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

2   **Running Head:** Carbon dynamics from Canadian and US swamps

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

20

21

22   **Abstract**

23   Swamps are a highly significant wetland type in North America both in terms of areal extent and their

24   role in terrestrial carbon cycling. These wetlands, characterized by woody vegetation cover, encompass a

25   diverse suite of ecosystems, including broad-leaved, needle-leaved, mixedwood or shrub/thicket swamps.

26   Uncertainties in the role of swamps in carbon uptake and release continue to be substantial due to

27   insufficient data on variabilities in carbon densities across diverse swamp types and relatively few flux

28   measurements from swamp sites. Robust measurements of rates of vertical accretion of swamp soils and

29   the associated long-term rates of carbon accumulation, alongside measurements of carbon losses from

30   swamps, are needed for emerging frameworks for carbon accounting, and for assessments of the impacts

31   of climate warming and land use change on this important wetland type. Based on data compilation, we

32   present here a comparative analysis from a series of North American swamp sites on carbon dioxide,

33   methane and dissolved organic carbon fluxes, aboveground biomass, net primary productivity, and soil

34   carbon properties including bulk densities, organic carbon contents, peat depths, rates of vertical

35   accretion, and rates of long-term carbon accumulation. We compare these properties for four major

36   swamp types: needle-leaved, broad-leaved, mixedwood and shrub/thicket swamps. We show differences

37   in carbon fluxes, biomass and NPP across the four types, with broad-leaved swamps having the largest

38   CH_4 flux, highest soil bulk densities, thinnest peat depths and lowest soil organic matter contents, whereas

39   needle-leaved swamps have the smallest CH_4 flux, highest aboveground biomass and highest NPP. We

40   show high soil carbon stocks ($kgC\ m^{-2}$) in all types of swamps, even those where organic deposits were

41   too shallow to meet the definition of peat. However, we note there is a significant lack of studies focused

42   on swamp carbon dynamics despite their abundance across Canada and the United States.

43   **1.0 Introduction**

44   Wetlands are a key component of the terrestrial carbon cycle and important for climate change mitigation

45   (e.g., Humpenöder et al., 2020). Swamps can make up large areas of wetland regions across Canada and

46   the USA and yet are vastly understudied in comparison to other wetland types. There are also large

47   variations in the literature with regards to the definition of what a swamp is and what classification they

48   fall under – peatland, non-peatland (mineral) or both, although many agree that swamps are wetlands with

49   at least 25% tree cover (e.g., Nahlik and Fennessy 2016, National Wetlands Working Group. 1997; AWI

50   2018).

51   In swamps, also known as treed/shrub wetlands, the presence of hydric soil conditions, wetland-adapted

52   vegetation and anaerobic microbial communities significantly influence not only the amount of soil

53   carbon present but the different pathways for carbon fluxes and rates of transfer (Trettin and Jurgensen,

54   2003). For example, the typical high-water tables found in swamps can lead to increased carbon storage

55   through reduced decomposition (Middleton, 2020). However, higher water tables are also conducive to

56   higher methane (CH_4) production and emissions in comparison to some other wetland types such as bogs

57   (Moore and Knowles, 1989). The variable nature of the hydrology of these systems can also result in

58   dynamic dissolved organic carbon (DOC) export rates (Mulholland, 1981). Swamps typically have high

59   tree cover, therefore can typically have greater above and belowground biomass and larger rates of net

60   primary productivity (NPP) in comparison to other treed wetland types such as bogs and fens.

61   Furthermore, this also means they can have increased levels of litter input in comparison to other wetland

62   types (Stoler and Relyea, 2019), leading to higher rates of carbon input and consequently, high rates of

63   organic matter accumulation.

64   Swamps have been documented to occupy a substantial portion of wetland area in North America,

65   although spatial distribution maps cannot be explicit yet due to varying regional definitions and potential

66   overlaps with other wetland types. For example, in the conterminous United States, it is estimated that

67   swamps make up approximately 49% of the wetland area, while in Alaska, shrub-dominated wetlands

68   make up approximately 68% of the wetland area, with forested wetlands only covering approximately 8%

69   (Hall et al., 1994). For Canada, swamps may represent the second most abundant wetland class, at nearly

70   9% of wetland landcover, second to marshes (~ 12%) (Amani et al. 2019). Furthermore, Riley (1994) note

71   that peat-forming conifer swamps are the dominant wetland type in northern Ontario, accounting for

72   nearly 40-60% of the peatland area. Yet, Tarnocai (2006) estimates that swamps cover only 1% of the

73   total Canadian wetland area. In southern Ontario, where wetland drainage and anthropogenic impacts are

74   widespread, the current 'tree swamp' cover is estimated about 76% and 'shrub swamp' is 11% in spatial

75   cover (Byun et al 2018). Given the overall significant areal extent of these wetland types, it is imperative

76   that we improve on the state of our current knowledge of carbon cycling in swamp wetland systems.

77   Despite the significant spatial extent and importance in regional carbon cycling, swamps are largely

78   missing from national and global greenhouse gas inventories. In Canada, for example, the recently

79   developed Canadian Model for Peatlands (CaMP, Bona et al., 2020) tracks carbon fluxes for 11 different

80   peatland types. However, because of insufficient data to parameterize or calibrate the model for swamps,

81   they are not included in the final estimates (Bona et al., 2020). Additionally, Canadian peatland mapping

82   products used in the CaMP model do not map swamp distributions at the national scale (Webster et al.,

83   2018). Available estimates from US national wetland inventories indicated that shrub-dominated or

84   forested wetlands, classes in which swamps would be included, are highly significant in terms of soil

85   carbon storage (Nahlik and Fennessy, 2016), although there remain important gaps in available data on

86   both quantity and types of organic matter present in swamp soils. Similarly, recent datasets of boreal and

87   arctic lake and wetland CH_4 flux and area were unable to include swamps as their own category, lumping

88   them with other wetland types, largely due to a lack of CH_4 data but also due to the wide range of

89   hydrological and nutrient conditions across swamp types (Kuhn et al., 2021; Olefeldt et al., 2021).

90   Without clear understanding of swamp carbon stocks and fluxes and how they vary from other wetland

91   types, particularly bogs and fens with which they are currently grouped in many datasets and models, the

92   potential error in regional estimates of present and future carbon exchange will remain unknown.

93   Therefore, given the documented large but potentially poorly constrained spatial extent of these

94   ecosystems across both Canada and the USA, a better understanding of variability in carbon stocks and

95   fluxes in is required to support both future improved wetland mapping and climate and earth system

96   modelling efforts. Thus, this study compares vegetation biomass and net primary productivity, carbon

97   dioxide (CO_2) and methane (CH_4) fluxes, dissolved organic carbon (DOC) concentration and export, and

98   soil carbon stocks from four distinct swamp typesacross Canada and the United States. We aim to answer

99   the following questions: (1) How variable are C fluxes and stocks among swamp types; (2) How do

100   swamp C fluxes and stocks compare to other wetland and upland ecosystems; and (3) What are the most

101   significant research needs to better quantify the role of swamps in the global carbon cycle?

102

103   **2.   Methods and Materials**

104   *2.1 Classification of swamps*

105   The Canadian Wetland Classification System (NWWG, 1997) defines swamps as belonging to both

106   mineral and organic wetland classes. However, the provincial Alberta Wetland Inventory (AWI, 2018)

107   classifies a swamp as 'a mineral wetland with water levels near, at or above the ground surface for

108   variable periods during the year which contains either more than 25% tree cover of a variety of species or

109   more than 25% shrub cover'. A similar definition is used by the Province of Québec, where organic treed

110   wetlands (non-bog or fen) are defined as peatlands (Bazoge et al., 2014). Definitions of swamps used in

111   the Province of Ontario also emphasize >25% tree or (Riley 1994; Government of Ontario, 2014) or tall-

112   shrub cover, and soils may be either mineral or organic (NWWG, 1997). In the United States, swamps are

113   often classified simply as a forested wetland (Cowardin et al., 1979) or by any number of names including

114   palustrine forested wetland, palustrine shrub wetland, vernal pools, bottomwood/bottomland or floodplain

115   forests. These discrepancies likely occur because swamps are often categorized based on their tree cover

116   and can be easily mis-classified as uplands or other treed wetlands i.e., bogs or fens (Locky et al., 2005).

117   Species that can be strictly found only in swamps in some regions may be found in upland regions in

118   others, further confusing the classification of swamps. Furthermore, swamps can exhibit seasonal water

119   table fluctuations (Zoltai and Vitt 1995; Devito and Mendoza, 2007) that can lead to their

120   misclassification as fens or other treed wetlands.

121   Therefore, we have not created a new classification of swamp types, rather we relied on original author

122   descriptions or classifications, placing each site into one of four dominant swamp type categories defined

123   based on dominant vegetation cover. These categories include broad-leaved swamps, needle-leaved

124   swamps, mixedwood swamps co-dominated by a mixture of broad-leaved and needle-leaved species, and

125   shrub or thicket swamps dominated by tall shrubs (Table 1, Figure 1). Swamps included in this synthesis

126   may either be on mineral or organic soil. Our study is focused on only freshwater swamps/forested

127   wetlands; therefore, mangrove forests were excluded from our data search. We focus exclusively on

128   freshwater swamps because coastal processes and marine influence add considerable variability in terms

129   of gas fluxes, sediment accretion and carbon accumulation (Rovai et al., 2018) and would invalid

130   comparisons with freshwater swamps.

131

132   *2.2 Data collection for carbon fluxes, vegetation biomass and net primary productivity (NPP)*

133   To locate all papers that have reported soil carbon dioxide (CO_2), methane (CH_4) fluxes, dissolved

134   organic carbon (DOC), vegetation biomass and above/belowground net primary productivity (NPP) from

135   swamps and forested wetlands (not explicitly classified as bogs or fens), we performed a comprehensive

136   search on Web of Science (accessed between September 2019 and November 2020) using the key words:

137   "methane" OR "CH_4" OR "carbon dioxide" OR "CO_2" OR "dissolved organic carbon OR "DOC" OR

138   "net primary productivity" OR "NPP" OR "net primary production" OR "biomass" OR "swamp" OR

139   "forested wetland" OR "slough" OR "forested hollow" OR "forested pool" OR "vernal pool" OR

140   "forested peatland" OR "wooded pond" OR "pocosins" OR "carr". We also checked references within

141   relevant papers and book chapters and utilized summary tables provided. Only studies using the static

142   chamber method were used for summaries of soil CO_2 and CH_4 flux due to a lack of studies using the

143   eddy covariance technique in swamp ecosystems. This resulted in 15 papers for CH_4 fluxes, 6 papers for

144   CO_2 fluxes, 7 papers for DOC and > 20 papers for NPP/biomass across both Canada and the United

145   States. We extracted information on wetland type and location. When the data were presented in figures,

146   mean values and standard error were extracted using WebPlotDigitizer

147   (https://automeris.io/WebPlotDigitizer/). Carbon dioxide fluxes were converted to g CO_2 m^{-2} d^{-1} and CH_4

148   fluxes were converted to mg CH_4 m^{-2} d^{-1} for consistency. Due to limited year-round data, we only present

149   data from May – September where possible. Some studies report biomass and productivity only for the

150   forest stand in the swamp (e.g., Conner and Day, 1976; Megonigal and Day, 1988; McKee et al., 2013);

151   however, as the overstory tree or tall shrub layer in swamps accounts for over 90% of aboveground

152   biomass and at least 80% of aboveground NPP (Reader and Stewart, 1972; Parker and Schneider, 1975),

153   reported values will only slightly underestimate the ecosystem totals. In contrast, in bald cypress swamps,

154   cypress knees can represent up to 17.9% of the total aboveground biomass carbon stock, illustrating the

155   importance of including all biomass components for the tree layer (Middleton, 2020).

156

157   *2.3 Data collection for soil carbon*

158   A dataset was compiled to compare swamp soil properties across the four swamp types. The data were

159   extracted mainly from three databases: a wetland database for the Western boreal, subarctic, and arctic

160   regions of Canada (ZDB) (Zoltai et al., 2000), surveys of peat and peatland resources for southeastern,

161   northwestern and northeastern Ontario (RDB) (Riley 1994a, b; Riley and Michaud, 1989) and the

162   Neotoma Paleoecology Database (NDB) (Williams et al., 2018). Swamp classification systems used in

163   ZDB and RDB included the four swamp types considered here and original classifications were applied.

164   In addition to the 24 sites classified as swamps in ZDB, a sub-set (N = 75) of sites not named as

165   "swamps" but classified as "forested fens" or "forested bogs" were included for comparison, recognizing

166   that a consistent terminology is lacking. To identify NDB sites corresponding to swamps or forested

167   wetlands, the "advanced" search menu was used with the following settings: "collection type" was set to

168   "core"; "deposit" was set to include "swamp", "tidal freshwater forested wetland", "slough", "small

169   hollow" or "vernal pool". Further, all sites with site names containing any of the following terms were

170   also reviewed: "swamp", "forested wetland", "slough", "forested hollow", "forested pool", "vernal pool",

171   "forested peatland", "wooded pond", "pocosin" or "carr". The full list of sites included, and original

172   references, are found in the Supplementary Information. The NDB sites were placed into one of the four

173   swamp types based on author descriptions in the original publications.

174

175   All sites used for comparisons of swamp soil properties included some combination of bulk density (BD,

176   g cm^{-3}), percent organic matter (%OM), ash content (%), percent organic carbon (%OC), percent total

177   carbon (%TC), qualitative descriptions of sediment type (peat vs mineral soil), peat depth (cm) and age-

178   depth relationships derived from radiocarbon dating. For each core, mean/median/standard

179   deviation/maximum/minimum/inter-quartile range (IQR) values were calculated or extracted from

180   original sources for BD, %OM, %OC. Only direct measurements of %OC are reported; no conversions

181   were done from %OM. Ash content was converted to OM% using the relationship Ash% + OM% =

182   100%. Then, the means of each variable from each core, and peat depths, were used to consider

183   variability in peat properties within and between the four swamp categories (Table 1). We report mean

184   BD, mean OM/OC/TC and mean peat thicknesses (cm) for the swamp peat sections (>30% OM) in the

185   available cores for each swamp category. Mineral sections with <30% OM were not included in these

186   comparisons to facilitate comparisons with other peat-forming wetlands. Because core sections with

187   <30% OM may still contain important carbon stocks and considering the difficulties in defining the

188   boundaries of swamp peat within cores without detailed macrofossil or other palaeoecological analyses,

189   we also report mean values for BD, %OM, and %OC by depth, 0-30 cm, 30-60 cm, 60-90 cm, and 90-120

190   cm, for the entire profiles (including both mineral and organic sections) for each swamp type, after Nahlik

191   and Fennessy (2016). These mean values by depth also include sections of the soil cores that do not meet

192   the definition of peat, and thus we are capturing both mineral and organic swamp soil types. Carbon

193   stocks were calculated for each section by multiplying organic carbon densities (g C cm^{-3}) by depth

194   intervals (cm) and converting to the standard units of kgC m^{-2} or t ha^{-1} (Howard et al., 2014). Carbon

195   densities are defined as the product of BD (g cm^{-3}) and %OC.

196

197   When age-depth relationships were available, from radiocarbon or other radioisotope dating, rates of

198   vertical accretion (cm yr^{-1}) were calculated for the swamp peat sections. The mean peat accretion rate (cm

199   yr^{-1}) was calculated for each core from the lowermost age control point and associated depth. In the cases

200   where this information as well as bulk density and organic matter content were available, average long-

201   term apparent carbon accumulation rates (aCAR, g C m^{-2} yr^{-1}) were calculated using basal ages of the

202   swamp peat sections of the core (Chambers et al. 2010).

203

204   **2.4 Data analysis**

205   All analyses were performed in R 3.5.3 (R Core Team, 2019). Analysis of variance (ANOVA) and post-

206   hoc Tukey tests (*Lsmeans*; Lenth, 2016) were used to determine statistical significance of any differences

207   between the swamp peat core sections from the four swamp types in terms of bulk density and organic

208   matter content. Linear regressions were used to look at relationships between water table depth and both

209   NPP and CH$_4$ fluxes. Only three of the studies looking at CO$_2$ fluxes reported water table depth so no

210   relationship could be calculated.

211
212   **3.   Results**

213   *3.1 Vegetation biomass and net primary productivity (NPP)*

214   Most data for biomass and NPP in swamps has been collected in the eastern United States in warm

215   temperate to sub-tropical environments, with only approximately 10% of the records north of 40°N

216   (Figure 2A). Due to this geographic distribution, needle-leaved swamps in this dataset were dominated by

217   bald cypress. Average aboveground biomass was greatest in needle-leaved swamps (21.4 ± 13.2 kg m^{-2}),

218   followed by broad-leaved (20.1 ± 10.1 kg m^{-2}) and mixedwood (19.3 ± 12.0 kg m^{-2}) swamps, with

219   shrub/thicket swamps having on average less than one quarter of the aboveground biomass of the forested

220   swamps (Table 2).

221 Aboveground NPP was more similar between swamp classes with average values of 0.91, 0.94, 1.03, and

222 1.57 kg m^{-2} yr^{-1} for shrub, mixedwood, broad-leaved, and needle-leaved, respectively. We found a

223 negative relationship between depth of water table and NPP (Figure 3), with NPP decreasing as water

224 tables become shallower.

225 Few studies have measured belowground biomass in swamps. We found only six studies (all needle-

226 leaved swamps), reporting data from 12 stands with an average across all swamp types of 1.8 kg m^{-2}. This

227 represents less than 10% of total biomass in treed swamp classes. Belowground NPP was measured in

228 only three studies (needle-leaved swamps only) across seven stands with an average value of 0.21 kg m^{-2}

229 yr^{-1}.

230 *3.2 Carbon dioxide (CO$_2$) and methane (CH$_4$) fluxes*

231 Very few studies have looked at soil CO_2 fluxes from swamps (7 studies across 13 sites: Figure 2B)

232 (Table 3). Largest emissions were found from a mixedwood swamp in southern Ontario, Canada with a

233 growing season mean flux of approximately 12.5 ± 15.6 g CO_2 m^{-2} d^{-1}. Only one study from Kendall et al.

234 (2020) in Nova Scotia, Canada, looked at CO_2 flux from both broad-leaved and needle-leaved swamps

235 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.

236 Similarly, soil CH_4 flux measurements from swamps are also lacking (Table 4). We found only 15 studies

237 (covering 23 sites: Figure 2B) reporting soil CH_4 fluxes. Furthermore, there is a distinct lack of studies

238 from broad-leaved, needle-leaved and shrub/thicket swamps, with mixedwood swamps dominating the

239 literature with 13 sites (Figure 2). The largest CH_4 flux was found to come from broad-leaved swamps

240 with a growing season mean flux of 126.5 ± 33.9 mg CH_4 m^{-2} d^{-1}. Needle-leaved swamps had the lowest

241 mean flux at 13.5 ± 10.3 mg CH_4 m^{-2} d^{-1}. The largest fluxes from all swamp types came from swamps

242 located in the temperate to sub-tropical regions of southeastern USA, with average fluxes becoming

243 smaller as you move further north towards the boreal zone. However, the one shrub/thicket study from

244 Roulet et al. (1992) noted a flux of approximately 34.9 mg CH_4 m^{-2} d^{-1} from a site in northern Ontario.

245 Nearly all sites were a source of CH_4 to the atmosphere during the growing season. In line with many

246 studies looking at CH_4 emissions from wetlands (Calabrese et al., 2021), CH_4 fluxes increased with

247 increasing water table level (Figure 4); however, this relationship is based on a limited dataset as

248 unfortunately not every study reported water table depth.

249

250 *3.3 Dissolved organic carbon (DOC) concentration and export*

251 Comparing DOC concentration among studies was complicated by the different sampling methods

252 applied. Some studies monitored DOC only in surface water during flooded periods (Battle and Golladay,

253   2001), others in stream water (Galloway and Branfireun, 2004) and others in soil pore water. When

254   measured in soils, the depth of measurement varied (see Table 5). Comparing across these varied samples,

255   average DOC concentration in swamp soil pore water was 11.1 to 86.7 mg L^{-1} across 10 study sites.

256   Surface water concentrations were generally lower and less variable at 15.2 to 27.1 mg L^{-1}.

257   We found three studies reporting net DOC export from six swamps (Mulholland, 1981; Devito et al.,

258   1989; D'Amore et al., 2015) with an average of 30.6 g C m^{-2} yr^{-1} (Table 5). As hydrology varies between

259   swamps, care must be taken to account for both DOC inputs and outputs to the swamp in order to

260   determine the DOC load attributable to the swamp alone (i.e., net DOC export).

261   *3.4 Soil carbon stocks*

262   A total of 247 swamp cores were used for comparisons of soil properties (Table S2). All swamp types

263   have high carbon densities, reflecting a combination of high organic matter contents and/or high bulk

264   densities (Table 6); mean bulk densities are typically higher than those reported for northern bogs and

265   fens (Loisel et al., 2014). Comparisons by ANOVA and post-hoc Tukey tests indicate that broad-leaved

266   swamps have significantly higher bulk densities than the other three swamp types (F = 16.1, df = 4, *p*

267   <0.01) and lower organic matter contents (F = 13.6, df = 4, *p* <0.01) (Figure 5). Other swamp types were

268   not statistically different from each other in terms of bulk density or organic matter content.

269   Of the four swamp types considered here, needle-leaved swamps have the highest rates of peat vertical

270   accretion. Peat vertical accretion is an order of magnitude lower in broad-leaved swamps, and peat depths

271   are also lowest in broad-leaved swamps (Table 6). Mixedwood and needle-leaved swamps are similar in

272   terms of soil properties, but mixedwood swamps are less abundant in the dataset. Shrub/thicket swamps

273   had lower peat depths than needle-leaved or mixedwood swamps, and no data were available to calculate

274   accretion rates. Lower above-ground biomass in shrub/thicket swamps (Table 2) may result in lower

275   organic matter inputs, contributing to lower peat depths. The non-swamp forested wetlands in the ZDB

276   (consisting of forested fens and bogs), have significantly lower bulk densities (Figure 5; ANOVA F =

277   12.9, df = 4, *p* <0.01) than sites explicitly classified as broad- and needle-leaf swamps but organic matter

278   contents are not distinct from other swamp types.

279   Swamp of all kinds hold significant soil carbon stocks (Table 7). The average 0–90 cm carbon stock for

280   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).

281   This is close to the reported mean carbon stock (61.5 ± 6.3 for 0–100 cm, kgC m^{-2}) for 65 freshwater

282   inland organic soil wetlands (Nahlik and Fennessy, 2016), however the sites of Nahlik and Fennessy

283   (2016) includes all types of inland organic-soil wetlands, not just swamps.

284 **4. Discussion**

285 This study synthesizing swamp carbon stocks and emissions from a range of sites across Canada and the

286 United States clearly indicates that these ecosystems are important components of the terrestrial carbon

287 cycle. For example, swamp aboveground biomasses (Table 2) are clearly larger than other wetland types

288 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

289 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

290 marshes (~1.2 kg m^{-2} y^{-1}) (Bona et al., 2018). Growing season bog and fen CH$_4$ fluxes from a range of

291 Canadian sites are comparable to mixedwood and shrub/thicket swamp sites at 35.8 and 40.8 mg CH$_4$ m^{-2}

292 d^{-1}, respectively (Table S1; Webster et al. 2018) but smaller than broad-leaved swamps. Swamp soil

293 carbon stocks are clearly larger than forest soil carbon stocks at 4–5 times greater than the average soil

294 values for all forest soils in conterminous US (Domke et al., 2017). The summarized carbon values for

295 the swamps (Figure 6) can be compared to the other ecosystems (Table S1).

296 While we are unable to determine how representative the sites are, our results provide key information for

297 the next steps in quantifying the role of swamps in regional and national carbon cycling. Furthermore,

298 until we have a better understanding of the spatial distribution of swamps across North America, we do

299 not know the full extent of conditions pertaining to climate and local hydrology that promotes the

300 development of these wetlands (see Figure 2 for distribution of studies). This makes a full assessment of

301 the representativeness of existing studies difficult, if not impossible. Thus, the following discussions

302 mostly focus on the comparison among four types of swamps and recognize knowledge gaps for future

303 studies.

304 *4.1 Vegetation biomass and aboveground NPP*

305 The mean aboveground biomass from the compiled swamp database of 194 t ha^{-1} (19.4 kg m^{-2}) falls

306 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})

307 determined from compiled forest inventory data across the United States and Canada (Zhu et al., 2018).

308 NPP depends on stand age, declining as forests reach maturity (Kurz et al. 2013; Zhu et al., 2018);

309 average NPP in Canada's managed forests were estimated as ~0.35 kg C m^{-2} yr^{-1} (Stinson et al., 2011),

310 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}

311 assuming 50% C content in biomass. As mentioned above, swamp aboveground biomass and NPP were

312 higher than the mean wooded bog and wooded fen aboveground biomass illustrating the taller trees and

313 denser cover of woody vegetation that define swamps in comparison to other wetland classes. Forest

314 biomass increases with increasing mean annual temperature and precipitation (Zhu et al., 2018) and this is

315 likely also the case for swamps. However, Megonigal et al. (1997) observed that swamp NPP had a

316   negative relationship with the depth of inundation likely due to stress causes by anoxic soil conditions.

317   We observed a similar trend across the compiled aboveground NPP data for sites that also reported water

318   table position (Figure 3). Given that most of the biomass measurements in the literature are from south of

319   40°N (Figure 2), the mean value presented here is likely an overestimate of biomass in cool temperate and

320   boreal swamps. This illustrates the need for better characterization of northern swamp biomass and NPP.

321   Belowground biomass made up a relatively small proportion of total biomass in swamps, resulting in a

322   belowground:aboveground biomass ratio of 0.1:1, but this is based on a small number of studies. This is

323   smaller than ratios determined for generic forests (Li et al., 2003). In some peatland ecosystems,

324   belowground biomass may exceed aboveground biomass (e.g., Murphy et al., 2009). Shallow water table

325   position or flooded conditions likely limit root growth in swamps, resulting in shallow rooted trees.

326   However, more research is needed to better quantify belowground biomass and NPP, including

327   contributions of understory species.

328   *4.2 CO_2 and CH_4 fluxes and DOC export*

329   Due to the distinct lack of soil CO_2 flux measurements in the literature, it is difficult to present a full

330   understanding on dynamics of CO_2 fluxes from swamps (see Figure 2 for lack of spatial representation).

331   As with other wetland types, the hydrological condition of swamps is likely a strong control on CO_2

332   emissions. High water tables can lead to a reduction in CO_2 production and lower emissions (Davidson et

333   al. 2019). Conversely, as water table levels drop, CO_2 emissions may increase as the oxic zone within the

334   soil column increases. Soil temperature is also a strong control on CO_2 emissions from wetland soils

335   (Gutenberg et al. 2019). Unfortunately, there is a distinct lack of ecosystem scale C exchange

336   measurements in swamps, therefore it is difficult to estimate the total C exchange from these ecosystems,

337   especially as the studies compiled in this synthesis is not looking at carbon uptake of the understory

338   vegetation and the exchange with the trees (especially as root respiration is likely present).

339   From the published literature, CH_4 emissions were substantially higher (mean emissions: 85 mg CH_4 m^{-2}

340   day^{-2}) in broad-leaved swamps compared to other swamp classes (mean emissions: needle leaved: 11.2

341   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

342   including the majority of swamps being found in temperate and subtropical locations, leading to warmer

343   soil temperatures. Furthermore, the deciduous species found in broad-leaved swamps are likely to

344   generate greater amounts of more labile litterfall, which can increase CH_4 production and emissions

345   (Amaral and Knowles, 1994; Kang and Freeman, 2002; Koh et al., 2009). One of the strongest controls

346   on CH_4 production and emissions is water table position (Calabrese et al. 2021), with the highest

347   production being found in the anoxic zones of submerged soils (Abdalla et al., 2016). Swamps can often

348   be inundated or flooded for significant periods of the year (Day et al., 1988; Day and Megonigal, 1993),

349   causing anoxic soil conditions and leading to increased rates of both CH_4 production and emissions.

350   However, this relationship can be quite complex (Moore and Knowles, 1989). Water table position within

351   the soil column is of critical importance in controlling CH_4 emissions (Moore and Knowles, 1989;

352   Davidson et al., 2019). Although both CH_4 fluxes and water table depths from the literature are lacking,

353   we did find a relationship between increasing water table depth (i.e., water tables close to or above the

354   surface of the ground) and larger CH_4 fluxes (Figure 4). Swamps can also often have higher CH_4 emission

355   rates than other peatland types due to the presence of permanent open pools of water (Bubier et al., 1995).

356   However, these flashy hydrological conditions that often occur in swamps can also allow for significant

357   dry periods throughout the year, leading to increased levels of CH_4 oxidation (Megonigal and Schelsinger,

358   2002; Koh et al., 2009). In river-floodplain swamps, the mixing of oxygen-rich river water into the water

359   column following flooding may also result in lower emissions, reducing methanogenesis (Pulliam, 1993;

360   Koh et al., 2009).

361   Although numerous studies across the world are now highlighting the importance of wetland trees as a

362   source or sink of CH_4 (Pangala et al., 2013, 2015; Covey and Megonigal 2018), there are a lack of studies

363   on tree CH_4 dynamics in swamps across Canada and the United States, therefore we did not include them

364   in this study. However, there is a potential for tree emissions to enhance the overall CH_4 emissions from

365   swamps, acting as a conduit for plant-mediated transport of CH_4, similar to aerenchymatous vegetation

366   such as sedges (Whalen, 2005). Tree emissions are typically from living trees; however, it can be

367   challenging to distinguish between the source of methanogenesis and whether the trees themselves are

368   producing CH_4 or whether they just act as a conduit (Covey and Megonigal 2018). It was estimated that

369   CH_4 emission rates from *Taxodium distichum* (bald cypress) knees in a swamp in North Carolina was

370   approximately 2.3 μmol CH_4 m^{-2} stem h^{-1} (Pulliam and Meyer, 1992).

371   Comparison of DOC concentration in soils among studies is complicated by the different sampling

372   designs employed (i.e., timing of measurements, depths samples, etc.). With that in mind, mean soil DOC

373   concentrations in swamps, 9.1–86.7 (Table 5) is slightly lower, but generally within the range of mean

374   values, 36–78 mg L^{-1}, reported for bogs and fens in North America (McKnight et al., 1985; Moore, 2003;

375   Kane et al., 2010; Khadka et al., 2016; Orlova et al., 2020). Although few studies report swamp-specific

376   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

377   and bog with mean values in North America of 5 and 22 g C m^{-2} yr^{-1}, respectively (Evans et al., 2016).

378   Thus, swamps play an important role in fluvial carbon exports and several studies report that catchment

379   scale DOC export is well-correlated to wetland area in regions where much of the wetland area is made

380   up of swamps (Creed et al., 2008; O'Connor et al., 2009; Casson et al., 2019).

381   *4.3 Soil carbon stocks*

382   Swamps, especially peat swamps, can have substantial organic matter accumulation due to persistent

383   waterlogged conditions and slower decomposition rates compared to the surrounding upland forest. For

384   example, Byun et al. (2018) showed that conifer (needle-leaved) swamps have the largest soil carbon

385   stock of wetland types in Southern Ontario (Canada) and have higher peat carbon densities than average

386   northern fens and bogs (Loisel et al., 2014). This likely relates to higher bulk densities as long-term rates

387   of peat vertical accretion in needle-leaved and mixedwood swamps (0.03 – 0.04 cm yr^{-1}, Table 6) are

388   similar to typical values from northern bogs or fens (e.g., Bysouth and Finkelstein, 2020). The high rates

389   of peat vertical accretion with the deeper peat deposits in needle-leaved and mixedwood swamps (Table

390   6) may result from a combination of acidic leaf litter, recalcitrance of needle leaves, and associated plants

391   that promote peat accumulation, including *Sphagnum* mosses in boreal regions (Le Stum-Boivin et al.,

392   2019). The proportional abundance of needle-leaved vs. broadleaved trees used to distinguish between

393   "mixedwood", and "needle-leaved" swamp varies (i.e., Dahl and Zoltai 1997). Thus, inconsistencies in

394   criteria used to define these swamp types could relate to the similarity between these two categories in

395   terms of soil properties.

396   The broad-leaved swamps considered here were distinct from the others swamp types in terms of higher

397   bulk densities and lower organic matter contents (Table 6; Figure 5). These trends may reflect the more

398   readily humified leaf litter produced by broad-leaved trees, and the hydrological setting. Broad-leaved

399   swamps are often characterized by seasonal inundation, with pooling water early in the growing season

400   related to snowmelt and runoff in some regions, thus adding inorganic material to the soil profile. Surface

401   runoff is also likely important for other swamp types as well; many swamps are situated in either riparian,

402   coastal or bottomland settings. The combination of high bulk densities and persistence of anoxic

403   conditions for at least part of the year results in high carbon stocks for the upper parts of the profiles in

404   broad-leaved swamps (Figure 5). Overall peat depths and organic matter contents are lower in broad-

405   leaved swamps, likely as a result of seasonal declines in water table position and oxic conditions

406   conducive to decomposition and CO_2 fluxes. Nevertheless, we show that even "mineral swamps" may

407   contain significant carbon stocks, particularly when deeper soil profiles are taken into consideration.

408   Paleoecological studies of long-term swamp development show the importance of ecological succession

409   and long-term hydroclimatic change, resulting in variability in swamp substrates at depth (Whitehead,

410   1972; McLachlan and Brubaker, 1995; Byun et al., 2021). These processes can ultimately result in

411   significant carbon stocks underlying present day swamps of all types.

412   A comparison of the available data on above-ground biomass in swamps (Table 2) with the soil carbon

413   stocks (Table 7) corroborates the findings of Beaulne et al. (2021) that soil carbon stocks in forested

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

422 **5.   Future research directions**

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

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

444 Additional data are needed to improve the comparisons among swamp vegetation classes across both
445 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.

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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800 **Tables**
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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

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Table 2. Summary of mean ($\pm$ 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

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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

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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

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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

	Coordinates	Soil	Tree species	Understory		Reference
			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 (g m^{-2} 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)

813

Figures

816
817 **Figure 1**. Example photographs of the four main swamp types A) broad-leaved (location: Ontario, Canada) (photo
818 credit: Dean Hiler) B) needle-leaved (location: Alberta, Canada) (photo credit: Scott J. Davidson) C) mixedwood
819 (location: Ontario, Canada) (photo credit: Scott J. Davidson) D) shrub/thicket (location: Michigan, USA) (photo
820 credit: Lars Brudvig)
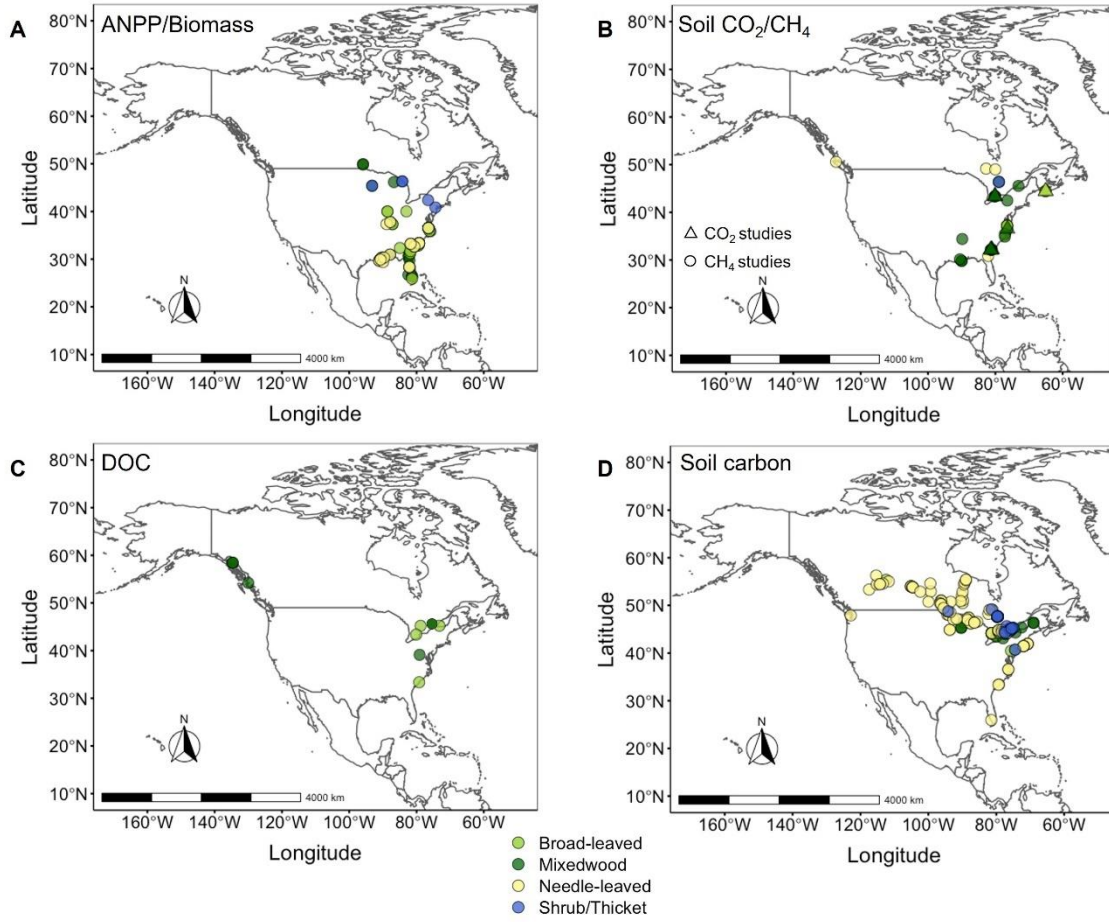
821
Figure 2. Locations of study sites for A) aboveground net primary productivity (ANPP) and biomass, B) soil carbon dioxide (CO_2) and methane (CH_4) fluxes, C) dissolved organic carbon (DOC) and D) soil carbon.

824
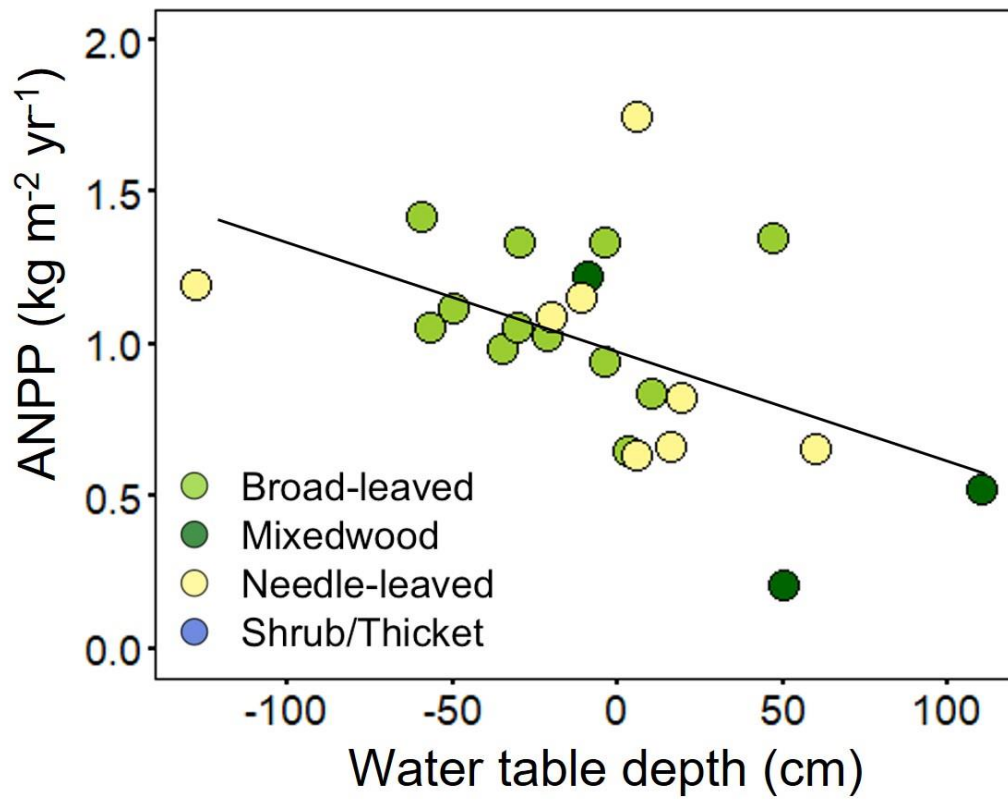
Figure 3. Aboveground net primary productivity (ANPP) as a function of water table depth (cm). A positive water table depth value indicates the water level is above the ground surface. Linear regression; y=-0.0036x+0.9799, R^2 = 0.25, p = 0.01.
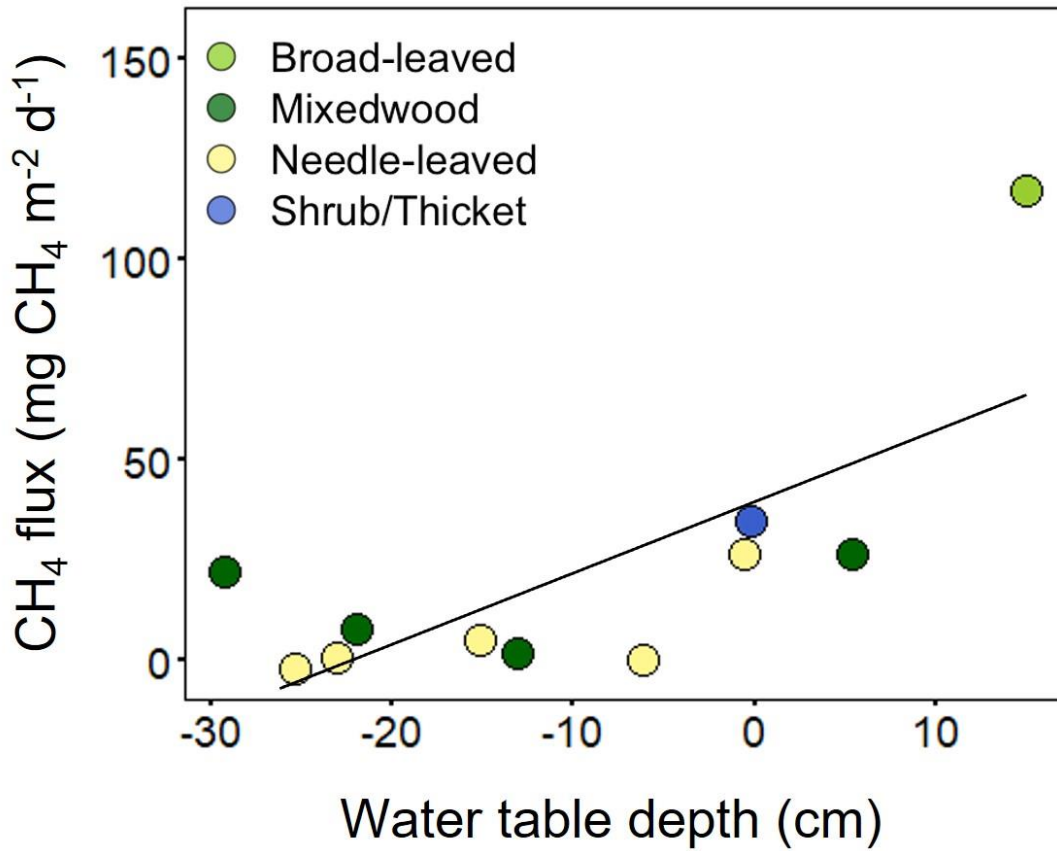
Figure 4. Swamp methane (CH_4) flux as a function of water table depth (cm). A positive water table depth value indicates the water level is above the ground surface. Due to lack of studies reporting both CH_4 flux and water table depth, we do not categorize by swamp type. Linear regression; y=-1.7395x+39.867, R^2 = 0.52, p = 0.011.
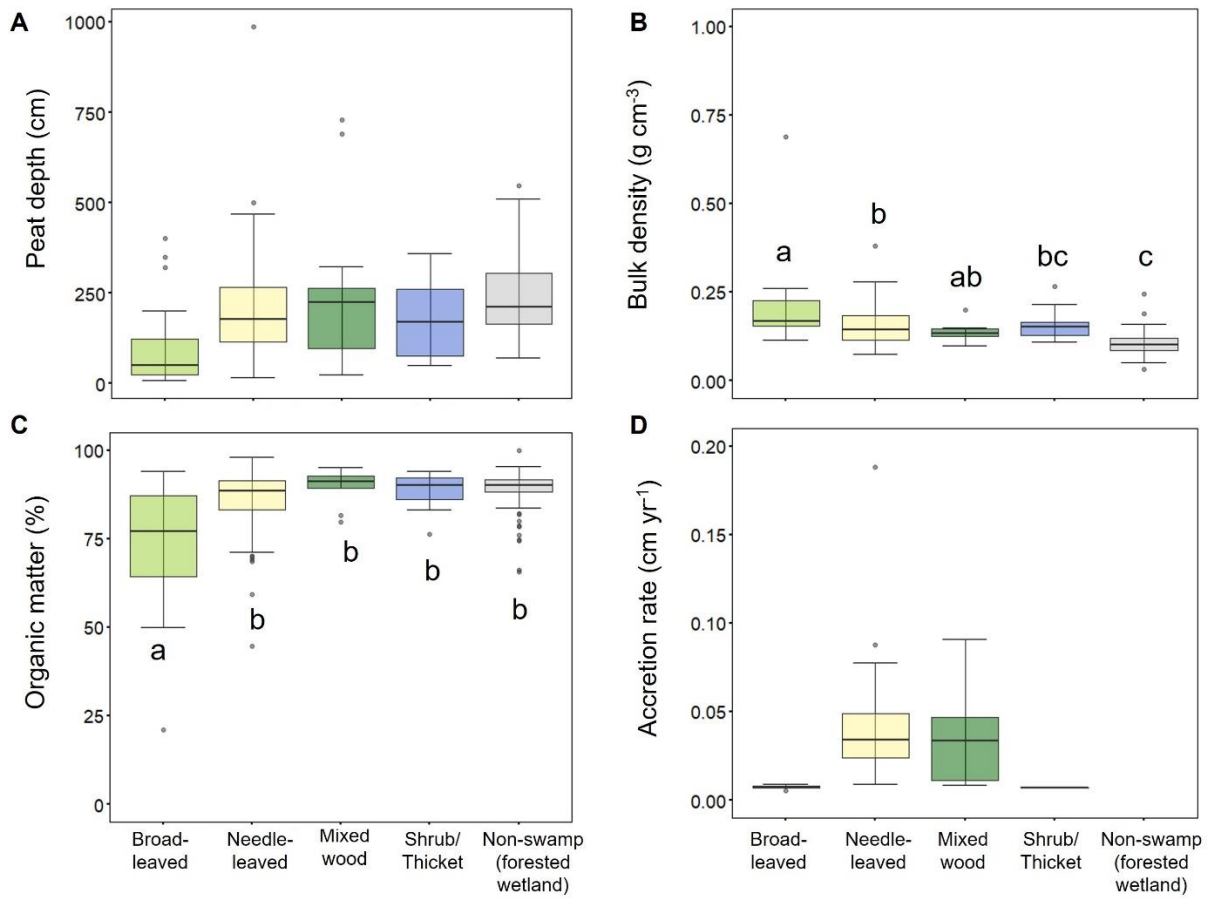
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835
836 **Figure 5.** A) peat depth (cm), B) bulk density (g cm^3), C) organic matter (%) and D) rate of peat accretion (cm yr^{-1})
837 for the four swamp types as well as forested wetlands not classified as specifically as "swamps" in ZDB (Zoltai et
838 al., 2000). Each point represents the mean value of one profile (only peat sections included). Lower case letters
839 indicate significant difference between swamp types (analysis of variance, p < .0001).
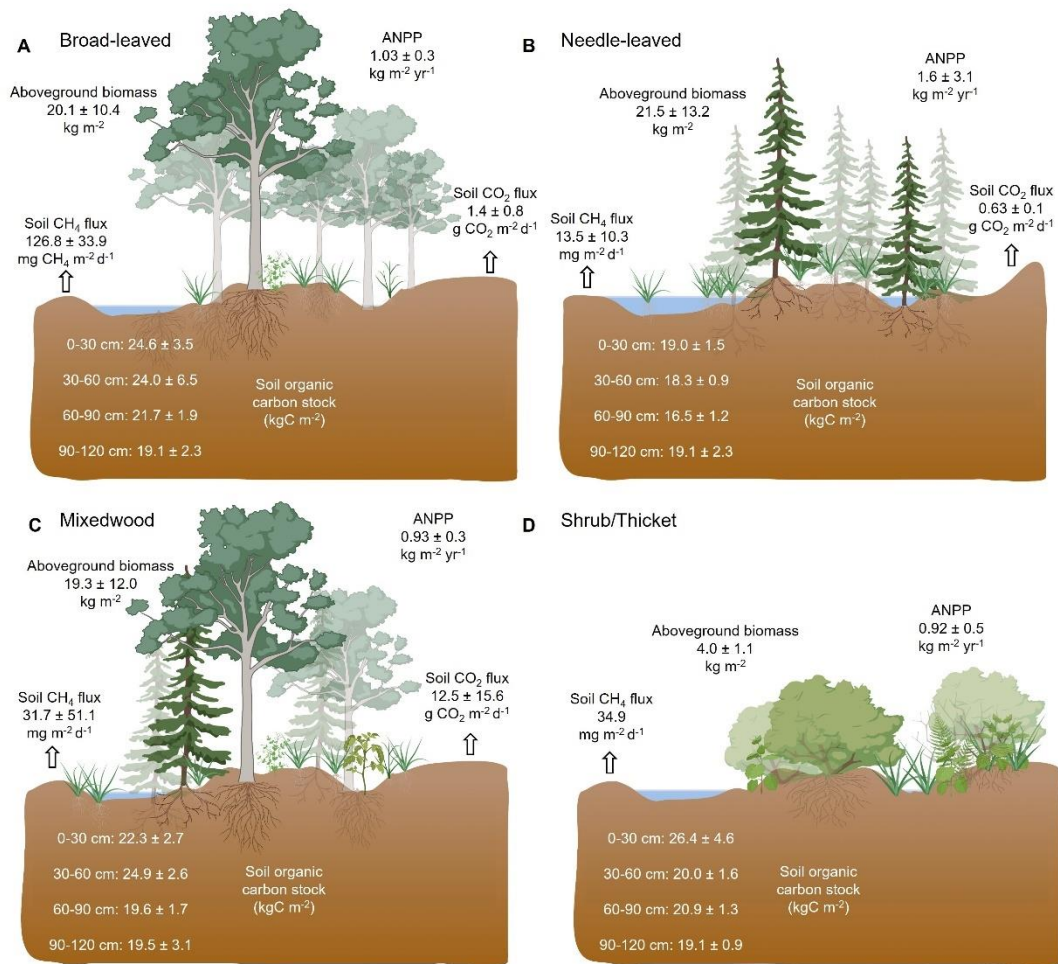
840
841 **Figure 6.** Summary of seasonal growing season mean (± SD) aboveground net primary productivity (ANPP),
842 aboveground biomass, CO_2 flux, CH_4 flux and total soil organic carbon stock for depths 0-30 cm, 30-60 cm, 60-90
843 cm and 90-120cm where available for A) broad-leaved, B) needle-leaved, C) mixedwood and D) shrub/thicket
844 swamps from the published literature. Soil CO_2 flux for broad-leaved and needle-leaved swamps is from one study.
845 No soil CO_2 flux measurements were found for shrub/thicket swamps. Please see Tables 1-7 for sample sizes used to
846 calculate the means shown here. Aboveground biomass and ANPP are presented in kg dry weight m^{-2} and kg dry
847 weight m^{-2} yr^{-1} respectively.