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Seasonal controls on methane flux components in a boreal peatland - combining plant removal and stable isotope analyses

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Abstract. Wetlands are the largest natural source of atmospheric methane and highly vulnerable to climate change. In our study we aim to better understand the environmental controls on the strength and seasonal variation of methane flux components from hollows, typically the high-emitting wettest microtopographic features in a boreal bog. We measured methane fluxes from intact vegetation as well as on vegetation removal treatments and analyzed pore water methane concentrations and stable carbon isotopes of dissolved and emitted methane. Using these data, we quantified the rates of total methane emission, methane oxidation and plant-mediated methane transport for the summer and shoulder seasons of 2021 and 2022. Total methane emissions from areas with intact vegetation range from 13 to 2171 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ during shoulder seasons and summer months and are mainly controlled by the leaf area of aerenchymatous plants. Methane oxidation in the *Sphagnum* moss layer decreases total methane emissions by 82 ± 20 % while transport of methane through aerenchymatous plants increases methane emissions by 80 ± 22 %. Both methane oxidation and plant-mediated methane transport rates follow a seasonal cycle with lower but still significant rates during the shoulder seasons compared to the summer months. As a net effect, the presence of *Sphagnum* mosses and vascular plants reduces methane emissions from the study site. This balance, however, appears to be highly sensitive to climate change, i.e. increasing soil temperatures and changing leaf area and composition of the wetland vegetation. The provided insights can help to improve the representation of environmental controls on the methane cycle and its seasonal dynamics in process-based models to more accurately predict future methane emissions from boreal peatlands.

1 Introduction

Wetlands are the largest natural source of atmospheric methane (CH_4) (Saunois et al., 2016), a greenhouse gas with 45 times the mass-based sustained-flux global warming potential of CO_2 on a 100-year timescale (Neubauer, 2021). The response of wetland CH_4 emissions to a changing climate remains highly uncertain, partly due to a high degree of uncertainty in CH_4 process parameterization in large-scale CH_4 emission models (Melton et al., 2013).

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In the boreal biome the dominant wetland type are peatlands, where organic material decomposes only partially and accumulates as peat due to anoxic conditions below the water table. These ecosystems thus form a globally important carbon storage of 500 Gt of C (Yu, 2012). CH_4 emissions from peatlands are controlled among others by soil temperature (Dunfield et al., 1993), water table depth (Dise et al., 1993; Ström and Christensen, 2007), and vegetation composition (Ström et al., 2005; Dorodnikov et al., 2011; Korrensalo et al., 2022; Riutta et al., 2020) - environmental variables that are strongly affected by climate change. With globally rising atmospheric temperatures and CO_2 concentrations we expect a shift in vegetation communities as well as hydrologic feedbacks (Yuan et al., 2021) that will likely result in a widespread drying trend in boreal peatlands (Zhang et al., 2022; Mullan et al., 2019). Changes in environmental conditions might considerably affect peatland CH_4 emissions in the near future, thereby altering atmospheric CH_4 concentrations. Depending on the direction of the change this can potentially result in a positive feedback loop between increasing CH_4 emissions and increasing air temperatures.

The CH_4 flux in peatlands is the net of CH_4 produced by methanogenic archaea under anaerobic conditions below the water table and CH_4 oxidized to CO_2 by methane oxidizing bacteria mostly under aerobic conditions. Rates of CH_4 oxidation, CH_4 storage in the peat, and CH_4 emission are affected by the pathway of CH_4 transport - diffusion, plant-mediated transport, or ebullition (Lai, 2009). Each of the three components of CH_4 flux, production, oxidation, and transport, is associated with its own set of environmental and ecological controls. Changes in environmental and ecological variables might therefore affect the individual components of CH_4 flux differently. Moreover, their effect on the flux components might also differ by season. It is therefore crucial to separately investigate the controls on the CH_4 flux components as well as their interactions and seasonal variation to draw conclusions on the net effect of environmental changes on CH_4 emissions from peatlands.

The vegetation composition of a peatland influences all three components of CH_4 fluxes. Vascular aerenchymatous plants can enhance CH_4 emissions through plant-mediated CH_4 transport and substrate supply for methanogenesis or reduce CH_4 emissions through oxygen leakage into the rhizosphere of aerenchymatous plants, thereby supporting CH_4 oxidation (Joabsson et al., 1999). The magnitude and relative importance of each of these effects depends on the plant species (Schimel, 1995; Ström et al., 2005; Dorodnikov et al., 2011; Korrensalo et al., 2022). *Sphagnum* mosses can significantly enhance CH_4 oxidation rates through a symbiosis with methane oxidisers, which provide *Sphagnum* mosses with CO_2 and use the oxygen released from moss photosynthesis (Larmola et al., 2010; Kip et al., 2010). Vegetation composition can therefore influence the balance between CH_4 production and consumption and thus affects the net CH_4 flux in a peatland.

The magnitude and importance of CH_4 flux components can be investigated using the natural abundance of stable carbon isotopes in CH_4 (e.g., Knoblauch et al., 2015; Marushchak et al., 2016) and plant removal experiments (e.g., Riutta et al., 2020; Galera et al., 2023), but these two methods have rarely been applied in the same study. Combining the two methods allows us to more directly relate differences in CH_4 fluxes between intact vegetation and plant removal treatments to specific processes within the CH_4 cycle. Based on this, environmental controls on CH_4 flux components as well as their seasonal dynamics can be identified.

Incorporating such new insights on the interaction between environmental conditions and CH_4 flux components from peatlands into process-based models will greatly improve our prediction of future natural CH_4 emissions.

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The aim of this study is to evaluate seasonal differences in the processes controlling net CH_4 emissions and their components. The objectives were to quantify seasonal differences in (1) CH_4 emissions; (2) plant-mediated CH_4 transport; and (3) CH_4 oxidation and how these components are controlled by environmental and ecological factors. We achieve this by combining manual chamber measurements and pore water analysis for CH_4 concentrations and stable C-CH_4 isotopes with a vegetation removal experiment isolating the effects of vascular plants and *Sphagnum* mosses on CH_4 fluxes within wet hollows of a boreal bog. Bogs are peatland ecosystems that are not connected to the ground water and receive water and nutrients only through precipitation, and typically have a high spatial variation in their microtopography. Within the studied bog, we focus on hollows that typically have highest CH_4 emissions of all bog microtopographical features (Turetsky et al., 2014) and are the most sensitive to climate change (Kokkonen et al., 2019).

2 Methods

2.1 Study site

The study was carried out in 2021 and 2022 in an ombrotrophic bog, which is part of the Siikaneva peatland complex located in Southern Finland (61°50′ N, 24°12′ E, 160 m a.s.l), within the southern boreal vegetation zone (Ahti et al., 1968) (Figure 1a).

According to the 30-year averages (1993-2022) from the Juupajoki-Hyytiälä weather station (Finnish Meteorological Institute, 2023a) that is located 6.3 km east from the bog site, the area has an average annual temperature of 4.1 °C and average temperatures in January and July of -6.5 °C and 16.4 °C, respectively. The mean annual precipitation sum is 688 mm of which about one third falls as snow (Riutta et al., 2020). The region is typically snow-covered for 190 days between October 24th and April 30th. The growing season, comprising all days between the first five-day period with average temperatures above 5 °C and the first five-day period with average temperatures below 5 °C (Finnish Meteorological Institute, 2023b), on average lasts for 167 days between April 27th and October 11th.

Annual mean temperatures were similar to the 30-year average in 2021 and 0.7 °C higher in 2022. Mean temperatures in January were 0.1 °C lower in 2021 and 1.2 °C higher in 2022 than the 30-year average. Mean temperatures in July were 2.4 °C higher in 2021 and similar to the 30-year average in 2022. The annual precipitation sums in 2021 and 2022 were 19 and 28 mm higher than the 30-year average.

Siikaneva bog has a pronounced microtopography ranging from open-water pools and low-lying bare peat surfaces to drier and higher hummocks with wet hollows and intermediate lawns in between. Each microtopography type shows characteristic plant communities (Korrensalo et al., 2018b) and nutrient concentrations in the surface peat (Korrensalo et al., 2018a). In this study we focused on the wet hollows, which cover about 20 % of Siikaneva bog (Alekseychik et al., 2021), making it the second largest microtopography type in Siikaneva bog after the lawns. The vegetation in the hollows typically consists of a moss layer formed by *Sphagnum cuspidatum* and *Sphagnum majus* as well as the aerenchymatous vascular sedges *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris* (Korrensalo et al., 2018b). The soil at the hollows was classified as Histosol consisting of slightly decomposed peat with a pH of 4.4 measured down to 30 cm depth.

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2.2 Experimental design

This study used a vegetation removal experiment, established in 2016, with one control plot and two treatments that allowed us to isolate the effects of vascular vegetation and moss on CH_4 emissions. The control plot had intact natural vegetation including *Sphagnum* mosses and vascular plants (peat-sphagnum-vascular, or PSV), one treatment had all vascular plants removed and only the *Sphagnum* moss layer remaining (PS), and another treatment had all vegetation removed, leaving behind a bare peat surface (P) (Figure 1c). Polypropylene root barrier fabric was installed 70 cm deep in the ground around an area of about 0.6 m^2 surrounding the PS and P treatments to keep vascular plants from growing back to the vegetation removal area. There are five spatial replicate plot clusters within the hollow microtopography type placed along a boardwalk in Siikaneva bog (Figure 1b). Each of the plot clusters comprises one control plot and one of each vegetation treatment (Figure 1c). Aluminum collars for manual chamber measurements of CH_4 are permanently installed at the PSV and PS plots while the P plots are covered with a wooden frame holding the moss layer on net fabric that is removed for collar placement on the measurement day.

The data for this study was collected during seven field campaigns that took place in July, August and October 2021 and in May, July, September and October 2022 (Figure A1). We captured summer and fall conditions at Siikaneva bog in 2021, and spring, summer and fall conditions in 2022 with our measurement campaigns. In summer 2021, the measurement campaigns took place just after the air temperature had reached its annual maximum and when the water table was at its annual minimum. The measurements in fall 2021 were taken after an extended period of strong precipitation (not shown) so that the water table reached a seasonal maximum. During the measurement campaign in spring 2022, the surface soil temperature had just risen above 0 $^{\circ}\mathrm{C}$ and daily average air temperatures rose above 10 $^{\circ}\mathrm{C}$ for the first time of the year, melting the last isolated patches of snow and ground ice and starting the growing season. The water table started to decrease from its annual maximum that had been reached during peak snow melt. The summer measurement campaign in 2022 took place right after air and soil temperatures had reached their maxima of the year. The water table reached a first minimum following an extended period without precipitation in late June. Between the measurement campaigns in September and October 2022, average air and soil temperatures decreased by about 5 $^{\circ}\mathrm{C}$ and the water table rose by about 2 cm.

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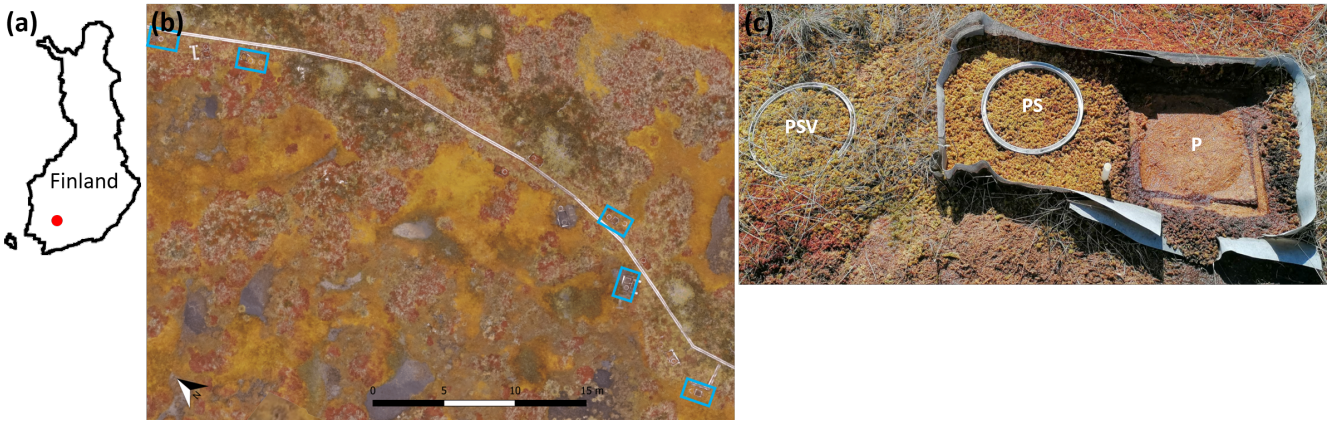


Figure 1. Location of (a) Siikaneva bog in Finland, (b) the five spatial replicates of chamber measurement plot clusters within Siikaneva bog, and (c) the control plot and the two vegetation treatments within one plot cluster (PSV: intact vegetation plot including *Sphagnum* mosses and vascular plants; PS: *Sphagnum* moss plot with vascular plants removed; P: peat plot with all vegetation removed). The drone image in (b) was taken and processed in August 2022 by Lion Golde and Tabea Rettelbach (AWI).

2.3 Quantifying CH_4 fluxes

2.3.1 Manual chamber measurements

During each of the field campaigns we measured the CH_4 fluxes manually on each of the 15 plots using a transparent chamber. Each plot was usually measured twice - once under normal light conditions and once under dark conditions, with blackout fabric covering the chamber. In July 2021 measurements were additionally performed at two different levels of incomplete shading using one or two layers of net fabric, respectively. For the flux measurements we placed a transparent cylindrical chamber with a volume of 36 l (inner height of 39.0 cm and an inner diameter of 34.4 cm) on the collar (inner diameter: 30.7 cm). Since the chamber was larger in diameter than the collar, we attached a rubber seal at the bottom of the chamber in 2021. In 2022, we used a 3D-printed adapter (added height: 8 cm) to connect the collar and the chamber. Both the collars and the adapter had a rim at the top that we filled with water to seal the connections. For each measurement we kept the chamber closed for 3 min (2021) or 5 min (2022) and continuously recorded the CH_4 and CO_2 concentrations inside the chamber at a frequency of 1 Hz using an in-line gas analyzer (Licor LI-7810 in summer 2021 and additionally LGR Microportable Greenhouse Gas Analyzer (MGGA) in fall 2021 and in 2022). Prior to each measurement we ventilated the chamber until the CH_4 and CO_2 concentrations inside the chamber were back to ambient conditions.

Two fans with Peltier elements continuously mixed and cooled the air inside the chamber. The temperature inside the chamber was measured with a HOBO temperature sensor at a frequency of 1 Hz. Despite the cooling, the temperature inside the chamber increased by more than 1 °C in 20 % and by more than 2 °C in 10 % of the measurements between May and August. In September and October, the temperature increase inside the chamber remained within 0.5 °C of the ambient air temperature during 90 % of the measurements.

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2.3.2 Flux calculations

We removed the first 25 s of each measurement to account for potential initial disturbances caused by the chamber placement. We then applied three steps of quality control. First, we visually checked the change in CH_4 concentration over time during each chamber measurement for measurement errors, obvious leakage from the chamber (temporary decrease in gas concentration) and excessive CH_4 ebullition (less than 30 s between ebullition events) and excluded the respective measurements (14 % of measurements excluded). Next, we visually checked the remaining measurements for episodic ebullition events. We classified every obvious sudden step increase in CH_4 concentrations as ebullition if, after the increase, the CH_4 concentration did not return to a level similar to before the increase. Ebullition events were detected during 20 % of the measurements that we considered for flux calculation. We split the measurements showing ebullition events into time periods of diffusive and ebullitive CH_4 emissions (modified from Hoffmann et al., 2017). For this, we marked all consecutive rows of three or more data points as ebullition events that showed a CH_4 concentration change from its predecessor of more than 75 percentile + 0.7×IQR or less than 25 percentile - 0.7×IQR of the measurement. We then extracted the longest series of consecutive data points that were not classified as ebullition for flux calculation. We visually checked the performance of this algorithm and manually adjusted the time periods of non-ebullitive CH_4 emissions where needed. We then visually identified measurements that showed an exponential increase in CH4 concentrations at the beginning of the measurement (20 % of the measurements). Some studies suggest that the rate of change in CH_4 concentrations in the chamber decreases over time with increasing equilibration between soil gas concentrations and concentrations in the chamber headspace. They conclude that the higher slope in CH_4 concentrations at the beginning of each measurement is best suited for flux estimation (e.g., Hutchinson and Mosier, 1981; Pedersen et al., 2010; Forbrich et al., 2010). Efforts to evaluate the performance of different models for flux calculations indicate that process-based models should only be applied with much caution to assure that model assumptions are met and additional information like soil gas concentrations should be considered to identify the reason for the observed nonlinear behaviour (Forbrich et al., 2010; Pirk et al., 2016). In our study, we observed an exponential increase in chamber concentrations mainly at sites with high pore water concentrations and despite short chamber closures and relatively low headspace CH_4 concentrations in the comparatively large chamber. This points towards a steady ebullition of micro bubbles caused by the chamber placement rather than a saturation effect. We therefore manually extracted the time periods of linear concentration change towards the end of the measurements for flux calculation. We then determined the CH_4 fluxes as the slope of linear fits to all time periods extracted for flux calculation. To convert the mole fractions of CH_4 in dry air, as measured by the gas analyzer, to molar concentrations we used the ideal gas law with the mean temperature recorded inside the chamber during the measurement and with standard atmospheric pressure.

We quantified the effect of vascular plants on the CH_4 fluxes ($F_{CH_4,vascular}$) by subtracting the CH_4 fluxes measured at the PS plots ($F_{CH_4,PS}$) from the fluxes measured at the respective PSV plots ($F_{CH_4,PSV}$) on the same day and under the same light conditions (Equation 1).

$$F_{CH_4,vascular} = F_{CH_4,PSV} - F_{CH_4,PS} \quad (1)$$

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We similarly quantified the effect of the *Sphagnum* moss layer on the CH_4 fluxes ($F_{CH_4,Sphagnum}$) by subtracting the fluxes at the P plots ($F_{CH_4,P}$) from the fluxes at the respective PS plots on the same day and if available under the same light conditions (Equation 2). In cases where the flux measurement at the P plot was only available for one light level, we used this same flux value for calculation with all light levels applied at the respective PS plot.

$$F_{CH_4,Sphagnum} = F_{CH_4,PS} - F_{CH_4,P} \quad (2)$$

We excluded cases where both $F_{CH_4,vascular}$ and $F_{CH_4,Sphagnum}$ were negative, that is when emissions from the PS treatment were higher than emissions from both the respective P and PSV plot. We assume that these unexpected observations are caused by processes other than the direct vegetation effects, such as spatial or temporal variation in CH_4 emissions or steady ebullition of micro-bubbles from the PS treatments.

2.4 Carbon stable isotope signatures of emitted and pore water CH_4, concentrations of dissolved CH_4 in the pore water, and dissolved organic carbon

In addition to the CH_4 fluxes, during the measurement campaigns in 2022, we measured the δ^{13}C-values of the emitted and pore water CH_4 at each measurement plot. Samples for emitted and for pore water CH_4 of the same measurement plot were always taken on the same day. Only at one plot in May and in September 2022 samples for emitted and for pore water CH_4 had to be taken on consecutive days due to bad weather conditions.

To determine the δ^{13}C-values of emitted CH_4 we took 30 ml manual gas samples from the chamber headspace every 5 min during 25 min chamber closures at all PSV, PS and P plots under light conditions. 25 ml of the gas samples were transferred into evacuated 12 ml glass vials (Labco Exetainer).

For the measurement of pore water dissolved organic carbon (DOC) and δ^{13}C-CH_4 values and CH_4 concentrations we took 20 ml as well as 30 ml water samples in 60 ml syringes from three depths, representing conditions within the *Sphagnum* layer (7 cm), as well as within (20 cm) and below (50 cm) the main root zone (Korrensalo et al., 2018a), next to each PSV plot and from the vegetation removal area including the PS and P plots. We assume that samples taken at 20 and 50 cm depth (underneath the moss layer) from the vegetation removal area are representative of the conditions underneath both the PS and P plots. To extract the water samples from the peat, we used a metal sampling probe with a small hole at the end that we inserted into the peat up to the desired sampling depth.

The water samples for DOC were acidified with HCl and stored under cool (4 $^{\circ}\mathrm{C}$) and dark conditions until DOC was quantified as non purgeable organic carbon (NPOC) using a Shimadzu TOC-L analyzer.

The water samples for analysis of dissolved CH_4 we kept cooled until the evening of the same day. Then we added 30 ml of N_2 to the syringes containing the water samples, shook them for two minutes to equilibrate the gas concentrations in water and gas volume and transferred the gas phase into evacuated 12 ml glass vials (Labco Exetainers). To derive the actual pore water gas concentrations from the concentrations measured after equilibrating pore water and headspace gas concentrations, we used Henry's law, considering the temperature dependence of gas solubility (Lide and Frederikse, 1996). The glass vials were sealed

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Preprint. Discussion started: 4 January 2024
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with hot glue and the samples were analyzed for CH_4 and CO_2 concentrations as well as for δ^{13}C-CH_4 and δ^{13}C-CO_2 by Cavity Ring-Down Spectroscopy (CRDS; Picarro G2201-I Isotopic Analyzer + autosampler SAM) within one month after sampling.

Prior to analysis with the isotopic analyzer, the soil gas samples had to be diluted by up to 1/250 with CO_2 and CH_4 free synthetic air (purity $\geq$ 99,999 %) to obtain the optimal concentration range for CH_4 (2 – 200 ppm) and CO_2 (400 – 7000 ppm). Due to different dilutions, sometimes several subsamples of the same gas sample were measured. For the further data analysis, we used the gas concentrations measured in the least diluted sample and the δ^{13}C-values obtained from the dilutions that produced gas concentrations within the optimal range for the isotopic analyzer.

After the sample analysis three corrections were applied to the measurement data. (1) The concentrations of CO_2 and CH_4 had to be corrected for dilution. This correction was based on the measurement of a dilution series of a standard gas (100 ppm CH_4, 1 % CO_2) with nine levels of dilution ratios between 1 and 1/100 within each sample batch of max. 150 samples. A linear regression was performed between the measured gas concentrations and the theoretical gas concentrations calculated for the standard gas concentrations using the respective dilution factors. This regression was then used to correct the measured gas concentrations of the soil gas samples for their actual dilutions. (2) The δ^{13}C-values were corrected for the day-to-day drift. For this, samples of a reference gas (CH_4 concentration: 10 ppm, CO_2 concentration: 2000 ppm; δ^{13}C-CH_4: -41.5 ‰, δ^{13}C-CO_2: -35.6 ‰) were added at the beginning and at the end of each sample batch as well as after every 15 samples within the sample batch. The offset of the average of measured δ^{13}C-values per autosampler run from the actual δ^{13}C-values of the reference gas was used to correct the δ^{13}C-values of the gas samples. (3) The δ^{13}C-values were corrected for non-linearity as a function of the gas concentration since we observed non-linearity of the δ^{13}C-values in the low concentration range. First, we determined the default δ^{13}C-values of the standard gas as the average δ^{13}C-value of the standard gas at dilutions that produced gas concentrations similar to the reference gas concentrations (dilution of 0.08 for CH_4 and 0.2 for CO_2). For each standard gas sample, the offset of the δ^{13}C-value from the default δ^{13}C-value was determined. Next, we fitted a quadratic model to this offset for each autosampler run with the inverse of the gas concentration as an independent variable. Depending on the measured gas concentration a correction factor was then calculated and applied for each measured δ^{13}C-value. We estimate an analytical uncertainty of 0.4 and 0.2 ‰ for the δ^{13}C-values and of 0.2 and 46 ppm for the concentrations of CH_4 and CO_2, respectively, based on the standard deviation of the reference gas values after all three corrections.

We used the gas samples taken from the chamber headspace to estimate the δ^{13}C-values of the CO_2 and CH_4 emitted from the soil as the intercept of a linear regression function describing the δ^{13}C-values as a function of the inverse of the gas concentration (Keeling estimate) (Keeling, 1958, 1961).

For comparison with the fluxes determined from the gas analyzer measurements we furthermore estimated the CO_2 and CH_4 fluxes as the slope of a linear regression line through the gas concentrations over the measurement time.

For quality control of the gas fluxes and emission-δ^{13}C calculated from the gas concentrations and δ^{13}C values in the chamber gas samples we visually inspected the simultaneous high-frequency continuous CH_4 concentration measurements of the portable gas analyzer. We excluded concentration and δ^{13}C measurements from manual gas samples that were separated by ebullition events from our flux calculations and δ^{13}C estimates of CH_4 emissions. In cases where ebullition occurred between every manual sample, the entire measurement was discarded. Measurements were also discarded if the portable gas analyzer

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measurements showed a concentration change that obviously deviated from a linear or exponential form and if the gas concentrations in the manual samples deviated irregularly from the portable gas analyzer measurements (7 % of the chamber measurements). We furthermore discarded all Keeling estimates with R^2 values below 0.8 (another 53 % of the chamber measurements). Low R^2 values particularly occurred at low gas fluxes. Due to the generally low fluxes, all but one Keeling estimate from the PS plots had to be discarded (94 % of the measurements at the PS plots). For the PSV plots 22 % and for the P plots 42 % of the Keeling estimates had to be discarded.

2.5 Collecting environmental data

2.5.1 Environmental controls on CH_4 fluxes

As potential environmental controls on diffusive CH_4 fluxes and their components we considered peat temperatures, water table depth, total leaf area, and leaf area of aerenchymatous plants. Peat temperatures at 7 and 20 cm depth were measured manually with a rod thermometer at intact vegetation (next to the PSV plot) and under vegetation removal (PS and P treatments) right after the pore water sampling. The water table depth was measured manually on the days of flux measurements and pore water sampling in perforated plastic tubes that are permanently installed in the peat at average surface elevation once per plot cluster.

We determined the leaf area index (LAI) inside each PSV plot following Wilson et al. (2007). We estimated the average number of leaves per square meter of area for each vascular plant species by counting their leaves within each PSV plot over the growing season on three days in 2021 and on five days in 2022. To determine the average leaf sizes we collected samples of each species from the measurement site on the day of leaf counting and measured their leaf area with a LI-3000 Portable Area Meter (LICOR, Lincoln, Nebraska). We applied correction factors to the measured average leaf areas to account for the typical leaf shape of each vascular plant species (Op de Beeck et al., 2017). We then calculated the LAI on the sampling days for each vascular plant species present in each PSV plot by multiplying the respective leaf number with the average leaf area per m^2. We reconstructed the LAI of each vascular plant species for each growing season day in 2022 using the log-normal curve version of the model presented by Wilson et al. (2007). For 2021, the curve could not be fitted because of too few sampling days. We therefore linearly interpolated the LAI between the sampling days. We calculated the total LAI of each PSV plot as the sum of the LAI of all vascular plants present at the measurement plot (LAI_{tot}). The LAI of aerenchymatous plants (LAI_{aer}) was determined as the sum of LAI of the aerenchymatous species present in the hollow microtopography type, namely *C. limosa*, *S. palustris*, *R. alba* and *Eriophorum vaginatum*. Outliers in the flux data were excluded from the calculation of both vegetation effects.

2.5.2 Meteorological conditions

To characterize the meteorological conditions at the study site in 2021 and 2022 we used air temperature, water table depth and snow depth measured at the weather station in Siikaneva fen (Alekseychik et al., 2023), about 1.3 km southeast of Siikaneva bog. We corrected air temperature measurements for conditions at the bog site based on a linear regression between bog and fen data between 2011 and 2016 when measurements were still being performed at both sites and added some noise to the time

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series. Additionally, we used the water table depth and the peat temperature at 2 cm depth, recorded four times per day at four spatial replicates within the hollow microtopography type at Siikaneva bog starting in July 2021. To verify the timing of onset and complete thaw of the snow cover we used the pictures of a phenocam installed at Siikaneva bog and overlooking a hollow area (https://phenocam.nau.edu/webcam/sites/siikanevabog/).

To separate the measurement years into seasons we used the threshold temperatures of below 0 °C in winter, between 0 and 10 °C in spring and fall, and above 10 °C in summer, given by the Finnish Meteorological Institute (2023b). We modified this definition by only recognizing a change between seasons when daily average air temperatures were above the lower threshold (0 °C for spring, 10 °C for summer) or below the upper threshold (10 °C for fall, 0 °C for winter) for at least 3 consecutive days and when periods of consecutive days with average temperatures below the lower or above the upper threshold did not exceed 3 days. Since surface soil temperature data was available for Siikaneva bog we defined the growing season as the snow-free time period where soil temperatures at 2 cm depth were continuously above 0 °C.

2.6 Applying statistical analyses

Similar environmental conditions during the growing seasons of 2021 and 2022 (Figure A1) allowed us to aggregate the CH_4 fluxes across the two measurement years. CH_4 fluxes did not differ significantly between light conditions ($t_{(64)} = 1.178$, $p = 0.2432$). We therefore treated light and dark measurements as temporal replicates in the data analysis.

We used linear mixed-effects models to test whether the measured CH_4 fluxes, pore water CH_4 concentrations and δ^{13}C-CH_4 values differed significantly between seasons, between control plot and vegetation treatments and, for the pore water gas data, between sampling depths. We furthermore applied linear mixed-effects models to identify environmental variables controlling the CH_4 fluxes from the control plot and from both vegetation treatments as well as the vegetation effects on CH_4 fluxes. As potential environmental controls we considered peat temperatures at 7 and 20 cm depth, water table depth, LAI_{tot} and LAI_{aer}. As expected, we found a strong positive correlation ($r > 0.8$) between LAI_{tot}, LAI_{aer} and the peat temperatures at 7 and 20 cm depth and therefore did not include combinations of these four variables in the same model. We used the function lme of the package nlme to construct the models. We included the spatial replicates and, in the case of the flux data, the year as random effects to account for the randomized block design with repeated measures. We used the AIC value (Akaike information criterion) to evaluate whether the addition of a fixed predictor significantly improved the model compared to the simpler one. Univariate models explained best the variation in all but one flux data set. Only for the fluxes from the P treatments a multivariate model performed better. To achieve normality of the residuals (tested using the Shapiro-Wilk test with the function shapiro.test), the CH_4 fluxes had to be logarithmically transformed prior to statistical analyses. Despite containing some outliers we decided not to transform the vegetation effects on CH_4 emissions since both vascular plant effects and *Sphagnum* moss layer effects included positive as well as negative values. We applied the post-hoc Tukey's HSD (honestly significant difference) test to the model results to identify significant differences between combinations of control plot or vegetation treatment, season and sampling depth using the glht function of the package multcomp. All statistical analyses were done in the R environment (version 4.3.0).

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3 Results

3.1 CH_4 fluxes

3.1.1 CH_4 fluxes at the vegetation removal treatments compared to the control plots

The CH_4 emissions from both control plots and vegetation treatments ranged between a minimum of 2 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ measured in fall and a maximum of 2225 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ in summer (Figure 2a). The presence of *Sphagna* (PS treatment) decreased the CH_4 emissions compared to the bare peat (P treatment). The additional presence of vascular plants (PSV plot) increased the CH_4 emissions but they still remained below the emissions from the bare peat (P treatment). The strength of the vegetation effects on the CH_4 emissions differed by season, with the *Sphagna* decreasing and the vascular plants increasing the CH_4 emissions most strongly in summer, followed by fall and then spring (significant treatment by season interaction ($F_{(4,187)}$ = 7.393, $p < 0.0001$)).

The CH_4 emissions from both control plots and vegetation treatments followed a seasonal cycle with the mean fluxes increasing between spring and summer and then decreasing again towards fall. The seasonal variation in CH_4 emissions differed by vegetation treatment, with the mean shoulder season (spring and fall) emissions from the PSV, PS and P treatments being 31, 16 and 41 % of the respective summer emissions. While emissions from the PSV plots were similar in spring and in fall, fall emissions were lower than spring emissions at the PS plots. At the P plots, the opposite pattern was observed with higher emissions in fall than in spring.

An increase in each of the considered environmental and ecological predictors (LAI_{tot}, LAI_{aer}, peat temperatures at 7 and at 20 cm depth, and water table depth) resulted in higher CH_4 emissions from the intact vegetation (PSV plots) (Table A1). The increase of CH_4 emissions with increasing LAI_{aer} explained most of the variation in the fluxes at the PSV plots. CH_4 emissions from the *Sphagnum* treatments (PS treatments) increased with higher peat temperatures at 7 and at 20 cm depth (Table A2). The variation in the CH_4 fluxes at the PS treatments was best explained by a combination of the fluxes increasing with increasing peat temperatures at 20 cm depth and with higher water table. Most of the variation in CH_4 emissions from the bare peat (P treatments) was explained by an increase of emissions with increasing peat temperature at 20 cm depth (Table A3). Furthermore, CH_4 emissions from the P treatments were higher at lower water tables.

3.1.2 Vascular plant effects on CH_4 fluxes

The presence of vascular plants led to a mean increase in CH_4 emissions in all seasons (Figure 2a). Mean vascular plant-related increments in CH_4 fluxes significantly affected the CH_4 emissions in summer and fall. Their magnitude differed significantly between the seasons ($F_{(2,42)}$ = 5.677, p = 0.0066)) with the increase in the shoulder seasons being 30 % of the summer increase in CH_4 emissions. The effect of the vascular plants accounted for 81 ± 20 % and 62 ± 63 % of the CH_4 emissions from the PSV plots in summer and during the shoulder seasons, respectively. The full range of vascular plant effects was between a decrease in CH_4 emissions by 401 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ and an increase in CH_4 emissions by 960 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ compared to the moss plot (PS treatment) emissions, ignoring an outlier of 1886 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ in summer (Figure 2b).

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An increase in each of the considered environmental and ecological predictors (LAI_{tot}, LAI_{aer}, peat temperatures at 7 and at 20 cm depth, and water table depth) lead to an increase in the vascular plant-related increment in CH_4 emissions (Table A4). Vascular plants particularly lead to a stronger increase in CH_4 emissions at higher peat temperatures at 7 cm depth.

3.1.3 Effects of the *Sphagnum* moss layer on CH_4 fluxes

The presence of *Sphagna* (PS treatment) reduced mean CH_4 emissions in all seasons with the effect being significant in summer and fall (Figure 2a). The magnitude of the *Sphagnum*-related reduction in CH_4 emissions varied significantly between the seasons ($F_{(2,51)} = 6.010$, $p = 0.0045$)) with the shoulder season decrease being 41 $\%$ of the summer decrease. The presence of *Sphagna* on average decreased the CH_4 by 80 ± 27 $\%$ and 83 ± 17 $\%$ in summer and during the shoulder seasons, respectively compared to the bare peat (P treatments) emissions. Individual effects of *Sphagna* on CH_4 emissions ranged from a decrease by 2056 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ to an increase by 61 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ compared to the bare peat (P treatment) emissions (Figure 2c).

None of the relevant potential environmental and ecological controls that we considered in our study (peat temperatures and water table depth) nor their combination influenced the effect of the *Sphagnum* layer on CH_4 fluxes (Table A5).

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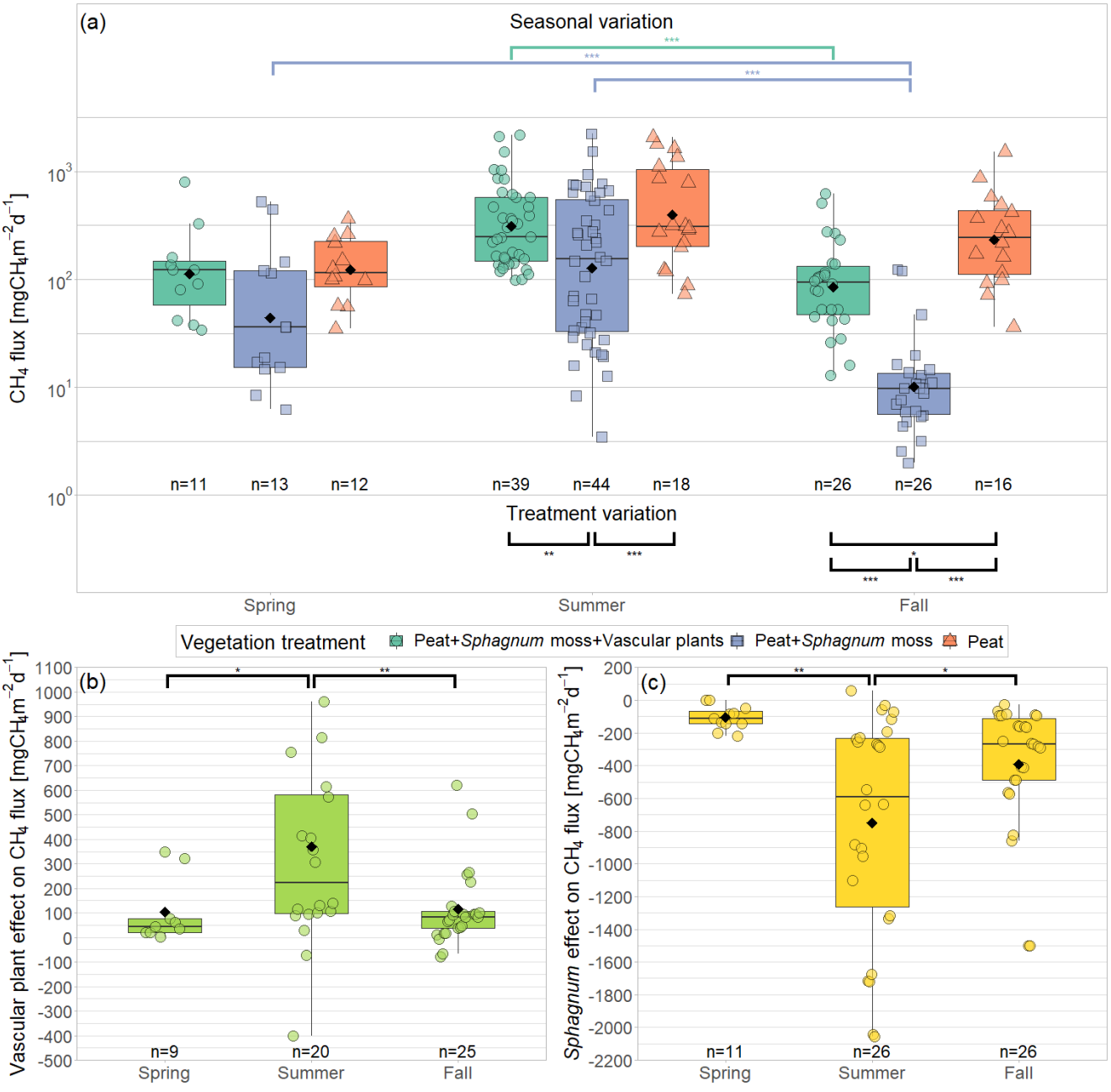


Figure 2. CH_4 fluxes (displayed on a logarithmic y-axis) (a), vascular plant effects (b) and *Sphagnum* moss layer effects (c) on CH_4 fluxes by season and vegetation treatment. Circles show the individual values, the boxplot shows the median (horizontal line), 25th and 75th percentiles (hinges) and smallest/largest values, no more than 1.5 times the inter-quartile range from the hinges (whiskers). Values above/below the whiskers are classified as outliers. Mean values are given as black diamonds. The statistics in (a) are based on the logarithmically transformed flux data. Brackets in (a) connect pairs of flux groups that differ significantly from one another. Brackets displayed under "Seasonal variation" show differences between the seasons within one treatment group. Brackets displayed under "Treatment variation" show differences between treatment groups within one season. The number of asterisks next to the bracket indicates the significance level of the difference: ***: 0<p<0.001, **: 0.001<p<0.01, *: 0.01<p<0.05. Numbers of observations (n) in each group of data are given below the boxes. An outlier in the vascular plant effects of 1886 $\mathrm{mgCH_4\ m^{-2}\ d^{-1}}$ is not displayed in figure (b) but was included in the statistical analysis and in the creation of the boxplots.

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3.2 Pore water properties

3.2.1 CH_4 pore water concentrations

The CH_4 pore water concentrations ranged from 3 $\mu mol\,L^{-1}$ at 7 cm depth in summer to 745 $\mu mol\,L^{-1}$ at 20 cm in spring, both underneath the vegetation removal experiment (PS and P treatment) (Figure 3a).

On average, pore water concentrations were lower under intact vegetation (PSV plot), being 64 % of the concentrations underneath the vegetation removal (PS and P treatments) across all seasons and sampling depths ($F_{(1,105)} = 28.267$, $p < 0.0001$).

Pore water concentrations generally increased with depth ($F_{(2,105)} = 14.587$, $p < 0.0001$). On average, mean concentrations at 7 and 20 cm depth were 57 and 91 % of the concentrations at 50 cm depth, respectively.

Pore water CH_4 concentrations did not differ significantly between the seasons ($F_{(2,106)} = 1.599$, $p = 0.2070$). Figure 3a, however, indicates a decrease in pore water concentrations between spring and summer. The decrease was strongest at 7 and 50 cm depth under intact vegetation (PSV plot) and at 20 and 50 cm depth underneath the vegetation removal (PS and P treatments). Between summer and fall, pore water concentrations under the intact vegetation remained similar at all depths and increased underneath the vegetation removal at 7 and 20 cm depth.

3.2.2 Stable $^{13}C/^{12}C$ isotope values in pore water and emitted CH_4

Pore water δ^{13}C-CH_4 values ranged from -72.7 ‰ at 20 cm depth under intact vegetation (PSV plot) in spring to -30.6 ‰ at 7 cm depth underneath the vegetation removal (PS and P treatments) in summer.

Pore water CH_4 under intact vegetation (PSV plot) was more enriched in ^{13}C than underneath the vegetation removal treatments (PS and P), especially in summer and fall and at 7 and 20 cm depth, showing in a significant difference between δ^{13}C-CH_4 values at the control plots compared to the vegetation removal treatments ($F_{(1,99)} = 13.681$, $p = 0.0004$) (Figure 3b).

Pore water CH_4 became more enriched in ^{13}C towards the peat surface. The depth profile of δ^{13}C-CH_4 values differed between the seasons (interaction between season and sampling depth, $F_{(4,99)} = 3.933$, $p = 0.0053$). In spring, the differences in δ^{13}C-CH_4 values between control plots and vegetation removal treatments as well as between sampling depths were small and pore water CH_4 was more depleted in ^{13}C compared to summer and fall. In summer and fall, pore water CH_4 became more enriched in ^{13}C, especially at 7 and 20 cm depth under intact vegetation (PSV plots) and at 7 cm depth underneath the vegetation removal (PS and P treatments). Between summer and fall, δ^{13}C-CH_4 values remained similar at 20 and 50 cm depth while pore water CH_4 became more depleted in ^{13}C at 7 cm depth at both control plots and vegetation removal treatments.

While CH_4 generally became more enriched in ^{13}C, pore water CO_2 became more depleted in ^{13}C towards the peat surface (Figure A2).

δ^{13}C of emitted CH_4 ranged from -83.9 ‰ at intact vegetation (PSV plot) to -45.1 ‰ at bare peat (P treatment), both in spring. All but one δ^{13}C estimate for CH_4 emissions from the moss plots (PS treatment) had to be discarded due to low accuracy of the Keeling estimates, mostly related to low emission rates.

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CH_4 emitted from intact vegetation (PSV plot) was significantly more depleted in ^{13}C compared to the CH_4 emitted from bare peat (P treatment) ($F_{(1,26)}$ = 41.349, $p < 0.0001$). CH_4 emitted from both control plots and bare peat treatments was significantly more depleted in ^{13}C in fall compared to spring and summer ($F_{(2,26)}$ = 5.277, $p = 0.0119$).

CH_4 emitted from intact vegetation (PSV plot) was more depleted in $\delta^{13}C$ than the respective pore water CH_4 at 7 cm depth while at bare peat, $\delta^{13}C$ values of CH_4 remained similar upon emission. This shows in a significant difference in isotopic fractionation upon emission between control plot and bare peat treatment ($F_{(1,58)}$ = 15.101, $p = 0.0003$).

3.2.3 Dissolved organic carbon

Pore water DOC ranged between 11 and 38 $\mathrm{mg\,L^{-1}}$. DOC values were higher in summer than during the shoulder seasons and showed little variation with depth. In the shoulder seasons, DOC showed a more pronounced depth profile of values decreasing with depth in spring and increasing with depth in fall. This seasonal variation in the depth profile shows in a significant effect of the depth and season interaction on DOC ($F_{(1,192)}$ = 7.651, $p < 0.0001$). Pore water DOC did not differ significantly between the control plots and the vegetation removal treatments ($F_{(1,199)}$ = 2.071, $p = 0.1517$).

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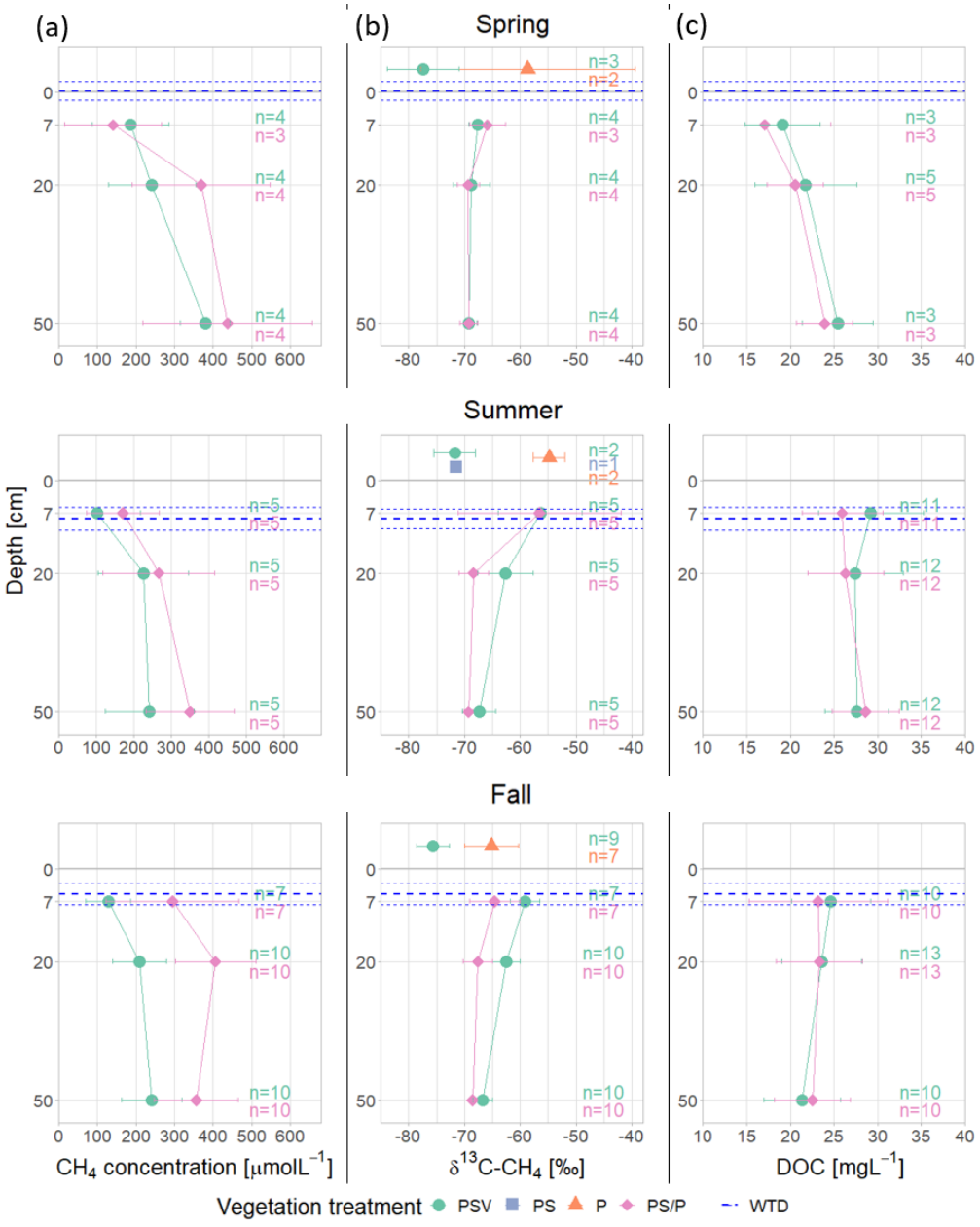


Figure 3. Mean and standard deviation of dissolved pore water CH_4 concentrations (a), δ^{13}C-CH_4 values (b) and DOC (c) by season, vegetation treatment and sampling depth. Control plot and vegetation treatments are the following: PSV: intact vegetation including *Sphagnum* mosses and vascular plants; PS: *Sphagnum* moss with vascular plants removed; P: peat with all vegetation removed. Pore water data is combined for the PS and P plots because the vegetation removal treatments were collocated. The δ^{13}C values of emitted CH_4 are displayed above the soil surface (depth of 0 cm). The blue dashed lines indicate the mean and standard deviation of the water table depth during the respective measurement campaigns. Numbers of observations (n) in each group of data are given in the figure.

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4 Discussion

In our study, we combined measurements of CH_4 emissions from vegetation removal experiments in wet hollows of a boreal bog with pore water CH_4 concentration and isotopic data. We aimed to quantify and to explain seasonal differences in the components of CH_4 emissions (production, oxidation, transport) considering their environmental and ecological controls. We found that the presence of vascular plants generally increased the CH_4 emissions while the presence of *Sphagnum* moss reduced the CH_4 emissions from our study site. During the shoulder seasons both vegetation effects were lower than in summer but still significantly affected the CH_4 emissions.

4.1 Vascular plant effects on CH_4 fluxes and plant-mediated CH_4 transport

In our study, CH_4 emissions were generally higher in the presence of vascular plants (Figure 2a,b) as expected based on previous studies suggesting a dominance of vascular plant effects that increase CH_4 emissions namely plant-mediated CH_4 transport, reducing the availability of CH_4 for CH_4 oxidation, and substrate supply for methanogenesis (Whiting and Chanton, 1992; Frenzel and Rudolph, 1998; Ström et al., 2012; Henneberg et al., 2016). Altogether, the net effect of vascular aerenchymatous plants on CH_4 emissions from wetlands is the sum of those enhancing processes and processes reducing CH_4 emissions namely oxygen leakage into the rhizosphere of aerenchymatous plants, thereby supporting CH_4 oxidation (Joabsson et al., 1999).

Vascular plant effects were smaller during the shoulder seasons but still significantly increased CH_4 emissions (Figure 2b) even in spring when there were only old, dead leaves of aerenchymatous plants and in fall when the majority of their leaves were already brown. This indicates that the increasing effects of vascular plants on CH_4 fluxes can persist even after complete leaf senescence, although at a lower rate, as shown for the plant-mediated CH_4 transport by Roslev and King (1996) and Korrensalo et al. (2022). Besides the leaf area of aerenchymatous plants and the peat temperatures which directly influence the plant transport and substrate supply through controlling the biomass of aerenchymatous plants, water table depth also significantly affected the seasonal variation of vascular plant effects, which is in line with Korrensalo et al. (2022). In summer, when water table depths were lower, a thicker aerobic peat layer led to higher potential CH_4 oxidation rates. This is supported by the negative correlation of CH_4 emissions from the moss (PS) treatments with the water table depth. The transport of CH_4 through aerenchymatous plants passes by this relatively thicker oxidation zone, leading to a stronger vascular plant effect than at higher water tables.

The high summertime contribution of vascular plant effects to total CH_4 emissions of 82 ± 20 % could be explained by efficient plant-mediated CH_4 transport. The previously reported proportions of plant transport range from 70 % to more than 90 % of the total CH_4 emissions (Whiting and Chanton, 1992; Schimel, 1995; Riutta et al., 2020; Knoblauch et al., 2015), indicating that plant transport is the primary pathway for CH_4 emissions in the presence of aerenchymatous plants (Van Der Nat and Middelburg, 1998). The large range of positive vascular plant effects accounting for 1 to 99 % of the CH_4 emissions, furthermore matches the proportions of plant-mediated CH_4 transport of 6 to 90 % reported for Siikaneva bog between May and October by Korrensalo et al. (2022). The high mean vascular plant effect found in our study can be explained by the generally high abundance of *S. palustris* compared to other aerenchymatous species in our measurement plots (Figure A1c). Vascular

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Preprint. Discussion started: 4 January 2024
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plant effects on CH_4 emissions were found to be highly species-dependent (Schimel, 1995; Ström et al., 2005; Dorodnikov et al., 2011; Korrensalo et al., 2022) and *S. palustris* was reported to transport the most CH_4 of all aerenchymatous bog plant species studied by Dorodnikov et al. (2011) and Korrensalo et al. (2022).

Individual cases in summer and fall where the presence of vascular plants led to a decrease in CH_4 emissions (Figure 2b) might be related to strong oxygen leakage through aerenchymatous plants allowing for CH_4 oxidation in their otherwise anaerobic rhizosphere. CH_4 emissions in the presence of vascular plants might however also be reduced due to processes other than the direct effect of aerenchymatous plants, such as the potentially high spatial and temporal variability of CH_4 emissions and their components (production, oxidation and transport). In addition, aerenchymatous plants may decrease pore water CH_4 concentrations through efficient plant transport, which then decreases the diffusive CH_4 emissions from the same areas (Chanton, 2005). This might thus have led to an underestimation of plant transport rates in these cases.

The concentrations of CH_4 dissolved in the pore water suggest that effective plant-mediated transport is primarily responsible for the increase in CH_4 emissions in the presence of vascular plants. Pore water CH_4 concentrations were 43 ± 24 % lower when vascular plants were present (Figure 3a) which is in line with the about 50 % lower pore water CH_4 concentrations in the presence of vascular plants found in some earlier studies (Wilson et al., 1989; Chanton et al., 1989; Chanton, 1991). Whiting and Chanton (1992) on the contrary found that clipping of aboveground vegetation reduces pore water CH_4 concentrations and explained their observation by the production of root exudates, senescence and decay of vascular plants providing substrates for CH_4 production. The lower pore water concentrations in our study thus indicate that efficient plant-mediated transport prevented an accumulation of CH_4 inside the peat. Accordingly, in the absence of vascular plants pore water concentrations were high, especially in fall and in spring following the high CH_4 production rates of the previous summer. The missing difference in DOC values between plots with and without vascular plants similarly suggests that the presence of vascular plants does not significantly affect the substrate availability for CH_4 production, although this does not rule out the possibility that certain more specific plant root exudates such as acetate could have been better associated with CH_4 production (Ström et al., 2003).

The importance of plant-mediated CH_4 transport is furthermore indicated by the substantial depletion of pore water CH_4 in ^{13}C upon emission (Figure 3b) in the presence of vascular plants. As expected for a bog, hydrogenotrophic methanogenesis (using H_2 and CO_2 to produce CH_4) dominated over acetoclastic methanogenesis (using acetate as an electron acceptor) year-round below the main root zone as indicated by the low $\delta^{13}C$-CH_4 values and the high $\delta^{13}C$-CO_2 values (Whiticar, 1999) at 50 cm depth (Figure A2). The enrichment of pore water CH_4 in ^{13}C within the rhizosphere of vascular plants (at 7 and 20 cm sampling depth) compared to pore water CH_4 below the rhizosphere or in the absence of vascular plants in summer and fall could have been caused by different processes associated with vascular plants (plant transport, rhizospheric oxidation, acetoclastic CH_4 production from root exudates) (Chanton, 2005; Popp et al., 1999). In our study, the stronger overall ^{13}C-enrichment of dissolved CH_4 between production and emission in the presence of vascular plants can at least partly be explained by the preferential emission of $^{12}CH_4$, suggesting that rhizospheric oxidation did not play a major role in our study (Chanton, 2005). ^{13}C-depletion between rhizospheric and emitted CH_4 of 1 to 27 ‰ was similar to the isotopic fractionation of 1 to 15 ‰

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reported in previous studies for diffusive CH_4 transport through aerenchymatous plants (Chanton et al., 1992a, b; Tyler et al., 1997; Popp et al., 1999).

4.2 Effect of the *Sphagnum* moss layer on CH_4 fluxes and CH_4 oxidation rates

We found that areas with a *Sphagnum* moss layer (PS treatment) generally showed lower CH_4 emissions than bare peat (P treatment) (Figure 2a). Pore water CH_4 concentrations in the aerobic *Sphagnum* layer were lower (Figure 3a) and the dissolved CH_4 was more enriched in ^{13}C (Figure 3b) than in the deeper, anoxic peat layers (20 cm, 50 cm). This indicates that CH_4 oxidation predominantly occurred in the aerobic surface layer of *Sphagnum* moss.

The presence of a *Sphagnum* moss layer significantly decreased CH_4 emissions by an average of 82 ± 20 % across all seasons. This is in line with the fivefold increase in CH_4 emissions upon removal of the moss layer in *Sphagnum*-dominated hollows of ombrotrophic peat bogs found by Kip et al. (2010). The decrease in CH_4 emissions related to moss layer effects in our study agrees with the high mean value and high variability of oxidation rates in the aerobic surface layer and in the rhizosphere of wetlands reported in the literature (Segers, 1998; Roslev and King, 1996).

The decrease in CH_4 emissions related to the *Sphagnum* layer was significantly stronger in summer than during the shoulder seasons (Figure 2c). We could not identify a significant effect of any of the considered explanatory variables on the *Sphagnum* effects. This, as well as the unexpected increase in CH_4 emissions in the presence of *Sphagna* during one individual summer measurement might be related to other processes besides oxidation contributing to the difference in CH_4 emissions from bare peat (P treatment) and *Sphagnum* plots (PS treatment). Contrary to our assumptions, the moss layer might affect not only the consumption but also the production or the storage of CH_4 in the soil. In addition, temporal and spatial variations between the CH_4 emissions from the two vegetation removal treatments might add further uncertainty to our calculation approach. Furthermore, actual oxidation rates under natural conditions, that is in the presence of vascular plants (PSV), probably differ from our estimations for the moss (PS) treatments by the combined effect of CH_4 bypassing the aerobic surface layer through plant transport, thereby avoiding oxidation, and rhizospheric oxidation in the presence of vascular plants. Despite the missing effect of environmental variables on the *Sphagnum*-related decrease in CH_4 emissions, we can get an indication of the seasonal controls on CH_4 oxidation rates from the variables explaining the CH_4 emissions from the PS and P treatments. Reduced CH_4 emissions from moss surfaces (PS treatment) at lower water tables are potentially related to higher oxidation rates in summer due to a thicker aerobic oxidation layer. More CH_4 was furthermore emitted from both vegetation removal (PS and P) treatments at higher peat temperatures at 20 cm depth, indicating higher methanogenic activity at higher peat temperatures in the anaerobic soil (Dunfield et al., 1993). The higher production rate might have resulted in a higher availability of substrate for CH_4 oxidation in the summer months and therefore higher oxidation rates. Previous studies have demonstrated a seasonal variation in CH_4 oxidation rates that was related to an increase in methanotrophic activity with increasing soil temperatures in the oxidation layer (Whalen and Reeburgh, 1996; Zhang et al., 2020). However, CH_4 production was shown to depend much stronger on the temperature than CH_4 oxidation (Dunfield et al., 1993). In cases where oxidation is limited by the availability of CH_4, peat temperatures in the anaerobic zone might therefore have a stronger effect on oxidation rates than the temperatures in the oxic surface layer. A dependence of CH_4 oxidation rates on the availability of CH_4 in the peat together with lower water

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tables could explain the higher oxidation rates in fall compared to spring (Figure 2c). Pore water CH_4 concentrations at the vegetation removal (PS and P treatments) were high in fall (Figure 3a) following high production rates during the summer months and accumulation in the pore water due to missing plant transport, providing abundant substrate for CH_4 oxidation.

The importance of CH_4 oxidation in the aerobic surface layer also shows in the depth profiles of stable C isotope values and of concentrations of dissolved pore water CH_4, both in summer as well as during the shoulder seasons. Close to the surface (7 cm depth) CH_4 concentrations were lower and pore water CH_4 was more enriched in ^{13}C compared to deeper layers (20 and 50 cm depth) in all seasons (Figure 3a,b). This can be explained by CH_4 oxidation in the *Sphagnum* layer, converting CH_4 into CO_2 and discriminating against ^{13}C (Whiticar, 1999). The about 10 cm thick moss layer usually coincided well with the aerobic surface layer above the water table. We therefore conclude that most CH_4 oxidation took place in the aerobic surface layer while there is no indication of significant anaerobic CH_4 oxidation in deeper, anaerobic peat layers. We can assume that CH_4 oxidation was negligible at the bare peat (P treatments), since the water table at those treatments was usually at or above the peat surface.

Apart from providing aerobic conditions for CH_4 oxidation under unsaturated conditions, the moss layer may further support CH_4 oxidation through a loose symbiosis between *Sphagnum* species and methanotrophs (Larmola et al., 2010; Kip et al., 2010). In such a symbiosis, methanotrophs benefit from the oxygen supplied by the mosses through photosynthesis and the mosses from the CO_2 released from CH_4 oxidation by methanotrophs (Liebner et al., 2011). This link between CH_4 oxidation and moss-associated photosynthesis is typically characterized by higher oxidation rates occurring at higher water tables when the *Sphagnum* moss is submerged (Larmola et al., 2010; Kip et al., 2010) and by a strong dependence of CH_4 emissions on light exposure (Liebner et al., 2011). In our study we did not find a significant light-dependence of net CH_4 emissions and the negative correlation of CH_4 emissions from the moss (PS) treatments with the water table depth indicates higher oxidation at lower water tables which is in line with Roslev and King (1996) and Perryman et al. (2023). We therefore conclude that the role of the moss layer as an aerobic surface layer above the water table in our study dominates over the symbiotic effects specific to *Sphagnum* moss.

4.3 Environmental controls on the strength and seasonal cycle of CH_4 emissions

CH_4 flux is the net of CH_4 production and CH_4 oxidation. The pathways of CH_4 transport further affect CH_4 fluxes by influencing the percentage of produced CH_4 that is either stored in the peat, oxidized or directly emitted to the atmosphere. It is therefore important to know how temperature, water table, and plant phenology interact to control the components of CH_4 fluxes (production, oxidation and transport) over the year.

We found that CH_4 emissions from intact vegetation (PSV plot) were highest in summer and weaker but still significant during the shoulder seasons (Figure 2a). Similar to Korrensalo et al. (2018b) this seasonal cycle in CH_4 emissions followed the LAI_{tot} and the LAI_{aer} as well as the peat temperatures in the aerobic (7 cm depth) and anaerobic peat layers (20 cm depth). Contrary to Korrensalo et al. (2018b), we also found an unexpected increase in CH_4 emissions with lower water table.

Variations in the LAI_{aer} best explained the seasonal variations in CH_4 emissions from intact vegetation (PSV plot). A higher leaf area of aerenchymatous plants allowed for more plant transport which resulted in increased CH_4 emissions through a more

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direct emission of produced CH_4, bypassing the aerobic oxidation layer. Since aerenchymatous plants accounted on average for 92 ± 11 % of the total leaf area in our study plots (Figure A1), LAI_{tot} had no significant effect on the CH_4 emissions when the effect of LAI_{aer} was already regarded.

The accumulation of CH_4 in the pore water in the absence of plant-mediated transport leads to a temporal decoupling between CH_4 production and emission, showing in the high pore water concentrations and the relatively high sustained CH_4 emissions from bare peat (P) in fall (Figure 3a), following peak CH_4 production during the summer months. Limiting our observations to the growing season may therefore have led to an overestimation of the enhancing effect of plant transport on total CH_4 emissions in our study. Year-round CH_4 flux measurements could allow us to assess the annual CH_4 balance by vegetation treatment in order to investigate if plant transport significantly increases net annual CH_4 emissions or if CH_4 emissions in the absence of vascular plants are mostly just delayed to the non-growing season.

By reducing pore water CH_4 concentrations (Figure 3a), plant-mediated CH_4 transport affects the rates of the other emission pathways for CH_4, i.e., diffusion and ebullition. At lower pore water concentrations there is a lower concentration gradient between peat and atmosphere reducing diffusive CH_4 transport (Chanton, 2005). Lower pore water concentrations due to efficient plant transport might similarly decrease CH_4 ebullition by preventing gas bubbles in the peat from becoming sufficiently large to move to the surface (e.g., van den Berg et al., 2020). This shows in the higher number of ebullition events occurring at the vegetation removal treatments compared to the intact vegetation (Figure A3). Most ebullition events occurred from bare peat (P) and their frequency followed the seasonal change in water table depth. This shows that ebullition is particularly important at non-vegetated plots where we expect pore water CH_4 concentrations to be even higher due to the missing oxidation layer and where water tables are highest (Männistö et al., 2019). While diffusive CH_4 transport through the water phase is conducive to CH_4 oxidation, a part of the CH_4 transported by ebullition bypasses the oxidation layer and is directly emitted to the atmosphere as indicated by the lower but still significant number of ebullition events occurring at the moss (PS) treatments.

Higher soil temperatures in the deeper, anoxic peat layers led to a net increase in CH_4 emissions probably because more CH_4 was produced at higher temperatures due to higher methanogenic activity (Dunfield et al., 1993). Additionally, higher peat temperatures in the anaerobic soil also correlated with higher CH_4 oxidation rates, thereby counteracting the increase in CH_4 emissions, probably because higher CH_4 production rates at higher temperatures provided more CH_4 for oxidation by methanotrophs. In winter at Siikaneva, when the top soil layer freezes, the dampening effect of oxidation on CH_4 emissions might however be disabled while CH_4 production continues in the deeper unfrozen soil layers. This might result in an accumulation of CH_4 underneath the frozen layer as indicated by the high soil gas concentrations in deeper peat layers in spring (Figure 3a) which can then be released upon thaw in a pulse emissions (Zona et al., 2016; Friborg et al., 1997; Alm et al., 1999; Tokida et al., 2007). Increased CH_4 concentrations at higher temperatures in the aerobic soil layer are probably mostly an indirect effect of the peat temperatures being correlated with LAI_{aer}.

Contrary to Korrensalo et al. (2018b), we found that water table had a significant effect on CH_4 emissions with higher CH_4 emission occurring at lower water tables. Since CH_4 oxidation rates did not correlate with water table, this is probably mostly an indirect effect related to low water tables occurring at times of high air and peat temperatures.

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The high emission rates in our study might already indicate a trend of increased CH_4 emissions resulting from increased peat temperatures following climate warming, especially when comparing our measurements to previous years (Korrensalo et al., 2018b). When excluding the lowest and highest 2.5 % of all fluxes, the CH_4 emissions measured in our study at intact vegetation (PSV plots) ranged from 25 to 1590 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ (Figure 2) which is significantly higher than the range of -7 to 387 $\mathrm{mgCH_4\,m^{-2}\,d^{-1}}$ reported for Siikaneva bog for the growing seasons of 2012, 2013 and 2014 by Korrensalo et al. (2018b). Summer air temperatures and therefore peat temperatures were higher in 2021 and 2022 compared to 2012, 2013 and 2014.

By affecting the balance between the enhancing effect of plant transport and the reducing effect of CH_4 oxidation, the composition and the leaf area of the vegetation strongly controlled the CH_4 emissions throughout the growing season. The attenuating effect of CH_4 oxidation dominated over the enhancing effect of plant transport on CH_4 emissions throughout the growing season (Figure 2b,c). Because aerenchymatous plants reduce the amount of CH_4 available for oxidation by transporting it past the aerobic surface layer, actual oxidation rates in the presence of aerenchymatous plants are probably lower than the oxidation rates that we calculated for the moss plots (PS treatments). Despite this likely overestimation of actual oxidation rates, the total vegetation present in the hollows of Siikaneva bog still reduced the CH_4 emissions from the measurement site compared to the bare peat (P treatment) emissions (Figure 2a).

5 Conclusions

This study identifies environmental controls on CH_4 emissions from boreal peatlands by quantifying seasonal variations in CH_4 fluxes, plant-mediated CH_4 transport and CH_4 oxidation in the hollows of Siikaneva bog, Southern Finland.

The species composition, leaf area and seasonal dynamics of peatland vegetation largely control CH_4 transport and CH_4 oxidation rates as well as their seasonal variation. The reduction of CH_4 emissions by oxidation in the *Sphagnum* moss layer currently outweighs the increase in CH_4 emissions due to CH_4 transport through aerenchymatous plants during both summer and shoulder seasons. By controlling the balance between oxidation and plant transport, vegetation properties thus significantly affect the strength and seasonal variation in CH_4 emissions from boreal peatlands even after plant senescence and can potentially make the difference between net consumption or net emission of CH_4.

This vegetation controlled balance suggests that the CH_4 cycle in boreal peatlands is highly sensitive to changes in vegetation properties and their seasonal dynamics. By influencing the species composition, growing season length, and leaf area of peatland vegetation, changes in air and soil temperatures and in hydrological conditions due to climate warming will therefore in addition to their direct effects also indirectly affect peatland CH_4 emissions.

Better understanding the effect of peatland vegetation on CH_4 emissions and its seasonal dynamics and incorporating it into process-based models will therefore greatly improve our estimates of future CH_4 emissions from boreal peatlands under the changing climate.

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Data availability. All measurement data including the CH_4 flux estimates, $\delta^{13}C$ of emitted CH_4, concentrations and $\delta^{13}C$ of CH_4 dissolved in the pore water, DOC, LAI, soil temperatures and water table depths at our measurement sites has been submitted to Pangaea. The data set has passed an initial check and has been approved for the next steps in the editorial workflow. The data will be openly available online on Pangaea before mid March.

Appendix A

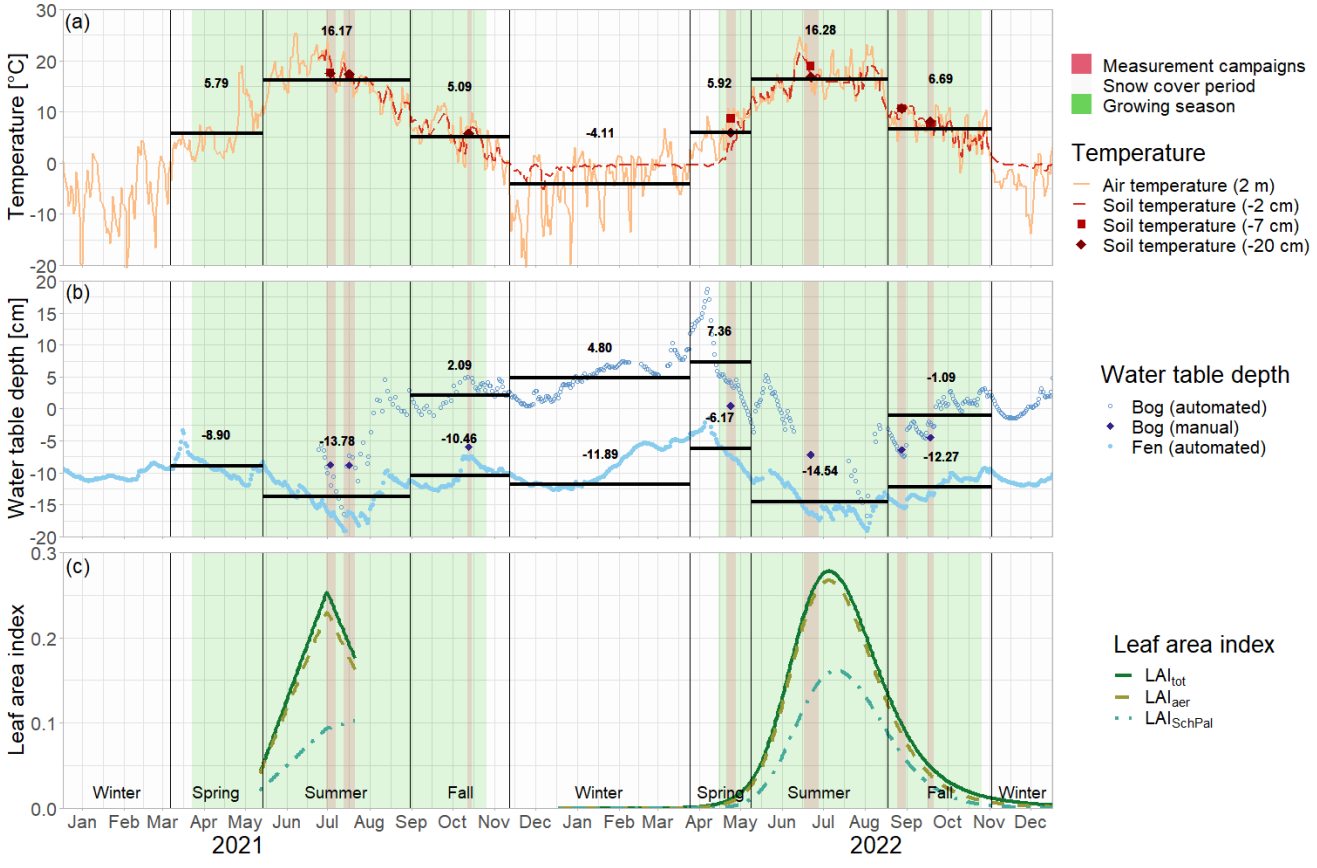


Figure A1. Daily mean air and soil temperatures (a), daily mean water table depth (b), and daily leaf area index of the total vegetation (LAI_{tot}), aerenchymatous plants (LAI_{aer}) and *Scheuchzeria Palustris* (LAI_{SchPal}) (interpolated and modeled based on field measurements for 2021 and 2022, respectively) (c) at Siikaneva bog in 2021 and 2022. The snow cover period is the time period between the first and the last day of snow cover even if interrupted by snow-free days. Water table depth at the nearby Siikaneva fen site is given to show the general course of the water table over the year at times where no water table measurements were available for Siikaneva bog. Individual markers in (a) and (b) give the mean peat temperatures and water table depths measured manually at the measurement plots during the field campaigns. Seasonal mean air temperatures and water table depths are given as horizontal lines and noted in the figures.

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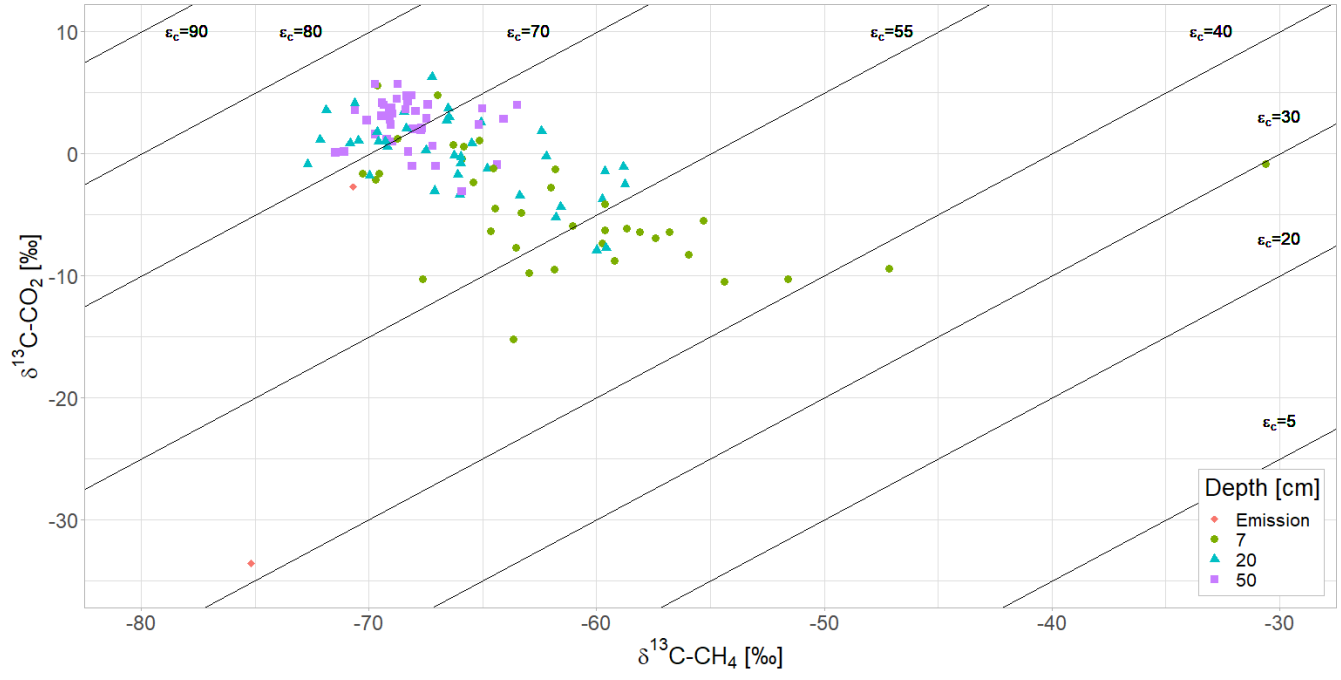


Figure A2. δ^{13}C of pore water and emitted CH_4 and CO_2 by sampling depth with isotope fractionation lines ϵc with isotope separation factor $\epsilon_C \approx \delta^{13}C\text{-}CO_2 - \delta^{13}C\text{-}CH_4$ (following Whiticar, 1999).

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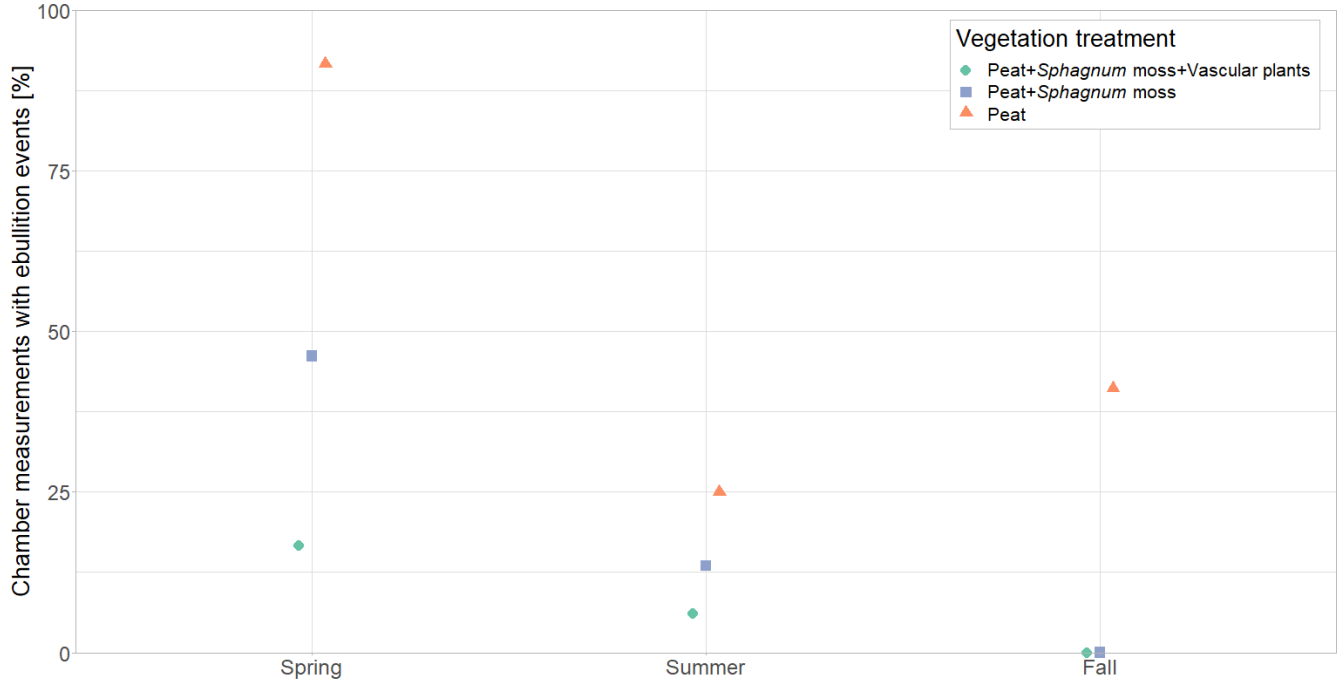


Figure A3. Number of flux measurements during which one or more ebullition events were detected by visual inspection of the CH_4 concentration time series normalized by the total number of measurements. Measurements that were discarded from flux calculation due to excessive ebullition are included in this figure.

Table A1. Parameter estimates for linear models for CH_4 flux from PSV plots. Estimate values, standard error (SE), degrees of freedom (DF), test statistics *t* and *p* are given to the fixed predictors of the model as well as conditional pseudo-R-squared for generalized mixed effects models (R^2).

Parameter	Value	SE	DF	t	p	R^2
LAIaer	4.74	0.95	59	4.975	<0.0001	0.48
LAItot	4.55	0.93	59	4.909	<0.0001	0.51
Tsoil7	0.08	0.02	50	3.917	<0.0001	0.34
Tsoil20	0.09	0.02	55	4.710	<0.0001	0.39
WTD	0.13	0.03	61	4.122	<0.0001	0.50

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Table A2. Parameter estimates for linear models for CH_4 flux from PS treatment. Estimate values, standard error (SE), degrees of freedom (DF), test statistics *t* and *p* are given to the fixed predictors of the model as well as conditional pseudo-R-squared for generalized mixed effects models (R^2). The model that best explained the variation in the data is highlighted with a blue box.

Parameter	Value	SE	DF	t	p	R^2
univariate models						
Tsoil7	0.20	0.03	57	6.380	<0.0001	0.59
Tsoil20	0.18	0.04	63	5.017	<0.0001	0.44
WTD	0.11	0.06	68	1.949	0.0555	0.33
multivariate model						0.71
Tsoil20	0.45	0.06	62	7.477	<0.0001	
WTD	-0.43	0.08	62	-5.139	<0.0001	

Table A3. Parameter estimates for linear models for CH_4 flux from P treatment. Estimate values, standard error (SE), degrees of freedom (DF), test statistics *t* and *p* are given to the fixed predictors of the model as well as conditional pseudo-R-squared for generalized mixed effects models (R^2). The model that best explained the variation in the data is highlighted with a blue box.

Parameter	Value	SE	DF	t	p	R^2
Tsoil7	0.02	0.03	27	0.710	0.4840	0.56
Tsoil20	0.07	0.02	31	2.911	0.0066	0.62
WTD	0.09	0.03	31	3.293	0.0025	0.70

Table A4. Parameter estimates for linear models for the effect of vascular plants on CH_4 fluxes. Estimate values, standard error (SE), degrees of freedom (DF), test statistics *t* and *p* are given to the fixed predictors of the model as well as conditional pseudo-R-squared for generalized mixed effects models (R^2). The model that best explained the variation in the data is highlighted with a blue box.

Parameter	Value	SE	DF	t	p	R^2
LAIaer	1306.08	523.25	37	2.496	0.0171	0.45
LAItot	1214.66	496.97	37	2.444	0.0194	0.46
Tsoil7	37.76	9.22	31	4.097	0.0003	0.62
Tsoil20	22.18	7.87	36	2.820	0.0078	0.42
WTD	30.60	12.99	39	2.355	0.0236	0.46

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Table A5. Parameter estimates for linear models for the effect of *Sphagnum* moss on CH_4 fluxes. Estimate values, standard error (SE), degrees of freedom (DF), test statistics *t* and *p* are given to the fixed predictors of the model as well as conditional pseudo-R-squared for generalized mixed effects models (R^2).

Parameter	Value	SE	DF	t	p	R^2
Tsoil7	-1.34	8.64	42	-0.155	0.8774	0.82
Tsoil20	12.56	8.28	46	1.517	0.1362	0.83
WTD	14.65	10.03	48	1.460	0.1507	0.90

Author contributions. EST, AK and EM designed and installed the experimental setup. CCT, AK, LvD and KJ planned the measurements and sampling performed during the field campaigns. KJ conducted the flux measurements and the pore water sampling and processed the flux data. EM performed the field sampling, measurements and processing of the LAI data. MEM and KJ analyzed the pore water gas samples. MEM wrote the R scripts to process and correct the gas concentrations and stable carbon isotope ratios of the pore water gas samples. CCT, LvD and KJ processed the meteorological data. KJ performed the data analysis. The manuscript was written by KJ and commented on by all authors. CCT and CK supervised the project.

Competing interests. The authors declare that they have no conflict of interest.

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