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The unrecognized importance of carbon stocks and fluxes from swamps in Canada and the USA

Running Head: Carbon dynamics from Canadian and US swamps

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Swamp, forested wetland, carbon flux, organic matter, carbon stocks

Abstract

Swamps are a highly significant wetland type in North America both in terms of areal extent and their role in terrestrial carbon cycling. These wetlands, characterized by woody vegetation cover, encompass a diverse suite of ecosystems, including broad-leaved, needle-leaved, mixedwood or shrub/thicket swamps. Uncertainties in the role of swamps in carbon uptake and release continue to be substantial due to insufficient data on variabilities in carbon densities across diverse swamp types and relatively few flux measurements from swamp sites. Robust measurements of rates of vertical accretion of swamp soils and the associated long-term rates of carbon accumulation, alongside measurements of carbon losses from swamps, are needed for emerging frameworks for carbon accounting, and for assessments of the impacts of climate warming and land use change on this important wetland type. Based on data compilation, we present here a comparative analysis from a series of North American swamp sites on carbon dioxide, methane and dissolved organic carbon fluxes, aboveground biomass, net primary productivity, and soil carbon properties including bulk densities, organic carbon contents, peat depths, rates of vertical accretion, and rates of long-term carbon accumulation. We compare these properties for four major swamp types: needle-leaved, broad-leaved, mixedwood and shrub/thicket swamps. We show differences in carbon fluxes, biomass and NPP across the four types, with broad-leaved swamps having the largest CH_4 flux, highest soil bulk densities, thinnest peat depths and lowest soil organic matter contents, whereas needle-leaved swamps have the smallest CH_4 flux, highest aboveground biomass and highest NPP. We show high soil carbon stocks (kgC m^{-2}) in all types of swamps, even those where organic deposits were too shallow to meet the definition of peat. However, we note there is a significant lack of studies focused on swamp carbon dynamics despite their abundance across Canada and the United States.

1.0 Introduction

Wetlands are a key component of the terrestrial carbon cycle and important for climate change mitigation (e.g., Humpenöder et al., 2020). Swamps can make up large areas of wetland regions across Canada and the USA and yet are vastly understudied in comparison to other wetland types. There are also large variations in the literature with regards to the definition of what a swamp is and what classification they fall under – peatland, non-peatland (mineral) or both, although many agree that swamps are wetlands with at least 25% tree cover (e.g., Nahlik and Fennessy 2016, National Wetlands Working Group. 1997; AWI 2018).

In swamps, also known as treed/shrub wetlands, the presence of hydric soil conditions, wetland-adapted vegetation and anaerobic microbial communities significantly influence not only the amount of soil carbon present but the different pathways for carbon fluxes and rates of transfer (Trettin and Jurgensen, 2003). For example, the typical high-water tables found in swamps can lead to increased carbon storage through reduced decomposition (Middleton, 2020). However, higher water tables are also conducive to higher methane (CH_4) production and emissions in comparison to some other wetland types such as bogs (Moore and Knowles, 1989). The variable nature of the hydrology of these systems can also result in dynamic dissolved organic carbon (DOC) export rates (Mulholland, 1981). Swamps typically have high tree cover, therefore can typically have greater above and belowground biomass and larger rates of net primary productivity (NPP) in comparison to other treed wetland types such as bogs and fens. Furthermore, this also means they can have increased levels of litter input in comparison to other wetland types (Stoler and Relyea, 2019), leading to higher rates of carbon input and consequently, high rates of organic matter accumulation.

Swamps have been documented to occupy a substantial portion of wetland area in North America, although spatial distribution maps cannot be explicit yet due to varying regional definitions and potential overlaps with other wetland types. For example, in the conterminous United States, it is estimated that swamps make up approximately 49% of the wetland area, while in Alaska, shrub-dominated wetlands make up approximately 68% of the wetland area, with forested wetlands only covering approximately 8% (Hall et al., 1994). For Canada, swamps may represent the second most abundant wetland class, at nearly 9% of wetland landcover, second to marshes (~ 12%) (Amani et al. 2019). Furthermore, Riley (1994) note that peat-forming conifer swamps are the dominant wetland type in northern Ontario, accounting for nearly 40-60% of the peatland area. Yet, Tarnocai (2006) estimates that swamps cover only 1% of the total Canadian wetland area. In southern Ontario, where wetland drainage and anthropogenic impacts are widespread, the current 'tree swamp' cover is estimated about 76% and 'shrub swamp' is 11% in spatial cover (Byun et al 2018). Given the overall significant areal extent of these wetland types, it is imperative that we improve on the state of our current knowledge of carbon cycling in swamp wetland systems.

Despite the significant spatial extent and importance in regional carbon cycling, swamps are largely missing from national and global greenhouse gas inventories. In Canada, for example, the recently developed Canadian Model for Peatlands (CaMP, Bona et al., 2020) tracks carbon fluxes for 11 different peatland types. However, because of insufficient data to parameterize or calibrate the model for swamps, they are not included in the final estimates (Bona et al., 2020). Additionally, Canadian peatland mapping products used in the CaMP model do not map swamp distributions at the national scale (Webster et al., 2018). Available estimates from US national wetland inventories indicated that shrub-dominated or forested wetlands, classes in which swamps would be included, are highly significant in terms of soil carbon storage (Nahlik and Fennessy, 2016), although there remain important gaps in available data on both quantity and types of organic matter present in swamp soils. Similarly, recent datasets of boreal and arctic lake and wetland CH_4 flux and area were unable to include swamps as their own category, lumping them with other wetland types, largely due to a lack of CH_4 data but also due to the wide range of hydrological and nutrient conditions across swamp types (Kuhn et al., 2021; Olefeldt et al., 2021). Without clear understanding of swamp carbon stocks and fluxes and how they vary from other wetland types, particularly bogs and fens with which they are currently grouped in many datasets and models, the potential error in regional estimates of present and future carbon exchange will remain unknown.

Therefore, given the documented large but potentially poorly constrained spatial extent of these ecosystems across both Canada and the USA, a better understanding of variability in carbon stocks and fluxes in is required to support both future improved wetland mapping and climate and earth system modelling efforts. Thus, this study compares vegetation biomass and net primary productivity, carbon dioxide (CO_2) and methane (CH_4) fluxes, dissolved organic carbon (DOC) concentration and export, and soil carbon stocks from four distinct swamp typesacross Canada and the United States. We aim to answer the following questions: (1) How variable are C fluxes and stocks among swamp types; (2) How do swamp C fluxes and stocks compare to other wetland and upland ecosystems; and (3) What are the most significant research needs to better quantify the role of swamps in the global carbon cycle?

2. Methods and Materials

2.1 Classification of swamps

The Canadian Wetland Classification System (NWWG, 1997) defines swamps as belonging to both mineral and organic wetland classes. However, the provincial Alberta Wetland Inventory (AWI, 2018) classifies a swamp as ‘a mineral wetland with water levels near, at or above the ground surface for variable periods during the year which contains either more than 25% tree cover of a variety of species or more than 25% shrub cover’. A similar definition is used by the Province of Québec, where organic treed wetlands (non-bog or fen) are defined as peatlands (Bazoge et al., 2014). Definitions of swamps used in the Province of Ontario also emphasize >25% tree or (Riley 1994; Government of Ontario, 2014) or tall-shrub cover, and soils may be either mineral or organic (NWWG, 1997). In the United States, swamps are often classified simply as a forested wetland (Cowardin et al., 1979) or by any number of names including palustrine forested wetland, palustrine shrub wetland, vernal pools, bottomwood/bottomland or floodplain forests. These discrepancies likely occur because swamps are often categorized based on their tree cover and can be easily mis-classified as uplands or other treed wetlands i.e., bogs or fens (Locky et al., 2005). Species that can be strictly found only in swamps in some regions may be found in upland regions in others, further confusing the classification of swamps. Furthermore, swamps can exhibit seasonal water table fluctuations (Zoltai and Vitt 1995; Devito and Mendoza, 2007) that can lead to their misclassification as fens or other treed wetlands.

Therefore, we have not created a new classification of swamp types, rather we relied on original author descriptions or classifications, placing each site into one of four dominant swamp type categories defined based on dominant vegetation cover. These categories include broad-leaved swamps, needle-leaved swamps, mixedwood swamps co-dominated by a mixture of broad-leaved and needle-leaved species, and shrub or thicket swamps dominated by tall shrubs (Table 1, Figure 1). Swamps included in this synthesis may either be on mineral or organic soil. Our study is focused on only freshwater swamps/forested wetlands; therefore, mangrove forests were excluded from our data search. We focus exclusively on freshwater swamps because coastal processes and marine influence add considerable variability in terms of gas fluxes, sediment accretion and carbon accumulation (Rovai et al., 2018) and would invalid comparisons with freshwater swamps.

2.2 Data collection for carbon fluxes, vegetation biomass and net primary productivity (NPP)

To locate all papers that have reported soil carbon dioxide (CO_2), methane (CH_4) fluxes, dissolved organic carbon (DOC), vegetation biomass and above/belowground net primary productivity (NPP) from swamps and forested wetlands (not explicitly classified as bogs or fens), we performed a comprehensive search on Web of Science (accessed between September 2019 and November 2020) using the key words: “methane” OR “CH_4” OR “carbon dioxide” OR “CO_2” OR “dissolved organic carbon OR “DOC” OR “net primary productivity” OR “NPP” OR “net primary production” OR “biomass” OR “swamp” OR “forested wetland” OR “slough” OR “forested hollow” OR “forested pool” OR “vernal pool” OR “forested peatland” OR “wooded pond” OR “pocosins” OR “carr”. We also checked references within relevant papers and book chapters and utilized summary tables provided. Only studies using the static chamber method were used for summaries of soil CO_2 and CH_4 flux due to a lack of studies using the eddy covariance technique in swamp ecosystems. This resulted in 15 papers for CH_4 fluxes, 6 papers for CO_2 fluxes, 7 papers for DOC and > 20 papers for NPP/biomass across both Canada and the United States. We extracted information on wetland type and location. When the data were presented in figures, mean values and standard error were extracted using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/). Carbon dioxide fluxes were converted to g CO_2 m^{-2} d^{-1} and CH_4 fluxes were converted to mg CH_4 m^{-2} d^{-1} for consistency. Due to limited year-round data, we only present data from May – September where possible. Some studies report biomass and productivity only for the forest stand in the swamp (e.g., Conner and Day, 1976; Megonigal and Day, 1988; McKee et al., 2013); however, as the overstory tree or tall shrub layer in swamps accounts for over 90% of aboveground biomass and at least 80% of aboveground NPP (Reader and Stewart, 1972; Parker and Schneider, 1975), reported values will only slightly underestimate the ecosystem totals. In contrast, in bald cypress swamps, cypress knees can represent up to 17.9% of the total aboveground biomass carbon stock, illustrating the importance of including all biomass components for the tree layer (Middleton, 2020).

2.3 Data collection for soil carbon

A dataset was compiled to compare swamp soil properties across the four swamp types. The data were extracted mainly from three databases: a wetland database for the Western boreal, subarctic, and arctic regions of Canada (ZDB) (Zoltai et al., 2000), surveys of peat and peatland resources for southeastern, northwestern and northeastern Ontario (RDB) (Riley 1994a, b; Riley and Michaud, 1989) and the Neotoma Paleoecology Database (NDB) (Williams et al., 2018). Swamp classification systems used in ZDB and RDB included the four swamp types considered here and original classifications were applied. In addition to the 24 sites classified as swamps in ZDB, a sub-set (N = 75) of sites not named as "swamps" but classified as "forested fens" or "forested bogs" were included for comparison, recognizing that a consistent terminology is lacking. To identify NDB sites corresponding to swamps or forested wetlands, the "advanced" search menu was used with the following settings: "collection type" was set to "core"; "deposit" was set to include "swamp", "tidal freshwater forested wetland", "slough", "small hollow" or "vernal pool". Further, all sites with site names containing any of the following terms were also reviewed: "swamp", "forested wetland", "slough", "forested hollow", "forested pool", "vernal pool", "forested peatland", "wooded pond", "pocosin" or "carr". The full list of sites included, and original references, are found in the Supplementary Information. The NDB sites were placed into one of the four swamp types based on author descriptions in the original publications.

All sites used for comparisons of swamp soil properties included some combination of bulk density (BD, g cm^{-3}), percent organic matter (%OM), ash content (%), percent organic carbon (%OC), percent total carbon (%TC), qualitative descriptions of sediment type (peat vs mineral soil), peat depth (cm) and age-depth relationships derived from radiocarbon dating. For each core, mean/median/standard deviation/maximum/minimum/inter-quartile range (IQR) values were calculated or extracted from original sources for BD, %OM, %OC. Only direct measurements of %OC are reported; no conversions were done from %OM. Ash content was converted to OM% using the relationship Ash% + OM% = 100%. Then, the means of each variable from each core, and peat depths, were used to consider variability in peat properties within and between the four swamp categories (Table 1). We report mean BD, mean OM/OC/TC and mean peat thicknesses (cm) for the swamp peat sections (>30% OM) in the available cores for each swamp category. Mineral sections with <30% OM were not included in these comparisons to facilitate comparisons with other peat-forming wetlands. Because core sections with <30% OM may still contain important carbon stocks and considering the difficulties in defining the boundaries of swamp peat within cores without detailed macrofossil or other palaeoecological analyses, we also report mean values for BD, %OM, and %OC by depth, 0-30 cm, 30-60 cm, 60-90 cm, and 90-120 cm, for the entire profiles (including both mineral and organic sections) for each swamp type, after Nahlik and Fennessy (2016). These mean values by depth also include sections of the soil cores that do not meet the definition of peat, and thus we are capturing both mineral and organic swamp soil types. Carbon stocks were calculated for each section by multiplying organic carbon densities (g C cm^{-3}) by depth intervals (cm) and converting to the standard units of kgC m^{-2} or t ha^{-1} (Howard et al., 2014). Carbon densities are defined as the product of BD (g cm $^{-3}$) and %OC.

When age-depth relationships were available, from radiocarbon or other radioisotope dating, rates of vertical accretion (cm yr^{-1}) were calculated for the swamp peat sections. The mean peat accretion rate (cm yr^{-1}) was calculated for each core from the lowermost age control point and associated depth. In the cases where this information as well as bulk density and organic matter content were available, average long-term apparent carbon accumulation rates (aCAR, g C m^{-2} yr^{-1}) were calculated using basal ages of the swamp peat sections of the core (Chambers et al. 2010).

2.4 Data analysis

All analyses were performed in R 3.5.3 (R Core Team, 2019). Analysis of variance (ANOVA) and post-hoc Tukey tests (*Lsmeans*; Lenth, 2016) were used to determine statistical significance of any differences between the swamp peat core sections from the four swamp types in terms of bulk density and organic matter content. Linear regressions were used to look at relationships between water table depth and both NPP and CH_4 fluxes. Only three of the studies looking at CO_2 fluxes reported water table depth so no relationship could be calculated.

3. Results

3.1 Vegetation biomass and net primary productivity (NPP)

Most data for biomass and NPP in swamps has been collected in the eastern United States in warm temperate to sub-tropical environments, with only approximately 10% of the records north of 40°N (Figure 2A). Due to this geographic distribution, needle-leaved swamps in this dataset were dominated by bald cypress. Average aboveground biomass was greatest in needle-leaved swamps (21.4 ± 13.2 kg m^{-2}), followed by broad-leaved (20.1 ± 10.1 kg m^{-2}) and mixedwood (19.3 ± 12.0 kg m^{-2}) swamps, with shrub/thicket swamps having on average less than one quarter of the aboveground biomass of the forested swamps (Table 2).

Aboveground NPP was more similar between swamp classes with average values of 0.91, 0.94, 1.03, and 1.57 kg m^{-2} yr^{-1} for shrub, mixedwood, broad-leaved, and needle-leaved, respectively. We found a negative relationship between depth of water table and NPP (Figure 3), with NPP decreasing as water tables become shallower.

Few studies have measured belowground biomass in swamps. We found only six studies (all needle-leaved swamps), reporting data from 12 stands with an average across all swamp types of 1.8 kg m^{-2}. This represents less than 10% of total biomass in treed swamp classes. Belowground NPP was measured in only three studies (needle-leaved swamps only) across seven stands with an average value of 0.21 kg m^{-2} yr^{-1}.

3.2 Carbon dioxide (CO_2) and methane (CH_4) fluxes

Very few studies have looked at soil CO_2 fluxes from swamps (7 studies across 13 sites: Figure 2B) (Table 3). Largest emissions were found from a mixedwood swamp in southern Ontario, Canada with a growing season mean flux of approximately 12.5 ± 15.6 g CO_2 m^{-2} d^{-1}. Only one study from Kendall et al. (2020) in Nova Scotia, Canada, looked at CO_2 flux from both broad-leaved and needle-leaved swamps and found growing season soil CO_2 fluxes of 1.4 ± 0.8 and 0.63 ± 0.1 g CO_2 m^{-2} d^{-1} respectively.

Similarly, soil CH_4 flux measurements from swamps are also lacking (Table 4). We found only 15 studies (covering 23 sites: Figure 2B) reporting soil CH_4 fluxes. Furthermore, there is a distinct lack of studies from broad-leaved, needle-leaved and shrub/thicket swamps, with mixedwood swamps dominating the literature with 13 sites (Figure 2). The largest CH_4 flux was found to come from broad-leaved swamps with a growing season mean flux of 126.5 ± 33.9 mg CH_4 m^{-2} d^{-1}. Needle-leaved swamps had the lowest mean flux at 13.5 ± 10.3 mg CH_4 m^{-2} d^{-1}. The largest fluxes from all swamp types came from swamps located in the temperate to sub-tropical regions of southeastern USA, with average fluxes becoming smaller as you move further north towards the boreal zone. However, the one shrub/thicket study from Roulet et al. (1992) noted a flux of approximately 34.9 mg CH_4 m^{-2} d^{-1} from a site in northern Ontario. Nearly all sites were a source of CH_4 to the atmosphere during the growing season. In line with many studies looking at CH_4 emissions from wetlands (Calabrese et al., 2021), CH_4 fluxes increased with increasing water table level (Figure 4); however, this relationship is based on a limited dataset as unfortunately not every study reported water table depth.

3.3 Dissolved organic carbon (DOC) concentration and export

Comparing DOC concentration among studies was complicated by the different sampling methods applied. Some studies monitored DOC only in surface water during flooded periods (Battle and Golladay, 2001), others in stream water (Galloway and Branfireun, 2004) and others in soil pore water. When measured in soils, the depth of measurement varied (see Table 5). Comparing across these varied samples, average DOC concentration in swamp soil pore water was 11.1 to 86.7 mg L^{-1} across 10 study sites. Surface water concentrations were generally lower and less variable at 15.2 to 27.1 mg L^{-1}.

We found three studies reporting net DOC export from six swamps (Mulholland, 1981; Devito et al., 1989; D'Amore et al., 2015) with an average of 30.6 g C m^{-2} yr^{-1} (Table 5). As hydrology varies between swamps, care must be taken to account for both DOC inputs and outputs to the swamp in order to determine the DOC load attributable to the swamp alone (i.e., net DOC export).

3.4 Soil carbon stocks

A total of 247 swamp cores were used for comparisons of soil properties (Table S2). All swamp types have high carbon densities, reflecting a combination of high organic matter contents and/or high bulk densities (Table 6); mean bulk densities are typically higher than those reported for northern bogs and fens (Loisel et al., 2014). Comparisons by ANOVA and post-hoc Tukey tests indicate that broad-leaved swamps have significantly higher bulk densities than the other three swamp types (F = 16.1, df = 4, p <0.01) and lower organic matter contents (F = 13.6, df = 4, p <0.01) (Figure 5). Other swamp types were not statistically different from each other in terms of bulk density or organic matter content.

Of the four swamp types considered here, needle-leaved swamps have the highest rates of peat vertical accretion. Peat vertical accretion is an order of magnitude lower in broad-leaved swamps, and peat depths are also lowest in broad-leaved swamps (Table 6). Mixedwood and needle-leaved swamps are similar in terms of soil properties, but mixedwood swamps are less abundant in the dataset. Shrub/thicket swamps had lower peat depths than needle-leaved or mixedwood swamps, and no data were available to calculate accretion rates. Lower above-ground biomass in shrub/thicket swamps (Table 2) may result in lower organic matter inputs, contributing to lower peat depths. The non-swamp forested wetlands in the ZDB (consisting of forested fens and bogs), have significantly lower bulk densities (Figure 5; ANOVA F = 12.9, df = 4, p <0.01) than sites explicitly classified as broad- and needle-leaf swamps but organic matter contents are not distinct from other swamp types.

Swamp of all kinds hold significant soil carbon stocks (Table 7). The average 0–90 cm carbon stock for four swamp types reported here ranges from 53.8–70.3 kgC m^{-2}, with a mean of 64.5 kgC m^{-2} (Table 7). This is close to the reported mean carbon stock (61.5 ± 6.3 for 0–100 cm, kgC m^{-2}) for 65 freshwater inland organic soil wetlands (Nahlik and Fennessy, 2016), however the sites of Nahlik and Fennessy (2016) includes all types of inland organic-soil wetlands, not just swamps.

4. Discussion

This study synthesizing swamp carbon stocks and emissions from a range of sites across Canada and the United States clearly indicates that these ecosystems are important components of the terrestrial carbon cycle. For example, swamp aboveground biomasses (Table 2) are clearly larger than other wetland types such as treed bog and fen (1.2 – 2.3 kg m^{-2}) or marsh (~1.2 kg m^{-2}) (Bona et al., 2018). Also, aboveground NPP are larger in swamps than reported for fens (0.2-0.4 kg m^{-2} y^{-1}), bogs (0.3-0.4 kg m^{-2} y^{-1}), and marshes (~1.2 kg m^{-2} y^{-1}) (Bona et al., 2018). Growing season bog and fen CH_4 fluxes from a range of Canadian sites are comparable to mixedwood and shrub/thicket swamp sites at 35.8 and 40.8 mg CH_4 m^{-2} d^{-1}, respectively (Table S1; Webster et al. 2018) but smaller than broad-leaved swamps. Swamp soil carbon stocks are clearly larger than forest soil carbon stocks at 4–5 times greater than the average soil values for all forest soils in conterminous US (Domke et al., 2017). The summarized carbon values for the swamps (Figure 6) can be compared to the other ecosystems (Table S1).

While we are unable to determine how representative the sites are, our results provide key information for the next steps in quantifying the role of swamps in regional and national carbon cycling. Furthermore, until we have a better understanding of the spatial distribution of swamps across North America, we do not know the full extent of conditions pertaining to climate and local hydrology that promotes the development of these wetlands (see Figure 2 for distribution of studies). This makes a full assessment of the representativeness of existing studies difficult, if not impossible. Thus, the following discussions mostly focus on the comparison among four types of swamps and recognize knowledge gaps for future studies.

4.1 Vegetation biomass and aboveground NPP

The mean aboveground biomass from the compiled swamp database of 194 t ha^{-1} (19.4 kg m^{-2}) falls within the broad range of mature forest biomass of 33 to 982 t ha^{-1} (average 355 t ha^{-1} = 35.5 kg m^{-2}) determined from compiled forest inventory data across the United States and Canada (Zhu et al., 2018). NPP depends on stand age, declining as forests reach maturity (Kurz et al. 2013; Zhu et al., 2018); average NPP in Canada’s managed forests were estimated as ~0.35 kg C m^{-2} yr^{-1} (Stinson et al., 2011), lower than the mean value from the compiled swamp data of 1.1 kg m^{-2} yr^{-1}, or ~0.55 kg C m^{-2} yr^{-1} assuming 50% C content in biomass. As mentioned above, swamp aboveground biomass and NPP were higher than the mean wooded bog and wooded fen aboveground biomass illustrating the taller trees and denser cover of woody vegetation that define swamps in comparison to other wetland classes. Forest biomass increases with increasing mean annual temperature and precipitation (Zhu et al., 2018) and this is likely also the case for swamps. However, Megonigal et al. (1997) observed that swamp NPP had a negative relationship with the depth of inundation likely due to stress causes by anoxic soil conditions. We observed a similar trend across the compiled aboveground NPP data for sites that also reported water table position (Figure 3). Given that most of the biomass measurements in the literature are from south of 40°N (Figure 2), the mean value presented here is likely an overestimate of biomass in cool temperate and boreal swamps. This illustrates the need for better characterization of northern swamp biomass and NPP.

Belowground biomass made up a relatively small proportion of total biomass in swamps, resulting in a belowground:aboveground biomass ratio of 0.1:1, but this is based on a small number of studies. This is smaller than ratios determined for generic forests (Li et al., 2003). In some peatland ecosystems, belowground biomass may exceed aboveground biomass (e.g., Murphy et al., 2009). Shallow water table position or flooded conditions likely limit root growth in swamps, resulting in shallow rooted trees. However, more research is needed to better quantify belowground biomass and NPP, including contributions of understory species.

4.2 CO_2 and CH_4 fluxes and DOC export

Due to the distinct lack of soil CO_2 flux measurements in the literature, it is difficult to present a full understanding on dynamics of CO_2 fluxes from swamps (see Figure 2 for lack of spatial representation). As with other wetland types, the hydrological condition of swamps is likely a strong control on CO_2 emissions. High water tables can lead to a reduction in CO_2 production and lower emissions (Davidson et al. 2019). Conversely, as water table levels drop, CO_2 emissions may increase as the oxic zone within the soil column increases. Soil temperature is also a strong control on CO_2 emissions from wetland soils (Gutenberg et al. 2019). Unfortunately, there is a distinct lack of ecosystem scale C exchange measurements in swamps, therefore it is difficult to estimate the total C exchange from these ecosystems, especially as the studies compiled in this synthesis is not looking at carbon uptake of the understory vegetation and the exchange with the trees (especially as root respiration is likely present).

From the published literature, CH_4 emissions were substantially higher (mean emissions: 85 mg CH_4 m^{-2} day^{-2}) in broad-leaved swamps compared to other swamp classes (mean emissions: needle leaved: 11.2 mg CH_4 m^2 d^1 and mixedwood: 35 mg CH_4 m^{-2} d^{-1}). This could be due to several different reasons including the majority of swamps being found in temperate and subtropical locations, leading to warmer soil temperatures. Furthermore, the deciduous species found in broad-leaved swamps are likely to generate greater amounts of more labile litterfall, which can increase CH_4 production and emissions (Amaral and Knowles, 1994; Kang and Freeman, 2002; Koh et al., 2009). One of the strongest controls on CH_4 production and emissions is water table position (Calabrese et al. 2021), with the highest production being found in the anoxic zones of submerged soils (Abdalla et al., 2016). Swamps can often be inundated or flooded for significant periods of the year (Day et al., 1988; Day and Megonigal, 1993), causing anoxic soil conditions and leading to increased rates of both CH_4 production and emissions. However, this relationship can be quite complex (Moore and Knowles, 1989). Water table position within the soil column is of critical importance in controlling CH_4 emissions (Moore and Knowles, 1989; Davidson et al., 2019). Although both CH_4 fluxes and water table depths from the literature are lacking, we did find a relationship between increasing water table depth (i.e., water tables close to or above the surface of the ground) and larger CH_4 fluxes (Figure 4). Swamps can also often have higher CH_4 emission rates than other peatland types due to the presence of permanent open pools of water (Bubier et al., 1995). However, these flashy hydrological conditions that often occur in swamps can also allow for significant dry periods throughout the year, leading to increased levels of CH_4 oxidation (Megonigal and Schelsinger, 2002; Koh et al., 2009). In river-floodplain swamps, the mixing of oxygen-rich river water into the water column following flooding may also result in lower emissions, reducing methanogenesis (Pulliam, 1993; Koh et al., 2009).

Although numerous studies across the world are now highlighting the importance of wetland trees as a source or sink of CH_4 (Pangala et al., 2013, 2015; Covey and Megonigal 2018), there are a lack of studies on tree CH_4 dynamics in swamps across Canada and the United States, therefore we did not include them in this study. However, there is a potential for tree emissions to enhance the overall CH_4 emissions from swamps, acting as a conduit for plant-mediated transport of CH_4, similar to aerenchymatous vegetation such as sedges (Whalen, 2005). Tree emissions are typically from living trees; however, it can be challenging to distinguish between the source of methanogenesis and whether the trees themselves are producing CH_4 or whether they just act as a conduit (Covey and Megonigal 2018). It was estimated that CH_4 emission rates from *Taxodium distichum* (bald cypress) knees in a swamp in North Carolina was approximately 2.3 μmol CH_4 m^{-2} stem h^{-1} (Pulliam and Meyer, 1992).

Comparison of DOC concentration in soils among studies is complicated by the different sampling designs employed (i.e., timing of measurements, depths samples, etc.). With that in mind, mean soil DOC concentrations in swamps, 9.1–86.7 (Table 5) is slightly lower, but generally within the range of mean values, 36–78 mg L^{-1}, reported for bogs and fens in North America (McKnight et al., 1985; Moore, 2003; Kane et al., 2010; Khadka et al., 2016; Orlova et al., 2020). Although few studies report swamp-specific DOC export, available values of 19.2 to 49.8 g C m^{-2} yr^{-1} are on the high end of those reported for fens and bog with mean values in North America of 5 and 22 g C m^{-2} yr^{-1}, respectively (Evans et al., 2016). Thus, swamps play an important role in fluvial carbon exports and several studies report that catchment scale DOC export is well-correlated to wetland area in regions where much of the wetland area is made up of swamps (Creed et al., 2008; O'Connor et al., 2009; Casson et al., 2019).

4.3 Soil carbon stocks

Swamps, especially peat swamps, can have substantial organic matter accumulation due to persistent waterlogged conditions and slower decomposition rates compared to the surrounding upland forest. For example, Byun et al. (2018) showed that conifer (needle-leaved) swamps have the largest soil carbon stock of wetland types in Southern Ontario (Canada) and have higher peat carbon densities than average northern fens and bogs (Loisel et al., 2014). This likely relates to higher bulk densities as long-term rates of peat vertical accretion in needle-leaved and mixedwood swamps (0.03 – 0.04 cm yr^{-1}, Table 6) are similar to typical values from northern bogs or fens (e.g., Bysouth and Finkelstein, 2020). The high rates of peat vertical accretion with the deeper peat deposits in needle-leaved and mixedwood swamps (Table 6) may result from a combination of acidic leaf litter, recalcitrance of needle leaves, and associated plants that promote peat accumulation, including *Sphagnum* mosses in boreal regions (Le Stum-Boivin et al., 2019). The proportional abundance of needle-leaved vs. broadleaved trees used to distinguish between "mixedwood", and "needle-leaved" swamp varies (i.e., Dahl and Zoltai 1997). Thus, inconsistencies in criteria used to define these swamp types could relate to the similarity between these two categories in terms of soil properties.

The broad-leaved swamps considered here were distinct from the others swamp types in terms of higher bulk densities and lower organic matter contents (Table 6; Figure 5). These trends may reflect the more readily humified leaf litter produced by broad-leaved trees, and the hydrological setting. Broad-leaved swamps are often characterized by seasonal inundation, with pooling water early in the growing season related to snowmelt and runoff in some regions, thus adding inorganic material to the soil profile. Surface runoff is also likely important for other swamp types as well; many swamps are situated in either riparian, coastal or bottomland settings. The combination of high bulk densities and persistence of anoxic conditions for at least part of the year results in high carbon stocks for the upper parts of the profiles in broad-leaved swamps (Figure 5). Overall peat depths and organic matter contents are lower in broad-leaved swamps, likely as a result of seasonal declines in water table position and oxic conditions conducive to decomposition and CO_2 fluxes. Nevertheless, we show that even "mineral swamps" may contain significant carbon stocks, particularly when deeper soil profiles are taken into consideration. Paleoecological studies of long-term swamp development show the importance of ecological succession and long-term hydroclimatic change, resulting in variability in swamp substrates at depth (Whitehead, 1972; McLachlan and Brubaker, 1995; Byun et al., 2021). These processes can ultimately result in significant carbon stocks underlying present day swamps of all types.

A comparison of the available data on above-ground biomass in swamps (Table 2) with the soil carbon stocks (Table 7) corroborates the findings of Beaulne et al. (2021) that soil carbon stocks in forested boreal peatlands are several-fold higher in than those of trees. Beaulne et al. (2021) show a shift toward greater dominance of the soil fraction along a swamp to forested bog gradient, and this is also shown in our comparison of boreal swamps with forested fens or bogs (Zoltai et al., 2000; Table 6). The forested fens and bogs contain deeper peat and presumably lower tree biomass although there were few sites with paired measurements of both above ground biomass and soil carbon stocks. Higher bulk density in swamp soils as compared to forested bog or fen peat may relate to hydrological regime, more frequent flooding and greater influence of surface runoff. These findings support the idea that nuanced classification systems are required to distinguish swamps from forested fens and bogs.

5. Future research directions

Our results highlight the importance of swamps for wetland carbon storage in Canada and the United States and show important carbon cycling differences among swamps (as defined by vegetation). However, the criteria to categorize swamps are poorly defined and vary across regions. Both structural and functional criteria are used to define swamps. While most classifications seem to agree on swamps having a minimum tree or tall shrub cover of >25%, a structural characteristic that can be derived from remote sensing, classifications do not agree on whether swamps can accumulate peat or not, a function more difficult to assess from remote sensing products, and only indirectly. Furthermore, even when swamp definitions include forested wetlands on organic soils, specific forested peatland types are excluded from the swamp category (treed bogs or fens), even when tree cover is >25%, further complicating the classification. The comparisons presented here highlight the importance of vegetation cover in defining swamps, alongside the hydrological regime, which is often characterized by seasonal flooding, riparian, coastal or bottomland settings. Swamps can accumulate significant amounts of peat, or not, but we show that regardless of any organic vs. mineral swamp definitions, all swamp types are important in terms of carbon accumulation and fluxes.

There is an urgent need to update maps of swamp distributions using a consistent definition across regions. We were unable to estimate total C stocks in swamps across North America, not only due to a lack of soil carbon and flux data, but also due to a lack of reliable maps given the huge variation in swamp cover among existing sources. Future research focused on the mapping of swamps should combine the use of optical imagery to identify the dominant vegetation with methods that map topographic or wetness (e.g., terrain mapping e.g., Creed et al. 2008; Lidberg et al., 2020) or microwave earth observation (e.g., Townsend, 2001).

Additional data are needed to improve the comparisons among swamp vegetation classes across both climate and hydrological regions and to test some of the ideas suggested here. Broad-leaved swamps stand out as distinct from the other three categories owing to higher bulk densities, thinner peat depths and higher CH_4 emissions, likely reflecting strongly seasonal hydrological regimes and ecological conditions. Needle-leaved swamps are particularly important in terms of above-ground biomass and these swamp systems can slowly accumulate significant peat depths over long periods of time, resulting in large soil carbon stocks that cannot be replaced on short- or medium-term timescales following disturbance. However, there were generally fewer than 10 sites available for estimating total soil carbon stocks for each swamp type and the representativeness of the existing studies for capturing the range of hydrological and chemical conditions across swamps remains unclear. Significantly more field sampling is needed to determine the drivers of variability in soil carbon stocks to inform upscaling efforts as well as land use planning. In conclusion, we show that all swamp types are important in carbon cycling. This prevalent yet understudied wetland type in North America must be taken into consideration in land-based climate change mitigation efforts.

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Data Availability Statement

Any data that support the findings of this study are included within the article, supplementary information and publicly available where applicable.

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Tables

Table 1. Examples from selected regions of Canada and the United States of typical dominant trees and shrubs for the four swamp types

Swamp type	**Examples and typical taxa**	**Example References**
Broad-leaved	Hardwood swamps dominated by *Acer rubrum, A. saccharinum* and *Fraxinus nigra*, with *Betula papyrifera, Fagus grandifolia, Fraxinus pennsylvanica, Populus balsamea*, or *Ulums americana* as sub-dominants. Southeast USA: Tupelo swamps dominated by *Nyssa* spp.	Dahl and Zoltai 1997 Riley 1994a, b Burns and Honkala 1990
Needle-leaved	Nutrient-poor acid swamps dominated by *Picea glauca*, *P. mariana*, or *Larix laricina* with *Abies balsamea*; or US Coastal plain: *Chamaecyparis thyoides* dominant Nutrient-rich, minerotrophic swamps dominated by *Thuja occidentalis* and/or *Larix laricina* Bald-cypress swamps (*Taxodium distichum*) (Southeastern USA and Gulf Coastal Plains) *Tsuga heterophylla* and *Chamaecyparis nootkatensis* (Maritime west coast)	Riley 1994a, b Riley and Michaud 1989 Burns and Honkala 1990
Mixedwood	Co-dominance by both deciduous and coniferous species such as *Fraxinus nigra* and *Thuja occidentalis*, and may include combinations of other subdominant trees such as *Picea* spp., *Abies balsamea, Acer rubrum* and/or *Populus balsamifera*	Riley 1994a, b Dahl and Zoltai 1997
Shrub/ Thicket	Dominance by tall shrubs such as *Alnus rugosa, Betula pumila, Cephalanthus occidentalis, Cornus racemosa, Cornus stolonifera, Ilex verticillata, Rhus vernix*, or *Salix* spp.	Riley 1994a, b

Table 2. Summary of mean (± SD) aboveground net primary productivity (ANPP) and aboveground biomass from swamps and forested wetlands across Canada and the United States. Values are presented in kg dry weight m^{-2} and kg dry weight m^{-2} yr^{-1}

Swamp type	**Aboveground net primary productivity ($kg\ m^{-2}\ yr^{-1}$)**	**Aboveground biomass ($kg\ m^{-2}$)**	**Number of studies**
Broad-leaved	1.03 ± 0.3	20.1 ± 10.4	10
Needle-leaved	1.57 ± 3.1	21.5 ± 14.8	20
Mixedwood	0.94 ± 0.3	19.3 ± 12.0	11
Shrub/Thicket	0.92 ± 0.5	4.0 ± 1.1	3

Table 3. Summary of mean (± SD where available) growing season soil carbon dioxide (CO_2) flux and associated environmental variables from swamps and forested wetlands across Canada and the United States.

Swamp type	Location	Water table depth (cm) bgs[a]	Soil type	Dominant tree species	Dominant understory species	CO_2 flux ($g\ m^{-2}\ d^{-1}$)	Reference
Broad-leaved	44.3 °N, 65.1 °W	-	Organic	*Tsuga canadensis, Abies balsamea, Acer rubrum,*	*Sphagnum* spp., *Rubus pubescens, Pteridium aquilinum*	1.4 ± 0.8	Kendall et al. 2020
Needle-leaved	44.3 °N, 65.1 °W	-	Organic	*Acer rubrum, Tsuga canadensis, Pinus strobus, Larix laricina*	*Rubus hispidus, Pleurozium schreberi, Carex* spp	0.6 ± 0.2 0.7 ± 0.4	Kendall et al. 2020[b]
Mixedwood	29.5 °N, 90.1 °W	24.0	Mineral	*Taxodium distichum, Fraxinus profunda*	-	1.4 ± 34.2 1.1 ± 34.4	Yu et al. 2008
	42.2 °N, 76.2 °W	20-35	Organic	*Acer rubrum, Tsuga* spp.	-	2.1	Miller et al. 1999
	43.2 °N, 80.1 °W	-26.5 -33.5 -0.4	Organic	*Larix laricina, Thuja occidentalis, Acer rubrum, Populus tremuloides*	-	50.3 ± 7.3 32.2 ± 6.5 15.8 ± 3.6	Davidson et al. 2019[c]
	36.3 °N, 76.2 °W	-	Organic	*Taxodium distichum, Chamaecyparis thyoides, Pinus serotina, Acer rubrum, Nyssa sylvatica*	-	11.32	Gutenberg et al. 2019
	32.1 °N, 81.1 °W	-	Mineral/organic	*Taxodium distichum, Nyssa aquatica*	*Polygonum hydropiperoides, P. arifolium, Thelypteris* sp., *Carex* spp., *Commelina diffusa, Toxicodendron radicans, Iris* sp.	4.3 3.9 2.2	Krauss and Whitbeck 2012[c]

a. Below ground surface
b. Two sub-sites
c. Three sub-sites
\- Indicates no data available

Table 4. Summary of mean (± SD where available) growing season soil methane (CH_4) flux and associated environmental variables from swamps and forested wetlands across Canada and the United States.

Swamp type	**Location**	**Water table depth (cm) bgs**[a]	**Soil type**	**Dominant tree species**	**Dominant understory vegetation**	**CH_4 flux ($mg\ m^{-2}\ d^{-1}$)**	**Reference**
Broad-leaved	45.5 °N, 73.1 °W	-15.1	Organic			4.7	Moore and Knowles 1990
	44.3 °N, 65.1 °W	-	Organic	*Tsuga canadensis, Abies balsamea, Acer rubrum,*	*Sphagnum* spp., *Rubus pubescens, Pteridium aquilinum*	0.04 ± 0.8	Kendall et al. 2020
	37.1 °N, 73.3 °W	15	Mineral	*Acer rubrum, Quercus bicolor, Fraxinus tomentosa*	*Typha latifolia, Peltandra virginica, Saururus cernus, Polygonum coccineum*	117 155 83 152	Wilson et al. 1989[b]
Needle-leaved	49.1 °N, 82.4 °W	-29.2	Organic	*Picea mariana,*	*Warnstorfia fluitans, Warnstorfia exannalatus*	21.9	Bubier et al. 1992a
	49.0 °N, 80.0 °W	5.42	Organic	*Picea mariana,*	-	26.6	Bubier et al. 1992b
	44.3 °N, 65.1 °W	-	Organic	*Acer rubrum, Tsuga canadensis, Pinus strobus, Larix laricina*	*Rubus hispidus, Pleurozium schreberi, Carex* spp	-0.005 ± 0.03 0.05 ± 0.09	Kendall et al. 2020[c]
	30.5 °N, 82.1 °W	-	Organic	*Taxodium* sp.	-	9.8	Harriss and Sebacher 1981
	46.2 °N, 78.6 °W	-13.1	Organic	*Thuja occidentalis, Larix laricina*	-	1.9	Roulet et al. 1992

	50.3 °N, 127.2 °W	-22	Organic	*Thuja plicata*	-	19.3	Christiansen et al. 2016
Mixedwood	43.2 °N, 80.1 °W	-26.5 -33.5 -0.4	Organic	*Larix laricina, Thuja occidentalis, Acer rubrum, Populus tremuloides*	-	0.7 ± 10.7 -2.0 ± 6.6 26.5 ± 58.7	Davidson et al. 2019[c]
	36.3 °N, 76.2 °W	-	Organic	*Taxodium distichum, Chamaecyparis thyoides, Pinus serotina, Acer rubrum, Nyssa sylvatica*	-	2.9	Gutenberg et al. 2019
	32.1 °N, 81.2 °W	-	Organic	*Quercus laurifolia, Liquidambar styraciflua, Taxodium distichum*	-	28.8	Pulliam 1993
	34.2 °N, 89.5 °W	-	Organic	*Quercus marilandica, Quercus. alba, Pinus taeda, Taxodium distichum*	-	140.4	Koh et al. 2009
	46.2 °N, 78.6 °W	-6	Organic	*Thuja occidentalis, Abies balsamea, Fraxinus nigra, Acer rubrum*	-	0.2	Roulet et al. 1992
	32.1 °N, 81.1 °W	-	Mineral/organic	*Taxodium distichum, Nyssa aquatica*	*Polygonum hydropiperoides, P. arifolium, Thelypteris* sp., *Carex* spp., *Commelina diffusa, Toxicodendron radicans, Iris* sp.	3.02 ± 0.04 5.02 ± 0.06 0.2 ± 4.6	Krauss and Whitbeck 2012[c]
	30.1 °N, 90.3 °W	-	Mineral/organic	*Taxodium distichum, Nyssa aquatica*	-	146 ± 199	Alford et al. 1997

	34.5 °N, 77.1 °W	-	Mineral/organic	*Acer rubrum*	*Rosa* sp.	37.9 ± 33.6	Kelley et al. 1995
Shrub/Thicket	46.2 °N, 78.6 °W	-	Organic	-	*Salix pedicellaris,* *Cornus sericea,* *Alnus incana,* *Betula nana*	34.9	Roulet et al. 1992

a. Below ground surface
b. Four sub-sites
c. Three sub-sites
\- Indicates no data available

Table 5. Summary of mean (± SD where available) dissolved organic carbon (DOC) concentration and export and associated environmental variables from swamps and forested wetlands across Canada and the United States.

Swamp category	**Location**	**Soil type**	**Dominant tree species**	**Dominant understory species**	**Soil DOC concentration ($mg\ L^{-1}$)**	**Reference**
Broad-leaved	47.1 °N, 84.4 °W	Organic	*Acer saccharum* Marsh.	-	9.1 (3.6 – 21.7)[a]	Creed et al. 2013
Needle-leaved	58.5 °N, 134.5 °W	Organic	-	-	25.6 (15.7 – 37.8)[b]	D'Amore et al. 2015
	54.2 °N, 130.25 °W	Mineral/organic	*Picea sitchensis*, *Tsuga mertensiana*, *Thuja plicata*	*Chamaecyparis nootkatensis*, *Lysichitum americanum*	18.8 (± 3.6)	Fitzgerald et al. 2003
	54.2 °N, 130.25 °W	Organic	*Tsuga heterophylla*, *Thuja plicata*, *Pinus contorta*, *Chamaecypari nootkatensis*	*Vaccinium* spp., *Pleurozium* spp., *Sphagnum* spp., *Oplopanax horridus*, *Lysichitum americanum*	17.6 (± 7.0)[c] 11.1 (± 6.0)[d]	Emili and Price 2013
	46.2 °N, 86.7 °W	Organic	*Picea mariana*	-	32 (9 – 99)[e]	McLaughlin et al. 1994
	39.1 °N, 79.6 °W	Organic	*Picea rubens*	*Rhododensron maximum*, *Sphagnum girgensohnii*, *Carex canescens*	86.7 (36 – 174)[f]	Yavitt 1994
Mixedwood	45.2 °N, 73.2 °W	Organic	*Betula allenghaniensis*, *Tsuga cadensis*, *Acer rubrum*, *Thuja*	*Onoclea sensibilis*, *Dryopteris spinulosa*,	59 (41 – 81)[h]	Dalva and Moore 1991

			occidentalis, Fraxinus nigra	*Lycopodium lucidulum*		
	33.3 °N, 79.2 °W	Mineral/organic	*Taxodium distictum, Nyssa aquatica, Nyssa sylvatica*	-	42.7 (31.4 – 55.0)[f]	Chow et al. 2013
					Surface water DOC concentration (mg L^{-1})	
Needle-leaved	58.5 °N, 134.5 °W	Organic	-	-	15.2 27.1 24.6	D’Amore et al. 2015
	31.2 °N, 84.47°W	Organic	*Taxodium ascendens, Nyssa biflora*	-	19.9 (15.1 – 28.2)	Battle and Golladay 2001
Mixedwood	43.3 °N, 80.1 °W	Organic	*Larix laricina, Thuja occidentalis, Acer rubrum, Populus tremuloides*	-	11.3 (6.1 – 18.4)	Galloway and Branfireun 2004
					DOC export (g C m^{-2} yr^{-1})	
Broad-leaved	35.4 °N, 77.2 °W	Organic	*Acer rubrum, Fraxinus caroliniana, Nyssa syltvatica*	-	26	Mulholland 1981
Needle-leaved	58.5 °N, 134.5 °W	Organic	-	-	20.7 49.8 19.2	D’Amore et al. 2015
	45.2 °N, 78.8 °W 45.4 °N, 79.1 °W	Organic	*Picea mariana, Thuja occidentalis*	*Alnus* spp. *Ilex verticillata*, *Sphagnum* spp.	33.5 34.5	Devito et al. 1989

a. Measured in upper 90 cm
b. Average of concentrations at 25 and 50 cm depth across all three study sites
c. From organic soil horizons
d. From mineral soil horizons
e. Measured at 30 cm depth
f. Measured in profiles in the upper 50 cm of soil
g. Measured at 5-10 cm depth

Table 6. Means of peat properties by swamp type. OM = organic matter OC = organic carbon; aCAR = apparent rate of carbon accumulation. Means calculated based on peat section of soil profile. Values reported as mean ± standard deviation (number of samples used in calculation)**.** For medians and inter-quartile ranges, see Figure 5.

Swamp category	**Total number of cores**	**Peat depth (cm)**	**Bulk density (g cm^{-3})**	**OM (%)**	**OC (%)**	**Accretion rate (cm y^{-1})**	**aCAR ($\text{g m}^{-2}\ \text{yr}^{-1}$)**
Broad-leaved	24	101 ± 112 (24)	0.204 ± 0.064 (21)	73.2 ± 18.3 (20)	40.5 ± 9.0 (8)	0.00737 ± 0.00153 (4)	-
Needle-leaved	109	199 ± 136 (108)	0.153 ± 0.055 (88)	86.2 ± 8.21 (97)	46.7 ± 13.9 (27)	0.044 ± 0.031 (39)	30.3 ± 20.6 (28)
Mixedwood	21	236 ± 186 (20)	0.136 ± 0.026 (12)	90.0 ± 4.8 (12)	47.6 ± 4.2 (11)	0.037 ± 0.029 (8)	-
Shrub/Thicket	17	181 ± 103 (17)	0.156 ± 0.044 (16)	88.6 ± 4.84 (16)	44.7 ± 10.1 (14)	0.007 (1)	-
Non-swamp (forested wetland)[a]	76	237 ± 100 (76)	0.103 ± 0.032 (75)	88.6 ± 5.94 (76)	-	-	-

[a] Based on Zoltai et al. 2000 dataset; these include forested bogs and fens

Table 7. Mean (± SE) soil properties and organic carbon stocks by depth for each swamp type from 0-120 cm. Depths based on midpoint of sampling interval. Number of samples used in calculation shown in ( ).

Swamp Type	Depth (cm)	Bulk density (g cm^{-3})	Organic Matter (%)	Organic Carbon (%)	Total Carbon (%)	Organic Carbon Stock (kgC m^{-2})
Broad-leaved	0-30	0.30 ± 0.04 (18)	65 ± 5.2 (18)	34.5 ± 4.0 (7)	44.7 ± 1.5 (6)	24.6 ± 3.5 (5)
	30-60	0.60 ± 0.13 (15)	49.6 ± 9.7 (15)	44.3 ± 2.7 (3)	45.0 ± 1.6 (5)	24.0 ± 6.5 (3)
	60-90	0.58 ± 0.18 (9)	52.6 ± 13.7 (9)	38.1 ± 11.5 (4)	0.58 ± 0.18 (9)	21.7 ± 1.9 (3)
	90-120	0.16 ± 0.03 (5)	82.3 ± 6.3 (5)	47.7 ± 2.4 (4)	0.16 ± 0.03 (5)	19.1 ± 2.3 (4)
Needle-leaved	0-30	0.18 ± 0.02 (54)	87.3 ± 1.1 (64)	44.4 ± 0.8 (23)	0.18 ± 0.02 (54)	19.0 ± 1.5 (23)
	30-60	0.17 ± 0.02 (50)	85.4 ± 2.0 (59)	47.1 ± 1.0 (19)	0.17 ± 0.02 (50)	18.3 ± 0.9 (19)
	60-90	0.23 ± 0.03 (40)	90.3 ± 3.1 (49)	47.2 ± 1.3 (10)	0.23 ± 0.03 (40)	16.5 ± 1.2 (10)
	90-120	0.16 ± 0.01 (28)	86.4 ± 2.2 (36)	48.4 ± 0.7 (9)	0.16 ± 0.01 (28)	18.4 ± 1.9 (9)
Mixedwood	0-30	0.17 ± 0.01 (11)	89.7 ± 0.8 (11)	45.2 ± 1.2 (9)	0.17 ± 0.01 (11)	22.3 ± 2.7 (9)
	30-60	0.19 ± 0.02 (5)	91.4 ± 1.6 (5)	49.4 ± 1.2 (4)	0.19 ± 0.02 (5)	24.9 ± 2.6 (4)
	60-90	0.18 ± 0.03 (5)	88.7 ± 2.1 (5)	43.4 ± 2.6 (4)	0.18 ± 0.03 (5)	19.6 ± 1.7 (4)
	90-120	0.17 ± 0.04 (3)	92.3 ± 0.8 (3)	47.8 ± 2.3 (2)	0.17 ± 0.04 (3)	19.5 ± 3.1 (2)
Shrub/Thicket	0-30	0.20 ± 0.03 (8)	90.0 ± 1.5 (8)	44.7 ± 4.1 (8)	0.20 ± 0.03 (8)	26.4 ± 4.6 (8)
	30-60	0.14 ± 0.01 (6)	89.1 ± 2.9 (6)	46.7 ± 2.8 (6)	0.14 ± 0.01 (6)	20.0 ± 1.6 (6)
	60-90	0.15 ± 0.01 (8)	89.1 ± 2.0 (8)	48.5 ± 1.4 (7)	0.15 ± 0.01 (8)	20.9 ± 1.3 (7)
	90-120	0.15 ± 0.02 (4)	87.7 ± 5.2 (4)	45.2 ± 4.2 (4)	0.15 ± 0.02 (4)	19.1 ± 0.9 (4)

Figures

Figure 1. Example photographs of the four main swamp types A) broad-leaved (location: Ontario, Canada) (photo credit: Dean Hiler) B) needle-leaved (location: Alberta, Canada) (photo credit: Scott J. Davidson) C) mixedwood (location: Ontario, Canada) (photo credit: Scott J. Davidson) D) shrub/thicket (location: Michigan, USA) (photo credit: Lars Brudvig)

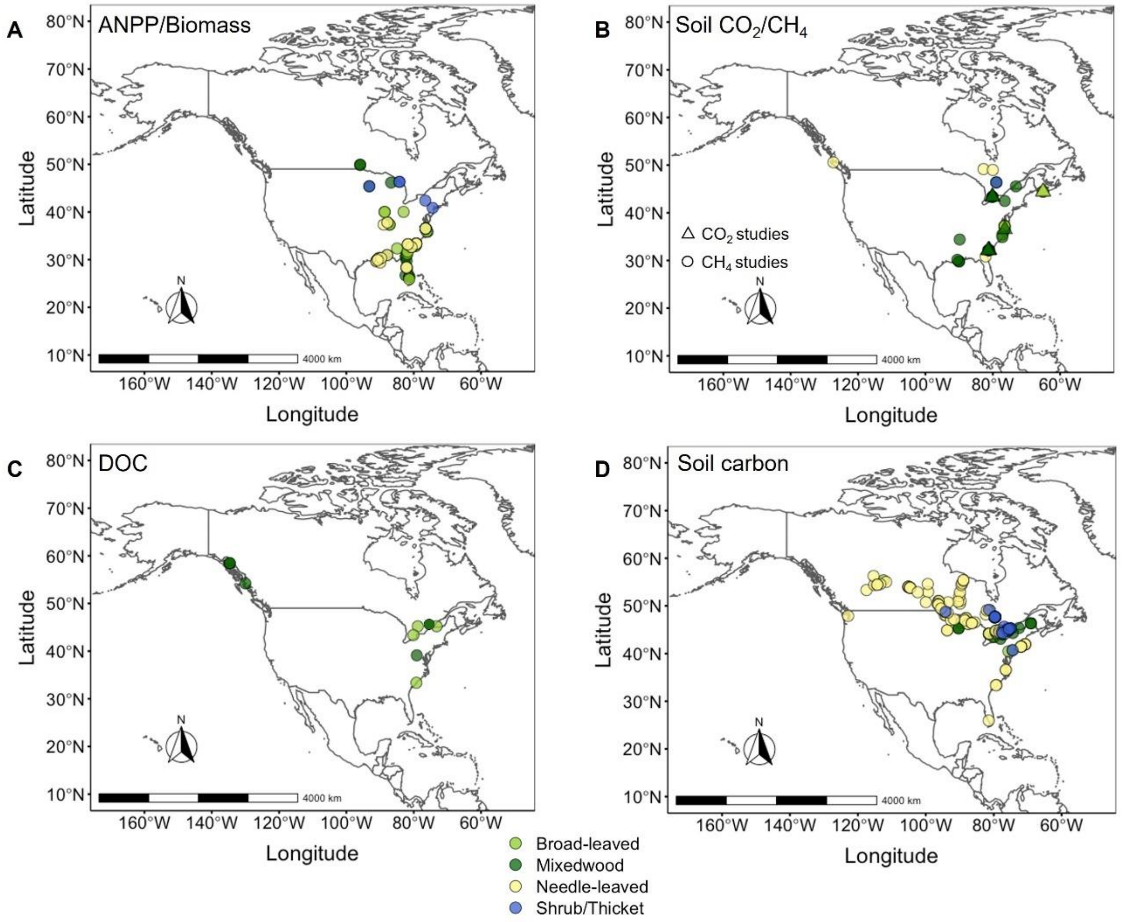

Figure 2. Locations of study sites for A) aboveground net primary productivity (ANPP) and biomass, B) soil carbon dioxide (CO_2) and methane (CH_4) fluxes, C) dissolved organic carbon (DOC) and D) soil carbon.

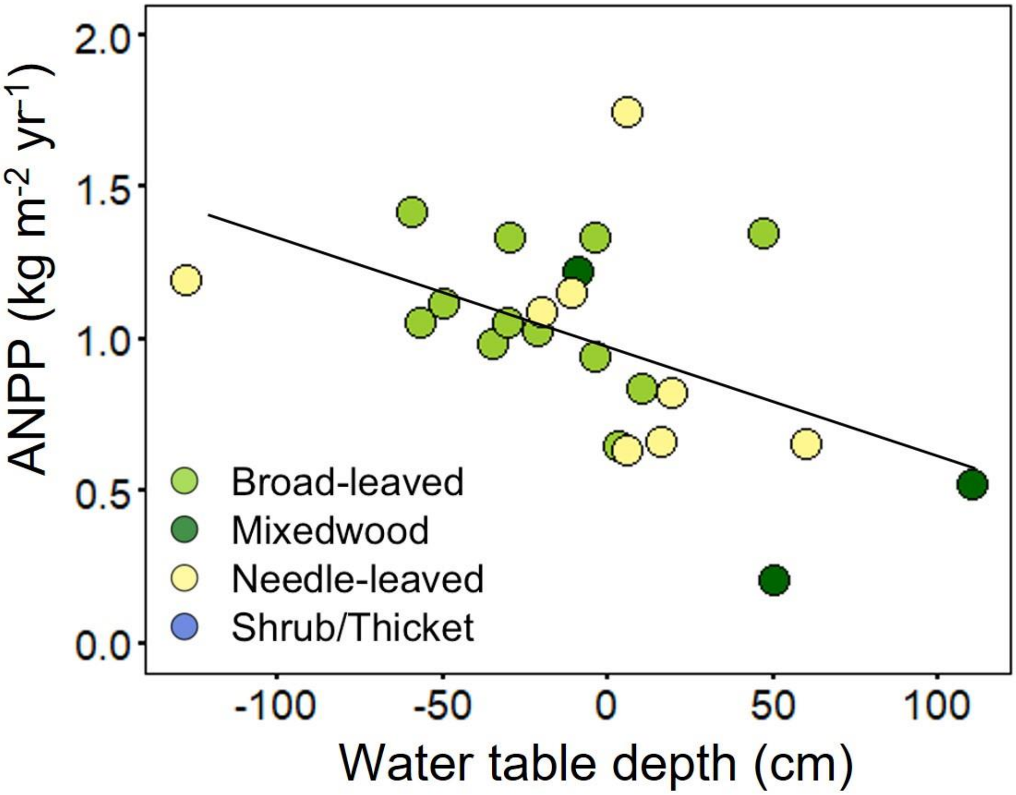

Figure 3. Aboveground net primary productivity (ANPP) as a function of water table depth (cm). A positive water table depth value indicates the water level is above the ground surface. Linear regression; $y=-0.0036x+0.9799$, $R^2 = 0.25$, $p = 0.01$.

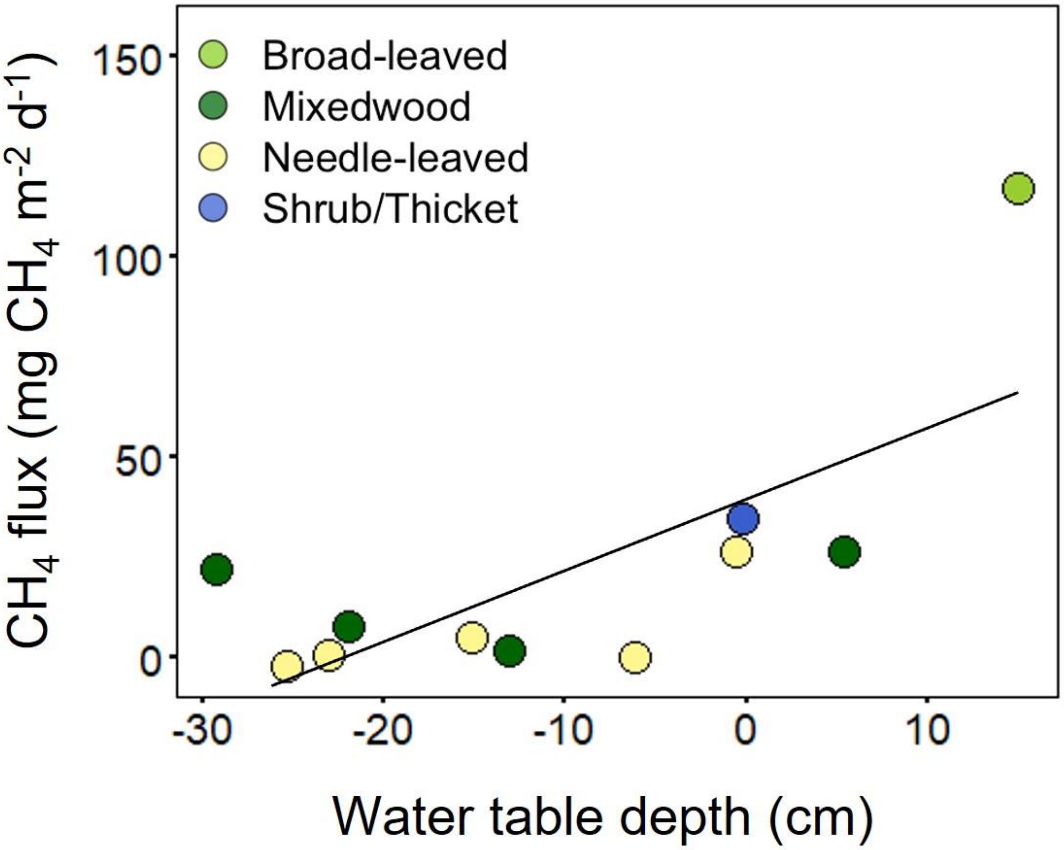

Figure 4. Swamp methane (CH_4) flux as a function of water table depth (cm). A positive water table depth value indicates the water level is above the ground surface. Due to lack of studies reporting both CH_4 flux and water table depth, we do not categorize by swamp type. Linear regression; $y=-1.7395x+39.867$, $R^2 = 0.52$, $p = 0.011$.

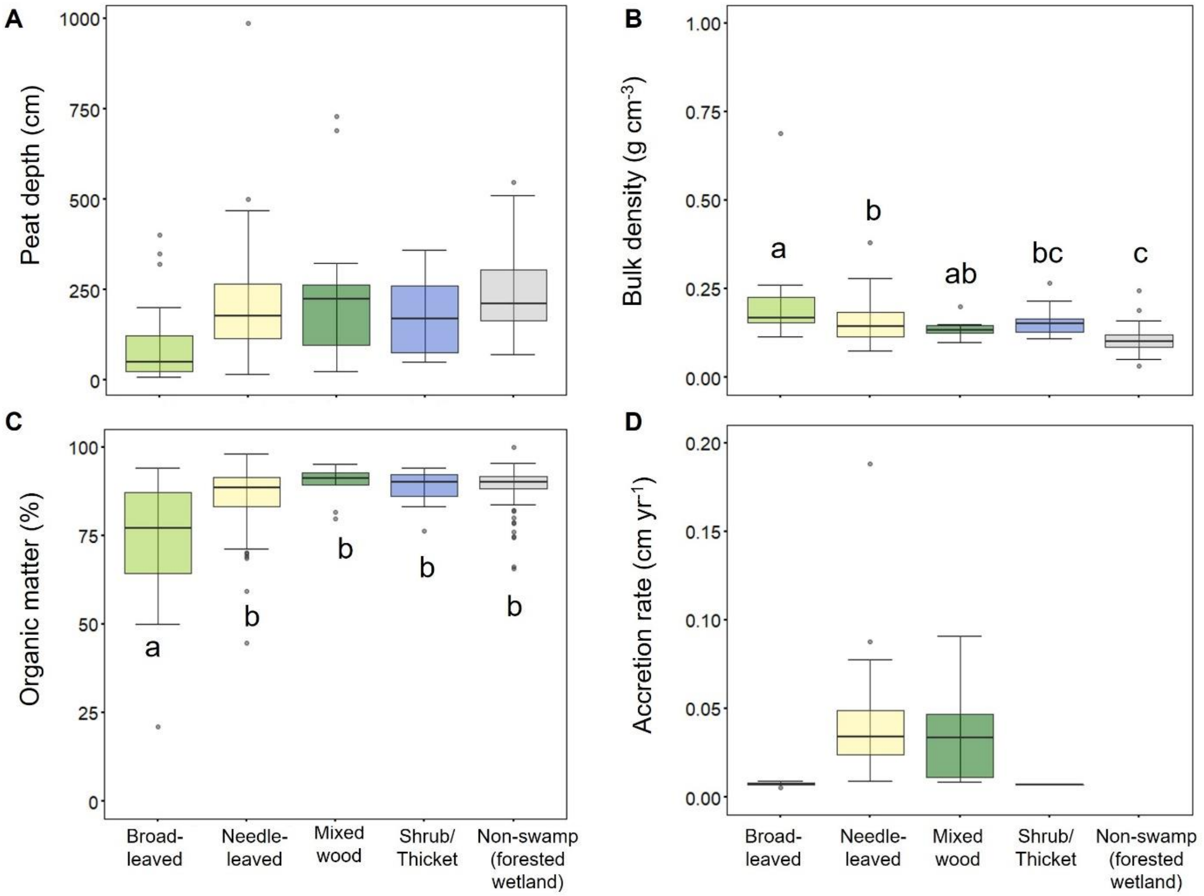

Figure 5. A) peat depth (cm), B) bulk density (g cm^3), C) organic matter (%) and D) rate of peat accretion (cm yr^{-1}) for the four swamp types as well as forested wetlands not classified as specifically as "swamps" in ZDB (Zoltai et al., 2000). Each point represents the mean value of one profile (only peat sections included). Lower case letters indicate significant difference between swamp types (analysis of variance, p < .0001).

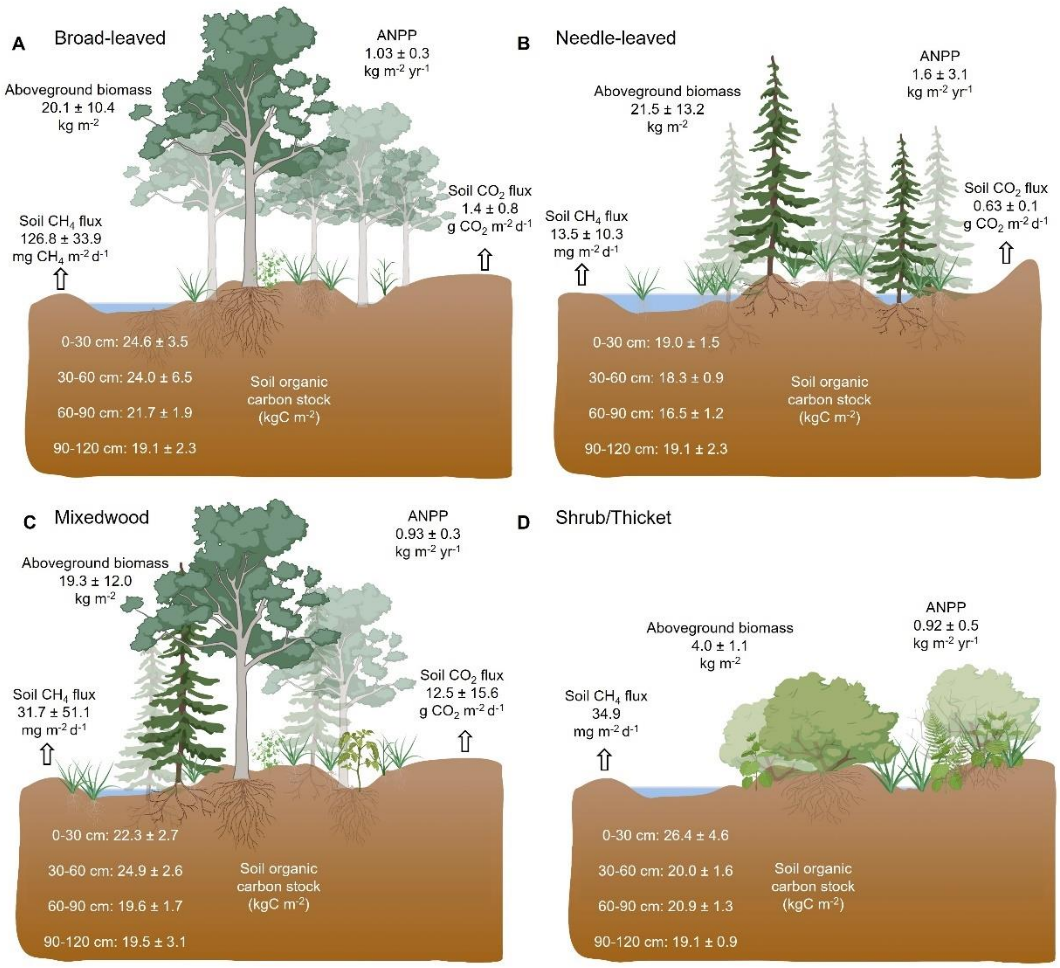

Figure 6. Summary of seasonal growing season mean (± SD) aboveground net primary productivity (ANPP), aboveground biomass, CO_2 flux, CH_4 flux and total soil organic carbon stock for depths 0-30 cm, 30-60 cm, 60-90 cm and 90-120cm where available for A) broad-leaved, B) needle-leaved, C) mixedwood and D) shrub/thicket swamps from the published literature. Soil CO_2 flux for broad-leaved and needle-leaved swamps is from one study. No soil CO_2 flux measurements were found for shrub/thicket swamps. Please see Tables 1-7 for sample sizes used to calculate the means shown here. Aboveground biomass and ANPP are presented in kg dry weight m^{-2} and kg dry weight m^{-2} yr^{-1} respectively.