Plant community composition controls spatial variation in year-round methane fluxes in a boreal rich fen

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Abstract Climate change is expected to impact the methane (CH_4) budget of boreal peatlands, highlighting the need to understand the factors that influence methane cycling, including plant community structure. In northern peatlands, the majority of methane is transported through plants, and the magnitude of this process is strongly linked to plant community composition. Therefore, detailed information about the role of plants regulating year-round methane fluxes is highly valuable. This paper explores the causes of spatial variability in plot-scale methane fluxes in a northern boreal rich fen. Methane fluxes were measured using the manual chamber technique in the context of fine-scale biomass variations in plant community compositions from 36 study plots over 232 days throughout a full year. The mean methane flux rates for snow-free and snow seasons were 2.55 and 0.21 mg $CH_4/m^2/h$, respectively. We found a significant correlation between methane fluxes and a ~~vascular~~ plant ~~cluster~~community type associated with the ~~occurrence~~presence of ~~the~~ sedge *Carex rostrata* during three studied periods: year-round, snow-free and snow season ~~periods. More precisely,~~. *C. rostrata* ~~grew~~was present at ~~the point~~13 out of ~~flux measurement in 13~~ 36 plots, and these 13 plots contributed 44–49 % of the total measured methane fluxes ~~originated from these plots during the three periods~~. The biomass of vascular plants, sedges, and *C. rostrata*, as well as the ratio of vascular plant to bryophyte biomass, also significantly correlated with methane fluxes ~~in~~during year-round and snow-free ~~season~~seasons. By identifying vegetation-driven emission hotspots, these results can enhance efforts to upscale emission predictions and improve ecosystem-scale methane ~~modelling~~modeling. Thus, our findings provide valuable insights for predicting realistic future changes in peatland methane emissions throughout the year.

1 Introduction

Northern peatlands are an intrinsic part of the global carbon cycle and currently, these peatlands store more than a third of all terrestrial carbon, act as strong sinks of carbon dioxide (CO_2) and are among the main natural terrestrial source of methane

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(CH_4) (Ramage et al., 2024; Schuur et al., 2022). Indeed, ~~natural~~ wetlands produce ~~22–30~~about 25 % of the ~~global~~total methane emissions that are still considered an important source of uncertainty in the global methane budget (Saunois et al., ~~2020~~2024). The uncertainty arises from several factors: the relative contributions of methane emissions from tropical and northern wetlands, how these regions respond to rising temperatures, and the ~~spatial and temporal dynamics~~spatiotemporal patterns of the emissions (Christensen, 2024; Yuan et al., 2024).

Climate change is predicted to affect the hydrology of peatlands by increasing the water table depth (WTD) (Evans et al., 2021; Helbig et al, 2020; Swindles et al., 2019), which is one of the most well-known regulators of methane ~~dynamics~~fluxes along with temperature and vegetation (Turetsky et al., 2014). According to several studies, an increased WTD would decrease methane fluxes (e.g. Pearson et al., 2015; Riutta et al., 2020) and increase the rate of decomposition and soil CO_2 emissions (Ma et al., 2022). ~~This~~These ecosystem~~ process is~~-level processes are complex, though, as the increasing level of atmospheric CO_2 is predicted to enhance plant productivity (Forkel et al., 2016) and thereby the rate of root exudation (Nielsen et al., 2017~~), leading~~) that via priming leads to greater methane emissions (Turner et al., 2020; Waldo et al., 2019). The expected rise in methane production could be balanced by increased methane oxidation in the topsoil~~ layers~~, which is a probable response to enhanced microbial activity and oxygen availability caused by rising temperatures (Zhang et al. 2021). Warming climate may, however, also increase the areal cover of wet fens in the Arctic region due to permafrost thaw, which could potentially create new sources for methane release (e.g. Christensen et al., 2023; Grimes et al., 2024).

~~In addition to hydrology, vegetation~~Vegetation type and responses to environmental changes are highly relevant for methane flux dynamics, as up to 90 % of ecosystem-level methane ~~in northern peatlands~~ is transported through plants in northern peatlands (Ge et al., 2023; Korrensalo et al., 2022). The aerenchymatous tissues of certain vascular plant species allow methane to move from ~~deeper~~anoxic soil through the plant, thus avoiding the oxidation in ~~upper~~oxic soil layers (Ge et al., 2023; Joabsson et al., 1999~~). Indeed~~) and, indeed, plant species and their specific traits have been found to reliably predict methane flux rates~~ better than any studied abiotic factor~~ (Korrensalo et al., 2022). *Sphagnum* mosses of wet environments can also host methanotrophic microbes and thus have a potential to ~~oxidate~~oxidize methane and affect the magnitude of the total emissions (Larmola et al., 2010). Climate change is predicted to accelerate the natural vegetational succession in boreal rich fens towards *Sphagnum*-dominated plant communities even in stable hydrological conditions (Kolari et al., 2021), which could have major impacts on methane ~~dynamics.~~production and release. To improve our understanding and the predictions of future methane emissions, it is important to have more focus on the vegetation composition and the specific plant species controlling the magnitude of the fluxes (Riutta et al., 2020).

The relationship between plant community composition and methane fluxes remains an important topic of study (e.g. Lai et al., 2014; Riutta et al., 2007; Ström et al., 2015) and research on individual plant species has shown significant variation in the magnitude of flux rates and transport efficiencies (e.g. Bhullar et al., 2013; Koelbener et al., 2010; Korrensalo et al., 2022). ~~Studies~~ However, year-round methane flux data from northern boreal rich fens ~~with extensive, year-round,~~ at the plot-scale ~~flux data~~ are~~, however,~~ limited. This study aims to better understand the causes behind local spatial ~~differences~~variability of methane fluxes year-round, and to provide a new perspective on assessing plant-mediated methane emissions. To this end,

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we focus on fine-scale variations in plant community composition based on species' biomass, using non-destructive in situ methods. We intend to answer the following questions: (1) Do methane flux variations correlate with plant community type at a study plot scale? (2) Does plant community composition correlate with methane flux variability alone or in combination with other environmental factors? We hypothesize that (1) the plant community composition affects the methane flux and that (2) the flux is highest on study plots with largest biomass of vascular plants in absolute terms or in proportion to the biomass of bryophytes.

2 Materials and methods

2.1 Study site

This study was implemented in Puukkosuo, an open and slightly sloping calcareous fen located in the northern boreal zone at Oulanka National Park in Kuusamo, Northeast Finland (66.377299° N, 29.308062° E) (Fig. 1). The long-term (1992–2022) mean annual, January and July temperatures ~~from the normal period of 1992–2022~~ were 0.6, -13.0, and 15.3 °C, respectively, and the mean annual precipitation was 557.4 mm. The study period (19.10.2021–31.10.2022) was slightly warmer and drier than the ~~normal period~~ long-term mean with temperatures 0.9, -11.4, and 16.5 °C, respectively, and with total annual precipitation of 528.8 mm. ~~The mean pH during~~During the snow-free season of 2022, the mean pH (n=179) measured from peat porewater at approximately 10 cm depth, was 7.0, ranging from 6.74 to 7.38.~~-~~ The deepest measured water table was 9.3 cm below the peat surface, while the highest was 7.0 cm above the surface (Fig. A1). The plot-scale variation in WTD ~~fluctuated only slightly:~~ during the snow-free season of 2022 ~~the variation in WTD throughout the fen~~ was ~~6,~~3.8–9.1 cm ~~on~~with an average of 6.5 cm. The vegetation at the site is dominated by ~~graminoids~~vascular plants typical of rich fens (*Carex* ~~sp~~spp., *Trichophorum* ~~sp~~spp., *Molinia caerulea*~~), herbaceous plants (~~, *Potentilla erecta*, *Menyanthes trifoliata*), as well as brown mosses (*Scorpidium cossonii, Campylium stellatum*, *Cinclidium stygiym*) and peat mosses (*Sphagnum* spp., mostly *S. warnstorfii*).

2.2 Experimental design

The study area was approximately one hectare in size and included 12 spatial blocks. Each block had three study plots resulting in 36 study plots. The plots were established in summer 2018, and the size of a plot was 2 m × 3.5 m which included a 0.5 m wide buffer zone. Wooden boardwalks, built to minimize stepping on the surface of the peat, led to the plots. Half of the study plots (n=18) were located inside a fence, built in spring 2019, to exclude grazing by reindeer (Fig. 1). At the time of this study, the exclusion had lasted for 2–3 years. The location of the plots and the fence followed the hydrological gradient of the fen (Fig. 1). The study plots were also assigned to snow level manipulations that were started in January 2019. Within each block, one plot was an untreated control with ambient snow level, one a snow removal plot where the snow depth was maintained at 0.25 m throughout the snow season, and one plot a snow addition plot, where the snow from the removal plot was placed. The snow treatments had no statistically significant effects on the methane fluxes (Fig. B6).

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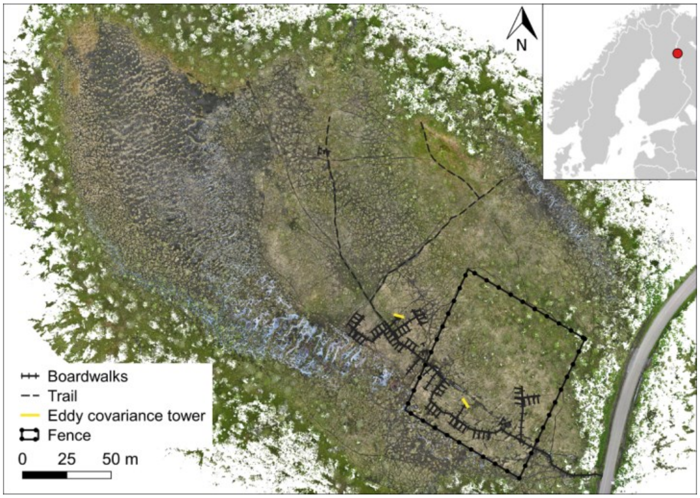

Figure 1. A map of ~~the study system,~~ Puukkosuo rich fen showing the location of boardwalks, experimental area and the fence excluding reindeer. The small inset shows the location of the study area, Oulanka, in NE Finland. Orthomosaic © Petra Korhonen 2024.

2.3 Methane flux measurements

For ~~manual~~ methane flux measurements, a round PVC collar (inner diameter 29.5 cm) was inserted approximately 5 cm into the ground in the rear end of each plot in September 2020. During 19.10.2021–31.10.2022, we measured methane fluxes (mg $CH_4/m^2/h$) over 232 individual days between 8 am and 6 pm, ~~doing measurements from~~conducting one measurement per plot per day. On most days, only half ~~(n=18)~~ of the ~~study~~ plots ~~per day.~~were measured using randomized plot selection. We used manual, closed chamber technique (e.g. Christensen et al., 2000) with a portable LI-COR $CH_4/CO_2/H_2O$ Trace Gas Analyzer (LI-7810) and a transparent ~~Plexiglas~~polycarbonate chamber (height 38 cm, diameter 29 cm) equipped with a small fan to circulate the air inside the chamber (Fig. 2a). For each measurement during snow-free season, the chamber was placed on the PVC collar for an airtight seal (Fig. 2b). Each measurement lasted for 5 minutes. During winter, when snow covered the collars and it was not possible to place the chamber directly on them, we measured the fluxes on top of the snowpack, also known as floating chamber technique~~.~~, to avoid disturbance to the snow and methane diffusion (Björkman et al., 2010~~). These~~) and consequently to the experimental plots. In comparison to the snow-free season, these measurements were taken at a slightly different spot closer to the boardwalks~~ to avoid unnecessary disturbance to the snowpack. Clearing the measuring points from snow would have caused excessive disturbance to both the snowpack and the continuous flux measurements, making the possible dilution of the flux during diffusion through the snowpack inevitable (Björkman et al., 2010).~~. Due to these limitations,

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snow season flux measurements should be examined with caution. Altogether, ~~4319~~4121 individual measurements were ~~taken, of which 4121 were successful and~~ used in this study.

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To calculate methane flux rates for each plot, we used a Python script that calculated the slope of methane concentration change during three centremost minutes of a five-minute measurement period and computed the flux in mg $CH_4/m^2/h$ using ambient air pressure and air temperature at the time of each measurement (linear regression model, e.g. Pirk et al., ~~2017~~2016a). We accepted the measurements with an R^2 value ≥ 0.95 (n = 3589) and inspected all the rest (n = 691) individually, leaving out measurements showing very strong non-linearity or any other sign of failed measurement (n = 159). We examined the fluxes in three periods: 1) year-round (19.10.2021–31.10.2022), 2) snow-free (13.5.–26.10.2022), and 3) snow season (19.10.2021–12.5.2022 and 27.10.–31.10.2022). Snow-free ~~and snow seasons~~season presented a period when we were ~~defined by the snow cover and the ability~~able to measure ~~the~~ fluxes on the collar~~.~~ (part of the experimental plot or the experimental site could be covered with snow). Snow covered season presented a season when we measured the fluxes on top of the snow, not on the collar. Annual accumulated flux (1.11.2021-31.10.2022) was estimated by calculating a 24-hour accumulated flux for each available datapoint by multiplying the hourly mean flux by 24. These daily flux values were then summed to obtain the annual total. The days which were missing a measurement were given the value from a previous measurement~~. In the annual accumulated flux calculations, we assumed that~~, assuming the fluxes did not vary remarkably diurnally or over the days.

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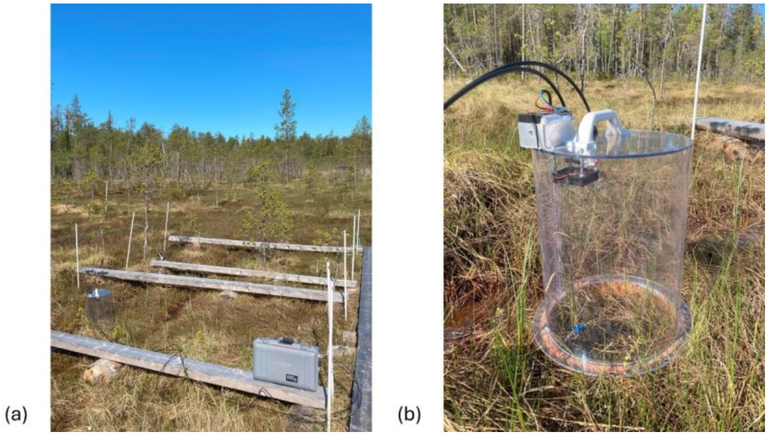

Figure 2. A flux measurement carried out with (a) a portable LI-COR Trace Gas Analyzer and (b) a clear ~~plexiglas~~polycarbonate chamber placed on a round collar installed at each plot in 2020. Photos by Eeva Järvi-Laturi.

2.4 Plant community data

We studied the plant communities by identifying ~~the~~ species and their abundance within each collar~~ and estimating their biomasses (BM) from separately collected~~ , collecting separate biomass samples from outside of the main research area, and using the mean biomass (BM) value of each species' samples to determine the community composition within each collar. Plant surveys and sample collection were done during 25.7.–12.8.2022.

To survey the vascular plant (VP) species ~~(n=31)~~ within ~~each collar~~the collars, we counted each aboveground shoot individually and separated them into ~~fertile~~flowering and ~~sterile~~non-flowering categories~~.~~, as the flowering shoots may hold higher biomass than the non-flowering ones. Altogether, 31 vascular plant species were identified from the study site. We collected separate biomass samples of each identified species. The biomass sampling was randomized by first selecting an area where vegetation heights resembled the heights of the vegetation within the collars. Then, we randomly threw a marker and selected the first ten non-flowering individuals of target vascular plant species close to the marker. Additionally, we collected ~~separate samples (n=10~~ ten flowering individuals for ~~both fertile and sterile shoots) of each identified~~those species~~ for BM estimation by cutting~~, which were found flowering within the ~~shoot~~collars. Shoots were cut at the peat surface. For uncommon species (*Angelica sylvestris*, *Carex dioica*, *Carex panicea*, *Dactylorhiza* sp., *Drosera* sp., *Eriophorum angustifolium*, *Festuca ovina*, *Pinguicula* sp., *Saussurea alpina* and *Viola epipsila*), randomization could not be put into practice. For these, samples were collected from where they could be found.

For bryophytes, we visually estimated the percentage ~~coverage~~cover of each species~~ (n=10)~~ within each collar. Altogether, 10 bryophyte species were identified from the study site. We took either three samples ~~covering~~representing 5 % (diam. 6.6 cm) or one sample representing 1 % (diam. 2.95 cm) of the collar area ~~for the five most common species, and one sample covering 1 % of the area~~ with small plastic jars. The larger sample size was collected for species that could easily be found in pure patches (*Aulacomnium palustre, Campylium stellatum, Scorpidium cossonii, Sphagnum* spp. and *Tomentypnum nitens*), and the smaller sample size for the remaining~~ five species,~~ , more scattered and sparse species (*Aneura pinguis, Cinclidium stygium, Fissidens adianthoides, Mesoptychia rutheana* and *Paludella squarrosa*). The sampling locations were selected so that the target bryophyte species could be found as "pure monoculture" as possible. We then ~~cut them~~cleaned the samples of other species and litter, removed the non-living parts, and included only the colorful or leafy parts to represent the aboveground biomass. ~~All BM samples were collected outside of the main research area nearby the study plots. We~~

For BM estimation, we dried the samples (n=454) in a hot air circulation oven at 40 °C for minimum of two days and weighed them ~~in a laboratory using a Denver Instrument SI-234 analytical scale with a four decimal precision (Table A1).~~with a four decimal precision (Denver Instrument SI-234, Table A1). The dry weights were normalized either by shoot (vascular plant, g/shoot) or by cover percent (bryophyte, g/1 %). For each vascular plant species, we used the total number of shoots, separated by flowering and non-flowering categories, within a collar, multiplied by the mean dry mass per shoot to obtain total species BM for each collar. For each bryophyte species, we used the total percentage cover within a collar, multiplied by the mean dry mass per 1 % area to obtain total species BM for each collar. We also calculated a VP to bryophyte BM ratio for

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2.5 Environmental variables

We used weekly measures of WTD from June to October from regular measuring points located approximately 1 m from the methane flux measurement points. At every plot, soil temperature was recorded with 10-min intervals at 5 cm depth (model p107 CS CR1000, Campbell Scientific Inc., Logan, UT, USA). In October 2023, we measured peat layer thickness at the rear edge of each study plot with a thin, metallic 300 cm long auger. To determine peat chemistry, we collected pore-water during frost-free periods. In the beginning of snow-free season 2022, rhizon samplers (Rhizosphere Research Products, The Netherlands) were installed (10 cm depth) for pore water sampling in the middle of the collar in each experimental plot. Pore water was sampled five times during the frost-free periods (31 May, 29 June, 22 July, 28 August, 29 September). Samples were collected into evacuated opaque syringes over a period of 24–48 h, filtered (0.45 µm, sterile nylon, Sarstedt, Germany) and frozen (−18 °C). Thawed samples from all sampling campaigns were analyzed for pH (913 pH/DO Meter, Metrohm), dissolved organic (DOC) and inorganic carbon (~~DOC,~~ DIC; Shimadzu DOC-VCX, Trios) and dissolved organic nitrogen (DON), ammonium (NH_4~~)~~$^+$) and nitrite + nitrate (NO_2~~+~~$^-$ + NO_3~~;~~$^-$; AA500 Seal Analytical) and for DOC and DON reported as mg/l and for NH_4^+ and NO_2~~+~~$^-$ + NO_3^- as µg/l. In analyses, we used the mean value of each measured variable. Additionally, we ~~observed~~estimated the ~~amount~~percentage cover of litter inside the collar ~~(%) and the microtopography around the collar (flark/intermediate/hummock)~~ while identifying the vegetation.

2.6 Data analyses

To analyse the vegetation, we divided the plant communities into three species combinations: 1) all species, 2) VPs, and 3) bryophytes. We analysed these combinations separately using plant BM estimates (see 2.4) by hierarchical cluster analysis using Sorensen (Bray–Curtis) distance measure and Flexible Beta group linkage method (McCune et al., 2002) with beta-value of -0.25. Clusters with less than six samples (study plots) were discarded. To evaluate which species were statistically most connected to the different clusters, we carried out an indicator species analysis separately to all three species combinations. We tested the differences between the clusters with Tukey's ~~HSD (~~Honestly Significant Difference (HSD) test ~~and~~following an Analysis of Variance (aov function, R Core Team, 2024) to assess the ~~clusters'~~significance of clusters in relation to methane fluxes in different time periods (snow-free, year-round and snow season~~) with linear regression models using the lm function (R Core Team, 2024). We~~). With clustered data, we performed detrended correspondence analysis (DCA) to identify patterns in species composition and canonical correspondence analysis (CCA) to relate the species composition to environmental variables (McCune et al., 2002). We conducted the analyses separately for VPs and bryophytes to determine the main environmental factors characterizing the composition of these plant communities. Pairwise correlations between multiple BM and environmental variables were examined with a separate CCA, using snow-free season averages. The resulting Pearson

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correlation matrix (Table B2) provides insights into these relationships. Finally, we conducted local regression models (LOESS, locally estimated scatterplot smoothing) to ~~study the significance~~explore nonlinear trends between ~~BM~~various variables and methane fluxes in relation to VP clusters.

~~We estimated the plot-scale aboveground BM of each plant species using a mean dry mass from separate samples (Table A1). We also calculated a VP to bryophyte ratio (%) for each plot (Table A2) and analyzed the relationships of multiple BM and environmental variables with a correlation matrix (Table B2).~~ Cluster, indicator species and correspondence analyses were implemented with PC-ORD version 7.09 (McCune and Mefford, 2018). Regression models and Tukey's HSD tests were performed using RStudio version 2024.4.2.764 (Posit team, 2024). Both programmes were used for data visualization: PC-ORD for cluster dendrograms, boxplots, and ordination graphs, RStudio for line graphs and scatterplots. Significance was defined as $p < 0.05$. We used the following R packages: readxl v1.4.3 (Wickham and Bryan, 2023), dplyr v1.1.4 (Wickham et al., 2023a), tidyr v1.3.1 (Wickham et al., 2024), ggplot2 v3.5.1 (Wickham, 2024), forcats v1.0.0 (Wickham, 2023), scales v1.3.0 (Wickham et al., 2023b), paletteer v1.3.0 (Hvitfeldt, 2021), ggnewscale v0.5.0 (Campitelli, 2024) and viridis v0.6.5 (Garnier et al., 2024). R scripts were created with the assistance of Microsoft 365 Copilot, an AI-powered productivity tool.

3 Results

3.1 Methane fluxes

~~Methane fluxes were the highest during~~During the snow-free season, methane fluxes were the highest, ranging from 0.02 to 9.17 mg $CH_4/m^2/h$ (i.e., 0.48–220 mg $CH_4/m^2/d$), with an overall mean of 2.55 mg $CH_4/m^2/h$~~. The variation in methane fluxes across all study plots was also greatest during~~ (i.e., 61 mg $CH_4/m^2/d$). During this ~~period, with~~season, the mean of plot-scale methane fluxes ~~varying between~~ranged from 0.51 ~~and~~to 4.67 mg $CH_4/m^2/h$~~.~~, and daily coefficient of variation spanned from 38.9 % to 85.4 %. The highest individual fluxes per plot varied between 1.51 and 9.17 mg $CH_4/m^2/h$. The lowest flux values of the snow-free period (0.02–1.18 mg $CH_4/m^2/h$) were measured in May after a spring burst (1.4.–12.5.2022), and at the end of the season in late October (Fig. 3). The magnitude of the spring burst differed among the plots, with ~~the~~ maximum individual fluxes ranging from 0.15 to 6.65 mg $CH_4/m^2/h$. During the snow season, ~~the~~ flux measurements fluctuated between 0 and 6.65 mg $CH_4/m^2/h$ (i.e., 0–160 mg $CH_4/m^2/d$), with an overall mean ~~flux was~~of 0.21 mg $CH_4/m^2/h$~~, with the~~ (i.e., 5 mg $CH_4/m^2/d$). The mean of plot-scale fluxes ~~ranging~~ranged from 0.07 to 0.56 mg CH_4/~~m^2/h.~~m^2/h, and daily coefficient of variation spanned from 39.3% to 300.4%. Further, the snow season fluxes accounted on average for 8.2% of the estimated annual accumulated flux, with values ranging from 2.3 % up to 21.3 % across the study plots (Table B3). On a year-round scale, the overall mean flux was 1.37 mg $CH_4/m^2/h$, with mean fluxes varying between 0.29 and 2.52 mg $CH_4/m^2/h$~~.~~, and daily coefficient of variation ranging from 38.9 % to 300.4 %.

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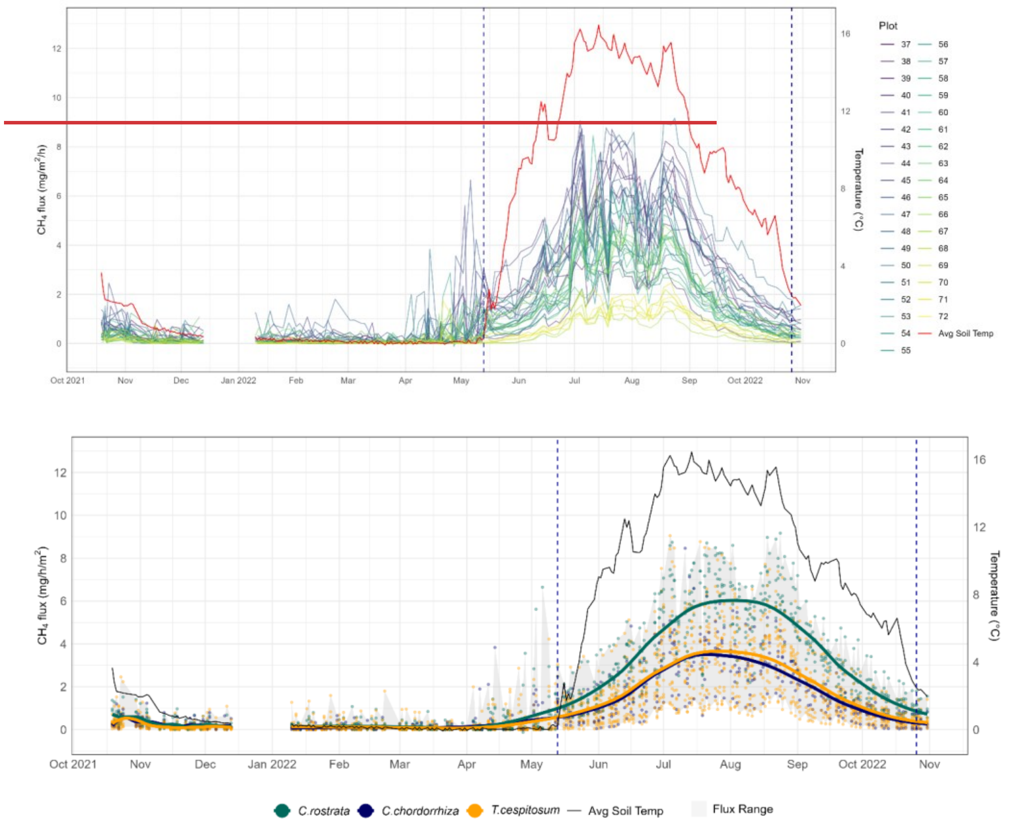

Figure 3. Year-round ~~plot-scale~~ methane ~~flux~~fluxes (mg $CH_4/m^2/h$) ~~and mean soil temperature at 5 cm depth from the end of October 2021 to the end of October 2022. The red line represents the~~at Puukkosuo with average soil temperature ~~of all plots, while the other lines represent a manually measured flux of each~~at 5 cm depth. The grey flux range shows the overall variation of the fluxes. Smoothed conditional means (LOESS method) and data points, representing individual ~~study plot.~~plot-scale flux measurements, are segregated by vascular plant clusters defined in section 3.2. The vertical dashed lines mark the start and end of the snow-free season (13.5.–26.10.2022).

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3.2 Plant community structures

The plots differed in their plant community structures, with wide variation in plant BM. VP BM per plot ranged from 62.1 g/m^2 to 486 g/m^2, while the bryophyte BM ~~varied between~~ranged from 65.1 g/m^2 ~~and~~to 269 g/m^2. The lowest total BM for an individual plot was 167 g/m^2, while the highest was 674 g/m^2. The percentage of VPs in the total BM varied between 21 % and 72 % (Table A2). ~~Species~~The species producing the most BM, based on combined dry mass estimates from all plots, were sedges *Carex lasiocarpa* (122 g) and *C. rostrata* (84 g), and bryophytes *Scorpidium cossonii* (193 g), *Campylium stellatum* (113 g), and *Sphagnum* spp. (92 g) (Table A3).

The cluster and indicator species analyses for all species, VPs, and bryophytes all yielded three clusters (groups of plots) with significant ($p < 0.05$) indicator species statistically connected to the clusters (Figs. B1–B3). The cluster analyses indicated that bryophytes (*Sphagnum* spp., *S. cossonii*, and *C. stellatum*) showed the strongest connection to the clusters when analyses were done with all plant species or bryophytes (Figs. B1, B3). On the other hand, when analysing VPs alone, the clusters connected mostly with different sedges ~~connected with the clusters [~~(*C. rostrata* ~~(~~with the first, *C.*~~ros), C.~~ *chordorrhiza* ~~(C.cho),~~with the second, and *Trichophorum cespitosum, C. lasiocarpa*, and *Potentilla erecta* (a forb) with the third cluster). From here on, the clusters are referred to as *C. rostrata*-cluster, *C. chordorrhiza*-cluster, *and T.*~~ces)].~~ *cespitosum*-cluster, respectively. The characteristics of each VP cluster, including their community structure and indicator species, were studied by comparing the indicator values of the ~~VP~~ species (Table B1). The results demonstrated that the plant communities differed between the clusters, as most species were abundant in only one or two clusters, and only three species (*Campylium stellatum*, *Vaccinium oxycoccos*, and *Scorpidium cossonii*) were common in all clusters (Table B1). We also found an association between *Sphagnum* mosses and *C. rostrata* in the plant communities: the *C. rostrata*-cluster had the highest abundance of *Sphagnum* mosses among the three vascular plant clusters (Table B1). The spatial division of the vascular plant communities was clear – the *C. rostrata*-community plots were all located in the upper part of the sloping fen, while the other two clusters were more widely distributed (Fig. B7). ~~,~~

3.3 Clusters' relation to methane fluxes

An Analysis of Variance (ANOVA) revealed that VP clusters correlated significantly with snow-free season ($F = 10.71$, $p < 0.001$) and year-round ($F = 10.92$, $p < 0.001$) methane fluxes but not with snow season fluxes ($F = 2.14$, $p > 0.05$). ~~Here and in the following, significance is defined as p < 0.05. The~~Tukey's HSD test indicated that *C.*~~ros~~ *rostrata*-cluster, which had the highest fluxes especially during snow-free season (Fig. 43), differed significantly from ~~the~~ *C.*~~Cho~~ *chordorhhiza*- and *T.*~~Ces~~ *cespitosum*-clusters in snow-free ($p < 0.01$ and $p < 0.001$, respectively) and year-round periods ($p < 0.01$ and $p < 0.001$, respectively) but not in snow season (Fig. ~~5a~~4a). There were no significant differences between *C.*~~cho~~ *chordorrhiza*- and *T.*~~ces~~ *cespitosum*-clusters in any of the periods~~.~~ (Fig. 4a–c). All species-clusters did not correlate significantly with methane fluxes in any period ($F = 1.51$, $p > 0.2$ for snow-free, $F = 1.45$, $p > 0.2$ for year-round, and $F = 0.57$, $p > 0.5$ for snow season, Fig. 4b). Similarly, the bryophyte clusters did not correlate significantly with methane fluxes ($F = 1.23$, $p > 0.3$ for snow-free, $F = 1.26$, $p > 0.2$ for year-round, and $F = 0.90$, $p > 0.4$ for snow season~~) (Figs. 5b, c~~, Fig. 4c).

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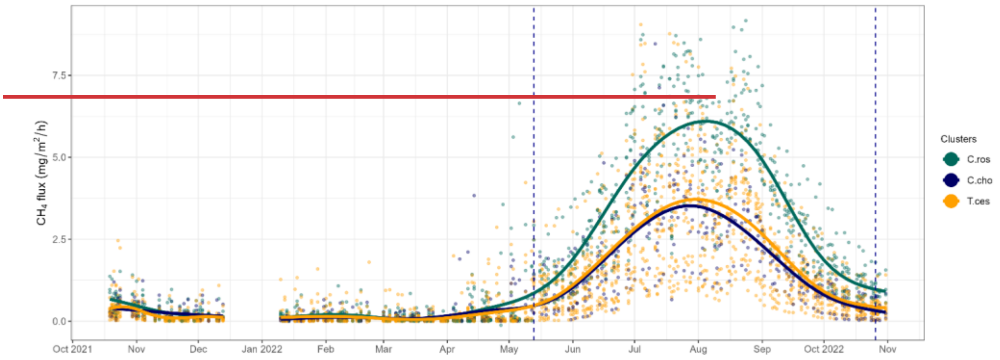
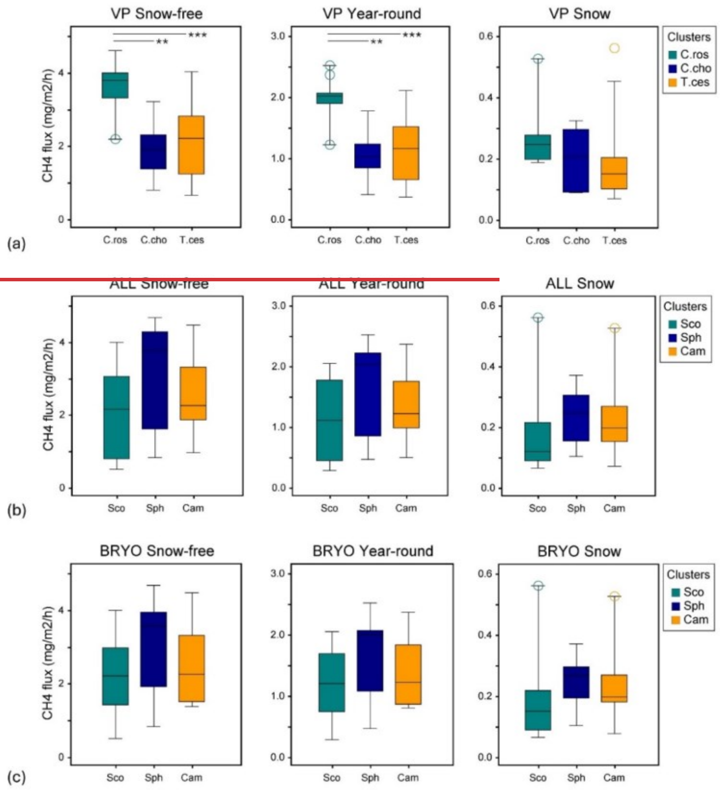


~~**Figure 4. Year-round methane fluxes of Puukkosuo with smoothed conditional means segregated by vascular plant clusters. See Fig. 5 for cluster abbreviations. Each dot in the graph represents one manual flux measurement. The vertical dashed lines mark the start and end of the snow-free season (13.5.–26.10.2022).**~~


VP Snow-free
VP Year-round
VP Snow
CH4 flux (mg/m2/h)
***
**
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ALL Snow
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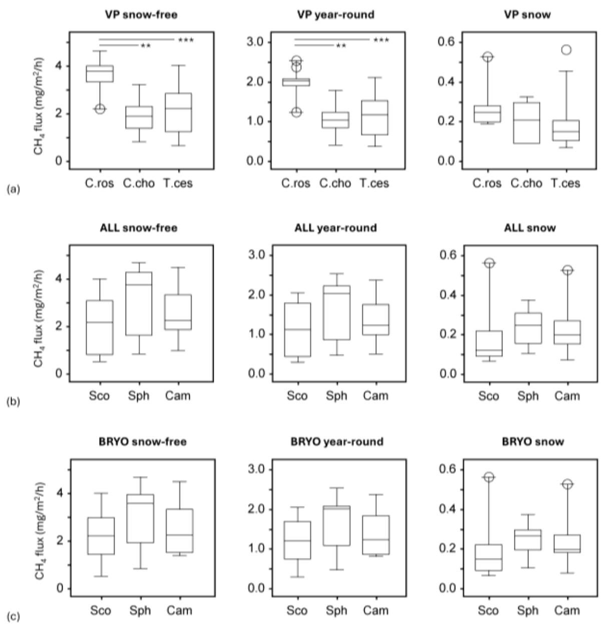

Figure 4.~~Figure 5.~~ Methane fluxes in snow-free season (left panel), the whole year (middle panel), and snow season (right panel), as divided by cluster analyses of (a) vascular plants (VP), (b) all species (ALL) and (c) bryophytes (BRYO). Abbreviations for the clusters and the species with highest fidelity according to indicator species analysis: C.Ros = *C. rostrata*, C.Cho = *C. chordorrhiza*, T.Ces = *C. lasiocarpa*, *P. erecta*, and *T. cespitosum*, Sco = *S. cossonii*, Sph = *Sphagnum* spp. and Cam = *C. stellatum*. Asterisks above the bars denote significant differences between the clusters at the level $p < 0.01$ and $p < 0.001$ ***.**

3.4 Ordination analyses

Within VP communities, the *C.* ~~ros~~*rostrata*-cluster diverged from the *C.*~~cho~~ *chordorrhiza*- and *T.*~~ces~~ *cespitosum*-clusters in both detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA~~,~~), while the *C.*~~Cho~~ *chordorrhiza*- and *T.*~~Ces~~ *cespitosum*-clusters ~~showed a clear distinction~~ diverged in DCA, but not in CCA (Fig. B4a–b). ~~Similarly, in~~In bryophyte communities, the ~~Sph~~*Sphagnum*-cluster diverged from the ~~Sco~~*S. cossonii*- and ~~Cam~~*C. stellatum*- clusters in both DCA and CCA, while the ~~Sco~~*S. cossonii*- and ~~Cam~~*C. stellatum*-clusters ~~showed a clear distinction~~diverged in DCA, but not in CCA (Fig. B5a–b). The main compositional gradients of VP and bryophyte communities displayed different correlation patterns with environmental variables. The first ordination axis of the VP communities correlated with snow-free and year-round methane fluxes (r = 0.775 and 0.782 in DCA, r = -0.856 and ~~-~~-0.866 in CCA, respectively, Fig. B4a–b). Additionally, the first ordination axis correlated with snow season fluxes (r = 0.445 in DCA, -0.402 in CCA). The correlation was also

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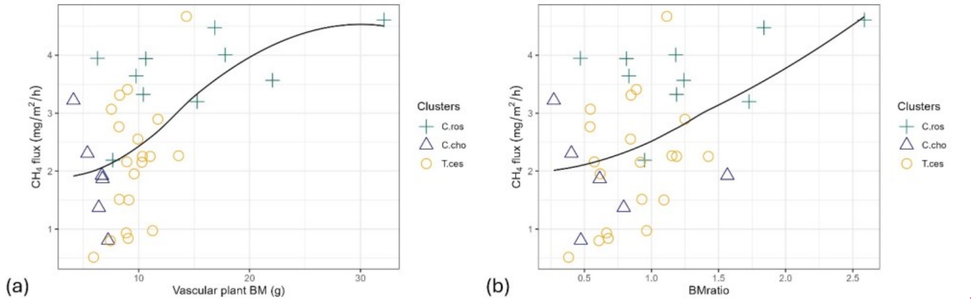
3.5 BM, environmental variables and methane

~~The~~In the Pearson correlation matrix (Table B2), the total BM of VPs correlated with the total BM of sedges (r = 0.98) and the total BM of *C. rostrata* (r = 0.93) indicating that sedges were the main functional group of VPs, and *C. rostrata* the main VP species, producing BM in our study site. The BM variables that had a significant pairwise correlation with methane fluxes in year-round and snow-free season were the total BM of VPs ($p < 0.001$~~) (Fig. 6a~~), the total BM of sedges ($p < 0.001$), the total BM of *C. rostrata* ($p < 0.001$~~) (Fig. 7~~), and the ratio ~~between~~of VP ~~and~~to bryophyte ~~biomasses (from here called the~~ BM ~~ratio)~~ ($p < 0.01$) (Fig. ~~6b~~5a–d). Significant correlations during the snow season were not discovered. Environmental variables that had a significant pairwise correlation with methane fluxes in snow-free and year-round periods were pH ($p < 0.05$ and $p \leq 0.01$, respectively, Fig. 5e) and combined concentration of NO_3^- and NO_2^- in peat pore water ($p < 0.05$ for both periods, Fig. 5f). There was no significant correlation between methane fluxes and WTD or soil temperature in any period. All correlation coefficients are listed in a correlation matrix in Table B2.



~~Figure 6. The~~ We found that when *C. rostrata* BM was 0 g, there was large variation in the magnitude of methane flux (Fig. 5c). Therefore, we additionally examined the clusters' relation to fluxes in plots without any *C. rostrata* shoots (23 plots out of 36), as well as the relationship between methane fluxes and environmental variables using linear regression models (lm function, R Core Team, 2024). This revealed that, in the absence of *C. rostrata*, pH and litter cover were the primary

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environmental drivers of snow-free season methane fluxes, showing significant relationships ($p < 0.001$ and $p = 0.01$, respectively) and Pearson correlation values of -0.66 and -0.29, respectively.

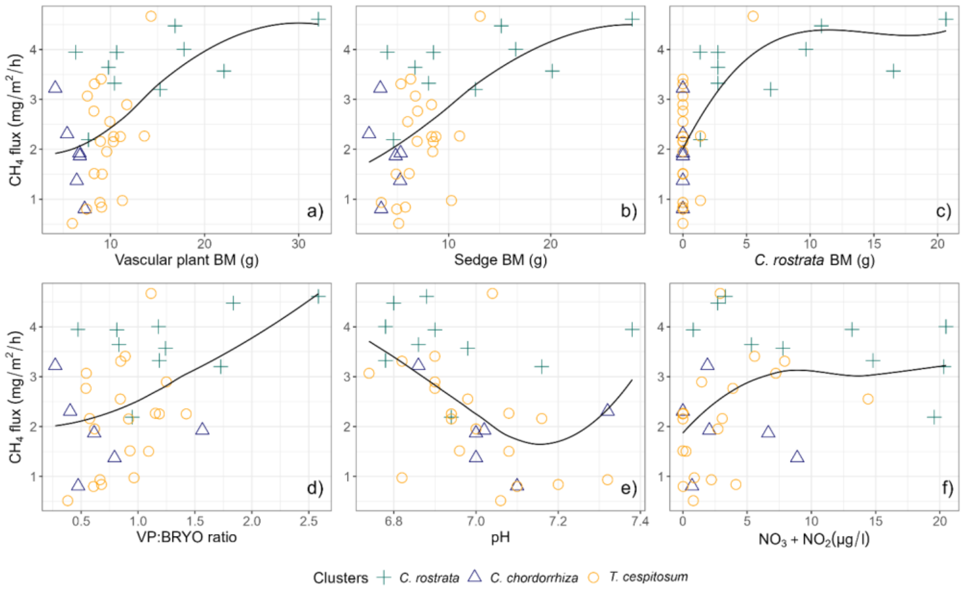

Figure 5. Scatterplots showing the relationships between methane (CH_4) flux (mg/~~m²/~~m²/h) and ~~(~~environmental variables: a) total biomass (BM) of vascular plants (~~g of dry weight) (~~p < 0.001, r = 0.54~~) and ()~~, b) ~~biomass~~total BM of sedges (p < 0.001, r = 0.57), c) BM of *C. rostrata* (p < 0.001, r = 0.60), d) BM ratio of vascular plants and bryophytes (p < 0.01, r = 0.45~~) segregated by~~), e) pH (p < 0.05, r = -0.38), and f) NO_3+NO_2 concentration (p < 0.05, r = 0.34) across different vascular plant clusters. ~~See Fig. 5 for cluster abbreviations~~Vascular plant clusters are defined in section 3.2. The smoothing lines were fitted using local polynomial regression (LOESS) with a span value of 1. Biomass values are in grams (g) of dry weight.

4 Discussion

4.1 Methane flux variation over time and space

During the snow-free season, ~~the range of~~methane fluxes ~~was 0.02–9.17 mg $CH_4/m^2/h$ (i.e., ~~ranged from 0.48~~–~~ to 220 mg $CH_4/m^2/d$~~),~~, with ~~the~~an overall mean ~~being 2.55 mg $CH_4/m^2/h$ (i.e.,~~of 61~~-~~ mg $CH_4/m^2/d$~~).~~. Similar ~~flux rates ranging from ~30–300 mg $CH_4/m^2/d$, with a mean of ~100 mg $CH_4/m^2/d$ during June–October (Jammet et al., 2017)~~ fluxes have been measured from a northern boreal rich ~~fens. The~~ fen (Jammet et al., 2017). We observed that snow season ~~fluxes'~~fluxes, with a range ~~was~~

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~~0–6.65 mg $CH_4/m^2/h$ (i.e.,~~from 0–160 mg $CH_4/m^2/d$~~), with~~ and an overall mean ~~being 0.21 mg $CH_4/m^2/h$ (i.e.,~~of 5 mg $CH_4/m^2/d$~~). Further, the snow season fluxes~~ , accounted ~~on average~~ for ~~8.~~2.3–21.3 % of the estimated annual accumulated flux~~, with values ranging from 2.3 % up to 21.3 % across the study plots~~ (Table B3). ~~Even though~~Although we measured fluxes on top of an undisturbed snowpack~~ – which may underestimate the magnitude of the fluxes to some extent (e.g. Björkman et al., 2010) –~~ , our results ~~are in line~~align with a study from ~~boreal~~ fens in central Finland, where 6–17 % of the annual methane release was observed during wintertime~~,~~ when measuring ~~the~~ fluxes on peat surface after clearing the ~~spots from~~ snow (Alm et al., 1999). ~~Given that~~We acknowledge that direct measurements from the ground surface would have improved our ability to connect winter fluxes with the studied plant communities. However, we do not expect significant differences in flux values obtained using a closed chamber on top of the snowpack, as methane diffusion through the snowpack may be relatively unrestricted (Alm et al., 1999; Pirk et al., 2016b). Since winter may account for up to 20 % of the annual methane flux in boreal fens~~,~~ (this study, Alm et al., 1999), any changes in wintertime processes may impact future methane emissions from these regions. ~~Our~~Therefore, our results highlight the importance of including winter in methane flux studies, as this information may help ~~to~~ reduce the current large uncertainties in the net carbon balance. Furthermore, the reduced variability of fluxes and the lack of significant variation among vegetation clusters during mid-winter (Figs. 3, 4) suggest that winter fluxes could be effectively captured even with lower but more optimized sampling efforts, aiding in the estimation of annual emissions (Vargas and Le, 2023).

Flux rates during the snow-free season reached up to 9.17 mg $CH_4/m^2/h$ ~~in~~at certain study plots ~~45 and 50~~, while they never exceeded 2 mg $CH_4/m^2/h$ in ~~study plots 67, 68, 71 and 72~~some others (Fig. 3). The high ~~fluxes in plot 50 may partly be explained by the high biomass~~BM of vascular plants, and ~~*Carex rostrata*. Indeed, the~~especially presence ~~of~~ *C. rostrata* ~~appears generally important for~~, contributes to the spatial variability in fluxes: all plots with more than five flux measurements exceeding 6 mg $CH_4/m^2/h$ (n = 9) contained *C. rostrata* shoots~~. In contrast,~~ but only three out of 19 plots that never recorded fluxes above 6 mg $CH_4/m^2/h$ contained *C. rostrata*. However, *C. rostrata* biomass cannot be the sole factor of high methane fluxes, as one plot ~~45 did not contain any~~containing no *C. rostrata* shoots~~.~~ also measured fluxes up to 9.05 mg $CH_4/m^2/h$ (see 4.3). Unlike the snow-free season, the high flux values ~~from plots 43, 46, 47, 49~~ during the spring burst at the end of the snow season could not be explained by ~~vegetation~~plant biomass or any other studied environmental variable. Other reasons for the spatial variation in flux rates may include species-specific plant traits such as rooting characteristics (Ge et al., 2023), ecohydrological aspects such as peat water holding capacity (Zhang et al., 2020), or ~~the role of microbiota~~microbial metabolic interactions such as nutrient cycling (Kujala et al., 2024; Yavitt et al., 2012~~).~~), which contribute to soil conditions, substrate availability, and microbial activity. Interestingly, the methane fluxes from *C. rostrata*-community plots were the highest from late July to late August (Fig. 43) when vegetation at our site remained predominantly green, even though fluxes from *C. rostrata* shoots have been reported to be the highest ~~in early autumn~~ when leaves are senescing (Ge et al., 2024). The period from late July to late August may coincide with the peak development of permeable root surface area ~~and aerenchyma~~ (Reid et al., 2015~~). The~~) which extent ~~of permeable root surface~~, in turn, is a key factor influencing methane transport in plants

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(Henneberg et al., 2012). Therefore, the seasonal changes in methane flux rates associated with *C. rostrata* may be controlled by the belowground parts of the plant (Ge et al., 2024).

4.2 Plant communities, biomass and methane

~~While previous studies have shown substantial vegetation–methane flux correlations during~~During the growing season ~~(e.g.,~~ vegetation is known to correlate substantially with methane fluxes (e.g. Lai et al., 2014; Riutta et al., 2007; Ström et al., 2015), ~~our research extends this to year-round scale, finding~~but we found significant correlations ~~in all studied time periods; snow-free,~~ year-round ~~and snow season, and thus~~ supporting our first hypothesis. ~~We acknowledge that the measured snow season fluxes might not fully represent the identified plant communities, as the measurements were not taken straight above the collars and the flux rates from different parts of the plots may differ to an unknown extent. However~~Thus, our results indicate that the influence of plant communities on methane flux dynamics is not limited to active growing season or plant senescence, and that some species are likely to be more efficient at supporting methane production and transport, even under the snowpack. Indeed, continuous production and spatial variation in methane flux rates has been observed throughout the cold season, and the variation has been associated with differences in plant community composition and the adjoining differences in substrate quantity and quality (Pirk et al., 2016b). However, the significant correlation between vegetation and methane fluxes during the snow season identified by CCA, but not by linear regression models, suggests that the relationship between vegetation and snow season methane fluxes is complex and non-linear.

~~The differences in plant community structures between the study plots, in relation to methane fluxes, were discovered when the focus of cluster and indicator species analyses was set solely on vascular plants (Fig. 5a). The clusters were mostly associated with different sedges and had only three species (*Campylium stellatum*, *Vaccinium oxycoccos*, and *Scorpidium cossonii*) common to all clusters (Table B1). At the peatland level, the~~Both the total vascular plant biomass and the ratio of vascular plant to bryophyte biomass correlated significantly with methane fluxes during snow-free and year-round periods, supporting our second hypothesis (Fig. 5a, d; Table B2). There was a strong correlation between the biomass of vascular plants, sedges and *C. rostrata* (Table B2). Additionally, the biomass of vascular plants, sedges and *C. rostrata* also correlated with methane fluxes (Fig. 5a–c; Table B2). These findings suggest ~~spatial division of the vascular plant communities was clear – the *C. rostrata* community plots were all located in the upper part of the sloping fen, while the other two clusters were more widely distributed (Fig. B7). Edaphic factors, such as water table depth and pH, are generally identified as the main determinants of dominant plant species, species differentiation, and plant community composition in mires (Brancaleoni et al., 2022; Laitinen et al., 2024). However, in our study, these factors could not explain the distribution of the vascular plant communities. The distribution of bryophyte communities and the biomass of *Sphagnum* mosses, on the other hand, correlated with these variables (Table B2). Indeed, the ratio of *Sphagnum* to brown mosses might be more significant in determining the composition of vascular plant species in a fen, as most fen-specialist species prefer environments abundant in bryophytes other than *Sphagnum* (Singh et al., 2019). This could explain the distribution of plant communities at our study site, as our analyses showed that bryophytes had the strongest connection to the overall plant community composition when all plant species were~~

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~~considered (Fig. B1). Additionally, there was an association between *Sphagnum* mosses and the fen generalist species *C. rostrata* in the plant communities: the *C. rostrata* cluster had the highest abundance of *Sphagnum* mosses among the three vascular plant clusters (Table B1).~~

~~4.3 The role of plant biomass~~

~~The second hypothesis behind this study was that methane fluxes would be higher on plots where vascular plant biomass is high, either in absolute terms or relative to bryophyte biomass. Our findings supported this, as both total vascular plant biomass and the biomass ratio of vascular plants and bryophytes significantly correlated with methane fluxes during snow-free and year-round periods (Fig. 6, Table B2). The strong correlation between total vascular plant biomass and the biomass of sedges and *C. rostrata*, as well as the even stronger correlation of sedge and *C. rostrata* biomasses with methane fluxes (Table B2), suggests~~, similar to earlier studies (e.g. Ge et al., 2023; Korrensalo et al., 2022), that plant functional type and species largely determine the magnitude of the fluxes. High amounts of vascular plant, sedge, and *C. rostrata* biomass likely enhance methane production and release by supplying labile organic ~~matter~~ carbon substrates for methanogenesis ~~and providing pathways for substrates to reach anoxic peat layers~~ through deep root systems throughout the year~~-round~~ (Alm et al., 1999; Joabsson et al., 1999, Saarinen, 1996). High flux rates from *C. rostrata* dominated plots (Fig. 7) may be due to the species' high methane transport rate (Ge et al., 2023), ~~low oxidation potential (Ström et al., 2005), and~~ the high porosity ~~and large aerenchyma~~ of its roots (Ge et al., 2023~~). High biomass of *C. rostrata* may also drive winter methane fluxes, as this species is both biennial (Saarinen, 1998)~~), and a low capacity to oxidize methane into CO_2 in the rhizosphere (Ström et al., 2005). Additionally, the perennial nature and deep rooting~~, and can therefore provide labile carbon to deeper peat layers~~ traits of *C. rostrata* (Saarinen, 1996~~) supporting~~; 1998) could support methane production ~~year-round.~~and transport during the cold season by providing substrates for microbial processes in deeper peat layers and a potential pathway from belowground to the atmosphere. Approximately 40 % of *C. rostrata* shoots at our study site overwinter green (Cunow et al., unpublished data), indicating the potential to transport gases also during wintertime. Moreover, the significant correlation between the ~~variable of BM~~ ratio of vascular plant to bryophyte biomass and methane fluxes brings a new perspective to the discussion, as previous studies have mainly focused on finding differences between single plant species (e.g. Bhullar et al., 2013; Ge et al., 2023; Koelbener et al., 2010; Korrensalo et al., 2022) or their role in a plant community (e.g. Lai et al., 2014; Riutta et al., 2007; Ström et al., 2015). ~~BM~~This biomass ratio could ~~act~~ be obtained remotely (e.g., multispectral imaging, Wolff et al., 2023) and potentially used as a predictive parameter for ~~predicting~~modeling peatland methane ~~flux of peatlands and be used in remote sensing and modelling studies~~fluxes.

A majority (75 %) of the highest methane fluxes observed in this study originated from *C. rostrata* dominated plots. However, the magnitude of the fluxes was not solely dictated by ~~the amount of~~ C. *rostrata* biomass; the fluxes increased rapidly in a non-linear manner and only slightly with higher biomass, being relatively high and stable in most *C. rostrata*-cluster plots (Fig. ~~7~~5c). As a species with high gas transport efficiency, even a single *C. rostrata* shoot can transport a substantial volume of gases – potentially the same amount as a community with multiple shoots, where gas transport is

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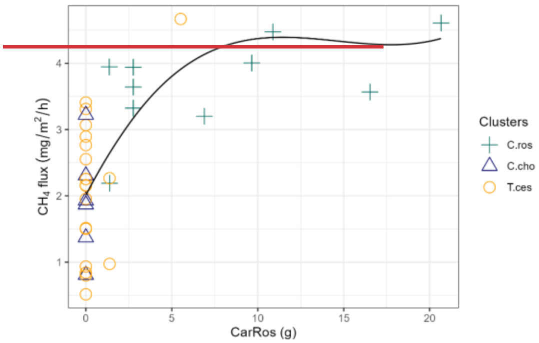
distributed among many individuals (Koelbener et al., 2010; Korrensalo et al., 2022). This division of gas transport among ~~more~~multiple shoots could explain the observed saturation in ~~the~~ methane flux rates~~ with~~: as the ~~higher~~ biomass of *C. rostrata*~~.~~ ~~Nevertheless, this does not imply~~ increases, the total flux remains consistent regardless of the number of shoots. In our analysis, an increase in biomass corresponds to a higher number of shoots, and therefore we cannot argue that the size of individual *C. rostrata* shoots ~~has no~~did not impact ~~on~~ the plant's methane transport efficiency~~. For the analyses, a mean biomass was used for each species, and all individual shoots were assigned the same estimate weight. Consequently, an increase in biomass corresponds to a higher number of shoots~~.



~~**Figure 7. The relation of snow-free season methane fluxes (mg/m²/h) and the biomass of *C. rostrata* (g of dry weight) (p < 0.001, r = 0.60) segregated by vascular plant clusters. See Fig. 5 for cluster abbreviations.**~~

4.~~4~~3 Environmental factors ~~explaining spatial variation of~~and methane ~~fluxes~~

We also asked if the spatial variability of methane fluxes could be explained by the combination of plant communities and environmental variables~~. Our results indicate~~ , and found that vegetation composition was the primary driver of this ~~variability, as~~variation. However, in some cases, the role of an environmental variable seemed to depend on the presence of plants. Firstly, we analyzed snow-free season methane fluxes from plots without any *C. rostrata* shoots and found that pH and litter cover emerged as main drivers of methane fluxes. However, as the significance of pH lowered when including the plots with *C. rostrata*, it is likely that the significant relationship between methane fluxes and pH in snow-~~-~~free and year-round periods is ~~likely also~~ explained through vegetation ~~(Jimenez-Alfaro et al., 2023; Keith et al., 2022). The positive correlation of~~ . Secondly, when *C. rostrata* was present, NO_3^- and NO_2^- levels ~~and~~correlated positively with methane fluxes during snow-~~-~~free and year-round periods ~~was~~ . In plots without *C. rostrata* shoots, this significant relationship disappeared, suggesting that the positive correlation is related to the presence of the species. The positive correlation was unexpected, as these compounds ~~have~~ usually ~~been found to~~ inhibit ~~methane production~~methanogenesis (e.g. Knorr & Blodau, 2009). ~~However, recent studies have~~More precisely, higher levels of NO_3^- may promote methane oxidation, leading to lower fluxes (Song et al., 2022), but the impact of these electron acceptors remains debated ~~their impact on methane production~~ (Zhang et al., 2021). Thus, our findings

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underscore the need for further investigation into the interaction between *C. rostrata* and NO_3^- and NO_2^- in driving methane fluxes.

Water table depth~~, which~~ is commonly thought to regulate methane fluxes in peatlands (Lai, 2009; Turetsky et al., 2014~~),~~) but did not correlate with methane fluxes at our site in any period. Indeed, in ~~constantly wet~~ fens with a stable water table, such as our study site~~,~~ (standard deviation of WTD 1.05–2.78 cm), the depth of the water table may not control the variability of the fluxes (e.g. Ge et al., 2023). ~~The thickness of the peat~~Peat layer did not ~~correlate~~show a significant pairwise correlation with methane fluxes~~,~~ which supports the previous findings that most of methane ~~released from peatlands~~ is produced from the fresh root litter and root exudates instead of old, recalcitrant peat (Ström et al., 2012). However, peat ~~depth~~layer thickness correlated significantly with the first ordination axis in CCA and had a significant pairwise correlation with the biomass of vascular plants, sedges, and *C. rostrata*, as well as the biomass ratio of vascular plants and bryophytes (Table B2), all of which were proxies for higher methane fluxes. ~~Further, peat temperature did not correlate with the fluxes.~~This suggest that peat layer composition and depth can also impact methane production through an indirect relationship. Lastly, methane fluxes did not correlate with peat temperature at 5 cm depth. Indeed, methane fluxes in boreal rich fens associate with deeper soil temperatures, which connect to water table position, rather than with surface temperatures influenced by air temperature (Olefeldt et al., 2017). All these findings highlight that vegetation, rather than environmental factors, was the main driver of methane fluxes at our site.

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Conclusions

Our ~~manually measured~~ year-round methane flux data ~~from a northern boreal rich fen~~ showed significant spatial and temporal variations in flux magnitude~~.~~ in a northern boreal rich fen. Plant community composition, particularly the biomass of ~~*Carex*~~*C. rostrata*, ~~demonstrated a strong potential causality in explaining~~effectively explained the plot-scale spatial variation of methane fluxes during snow free and year-round periods. Multivariate analysis also revealed ~~a moderate correlation between snow season fluxes and a vascular plant cluster most strongly associated with the presence of *C. rostrata*. These findings answer our first research question and support our hypothesis that plant community composition affects the flux. Environmental variables that significantly correlated with methane fluxes were pH and the combined concentrations of nitrate and nitrite in peat pore water during snow-free and year-round periods. These findings answer our second research question and indicate that plant community composition drives methane flux variability, both alone and in combination with other environmental factors. The~~that a vascular plant cluster characterized by *C. rostrata* correlated with snow season methane fluxes. In addition, the total biomass of vascular plants and the ratio of vascular plant to bryophyte biomass also showed a significant positive relationship with methane fluxes in both year-round and snow-free seasons~~, confirming our second hypothesis that higher~~. On the other hand, the role of other environmental factors, such as pH and nitrogen, in driving methane fluxes ~~occur in plots with higher vascular plant biomass or a higher vascular plant~~was subtle and seemed to ~~bryophyte biomass ratio. In addition to further research~~depend on ~~plant properties, particularly species-specific traits (Ge et al., 2023), which is crucially needed for northern~~

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~~boreal fens, our~~vegetation. Our findings suggest that the biomass ratio of vascular plants and bryophytes could ~~potentially~~ be used as a parameter for predicting methane emissions~~. This biomass ratio could also be valuable in remote sensing and modelling studies of peatlands with vegetation structure~~ at study sites with similar vegetation to ~~our study site~~ours. Importantly, these findings ~~provide valuable insights for predicting realistic~~help to predict more accurately and realistically future changes in peatland methane emissions ~~throughout the year~~, which is essential for estimating the potential impacts of ongoing climate change ~~(Riutta et al., 2020).~~.

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Appendices

Appendix A with additional site information. Appendix B with additional figures and tables of the results.

Data availability

Full datasets used are available on request.

Author contribution

MV, RP, MM and TRC designed the experimental setup of the study site. EJL, TT, TRC and JL designed the study. EJL sampled the vegetation and performed the statistical analyses with assistance from JL, EK and TT. EJL, JL and EK were responsible for data curation. EK and MM wrote the code for the flux calculations. MV designed and provided resources for sampling the water chemistry. Resource management of the data collection were overseen by RP. Manual methane flux measurements, pore water sampling and water level measurements were conducted by numerous individuals, including EJL and EK. EJL prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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