



Plant mediated methane efflux from a boreal peatland complex

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Abstract

Purpose Aerenchymous plants are an important control for methane efflux from peatlands to the atmosphere, providing a bypass from the anoxic peat and avoiding oxidation in the oxic peat. We aimed to quantify the drivers of aerenchymous peatland species methane transport and the importance of this process for ecosystem-scale methane efflux.

Methods We measured seasonal and interspecies variation in methane transport rate per gram of plant dry mass at a boreal fen and bog, which were upscaled to ecosystem-scale plant methane transport.

Results Methane transport rate was better explained by plant species, leaf greenness and area than by environmental variables. Leaves appeared to transport

methane even after senescence. Contrary to our expectations, both methane transport rate and the proportion of plant transport were lower in the fen (with greater sedge cover) than in the bog site. At the fen and bog, average methane transport rate was 0.7 and 1.8 mg g⁻¹ d⁻¹, and the proportion of seasonally variable plant transport was 7–41% and 6–90%, respectively. Species-specific differences in methane transport rate were observed at the ecosystem-scale: *Scheuchzeria palustris*, which accounted for 16% of the aerenchymous leaf area in the fen and displayed the greatest methane transport rate, was responsible for 45% of the ecosystem-scale plant transport.

Conclusion Our study showed that plant species influence the magnitude of ecosystem-scale methane emissions through their properties of methane transport. The identification and quantification of these properties could be the pivotal next step in predicting plant methane transport in peatlands.

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Introduction

Wetlands with vegetation that is adapted to water saturated conditions (Pan et al. 2020) are the largest single natural source of methane (CH₄), the greenhouse gas, (Zhang et al. 2017; Saunio et al. 2020), with a global warming potential 28 to 34 times that of carbon dioxide (CO₂) on a 100-year timescale (IPCC 2013). Aerenchymous tissue is characteristic to many wetland plants and is an adaptation that provides an oxygen supply to the roots of wetland plants but also acts simultaneously as a major conduit for CH₄ efflux to the atmosphere (Fig. 1; Schimel 1995; Pedersen et al. 2021). While the recent increase in the atmospheric CH₄ concentration has been partly attributed to wetlands (Kirschke et al. 2013; Zhang et al. 2021), the uncertainties in the estimates of current and future CH₄ emissions remain large (O'Connor et al. 2010;

Saunio et al. 2020), which partly results from the poorly quantified mechanisms through which plants impact CH₄ oxidation and release, as addressed in modeling work (Li et al. 2010; Wania et al. 2010; Zhang et al. 2017; Raivonen et al. 2017).

In northern peat accumulating wetlands (i.e., peatlands), aerenchymous plants are important in regulating CH₄ emissions (Fig. 1) as their presence has been observed to lead to lower pore water CH₄ concentrations and greater net efflux of CH₄ (Green and Baird 2012; Henneberg et al. 2016; Strack et al. 2017). Their abundance is greatest at sites and surfaces where the water level is close to the soil surface (Laine et al. 2012; Korrensalo et al. 2018a; Fig. 1). When CH₄ bypasses the oxic peat and live *Sphagnum* layers via aerenchymous plants, a larger proportion of CH₄ produced in the anoxic peat layer may avoid oxidation by the methanotrophic microbes in the aerobic peat layer and be released to the atmosphere (Schimel 1995; Whalen 2005; Turner et al. 2020; Fig. 1). The estimated proportion of plant transport of the total site-level CH₄ efflux varies widely from 27 to 98%

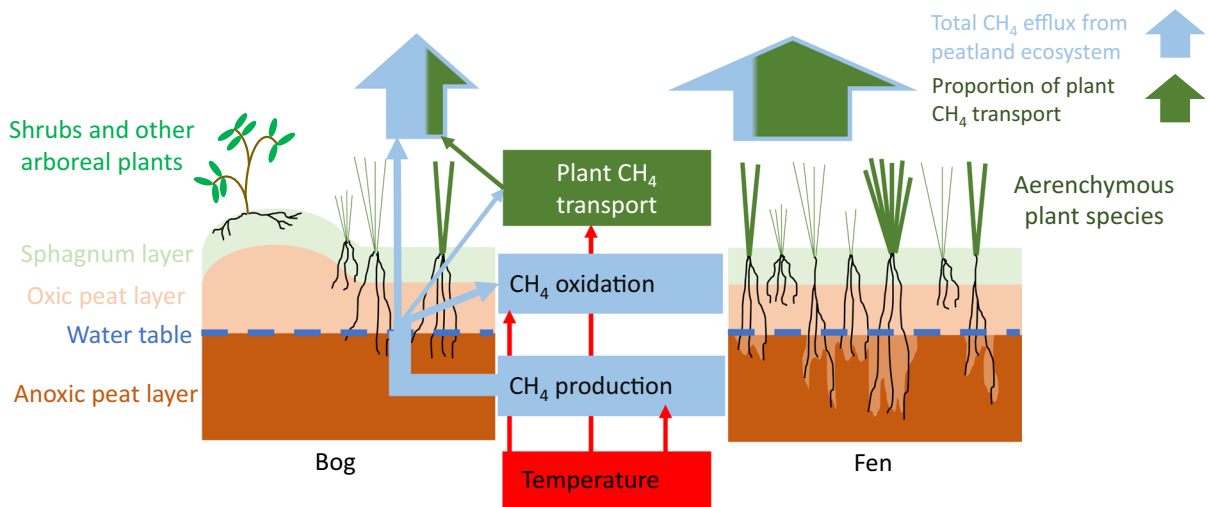


Fig. 1 Schematic presentation of plant methane (CH₄) transport in fens and bogs; the main peatland types of the boreal region. Vegetation in rainwater-fed, nutrient-poor bogs with a surface topography that varies from shrub dominated drier hummocks to sedge dominated wet hollows provides less suitable litter for methanogenesis than sedge-dominated minerotrophic fens. Sedges and other aerenchymous plant species act as conduits of CH₄ to the atmosphere, bypassing oxidation by methanotrophic microbes in the oxic peat and living moss layer, with only negligible oxidation along this bypass route (Turner et al. 2020). Simultaneously, they transport oxygen

into the anoxic peat layer (light color around the sedge roots) (Fritz et al. 2011; Münchberger et al. 2019). Both CH₄ production and oxidation are regulated by spatially and seasonally varying water levels and soil temperatures (Turetsky et al. 2008; Larmola et al. 2010; Yrjälä et al. 2011), and the same control may also apply to the capacity of plants to transport CH₄ (Shannon and White 1994). Aerenchymous plant species may vary in their capacity to transport CH₄ (Bhullar et al. 2013) and increase the overall CH₄ efflux (Strack et al. 2017), which results in sedge-dominated fens exhibiting greater CH₄ emissions than bogs (Turetsky et al. 2014)

(Morrissey and Livingston 1992; Shannon et al. 1996; Kutzbach et al. 2004; Dorodnikov et al. 2011; Knoblauch et al. 2015). Studying plant CH₄ transport over seasonally changing environmental conditions and at sites with different vegetation types might be the key in developing a mechanistic understanding of this process.

A mechanistic understanding of how plants regulate peatland CH₄ cycling would improve projections of future CH₄ emissions under a changing climate. Climate change will affect the CH₄ cycle both directly through changes in abiotic drivers, such as temperature and moisture (Fig. 1), and indirectly through the resultant successional changes in vegetation. In peatlands, vegetation is known to be especially sensitive to changes in hydrology (Talbot et al. 2010; Tahvanainen 2011; Mäkiranta et al. 2018; Kokkonen et al. 2019) and appears to be a stronger control on CH₄ cycling than temperature (Ward et al. 2013; Peltoniemi et al. 2016; Riutta et al. 2020). The abiotic and biotic drivers are strongly linked, e.g., once the water table falls below a certain threshold level the impact of vegetation on CH₄ fluxes diminishes (Waddington et al. 1996; Strack et al. 2006; Riutta et al. 2020). The change in vegetation resulting from a drier and warmer climate is expected to differ between peatland site types and microforms, causing contrasting impacts on CH₄ production. In minerotrophic fens, graminoids could become more abundant (Dieleman et al. 2015), which could support greater CH₄ production (Treat et al. 2015), while in rainwater-fed ombrotrophic bogs, a more hostile environment for methanogenesis could result from increased cover of shrubs (Breeuwer et al. 2009), which have recalcitrant litter for decomposition (Bragazza et al. 2013). However, the differences within a wide selection of plant species in CH₄ transport has not been previously studied in the field over a growing season to quantify the environmental controls of this process and how it regulates site-scale CH₄ efflux. Ongoing climate change and the expected associated successional change in peatland vegetation (Zhang et al. 2020) means that it is essential to know the extent that CH₄ transport rate is controlled by plant species and/or environmental conditions.

The aim of our study was to quantify the importance of different aerenchymous plant species and abiotic factors for controlling the plant CH₄ transport

rate from the peatland to the atmosphere. Further, we aimed to define the importance of CH₄ transport for the ecosystem-scale CH₄ efflux at a fen and a bog at different times of the growing season. For this, we upscaled plant transport measurements conducted over the growing season at a boreal fen and bog site to the ecosystem-scale and compared our results with eddy covariance (EC) measurements conducted at the two sites. We expected plant CH₄ transport rate to be regulated both by species characteristics and by seasonally variable temperature and moisture levels. We also hypothesized that the proportion of the ecosystem-scale CH₄ emission attributable to plant CH₄ transport would be greater in the fen site, which has a greater cover of aerenchymous species, than in the bog site (Fig. 1).

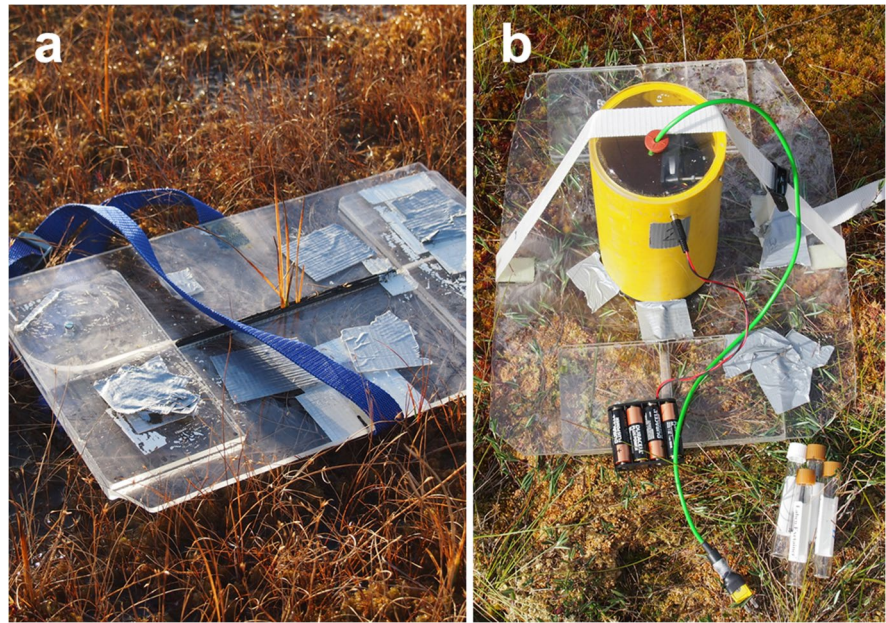
Materials and methods

Study site

The study was conducted in two peatland sites, both within the large Siikaneva peatland complex in Ruovesi, western Finland, located in the southern boreal vegetation zone (Ahti et al. 1968). The annual temperature sum in the area is 1318 degree days, annual rainfall is 707 mm, and the average annual, January and July temperatures are 4.2, −7.2 and 17.1 °C, respectively (30-year average values from the Juupajoki-Hyytiälä weather station, located 10 km from the site).

The bog site, located in the ombrotrophic part of the peatland complex, is characterized by large spatial variation in the water Table (WT) and vegetation composition (Korrensalo et al. 2018a). There is a gradient from high hummocks dominated by dwarf-shrubs, a few small Scots pine trees (*Pinus sylvestris*), and *Sphagnum* species typical of hummock environments to hollows dominated by ombrotrophic sedges (*Carex limosa*, *Rhynchospora alba*) and hollow *Sphagna*. The bog site also has open water pools and bare peat surfaces, with only a sparse cover of sedges. The fen site, located in the oligotrophic part of the peatland complex, is spatially more homogeneous and dominated by tall sedges (*Carex rostrata*, *C. lasiocarpa*) and *Eriophorum vaginatum* (Riutta et al. 2007). For more accurate description of the species

Fig. 2 The measurement chamber, plexiglass platform and plant sample a) before, and b) after the chamber has been attached on top and tightened with a belt. Soft foam sealant between the platform halves and on the bottom of the chamber ensures the airtightness of the system



composition at the bog and fen sites, see Korrensalo et al. 2018a and Riutta et al. 2007, respectively. The growing-season average WT in the bog and fen sites is 9 and 15 cm below the moss surface, respectively (unpublished data from May–September 2019, average of WT values at different vegetation communities, weighted by their areal cover within the sites). In the center of both sites, there is an EC tower reachable by a wooden boardwalk. To compare the WT between years, we used half-hourly WT depths relative to the moss surface that were continuously recorded on an intermediate lawn surface at both sites next to the EC tower. .

Methane efflux measurements

In the bog site, plant CH_4 transport rate was measured from all aerenchymous plant species present within the EC tower footprint, namely *C. limosa*, *E. vaginatum*, *R. alba*, *Scheuchzeria palustris* and *Trichophorum cespitosum*. In the fen site, measurements were conducted from the four most dominant aerenchymous species; *C. lasiocarpa*, *C. rostrata*, *E. vaginatum* and *S. palustris*, which together accounted for 89% of the aerenchymous leaf area index (LAI) at the site.

Between June–September in 2013, and May–October in 2014, measurements were carried

out on 3–5 samples per species within the EC tower footprint during each campaign, in total 8 and 11 campaigns at the bog site in 2013 and 2014, respectively, and 7 campaigns at the fen site in 2014. In 2013, the measurements were only carried out at the bog site, but both sites were studied in 2014. Measurements were conducted from the boardwalk whenever possible to avoid disturbing the peat and prevent CH_4 release as ebullition. To ensure that samples of the same species were always located more than 5 m apart, some measurements were conducted outside of the boardwalks, in which case any walking and movement at the measurement location was avoided.

Plant CH_4 transport rate (expressed per gram plant dry mass inside the chamber as $\text{mg CH}_4 \text{ g}^{-1} \text{ day}^{-1}$) was measured using custom-made cylinder-shaped chambers that varied in volume between 0.7 and 5.0 l. A plant sample of 2–104 leaves (depending on the growth form of the measured plant) belonging to the same species was separated from the peat and moss underneath, by two plexiglass plates that were attached together with a hinge and had a smooth rubber seal between them to avoid compression of the plant (Fig. 2a). The proportion of green leaves in the sample varied from 0 to 100% depending on the phase of the growing season. The sample was then covered with an opaque plastic chamber that

was sealed with the plate by a smooth rubber seal attached to the bottom of the chamber. Airtightness of the system was ensured by tightening a belt that extended from one plate to the other over the chamber. Finally, a rubber stopper was used to seal a vent hole in the top of the chamber (Fig. 2b). Each plant sample was measured for 35 min, during which four 20 ml air samples were drawn from the chamber with a syringe through the rubber stopper in the top of the chamber at 5, 15, 25 and 35 min after chamber closure. The air samples were then injected into evacuated 12 ml glass vials (Labco Limited, UK).

Simultaneous to the flux measurements, temperatures in the chamber (air) and peat at 5, 15 and 30 cm depth were recorded. WT was measured from a perforated plastic tube installed into the peat next to the sample after the WT level in the tube had stabilized for at least 30 min. After the flux measurement, the plant sample was cut with scissors and transported to the laboratory in a plastic bag. In each plant sample, the number of leaves was counted, the leaf area of brown and green leaf parts was measured with a scanner, and the dry weight was obtained for brown and green leaf parts separately after oven drying the sample at 60 °C for 24 h. Using these data, specific leaf area (SLA, $\text{m}^2 \text{g}^{-1}$) was calculated for each sample.

CH_4 concentration in the glass vials was analyzed with an Agilent Technologies 7890A gas chromatograph and Gilson GX-271 liquid handler. The CH_4 flux was calculated as the linear change in CH_4 concentration in relation to time, chamber volume and temperature. Nonlinear changes in CH_4 concentration that were visually detected, were surmised to have resulted from a leak in the chamber or in the vial and were excluded from the analysis. In total 6% of the measurements were excluded from the final dataset due to such nonlinearities.

In 2014, venting tubes were attached to each chamber to prevent the decrease in pressure inside the chamber when taking the gas samples. The other end of the venting tube was always kept in water during the measurement. These tubes did not significantly impact flux magnitude, which was tested by measuring the same plant samples with and without the tube ($n=8$, $p=0.100$). Therefore, the data measured with and without the tube (2013 and 2014, respectively) were pooled together.

Statistical methods

A t-test was used to test the significance of differences in plant CH_4 transport rates between 2013 and 2014 of all species in the bog site, and the difference in WT levels at the measurement locations of *E. vaginatum* and *S. palustris* growing in both sites.

We used linear mixed-effects models to quantify the differences in the plant CH_4 transport rate between aerenchymous species and sites, and to assess how well the measured plant characteristics and/or environmental variables were able to explain the plant CH_4 transport rate. Furthermore, we investigated whether species identity and site are needed to explain the plant CH_4 transport rate after environmental variables and measured plant characteristics have been taken into account. First, we constructed a model to assess the differences between species and sites with these two variables as fixed predictors and year and day of the year (DOY) as random effects, after determining that the differences between years and DOY were non-significant. Second, we constructed a model to assess the relative importance of plant characteristics, environmental variables, plant species, and site, where potential fixed predictors were added sequentially. After each new addition, Akaike Information Criterion (AIC) and a conditional F-test were used to evaluate whether the addition significantly improved the model. At this stage, potential fixed predictors for the model were DOY, environmental variables (air temperature, peat temperature at different depths, and WT), and plant characteristics (total leaf area in the sample, number of leaves in the sample, proportion of brown leaves and SLA). Next, we added plant species and site as fixed predictors and checked whether they improved the model. Site, plant species and DOY were included as categorical predictors, while the response shape for the other variables was visually assessed by plotting the residuals of the previous model against the next predictor to be added into the model. The best response shape was then selected using the AIC value and the conditional F-test. In addition to linear and second-degree polynomial responses, we used a constant response to the explanatory variable, to a visually determined threshold, and a second-degree polynomial response at values smaller or larger than the threshold as a third alternative. The final model

included the nested random effects of measurement year and DOY. Pairwise comparisons between the levels of categorical predictors were obtained by fitting the model repeatedly but each time holding a different level as a constant to which the other levels were compared. The residuals of the final model were normally distributed around a mean of zero. The model was fitted using function `lme` of package `nlme` (Pinheiro and Bates 2000) of R software (version 3.3.2.; R Core Team, 2020). The coefficients of the fixed and random part of the final model are presented in Supplementary information 1.

Eddy covariance measurements

During the study years, EC measurements were conducted in the bog and fen at a height of 3 m above the average moss surface. A METEK USA-1 sonic anemometer, a LI-7200 enclosed CO₂ and H₂O gas analyzer and a LI-7700 open-path CH₄ analyzer were used in the bog area (Männistö et al. 2019; Alekseychik et al. 2021), while the fen station was equipped with a METEK USA-1 sonic anemometer, a LI-7000 closed path CO₂ and H₂O gas analyzer, and a LGR GGA-24EP closed path CH₄ analyzer (Rinne et al. 2018).

The 10 Hz EC data were processed with the EddyUH software (Mammarella et al. 2016). First, all data were despiked according to Vickers and Mahrt (1997). Then, 2-D rotation was applied to the bog wind velocity components data after Reibmann et al. (2012), while the fen data were processed using a sector-wise planar fit after Mammarella et al. (2007), which was found to yield superior results. The spectral corrections were performed according to Mammarella et al. (2009). The calculated fluxes were filtered by the values of integral turbulence characteristics, skewness, kurtosis, flux stationarity and flux intermittency, following ICOS data processing protocols (Sabbatini et al. 2018; Nemitz et al. 2018). For further information on EC data processing, see Mammarella et al. (2016). The processed CH₄ and CO₂ fluxes were stored in the units of $\mu\text{mol m}^{-2} \text{s}^{-1}$. A friction velocity (u_*) threshold of 0.1 m s^{-1} was imposed on the calculated and quality controlled fluxes to exclude the periods when insufficient turbulent mixing affected the quality of the measured EC fluxes. The EC CH₄ flux was gap-filled using a

statistical model based on the relationship between the flux and the peat temperature at a 20 cm depth; for details, see Alekseychik et al. (2021) (bog site) and Rinne et al. 2018 (fen site).

Estimating site-level aerenchymous leaf area and biomass

Leaf area of aerenchymous plant species was defined in 0.36 m^2 sample plots; 18 in the bog site and 15 in the fen site. The sample plots covered the variation in vegetation within the site (Riutta et al. 2007; Korrensalo et al. 2019). Leaf area was estimated every three weeks over the growing seasons following Wilson et al. (2007). The average number of leaves per square meter of each species was estimated by counting the leaf number in five subplots ($8 \times 8 \text{ cm}$). The average size of one leaf was defined with a scanner from samples of corresponding species, which were taken from around the sample plots on each leaf area measurement day. The LAI of each species was defined by multiplying the average number of leaves by the average size of a leaf. Continuous LAI development of each species was then estimated by fitting a log-linear response to the observations (Wilson et al. 2007). Daily LAI values were converted to green biomass (BM, g m^{-2}) using the equations in Korrensalo et al. (2018a) and Mäkiranta et al. (2018). The species-wise daily biomass values at the sample plot scale were upscaled to the ecosystem-scale using the cover of plant community types within the EC tower footprint as presented in Korrensalo et al. (2018a) for the bog site and by Riutta et al. (2007) for the fen site. Total aerenchymous LAI and green biomass (LAI_{aer} and BM_{aer}) at each site and day was the sum of the species-specific LAI and green BM values.

Upscaling plant CH₄ transport

To quantify the proportion of plant CH₄ transport rate in the ecosystem-scale CH₄ efflux at the two sites, and to quantify the role of different plant species in ecosystem-scale CH₄ efflux at different times of the growing season, we upscaled the plant CH₄ transport rate ($\text{mg CH}_4 \text{ dry mass g}^{-1} \text{ day}^{-1}$), measured at the plant species-scale, to plant CH₄ transport per ground area ($\text{g CH}_4 \text{ m}^{-2} \text{ day}^{-1}$). Daily green BM of each species was multiplied by the seasonal mean plant CH₄ transport rate of

the corresponding species at that site. We used the seasonal mean transport rate for each species in upscaling, because no differences were found in plant CH₄ transport rate between the chamber measurement days, seasonally variable temperature or WT (see Results). To make the seasonal estimates comparable between years, we used the same time period from 1st of May to 30th of September for the upscaling at both years and sites. The CH₄ transport in the three plant species with low LAI values in the fen site that we did not measure was accounted for in upscaling by multiplying their daily green BM values by the mean CH₄ transport rate for all other fen species. The upscaled plant CH₄ transport rates represent only the CH₄ transported by the green BM at the sites. Senesced plant biomass data at the sites were not available and it is not known how long the senesced leaves may transport CH₄ (based on our measurements).

Results

Site conditions

In the bog site, where measurements were carried out during 2013 and 2014, WT in the continuous WT recordings at the intermediate lawn surface was lower in the drier year 2013 ($-14 \text{ cm} \pm 2 \text{ cm}$, May–September mean \pm standard deviation) than in 2014 (WT $-12 \text{ cm} \pm 3 \text{ cm}$). In 2014, when measurements were carried out in both sites, the fen site had a growing season (May–September) WT of $-7 \text{ cm} \pm 6 \text{ cm}$ with respect to the lawn surface. The seasonal maximum of BM_{aer} was greater in

2013 than in 2014 in the bog site (Table 1). The sedge-dominated fen site had a greater BM_{aer} value than the bog site during the 2014 growing season (Table 1).

Variability in plant CH₄ transport rate

At the bog site, plant CH₄ transport rates did not differ between the two measured years ($t=0.50$, $p=0.615$). In the bog site, aerenchymous plants were found to occur at wetter surfaces with shallower average WT than in the fen (Fig. 3c and d).

In the final linear mixed-effects model, plant CH₄ transport rate ($\text{mg CH}_4 \text{ dry mass g}^{-1} \text{ day}^{-1}$) was explained by plant species, total leaf area, the proportion of brown leaf area in the sample, and site (Fig. 4a–d). The differences between species largely reflected their habitat along the WT gradient at the two sites; species growing on the wettest surfaces (e.g., *S. palustris*) showed greater plant CH₄ transport rates than species growing on drier surfaces (e.g., *C. lasiocarpa*) (Figs. 3 and 4c). In general, the plant CH₄ transport rate was greater at the bog site than at the fen site ($p=0.002$). Of the two plant species measured at both the fen and bog in 2014, *E. vaginatum* was found at similar WT levels and exhibited similar plant CH₄ transport rates at both sites, while *S. palustris* grew in wetter conditions at the bog site and had a significantly greater CH₄ transport rate there than at the fen site (Fig. 3c and d). Plant CH₄ transport rate was reduced in samples with a greater total leaf area. The response shape that best explained the variability in the data was a second-degree polynomial decrease until LAI reached 18 cm^2 and then became constant (Fig. 4b). An increased proportion in brown leaf area decreased the plant CH₄ transport rate, but CH₄ was

Table 1 Seasonal cumulative methane (CH₄) efflux measured by the eddy covariance method and seasonal cumulative ecosystem-scale plant CH₄ transport derived from chamber measurements, both calculated for the time period 1.5.-30.9. in 2013

Site	Year	Seasonal CH ₄ efflux (Eddy covariance, g CH ₄ m ⁻²)	Seasonal plant CH ₄ transport (chambers, g CH ₄ m ⁻²)	Seasonal maximum BM _{aer} (g m ⁻²)	% plant transport of CH ₄ efflux, mean over the growing season \pm 95% CI	% plant transport of CH ₄ efflux, min/max over the growing season
Bog	2013	10.2	4.0	31.3	35.8 ± 2.5	5.9/59.6
Bog	2014	11.2	3.0	22.1	27.1 ± 2.2	7.4/89.6
Fen	2014	13.1	2.8	44.4	20.8 ± 1.0	7.4/41.2

and 2014, seasonal maximum aerenchymous biomass (BM_{aer}) and the proportion of plant CH₄ transport in ecosystem-scale CH₄ flux in the studied bog and fen sites

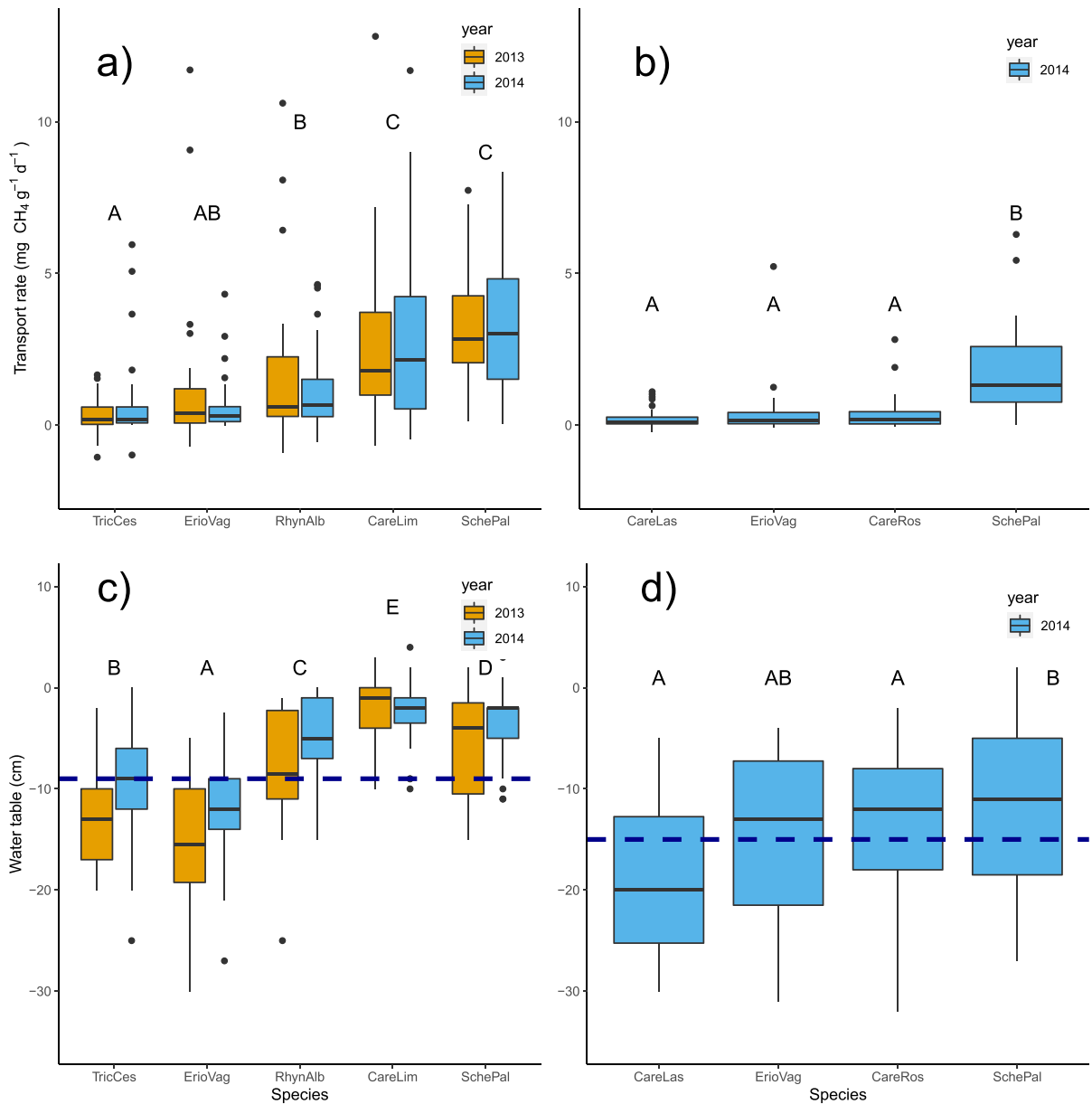


Fig. 3 Differences between aerenchymous plant species in a) and b) methane (CH₄) transport rate and c) and d) water Table (WT) at the sampling locations at the bog and fen site, respectively. Measurements were conducted in 2013 and 2014 at the bog site, and in 2014 only at the fen site. Upper and lower side of boxes denote the 25% and 75% percentiles. Line in the middle of the box denotes the median. The mean WT values at the two sites, measured as distance to the moss surface, are

indicated by dark blue dashed lines. Letters denote statistically significant ($p < 0.05$) differences between plant species. No significant difference was found in CH₄ transport rate between measurement years at the bog site. Abbreviated plant species names are TricCes = *Trichophorum cespitosum*, ErioVag = *Eriophorum vaginatum*, RhynAlb = *Rhynchospora alba*, CareLim = *Carex limosa*, SchePal = *Scheuchzeria palustris*, CareLas = *Carex lasiocarpa*, CareRos = *Carex rostrata*

transported at the non-negligible rate of 0.5 ± 0.9 (mean \pm standard deviation) mg CH₄ g⁻¹ day⁻¹ in samples consisting only of brown leaves.

Although a significant response of plant CH₄ transport rate to soil temperature at 15 cm depth and WT was initially detected, the latter abiotic

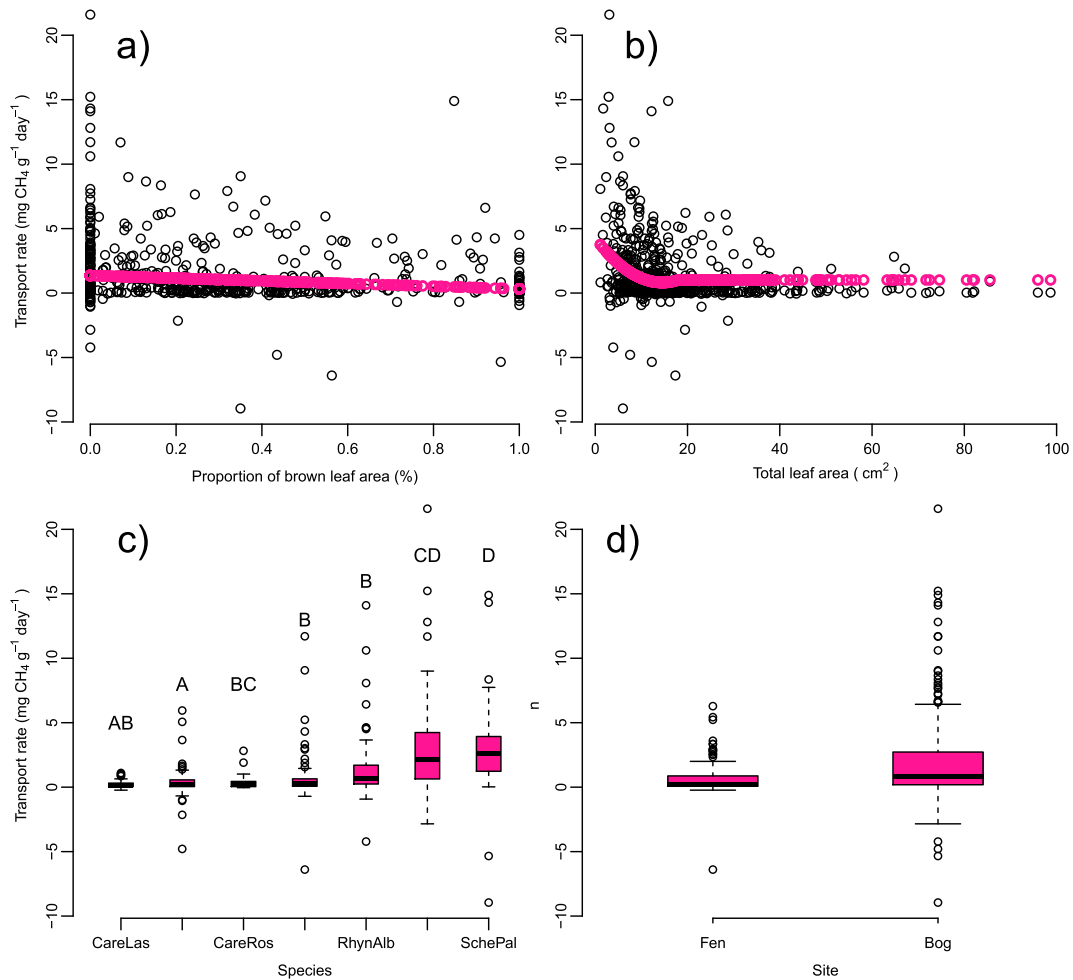


Fig. 4 Variables explaining plant methane (CH₄) transport and their response according to the linear mixed-effects model. The red datapoints in panels a) and b) show the model prediction when one factor at a time is allowed to vary within the range of the measured data and the other factors are set to constant (proportion of brown leaf area and total leaf area = mean of measured values, species = *Eriophorum vaginatum* at the bog site),

while the black datapoints represent measured data. Panel c) is based on the measured data from both sites pooled together, and panel d) is based on the measured data from all species and both years pooled together. The letters in panel c) denote statistically significant differences between aerenchymous species based on the mixed-effects model (Appendix 1). Full species names are as in Fig. 3

variables were no longer significant predictors once the variables described in the previous paragraph were included in the model. Brown leaf area was found to be a better predictor of plant CH₄ transport rate than peat temperature, and WT no longer significantly explained the plant CH₄ transport rate once species was included in the model. In a similar way, SLA and number of leaves were excluded from the model after the more powerful predictors were included.

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Impact of species in ecosystem-scale CH₄ transport

The extent of total CH₄ transport by the different aerenchymous species at the ecosystem-scale was modulated by their CH₄ transport rate. For example, *S. palustris* in the bog site comprised, on average, 13% of the aerenchymous LAI but accounted for 36% of total plant CH₄ transport due to its rapid CH₄ transport rate (Fig. 5a–e). In the fen site, *S. palustris* contributed on average 16% of the total aerenchymous LAI but accounted for

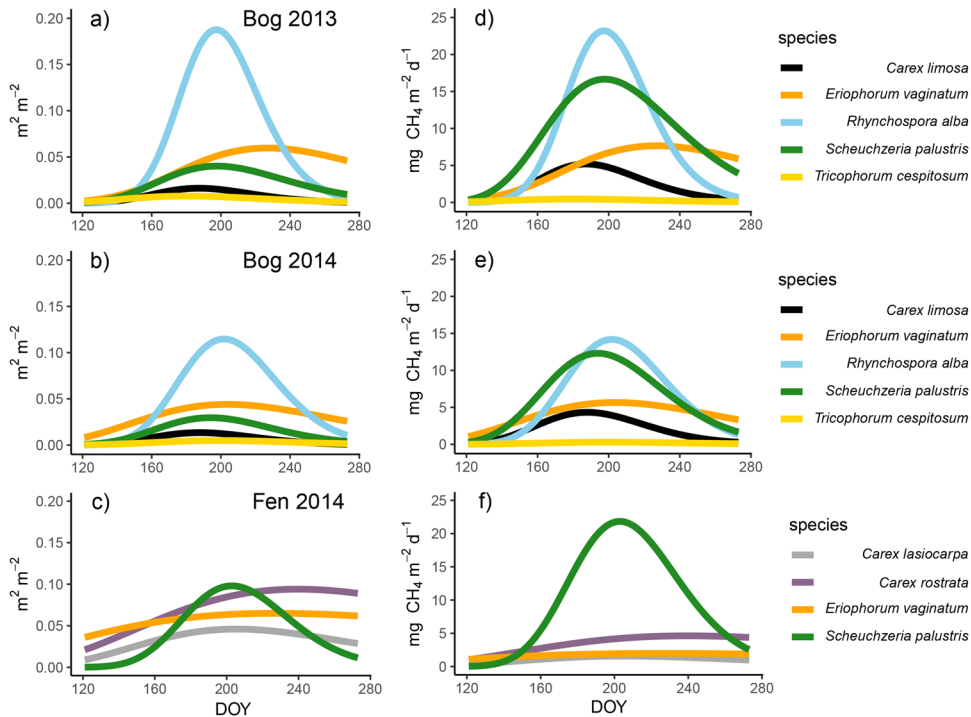


Fig. 5 Seasonal development of reconstructed green leaf area index (LAI) (a–c) and ecosystem-scale methane (CH₄) transport estimate (d–f) of each measured aerenchymous species at

the bog site in 2013 (a and d) and 2014 (b and e), and at the fen site in 2014 (c and f)

45% of the total CH₄ transport at the site (Fig. 5c and f). In contrast, *C. rostrata* in the fen site was observed to have the greatest LAI value for most of the growing season but due to its low CH₄ transport rate, exhibited low CH₄ transport at the ecosystem-scale.

Proportion of plant CH₄ transport of total CH₄ efflux

Both the seasonal cumulative plant CH₄ transport per ground area (g CH₄ m⁻²) and its proportion of the total CH₄ efflux at the ecosystem-scale were greater in the bog site than in the fen (Table 1, Fig. 6). In the bog, CH₄ transport and its proportion were greater in the drier year 2013 than in 2014 (Table 1, Fig. 6). Overall, the daily proportion of plant CH₄ transport of the CH₄ efflux measured by the EC tower varied over the growing seasons from 7 to 90% (Fig. 6). In the fen site, seasonal variation in the proportion of plant CH₄ transport, between 7 and 41% of the daily average CH₄ efflux, was

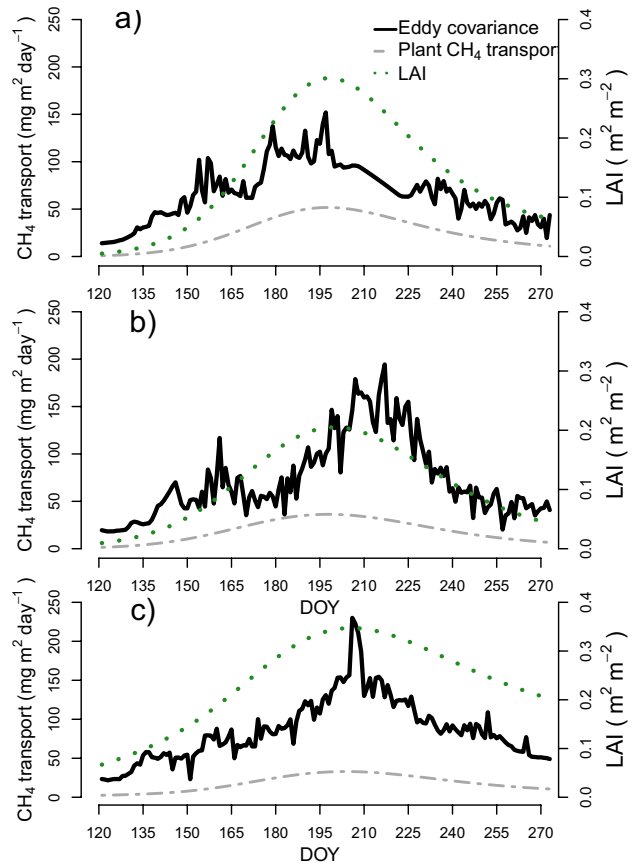
much lower than in the bog site in the same year, which exhibited proportions that ranged from 7 to 90% (Table 1). At both sites, the proportion was generally greatest at the beginning and at the end of the growing season (Fig. 6).

Discussion

The magnitude of measured CH₄ transport rate

The CH₄ transport rate values that we measured were in the same range as those reported per gram of plant dry mass by Shannon et al. (1996), which ranged from 1.23–4.49 mg CH₄ g⁻¹ day⁻¹ for a selection of aerenchymous bog plants, while other studies have reported only the rates per leaf area (Schimel 1995). Our values are in agreement with the measurements of Sebacher et al. (1985), although they only reported CH₄ emissions from the whole plant.

Fig. 6 Comparison of eddy covariance–derived daily cumulative estimates of ecosystem-scale methane (CH_4) efflux and daily plant CH_4 transport values upscaled from chamber measurements and daily aerenchymous green leaf area index (LAI) values in a) 2013 at the bog site, b) 2014 at the bog site, and c) 2014 at the fen site



Species rather than environmental factors explain CH_4 transport rate

In contrast to our hypothesis, none of the measured abiotic variables were able to explain the plant CH_4 transport rate when plant species were included. In our study, which covered a wide selection of aerenchymous plant species at two peatland sites, plant species and their properties (leaf area and proportion of senesced leaves) were better predictors of the CH_4 transport rate. These biotic variables correlated with WT and temperature but since they replaced these abiotic variables in the model, they also contain additional information. Peatland plant species have their niche along the WT gradient (Rydin 1993; Väliiranta et al. 2007) and, therefore, inherently carry information on the effect of WT on the CH_4 transport rate. Wet habitat species, such as *S. palustris* and *C. limosa*, showed greater CH_4 transport rates than hummock species. Accordingly, *S. palustris* had a reduced CH_4 transport rate in the

fen site where it grew in drier habitats than in the bog. Similarly, the proportion of brown leaves in the sample was correlated with the seasonal variation of temperature and WT, but displaced them in the final model.

Counterintuitively, total leaf area in the sample was found to decrease the CH_4 transport rate. Total leaf area correlates with root biomass (Korrensalo et al. 2018a); root surface area and volume which in turn are known to enhance plant CH_4 transport (Henneberg et al. 2012; Bhullar et al. 2013). However, our result is similar to previous studies in mesocosms (Bouchard et al. 2007; Koelbener et al. 2010) that found a negative correlation between CH_4 emissions and plant biomass. Greater root density may decrease the proportion of plant transport in total CH_4 efflux (Bhullar et al. 2013) as it will bring more oxygen into the anoxic zone and thus stimulate CH_4 oxidation in the peat (Ström et al. 2005; Münchberger et al. 2019). Larger and denser tussocks may be able to transport more oxygen into the peat (Fritz et al. 2011). In our

study, samples with greater leaf area values were often from species that have a tussock-like growth form. As such, our measured CH_4 transport rates represented the net effect the plant had on CH_4 transport, including also the enhancing effect on oxidation in the peat. Furthermore, with greater aboveground aerenchymous biomass, CH_4 in the peat might be distributed between more plants, which would leave less CH_4 to transport per unit of biomass.

The addition of plant species improved the explanatory power of our model. This implies that species is a proxy for other biological properties not measured in this study, but which are essential for predicting CH_4 transport. Currently, the prediction of various ecosystem functions, such as CO_2 cycling, biomass production, and resilience to perturbations, has been attempted using plant functional traits rather than species or plant functional groups (Funk et al. 2017; Rupp et al. 2019). However, work on traits specific to peatland plants has only just begun (Pan et al. 2019, 2020; Pedersen et al. 2021), and the extent that peatland C dynamics is explained by these traits has rarely been quantified. Net CH_4 efflux is known to be related to the presence of aerenchyma in plant tissue (Goud et al. 2017). Our study measured a wide variability in CH_4 transport rate between those species that possess aerenchyma tissues, which suggests that possession of aerenchyma alone is not sufficient to quantify the ability of plants to transport CH_4 . Root traits are known to be important in regulating CH_4 transport (Henneberg et al. 2012; Bhullar et al. 2013; Pan et al. 2019, 2020), but they are laborious to measure and cannot be used as a constant value due to within-species variability among peatland site types (Metsävainio 1931). This points to the need for further investigation of easily measurable plant functional traits related to CH_4 transport and net CH_4 emissions in peatland sites. Such traits could be, for example, the diameter of the shoot base, since some species appear to release CH_4 at the shoot base (Henneberg et al. 2012), or the diameter of leaf blades from where CH_4 commonly exits the plant (Morrissey et al. 1993; Schimel 1995; Kelker and Chanton 1997).

In this study, we observed a potential functional role of dead plant leaves beyond their role as substrate for methanogenesis (Ward et al. 2009). Although CH_4 transport rate decreased with the increasing proportion of brown leaves, completely senesced leaves also transported CH_4 to the atmosphere. The slower CH_4

transport rate of brown leaves could be due to collapsing aerenchymous tissue in the senescing leaves, as well as the overall slower CH_4 efflux in spring and autumn (Long et al. 2010; Rinne et al. 2020) when the proportion of brown leaves is greatest. When upscaling the CH_4 transport rate, we did not attempt to quantify the role of brown leaves in ecosystem-scale plant CH_4 transport, which may have caused a small underestimation in our autumn- and springtime plant transport estimates. In the case of deciduous species, brown leaf area development could be approximately estimated from seasonal peak leaf area, but it is not known how long brown leaves transport CH_4 before the collapse of the aerenchyma tissue structure. It is possible that CH_4 transport by brown leaves could play a role during warm spells in autumn, when the leaves have only recently senesced and the warm temperatures could stimulate CH_4 production.

CH_4 transport rate and proportion of plant CH_4 transport in fen and bog ecosystems

We observed a slower CH_4 transport rate in the aerenchymous species at the fen site with greater ecosystem-scale CH_4 efflux than in the bog site. The slower CH_4 transport rate observed in the fen plant species could reflect the greater ecosystem-scale aerenchymous biomass resulting in less CH_4 to transport per gram of dry mass. Our result is in line with Koelbener et al. (2010), who found that aerenchymous plants in less productive habitats produced greater CH_4 emissions than aerenchymous plant species typical of eutrophic sites, possibly due to the quality and quantity of substrate they provide for methanogenesis (greater production of organic acids with low molecular weights).

In contrast to our hypothesis, the fen site with the greater aerenchymous leaf area throughout the growing season accounted for a lower proportion of the total CH_4 efflux attributable to plant CH_4 transport than the bog site. Our results are also contrary to the model simulation of Raivonen et al. (2017), where the proportion of CH_4 efflux attributable to plant transport increased with increasing LAI values. However, in the same model simulations, the proportion of CH_4 efflux attributable to plant transport was negatively correlated with the total CH_4 efflux at the site (Raivonen et al. 2017), similarly to the fen (greater

total CH₄ efflux) and bog (lower total CH₄ efflux) in our study. The same effect was also observed within the growing season, as the proportion of total CH₄ efflux attributable to plant transport was greatest when the total efflux was lowest (at the beginning and end of the growing season). Previous studies at the plant community-scale have also demonstrated that plant communities dominated by species with rapid rate of CH₄ transport also display greater total CH₄ efflux (Morrissey and Livingston 1992; Ding et al. 2005), like the fen and bog sites in our study.

The smaller proportion of the ecosystem-scale CH₄ efflux attributable to plant CH₄ transport in our fen site could be at least partly explained by differences in CH₄ oxidation by methanotrophic microbes. The CH₄ oxidation potential has been reported to follow a Gaussian relationship to the growing season median WT of the microhabitat (optimum of about −3.5 cm) (Larmola et al. 2010). The site-level mean WT at the rather wet bog site studied here (−9 cm, which is also the median) was closer to this optimum than the WT at the fen site (−15 cm, median −16 cm). If the efficiency of CH₄ oxidation would indeed be greater at the bog site, plant-mediated transport of CH₄ past the oxidation zone could compose a larger proportion of ecosystem-scale CH₄ efflux than at the fen site, despite the greater CH₄ concentration in the fen peat (21% and 9% at 50 cm depth at the fen and bog, respectively, means of growing season 2018, Korrensalo et al., unpublished data). Therefore, the result could be different when comparing a dry bog to a wet fen. To confirm this, the contribution of plant transport to the overall CH₄ efflux at the site-level should be quantified at fen and bog sites with variable WT levels. Another explanation for the result could be the positive relationship between aerenchymous plant cover and rhizospheric oxidation (Münchberger et al. 2019), that may counteract the enhancing effect aerenchymous plant transport has on total CH₄ efflux. Further research is needed to find out if there could be an optimum density of aerenchymous plants that maximizes CH₄ emission by enhancing CH₄ transport and increasing CH₄ production through substrate availability, while simultaneously not accelerating rhizospheric oxidation to exceed these processes.

Differences between species in CH₄ transport rate impact ecosystem-scale plant CH₄ transport

Our estimates were within the same range as previous experimental studies that reported the proportions of total CH₄ efflux attributable to plant transport, albeit at the lower end of the previously reported range (Morrissey and Livingston 1992; Whiting and Chanton 1992; Schimel 1995; Kutzbach et al. 2004; Dorodnikov et al. 2011; Knoblauch et al. 2015). However, the clipping of aerenchymous plants that was conducted in some of the previous studies could have led to an overestimation of the proportion of CH₄ efflux attributable to plant transport due to simultaneously modifying substrate availability for methanogenesis through the removal of aboveground plant biomass and modifying CH₄ oxidation in the peat by cutting off the aerenchymous oxygen transport. Our chamber approach carries the potential error sources in LAI estimation, the conversion of LAI to BM, CH₄ transport measurements and the spatial vegetation inventory used in upscaling. The reliability of the combination of the two methods used here is supported by the close compatibility of EC measurements and closed chamber measurements upscaled to the ecosystem-scale in the earlier studies conducted in the same fen (Riutta et al. 2007) and bog (Korrensalo et al. 2018b) sites. Furthermore, opaque chambers used to quantify plant CH₄ transport create the potential bias by excluding light, which in some studies has been found to impact CH₄ efflux, potentially through stomatal closure (Morrissey et al. 1993) and when measuring plants with convective gas transport (Günther et al. 2014), while some studies report no effect of light in *Carex*-dominated surfaces (Günther et al. 2014; Luan and Wu 2014). However, the reliability of our ecosystem level CH₄ transport estimate is supported by the lack of diurnal course in CH₄ efflux in earlier studies from the same sites except a mild diurnal temperature effect (Riutta et al. 2007; Rinne et al. 2018; Knox et al. 2021). Further, within a peatland, light has been mainly reported to impact CH₄ efflux at dry hummock surfaces (Luan and Wu 2014; Mikkilä et al. 1995) that typically have low cover of aerenchymous species. Despite that, stomatal control of CH₄ transport has been suggested to be important only for certain aerenchymous plant species (Schimel et al. 1995), and thus the exclusion of light could potentially impact our CH₄ transport estimates through some individual plant species.

Our study suggests that the differences between plant species in their ability to transport CH₄ could have an impact on the ecosystem-scale CH₄ efflux. We found that the forb *S. palustris* exhibited the greatest contribution to ecosystem-scale plant CH₄ transport in the bog site despite its lesser contribution to ecosystem aerenchymous LAI. Furthermore, our results imply that the transport capacity of aerenchymous species could be a limiting factor for ecosystem-scale CH₄ efflux as the CH₄ transport rate did not vary over the growing season. Increased soil temperature in the middle of the summer stimulates CH₄ production (Dunfield et al. 1993), although a larger fraction of the CH₄ may end up oxidized if the transport capacity of the plants is limited. Ebullition is another transport route that bypasses the oxidation zone and is found to occur most in the middle of the summer, as previously reported at our bog site (Männistö et al. 2019). This could be an indicator of limited plant CH₄ transport, as ebullition is believed to occur when gas bubbles in the peat become sufficiently large in volume and is triggered by changes in air pressure (Tokida et al. 2007; Chen and Slater 2015), a phenomenon unlikely to happen with an effective plant CH₄ transport system.

Current models that describe peatland CH₄ cycling typically consider only the bulk biomass or LAI of aerenchymous plants when estimating the role of plant CH₄ transport at the ecosystem-scale (Wania et al. 2010; Raivonen et al. 2017), although our work suggests that the inclusion of plant CH₄ transport rate is also pivotal. For example, Wania et al. (2010) does not include aerenchymous plants other than sedges in their model due to their small contribution to ecosystem-scale NPP, but as addressed above, certain herbaceous species may contribute significantly to plant CH₄ transport. Neglecting species-specific differences in the CH₄ transport rate in the current process models could lead to both under- and overestimation of the role of plant transport in ecosystem-scale CH₄ efflux, depending on the species composition of the site. Some previous studies have found differences in CH₄ transport capacity between plant functional types, such as sedges and forbs (Ding et al. 2005; Bhullar et al. 2013). In this study, species belonging to the same plant functional type (sedges) displayed a wide variability in their CH₄ transport rates, and previously, even graminoid species of the same family were found to differ in their CH₄ transport

(Kao-Kniffin et al. 2010). The intraspecific variability in CH₄ transport rate observed here could be another potential error source in the models, although a fuller understanding of this variability requires measurements of a selection of plant species at varying site conditions, such as WT and peat CH₄ concentration. Defining separately the transport efficiency and intraspecific variability of all aerenchymous species might be unfeasible, but instead, identifying the traits that correlate with this process might be a better solution from the modeling perspective. Using these traits together with the correlations of CH₄ transport rate to WT and peat CH₄ concentration could be the key to including these species-specific and intraspecific differences in ecosystem-scale CH₄ models.

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Availability of data and material The plant CH₄ transport data associated with the manuscript has been submitted to PANGAEA repository for publication. On request, the data can also be obtained from the corresponding author. The eddy covariance data is available at SmartSMEAR portal (<https://smear.avaa.csc.fi/>). The leaf area data has been published in PANGAEA repository in Korrensalo A, Tuittila E-S, Uljas S (2019): Closed chamber measurements of net ecosystem exchange of CO₂ from Siikaneva bog, Finland. PANGAEA, <https://doi.org/10.1594/PANGAEA.905575>.

Authors' contributions The study was designed by AK and EST. AK was responsible for the field measurements of plant CH₄ transport, data processing and statistical analysis. PA, IM and TV conducted the eddy covariance measurements and processed the data. AK and EST wrote the manuscript with contributions from all other authors.

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Declarations

Conflicts of interest/competing interests The authors declare no conflicts of interest associated with this manuscript.

Code availability The code used to conduct the statistical analysis is available from the corresponding author on request.

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