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Warmer *Sphagnum* moss, less soil carbon loss: Anaerobic respiration and temperature response along a boreal forest-peatland ecotone

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Climate warming is predicted to rapidly change the local environmental conditions in peatland systems at high latitudes. This study explored soil respiration rates with microbial community compositions along a transect from well-drained upland forest to a *Sphagnum* moss peatland in boreal Finland. We found that soils from the upland forest and intermediate habitats incubated at 20°C generally produced more anaerobic CO_2 than the cooler incubation temperature groups (0, 4°C) and that the initial soil carbon content was the strongest geochemical and physical parameter correlated with cumulative CO_2 produced over the course of this 140 day incubation. Interestingly, bog samples were the exception to this, and were more productive at cooler temperatures. This implies that the controls on anaerobic CO_2 production in bogs differ from those in the soils of the surrounding habitats. This finding, along other parameters, such as soil carbon content, could give greater insights into potential carbon production in high-latitude soils.

Introduction

Wetlands play a significant role in the global carbon cycle as substantial carbon sinks (Yu *et al.* 2010; Bridgham *et al.* 2006). They contain roughly a third of the world's soil carbon, while only covering 5-8% of the Earth's surface (Mitch and Gosselink 2007). Of the estimated ~530 Pg of C in peatlands globally, over 80% is stored in high-latitude peatland systems (Hugelius *et al.* 2020). Peatlands efficiently use carbon from the atmospheric pool and sequester it in the terrestrial carbon pool through the slowed decomposition of vegetative organic matter, enabled by the acidic and waterlogged conditions within the peatland (Clymo 1987).

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However, many of the environmental-scale controls contributing to the sustained functionality of high-latitude wetlands, such as water table and vegetation composition, are predicted to undergo rapid change, with the progression of changing climatic conditions.

On a global scale, temperatures at high latitudes are increasing more rapidly than those at lower latitudes, disturbing the annual cycle of freeze and thaw in high-latitude peatlands (Kirtman *et al.* 2013; Byun *et al.* 2021). It remains uncertain how exactly climate warming will affect the carbon flux of northern wetland soils and vegetation, but generally it is agreed that these large carbon sinks have the potential to turn into a significant global net carbon source (Hanson et al 2020; Frolking *et al.* 2011). Peatland organic soil stability is heavily influenced by variables including regional climate, land use in the surrounding area, vegetation and peat chemical composition (Hodgkins *et al.* 2018; Keiluweit *et al.* 2016; Byun *et al.* 2021; Clymo and Hayward 1982; Crowther *et al.* 2016), all factors that are projected to undergo significant change with global climatic warming.

Though previous research has shown that organic soils generally respond to increased heat with increased greenhouse gas (GHG) production, the temperature response of (sub)arctic soil is generally poorly understood, and hardly follows the textbook knowledge of a temperature reaction rate of Q_{10} equaling 2 (Davidson and Janssens, 2006; Oertel *et al.* 2016). The *Sphagnum* mosses that dominate boreal and (sub)arctic bog vegetation has been shown to have variable anaerobic CH_4 responses to temperature treatments, with samples at greater depths being especially unresponsive to temperature fluctuations (Turetsky *et al.* 2012; Wilson *et al.* 2016). However, anaerobic CO_2 production response to temperature change in boreal peat soils is a known knowledge gap, and especially so in the ecotone soils around the bogs (Kolton *et al.* 2019). Net CO_2 flux is known to account for a larger component than net CH_4 flux in peatlands, though many ecosystem-scale parameters influence the exact ratio of the gasses (Frolking *et al.* 2011; Helbig *et al.* 2022). Given the predicted warming climatic trend, the exact quantifications of high-latitude organic matter (OM) response to temperature is of substantial interest to further refine climatic warming model predictions.

A commonly used method of estimating carbon (C) turnover and warming potential of soils are laboratory incubations. Laboratory (ex-situ) incubations are able to quantify the stability of organic molecules in soils, while being able to manipulate one dependent variable for each experimental group. Incubations have also shown to preserve the microbial communities within the soil, even when considering the limitations of a laboratory setting to organic matter C processing, such as the disturbance to the microbial community from field collection and shipment (Wilson *et al.* 2021). Recognizing and quantifying the relative abundances of the microbial taxa present can inform the robustness of the community to change, and inform about the conditions in the soil. Combining laboratory ex-situ incubation respiration rates with microbial community and diversity data allows insights into biogeochemical cycles happening in the soil column leading up to the collection of material in the field (Lin *et al.* 2014; Wilson *et al.* 2016).

Often overlooked in incubation studies is peatland soil's C lability in anaerobic environments, despite the availability of oxygen being one of the most important ecosystem scale controls on the microbial respiration pathways. Most studies have focused only on the surface of the soil, the acrotelm, and the largely oxic environment the top of the soil column is adapted for (Schädel *et al.* 2016, 2020; Kolton *et al.* 2019; Ren *et al.* 2024). However, fluctuating precipitation patterns will affect the hydrology of boreal habitats and consequently, the soil moisture (synonymous with ease of which oxygen can circulate within the soil column) is also predicted to undergo regional changes (Ruosteenoja and Jylhä 2021). Water slows gas exchange within the soil matrix, and in unsaturated conditions the most favorable electron receptor (O_2) is able to diffuse within the soil and spur OM decomposition. Studying soil columns layer-by-layer can show us the exact location of the most vulnerable C stocks and better predict the vulnerability of the system as a whole to changing climatic variables. To

better understand the potential metabolic pathways soil microbes use in response to shifting ecosystem-scale controls, additional experimental approaches aimed at exploring anaerobic pathways are essential to fill in these knowledge gaps.

Notably, the ecotone between the well-drained upland forest and the water saturated bog is included as an Intermediate margin zone. These habitats, also known as 'laggs', have been observed to be hotspots for biodiversity, though the hydrology and geochemistry of these zones have largely yet to be explored (Korpela 2004; Paradis *et al.* 2015). This knowledge gap in literature is largely hypothesized to be due to the difficulty of confidently delineating a habitat with considerable diversity, the relatively small areal coverage of the habitat zone, and geo-ecology experiments traditionally tending to prefer the homogeneity of larger systems (Fortin *et al.* 2000). Peatland — forest intermediate habitats, are known to be more sensitive to surrounding disturbances (examples include nearby agriculture development, ditching, or beaver behavior (Johnston and Naiman 1987)) but little is known about the margin itself, and less about the potential C cycling dynamics (Howie and van Meerveld 2011). The inclusion of the upland forest site in this study was made to extend the hydrologic gradient from ombrotrophic and fully-saturated peat soils to the endmember of well-drained podzol with less nutrient limitations. This was to fully explore the relative responses of the temperature treatments, despite upland forest soils only occasionally being in anerobic conditions in nature. We refer to the habitat zones here as: Bog, Intermediate, and Upland Forest.

This paper quantifies anaerobic CO_2 production and correlates it with microbial relative abundance using samples taken along a water-gradient-driven habitat transect from the Bog to Upland Forest aiming to discern the response of the soil biogeochemistry cycling to ecosystem scale controls. Previous literature has mostly used soils from temperate climates to show how organic soils respond to increased temperature with increased microbial respiration rates (Oertel *et al.* 2012). Here, we hypothesized that the soils from this transect from boreal Bog to Upland Forest habitat will respond with a similar positive correlation between respiration rate and temperature treatment, with the exception of soils composed of *Sphagnum* moss matter due to *Sphagnum*'s complex and recalcitrant biochemistry. The objective of this study was to characterize the soil substrate response to different temperature treatments, using soils from boreal habitats along a hydrologic gradient and at each soil horizon. We quantified anaerobic CO_2 production and sensitivity to temperature using an incubation experiment with samples along the hydrologic transect. The relative differences in production rates in response to laboratory incubation temperature directly improve our understanding of how vulnerable boreal peatlands and their surrounding habitats C stores are to climate warming.

Material and methods

Site description

Siikaneva peatland and the surrounding forested habitat (61.838440°N, 24.171650°E) is located in western Finland, within the boreal vegetation zone (Ahti, Hämet-Ahti, and Jalas, 1968). The site was chosen for the established research infrastructure, and the remoteness of this natural peatland habitat. Western Finland experiences daily temperature highs of 0°C in the winters and between 10 and 25°C in the summer growing season (lasting approx. 140 days, the length chosen for this incubation experiment). Annually, the region averaged 4.9°C and 58.2 mm of monthly precipitation in the last ten years from August 2011 to our sampling year of August 2021 (Finnish Meteorological Institute: accessed 2023). Siikaneva peatland had most recently seen water from the last observed rain on 29 and 30 July 2021 (10 days prior to soil core sampling). The peatland is not fed from any known groundwater source or adjoining waterbody. Soil core samples were taken along a water gradient from the Upland Forest, along the west-facing slope down to the Bog (Fig. 1). Habitat descriptions can be found in Table 1, and in further detail in the Supplementary Information.

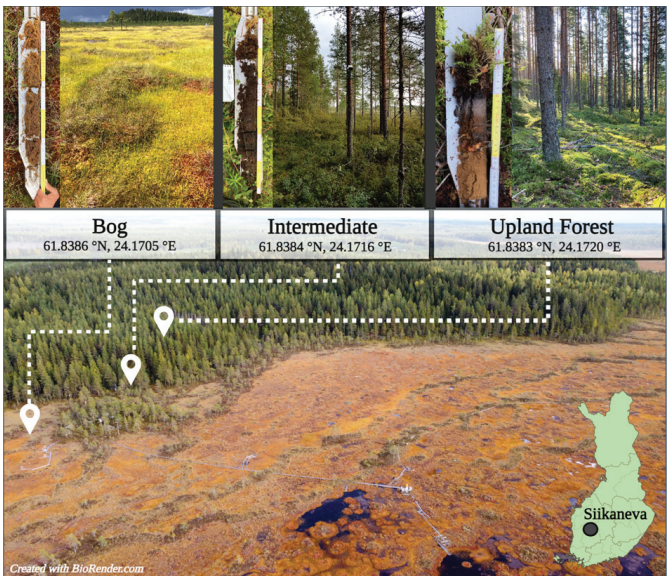

Fig 1. Sample site map. Our three sites represent three different habitats in the Siikaneva peatland and surrounding habitats (Western Finland). A boardwalk (visible in aerial view) transects the bog and provides infrastructure for other ongoing studies (such as continuous autochamber flux measurements and field meteorological stations). Inlaid, shows researchers' view of each field site, with image of cores directly to the left of their respective habitat. Drone image taken in August 2022 by T. Rettelbach and L. Golde.

Sample collection

Material was collected during late summer, around peak growing season in mid-August of 2021. Collection of material in Siikaneva was chosen to be near, but far enough to not affect the cluster of automatic and manual chamber measurement sites where data collection has been continuously for field flux measurements since 2021.

Four replicate cores each were taken at the Bog and Intermediate sites, and six replicates

Table 1. Soil Horizon Descriptions and Sampling Depth

Habitat	Surface Vegetation	Soil Class*	Bulk Density (g/cm^3)	Top of Horizon (cm)	Bottom of Horizon (cm)	Average Depth of Horizon (cm)	Soil Horizon Depth Group
Bog	*Sphagnum* moss lawn including: *Sphagnum papillosum, S. magellanicum* and *S. balticum*, some assorted sedges including from genus *Eriphorum*	O	0.03	0.0	30.0	15.0	Top
		O	0.09	30.0	50.0	40.0	Bottom
Intermediate	Scots pine (*Pinus sylvestris*), ground lichens (Cladonia spp.), blueberry shrub (*Vaccinium myrtillus*), feather mosses (*Hylocomium splenens*), some *Sphagnum* mosses	O	0.02	0.0	15.0	7.0	Top
		O	0.04	15.0	35.0	25.0	Middle
		O/M	0.18	35.0	50.0	42.5	Bottom
Upland Forest	Scots pine (*Pinus sylvestris*), ground lichens (Cladonia spp.), ferns (*Dryopteris dilatata*), feather mosses (*Hylocomium splenens*), glacial erratic boulders (granite rock)	O	0.03	0.0	15.0	7.5	Top
		M	0.19	15.0	25.0	20.0	Middle
		M	0.52	25.0	43.0	34.0	Bottom

Note: Photos of cores, surface vegetation can be seen in Fig. 1
*Soil Class denotes the soil being Organic or Mineral, with mineral being less than 20% C

were taken from the Upland Forest site. Spatial replicates were collected within approx. 25 m of the coordinates reported for each habitat (Fig. 1) and spaced as evenly as possible. Samples were taken from surface to bedrock in the Upland Forest and Intermediate site. In the bog, bedrock could be found no shallower than about 2 meters deep. Each soil core was subdivided by observed soil horizon in the field. The additional cores in the forest were taken due to the site having a significantly shallower soil layer before encountering bedrock. In the field, bagged samples were stored in a portable cooler. They were then frozen at –20°C in the dark for storage, until arrival at AWI Potsdam.

Geochemical laboratory analysis

After transport back to the laboratories, we combined the spatial replicates in each habitat by horizon. Subsamples of each soil horizon were taken for soil descriptive analytics. Results can be seen in Tables 1 and 2. Samples were freeze-dried, homogenized to a powder, and analyzed in duplicate on the carbon analyzer

Table 2. Soil Horizon Geochemical Properties

Habitat	Soil Horizon Depth Group	Soil Description	pH	Water Content %	TOC %	TN %	C:N
Bog	Top	Whole *Sphagnum* strands, suspended in bog water in floating mats, some sedges	4.10 ± 0.00	96.10 ± 4.21	44.05 ± 0.51	0.90 ± 0.01	49.38 ± 0.80
	Bottom	Partially decomposed *Sphagnum* moss. Medium brown in color	3.90 ± 0.00	96.61 ± 0.45	45.41 ± 0.18	1.51 ± 0.03	30.27 ± 0.61
Intermediate	Top	Mixture of mosses and moist organics	3.83 ± 0.20	93.77 ± 1.25	46.15 ± 0.13	1.43 ± 0.28	32.31 ± 6.33
	Middle	Homogenous, moist coffee-brown organics	3.90 ± 0.28	87.39 ± 1.80	46.02 ± 0.19	1.74 ± 0.14	26.46 ± 2.13
	Bottom	Black-colored organic layer, some grey mineral	4.53 ± 0.27	65.05 ± 3.92	16.54 ± 0.24	0.80 ±0.06	20.66 ± 1.57
Upland Forest	Top	Mixture of mosses and moist organics	3.46 ± 0.08	62.89 ± 8.00	35.98 ± 0.32	2.73 ± 0.05	13.20 ± 0.27
	Middle	Grey podzol mineral layer	3.77 ± 0.16	37.47 ± 11.52	5.44 ± 3.41	0.16 ± 0.00	33.57 ± 21.04
	Bottom	Tan-colored clay with frequent woody root intrusions (larger pieces removed before incubations)	4.47 ± 0.15	12.98 ± 2.29	2.43 ± 0.04	0.10 ± 0.01	25.44 ± 2.58

Note: n = 6 for pH and Water Content, n = 2 for TOC and TN. All numbers following "±" denote standard deviation.

(soliTOC, Elementar Analysensysteme — AWI Potsdam Carbon and Nitrogen Laboratory) for total organic C. For total nitrogen (N) we used a rapid N exceed (Elementar Analysensysteme, Germany) for generating the data. The pH of samples was taken from each replicate's pore water at the conclusion of the experiment. Bulk density was determined using the weight of the horizon's subsample and the known volume of the Eijelkamp peat corer for each core (n = 4 for the Bog and Intermediate habitats, and n = 6 for the Upland Forest site).

Incubation methods

To begin the incubation, the samples were thawed from –20°C to 4°C and each site's soil horizons were gently homogenized together in anoxic conditions (Don Whitley MACS MG-500 Anaerobic Chamber Workstation), and separated into pool replicates of each horizon to reduce heterogeneity between the spatial replicate cores. Each sterile 120 ml borosilicate vial received approximately 10 g wet weight of the homogenate sample with 5 ml of autoclaved tap water to create an anaerobic slurry. Samples were capped with sterile rubber septa, and crimped with aluminum seals. Vials remained sealed for the duration of the experiment to maintain constant moisture and the closure of the active microcosm system. Three temperature treatments (0, 4, 20°C) were introduced to the sample material as soon as the vials were capped (for each soil horizon there was two lab replicates, per temperature treatment), and they remained in the temperature incubator, except for brief gas chromatography (GC) headspace sampling. Blanks were also made that consisted solely of autoclaved tap water were made and ran in parallel, stored at the 4°C temperature incubator.

The entire sample preparation took place within the Don Whitley MACS MG-500 Anaerobic Chamber Workstation, with a constantly circulating, oxygen-free (N_2) headspace. Additionally, the samples were flushed with N_2 within a day after sealing, to ensure an anaerobic conditions. Aliquots of sample from the freshly thawed material was set aside and stored for microbial community composition, C and N analysis, water content measurement, and archive material (Wilson *et al.* 2021; Corbett *et al.* 2013; Schädel *et al.* 2020).

An equilibration period (25 days) was included at the experimental temperature to allow the sample to adjust to the temperature treatment and microbially exhaust any oxygen or other terminal electron receptors that may have been introduced during setup (Wilson *et al.* 2021). The equilibration temperatures were the same as those for the full 140 day run of the experiment: 0, 4, and 20°C. After an initial first week of sampling on days 0, 1, 3, and 7 the samples were measured once per week, then regularly after the first month. The vials were flushed as needed once the headspace reached 1,000 ppm CO_2 to represent field conditions over the 140-day sampling period. The headspace gas was analyzed with a Agilent Technologies 7890A GC System starting from the initial measurement. The same GC system was used throughout, with the same settings (column temperature was kept at 50°C, and helium was the carrier gas in the GC System). Before each vial was sampled, it was sterilized with ethanol and enflamed to ensure the headspace and sample maintained a sterile environment.

Production rate of CO_2 was determined by the difference in GHG concentration in vial headspace from one measurement, to the next and divided by the difference in days between measurement. The output (ppmv) was used in the Ideal Gas Law correction then this value was corrected for the volume of the sample with the added water, from the total 120 ml vial headspace volume. This corrected value then is also used to subtract the previous measurements flush residual, when the previous vial had measured $CO_2 \geq 1000$ ppm in the headspace of the vial. On "flush" days, the sample was measured, flushed with N_2, and measured again within the same hour. With the values corrected for the flush residual, the values were then converted from per unit vial, and then to per gram dry weight of sample inside each vial. Henry's Law was applied as autoclaved water had been added to the sample to ensure anaerobic conditions in the headspace. The aqueous CO_2 is accounted for in the values used. Values

were then normalized to gram dry weight of sample, and to per gram soil carbon. The cumulative production was calculated by summing the difference between measurements, and normalizing to the gram dry weight of sample, and to gram soil carbon (Robertson *et al.* 1999). Triplicate blanks with only autoclaved water were measured on each day of sampling, and the average of the three blank replicates difference between measurements was used as a benchmark of the minimum detected flux. Upon the conclusion of the incubation, samples were sacrificed, pH measured, baked, and weighed for the dry weight of each individual vial. The measurement of each day is reported in units of μg CO_2-C g DW^{-1} d^{-1} (μg C/gW/d) and μg CO2-C gC^{-1} d^{-1} (μg C/gC/d). While CH_4 was measured, the cumulative production was not significant and not further discussed.

Analysis of each soil horizon's temperature coefficient (known henceforth as the Q_{10}), was calculated. The Q_{10} is a standardized parameter used frequently in literature describing soil respiration activity as it relates to temperature differences (Hamdi *et al.* 2013). Q_{10}s represent the rates with a ten-degree temperature difference, here we fit an exponential equation from our data as our temperature differences are not ten (Eqs. 1 and 2 from Hamdi *et al.* 2013).

$$SR = Ae^{kT} \quad (1)$$

$$Q_{10} = e^{10k} \quad (2)$$

where Eq. 1 uses the rate of soil respiration (SR) with incubation temperature (T) with A and k as fitted parameters to calculate the Q_{10} value in Eq. 2.

Microbial community structure analysis

Samples were gently mixed together to homogenize the 4–6 spatial replicate cores, and care was taken to remove roots, leaf litter from surface, and rocks from deeper soil horizons. Aliquots for microbial community structure analysis were stored in Eppendorf vials and kept frozen at –30°C during the week that all horizons were gathered, then –80°C until analysis.

DNA extraction, PCR and sequencing

Total nucleic acids were extracted in duplicates using the PowerSoil-Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. Amplicon libraries were prepared by using barcoded primer pair sets (Uni515-F[5'-GTGTGYCAGCMGCCGCGGTAA-3'] / Uni806-R[5'-CCGGACTACNVGGGTWTCTAAT-3']) targeting the V3-V4 hypervariable regions of the 16S rRNA, with duplicates for each sample. PCR reactions (50 μL) contained 10× Pol Buffer C (Roboklon GmbH, Berlin, Germany), 25 mM $MgCl_2$, 0.2 mM dNTP mix (ThermoFisher Scientific), 0.5 mM each primer (TIB Molbiol, Berlin, Germany) and 1.25 U of Optitaq Polymerase (Roboklon, Berlin, Germany). The PCR program included an initial denaturation step at 95°C for 7 min, followed by 33 cycles at 95°C for 15 s, annealing at 60°C for 30 s, extension at 72°C for 30 s and a final extension step at 72°C for 5 min. After purification with the Agencourt AMPure XP kit (Beckman Coulter, Switzerland), the recovered PCR products were equilibrated into comparable equal amounts before pooling together with positive and negative controls. For the positive controls, we utilized a commercially available mock community (ZymoBIOMICS Microbial Community DNA Standard II; Zymo Research Europe, Freiburg, Germany). As for the negative controls, they consisted of the DNA extraction buffer and the PCR buffer. Sequencing was run in paired-end mode (2 × 300 bp) on Illumina MiSeq platform by Eurofins Scientific (Konstanz, Germany).

Data processing and analysis

DNA raw sequences were processed by a custom workflow. Demultiplexing was performed using Cutadapt v3.4 (http://dx.doi.org/10.14806/ej.17.1.200). The demultiplexed sequencing raw data was upload to the ENA (European Nucleotide Archive) with the project accession number PRJEB72044 (https://www.ebi.ac.uk/ena/browser/view/PRJEB72044). The resulting sequences were subjected to DADA2 v1.20 (Callahan *et al.* 2016), including filtering, derep-

lication, chimera detection, sequence merging, and the identification of amplicon sequence variants (ASVs). Taxonomy of ASVs was assigned by referring to the SILVA138 database (Xiang *et al.* 2013).

Statistical analysis of the incubation gas production and geochemical data was performed using R packages "tidyverse" (Wickham *et al.* 2019), "dplyr" (Wickham *et al.* 2023), and "stats" (R version 4.1.2). The incubation data set was uploaded up the PANGAEA and can be found with dataset number 964303 (https://doi.pangaea.de/10.1594/PANGAEA.964303) Fisher-Pitman Permutation tests were used to evaluate the significance in differences of CO_2 production of each soil horizon group using the R function "coin" (Hothorn *et al.* 2006) , as this study included multiple habitats and soil horizons, while constrained by $n = 2$ replicates per temperature treatment. Key parameters (included in the analysis was: total organic carbon (%), total carbon (%), total nitrogen (%), water content (%), pH, *pmoA* cell copies (see Fig. S8 in Supplementary Information), *mcrA* cell copies (see Fig. S9 in Supplementary Information), bulk density (g/cm^3), temperature of incubation (°C)) on measured CO_2 production variance were included in a principal component analysis (PCA) using the "vegan" package (Oksanen *et al.* 2022). Temperature sensitivity was determined from the calculation of the Q_{10} value, as described by Hamdi *et al.* 2013. Individual outlier measurements were removed on basis of visual inspection of measurements of incubation timeseries, four measurements were removed (of the total 605 headspace measurements) and determined to be from user error. A bubble plot was generated to visualize the microbial community composition at family level using ggplot2 package (v 3.4.2). The community data were collapsed at family level using the 'otuCollap' function of R package otuSummary (Yang 2020).

Results

Soil description

Properties of soil samples collected from Siikaneva peatland and surrounding habitats during August 2021 are shown in Tables 1 and 2. The Upland Forest and Intermediate site had a water table that was below the maximum coring depth of 50 cm and had soil moisture contents ranging from 16% to 96%.

Soil pH and bulk density generally increased with depth, except in the Bog (Table 2). pH ranged from 3.5 to 4.5 and was lowest in the surface Intermediate and Upland Forest samples. Bulk density was higher in mineral soils (mostly found in the Upland Forest and Intermediate site) and lowest in the organic soils of the Bog and topsoil of the other two habitats. In the bottom layers of the Intermediate and Forest site were a mix of O/M and mineral soil, with soil TOC contents < 20%. While the TOC content was largely similar in organic soils, the N content was not as evenly distributed and highest in the Forest Top soil. The largest C:N ratio was in Bog-top soil horizon. We found the lowest C:N values in the Forest-top (13.20) and Intermediate-bottom layers (20.66), as seen in Table 2.

Cumulative CO_2 production across the sites

Across sample groups, cumulative values of CO_2 production measured to day 140 ranged from an average of 1936 ± 160 μg CO_2-C g^{-1} DW (from the Intermediate-Top site, averaged replicates) to a 55.8 ± 18.5 μg CO_2-C g^{-1} DW from Upland Forest-Bottom samples (Fig. 2). Generally, the habitat that produced the most CO_2 per gram dry weight was the Intermediate site, followed by the Bog and Forest site respectively. Within the Intermediate site, the top (0-15cm) layer was significantly more productive in terms of CO_2 production over the course of the 140 days of incubation ($\chi^2 = 15.47$, d$f = 2$, $p = 0.0004$), producing 137% more CO_2 than in the middle layer and 171% more than the bottom layer within the habitat. The Upland Forest habitat also showed significant separations in CO_2 production by depth, but to a lesser degree (per μg CO_2-C g^{-1} DW, Kruskal-Wallis ($\chi^2 = 11.59$, d$f = 2$, $p = 0.003$)). The bog site's top and bottom layers were found to also be significantly different, but to a lesser extent than the preceding habitats ($Z = –2.46$, $p = 0.014$).

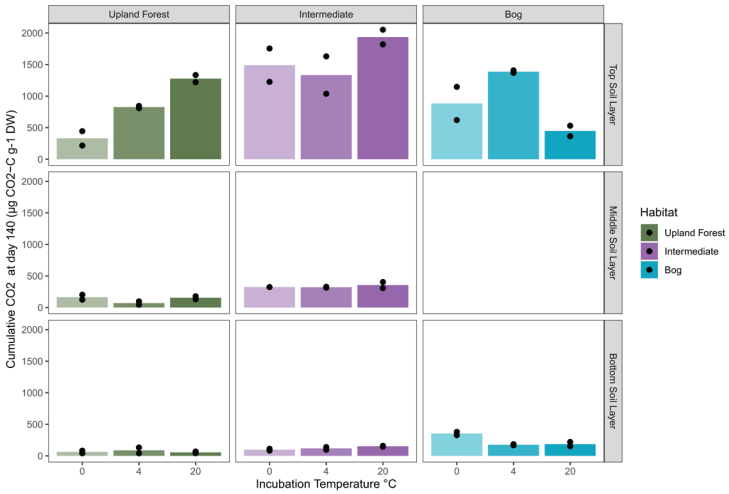

Fig 2. Cumulative CO_2-C production from the incubation of soil cores from Siikaneva peatland and surrounding habitat when normalized to gram dry weight of sample. Samples were taken along a hydrological transect, from the well-drained Upland Forest to the completely saturated Bog habitat (denoted by bar color). Intensity of color corresponds to the temperature that samples were incubated at for the duration of the 140 day experiment (also denoted on the x-axis: 0, 4, 20°C). The bars represent the average between the two replicates per treatment group, with the individuals represented as dots.

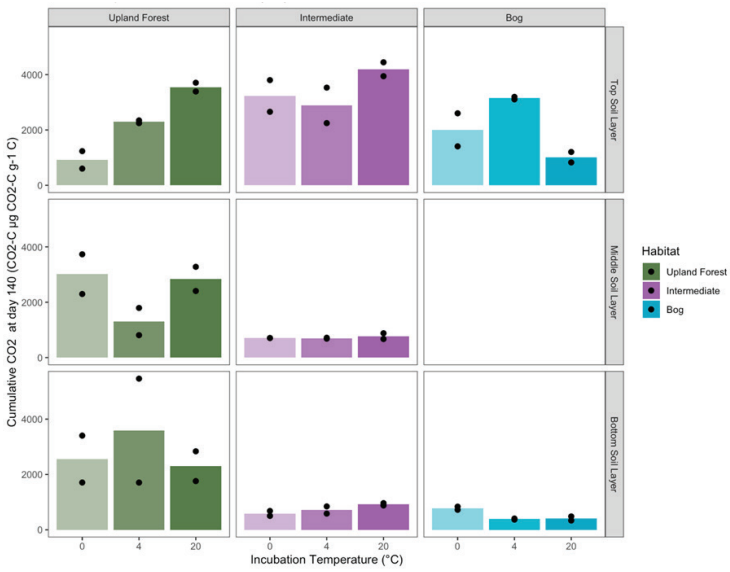

Fig 3. Cumulative CO_2-C production from the incubation of Siikaneva soil cores when normalized per gram soil C. Samples were taken along a hydrological transect, from the well-drained Upland Forest to the completely saturated Bog habitat (denoted by bar color). Intensity of color corresponds to the temperature that samples were incubated at for the duration of the 140 day experiment (0, 4, 20°C). The bars represent the average between the two replicates per treatment group, with the individuals represented as dots.

When considering production per gram carbon in the source material, the Upland Forest site was the most productive, followed by the Intermediate then the Bog (Fig. 3). Normalized to gram carbon, the Upland Forest site produced CO_2 at each soil horizon at a rate that was comparable to the top soil horizons (the most productive layer). In this paper, both metrics of C produced as *per gram dry weight* and *per gram soil C* are used. The expression of C produced in *per gram dry weight* is widely used in C decomposability literature and compares the quantity of soil C, while including the units expressed *per gram soil C* allows the quality of the sample C to be compared. . The Upland Forest site was the only site that's relationship between soil horizon and CO_2 productivity changed when assessing production normalized to the percentage of carbon in the sample.

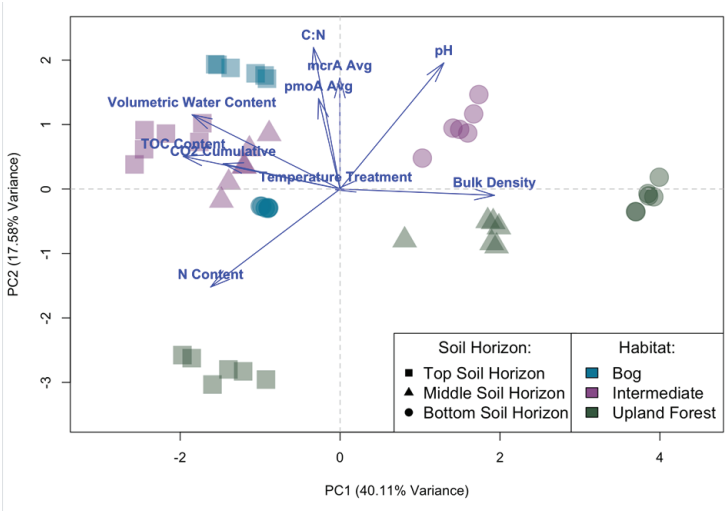

Fig 4. Biplot of the PCA with explanatory vectors. Each sample is represented as one data point, with color representing the habitat and shape representing the soil horizon. The length of vectors on the plot is proportional to the contribution of the variable to the component.

Bog habitat incubation results

The cumulative CO_2 produced by both depth groups (top 0-30cm and bottom 30–50cm; averaged laboratory replicates) ranged from 176 ± 12.1 (bottom horizon at 4°C) to 1390 ± 27.9 µg CO_2-C g^{-1} DW (top horizon at 4°C) with an overall mean of 573 µg CO_2-C g^{-1} DW (Fig. 2). The latter also produced the most cumulative CO_2 when normalized by gram C (3150 ± 63.3 µg CO_2-C g^{-1} C; Fig. 3). Overall, the bottom 30-50 cm was where the least CO_2 production occurred in this habitat. The lower depths of the bog were low in CO_2 production and largely unresponsive to the temperature treatment (Fig. 2).

Intermediate habitat incubation results

The cumulative CO_2 produced over 140 days from the Intermediate habitat ranged from 97.8 ± 20.8 (bottom horizon at 0°C) to 1940 ± 164 (top horizon at 20°C; µg CO_2-C g^{-1} DW) between averaged replicates (Fig. 2). The most CO_2-C was produced in the top soil horizon at 20°C, and the least amount of CO_2 production came from the bottom horizon of the soil column, in the treatment group incubated at 0°C. Samples, when normalized by gram C maintained the same superlatives of production groups (Fig. 3).

Upland Forest Habitat Incubation Results

The cumulative CO_2 produced over 140 days from the Upland Forest samples habitat ranged from 55.8 ± 18.5 (bottom horizon at 20°C) to 1280 ± 80.3 µg CO_2-C g^{-1} DW (top horizon at 20°C) While the differences between temperature treatments were not significant between soil horizon depth groups, this was the only habitat's bottom horizon that measured the least amount of CO_2 produced in the 20°C incubation temperature group When the cumulative CO_2-C values are normalized by sample material C, the quality of the C can be compared. Of note, the Forest-Middle and Forest-Bottom have comparable cumulative CO_2-C production to the Forest-Top layer when normalized to C, which was not the case when normalized only to production per gram dry weight of sample material (Figs. 2 and 3).

The temperature response of respiration rates

Overall, the effect of the incubation temperature treatments were less influential to the cumulative CO_2-C measured than hypothesized, with variable results from each habitat group (Fig. 4). In the principal component analysis, the temperature treatments were the shortest vector, and explained very little variance in the data. PC1

explained 40% of the variance and and the loadings for water content, nitrogen content and C content were negatively correlated indicating a negative relationship with PC1. The cumulative CO_2-C per gram dry weight was tightly correlated with C content of sample. The strongest positive correlation with PC1 was the sample bulk density, and the combination of these factors clearly separated out the soil horizons along this axis. PC2 explained 18% of the variance and was most strongly positively correlated with pH and negatively with N content. In the scope of the full 140 days and all temperature groups, the Q_{10} values remained relatively low (0.6–2.33), with the top layers showing the largest values (Table 3). When calculated for the low (0, 4°C) end temperature range, the Q_{10}s increased most remarkably in the Upland Forest soils (Table 3). This greater responsiveness to temperature sensitivity at low temperatures also coincides with lower Q_{10} values in the high (4, 20°C) range.

The Bog was the only habitat that had the most CO_2 production at 4°C, and not the 20°C incubation temperature. The Bog Top samples all produced more cumulative CO_2-C than the bottom soil horizon group, though interestingly, the bottom 30-50cm had the most CO_2 production in the 0°C incubation (354 ± 36.9 CO_2-C per g^{-1} DW), which was also true when normalized to gram C (780 ± 81.3 CO_2-C g^{-1} C). Within the temperature treatment, the Bog-Top (0–30 cm) and Bog-Bottom (30–50 cm) of the 4°C temperature group varied (see Figs. 2 and 3), with the Bog-Top layer producing approximately 10x more CO_2-C than the bottom layer.

Within the Intermediate habitat, the 20°C incubation temperature group produced the most cumulative CO_2 measured, with the Top soil horizon producing the most CO2-C (Fig. 2). The Intermediate's top 15 cm, middle 15–35 cm, and bottom 35–50 cm in 4°C had a wide range of cumulative CO_2-C production, in line with the diversity of soil types in this site. The lowest overall cumulative values came from the 0°C group, particularly Intermediate-Bottom samples.(Fig. 2 and Fig. S10 in the Supplmentary Information).

The Upland Forest samples overall CO_2-C production had a positive correlation with the temperature treatment of the incubations, but this was particularly observed in the Forest-Top 15 cm. The Forest-Middle 15–25 and the Forest-Bottom 25–43 cm did not show a visible relationship between incubation temperature and CO_2 production (Fig. 2), which was also the case for the other two habitats at the deeper soil horizons.

For all habitats, temperature strongly influenced the measurement point at which the largest flux was found ($\chi^2 = 11.84$, $df = 2$, $p = 0.002$), as well as the TOC % from sample measured at the start of the incubation ($\chi^2 = 16.69$, $df = 7$, $p = 0.019$). However, the length of the lag times (time from incubation Day 0 to day of measured maximum production rate) were not predictive of cumulative CO_2-C by day 140. Higher temperatures resulted in the maximum flux being closer to Day 0, and lower temperatures delayed the peak CO_2 production to as late as measurement day 71.

Table 3. Q_{10}s for CO_2 measured in anaerobic incubations from the Siikaneva peatland complex. The 'Low', 'High', and 'All' refer to the incubation temperature ranges included in the metric of temperature sensitivity.

Habitat	*Soil Horizon*	*Q_{10} Low (0, 4°C)*	*Q_{10} High (4, 20°C)*	*Q_{10} All (0, 4, 20°C)*
Upland Forest	Top	19.9	1.63	2.33
Upland Forest	Middle	0.157	2.17	1.49
Upland Forest	Bottom	18.8	0.744	1.18
Intermediate	Top	1.14	1.20	1.19
Intermediate	Middle	2.82	1.19	1.35
Intermediate	Bottom	4.08	1.27	1.50
Bog	Top	4.80	0.427	0.603
Bog	Bottom	0.191	1.02	0.800

Microbial data

In our study site, the three habitats each support a microbial community composition that reflects the defined differences of each habitat's soil geochemistry. The relationship between the biodiversity of the microbial community (as reflected in the Shannon index) and the CO_2 production per gram weight, and per gram soil C was highly significant (χ^2 = 38.16, df = 7, p = 2.83e-06; χ^2 = 28.19, df = 7, p = 0.0002).

The Bog site hosts a distinct microbial community, reflective of highly acidic, extremophile habitat typical of *Sphagnum* moss mires. In this site we found the community was dominated by *Acidobacteria* and *Protobacteria*. *Acidobacteria* is present in up to one third of all 16S rDNA sequences from *Sphagnum* moss bogs (Dedysh *et al.* 2006; Pankrotov *et al.* 2008) and describes a phylum of bacteria that can be found in many rather oligotrophic soil habitats but remains poorly understood taxonomically and functionally. The bog site showed the lowest alpha diversity of all sites (Shannon index: 4.88 for the Top soil horizon, 2.68 for the Bottom soil horizon). The bog site is the only site where a substantial abundance of methanogenic archaea (Rice Cluster II) was detected.

The Intermediate site had consistent microbial community structure throughout the soil column. This was the only habitat that had few differences in bacteria and archaea phyla by depth. Here, the soil community is represented by a diverse community of soil microbes, most notably from the Phylum *Actinobacteria* and *Proteobacteria* (Family: *Isosphaeraceae*). In the Intermediate site, we saw that the alpha diversity was highest in the top 15 cm depth group, and interestingly this was also the highest value of all soil horizons. The alpha diversity was relatively similar between the lower two soil horizons (Shannon index: 5.32 for the top, 4.70 for the middle soil horizon, and 5.30 for the bottom soil horizon in this habitat).

Generally, there was a wider distribution of microbial abundance, and diversity on the phylum level present in the Upland Forest site (Fig. 5). In this site, no group was measured at more than a 10% relative abundance. Notably, the presence of Archaea was no larger than 0.5% in any of the Upland Forest soil horizon depth groups and methanogens were not detected. The Upland Forest site had the highest measure of alpha diversity, when considering the soil column as a whole. Similar to the other two habitats, the highest measure of diversity was in the top layer (Shannon index: 5.75 for the top, 5.43 in the middle soil horizon and 5.44 in the bottom soil horizon).

Discussion

Soil properties and potential anaerobic decomposition

Of all the soil properties, we found that TOC was most strongly correlated with CO_2 production (Fig. 4). Soil C can be influenced by a number of factors such as degree of OM decomposition, decomposition pathways, and parent vegetation. (Clymo and Hayward 1982). Organic substrate quality and quantity has been known to be a significant influence on decomposition rates, but the exact relationship of soil C and decomposition is only starting to be more fully understood (Reichstein *et al.* 2005; Wetterstedt *et al.* 2010). For example, soil cores from the bog habitat had relatively high TOC content but low CO_2 production (Fig. 4). The dominant vegetation of the Bog (*Sphagnum* moss) is known to have high C content, mostly in the form of carbohydrates. However, C sampled from the dissolved organic C of *Sphagnum* extracts in bogs have been found to have a relatively low nominal oxidation state of the C, suggesting the sample is in an oxidation state unfavorable to be an electron donor to the terminal electron acceptors within the soil matrix, and thus be unfavorable to decomposition processes on a chemical level (Wilson *et al.* 2022). This low energetic potential of the molecular compounds within the *Sphagnum*-sourced OM is confounding, but can be explained by the Bog soils' saturation and acidic environment that is unfavorable to decomposition processes (LaRowe and van Cappellen 2011; Wilson *et al.* 2022). Introduction of terminal electron acceptors to soils experimentally (NO_3^-, SO_4^{2-}) have been found to increase the soil dissolved organic C's nominal oxidation state of C and stimulate

decomposition, resulting in increased respiration of CO_2 (Naughton *et al.* 2021). The conversation around how exactly *Sphagnum* resists decomposition despite its high C content is ongoing; many other potential factors (high phenolic content, nutrient limitation, etc) likely all contribute (van Breemen *et al.* 1995). The transect study design lends itself to the natural inclusion of variable soil parameters between habitats and each of the observed soil horizons, although the number of laboratory replicates was reduced as a result. This tradeoff limits the statistical power of the results, but examines the Upland Forest to Bog soil columns at a fine scale.

Furthermore, another indicator that the *Sphagnum* peat has low or inhibited energetic potential is the higher abundance of *Acidobacteria* in the Bog site. *Acidobacteria* are known to be oligotrophs able to compete in environments where resources are limited (Fierer *et al.* 2007). It is worth noting that in these low pH environments fungi have been shown to play an important role in C sequestration (Blagodatskaya and Anderson 1998; Wang *et al.* 2021), and present an opportunity for future studies to explore the relationship between fungi and C biogeochemistry. Additionally, the Bog habitat showed substantial abundance of methanogenic archaea indicating a lack of alternative electron acceptors other than those serving methanogenesis. Thus, anaerobic CO_2 production in this site may have been largely driven through methane production but not so much through thermodynamically more favorable processes like denitrification.

Both the Intermediate-Top and Upland Forest-Top had high soil C content, when compared to the other soil horizons (Table 2). Both sites were also characterized by a high abundance of *Actinobacteria* (Fig. 5), organisms that are suggested to cope well in environments where substrate concentrations are high (Ho *et al.* 2017). Although, the relationship with temperature and CO_2 produced varied with each horizon. We found that the Intermediate-Top at 20°C produced the most cumulative CO_2 per gram dry weight at the end of the 140 day incubation (1936 μg CO_2-C g^{-1} DW). The high productivity from the Intermediate site was unsurprising, on account of its microbiome likely being primed for dynamic temperature changes in both aerobic and anaerobic environments (Langlois *et al.* 2015; Nordström *et al.* 2022). Although the Intermediate habitat was above the water table when we collected samples from this site, we observed high water content and know that this habitat seasonally is covered with snow and is occasionally inundated with rainwater.

The Upland Forest site was the most productive when considering the CO_2 production in term of CO_2 per gram C in the sample source material (Fig. 3). These findings show the microbial community was able to metabolize the limited C at an equal, if not larger rate than the other horizons, a tribute to the adaptability of the microbial community to metabolize the limited C in their environment. The aerobic nature of the upland forest soils and prevalence of exudates from roots throughout the soil column all could contribute to the high utilization of available soil C. Roots are known to stimulate the soil microbial community, and the presence of roots here could also contribute to the Upland Forest having the highest Shannon index of the three habitats (Moore *et al.* 2015). Plant roots are also known to increase rates of soil organic matter decomposition. In a study 10 km away of our projects study site (the SMEAR II Hyytiälä Station: 61.7667°N, 24.2833°E) researchers aimed to see the role plant roots played in the balance of decomposition and organic matter formation in the Upland Forest soils. Adamczyk *et al.* (2019) processed the soil, placed in mesh bags of different sizes, and monitored over three years to assess root and fungal penetration, enabling subsequent enzyme and DNA analyses along with nitrogen quantification. They found that the presence of roots increases organic matter decomposition, while also increasing the nitrogen pool in the soil, which is significant for the extremely N limited podzol soils.

Similarly, surface samples in the Intermediate and Bog sites also showed higher anaerobic CO_2 production than deeper layers (Fig. 2). Though few studies have been done incubating Upland Forest and Intermediate equivalent habitats in anaerobic settings, the limited consensus from incubations show that these sites regularly experience thermal and hydrologically driven environmental change, and that they respond accordingly with large variations in microbial

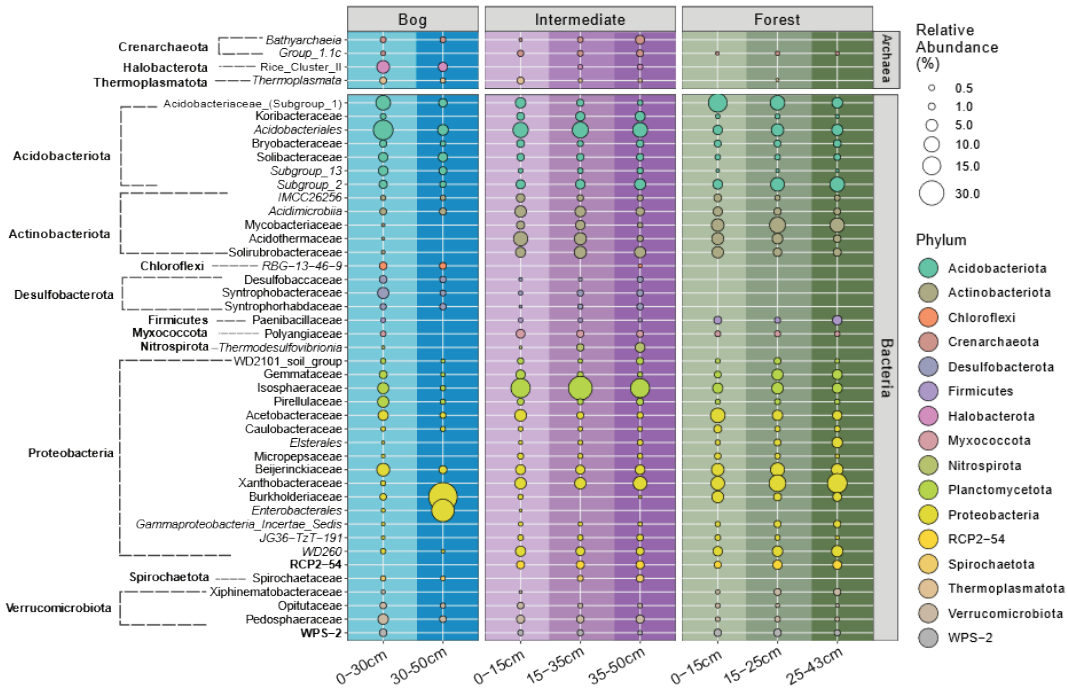

Fig. 5. Relative abundances of the microbial community structure in the Siikaneva peatland and surrounding habitats. Shown are those making up more than 0.25% of the total sequences. Bubbles presence represents taxonomic groups, and the diameter represents the percentage of abundance. Color used for emphasis of functional groups, habitat, and soil horizon of origin.

respiration patterns (Hartshorn *et al.* 2003; Oelbermann and Schiff 2008).

The soil moisture, and bulk density of the samples also had a strong positive correlation with CO_2 production. Soil horizons nearest to the surface (in the "top" depth group) had the highest CO_2 production and generally had the lowest bulk density, most TOC and as much, if not higher water contents than any other layer in its respective column (Fig. 2; Table 2). That the surface samples with the lower bulk density and high porosity had the most respiration activity was surprising in the sense that these would be the layers most exposed to oxygen in nature. However, one possible explanation is that samples at the top layer of the soil column are known to host more diverse and responsive microbial communities than horizons that are adapted to more the more stable and cooled anaerobic conditions of the lower depths. In fact, we did see a strong positive correlation between the Shannon diversity index and CO_2 produced, but this could be correlated with other contributing factors. Another noteworthy factor is lability of soil C throughout the soil column. Soil C at the surface is less degraded than soils at lower depths and thus, the carbohydrate-rich surface OM often contributes to a 'fast pool' of C respired to the atmosphere (Schädel *et al.* 2014).

We observed the most CO_2 produced (per gram dry weight) at the Intermediate top site, and the least in the lower mineral soil layers of the forest site (per gram dry weight). Here, we see that the combination of above-mentioned trend of low bulk density, high field soil moisture and (most relevantly) TOC is highest in the Intermediate site top layer. In C flux measurements at the nearby Lakkasuo mire (Lakkasuo: 61.800°N, 24.317°E), researchers set up a similar hydrologic gradient from Upland Forest to bog and measured CO_2 fluxes from *in situ* chamber measurements (Ťupek *et al.* 2008). They report that CO_2 was found to be largely influenced by the openness of the forest canopy, a feature that varies markedly in the dynamic conditions of the Intermediate site. The Bog site also has the

parameters that point to high potential CO_2 production (high VWC, high TOC, low BD) but the acidity of the waterlogged moss and the recalcitrant and confounding nature of the dominant vegetation (*Sphagnum* moss) is widely known to limit decomposition and C cycling processes (Clymo and Hayward 1982).

Our results indicated that the influence that pH may have played was likely obfuscated by the larger vector of influence that sample C composition had on CO_2 production, (Fig. 4; Table 2). We also measured the nitrogen content of each horizon and found both the highest and the lowest content of nitrogen (%) in the Upland Forest cores. In general, the Upland Forest data indicates that this habitat is particularly heterogeneous, indicating that this habitat needs more spatial and laboratory replicates to fully represent the soil C dynamics.

Depth had a negative correlation with nitrogen content in this habitat, with most of the nitrogen being contained in the top organic layer. Nitrogen in boreal forest soils and peatlands is a limiting factor for primary production and the nitrogen in these soils tend to be competitively recycled by the biota (Aerts *et al.* 1992; Wickland and Neff 2008; Kuhry and Vitt 1996). Vegetation in boreal forests and peatlands have been shown to have extraordinary adaptations on a cellular level to navigate N limitation, such as the feather moss (*Hylocomium splenens* — notably, the same species found in the Upland Forest and Intermediate site in this study) releasing chemo-attractants to targeted strains of N_2 fixing cyanobacteria when the moss is under N-limitation stress, forming a symbiotic relationship between the organisms (Bay *et al.* 2013). The elevated levels of N in the Forest-Top, Intermediate-Top and -Middle were likely as a result of this, as the feather mosses were ubiquitous throughout both habitats, and suggest that future studies exploring N cycling in these areas could be of interest (Stuiver *et al.* 2015). The ratio of carbon to nitrogen (C:N) found in each soil horizon was highest on the top of the soil horizon, due to the most fresh plant input, and decreased with depth/maturity, as found in previous literature where increasingly anaerobic conditions result in increasing loss of C (Janssen 1996; Kuhry and Vitt 1996).

While it is unexpected that we saw insignificant CH_4 production, the processes underlying methane production are sensitive to change and are influenced by a variety of inputs. In this study we postulate this lack of measured CH_4 is due to the resident methanogen community being unable to re-acclimatize after frozen transport, despite standard procedure being used, and a 25 day equilibration period before the start of the 140 days incubation.

Temperature Response

Generally, warmer temperatures produce more soil respiration products (Fang *et al.* 2005, 2006; Knorr *et al.* 2005; Davidson and Janssens 2006), but in this study, this relationship is shown to have an outlier in samples composed of *Sphagnum* moss (Fig. 4). In general, samples in the 20°C group were most productive in terms of cumulative CO_2 produced, especially at the top of the soil column. The top of the soil column in the boreal zone experiences large temperature fluctuations throughout the freeze-thaw seasonal cycles, and temperatures of 20°C and above are regular summertime highs in this region. The top soil samples (except for samples from the Bog) followed the expected response to temperature (having a higher incubation temperature treatment resulted in an increase of cumulative CO_2) which may indicate that the C availability there is of higher quality. With boreal regions expected to become warmer, the 'high' end temperatures included in this study are of particular interest to predicting future soil C production from these habitats.

The Bog samples did not respond to increased temperature, though produced more CO_2 at the 4°C in the Bog-Top and at 0°C in the Bog-Bottom than at 20°C (Fig. 2), in agreement with other anaerobic *Sphagnum*-dominated samples from boreal-latitude incubation experiments (Kolton *et al.* 2019). . The Bog's high TOC but minimal response to temperature could also indicate its higher composition of more recalcitrant forms of C, as each form of soil C likely has different interactions with the biotic environment at different temperatures. The low temperature sensitivity in the Bog could also suggest that

microbial community was not as well adapted for higher temperatures in the Bog as the well-drained sites were. Especially in the water-saturated Bog, the degree of connectivity between the soil horizons and how mobile microbial organisms, OM, nutrients, etc. are is an open question that should receive continued attention (Tfaily et al 2018). While this experiment shows that the microbial community in the Bog's lowest depths are respiring less CO_2 at 20°C, its plausible that warmer temperatures and precipitation changes allow the 'top' soil microbes to colonize lower depths in field conditions. Additionally, diversity in the structure of the SOM molecules and environmental inhibition of enzyme activity are examples of factors that could diminish the decomposition processes sensitivity to temperature changes in anaerobic environments, as mentioned above (Davidson and Janssens 2006) in addition to the presence of *Sphagnum* and its associated complex compounds (Wilson *et al.* 2022).

Across all plots, samples from the lower depth groups had decreased temperature response (Fig. 2). This is not to say that warming will result in less CO_2 production in nature, rather these results indicate that temperature is not likely the limiting factor for anaerobic CO_2 production in these soils. The sample Q_{10}s range from 0.6–2.33 and are within the range of previous high latitude wetland studies that report anaerobic incubations measuring CO_2 produce Q_{10} values of 0.67–4.10 (n = 219; Treat *et al.* 2015). In a global synthesis of available incubation studies, the global mean of soil Q_{10}s was found to be 2.04 ± 1.09 (n = 494; Hamdi *et al.* 2013), though most of these studies incubate material for less than a month and do not include (or have a much shorter) equilibration period than this studies 25-day incubation equilibration. The increase in Q_{10} values in the low range (0, 4°C) indicates a soil microbial community adapted for temperatures within this range, especially in the Upland Forest soils. Biogeochemical cycles in cold seasons have previously thought to have been relatively dormant, though increasing evidence shows that soil communities in high-latitude regions are still active throughout winter (McMahon et al 2009). These soils have been shown to have strong temperature responses and below 0°C (Schimel and Clein, 1996; Schimel and Mikan 2005), though understanding the mechanisms behind this near-zero response require further investigation with both laboratory and *in-situ* data.

Conclusion

We found that soil samples from the *Sphagnum* moss bog had the highest anaerobic CO_2 production at cooler temperatures, whereas the surrounding habitats responded positively to temperature. Additionally, the bog samples did not produce the most anaerobic CO_2 despite having the largest composition of initial soil carbon. Our findings underscore how the initial soil carbon content as the primary predictor of anaerobic-produced CO_2 for the soils in the Intermediate and Forest habitats, but the complex biochemistry of *Sphagnum* material indicates that this habitat is governed by different ecosystem-scale controls. We recommend including the intermediate peatland-forest ecotone in future geo-ecology experiments to further explore the dynamic and high production potential from this habitat. We also emphasize that the inclusion of initial soil carbon quantity into global climate models could have a high impact on refining climate scenario estimates.

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