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2 **Carbon stocks and fluxes from a boreal conifer swamp: filling a knowledge gap for**
3 **modelling the boreal C cycle**

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20 **Key Points:**

21 • Boreal conifer swamp wetlands are an underrepresented wetland class within wetland C
22   cycling measurements and modelling

23 • These swamps store large volumes of organic C in their aboveground biomass but most
24   importantly, in their soil organic carbon stock.

25 • We also found that the ground-layer of this site is a net source of GHGs during the
26   growing season

27 **Abstract**

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

42 source of C to the atmosphere. This study provides a much-needed insight into the C dynamics
43 of these under-valued wetland ecosystems and we highlight the need for a coordinated effort
44 across boreal regions to try to improve inventories of C stocks and fluxes.

45

46 **Plain language summary**

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

60

61 **1 Introduction**

62 Northern wetlands are an important component of the global carbon (C) cycle, storing a third of
63 the soil C pool in less than 5% of the global land area (Gorham, 1991; Xu et al. 2018; UNEP,
64 2022). Their ability to store C on millennial timescales is increasingly being acknowledged as an
65 important nature-based solution to climate change through protection and restoration efforts
66 (Strack et al. 2022). However, wetlands, including peatlands, are also the largest natural source
67 of methane (CH_4) to the atmosphere (Saunois et al. 2020), making it critical to quantify C storage
68 and fluxes accurately for C accounting efforts globally.

69 One northern wetland type that poses a unique challenge when quantifying C dynamics is
70 swamp. Swamps have a larger variation in their definitions in comparison to other wetland types
71 (for example, bogs and fens which have more nationally recognised definitions (Pakarinen, 1995;
72 Zoltai & Vitt, 1995)). These include being classified based on tree species/height and cover,
73 landform, hydrological regime, physiographic position relative to non-wetland landscapes, and
74 soil type (Davidson et al. 2022). Although they have variable definitions across the literature,
75 swamps across northern regions are generally identified by their highly variable hydrological
76 conditions and having at least 25% tree cover (with tree heights over 5 m i.e., NWWG, 1997;
77 Ducks Unlimited, 2021). Despite this, it can be challenging to identify and classify them in the
78 landscape (Locky et al. 2005; Davidson et al. 2022). For example, treed swamps may be
79 identified as upland forests, while wetter shrub swamps may be confused as fens (Locky et al.
80 2005). As such, they are often misclassified or overlooked in many wetland inventories, and it is
81 particularly difficult to spatially delineate swamps associated with other ecosystem types (e.g.,
82 on the margin of fens/bogs or uplands). Unlike other northern wetland types, such as bogs and
83 fens, swamps can be considered either mineral or peat-forming based on different wetland

84   classification schemes (NWWG, 1997). However, if strictly defined as only mineral wetlands,
85   significant C stocks are being missed from organic wetland inventories, despite nearly all swamp
86   sub-catogories demonstrating they not only meet organic soil depth definitions for peatlands, but
87   also hold significant C mass per unit area (Byun et al. 2018; Davidson et al. 2022; Dazé et al.
88   2022). Further, the variability in hydrological conditions in swamps, ranging from being
89   permanently flooded to seasonally indundated allow swamp trees to grow taller compared to
90   other forested wetland types, and therefore have ability to store more aboveground biomass
91   (Locky et al. 2005; Elmes et al. 2021).

92   Better characterizing C stocks in swamps is especially important given the potentially large
93   amount of organic matter and C stored in these ecosystems that is being overlooked. Accurately
94   quantifying the role swamps play within northern wetland C dynamics requires an understanding
95   of how these ecosystems differ from (or are similar to) other wetland types (Byun et al. 2018;
96   Beaulne et al. 2021). For example, Davidson et al. (2022) found that aboveground biomasses in
97   swamps (ranging from $4.0 - 21.5$ kg m^{-2}) are significantly larger than those found in treed bogs
98   and fens ($1.2 - 2.3$ kg m^{-2}), with swamps also having larger aboveground net primary
99   productivity (NPP) values than the range for bogs and fens, at $0.92 - 1.57$ kg m^{-2} yr^{-1} and $0.2 -$
100 0.4 kg m^{-2} yr^{-1}, respectively.

101   Developing relationships with water table and soil temperature in these ecosystems can be
102   difficult due to the variability in hydrological conditions, leading to constantly changing redox
103   conditions or lags/hysteresis – especially important for CH_4 production/emissions (Davidson et
104   al. 2019). Further, more tree cover means that shading could influence understory vegetation
105   productivity to a greater extent than other wetland types (Bisbee et al. 2001), and significant
106   litter inputs from the overstory means that soil respiration is not necessarily driven solely by
107   understory inputs (Webster et al. 2008), unlike many other wetland types (Phillips et al. 2010).

108   Despite key differences in the drivers of C cycling in swamps compared to other wetland types,
109   there remains few studies in northern regions as identified by Davidson et al. (2022). This is
110   especially true for the Boreal Region of Canada, which holds approximately 60% of the 1.1
111   million km^2 of peatland area within the country, with a significant portion of this area potentially
112   classified as swamp (Riley, 1994; Amani et al. 2019). These data gaps have led to their exclusion
113   from national greenhouse gas inventories and databases (e.g., IPCC, 2014; Kuhn et al. 2021),
114   land cover mapping (Olefeldt et al. 2021), and modelling efforts (Bona et al. 2020) and there are
115   few relevant process-based models that can be used to assess swamp ecosystem dynamics (Bona
116   et al. 2020). Developing such models and assessing the resilience of swamps to future
117   environmental change requires robust empirical data to allow for assessment of contemporary C
118   stocks, greenhouse gas exchanges and environmental drivers for both. Therefore, in this study we
119   aimed to (1) quantify the C stocks and fluxes at a representative wooded coniferous swamp
120   located in boreal Canada and (2) evaluate the key similarities and differences of this site to other
121   wetland types in the region.

122   **2 Materials and Methods**

123   **2.1 Study site**

124   The study was undertaken in a boreal wooded coniferous swamp (hereafter referred to as Heaven
125   Swamp), approximately 30 km north of Fort McMurray, Alberta, Canada (56°57'28.0"N
126   111°33'24.0"W). The study site is a fragment of swamp within a wider managed landscape. This
127   site is approximately 10 ha and was classified using the Ducks Unlimited Canada Alberta
128   Wetland Classification System (Ducks Unlimited, 2021). The hydrology of the site is largely
129   influenced by groundwater inputs from the surrounding upland landscape. The mean annual
130   temperature (1981-2010) is 1 °C, and mean annual precipitation is approximately 420 mm
131   (Environment Canada, 2017). This swamp is dominated by an overstory of *Picea mariana* (Mill,)
132   *Larix laricina* (Du Roi) K.Koch, Britton, (L.) and an understory of typical shrubs such as
133   *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Vaccinium oxycoccos* (L.) MacMill, and
134   *Vaccinium vitis-idaea* L. as well as mosses such as *Sphagnum squarrosum* (Crome) and feather
135   mosses, largely *Hylocomium splendens* (Hedw.) Schimp and *Ptilium crista-castrensis* (Hedw.)
136   De Not. All vegetation was identified to the highest taxonomic resolution possible in the field,
137   with nomenclature following the most recent records from the Integrated Taxonomic Information
138   System (ITIS, 2023).The peat depth within study locations at Heaven Swamp ranges between 2
139   and 3.5 m.

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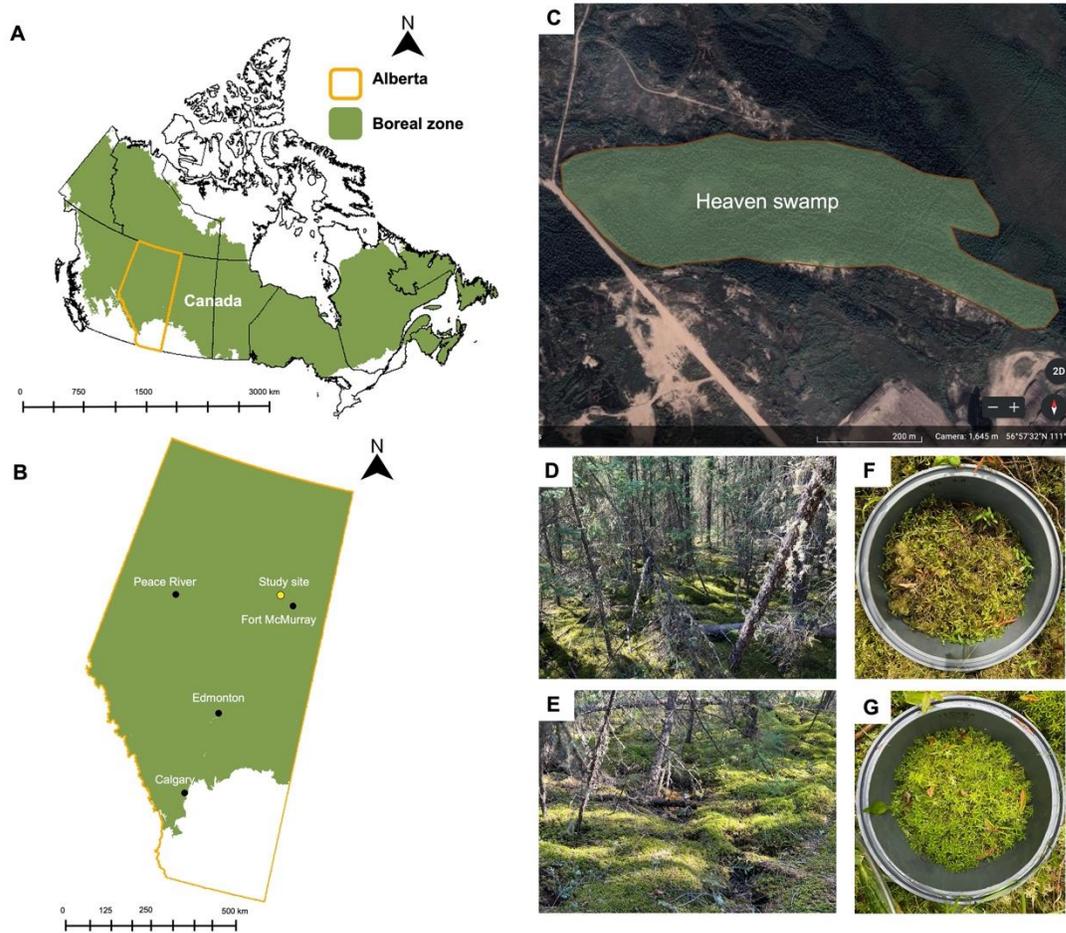
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143 **Figure 1.** The location of the boreal zone (NRCan North American boreal zone layer; Brandt, 2009) and Alberta
144 within Canada (A), the location of the study site within Alberta (B), the location of the study area (Heaven Swamp:
145 56°57′28″ N, 111°33′24″ W) (base map: Google Earth: TerraMetrics (Accessed 25/06/2023) (C) and photographs of
146 the typical tree density (D), example of understory vegetation community (E), example of representative feather
147 moss flux collar (F) and example of representative sphagnum flux collar (G). Maps shown in A and B are adapted
148 from Davidson et al. (2021).

149 2.2 Tree inventory and biomass

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

156 **Table 1.** Allometric equations used to estimate above and belowground biomass of trees at Heaven Swamp. AG:
157 aboveground biomass; DBH: diameter at breast height (1.4 m); TH: tree height; BG: belowground biomass

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

158

2.3 Peat characteristics

160 Peat cores were collected near the southwest corner of the tree inventory plots to determine the
161 soil C stocks of the uppermost 50 cm of peat (see Figure S1). A replicate core was taken at site
162 three for a total of 4 cores. Bulk density (g cm^{-3}) was determined on 10 cm depth intervals for a
163 total of 5 samples per core. Each sub-section was dried in the oven at 60 °C for 2 days or until
164 the sample reached constant weight. Organic matter (OM) content (%) was calculated using the
165 loss on ignition (LOI) method (Rowell, 1995). Approximately 2 g of each dried sample was
166 weighed and then burned in a muffle furnace at 550 °C for 3 hours. After burning the samples,
167 they were left to cool overnight and weighed post ignition. OM is calculated as the difference
168 between pre-ignition and post-ignition mass expressed as a percentage of pre-ignition mass. A 1
169 mg subsample was taken from each 10 cm depth interval for C and nitrogen (N) analysis. Each

170   subsample was ground to a fine powder using a Retsch ball mill and analysed for C and N
171   content using a 4010-elemental analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL
172   (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer at the University
173   of Waterloo, Canada. Soil organic carbon (SOC; kg m^2) content for each sub section was
174   calculated by first multiplying the bulk density (converted to kg m^3) by the total C content, and
175   then by 0.1 (in meters) to account for the depth of the sample. These values where then summed
176   to estimate the total soil C stock within the upper 50 cm.

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

181   $$SOC = 0.485*(peat\ depth;\ cm) + 13.532\ (\pm17\%)\qquad Eq.\ 1$$

2.4 Understory Vegetation

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

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

2.5 Carbon dioxide (CO_2) flux

200   Carbon dioxide (CO_2) fluxes were measured using the closed chamber method 12 times between
201   25th May and 16th August 2022 (representative of the growing season ranging from completely
202   snow free to the beginning of plant senescence). Within the two dominant vegetation
203   communities (feather moss and sphagnum), six PVC collars per community (co-located in
204   groups of three collars, height 15 cm x diameter 20 cm) were installed to a depth of
205   approximately 8 cm in May 2022. Collars were in place for one week before the first flux
206   measurements were taken. To investigate soil only fluxes of CO_2 (and CH_4), six more collars
207   were installed but the vegetation (originally feather moss) was clipped from within the collar at
208   soil level, totalling 18 collars. The height of the collar was measured from the soil surface to give
209   the correct chamber headspace volume for flux calculations.

210 CO_2 concentrations were measured in a clear acrylic chamber (20 cm diameter x 50 cm height)
211 placed on each flux collar, with water poured around the collar edge to create an airtight seal.
212 Measurements were collected at 15 s intervals for 105–120 s using a portable infrared gas
213 analyzer (EGM-4, PP Systems, Massachusetts, USA). A battery powered fan was used to mix the
214 chamber headspace. A thermocouple located within the chamber, attached to a thermometer was
215 used to measure air temperature during sampling. Relative humidity and photosynthetically
216 active radiation (PAR) were also measured within and on top of the chamber respectively with
217 sensors connected to the EGM-4. A neoprene sleeve was used to create fully dark conditions,
218 enabling ecosystem respiration (ER) to be measured. Order of sampling plots was randomised
219 daily to account for different light levels and solar angles throughout the day. Net ecosystem
220 exchange (NEE) is the overall exchange and direction of C movement between the atmosphere
221 and an ecosystem, here measured under full sun. Gross ecosystem productivity (GEP) is
222 calculated as the difference between NEE and ER. In this study, we use the sign conventions that
223 C uptake from the atmosphere is negative and emission to the atmosphere is positive. We
224 subtracted CO_2 emissions from the clipped plots from the vegetated plots to represent
225 autotrophic respiration. Raw data were inspected for linearity of fluxes, controlling for fit of $R^2 \geq$
226 0.75, except for fluxes that were relatively unchanging (<2 ppm over the closure period),
227 representing a flux close to zero. Quality control resulted in a data loss of 12%.

228 **2.6 Methane (CH_4) flux**

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

241 **2.7 Environmental variables**

242 A groundwater well made of PVC pipe (4 cm diameter x 100 cm long), slotted along the full
243 length and covered in mesh, was installed adjacent to each set of three co-located collars to
244 measure water table depth (WTD; relative to the ground surface). A soil temperature profile was
245 collected at each collar during each flux measurement at -30, -25, -20, -15, -10, -5, -2 cm from
246 ground surface. The first two rounds of flux measurements did not have WTD, or soil
247 temperature data collected due to the ground still being frozen.

248 **2.8 Statistical analysis**

249 All statistical analysis was undertaken in R version 3.6.1 (R Core Team, 2019), and all output
250 and models were inspected for normality and homogeneity of residuals (Zuur et al., 2009), with

251 statistical significance considered at α = 0.05. The relationship between C and organic matter
252 content in the upper 50 cm of the three peat profiles in this study was evaluated using the *lm*
253 (linear regression) function in R. The linear fit was forced through the origin to evaluate the ratio
254 between the two values.

255 Due to the C flux data being not normally distributed, an unpaired two-sample Wilcoxon test was
256 used to evaluate significant differences in CO_2 and CH_4 fluxes between the feathermoss and
257 sphagnum plots.

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

264 **3 Results**

265 **3.1 Above- and belowground C stocks**

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

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

289

290 **Table 2.** Total tree above and belowground biomass and tree height for trees < 1.6 m for the
291 three subplots at Heaven Swamp. Value in brackets is the standard deviation of the estimate from
292 the allometric equation converted as appropriate using error propagation rules.

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

293
294

295

296 **Table 3**. Total understory biomass for the three subplots at Heaven Swamp. Triplicates were
297 performed at each subplot (N=3). Value in brackets is the standard error of the mean.

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

	HS-1	HS-2	HS-3
Basal Area (m² ha⁻¹)	38.7	25.5	21.5
DBH Average (cm ± SD)			
Larix laricina (LL)	8.5 ± 5.0	3.5 ± 1.7	3.3 ± 2.7
Picea mariana (PM)	6.5 ± 4.0	6.1 ± 3.8	9.3 ± 3.7
N (LL,PM)	20,52	48,49	57,17
Stand Density (stems ha⁻¹)	7200	9700	7400

Carbon Stocks (kg C m⁻² ± SE)

	HS-1	HS-2	HS-3
Tree Aboveground	6.9 ± 1.4	4.2 ± 1.2	3.7 ± 0.5
Tree Belowground	1.6 ± 1.1	1.0 ± 1.0	0.9 ± 0.9
Understory x1000	0.014 ± 0.008	0.017 ± 0.016	0.044 ± 0.037
Soil Organic (upper 50 cm)	25.4	22.0	19.7
Total Soil Organic (minimum estimate)	121.9 ± 20.7	132.4 ± 22.5	128.5 ± 21.8
Peat Depth (N=9; m)	2.23 to >2.4	2.45 to >2.6	2.37 to >2.5

298

299 **Figure 2**. Schematic representation of the characteristics of the three sub-sites within the Heaven
300 Swamp complex. Aboveground tree biomass is shown in pale green. The biomass of the
301 dominant understory vegetation is shown in dark green. The relative depth of the upper 50 cm
302 soil organic layer and the estimated total soil organic layer are shown in light and dark brown
303 respectively (shading grey towards mineral layer at depth). Trees are not to scale but are
304 representative of the variation in canopy openness and species (LL = *Larix laricina*, PM = *Picea*
305 *mariana*). Tree counting was performed within a 10 × 10 m plot at each site. Standard errors are
306 shown by ± values.
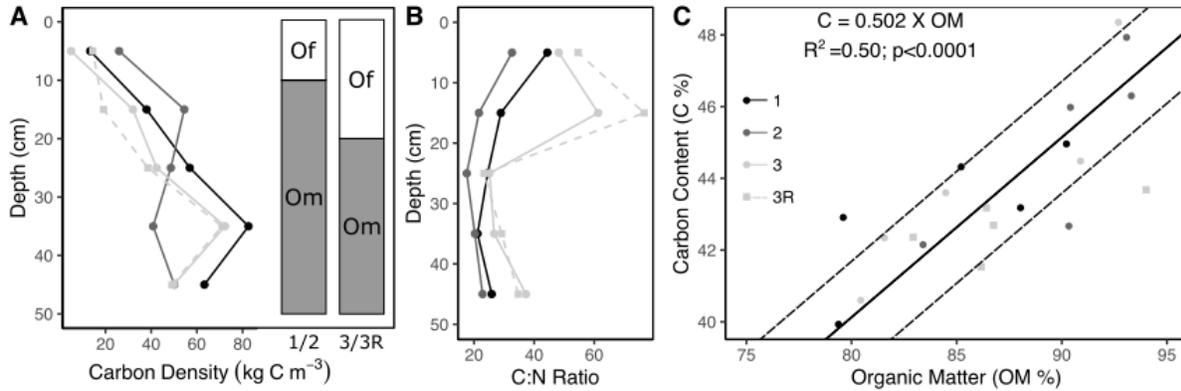
307

308 **Figure 3**. Belowground C density and soil classification (A), C:N ratio (B), and the relationship
309 between C and organic matter content (C) for the upper 50 cm peat profile from three plots at
310 Heaven Swamp. Linear regression in (C) was forced through (0,0) prior to fitting and dashed
311 lines are the residual standard error. Soil classification after Agriculture and Agri-food Canada
312 (1998). Of: organic-fibric; Om: organic-mesic.

3.2 CO$_2$ and CH$_4$ fluxes and associated environmental drivers

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

Despite having productive vegetation in the flux collars (Figure S2), understory NEE was largely positive across the measurement period (Figure 4C/5C), indicating that for the 2022 growing season, the understory was a net source of CO$_2$ to the atmosphere, due to larger losses of CO$_2$ via ER than uptake via GEP. Although the mean CO$_2$ fluxes were higher in the sphagnum plots than in the feather moss plots (Table 4), no significant difference in GEP (Wilcoxon signed rank test; z = -1.81, p = 0.07), ER (Wilcoxon signed rank test; z = -0.47, p = 0.63) or NEE (Wilcoxon signed rank test; z = -0.011, p = 0.9) was found. Likewise, although mean CH$_4$ flux were higher in the sphagnum plots (49.9 mg CH$_4$ m^{-2} d^{-1}) compared to the feather moss plots (30.6 mg CH$_4$ m^{-2} d^{-1}) the difference was not significant (Wilcoxon signed rank test; z = -1.27, p = 0.21) (Figure 5D). Clipped vegetation plots had much smaller fluxes than vegetated counterparts, with a mean ($\pm$ SD) soil CO$_2$ flux of 6.9 (4.6) g CO$_2$ m^{-2} d^{-1} and mean ($\pm$ SD) soil CH$_4$ flux of 5.3 (11.9) mg CH$_4$ m^{-2} d^{-1} (Figure S3). The difference in ER between clipped and unclipped plots (4.3 g CO$_2$ m^{-2} d^{-1}) indicates that understory plant respiration accounted for 44-48% of understory ER.

A significant relationship was found between NEE and WTD (LME, $F_{1,72}$ = 7.2, p = 0.0089; Figure 6A) but not for GEP and ER. A significant relationship was also found between NEE and soil temperature at 10 cm depth (LME, $F_{1,72}$ = 45.3, p < 0.001) and ER and soil temperature at 10 cm depth (LME, $F_{1,72}$ = 55.9, p <0.001; Figure 6B). The LME models explained 65% and 57% of the variance in NEE and ER respectively. The model only explained 12% of the variance in GEP. No significant relationship was found between GEP and soil temperature (LME, $F_{1,68}$ = 0.004, p = 0.9), however there was a significant relationship found between GEP and GCC (LME, $F_{1,68}$ = 8.01, p = 0.0061; Figure 6C), unlike NEE and ER. Finally, no significant relationship was found between CH$_4$ emissions and either WTD (Figure 6D) or soil temperature at 30 cm depth (LME, $F_{1,23}$ = 0.01, p = 0.9 and LME, $F_{1,23}$ = 1.8, p = 0.2 respectively).

Table 4. Summary (Mean $\pm$ SD) of the C flux (gross ecosystem productivity; GEP, ecosystem respiration; ER, net ecosystem exchange; NEE, eCH$_4$, soil temperature (ST) and water table depth at both vegetation flux collar types at Heaven Swamp.

Plot type	GEP	ER	NEE	CH$_4$	ST at 10 cm depth	ST at 30 cm depth	Water table depth
	g CO$_2$ m^{-2} d^{-1}			mg CH$_4$ m^{-2} d^{-1}	°C		cm bgs
feather moss	-1.8 (4.0)	12.6 (9.1)	10.5 (8.6)	30.6 (46.0)	11.9 (3.6)	8.5 (2.7)	12.2 (6.7)
sphagnum	-2.6 (3.6)	13.6 (9.7)	11.1 (10.5)	49.9 (74.7)	11.3 (3.9)	8.4 (2.9)	11.3 (5.7)

| clipped | - | 6.9[a] (4.6) | - | 5.3[a, b] (11.9) | 12.0 (3.2) | 7.9 (2.8) | 8.3 (11.1) |

[a] Soil only flux.
[b] CH_4 flux measurements for only May-June
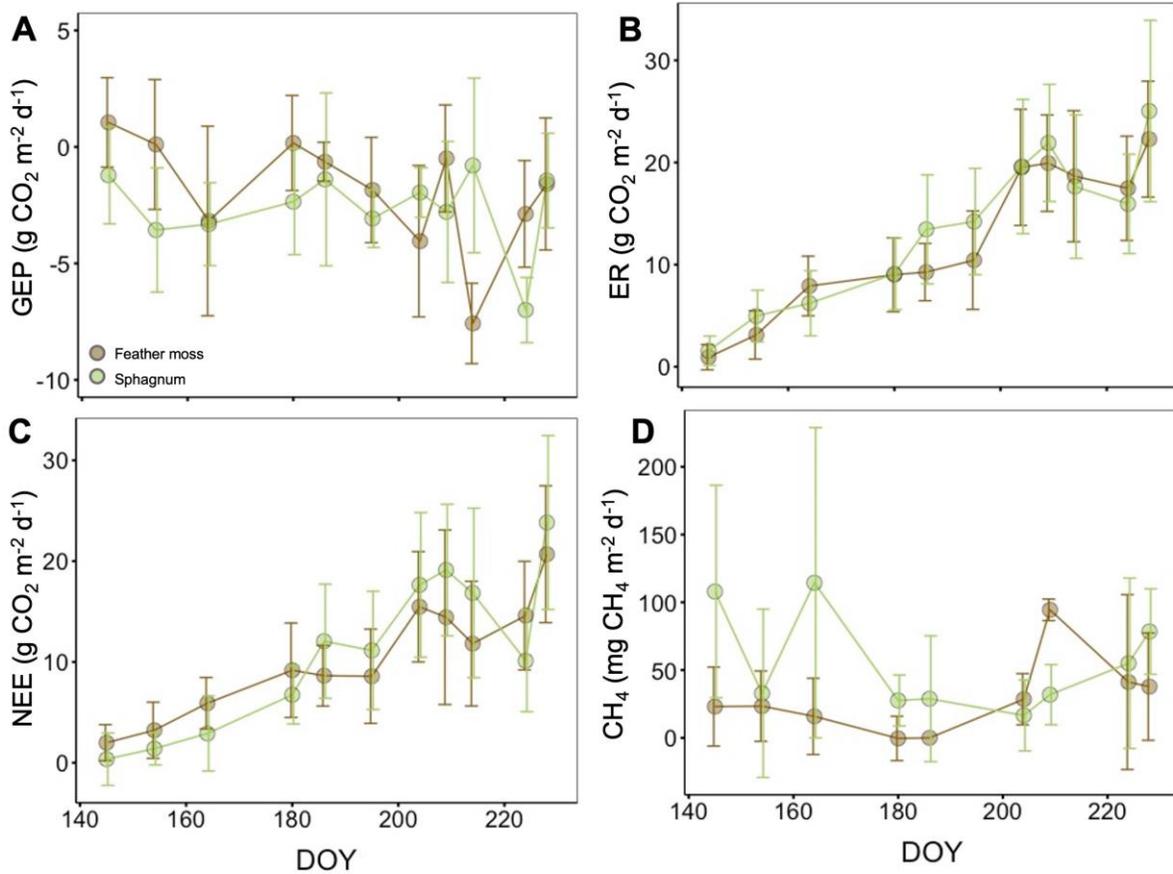
345

346 **Figure 4**. Time series plots of gross ecosystem productivity (GEP; g CO_2 m^{-2} d^{-1}) (A),
347 ecosystem respiration (ER; g CO_2 m^{-2} d^{-1}) (B), net ecosystem exchange (NEE; g CO_2 m^{-2} d^{-1}) (C)
348 and CH_4 flux (mg CH_4 m^{-2} d^{-1}) (D) measurements for both feather moss (n=6) and sphagnum
349 (n=6) collars at Heaven Swamp.
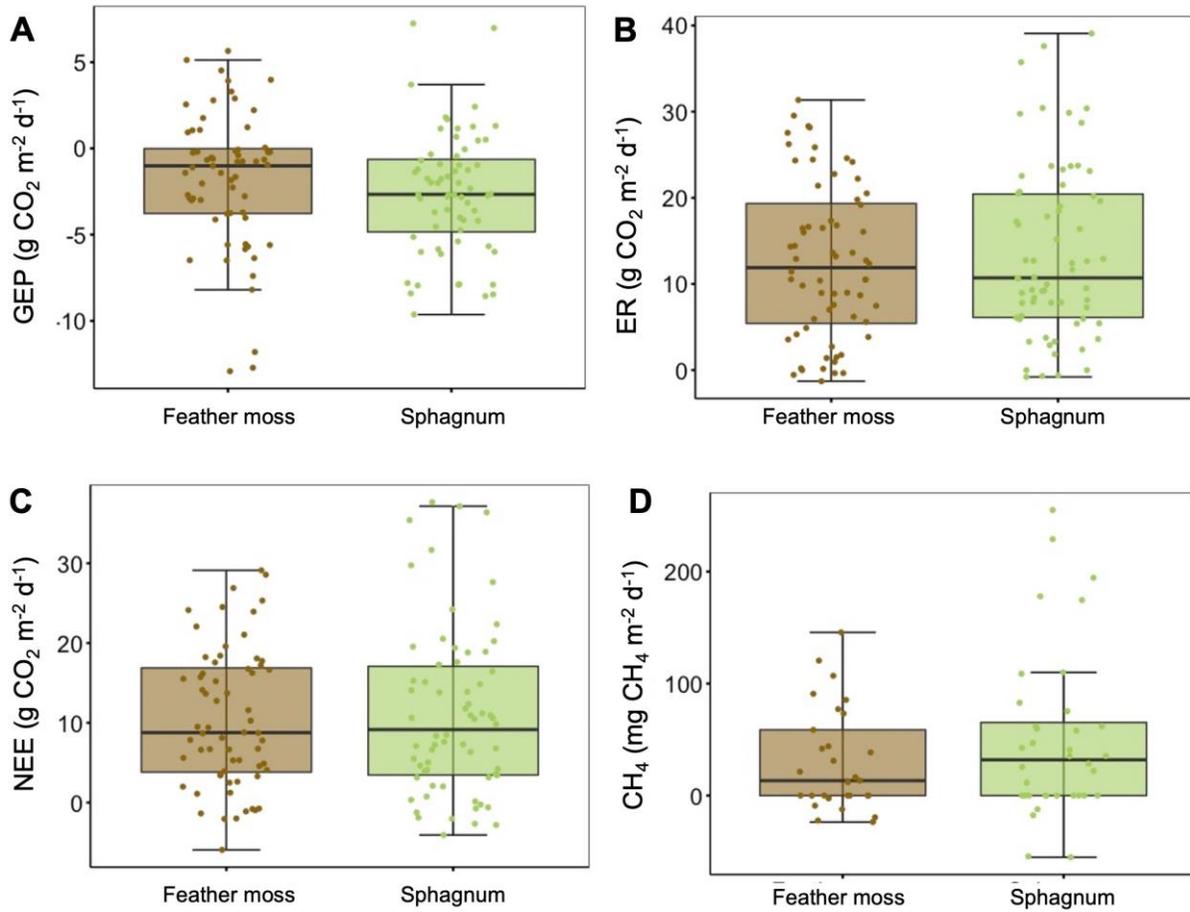
350
351 **Figure 5**. Gross ecosystem productivity (GEP; g CO_2 m^{-2} d^{-1}) (A), ecosystem respiration (ER; g
352 CO_2 m^{-2} d^{-1}) (B), net ecosystem exchange (NEE; g CO_2 m^{-2} d^{-1}) (C) and CH_4 flux (mg CH_4 m^{-2} d^{-1}
353 $^{-1}$) (D) measurements for both feather moss (n=6) and sphagnum (n=6) collars at Heaven Swamp.
354
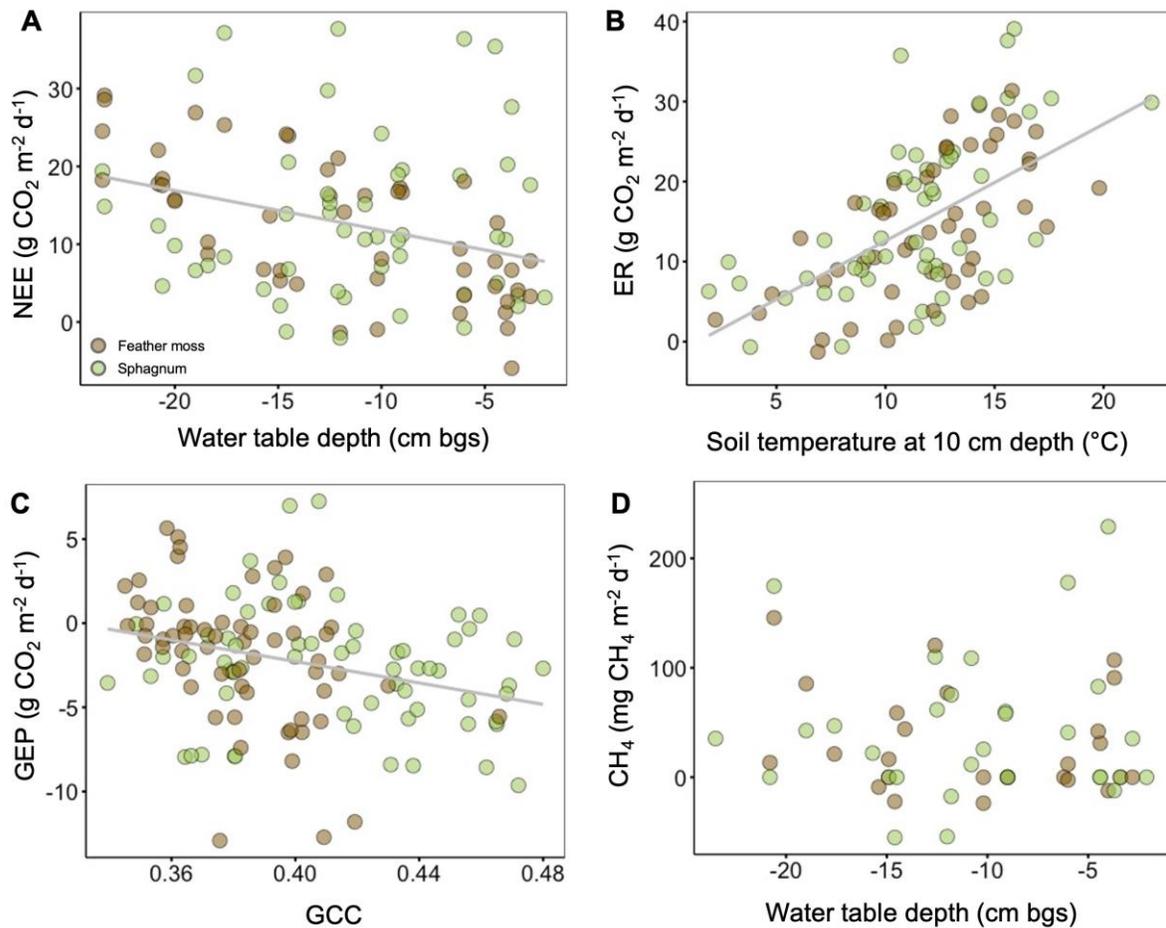
355
356 **Figure 6**. Relationship between water table depth (bgs; below ground surface) and net
357 ecosystem exchange (NEE; g CO_2 m^{-2} d^{-1}) (A), soil temperature at 10 cm depth (°C) and
358 ecosystem respiration (ER; g CO_2 m^{-2} d^{-1}) (B), green chromatic coordinate (GCC) and gross
359 ecosystem productivity (GEP; g CO_2 m^{-2} d^{-1}) (C) and water table depth (below ground surface)
360 and methane emissions (CH_4; mg CH_4 m^{-2} d^{-1}) for both vegetation plot types at Heaven Swamp.

361 **4 Discussion**

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

368 **4.1. Above- and belowground C stocks**

369 Overall, all plots contained sizeable stocks of C with an overall mean of 134 kg C m^{-2}. Mean
370 aboveground biomass was 5 kg C m^{-2}, which is low compared to the mean of all needle-leaved
371 swamps of 22 kg C m^{-2} (Davidson et al. 2022). However, most of the biomass measurements

372 synthesised by Davidson et al. (2022) are from south of 40 °N, and therefore their value is likely
373 to be unrepresentative of biomass C stocks in cool temperate and boreal swamps. Our value is
374 the same as mean estimates of aboveground C biomass for boreal forest in the same region
375 (Banfield et al. 2002), suggesting little difference between swamp and upland forest C stocks in
376 this region. The forest understory made a negligible contribution to total aboveground C stocks.
377 In contrast, approximately 95% of total C stocks were found as SOC. This was due to a
378 combination of deep peat (> 2m) and high C content; 50% of soil organic matter was C, in
379 keeping with synthesised data for northern herbaceous and woody peat (Loisel et al. 2014). As
380 such, our results are similar to those from forested peatlands in eastern Canada, where C stored
381 as tree biomass (1.5–5.7 kg C m^{-2}) was considerably less than SOC (23–170 kg C m^{-2}) (Magnan
382 et al. 2020; Beaulne et al. 2021). SOC stocks reported by Beaulne et al. (2021) and Magnan et al.
383 (2020) are smaller than ours (~ 130 kg C m^{-2}) because their peat depths were only 0.4–1 m. Our
384 SOC stock estimate is higher than those reported for upland boreal forests (ranging between 8
385 and 16 kg C m^{-2} (Banfield et al. 2002; Marty et al. 2015).

386 **4.2. CO_2 and CH_4 fluxes and associated environmental drivers**

387 Despite large belowground C stocks, over the course of the growing season the understory/soil of
388 Heaven Swamp was a source of both CO_2 and CH_4. There was no significant difference in CO_2
389 or CH_4 fluxes between feather moss and sphagnum collars. This result is at odds with work
390 suggesting differences in photosynthetic properties between these two moss groups (Kangas et
391 al. 2014) but may simply arise due to the low number of collar replicates. For CO_2, overall mean
392 GEP was -2.6 g CO_2 m^{-2} d^{-1}, whilst ER was 13.1 g CO_2 m^{-2} d^{-1}, resulting in a net efflux of CO_2.
393 ER correlated positively with soil temperature, reflecting the well-understood response of
394 microbial respiration to warmer conditions (Silvola et al. 1996). A similar result to Davidson et
395 al. (2021) was found in relation to increasing vegetation greenness (GCC) and GEP, showing
396 that more productive vegetation (i.e., greater CO_2 uptake) is related to green leaf phenology. In
397 general, there is a lack of measurements of swamp CO_2 fluxes, and those that do exist
398 overwhelmingly focus on soil fluxes only (Davidson et al. 2022). Nevertheless, our ER fluxes
399 are comparable to those from northern swamps (beyond 40°N) for which the collated mean is
400 14.7 g CO_2 m^{-2} d^{-1} (Davidson et al. 2022). Despite measured net emission measured for
401 understory NEE, our data do not necessarily suggest that Heaven Swamp is a net source of C to
402 the atmosphere. In northern swamps, litterfall inputs of C can be particularly high (e.g., 540 g m^{-2}
403) and outweigh gaseous C losses (Kendall et al. 2021). Similarly, NPP of trees could also offset
404 gaseous C losses (Laine et al. 1996), with estimates of NPP in black spruce stands ranging from
405 44 g dry mass m^{-2} yr^{-1} in a moderate rich fen in Alberta (Szumigalski and Bayley, 1996) to 144 g
406 C m^{-2} yr^{-1} in a black spruce stand with a 20 to 30 cm organic layer over mineral soil in
407 Saskatchewn (Gower et al. 1997) . Without measuring or modelling all CO_2 pathways in Heaven
408 Swamp, no firm conclusions can be drawn.

409 Overall mean CH_4 flux from feather moss and sphagnum collars was ~40 mg m^{-2} d^{-1}, which is
410 similar to the synthesis value for swamps given by Turetsky et al. (2014). The mean emission
411 from collars where vegetation was clipped was lower, at 5.3 mg m^{-2} d^{-1}. Methane measurements
412 from clipped collars only took place for two months, and thus are not directly comparable with
413 vegetated collars. However, we can estimate that understory autotrophic respiration was 4.3 g
414 CO_2 m^{-2} d^{-1}, substantially lower than the ER measured (~13 g CO_2 m^{-2} d^{-1}), a similar pattern
415 shown by Munir et al. (2017) in a drained black spruce bog. The lack of a relationship between

416   CH$_4$ flux and WTD is perhaps surprising, considering how WT is often viewed as a dominant
417   control on peatland CH$_4$ emission (e.g., Turetsky et al. 2014; Evans et al. 2021). However, this
418   relationship is frequently only apparent at large spatial/multi-site scales and/or over longer time
419   periods (Treat et al. 2007), and many studies do not find WTD as an overriding control (e.g.,
420   Laine et al. 2007; Levy et al. 2012; Green et al. 2018; Wen et al. 2020), including in swamps
421   (Koskinen et al. 2016). Within individual sites, WTD is not always an effective proxy for zones
422   of CH$_4$ production, because peat soils can be highly heterogeneous with oxic areas below the
423   water table and anoxic areas above it, over very small (cm^2) scales (Askaer et al. 2010).
424   Additionally, at our site WTD varied across a comparatively small range, 2-24 cm below the peat
425   surface. Other studies have suggested that WTD acts as a "cut-off" for CH$_4$ production, with
426   emissions increasing rapidly as WTD becomes shallower than 20-30cm (Couwenberg & Fritz,
427   2011; Levy et al. 2012; Evans et al. 2021; Hondula et al., 2021a). Furthermore, and in contrast to
428   both bogs and fens, swamps have a broad range of WTDs where large CH$_4$ emissions can occur
429   (Turetsky et al. 2014). Other studies of forested peatlands have observed large variation in CH$_4$
430   fluxes over small scales (e.g., 15 m, Korkiakoski et al. 2017). Thus, we assume in our study that
431   WTD was conducive to maintain CH$_4$ emissions throughout the measurement period, and other
432   factors (temperature, vegetation, soil structure, nutrients, etc) were implicated in driving
433   higher/lower emissions from day to day. A second possibility is that WTD and CH$_4$ were related,
434   but that this relationship was obscured due to hysteresis (e.g., Moore & Dalva, 1993; Laine et al.
435   2007).

4.3. Implications

437   Our results show that Heaven Swamp has sequestered large volumes of organic C in biomass and
438   soil and continues to play an active role in ecosystem-scale gaseous C cycling. SOC stocks at
439   Heaven Swamp (~ 130 kg C m^{-2}) are approximately the same as those in other Canadian
440   peatlands (50 – 220 kg C m^{-2}; Akumu & McLaughlin, 2013; Beilman et al. 2008) which, on face
441   value, suggests that boreal swamps are not "special cases" that require additional scrutiny and
442   should be included in estimates of boreal peatland area. However, this is only half of the story;
443   this site is classified as upland in the Alberta Biodiversity Monitoring Institute's Wetland
444   Inventory (DeLancey et al. 2020) and therefore soil C stocks would potentially not be fully
445   accounted for. The landscape-scale importance of northern swamps as "cryptic wetlands" has
446   long been recognised for aquatic C exports (Creed et al. 2003), but the unmapped "cryptic
447   carbon" these swamps hold is only now being properly considered. Emerging research in the
448   United States suggests that forested wetlands contain vast stores of previously unaccounted C
449   (Stewart et al. 2023). Similarly, although many forested wetlands are small (such as Heaven
450   Swamp), their abundant natures means that their cumulative CH$_4$ emissions can influence
451   landscape-scale budgets (Hondula et al. 2021b). Thus, there is a clear need to accurately map
452   these swamps, their hydrology, and their C stocks and fluxes, to properly inform regional,
453   national, and global budgets.

454   Furthermore, a timely accounting of the role these swamps play in C and greenhouse gas cycling
455   is also necessary to define a baseline from which future global change can be evaluated. This is
456   particularly relevant because boreal forests are predicted to experience the largest temperature
457   increase of any forest biome (Gauthier et al. 2015). Additionally, climate driven changes in
458   drought, fire regimes and biotic disturbance (e.g., bark beetle) all threaten to alter the stability of
459   boreal forests, and their associated carbon stocks and fluxes (Anderegg et al. 2020). The

460 magnitude and direction of future changes in the various components of swamp C and
461 greenhouse gas balances is hard to predict, due to non-linear responses and feedbacks (Bonan,
462 2008). However, for *P. mariana* (the dominant tree species at our site), a combination of
463 elevated air temperatures with increased soil water availability during spring will likely prolong
464 the growth season length by: (1) earlier initiation of bud break in developing shoots (Y0); (2)
465 accelerated shoot maturation; (3) earlier full photosynthetic recovery in overwintering needles;
466 and (4) a shift in key photosynthetic parameters. Together, these changes have the potential to
467 significantly increase net annual C uptake (Jensen et al. 2015). Balanced against this, research
468 from northern peatlands shows that rising temperatures could lead to increased peatland CH_4
469 production, or this might be outweighed by reduced CH_4 production and greater CH_4 oxidation
470 due to changes in water storage (Roulet et al. 1992). Climate-driven changes in vegetation
471 communities could also increase or decrease CH_4 emissions (Strack et al. 2006).

472 Clearly, how boreal swamps respond to climate, and other global changes, will potentially be
473 complex. For these reasons, and because of a current lack of data and biogeochemical
474 understanding, we call for the establishment of a coordinated swamp observatory throughout the
475 northern hemisphere. Measurements should include above and belowground carbon stocks; C
476 and greenhouse gas fluxes from soils and vegetation (Davidson et al. 2022), including tall tower
477 eddy covariance to measure landscape-scale exchange (e.g., Deshmukh et al. 2021); and high-
478 frequency water table data. Such measurement efforts need to be concerted and long-term. Only
479 by such an approach can these underappreciated northern wetlands be brought forward into the
480 spotlight, so long occupied only by bogs and fens.

481 **Acknowledgments**

494

495 **Conflict of Interest**

496 The authors declare that they have no known competing financial interests or personal
497 relationships that could have appeared to influence the work reported in this paper.
498
499

500 **Author contributions**
501 MS secured the funding; SJD and MS designed the study; EW, SC and MeS performed the data
502 collection and processing; SJD and MAD analysed the data with input from MS; and SJD, MAD
503 and MP wrote the paper. All authors edited the final draft.
504
505 **Open Research**

506 Data available via the Dryad Digital Repository: *Data will be uploaded once paper is accepted*
507 *for publication*
508

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