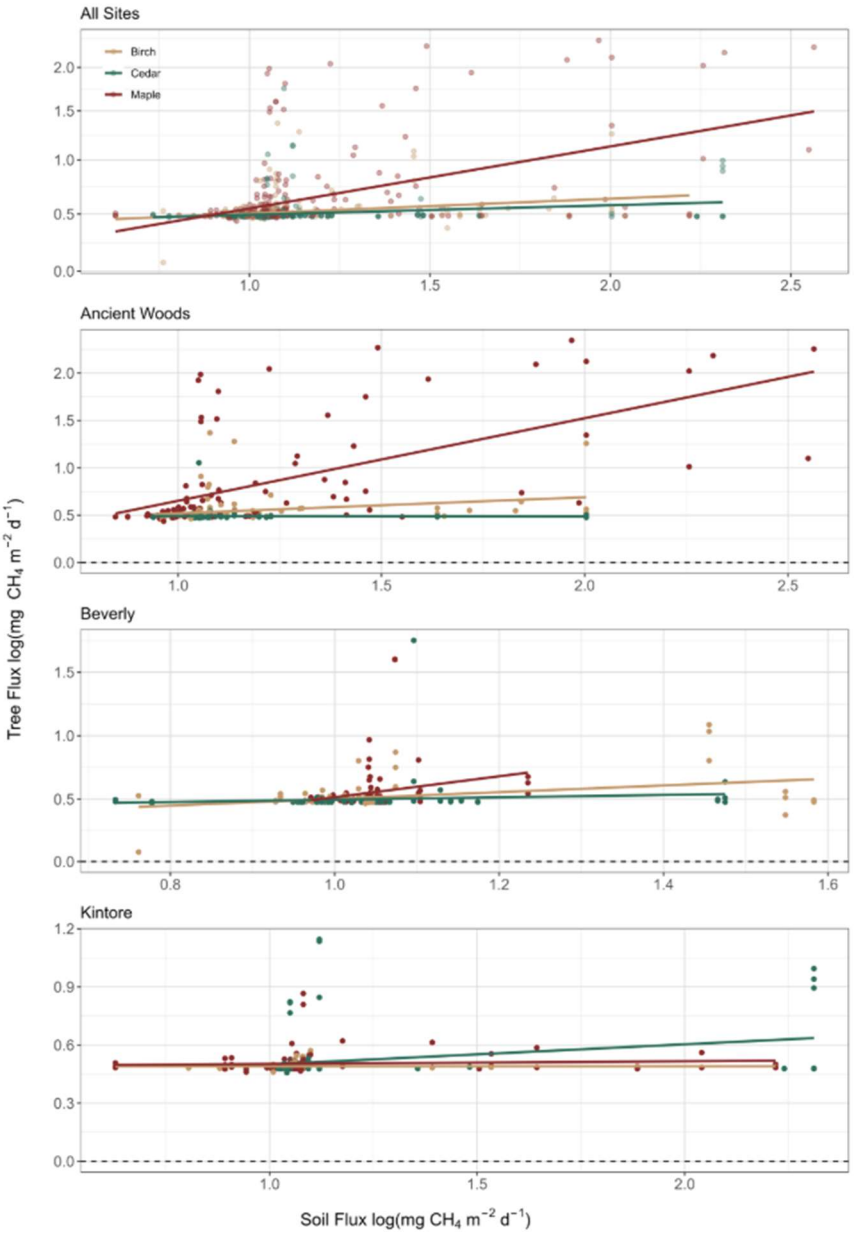


Figure 3.9 Relationship between soil CH_4 pool and tree stem CH_4 emissions showing the differences between species at each site. Points represent individual observations and lines represent the relationship trend. Methane flux was log10 transformed and is displayed on the transformed scale. Note that both x- and y-axes differ between plots.

3.3.3 Upscaling stem CH_4 flux to the community level

Measurements in autumn 2025 indicated that stem CH_4 flux was not significantly related to sampling height ($F_{1,78} = 0.027$, $p = 0.871$), and neither species ($F_{2,74} = 0.524$, $p = 0.594$) nor the Species × Height interaction ($F_{2,74} = 0.003$, $p = 0.997$) were significant. Estimated height slopes for birch, cedar, and maple were all close to zero and did not differ among species. Assuming that emissions were important only in the bottom 2 m of the tree stems (see methods), annual tree stem CH_4 emissions were highest at Ancient Woods, averaging 0.41 g CH_4 yr^{-1} (0.31 g C yr^{-1}) per square meter of swamp. Beverly and Kintore were much lower at 0.02 g CH_4 (0.01 g C) and 0.003 g CH_4 (0.002 g C) m^2 yr^{-1}, respectively.

3.4 Discussion

This study investigated the environmental and species-specific controls on tree stem CH_4 emissions in three temperate swamps in southern Ontario. This is the first study to measure tree stem CH_4 fluxes from *Betula alleghaniensis* and *Thuja occidentalis*, and one of the first on *Acer* spp (Hettwer et al. 2025: *A. rubrum*, Moisan et al. 2025: *A. sacccharinum*). Stem CH_4 emissions varied substantially among species, sites, and seasons, and were influenced by soil temperature, water-table position, and soil CH_4 availability. However, the importance of these drivers differed among sites and tree species, indicating that methane transport through trees is controlled by interacting environmental and physiological processes rather than a single universal mechanism.

3.4.1 Seasonality

Seasonality is a key aspect when considering temperate systems as it governs the timing and length of the growing season, air and soil temperatures, and water table position. Warming temperatures in the spring trigger soil thaw, making moisture and nutrients available to trees, vegetation, and microbes; methanogens in anoxic soils produce CH_4, that, with increasing sap flow and root activity, can be transported up the tree stems. In fact, we observed that stem CH_4 emissions were highest in the summer, peaking between May and July, and lowest in the winter, between November and February (Figure 3.4). Stem fluxes increased with both warming soil temperatures and as water tables neared the surface (Figure 3.8). Though there was no overall indication that the effect of ST depending on WT, responses differed between sites and species (Table 3.2; Figure 3.8). Soil CH_4 emissions similarly increased with WT and ST, resulting in increased stem emissions (Figure 3.9).

For soils, shifts between CH_4 sources in the summer and low CH_4 or slight sinks in the winter are typical of temperate ecosystems where weather conditions change seasonally (Dutaur & Verchot, 2007, Shoemaker et al. 2014, Covey & Megonigal 2019, Knox et al. 2019, Chapter 2: Schmidt et al. 2025, Chapter 4). Tropical ecosystems also experience seasonal shifts; however, as air and soil temperatures remain high year-round, they are instead driven by changes in precipitation regime, i.e., wet and dry seasons (Sakabe et al., 2021; Dalmagro et al., 2019; Griffis et al., 2020). Studies on cold-period soil and tree stem CH_4 emissions are limited, but freeze-thaw events appear to have relatively minor or inconsistent effects in temperate and hemi-boreal forested wetlands (Pangala et al. 2015, Mander et al. 2022, Ranniku et al. 2023). However, Mander et al. (2021) observed small increases in CH_4 fluxes when soil temperatures approached 0 °C, potentially caused by meltwater filling soil pores and causing short-term peaks in CH_4 production. In contrast, persistent snow cover has been associated with reduced soil CH_4 exchange, potentially by insulating soils, limiting gas diffusion, and reducing the intensity of freeze-thaw cycles (Mander et al. 2021, Borken et al. 2006).

3.4.2 Species differences

Positive soil – stem CH_4 relationships (Figure 3.9) indicate that soil CH_4 is being transported through the trees; however, the strength of the relationship depends on both species and site. We observed species-specific stem emissions that likely reflect differences in stem anatomy and gas transport efficiency rather than differences in soil CH_4 concentrations alone (Pangala et al. 2015). Although we did not measure these traits, differences between species have been explained by wood density (Pangala et al. 2013, 2015), stem anatomy and transport mechanisms (Pangala et al. 2015, Barba et al. 2019, Gauci 2025), tissue traits such as wood pH and moisture, and the number of methanogens and methanotrophs within the stem (Pangala et al. 2015, Moisan et al. 2025). Angiosperms (most broadleaf, deciduous, hardwood trees) generally emit more CH_4 than gymnosperms (most needle-leaved, coniferous, softwood, evergreen trees), and wetland trees typically emit more CH_4 than upland trees (Moisan et al. 2024, Wu et al. 2024). Thus, differences in maple compared to cedar may also reflect fundamental differences in whole-plant hydraulic and root traits. Gymnosperms generally have thicker, less highly branched fine roots and tracheid-based xylem composed of hollow, dead cells that connect through small valves, slowing water flow up the stem, whereas angiosperms typically have finer, more branched root systems and open vessels that increase hydraulic efficiency (Liese et al. 2017). Maples (hardwood angiosperms), consistently showed the strongest response to soil CH_4 and temperature, suggesting they may have more efficient transport of soil-derived CH_4; birch, also an angiosperm, had moderate responses. Conversely, cedars

(softwood gymnosperm), generally had weak relationships, which is consistent with evidence that wood traits and transport characteristics differ substantially between angiosperms and gymnosperms.

3.4.3 Site differences

Early data exploration indicated no significant effect of deeper (30 cm) soi temperature on tree stem CH4 flux, therefore we included only soil temperature at 10 cm depth as a predictor in our environmental model. Shallow soils likely control CH_4 production because 26 % of roots are found in the top 10 cm, 45 – 50 % in the top 20 cm, and 60 % within the top 30 cm in most temperate forests (Jackson et al. 1996, 1997). In wetlands and peatlands, the concentration of roots near the surface is often even more pronounced because deeper soils are regularly anoxic (He et al. 2023). Most absorptive roots, therefore, remain within the upper 20 – 30 cm of peat where oxygen availability is greatest (Murphy et al. 2010, Bhuiyan et al. 2017, Iverson et al. 2017). Additionally, total microbial activity is generally greatest within the top 10 – 30 cm of peat, and methanogens are most abundant and active immediately below the oxic surface layer, typically between 10 – 30 cm depth or just below the mean water table, where anoxic conditions and labile organic C are both present (Tian et al. 2023, Liu et al. 2025). These shallow depths receive fresh litter inputs, root exudates, warmer temperatures, and greater nutrient availabilities than deep anoxic zones, and decomposition in the near surface helps supply the substrates used by methanogens below (Kotsyrurbenko et al. 2019). In swamps, where WT fluctuates, the pattern is similar to peatlands but is even more tightly linked to WT position and tree root density than absolute depth. Methanogens concentrate in the active rooting zone as it creates microsites with varying oxygen concentrations and provides access to carbon exudates (Bechtold et al. 2025); the depth of the oxic layer has been found to be as little as 5 – 10 cm in some swamps (Megonigal & Schlesinger 2002).

The variability in the soil-tree CH_4 relationship between sites are likely driven by differences in local hydrologic conditions and CH_4 production. Many studies have shown that tree stem CH_4 emissions vary substantially among wetlands because of differences in water table position, hydroperiod, soil CH_4 production, nutrient availability, and vegetation composition (e.g., Pangala et al. 2015, Barba et al. 2019, Jeffrey et al. 2023, Gauci 2025). These factors influence both CH_4 production within the soil and the efficiency of transporting CH_4 within the soil and trees. The strong responses to environmental variables at Beverly suggest a tighter coupling between hydrologic conditions and methanogenesis, whereas the weaker responses at Kintore may reflect more stable hydrologic conditions or lower spatial variability in CH_4 production (Jeffrey et al. 2023). The high variability at Ancient Woods

is consistent with heterogeneous landscapes where local microtopography can affect tree ability to root, the specific conditions around those roots, and CH_4 production within the rooting zone (Pangala et al. 2015). Additionally, peat depth and composition modulate microbial activity and CH_4 production and movement. Despite frequently saturated conditions at both Ancient Woods and Beverly, shallower peat with higher mineral content at Ancient Woods may increase CH_4 production compared to the deep, high organic content peat at Kintore, and variable position of trees in relation to WT, saturation extent, and peat characteristics drive individual responses (Gauci 2025). For example, the maple at the edge of the depression in Ancient Woods that experienced the highest variability in
WT and frequently flooded during wet periods also had the greatest variability and highest emissions of all trees, suggesting that the conditions may have created a localized CH_4 hotspot.

3.4.4 Contribution to ecosystem emissions

Our tree stem CH_4 fluxes ranged from approximately 0.02 - 219 mg CH_4 m^{-2} of stem d^{-1}, with site and species means ranging from about 0.1 - 21 mg CH_4 m^{-2} d^{-1} and the contribution of stem fluxes to total ecosystem CH_4 varied over the study. Stem fluxes (per area of stem) were generally 0.86 - 70% of the soil CH_4 flux per area of ground, typically offsetting soil sink August – November and enhancing emissions the rest of the year. Although there are relatively few studies on tree stem CH_4 emissions in swamps, our results fall within the range reported for temperate forested wetlands and
swamps. Within a temperate *Alnus-Betula* swamp in the UK, individual trees emitted from near zero to > 100 mg CH_4 m^{-2} of stem d^{-1}, contributing 9 – 27 % of ecosystem CH_4, mostly during spring and winter (Pangala et al. 2015). Bitternut Hickory (*Carya cordiformis*) trees within a temperate upland forest in Delaware, USA were net sources of CH_4 at 0.68 - 3.52 mg m^{-2} of stem d^{-1}, peaking in late summer (Barba et al. 2021). The global average stem CH_4 flux from upland forests found by Wu et al. (2025) was -0.37 ± 28 mg m^{-2} of stem d^{-1}, while wetland forests were significantly higher at 121 ± 27 mg m^{-2} d^{-1}; stem CH_4 emissions also differed significantly between wetland ecosystems, averaging 139 ± 37.5 mg m^{-2} d^{-1} in inland and 77 ± 26.3 mg m^{-2} d^{-1} in coastal forested wetlands (Wu et al. 2025). Several species of trees in an Indonesian forested peatland released ~0.41 - 4.44 mg m^{-2} of stem d^{-1} (Pangala et al. 2012). Compared to the tropics and subtropics, however, temperate stem CH_4 emissions are quite low. Trees within the forested floodplains of the Amazon river basin emitted 7.92 - 13,944 mg CH_4 m^{-2} of stem d^{-1} (Pangala et al. 2017), while subtropical lowland forests in Australia were found to emit -0.48 - 1972 mg m^{-2} d^{-1} with emissions during the wet season exceeding the dry season by several orders of

magnitude (Jeffrey et al. 2020), and maximum stem emissions of ~3,256 mg CH_4 m^{-2} d^{-1} (Jeffrey et al. 2023).

Our study shows that trees in temperate swamps are important CH_4 pathways and that ignoring stems underestimates ecosystem CH_4 emissions. We show that tree species often follow similar patterns of emissions across different sites, but the magnitude is highly tied to site-specific conditions. While our study added three sites, three species, and hundreds of data points to the limited current knowledge, we only measured at one height, 1 m, which may have missed higher emission zones on the stem closer to the soil surface (Pangala et al. 2017, Barba et al. 2024), and thus underestimated tree stem CH_4 emissions. Additionally, the lack of patterns with height was likely because we measured stem height profiles at a time of year when CH_4 fluxes were low. Due to the prominence of site-specific differences, the direct effect of DBH could not be determined with only 3 trees per species per site. Future work should include height profiles throughout the season and explore the importance of DBH for explaining variation in CH_4 flux among individual trees for these species. Although we measured for nearly two years, we were limited in when we could sample, therefore we only measured during the day, missing any possibly diurnal trends, did not measure during extremes, such as very hot, cold, or rainy days, or measure equally across all months and seasons. Consequently, some of the patterns and relationships we found may have been dampened or exaggerated, and we may have missed hot moments of emissions that could greatly alter annual estimates. We also did not have multiple replicates of each site-canopy combination to assess if the conditions were truly site-specific or apply across each swamp type.

Therefore, more studies are needed, with detailed stem measurements across a range of stem heights and higher spatial and temporal distribution, enhanced by the creation and instrumentation of continuous/automated stem chambers (e.g., Brandle et al. 2019, Barba et al. 2021, Stahl et al. 2025). The addition of pore water CH_4 measurements would further refine and inform the relationship between soil and stem CH_4 fluxes, as would stem coring to assess tree traits such as wood density and structure. More frequent or continuous measurements of environmental conditions would help identify any lags or fine-scale relationships with WT, ST, etc. Sap flow measurements should be added to assess how stem fluxes are related to transpiration and transport of CH_4 rich water up the stem, as well as stem CH_4 concentrations. Finally, eddy-covariance towers above the swamp canopy help quantify emissions from upper branches and leaves, completing the CH_4 ecosystem budget, as has been shown for both CH_4 and CO_2 in the US and the Tropics (e.g., Sakabe et al. 2018, Wong et al. 2018, Griffis et al. 2020, Zhang et al. 2021, Wong et al. 2025).

Tree stem CH_4 emissions in temperate swamps are controlled by interacting environmental and species-specific factors. Soil temperate, water table position, and soil CH_4 availability all influence stem CH_4 emissions, but these relationships depend strongly on site conditions and tree genus. These findings show that predicting tree-mediated CH_4 emissions requires consideration of species composition and local hydrologic conditions rather than assuming a common response across swamps.

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3.6 Supplemental

Table S3.1 Monthly and annual precipitation and air temperature for each site in 2024 and 2025.

	Precipitation (mm)			Temperature (°C)		
	Ancient Woods	Beverly	Kintore	Ancient Woods	Beverly	Kintore
Jan-24	61.8	92.5	150.2	-4	-2.8	-3
Feb-24	22.1	27	91.1	-0.8	0	1
Mar-24	48	48.4	85.2	2.9	3.8	4
Apr-24	95.2	96.5	137.2	8	8.1	8
May-24	55.8	90.9	76.8	15.3	15.4	15
Jun-24	74.7	70.3	100	19.1	19.2	18
Jul-24	155.3	157	115.8	20.5	21.3	20
Aug-24	124.6	71.5	48	19.5	20.1	20
Sep-24	16.8	55.3	75.1	17.2	18	18
Oct-24	50.2	47.4	51.2	10.5	10.9	12
Nov-24	55.7	46.2	113.6	5.2	5.8	6
Dec-24	95.4	65.4	274.2	-2.2	-1.1	-1
Total	855.6	868.4	1318.4	9.3	9.9	9.8
Jan-25	44	21.5	85.2	-7.4	-6.3	-6
Feb-25	147	65.1	163.6	-6.5	-5.6	-5
Mar-25	62.4	63.8	270.6	1.4	2.1	2
Apr-25	57.6	74.8	198.4	7.3	7.2	7
May-25	91.8	94.5	362.2	12.5	12.2	12
Jun-25	76.4	79.8	262.6	19.9	19.7	20

Jul-25	48.6	36.9	180.8	21.7	22.4	22
Aug-25	40.2	39.7	42.7	18.6	19.8	20
Sep-25	29.4	56	132.3	16.3	17.6	17
Oct-25	37.2	61.6	21.5	9.7	10.8	11
Nov-25	59.6	33.1	211.9	2.7	3.3	3
Dec-25	91.6	74.2	365.3	-5.6	-4.6	-3
Total	785.8	701.0	2297.1	7.6	8.2	8.3
30 yr avg.	918.7	929.8	969	7.3	7.9	7.8

Table S3.2 Summary of water table, soil temperature, and soil moisture by site and year.

	2024			**2025**		
	Ancient Woods	Beverly	Kintore	Ancient Woods	Beverly	Kintore
Water Table (cm)						
Mean	-7.3	-22.4	-17.2	-20.4	-18.2	-26.2
Min	-60.0	-59.0	-56.0	-59.0	-55.0	-85.0
Max	24.0	15.0	1.0	46.0	8.0	2.0
Median	-2.0	-22.5	-12.0	-19.0	-18.0	-25.0
Range	84.0	74.0	57.0	105.0	63.0	87.0
Soil Temperature 10 cm (°C)						
Mean	13.6	13.8	14.4	10.1	11.4	13.6
Min	3.6	6.3	5.4	0.8	0.5	1.0
Max	20.6	19.2	22.0	28.8	20.6	21.9
Soil Moisture (%)						

Mean	64.2	60.2	59.5	65.5	71.3	60.2
Min	19.0	10.0	8.0	10.0	41.0	10.0
Max	85.0	86.0	87.0	85.0	85.0	85.0

Table S3.3 Summary output of the environmental model in Table 3.2.

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.461	0.053	785	8.6885	0.0000
WT	-0.001	0.002	785	-0.3003	0.7640
Site-Beverly	-0.082	0.087	18	-0.9487	0.3553
Site-Kintore	0.051	0.055	18	0.9246	0.3674
Soil CH_4	0.001	0.001	785	0.7418	0.4584
Species-Cedar	0.047	0.050	18	0.9517	0.3538
Species-Maple	-0.082	0.109	18	-0.7539	0.4607
T10	0.008	0.003	785	2.4421	0.0148
SM	0.000	0.000	785	0.1848	0.8534
WT:Site-Beverly	-0.001	0.003	785	-0.2517	0.8013
WT:Site-Kintore	0.001	0.002	785	0.5494	0.5829
WT:Species-Cedar	0.001	0.002	785	0.7262	0.4679
WT:Species-Maple	-0.002	0.004	785	-0.5435	0.5869
WT:T10	0.000	0.000	785	2.0211	0.0436
Site-Beverly:Soil CH_4	0.002	0.002	785	1.0113	0.3122
Site-Kintore:Soil CH_4	-0.001	0.001	785	-0.6973	0.4858
Site-Beverly:Species-Cedar	-0.019	0.085	18	-0.2205	0.8280

Site-Kintore:Species-Cedar	-0.081	0.066	18	-1.2191	0.2386
Site-Beverly:Species-Maple	0.047	0.131	18	0.3618	0.7217
Site-Kintore:Species-Maple	0.073	0.111	18	0.6601	0.5175
Site-Beverly:T10	0.002	0.005	785	0.4258	0.6703
Site-Kintore:T10	-0.007	0.003	785	-2.2234	0.0265
Site-Beverly:SM	0.001	0.001	785	0.7393	0.4599
Site-Kintore:SM	0.000	0.000	785	-1.0046	0.3154
Soil CH_4:Species-Cedar	-0.001	0.001	785	-0.5771	0.5640
Soil CH_4:Species-Maple	0.002	0.001	785	1.4524	0.1468
Species-Cedar:T10	-0.010	0.004	785	-2.6875	0.0074
Species-Maple:T10	0.044	0.009	785	4.9003	0.0000
WT:Site-Beverly:Species-Cedar	0.000	0.004	785	-0.0080	0.9937
WT:Site-Kintore:Species-Cedar	-0.003	0.003	785	-1.0117	0.3120
WT:Site-Beverly:Species-Maple	0.001	0.006	785	0.1826	0.8552
WT:Site-Kintore:Species-Maple	0.000	0.004	785	0.0392	0.9687
WT:Site-Beverly:T10	0.000	0.000	785	-0.6172	0.5373
WT:Site-Kintore:T10	0.000	0.000	785	-2.0195	0.0438
WT:Species-Cedar:T10	0.000	0.000	785	-2.0873	0.0372
WT:Species-Maple:T10	0.001	0.000	785	1.9705	0.0491
Site-Beverly:Soil CH_4:Species-Cedar	-0.001	0.004	785	-0.3283	0.7427
Site-Kintore:Soil CH_4:Species-Cedar	0.001	0.001	785	1.1658	0.2440

Site-Beverly:Soil CH_4:Species-Maple	-0.004	0.014	785	-0.2598	0.7951
Site-Kintore:Soil CH_4:Species-Maple	-0.002	0.001	785	-1.4806	0.1391
Site-Beverly:Species-Cedar:T10	0.005	0.006	785	0.7269	0.4675
Site-Kintore:Species-Cedar:T10	0.013	0.005	785	2.5470	0.0111
Site-Beverly:Species-Maple:T10	-0.037	0.010	785	-3.5461	0.0004
Site-Kintore:Species-Maple:T10	-0.043	0.009	785	-4.6815	0.0000
WT:Site-Beverly:Species-Cedar:T10	0.000	0.000	785	0.6516	0.5149
WT:Site-Kintore:Species-Cedar:T10	0.000	0.000	785	1.9265	0.0544
WT:Site-Beverly:Species-Maple:T10	0.000	0.000	785	-0.9094	0.3634
WT:Site-Kintore:Species-Maple:T10	0.000	0.000	785	-1.4943	0.1355

Table S3.4 Observed ranges of tree stem CH_4 by species and site. Minimum, maximum values and sample sizes (n) are shown to illustrate within-group variability.

Site	Species	Mean	Min	Max	Median	*n*
Ancient Woods	Birch	0.89	-0.17	20.45	0.11	97
Ancient Woods	Cedar	0.12	-1.49	8.32	0.02	97
Ancient Woods	Maple	20.82	-0.27	218.70	0.71	95
Beverly	Birch	0.43	-1.81	9.21	0.04	92
Beverly	Cedar	0.63	-0.05	53.38	0.01	95

Beverly	Maple	1.21	0.00	37.09	0.13	92
Kintore	Birch	0.09	-0.11	0.73	0.05	90
Kintore	Cedar	0.50	-0.14	10.97	0.02	113
Kintore	Maple	0.23	-0.11	4.34	0.06	96

Chapter 4

Carbon balance of four temperate swamps in southern Ontario, Canada

4.1 Introduction

Despite only covering approximately 6% of the earth's terrestrial surface, globally wetlands store over 30% of the total soil organic carbon (C) stock (Jackson et al. 2017, Poulter et al. 2021), with over half attributed to northern boreal peatlands where bogs and fens dominate (Hugelius et al. 2020). Tropical peatlands, located mainly in South America, Southeast Asia, and Central Africa, store 469–694 Gigatons of C in only 90 – 170 million hectares (Gumbricht et al., 2017, Ribeiro et al. 2019). Therefore, most wetland C inventories have focused on boreal and tropical wetlands, leading to a lack of information on other areas and wetland types, including swamps. 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).

Though definitions vary between regions, swamps are generally described as forested wetlands with > 30% canopy cover and seasonal or persistent surface water (NWWG 1997, Government of Ontario 2022). In Canada, swamps are estimated to represent up to 9% of national wetlands (Tarnocai 2006, Amani et al. 2019); in northern Ontario, conifer swamps make up 40–60% of peatlands (Riley 1994). Higher aboveground biomass has been found in swamps than in treed bogs and fens, or in marshes (Bona *et al.* 2018) and biomass in swamps is comparable to that of mature forests across Canada and the USA (Davidson *et al.* 2022). Dense, woody peat in swamps contains up to 4–5 times more C than forest soils across the USA (Domke *et al.* 2017). Carbon stocks held in swamp peat are 4–25 times higher than that of the trees in boreal black spruce forested peatlands (Magnan *et al.* 2020; Beaulne *et al.* 2021). This combination of large above and belowground carbon stocks suggests that swamps have the potential to represent carbon storage hotspots on the landscape.

Despite this, swamps are not fully considered in management and policy decisions and are often combined with other wetland types (Kuhn *et al.* 2021, Olefeldt *et al.* 2021) or absent as a specific category in current models of peatland C storage and cycling (Bona *et al.* 2018, Webster *et al.* 2018, Pontone *et al.* 2024). The absence of common, clear classification and lack of field data creates uncertainty in calculating existing soil C stocks and makes parametrizing models for swamps difficult (Yu *et al.* 2010, Bona *et al.* 2018, Byun *et al.* 2018, Dazé *et al.* 2022). Additionally, few studies

have quantified C fluxes and transfers between pools, such as net primary productivity of trees, litter inputs to the soil, and gaseous releases to the atmosphere (e.g., Reader and Stewart, 1972, Conner and Day Jr., 1976, Trettin and Jurgensen, 2003, Kendall et al. 2020, Davidson et al. 2022).

The C balance of an ecosystem, net ecosystem carbon balance (NECB) is the net sum of all C inputs (primarily through photosynthesis) and outputs (decomposition, fire, harvest, physical matter removal) over time (Chapin et al. 2006). A system's C balance determines if it is a source or a sink. An ecosystem's C balance is influenced by a wide range of factors, from local precipitation, water balance, and vegetation composition to disturbance such as climate change, fire, and land use change. Additionally, C is transferred between pools as, e.g., a tree moves from living vegetation biomass to deadwood upon death, and eventually to the soil pool as it decays (Bona et al. 2020). Although these processes are analogous to other wetlands and upland forests, plants within swamps are adapted to periods of anoxic soil conditions during the growing season; hydrologic inputs may come from groundwater, surface water, or precipitation and are closely related to geomorphic setting (Trettin and Jurgensen, 2002). The length of these periods of reduced oxygen availability influence vegetation productivity, decomposition, and CO_2 and CH_4 dynamics, where annual net productivity has been shown to decline with wetter conditions (Megonigal et al. 1997, Davidson et al. 2022). Additionally, temperature modulates these processes, as is shown broadly by the decrease in productivity with lower mean annual temperature and precipitation (Zhu et al. 2018), and by positive relationships between soil CO_2/CH_4 fluxes and soil temperature (Gutenberg et al. 2018, Davidson et al. 2019, Schmidt et al. 2025). Thus, hydrologic regime and soil temperature are likely dominant factors in swamp biogeochemical processes, but how this varies compared to other wetland types remains unclear.

This illustrates the need to quantify the current C stocks held in soils and above- and below-ground biomass and transfers between vegetation, soil, and atmosphere, particularly to provide the data needed for developing models of swamp C cycling. Additionally, current C exchange data in northern swamps is often based on the chamber method and limited to warmer months, missing important spatial and temporal variability and making it difficult to estimate an annual C budget (Blais et al. 2005). This study aims to address both of these issues by using multiple sampling methods and including as many pools and fluxes of C as possible. To address these gaps, we identified four study swamps in southern Ontario, Canada that represent a range of hydrogeomorphic setting and tree canopy

compositions. Sites were selected based on initial assessment during a synoptic study across 12 swamp study sites (Schmidt et al. 2025). At these four swamps, the specific objectives of this study were to:

(1) estimate the current C stocks held within soil, dead wood, trees, and understory vegetation,

(2) estimate the addition and losses of C to the ecosystem annually via growth and decay, and,

(3) determine if the study swamps are sources or sinks of C.

4.2 Methods

4.2.1 Study sites

As mentioned, four of the 12 sites from Chapter 2, Schmidt et al. (2025) were selected for a study that more fully captured spatial and temporal variation with all sites located in southern Ontario, between 42–44°N and 80–82°W (Figure 4.1). The swamps fall into three hydrogeomorphic settings and have organic or mineral-organic soils (Table 4.1). The study region falls within the humid continental climate zone, which is characterized by mild summers and relatively consistent precipitation across seasons. The average temperature of the coldest month is below 0 °C, while all months have average temperatures below 22 °C and at least four months have average temperatures of 10 °C or higher (CEC 2021). The study area has an average growing season of 188 days, with annual precipitation ranging from 900–1000 mm and the highest rainfall occurring during spring and fall (Government of Canada 2024). Southern Ontario has a high population density, ranging from 5–1000 people per square kilometer outside the Greater Toronto Area (CEC 2020b), and the landscape consists primarily of cropland interspersed with remnants of Carolinian and temperate continental forest (CEC 2020a, 2022). Although all study sites experience some degree of human activity, they were selected to ensure that no active canopy clearing had occurred within the previous 100 years. Therefore, disturbance was not specifically considered as an effect in this study.

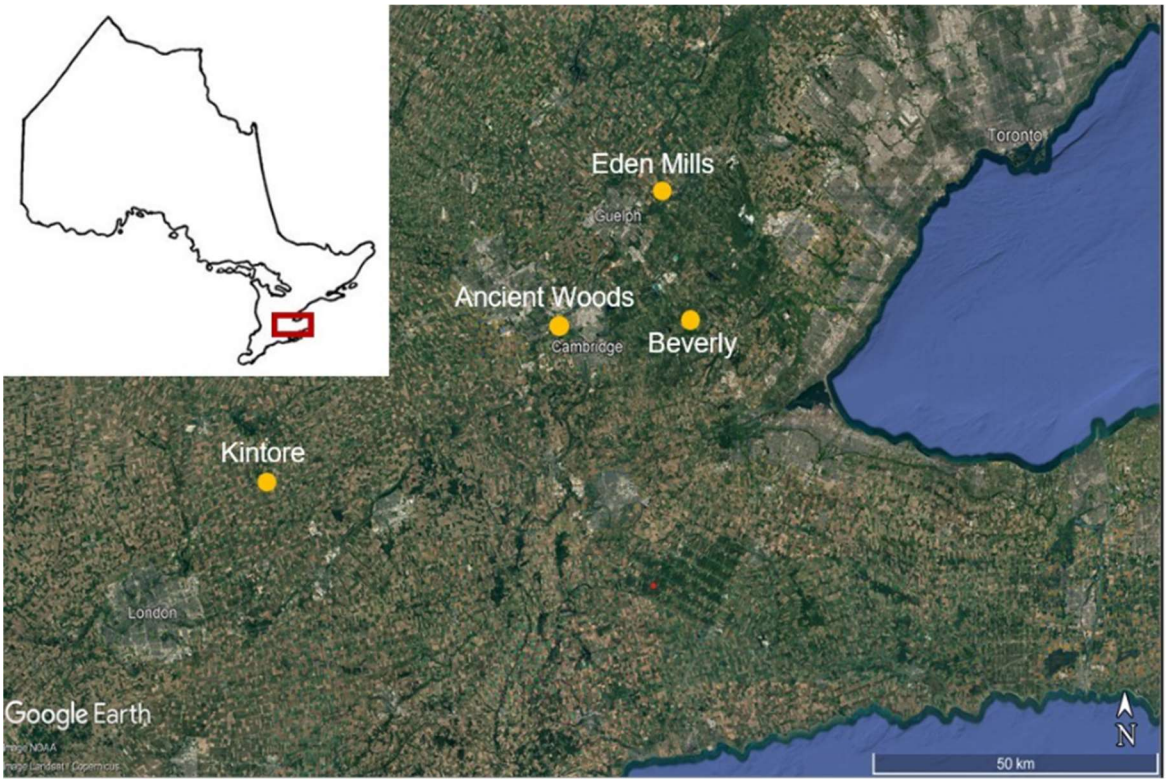


Figure 4.1 Map of site locations within study area and Ontario (inset). Base imagery from Google Earth, accessed 27-April-2026.

Table 4.1 Summary of sites.

Site	Hydrogeomorphic Setting	Canopy Type	Soil Type	Location
Ancient Woods (AW)	Basin	Broadleaf (mixed)	Mineral-Organic	43.3759, -80.3699
Beverly (B)	Flat	Broadleaf (mixed)	Organic	43.3841, -80.1050
Kintore (K)	Flat	Mixedwood	Organic	43.1614, -81.0050
Eden Mills (EM)	Riverine	Needleleaf	Organic	43.5706, -80.1522

Beverly Swamp is a mixedwood, flat swamp (Table 4.1, Fig 4.2). Unconfined flat swamps lack clear topographical boundaries or banks and often occur in glacial lake beds or outwash (NWWG 1997). The specific study area of Beverly Swamp used in this study had a predominantly broadleaf canopy, with peat soils (0.3–1.5 m) and a channelized stream running through it (Warren et al. 2001), indicating that it can

also be classified as a riparian swamp. Riparian swamps occur along the edges of rivers, streams, and lakes and are directly influenced by the water body; riverine swamps are situated along the banks of rivers and streams and often experience flooding when water levels are high (NWWG 1997). Dominant tree species included *Acer rubrum, Acer saccharinum*, and their hybrid, *Acer x freemanii*, *Betula alleghaniensis*, *B. papyrifera*, *Thuja occidentalis*, and *Fraxinus* spp. Understory vegetation was predominantly broadleaf saplings, and the ground layer consists of ferns, graminoids, forbs, patchy bryophytes, and large areas of bare peat.

The Ancient Woods swamp is a mixedwood, mineral-organic (0.2–0.6 m) basin swamp within which Bauman Creek originates from groundwater seepage (Table 4.1, Fig 4.2). Basin swamps are well-defined by the sides of the basin and occur in glacial deposits (e.g., kettle) or bedrock (NWWG 1997). Dominant tree species included *Acer* spp., *Betula alleghaniensis*, and *Thuja occidentalis*. The understory included broadleaf saplings and tall shrubs such as *Sambucus canadensis* and *Cornus* spp.; *Symplocarpus foetidus* makes up most of the ground cover from early spring to its senescence in mid- to late-June, after which bare peat dominates with patches of ferns, forbs, and bryophytes.

Kintore Swamp is a mixedwood flat swamp with peat soils 1–2 m deep (Table 4.1, Fig 4.2). Dominant tree species included *Tilia americana*, *Acer* spp., *Betula alleghaniensis*, and *Thuja occidentalis*. Understory species included *Lindera benzoin*, and *Cornus* spp.; the ground layer included large areas of *Symplocarpus foetidus* that transition to bare peat, and patchy forbs, graminoids, ferns, and bryophytes. A gravel road runs north to south through the swamp; plots were located on both sides to account for any potential effects on hydrology.

The Eden Mills swamp is a *Thuja occidentalis* riverine swamp along the Eramosa River with 0.3–1.0 m peat (Table 4.1, Fig 4.2). The understory was sparse *T. occidentalis* seedlings and ground layer vegetation was minimal, with patchy bryophytes and small areas of forbs, graminoids, and ferns in more open areas.



Figure 4.2 Photographs of study sites. Clockwise from top: Eden Mills, Kintore, Ancient Woods, Beverly. Photographs by M. Schmidt.

4.2.1 Biomass and soil carbon stocks

Tree surveys were conducted at all study sites in late July through early August 2022 as part of the synoptic study described in Schmidt et al. (2025). At each site, three 20 m × 20 m plots were used for tree measurements. All individuals ≥ 3 m tall were identified to species when possible, or otherwise to genus, and their diameter at breast height (DBH) was recorded. Dead standing stems were also measured for DBH, with height estimated for broken stems. Tree biomass (kg dry biomass converted to kg C m^{-2}) was estimated using allometric equations, assuming that wood contained 50% carbon (Lambert et al. 1996, Ung et al. 2008, Marscaro et al. 2011, Hamelin et al. 2015). Understory vegetation surveys and biomass estimates were conducted in July 2024 using 1 × 1 m quadrats. Two quadrats were sampled per carbon flux collar, with 12 flux collars per site (n=24 per site; see details below). Overhanging branches from young trees and shrubs ≤ 3 m tall were included in the samples. Vegetation was clipped at soil level, and branches were cut where they crossed the quadrat boundary. Biomass clippings and litter were placed in zip-top bags and kept at 4 °C for a maximum of 48 hours before drying at 60 °C until a stable weight was reached. Dry mass was recorded in g m^{-2}, and biomass was converted to estimated C stock using total C

values from bulk understory samples at each site (39–45%). These values were determined by combusting samples and converting them to gas using a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer in the Environmental Isotope Lab at the University of Waterloo. Belowground biomass was calculated as a proportion of aboveground tree biomass using equations from Li et al. (2011); this omits roots of ground layer plants resulting in a small underestimate.

Both fine and coarse woody debris were measured in three plots per site. Fine woody debris (FWD) - any branches, sticks, and twigs with a diameter less than approximately 7.5 cm - were collected with 1 x 1 m quadrats (National Forest Inventory 2021) to be dried and weighed in the laboratory. Coarse woody debris (CWD) was assessed using the line-intercept survey method (National Forest Inventory 2021). A 20 m transect of random orientation was marked and any log of >10 cm diameter at the smallest end that crossed the line was measured for length and the diameter of each end. Each was also assigned a decay class from 1 to 5 based on observed structural characteristics (Harmon et al. 2008). As we were unable to reliably identify the species of each log, a proportional average of the most common species was used to determine biomass (see S1 for detailed process). Site totals were calculated as the average of the three plots and organic C calculated as 49.3% of biomass (Harmon et al. 2013).

In 2024, four to six soil cores were collected near each C flux collar across the study sites using a Russian auger, extending to the confining mineral layer to determine soil C stocks. Cores were sectioned into 10 cm increments in the field, sealed in plastic zip-top bags, and transported to the laboratory. Samples were stored at 4 °C before being dried at 80 °C for 48 hours, after which dry bulk density was calculated by dividing dry mass by the initial sample volume (g cm^{-3}). Subsamples were analyzed for organic matter content (OM%) using loss on ignition (Kennedy & Woods 2013). Approximately 3 g of soil was placed in a pre-weighed ceramic crucible and heated in a muffle furnace at 550 °C for 4 hours. Organic matter content was determined from the mass lost relative to the initial sample mass, and organic C content was estimated by assuming that 50% of OM was carbon (Kennedy & Woods 2013). This assumption provided reasonable total C estimates based on carbon analyses of grab samples from the top 10 cm of soil, which fell within the range of variation in LOI estimates. Although this method also included inorganic C, inorganic C accounted for less than 0.01% of total C at these sites (Schmidt et al. 2025). Total C content for each depth increment was calculated by multiplying bulk density by organic C content, and total C (kg m^{-2}) per core was determined by summing all increments. Site-level soil C stocks were calculated as the average across all cores.

4.2.2 Soil CH_4 and CO_2 fluxes

We measured soil CO_2 and CH_4 fluxes simultaneously with a $CH_4/CO_2/H_2O$ Trace Gas Analyzer (LI-7810, LI-COR, Nebraska, USA) weekly from June to November 2023, monthly from January to April 2024, and weekly from May to November 2024 via the closed chamber method (Griffis *et al.* 2000). No measurements were taken in December due to site access limitations during hunting season. Twelve 20 cm diameter, 10 cm tall acrylic collars per site were permanently installed in a 30 m x 30 m equidistant grid to account for spatial and microtopographical variation and contained no vegetation. An acrylic chamber set into a corresponding groove in the collar created a seal and a small battery-operated fan continuously circulated the air within. Concentrations of CO_2 and CH_4 were measured every second within an opaque chamber (20 cm diameter x 40 cm tall) over a 3-minute closure, along with temperature and humidity within the chamber, resulting in a measure of soil respiration (CO_2 released from soil) and CH_4 flux. A circular floating chamber (27 cm diameter x 16.5 cm tall) positioned above the soil collar was used when water levels were >10 cm above surface. 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 connected to the LI-7810 enabled observation of chamber headspace concentration in real time, allowing for adjustments to the chamber to ensure a tight seal on the collar to obtain a clear, linear change in concentration during the chamber closure. 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. Order of plots was changed each visit to account for diurnal temperature changes. Further inspection for linearity and slope of the concentration change over the chamber closure was calculated using the processing tool PEDRO (Newton et al. 2025). Fluxes were accepted if $r^2 > 0.7$ (clear slope) or < 0.3 (flux nearly zero). After processing, 1,721 CO_2 and 1,724 CH_4 soil and 573 tree stem CH_4 fluxes were retained in the analysis, representing a loss of ~2% of data points each.

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), soil moisture (SM) of the top 10 cm was calculated as the average of 4 points surrounding the chamber via a Wet-2 Sensor and HH2 Moisture Meter (Delta-T Devices), and water table (WT) was measured as distance from surface in a dip well adjacent to each collar. Tree stem CH_4 fluxes were measured by Schmidt et al. (in preparation) and included here to ensure that this CH_4 emission pathway was included.

Annual CO_2 and CH_4 emissions were calculated using collar annual emissions. Monthly collar means were multiplied by the number of days in the month, then summed for the total annual flux per collar; total annual site flux was calculated as the average of annual collar fluxes. Annual uncertainty (standard deviation) was also calculated on the annual collar fluxes. Months with no field measurements were calculated as the average of the months preceding and following. CO_2 and CH_4 were multiplied by the proportion of C per compound to determine exchanges in mass of C m^{-2} y^{-1} (see S4.2 for example).

4.2.2 Annual Net Primary Productivity

Annual aboveground net primary productivity (ANPP) was calculated as the total amount of C, as organic matter, produced by the vegetation in a year. Tree cores were collected using an increment borer from nine individuals of *Acer* spp., *Betula alleghaniensis* and/or *papyrifera*, and *Thuja occidentalis* across Ancient Woods, Beverly, and Kintore in fall 2025. The thickness of the five most recent rings, representing 2025, 2024, 2023, etc., were measured and used to back-calculate DBH and biomass via allometric equations for each year; thus, incremental increase of wood and roots were calculated as the difference between years (Hamelin et al. 2015, Lambert et al. 1996, Li et al. 2003, Mascaro et al. 2011, Ung et al. 2008). No relationship between tree ring width and DBH was found, so a mean ring width was applied for each site. At Beverly, 16, 5, and 3% of the trees surveyed were *Acer* spp., *Betula* spp., and *Thuja occidentalis*, respectively. At Kintore, these species accounted for 22, 15, 0%, and 31, 6, and 6% at Ancient Woods. At Eden Mills *Thuja* made up 59% of trees with no *Acer* spp. or *Betula* spp. An average of the *Acer* spp. and *Betula* spp. was applied to any other broadleaf species, and an average of the *T. occidentalis* to needleleaf species. Belowground NPP was calculated as fine root turnover (FRT) plus the increase in estimated woody roots mass between the years using calculations from Li et al. (2011) and the tree surveys.

Twelve litter traps (0.5 x 0.5 m) per site were installed in September – October 2023 to catch leaves and twigs that fell from the canopy (adapted from Bernier *et al*. 2008). Each trap was collected once or twice each in October and November, dried, and weighed separately to obtain a mean value for the site. Litter traps were collected once more in April – May 2024 to include anything that fell over the winter and spring with this mass added to the site total. The mass of litter from each trap was averaged for each site and then added over time to calculate total annual production. Not collecting throughout the full year (i.e., no collection between May and September) likely missed some litter and slightly underestimated foliage NPP, however, temperate and boreal forest litterfall peaks in the fall, with a small increase in the spring of

reproductive material, and collection during the autumn captures an average of 72% of total aboveground litter in a given year (Bernier *et a*l. 2008, Zhang et al. 2014, Jevon et al. 2022).

Understory ANPP was estimated based on the understory biomass data. All herbaceous and woody material from understory plants but only foliage from the shrub layer was included in ANPP calculations; including woody material from the ground layer likely overestimated the total as not all was produced in that year; however, this is offset by likely underestimation as we did not account for ground layer root growth.

4.2.3 Statistical analysis

All analyses were conducted in the statistical analysis program R (R Core Team 2025). Variation of C stocks and greenhouse gas fluxes were analysed using linear mixed-effects models (lme; Pinheiro *et al.* 2016) to account for hierarchical sampling and repeated measurements. Carbon mass (kg C) was modelled as a function of site, vegetation level (canopy or understory) or component (foliage, wood, debris, etc.), and their interactions, with plot included as a random intercept. Soil CO_2 and CH_4 fluxes were modelled as functions of site, species, season, and environmental covariates (ST, SM, and WT depth), with collar or tree identity included as random intercepts. Methane fluxes were log-transformed to improve normality and homoscedasticity. Models were fitted using maximum likelihood, and collinear predictors were evaluated separately when necessary. Post-hoc comparisons were performed using estimated marginal means (emmeans; Lenth 2025) with Tukey adjustment. Model assumptions were assessed using residual diagnostics, and statistical significance was evaluated at $\alpha = 0.05$.

4.3 Results

4.3.1 Environmental Conditions

Total precipitation in 2023 at Ancient Woods and Beverly exceeded both the 2024 total and the 30-year average; both were lower than the 30-year average in 2024. At Eden Mills and Kintore neither year met the 30-year average and 2023 was drier than 2024. On average 2023 was approximately 0.5 °C cooler than 2024 (Environment and Climate Change Canada, 2026). Monthly and yearly precipitation and temperature data are available in Supplementary Table S4.1. Median WT at each site ranged from -5 to -27 cm in 2023 and -6.5 to -20 cm in 2024; WT was consistently deepest at Eden Mills and shallowest at Ancient Woods; consequently, SM in both years was similar at AW, B, and K while EM was drier. ST at 10 and 30 cm was approximately 2 °C warmer across all sites in 2024 and patterns were identical at both

depths; differences between sites in 2023 were small with much overlap, and only EM differed in 2024. Summary statistics for site-level environmental conditions are available in Supplementary Table S4.2.

4.3.2 Carbon Stocks

4.3.2.1 Biomass

Site-level differences in C stocks depended strongly on component (Fig 4.3); C stocks in understory, trees, and woody debris did not differ significantly among sites (all pairwise comparisons, $p \geq 0.7$). Living trees were the main contributor to total tree C stocks which ranged from 9.9 - 20.1 kg C m^{-2}. Woody debris, particularly coarse woody debris (logs), held 1.14 – 10.52 kg C m^{-2}. Understory biomass contributed relatively little to total stocks at 0.04 - 0.15 kg C m^{-2}.

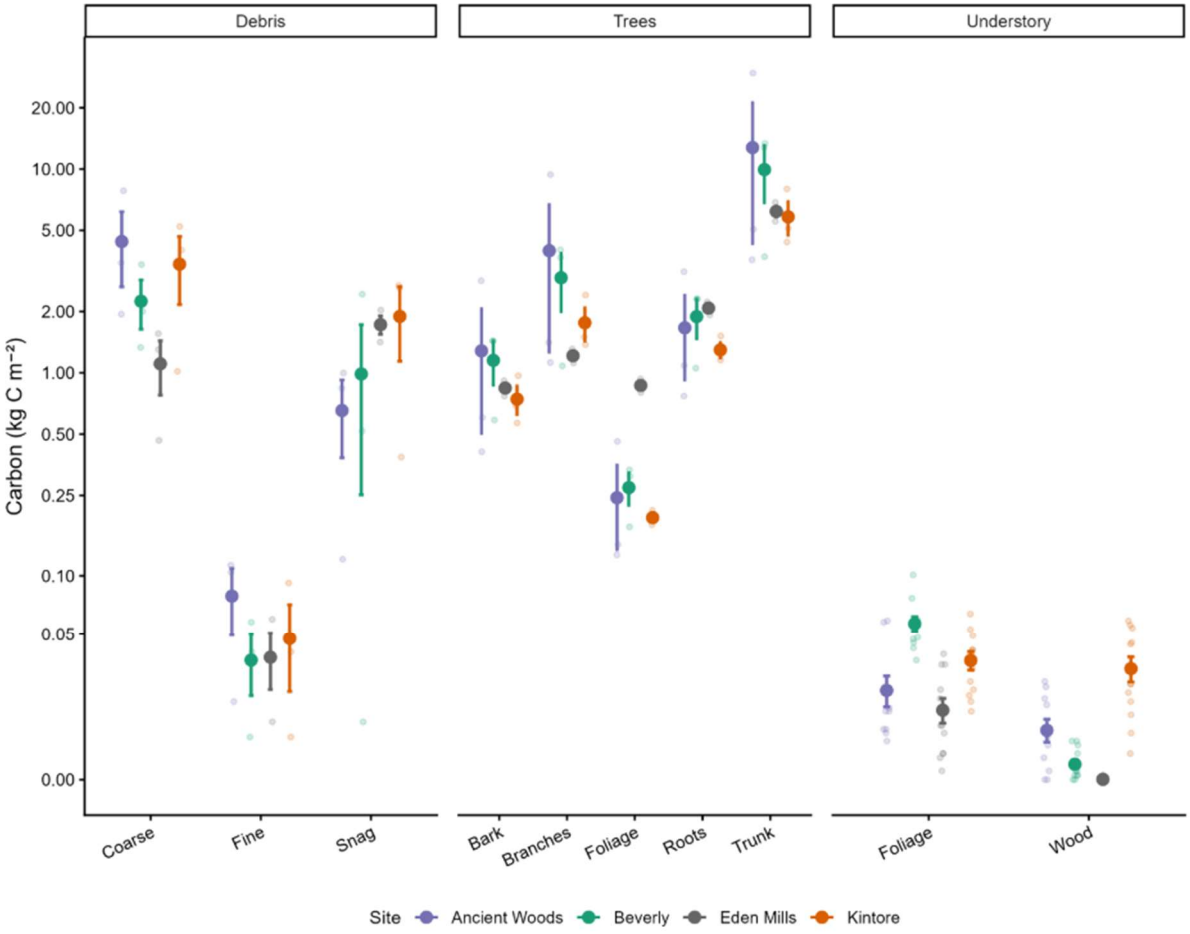


Figure 4.3 Mean (± SE) C stocks within components for each site. Points indicate individual observations; larger symbols show site means. Note that a pseudo-log scale is used for the y-axis.

4.3.2.2 Soil Carbon

Total soil C stocks varied widely among organic soil cores and sites, reflecting large differences in peat thickness to the mineral confining layer (Fig. 4.4). Mean peat depth ranged from 0.44 ± 0.11 m at Ancient Woods and 0.50 ± 0.22 m at Beverly to 0.60 ± 0.30 m at Eden Mills, with substantially thicker peat at Kintore (1.42 ± 0.34 m). The top 30 cm contained 13.0 kg C m^{-2} at Ancient Woods and 17.2, 17.4, 18.4 kg C m^{-2} at Beverly, Eden Mills, and Kintore, respectively. Mean total profile C stocks ranged from 20.4 ± 8.1 kg C m^{-2} at Ancient Woods, 32.6 ± 18.6 kg C m^{-2} at Beverly to 37.7 ± 23.6 kg C m^{-2} at Eden Mills, with markedly greater C storage at Kintore (85.8 ± 16.3 kg C m^{-2}). This translates to an equivalent soil mass (surface to 100 cm; Wendt and Hauser 2013) of 15.3, 20.0, 14.3, and 10.5 kg C m^{-}

^{2} at Ancient Woods, Beverly, Eden Mills, and Kintore, respectively. Total soil C stock increased with peat thickness across all sites (Fig. S1A), while C density, expressed as depth-weighted mean C per unit soil volume, varied among sites ($p < 0.0001$), with the greatest difference between Ancient Woods and Kintore (Fig. S4.1B). This suggests that total soil C storage is a function of both peat depth and C density.

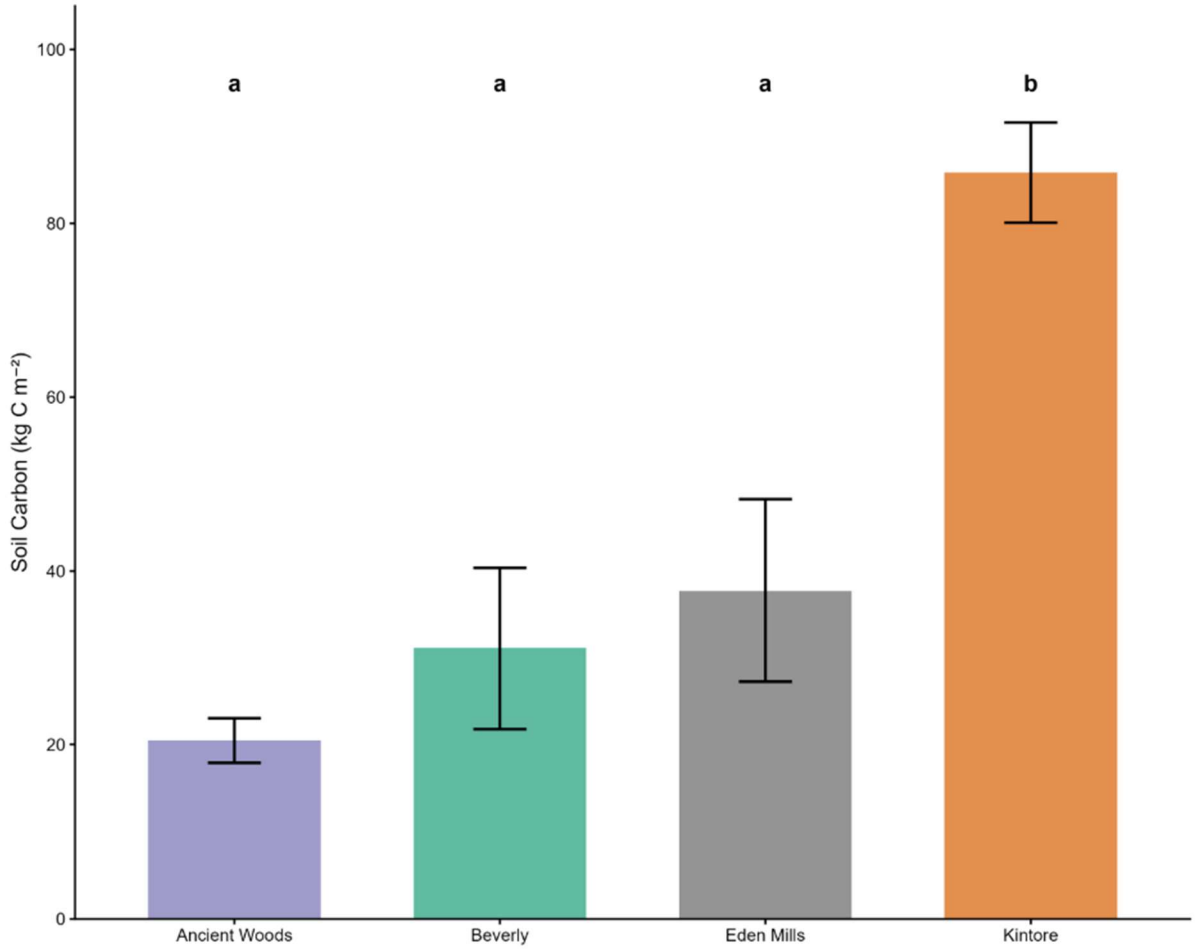


Figure 4.4 Mean (± SE) soil C stocks by site. Bars represent site-level means and error bars indicate standard errors calculated from variation among core-level measurements.

4.3.3 Fluxes of carbon between pools

4.3.3.1 Soil CO_2 Flux

Overall, soil CO_2 flux varied little between sites (12.9–18.1 g CO_2 m^{-2} d^{-1}), nor were there consistent effects of year or season across sites; the direction and magnitude of year-to-year change was different for each site (Year:Site $F_{3,1668}$= 5.0109, p = 0.0018). Within each year, sites differed slightly in mean CO_2 flux, but these differences were broadly consistent across years with highest CO_2 emissions in late summer (August–September) (Fig. 4.5). Average values for C fluxes are given in Supplementary Material Table S4.3.

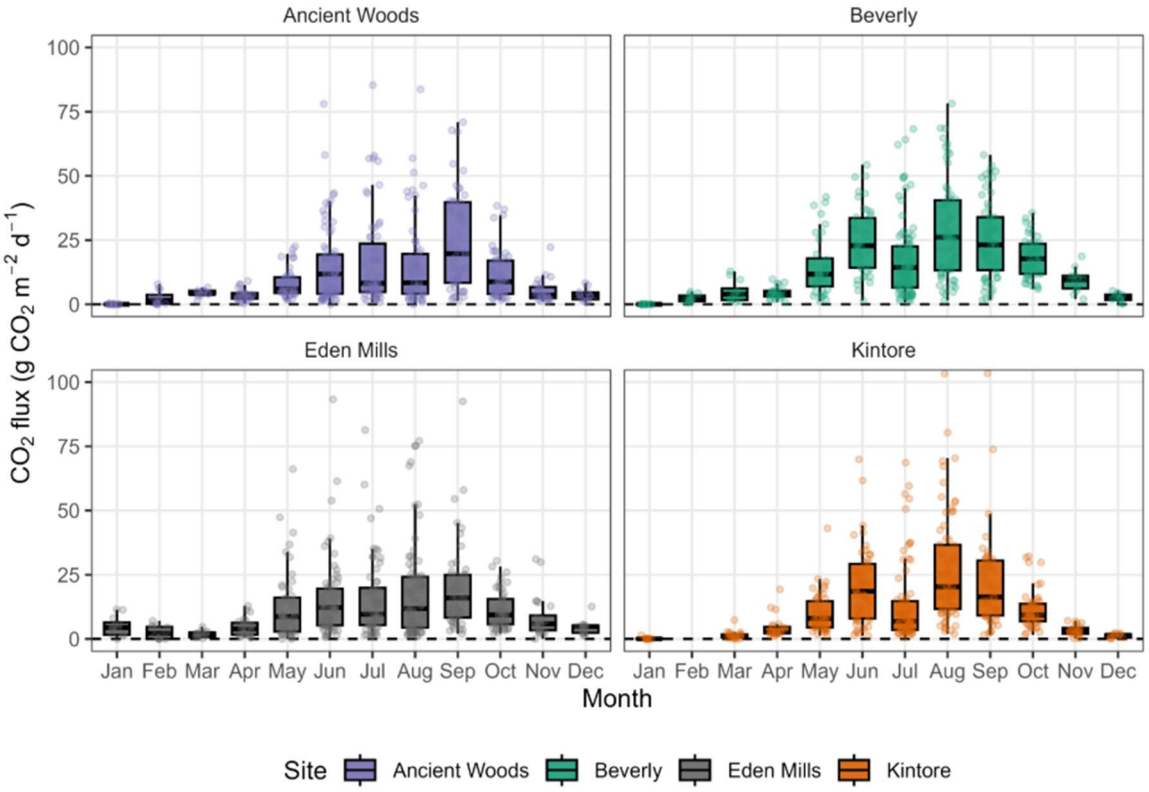


Figure 4.5 Monthly distributions of soil CO_2 flux across sites. Boxplots indicate medians and interquartile ranges, with jittered points showing individual measurements. The dashed horizontal line indicates zero flux. The y-axis is truncated at 100 g CO_2 m^{-2} d^{-1} to improve visualization of the majority of observations; six higher values are omitted from the display but included in all analyses (Kintore: n = 4: 103, 147, 147, 209 g CO_2 m^{-2} d^{-1}; Eden Mills: n = 2: 111, 154 g CO_2 m^{-2} d^{-1}).

Soil CO_2 respiration increased as WT declined below the soil surface ($F_{1,1625}$ = 346.79, p = <.0001), with the strongest responses at intermediate depths, and patterns were broadly consistent across sites (Fig 4.6). Near-surface SM (0–10 cm) explained substantially more variation in CO_2 flux than WT alone (ΔAIC = 193), while ST exerted a consistent positive effect across depths ($F_{1,1671}$ = 436.88, p <.0001; Fig. 4.7). A significant WT × ST interaction indicated that warming enhanced CO_2 emissions under deeper WTs, but temperature sensitivity declined as WT approached the soil surface ($F_{1,1623}$ = 143.63, p < 0.001; Fig 4.8). Combining monthly averages across the study period, annual emissions of CO_2 were 3.4 – 4.7 kg m^{-2} yr^{-1} from soils.

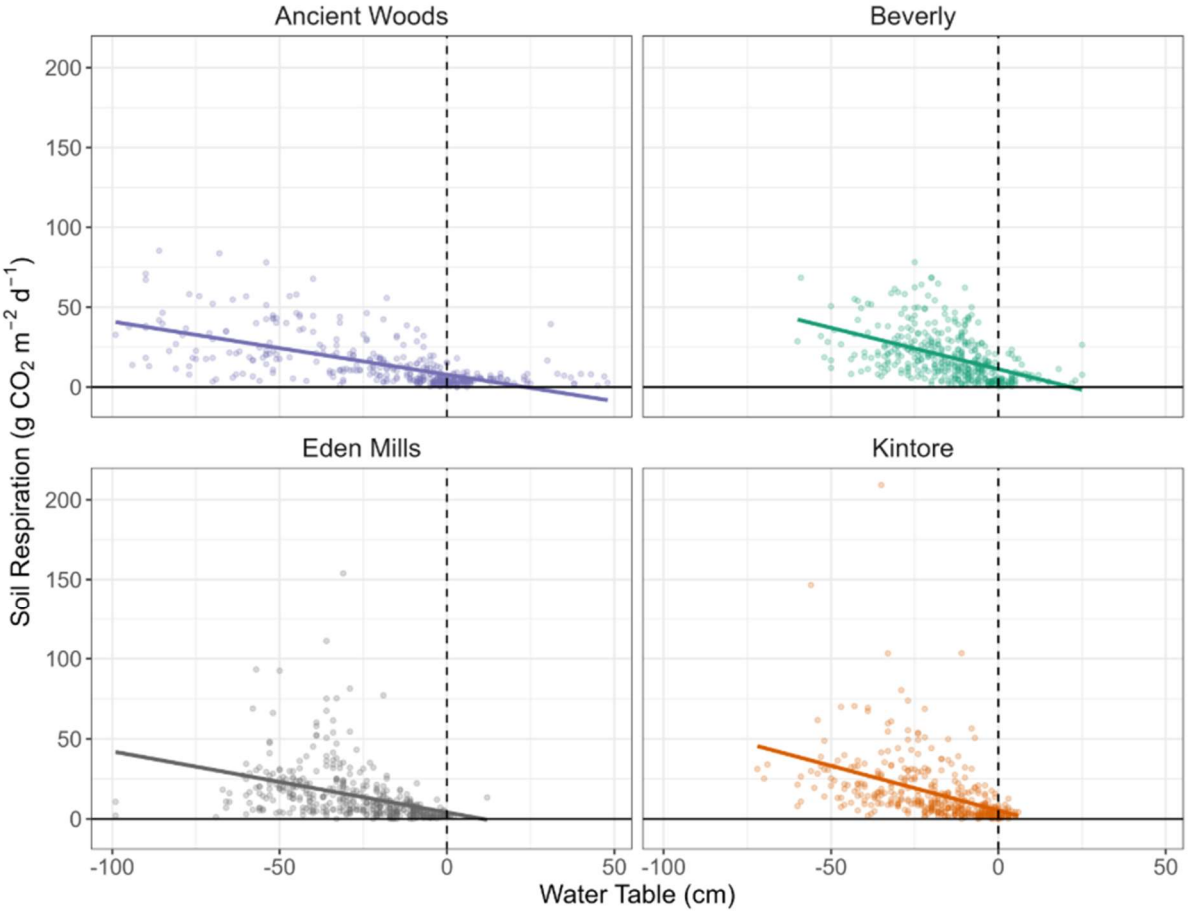


Figure 4.6 Relationships between water table and soil respiration. Water table is in cm, soil respiration is in log(CH4). Individual points represent measured data and lines show relationships.

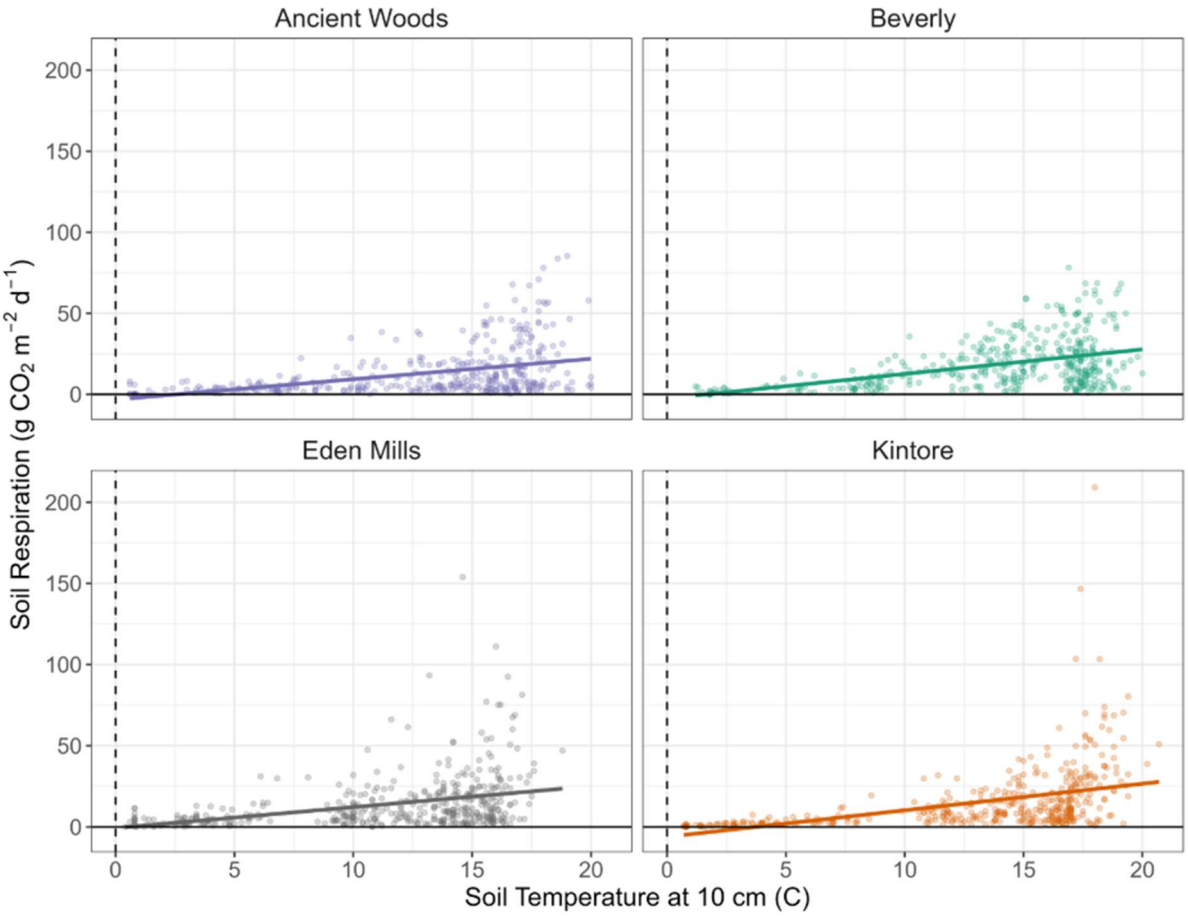


Figure 4.7 Relationship between soil CO_2 flux and soil temperature across the sites. Soil temperature is in °C, soil respiration is in log(CH_4). Individual points represent measured data and lines show relationships.

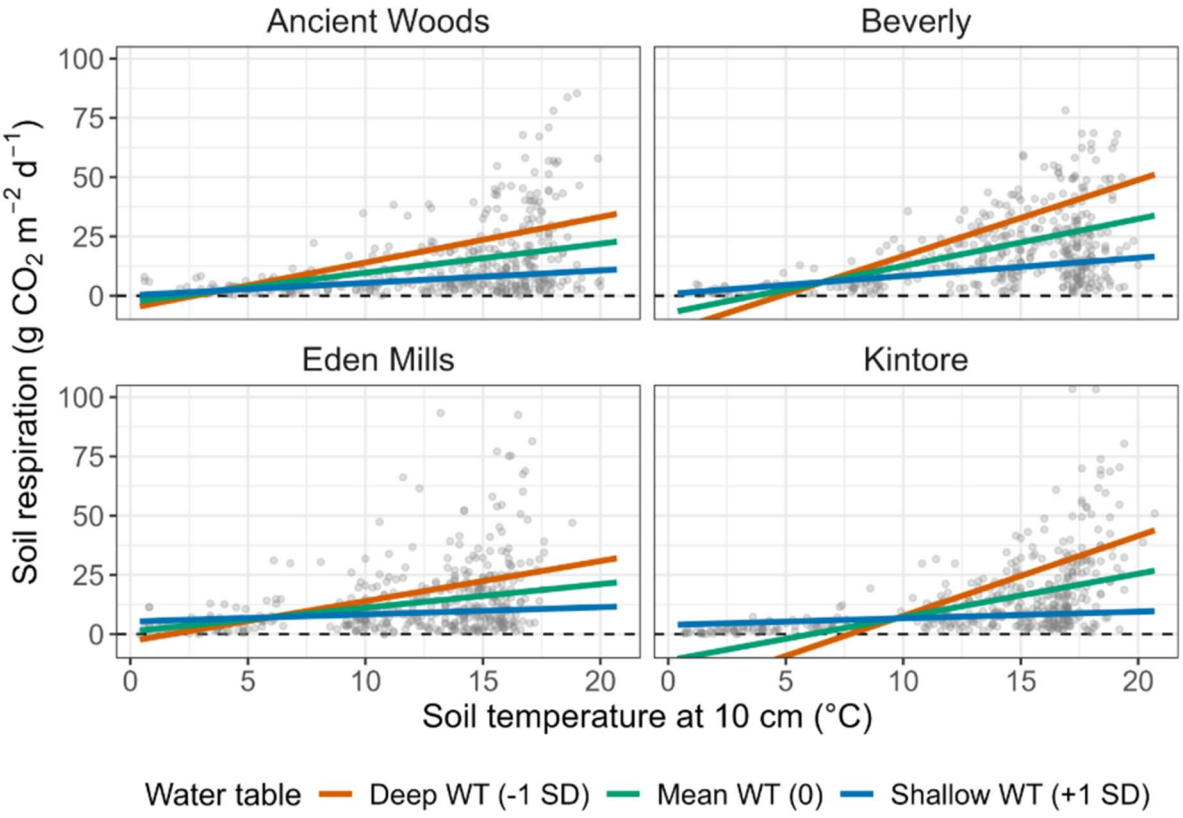


Figure 4.8 Interactive effects of water table depth and soil temperature on soil CO_2 flux. Lines show model-predicted CO_2 flux across the observed temperature range at deep, mean, and shallow water table positions. Temperature sensitivity was strongest under deeper water tables and weakened as the water table approached the soil surface.

4.3.3.2 Soil CH_4 Flux

Daily soil CH_4 fluxes varied more across sites than CO_2, ranging from -0.84 to 32.7 mg CH_4 m^{-2} d^{-1} ($F_{3,45}$ = 6.1996, p = 0.0013), with the highest fluxes at Ancient Woods and Beverly and lowest at Eden Mills (Fig 4.9). As with CO_2, there was no consistent main effect of year across sites; year-to-year differences varied among sites and were generally small relative to site-level variation. Within individual sites, interannual differences in CH_4 flux were weak or not statistically significant. Within each year, sites differed in mean CH_4 flux, suggesting that persistent site characteristics exerted stronger control over CH_4 dynamics than interannual variability during the study period.

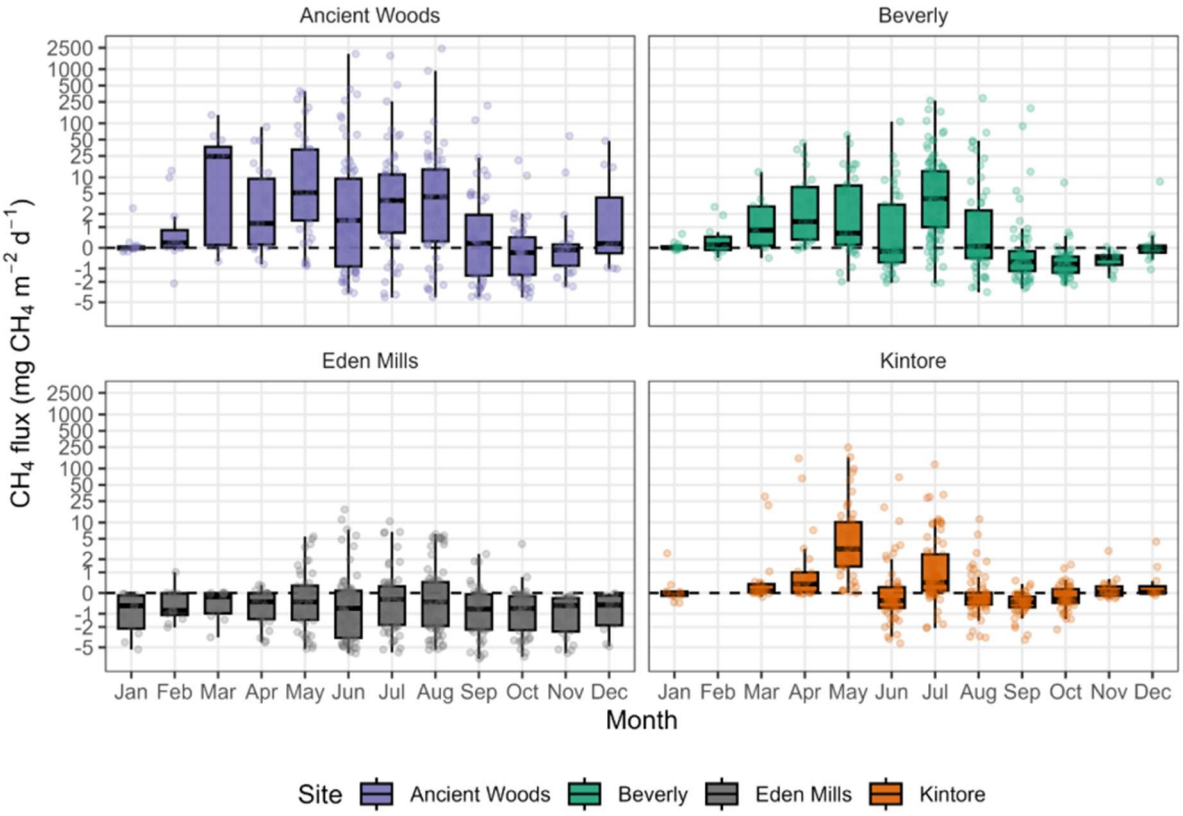


Figure 4.9 Monthly distributions of soil CH_4 flux across sites. Boxplots indicate medians and interquartile ranges, with jittered points showing individual measurements. The dashed horizontal line indicates zero flux. Note that a pseudo-log scale is used for the y-axis.

CH_4 emissions responded strongly to ST variation, with short-term, near-surface (10 cm) temperature deviations exerting a stronger positive effect than background (deeper soil, 30 cm) temperature ($F_{1,1674}$ = 37.1938, p <.0001; Fig 4.10). WT depth showed a weak negative association with CH_4, with emissions declining as the WT dropped below the soil surface ($F_{1,1628}$= 244.15, p <.0001; Fig 4.11). Significant interactions between ST and WT ($F_{1,1626}$ =20.410, p <.0001) indicated that temperature sensitivity depended on hydrologic conditions: warming effects were weak or negative under dry, deep WT but CH_4 emission increased sharply with warming under shallow WT (Fig 4.12), indicating that WT depth strongly constrained temperature-driven CH_4 production.

Combining monthly averages across the study period, annual emissions of CH_4 were 10.6 – 106.0 g m^{-2} yr^{-1} from soils. Emissions from tree stems as reported in Chapter 3 were 0.01 – 1.3 mg CH_4 m^{-2} yr^{-1}, accounting for < 1% of total ecosystem emissions.

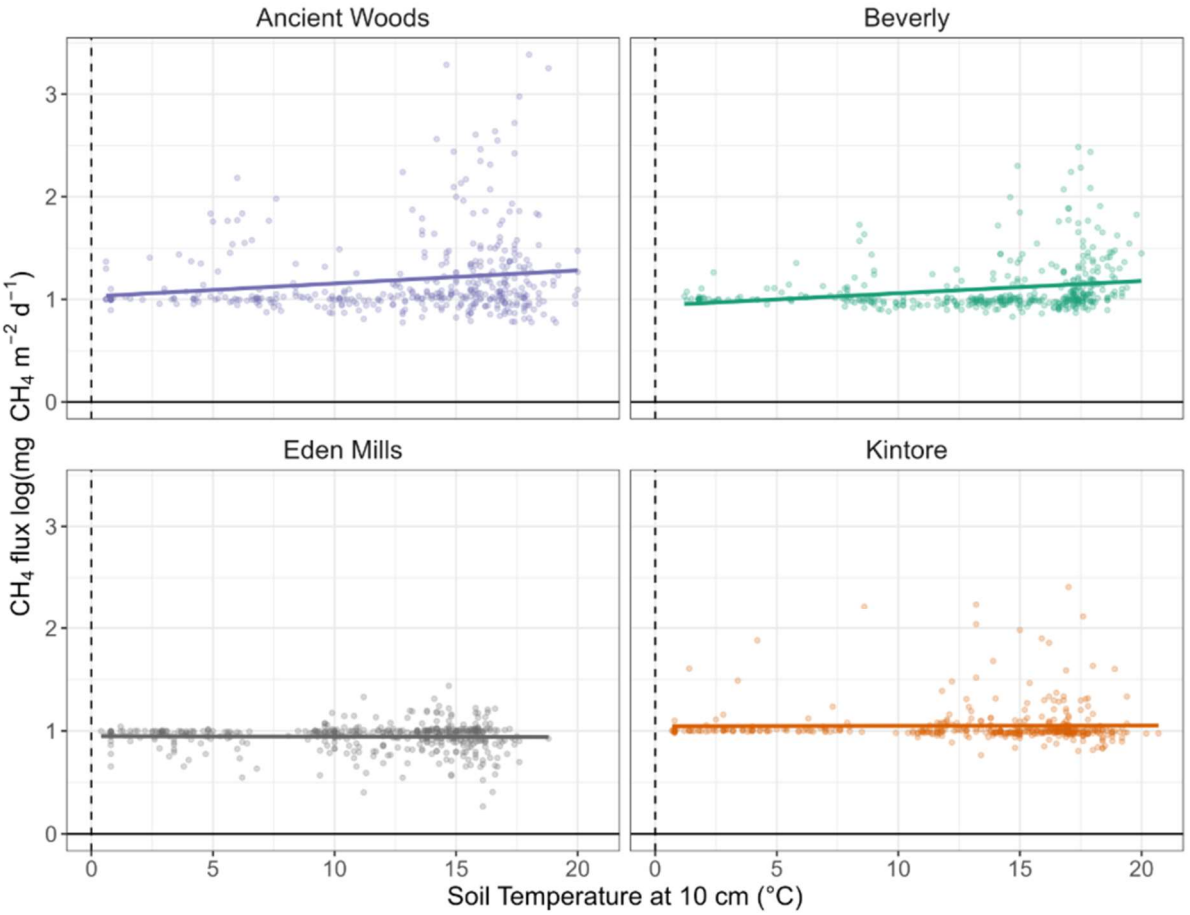


Figure 4.10 Relationship between soil CH_4 flux and soil temperature at 10 cm across the sites. Points represent individual data points and lines show relationships. Soil temperature is in °C and flux is in log(CH_4).

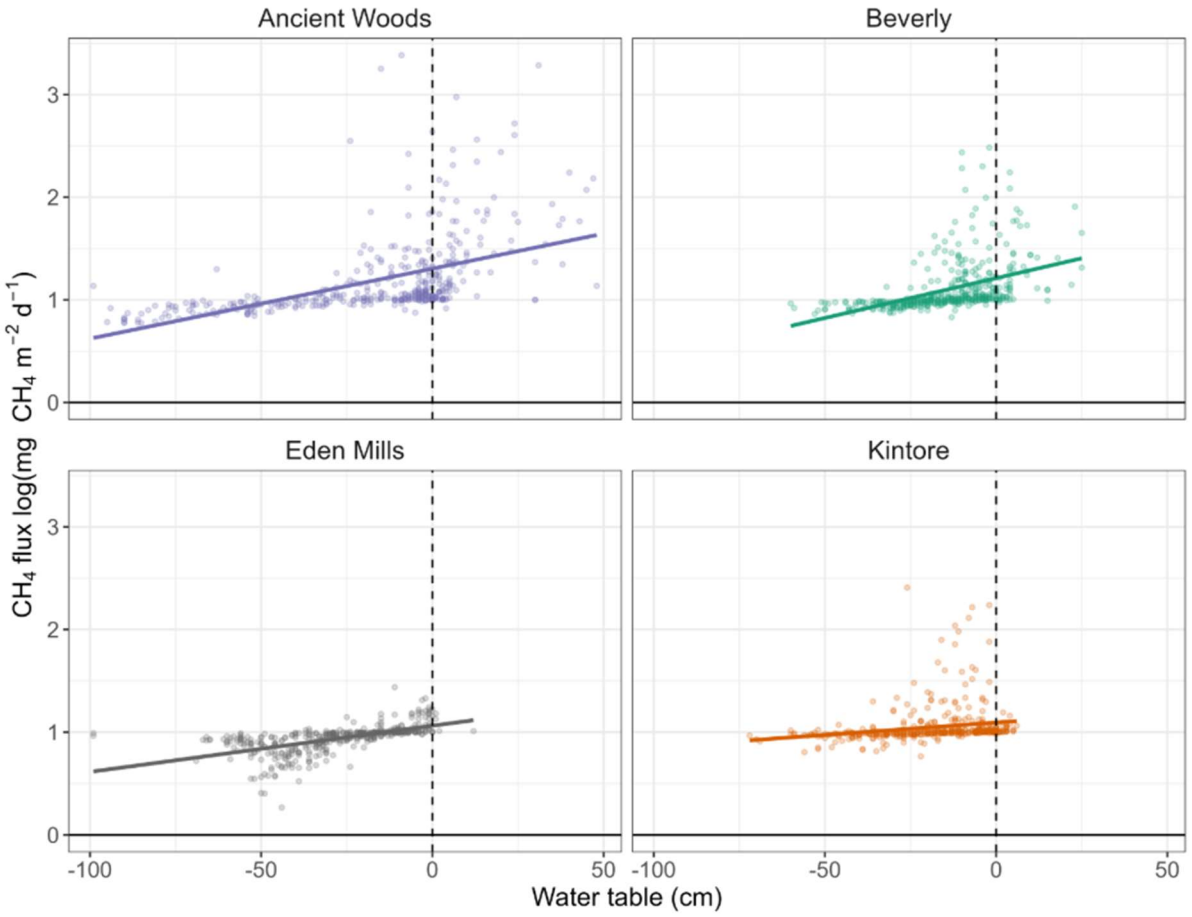


Figure 4.11 Relationship between soil CH_4 flux and water table across the sites. Points represent individual data points and lines show relationships. Water table is in cm and flux is in log(CH_4).

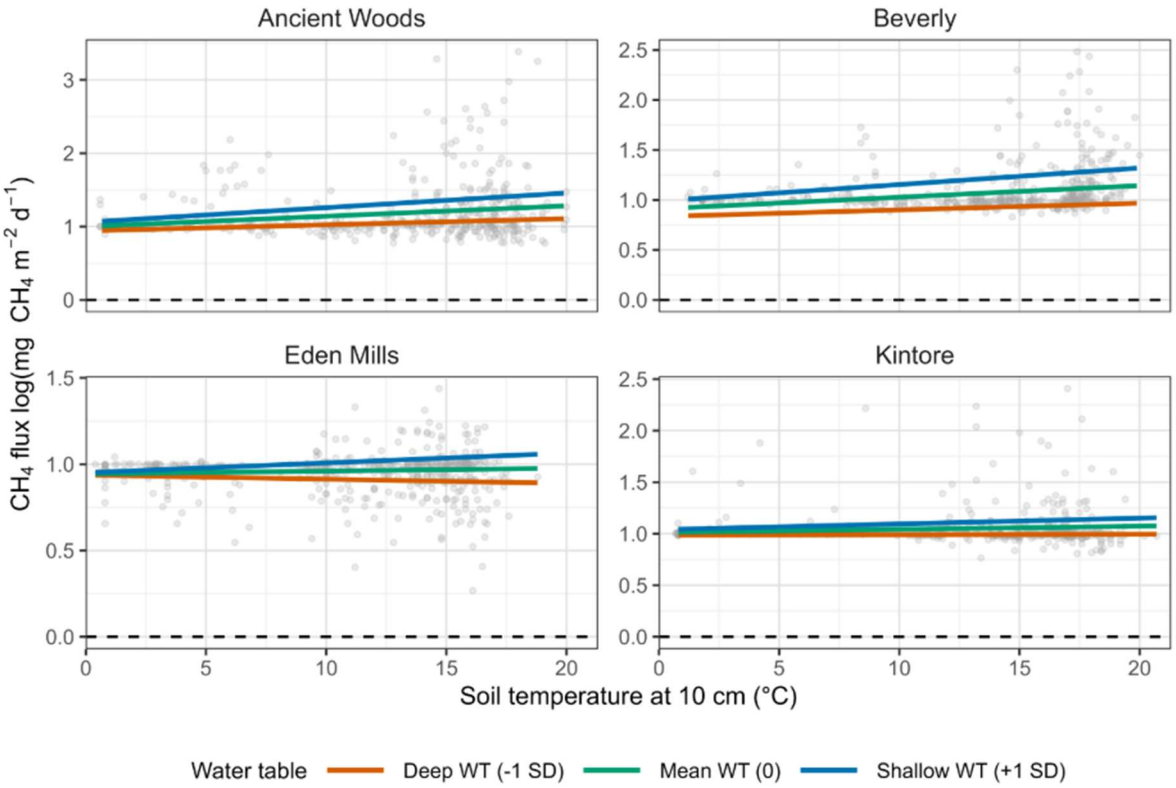


Figure 4.12 Relationship between soil CH_4 flux, water table, and soil temperature at 10 cm across the sites; CH_4 data values are in log(CH_4). Lines represent CH_4 flux under three moisture conditions: deep water table (dry soil conditions), mean water table, and shallow water table (wet conditions). Note y-axis vary between plots.

4.3.3.3 Annual Net Primary Productivity (NPP)

ANPP did not differ significantly among sites at either the tree or understory level (Tukey-adjusted pairwise tests: all $p \geq 0.56$; Fig 4.13). Foliage produced by trees (103 – 141 g C m^{-2}, as estimated from litterfall) was the largest component of annual C accrual and, subsequently, transferred from living biomass to the soil pool. Fine root production and incremental gain by woody roots of trees accounted for 86 – 216 g C m^{-2}, and tree stems and branches gained 333 – 721 g C m^{-2}. The understory accounted for 4 - 146 g C m^{-2}, primarily from foliage.

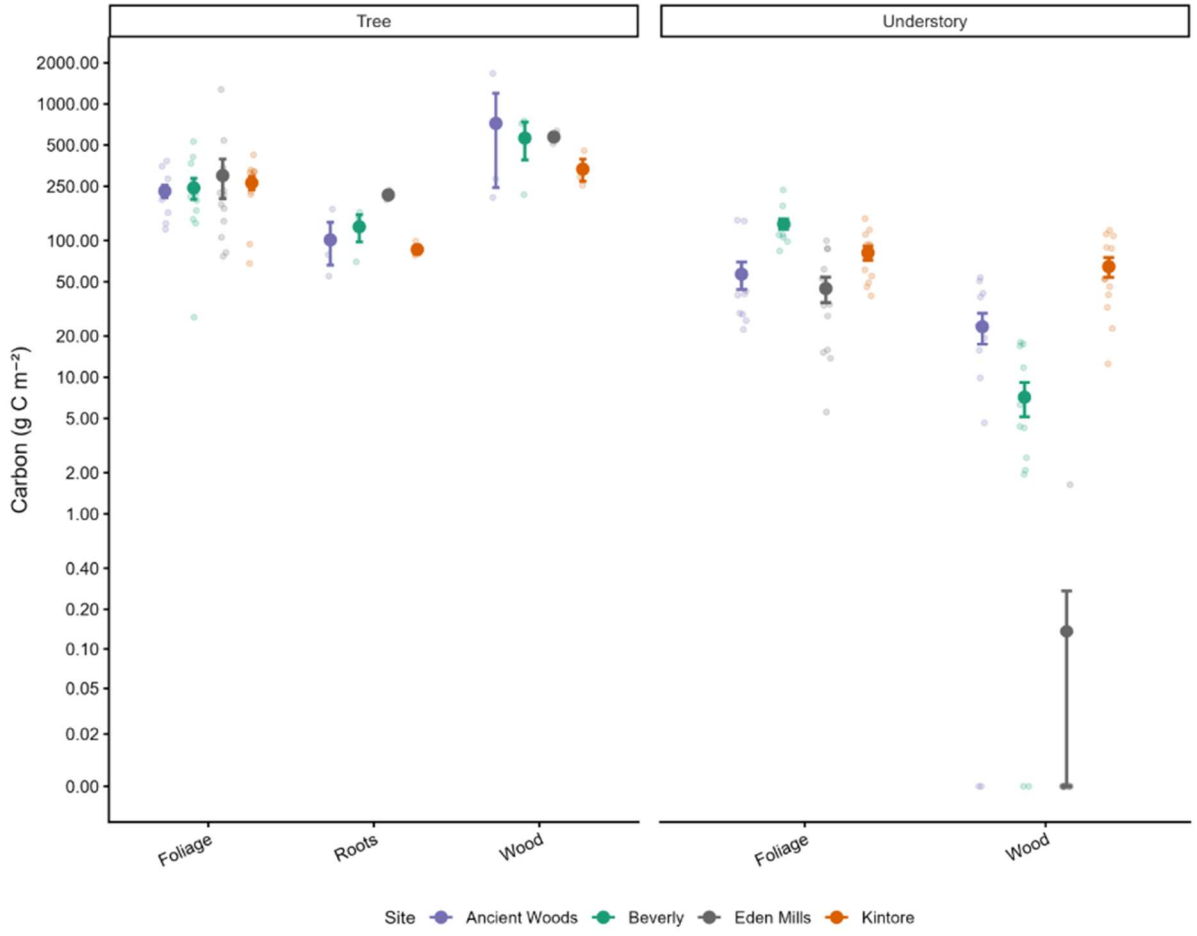


Figure 4.13 Annual Net Primary Productivity of trees and understory by component. Small points represent individual measurements; large points represent mean with standard error. Note that a pseudo-log scale is used for the y-axis.

4.3.3.4 Ecosystem Carbon Stocks and Annual Carbon Balance

Kintore had the highest total C stocks at 108.3 kg C m^{-2}, followed by Eden Mills and Beverly at ~51.5 kg C m^{-2} and Ancient Woods with 45.6 kg C m^{-2} (Table 4.2). Soils held 45 – 79% of total ecosystem C, followed by trees at 10 – 44%. Total annual C emitted from the swamps' soils ranged from 0.9 kg C m^{-2} at Ancient Woods to 1.2 kg C m^{-2} at Beverly, primarily from soil CO_2 respiration (Table 4.3). Trees accounted for the majority of NPP with understory taking up <30% that of the trees. Overall, uptake and storage of C (NPP) was lower than losses (soil and tree flux) at Beverly, Eden Mills, and

Kintore, making them slight sources of C to the atmosphere (< 1 kg C m^{-2} yr^{-1}; Table 4.4); Ancient Woods was a slight sink at -0.11 kg C $m^{-2}yr^{-1}$.

Table 4.2 Summary of existing C stocks. Values are means (standard deviations) in kg C m^{-2} yr-1. Replicates were averaged within plots and plots averaged within stock types. Level and ecosystem totals represent the sum of component means.

C Stocks (kg C m^{-2})					
	Component	**Ancient Woods**	**Beverly**	**Eden Mills**	**Kintore**
Woody Debris					
	Coarse	4.5	2.3	1.1	10.5
	Fine	0.1	0.0	0.0	0.0
	Snag	0.7	1.0	1.7	1.9
	Total	5.2 (2.0)	3.3 (1.7)	2.9 (0.2)	12.5 (4.7)
Soil					
	Mean Peat Depth (m)	0.4	0.5	0.6	1.4
	C Stock	20 (8)	33 (19)	38 (24)	86 (16)
Trees					
	Bark	1.3	1.2	0.8	0.7
	Branches	4.0	2.9	1.2	1.8
	Foliage	0.2	0.3	0.9	0.2
	Trunk	12.8	9.9	6.2	5.8
	Roots	1.7	1.9	2.1	1.3
	Total	19.9 (22.1)	16.2 (8.3)	11.2 (1.6)	9.8 (2.9)
Understory					
	Foliage	0.1	0.1	0.0	0.1
	Wood	0.0	0.0	0.0	0.1
	Total	0.1 (0.04)	0.1 (0.04)	0.0 (0.03)	0.1 (0.06)
Site Total		45.6 (23.6)	52.2 (20.5)	51.8 (23.6)	108.3 (17.2)

Table 4.3 . Summary of annual fluxes. Values are means (standard deviation) in g C m^{-2} yr^{-1}. Sign conventions are such that positive values indicate release to the atmosphere and negative values are uptake.

C Fluxes (g C m^{-2} yr^{-1})					
	Component	**Ancient Woods**	**Beverly**	**Eden Mills**	**Kintore**
Tree NPP					
	Foliage	-103	-106	-141	-118
	Roots	-101	-126	-216	-86
	Wood	-721	-563	-574	-333
	Total	-925 (825)	-795 (300)	-930 (70)	-537 (107)
Understory NPP					
	Foliage	-57	-132	-45	-82
	Wood	-23	-7	0	-64
	Total	-80 (43)	-140 (41)	-45 (33)	-146 (62)
Soil Flux					
	CH_4	8.6	1.6	-0.4	1.2
	CH_4-C	6.4 (13.4)	1.2 (1.6)	-0.3 (0.5)	0.9 (1.3)
	CO_2	3295	4488	3706	3632
	CO_2-C	890 (559)	1212 (419)	1001 (647)	981 (481)
	Total C	896 (559)	1213 (419)	1000 (676)	982 (481)
Tree Stem Flux					
	CH_4	1.3	0.1	0.0	0.0
	CH_4-C	1.0 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Site Total		-108 (998)	279 (517)	25 (680)	298 (497)

4.4 Discussion

Wetlands, particularly peatlands, are well known for their ability to store C in their soils, and upland forests recognized as important C sinks, largely due to tree biomass. Northern peatlands are estimated to store 415 ± 150 Gt of C (Hugelius et al. 2020), with ~272 ± 23 Gt sequestered in forested wetlands that cover ~8% of the boreal region (Pan et al.). However, research has tended to cluster in some areas and leave others understudied. Thus, literature on swamps is limited, and primarily focuses on tropical and subtropical swamps, where the climate is warmer and wetter than more northern latitudes (Davidson et al. 2022). Unlike temperate and boreal swamps, which experience a winter cessation of growth and greatly reduced microbial activity, tropical swamp forests maintain photosynthesis, respiration, and microbial

activity throughout the year because temperatures remain favorable. Seasonal changes in productivity are driven primarily by rainfall, flooding, and water-table dynamics rather than freezing temperatures (Malhi et al. 2012, Mitsch & Gosselink 2015).

Carbon storage in our sites was dominated by soils rather than aboveground biomass, with variation among sites driven primarily by differences in peat depth and C density. Despite contrasting hydrological conditions, tree, understory, and woody debris carbon pools were relatively consistent across sites, whereas soil carbon stocks varied more than fourfold. This suggests that long-term carbon accumulation is dependent on belowground processes over long timescales, and that peat stores more C than trees in forested wetlands (Beaulne et al. 2021). As in Magnan et al. (2023), we found a strong relationship between peat depth and total soil C; high C stocks at Kintore were the result of substantially deeper peat deposits, but differences in C density between sites show that C storage is not solely a function of depth. Soil depth has been noted as one of the most important factors in predicting soil C density of both mineral and organic soils with density decreasing linearly with depth, while soil C stocks often increase with depth due to higher soil mass (Hengl et al. 2017, Gross and Harrison 2019, Sothe et al. 2022). The mineral fraction in soils plays a role in this, as near the surface minerals are often saturated with C, reducing retention, and as C concentration decreases with depth, saturated minerals become more relevant to C storage (Hobley et al., 2015). Variations in C density reflect differences in litter inputs, decomposition rates, and peat composition, suggesting that both long-term accumulation and site-specific biogeochemical processes contribute to C storage.

A study by Byun et al. (2018) found that southern Ontario has lost over half of its historic wetlands to land use change, primarily cultivation, such that ~86% of the remaining extent is swamp. They estimated a cumulative C mass of the soil within conifer swamps of 180 ± 104 kg C m^{-2}, mixedwood 101 ± 58 kg C m^{-2}, and broadleaf 94 ± 76 kg C m^{-2}. These numbers are quite a bit higher than our sites at 20.44 ± 8.1 (Ancient Woods; broadleaf), 32.58 ± 18.6 (Beverly; broadleaf), 37.73 ± 23.6 (Eden Mills; conifer), and 85.84 ± 16.3 kg C m^{-2} (Kintore; mixedwood). However, their values were based on the Ontario Geological Survey's peat surveys of southeastern Ontario (SEO; Riley 1994) that focused on large, unforested, deep peat deposits for resource extraction between 44 and 46 °N latitude, and between Georgian Bay and 75 °W longitude (primarily north of Peterborough and Kingston and east of Lake Simcoe, with a subset near Parry Sound); the shallowest mean peat depth across survey areas was 1.4 m, while the majority were near or exceeded 2 m. Therefore, using the SEO peat survey depths potentially overestimated soil C stocks across the rest of southern Ontario, including our study area. For example, of

the 12 swamps studied in Schmidt et al. (2025), only five had peat depths that exceeded 50 cm. Though climatically similar, the SEO survey area is slightly cooler with a shorter growing season than the rest of southern Ontario, which may contribute to wetter conditions that reduce decomposition. Additionally, only 57% of the SEO ecoregion has been converted to agriculture compared to 78% agriculture, plus >7% developed land in southwestern Ontario (SWO), where the current study was situated (Crins 2009). Additionally, most of SEO has tile drainage installed in <5% of the area while much of SWO exceeds 30-50% (Byun et al. 2018).

Table 4.4 A comparison of values for aboveground biomass (AGB), belowground biomass (BGB), soil C stock, and depth measured of swamp and upland forests from the literature.

Ecosystem Type	Location	AGB (kg C m^{-2})	BGB (kg C m^{-2})	Depth (if stated) (m)	Soil C Stock (kg C m^{-2})	Author
Forested peatland	Canadian boreal	4.6 - 8.9	2.8 - 5.7		22 - 66	Beaulne et al. 2021
Marsh	Canada		1.2			Bona et al. 2018
Peatland	Canada			2	158	Sothe et al. 2022
Swamp	Southern Ontario, CA			0.5 - 1	28 - 45	This study
Swamp	Southern Ontario, CA			1	30 - 77	Barreto & Pironkova 2026
Swamp	Canada & USA	20		0.9	54 - 70	Davidson et al. 2022
Swamp	Southern Ontario, CA			0.33 - 0.5	20 - 35	Schmidt et al. 2025
Swamp	Canada		1.8			Bona et al. 2018
Treed bogs and fens	Canada		1.2 - 2.3			Bona et al. 2018
Upland	Conterminous USA				5.4	Domke et al. 2017
Upland	Global temperate biome	6 - 13			9.5	Lal 2005
Upland	Canada	4.1	1.3	2	68	Sothe et al. 2022
Upland	Boreal	3				Thurner et al. 2014
Upland	Temperate	5.4 - 6.4				Thurner et al. 2014
Upland forest	Canada		1.2			Smyth et al. 2013

Our estimated soil C stocks agree well with other North American swamps studies and highlight that swamps have greater soil C storage than upland forests. We observed that soil C stocks in the study swamps were similar to other swamp studies and much greater than values generally reported for upland forests (Table 4.4). Again, these differences could be due to shallower peat depths, as Baretto

and Pironkova (2026) also found a strong vertical stratification where deeper layers stored larger C pools than shallower layers. Additionally, differences in peat depths and C densities are likely influenced by site conditions such as geomorphic setting and hydrologic regimes (Megonigal and Day Jr. 1988), but these results highlight the large amounts of C stored in even shallow and mineral swamps.

These estimates also show that much more C is found in the soils than in the trees in forested wetland systems. Our sites held up to 10 times the C in peat compared to above and below ground biomass; on average biomass held only a third of the C than the soil did. The other studies show similar ratios at 20 – 35%, whereas AGB in upland forests held over 50 and up to ~85% of the C in the soils, an inverse relationship to organic systems. AGB in forested peatlands and swamps was 25 – 65% higher than upland forests; similarly, organic soils held > 55% of the C than upland soils. BGB in swamps is also higher than upland forests, storing approximately one third more C.

Soil CO_2 fluxes were relatively similar between sites and were primarily controlled by near-surface moisture and soil temperature. The strong increase in CO_2 fluxes as WT declined reflects the enhanced aerobic respiration under drier conditions, while the strong relationship of near-surface SM relative to WT suggests that microbial activity is more directly regulated by conditions in the upper soil layers (Blodau 2002, Bridgham et al. 2013). The interaction between temperature and hydrology further indicates that warming effects are contingent on oxygen availability; increased soil temperatures enhanced CO_2 emissions under dry conditions, but this effect diminished as soils became saturated and oxygen limitations constrained decomposition (Blodau 2002). Together, these results highlight the importance of coupling thermal and hydrological controls when predicting soil respiration in swamps. In contrast to CO_2, CH_4 fluxes were more spatially variable and more strongly influenced by site conditions. CH_4 emissions were primarily driven by WT, with ST affecting the rate of emission once wet conditions are present. Near-surface changes created stronger effects than background temperature conditions in deeper layers. Warming enhanced CH_4 emissions under wetter conditions but had little effect when WT was deep as increased oxygen constrained methanogenic activity. This interaction shows that hydrology does not control CH_4 flux magnitude in isolation but regulates how much temperature can drive production.

As with CO_2, this demonstrates that WT modifies temperature sensitivity and the importance of considering WT interactions with soil temperature. Despite differences in temperature and precipitation between years, interannual differences were small and inconsistent relative to site-level variation for both CO_2 and CH_4. This suggests that persistent site characteristics such as peat structure, hydrogeomorphic

setting, and soil chemistry have a stronger influence than short-term climate variability. This is demonstrated by the high and variable CH_4 values at Ancient Woods, where some of the collars were located within a pool and experienced dramatic changes in water table. Therefore, local spatial heterogeneity appears to be a stronger driver of soil greenhouse gas dynamics than temporal variability at annual timescales in these systems.

Beverly, Eden Mills, and Kintore acted as net C sources during the study period as ecosystem respiration outweighed annual C inputs from NPP. These losses were primarily driven by soil CO_2 emissions, with CH_4 contributing a smaller proportion of soil C losses. Despite substantial C storage, particularly in soils, these systems may be vulnerable to short-term C loss under certain environmental conditions. However, results from this study like reflect only short-term flux dynamics relative to long-term accumulation. Peat C stocks represent potentially centuries of net C sequestration, whereas annual C balance can fluctuate with environmental conditions. For example, at 15.9–20.9 g $m^{-2}d^{-1}$, growing season CO_2 soil fluxes from our sites were comparable to the range of North American swamps 0–50 g $m^{-2}d^{-1}$ found by Davidson *et al.* (2022). Similarly, growing season CH_4 emissions at our sites were well within the 0– >150 mg m^{-2} d^{-1} from Davidson et al. (2022) at -0.71 - 48.1 mg CH_4 m^{-2} d^{-1}, with Ancient Woods and Eden Mills acting as small CH_4 sinks. Growing season CH_4 fluxes from the swamps were also comparable to those of bogs and fens from a range of Canadian sites (35.8 ± 6.2 and 40.8 ± 5.1 mg CH_4 m^{-2} d^{-1}, respectively), as well as the mean of all temperate bogs and fens at 48.2 ± 16 mg CH_4 m^{-2} d^{-1} (Webster et al. 2018). Understory NEE across the southern Ontario sites in Schmidt et al. (2025) ranged from 1–24 g CO_2 m^{-2} d^{-1}, much higher than that of Canadian bogs (-4.9 ± 1.3 CO_2 $m^{-2}d^{-1}$) and fens (-3.5 ± 1.1 CO_2 $m^{-2}d^{-1}$) (Webster et al. 2018) due to lower understory cover, but aboveground NPP is larger in swamps (our sites: 0.91 - 1.57 kg C $m^{-2}yr^{-1}$; Davidson et al. 2022: 1.1 kg C $m^{-2}yr^{-1}$) than reported for fens (0.2–0.4 kg C $m^{-2}yr^{-1}$), bogs (0.3–0.4 kg C $m^{-2}yr^{-1}$), marshes (∼1.2 kg C $m^{-2}yr^{-1}$) (Bona et al 2018), or Canada's managed forests (0.35 kg C $m^{-2}yr^{-1}$; Stinson et al. 2011). These findings suggest that C dynamics in temperate swamps are driven by different controls across timescales; long-term C storage is determined by peat accumulation, while short-term GHG fluxes are regulated by temperature-moisture interactions influencing both soil organic matter cycling and overstory productivity. As a result, future warming may increase CH_4 emissions, particularly if conditions are able to sustain high water tables that support anaerobic processes. Conversely, increased prolonged dry periods may enhance CO_2 losses while limiting CH_4 emissions, potentially shifting the balance of GHG outputs, but could be offset by enhanced

overstory productivity and litter inputs. Fragmentation, conversion, and drainage result in isolated remnants, and these remnant swamps still account for a large portion of wetland in southern Ontario. Both within and surrounding swamps, anthropogenic disturbances may create drier conditions, in turn increasing soil C oxidation and reducing C stores and peat accumulation ability. How disturbance affects C exchange in these C storage hotspots requires additional study.

Although we aimed to measure the ecosystem C balance of our study swamps as completely as possibly, standard deviations of flux components, particularly soil C emissions were high resulting in a range for NECB that crossed zero for all sites. It should be noted that our study did not partition tree root respiration from soil respiration, and as such could result in an overestimation of soil C losses and an underestimation of net ecosystem carbon budgets. Additionally, annual values were calculated using monthly means of fluxes collected only during daylight hours, thus not accounting for potential lower fluxes overnight or on days not suited for fieldwork (rain, too hot, etc.). This large uncertainty highlights that additional studies are needed to further constrain C budgets. Additionally, our study did not include particulate or dissolved organic or inorganic carbon, which has been estimated at 19.2 - 49.8 g C $m^{-2}yr^{-1}$ export in North American swamps (Davidson et al. 2022). Therefore, future research should include ecosystem scale measures of C exchange in swamps (e.g., eddy covariance towers) to capture the full range of diurnal variation in C exchange and should include hydrologic C inputs and outputs. Research into decomposition and C accumulation rates in temperate mineral and organic swamps will help complete our understanding of the C budget and balance. Despite these limitations, this study provides new, field level data on how C moves through and is stored in temperate swamp systems and highlights that these ecosystem represent locally important stocks of both biomass and soil C. Incorporating these data into C accounting and modelling will help inform future policies of wetland conservation and restoration and management of swamps as natural climate solutions.

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4.6 Supplemental

Figure S4.1 Calculating proportional averages for unknown tree species.

Proportional averages for unknown species were found by

1. Calculate proportion of total stems per species from 20 x 20 m tree surveys
2. Calculate effective density per decay class as per Harmon et al. (2013)
   a. Sum species proportion * decomposition code density for each decay class
   b. Sum the squared average diameter of each log in each decay class
   c. Calculate volume per decay class with line intercept survey formula from National Forest Inventory (2021)
      i. Vk = 3.14^2/8L*sum(d^2)
3. Calculate biomass per decay class
   a. BMk = Vk*densityk

Table S4.1 Historic monthly, annual, and 30-year average precipitation for study period. Green cells indicate months included in growing season. Data obtained from Government of Canada. Weather station location names: 1. Kitchener/Waterloo; 2. Hamilton A; 3. Woodstock; 4. Roseville.

	Precipitation (mm)				Air Temperature (C)			
Month	Ancient Woods[1]	Beverly[2]	Eden Mills[4]	Kintore[3]	Ancient Woods[1]	Beverly[2]	Eden Mills[4]	Kintore[3]
23-Jan	49.4	75.5	80.6	22.5	-2	-1	-2	-1
23-Feb	58.4	85.4	42.4	16	-3	0	-2	0
23-Mar	69.9	117.2	114.7	55.5	-1	0	0	1
23-Apr	85.5	111.8	104.1	43.9	8	8	8	9
23-May	47	39.1	45.3	20.5	12	13	13	11
23-Jun	59.5	115.2	81.9	33.1	17	18	18	17
23-Jul	166.4	123.8	160	52	20	21	21	20
23-Aug	98.1	119	118.4	39.1	18	19	18	19
23-Sep	21.2	25.9	23.5	24.2	16	17	17	17
23-Oct	49.3	61.7	59.4	41	11	12	11	14
23-Nov	41.1	44.2	57.4	17.6	2	3	3	3
23-Dec	67.3	71.9	57.1	20	2	3	2	1
2023 Total	813.1	990.7	944.8	385.4	8	9	9	9
24-Jan	82.4	92.5	61.8	48	-4	-3	-4	-4
24-Feb	14.9	27	22.1	10.8	-1	0	-1	1
24-Mar	66	48.4	48	1.5	3	4	3	6
24-Apr	108	96.5	95.2	42	8	8	8	8

24-May	102.1	90.9	55.8	20	15	15	15	15
24-Jun	81.5	70.3	74.7	11.2	19	19	19	21
24-Jul	149	157	155.3	137.5	20	21	20	21
24-Aug	103.5	71.5	124.6	73.6	19	20	20	20
24-Sep	23.4	55.3	16.8	8.4	17	18	17	18
24-Oct	32	47.4	50.2	6.4	10	11	11	11
24-Nov	43.6	46.2	55.7	17	5	6	5	5
24-Dec	71.4	65.4	91.4	23	-2	-1	-2	-2
2024 Total	877.8	868.4	851.6	399.4	9	10	9	10
30 yr avg.	976	929.8	969	918.7	7	8	7	8

Table S4.2 Summary of site-level environmental variables.

Site	Growing Season						Non-Growing Season					
	Min WT* (cm)	**Max WT (cm)**	**Mean WT (cm)**	**Range (cm)**	**Mean ST 10 cm**	**Mean ST 30 cm**	**Min WT* (cm)**	**Max WT (cm)**	**Mean WT (cm)**	**Range (cm)**	**Mean ST 10 cm**	**Mean ST 30 cm**
Ancient Woods	-99	48	-16.8	147	15.3	14.3	-90	47	-14.9	137	5.74	6.96
Beverly	-60	25	-15.4	85	15.5	14.6	-44	10	-8.15	54	6.14	6.56
Eden Mills	-99	12	-25.2	111	13.5	12.8	-99	0	-30.8	99	4.72	5.94
Kintore	-72	5	-21.6	77	15.5	14.8	-44	6	-7.68	50	5.38	6.01

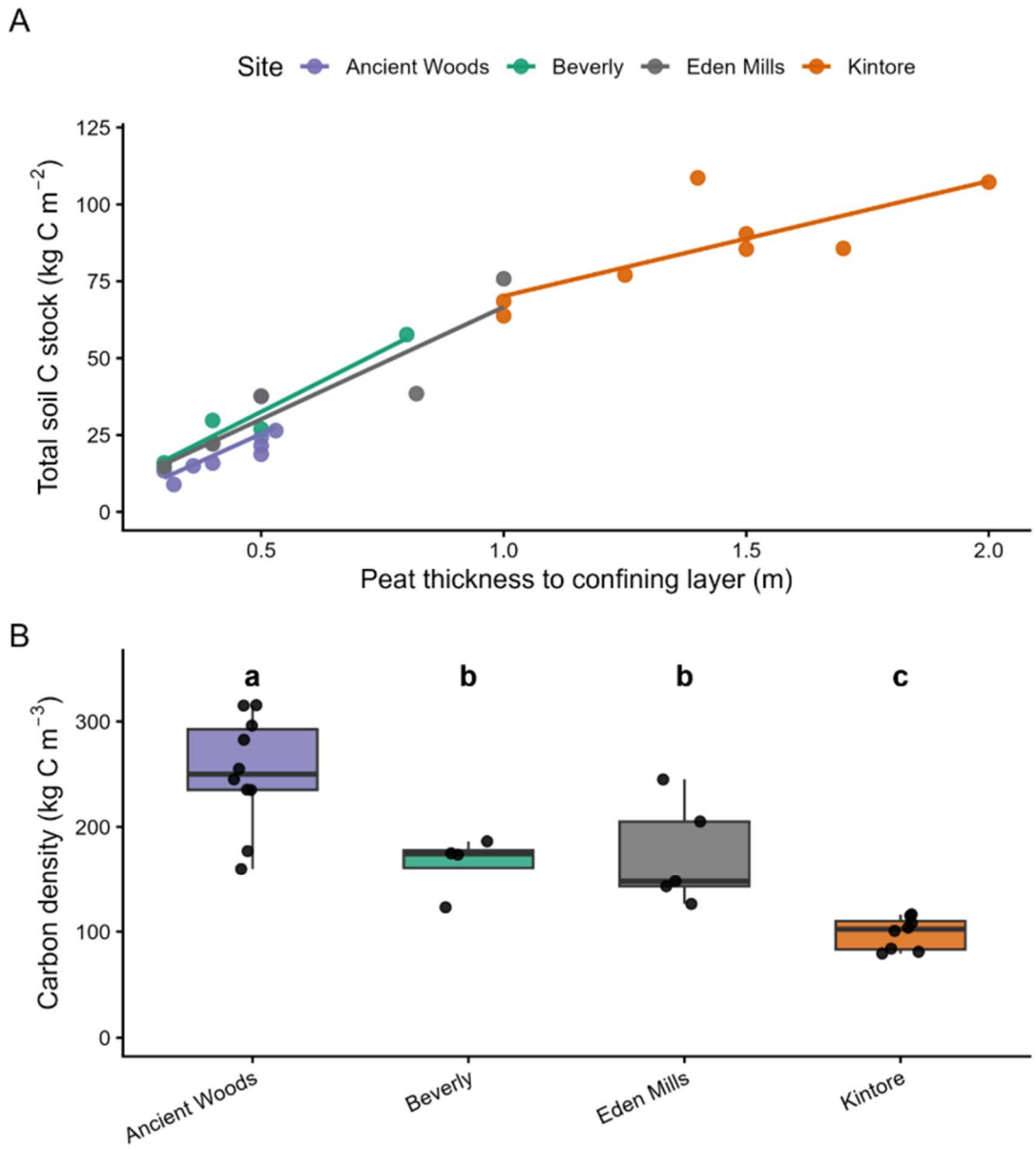


Figure S4.1 Factors influencing C storage in organic soils across sites. (A) Relationship between total soil C stock and peat thickness to the mineral confining layer for individual cores. Points represent individual cores, and lines show site-specific linear fits. (B) C density of organic soils by site, expressed as depth-weighted mean C density per core.

Table S4.4 Average CO_2 and CH_4 fluxes by month per site. CH_4 values are in mg $m^{-2}d^{-1}$, CO_2 values are in g $m^{-2}d^{-1}$.

	Ancient Woods		Beverly		Eden Mills		Kintore	
Month	Mean CH_4	Mean CO_2	Mean CH_4	Mean CO_2	Mean CH_4	Mean CO_2	Mean CH_4	Mean CO_2
January	0.21	0.06	0.07	0.02	-1.42	4.88	0.18	0.18
February	2.01	2.47	0.46	2.32	-0.64	2.70	196.92	0.84
March	777.52	4.38	2.14	4.93	-0.65	1.94	393.67	1.49
April	10.48	3.62	6.77	4.44	-0.91	4.47	9.94	4.44
May	46.41	8.30	6.57	14.90	-0.53	12.87	18.77	10.06
June	549.98	15.17	404.34	24.76	249.22	17.53	317.21	23.56
July	1667.50	16.85	16.32	17.25	-0.36	15.77	4.53	13.33
August	365.67	15.50	9.82	28.95	110.78	19.19	249.98	26.90
September	7.94	24.82	4.35	25.12	-1.50	19.88	-0.54	24.19
October	0.02	11.57	-0.66	18.11	-1.38	11.13	-0.20	11.48
November	2.55	5.35	-0.63	9.23	-1.67	8.33	0.21	3.32
December	6.75	3.72	0.58	2.67	-1.33	4.54	0.58	1.29

Chapter 5

Conclusion

This thesis addressed a critical gap in our understanding of carbon (C) cycling within temperate swamps. Although swamps occupy a substantial proportion of Canada's forested wetlands, they remain poorly represented in estimates of wetland C storage and greenhouse gas (GHG) dynamics (Tarnocai 2006, Byun et al. 2018, Amani et al. 2019). The overarching objective was to quantify soil and vegetation, with a particular focus on trees, carbon dioxide (CO_2) and methane (CH_4) dynamics and C storage across temperate swamps, while identifying the environmental factors controlling these processes.

5.1 Summary of findings

Temperate swamps are a significant but overlooked store of C with the ability to accrue deep organic soils and C rich mineral soils and sequester large amounts of C in tree biomass. Across 12 swamps in southern Ontario (Chapter 2), mineral, mineral-organic, and organic soils stored 11.6 - 35.5 kg m^{-2} of C within the top 50 cm. When sampled to the confining layer, peat depths of 0.2 - 2.0 m contained up to 86 kg C m^{-2} (Chapter 4). Comparatively, average soil C values for upland forests across U.S.A. are ~5.4 kg C m^{-2} (Domke et al. 2017), and estimated soil C across the global upland temperate biome is 9.6 kg C m^{-2} (Lal 2005). Soil was the pool that contained the largest C stocks within the swamps, and variation was driven primarily by differences in peat depth and C density; although C density varied, soil C increased with peat thickness (Chapter 4). Leaf litter was the main input of organic matter to soils and increased with broadleaf tree presence, accounting for 136 – 544 g C m^{-2}. Understory vegetation was the pool that held the least C regardless of community composition at 0.1 kg C m^{-2} or less, and trees and woody debris contained 13 – 25 kg C m^{-2}. In total, C stocks ranged from 46 – 108 kg C m^{-2}, and aboveground biomass far outweighs those of Canadian upland forests at 4.13 kg C m^{-2} (Sothe et al. 2022) and the global temperate biome at 6 – 13 kg C m^{-2} (Lal 2005).

Hydrology and temperature jointly regulated soil CO_2 and CH_4 dynamics. Mean WT and WT fluctuations were often determined by the hydrogeomorphic setting of the swamp and its connectivity to local ground and surface waters. Warmer, wetter soil conditions were conducive to higher CH_4 emissions, while drier conditions and deeper water tables shifted the balance towards CO_2 emissions. These patterns generally followed those of bogs and fens. Very dry conditions in swamps were observed to result in

minor CH_4 uptake by soil, which led to lower emissions in late summer than earlier in the season. Fluxes varied seasonally, peaking in summer and declining to near zero in winter, although they rarely reached zero. Soil C fluxes varied across sites, indicating that site-specific conditions are important to annual soil C exchange.

Trees influenced CH_4 emissions through species-specific transport pathways but rates of emissions also depended on site conditions (Chapter 3). A positive relationship with soil CH_4 flux supports the theory that CH_4 emitted from tree stems primarily originated within the soil and was transported up the stem via both passive and active mechanisms. Tree stems were generally sources of CH_4, with occasional moments of slight uptake, and mean fluxes per tree were 0.029 - 56.33 mg CH_4 m^{-2} of stem d^{-1}. Tree stem emissions followed similar seasonal patterns as soil CH_4 fluxes, peaking in summer and reaching their lowest values in winter, but species rates differed among sites. Overall, maple stems emitted the most CH_4, followed by birch and cedar; due to their different cell structure, gymnosperms transported and release less CH_4 than angiosperms. Stem CH_4 emissions followed the same response as soils to water table and soil temperature, but the magnitude varied among studied swamps. Scaled from area of stem to area of swamp, annual CH_4 emissions ranged from 0.003 g CH_4 (0.002 g C) to 0.41 g CH_4 m^{-2} yr^{-1} (0.31 g C yr^{-1}), up to 70% that of soil flux, offsetting or enhancing emissions throughout the year.

Together, these findings demonstrate that C storage and CO_2 and CH_4 cycling cannot be understood independently. Sites with greater peat accumulation may be able to modulate hydrological regimes that shallower or more mineral soils cannot, thereby influencing both soil CH_4 production and tree stem emissions. Likewise, the interaction between soil temperature and water table affected CH_4 production, while species-specific stem emissions suggest that vegetation influences the pathway by which and at what rate CH_4 reaches the atmosphere.

Most previous studies have investigated either C stocks or GHG fluxes, but relatively few involve both. By combining these, my doctoral research moved from asking “how much C is there?” to “what is the role of swamps in the C cycle?” Carbon stocks represent the cumulative result of long-term C accumulation (decades to millennia), whereas CO_2 and CH_4 fluxes represent C cycling over the short term (hours to years). In measuring both, we can evaluate whether current GHG fluxes are consistent with the large C stores observed in swamp soils, and whether these ecosystems remained relatively stable, lost, or accumulated C over the study period (2022-2025). Wetlands are unique because the same saturated conditions that slow decomposition and promote C storage also create anoxic conditions that favour CH_4

production. Considering only C storage may suggest that swamps have unequivocally climate benefits, while considering only CH_4 might overemphasize their potential contribution to global warming, much like excluding tree stem CH_4 emissions underestimates ecosystem contributions. Additionally, common environmental controls influenced both soil and stem dynamics, thus integrating C storage and GHGs provides a better mechanistic understanding of swamp functions than either dataset alone. The results of my research show, however, that swamps likely cannot be treated as a single ecosystem type. This thesis has shown considerable variability among sites in peat thickness, C stocks, CH_4 emissions, CO_2 respiration and uptake, environmental controls, and species effects. Therefore, grouping swamps with other forested wetlands or peatlands in regional assessments misses these differences.

5.2 Future research needs

Despite the contributions of this thesis, temperate swamps remain among the least studied and understood wetland types with several remaining knowledge gaps. To today, most wetland C research has focused on boreal peatlands, bogs, fens, and tropical wetlands. Temperate forested swamps, particularly in Canada, remain underrepresented. Therefore, we do not know how representative the sites chosen in this thesis are of temperate swamps across Ontario and Canada, or how C dynamics vary across climatic gradients. Although Chapter 2 included 12 swamps across southern Ontario, we do not conclusively know how swamp types differ (hardwood vs. softwood, mineral vs. organic, isolated vs. riparian, etc.). The spatial distribution of swamps across Canada remains uncertain, thus major uncertainties also remain regarding regional and national swamp C storage, peat depth and distribution within swamps, variability in bulk density and C density of peat in swamp soils, and the differences between mineral and organic swamp soils. Some inventories still classify swamps simply as mineral wetlands (ESRD 2015), despite evidence that many can contain peat exceeding 40 cm. As a result, swamp C stocks may be underestimated even when included in inventories.

This thesis measured CO_2 and CH_4 fluxes over a combined 3.5 years (June 2022 – Dec 2025), but this is still a relatively short time. To more accurately predict long-term GHG budgets, longer and more frequent studies are needed to examine interannual variability, responses to weather extremes such as drought and extreme precipitation events, shoulder-season and winter fluxes, freeze-thaw dynamics, and responses to long-term climate trends. Water table depth is often treated as the dominant environmental control, but swamps are highly complex systems and capturing the impact of duration of flooding, lateral groundwater inputs, surface water connectivity, preferential flow paths, microtopography, and short-term

hydrologic events would improve process-based understanding of GHG dynamics and ultimately flux predictions.

Studies on tree-mediated CH_4 transport and stem CH4 emissions have increased exponentially over the last few years, but many questions remain. The literature is still unclear on why some species emit much more CH_4 than others and what anatomical traits control it, and the role of sap flow and transpiration in CH_4 transportation (Pangala et al. 2015, Barba et al. 2019, Gauci 2025). Due to the lack of studies that integrate soil and stem fluxes, it is unclear how important stem emissions are relative to soil emissions.

Perhaps one of the greatest remaining challenges is in scaling measurements. While scaling soil emissions is relatively straight-forward, they do not always account for heterogeneity in understory vegetation, groundcover, shading, etc., that create spatial variability in fluxes. Additionally, assumptions are made about soil moisture, C content, soil depth, and the resulting C fluxes. Scaling tree stem fluxes is even more complicated as the steps require many measurements and estimates. Specifically, moving from chamber to stem requires tree diameters and height; from tree to stand requires detailed surveys on stand species composition and density. All these calculations also involve assumptions about representativeness of available stem flux measurements in space and time. Upscaling from stand to landscape and regional scales requires estimates of areal extent and swamp characteristics such as hydrogeomorphic setting, canopy, and stand composition. Eddy covariance measurements in swamps could help overcome some of these issues by directly measuring the combined effects of soils and trees on ecosystem scale C cycling. However, this combined approach limits our ability to understand environmental controls on individual processes as I have been able to do here. Therefore, this will require combining field measurements with remote sensing, airborne surveys, and ecosystem modelling.

As temperature and hydrology are such strong controls on C cycling, future climate change and land-use disturbance such as drainage for agriculture or conversion to urban land-use could substantially alter swamp GHG budgets. This leads to questions such as how swamps will respond to warmer temperatures, lower summer water tables, more frequent drought, extreme precipitation, changing snowpacks, and altered growing seasons. Without adequate information on how swamps function in the present, it becomes nearly impossible to predict how they will react in the future or support management of swamps as natural climate solutions. To inform management and policy decisions related to how swamps should be incorporated into national GHG inventories, and whether swamps should receive the same protections as peatlands future research should consider which swamps store the most C, which are most vulnerable

to C loss, and how drainage and restoration alter GHG emissions. While this thesis has started to fill some of these gaps for temperate swamps, boreal swamps also remain largely understudied and require attention in future research.

Taken together, these gaps indicate that temperate and boreal swamps remain disproportionately understudied relative to their potential importance in regional carbon cycling. While this thesis advances understanding by linking peat C storage with soil and tree GHG fluxes, significant uncertainties remain regarding the spatial variability of C stocks, the mechanisms regulating CH_4 production and transport in soil and trees, long-term responses to climate and land-use change, and the scaling of plot-level measurements to landscape and national carbon budgets. Addressing these gaps will be essential for accurately representing swamps in carbon accounting frameworks and for assessing their potential role in climate change mitigation and adaptation.

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