Small spatial ~~but large sporadic~~ variability in methane emission measured from a wet patterned boreal bog

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Abstract

We measured methane fluxes of a patterned bog situated in Siikaneva in southern Finland from six different plant community types in three growing seasons 2012–2014 using the static chamber method with chamber exposure of 35 minutes. A mixed effects model was applied ~~for~~ to quantify~~ing~~ the effect of the controlling factors on the methane flux.

The plant community types differed from each other in their water level, species composition, total leaf area (LAI_{TOT}) and leaf area of aerenchym~~at~~ous plant species (LAI_{AER}). ~~Excluding the highest 2.5 % of all fluxes,~~ M~~m~~ethane emissions ranged from -309 to ~~556~~ 1254 mg m^{-2} d^{-1}. Although methane fluxes increased with increasing peat temperature, LAI_{TOT} and LAI_{AER}, they had no correlation with water table or with plant community type. The only exception were higher fluxes from hummocks and high lawns than from ~~other plant community types~~high hummocks and bare peat surfaces in 2013 and from bare peat surfaces than from high hummocks in 2014. Chamber fluxes upscaled to ecosystem level for the peak season were of the same magnitude as the fluxes measured with the eddy covariance (EC) technique. In 2012 and in August 2014 there was a good agreement between the two methods, in 2013 and in July 2014, the chamber fluxes were higher than the EC fluxes.

Net fluxes to soil, indicating higher methane oxidation than production, were detected every year and on all community types. ~~Exceptionally high methane emissions up to 17 000 mg m^{-2}d^{-1} were measured sporadically in 2013 and 2014. These extreme emissions not detected in EC measurements we were not able to exclude as measurement errors and they did not correlate~~

~~with any measured variables.~~ Our results underline the importance of both LAI_{AER} and LAI_{TOT} in controlling methane fluxes and indicate need for automatized chambers to reliably capture localized events to support more robust EC method.

Keywords: leaf area index, peatland, peat temperature, plant community type, water table

1 Introduction

Mires or undrained Ppeatlands are wetland ecosystems where partly undecomposed organic material is stored as peat in anoxic conditions under the water ~~level~~table. Therefore, these ecosystems act as important sinks for carbon dioxide (CO_2), but on the other hand, they are also the largest natural source of methane (CH_4), which is a potent climate warming greenhouse gas (IPCC, 2014). Methane flux rate of a peatland ecosystem depends on the balance between microbial methane production and consumption. In peatlands, methane is produced in wet and anoxic conditions below the water table by anaerobic microbes, methanogens (Archaea) (Hanson and Hanson, 1996). It is released from peat to the atmosphere via three transport routes: by diffusion in the peat matrix, through aerenchym~~at~~ous vascular plants and by ebullition from water and bare peat surfaces (LeMer and Roger, 2001; Raghoebarsing et al., 2005). The consumption of methane is partly regulated by the proportions of these three routes. If the surface of peatland is not water-saturated, a part of the diffusing methane is oxidized in the upper aerobic peat layer or within *Sphagnum* mosses by methanotrophic bacteria (Hanson and Hanson, 1996; LeMer and Roger, 2001; Larmola et al., 2010), while the methane transported by plants (Bhullar et al., 2013) or bubbles is emitted directly to the atmosphere. Although large part of methane can be oxidized also in plants, such as rice (Bosse and Rudolph, 1997), so far significant methane oxidation has not been detected in bog plants, such as *Eriophorum angustifolium* and *E. vaginatum* (Frenzel and Rudolph, 1998). The processes of methane production, consumption and transport are affected by several environmental and ecological factors, such as water table (Dise et al., 1993), temperature (Dunfield et al., 1993), pH (Dunfield et al., 1993; Dedysh, 2002), quality and quantity of available substrate (Ström et al., 2003) as well as vegetation type and productivity (Bubier, 1995; Waddington et al., 1996; Joabsson et al., 1999). Current models of global methane budget are still uncertain due to limited knowledge of the relative contribution of different environmental factors controlling

65   methane fluxes (Riley et al., 2011). The largest source of uncertainty is the quantity of methane emissions from natural wetlands, such as peatlands (Riley et al., 2011; Melton et al., 2013).

Peatland ecology is strongly controlled by typically high water level and its spatial variation (Rydin and Jeglum, 2013). Importantly, water table determines the thickness of anaerobic and aerobic layers in peat, which may vary spatially within a peatland leading to different surface
70   types along the water table position gradient. Bogs are peatland ecosystems receiving nutrients only through atmospheric deposition, and typically characterized by strong spatial variation in water table. This results from pronounced microtopography varying from open pools and wet bare peat surfaces and hollows to intermediate lawns and drier and higher hummocks. Just as the thickness of aerobic peat layer differs between the surface types, the species composition
75   of plant community types varies (Kotiaho et al., 2013). Sedges with aerenchymatous tissue in their stems and roots, that allows transportation of oxygen to their roots, grow on the water-saturated surface types. Shrubs that lack aerenchymatous tissue, grow on higher surfaces with thicker aerobic layer. Together with plant community composition and environmental conditions, methane dynamics vary along the water table gradient as the amount of methane
80   transporting vegetation and the thickness of methane consuming aerobic layer change. It is generally considered that, the wetter the surface, the higher the methane emission (e.g. Bubier et al., 2005). However, recent studies based on spatial (Turetsky et al., 2014) and temporal variation (Rinne et al., 2017) indicate maximum fluxes at intermediate water table positions. Vegetation has recently been included in the process models as a controlling factor of methane
85   fluxes from peatlands (Li et al., 2016; Raivonen et al., 2017). However, these models do not yet take into account the impact of its spatial heterogeneity on methane fluxes.

Although there exists a wealth of studies that quantify methane emissions from different peatlands (reviewed by Turetsky et al., 2014; Wilson et al., 2016), most studies have been focused on fens that receive additional nutrients from the surrounding mineral soil, and support
90   higher amount of aerenchymatous vegetation compared to bogs (Turetsky et al., 2014). Studies on the spatial variation of methane emissions in bogs with varying plant community types are scarce (see however Waddington and Roulet 1996; Frenzel and Karofeld, 2000, Laine et al., 2007). Climate change is expected to alter water table and consequently the abundance of different plant community types in peatlands, leading to changes in ecosystem functions.
95   During the last decade, atmospheric methane concentration has shown an increasingly strong rise, and although the underlying reasons remain poorly understood (Kirschke et al., 2013) this increase has been associated with the microbially produced methane (Nisbet et al., 2016). As

atmospheric methane accelerates the global warming, it is crucial to be able to understand and model the carbon dynamics of peatlands, which are the largest natural source of methane and contain approximately one third of global soil carbon stock (Turunen 2002; Yu 2011). Better understanding on the microtopographical variation in the methane fluxes and their controlling factors enables better prediction of the effects of climate change on methane emissions from peatlands in the future.

In this study, we aimed to quantify spatial variation in methane fluxes and their controlling factors in a patterned boreal bog. We measured methane emissions in six different plant community types during three subsequent growing seasons. We compared methane flux, water table, peat temperature and leaf area of all vegetation (total LAI) and aerenchymatous vegetation (aerenchymatous LAI) between the plant community types for three growing seasons. Mixed effect model was used for quantifying the effect of the controlling factors on the methane flux. Fluxes measured with chambers were compared with methane flux measured with eddy covariance (EC) technique. We hypothesized that the plant community types differ in terms of environmental controls and, consequently, in their methane emissions. We expected wetter plant community types with aerenchymatous plant species to release more methane than drier plant community types.

2 Materials and methods

2.1 Study site

The study was conducted in the bog site of the oligotrophic peatland complex Siikaneva situated in southern Finland (61°50'N, 24°12'E), 160 m a.s.l., within the southern boreal vegetation zone (Ahti et al., 1968). The Siikaneva bog site is located 1.3 km north-west from Siikaneva fen site, studied before by e.g. Aurela et al. (2007), Rinne et al. (2007) and Riutta et al. (2007). According to the 30-year averages from the Juupajoki-Hyytiälä weather station that is located 6.3 km east from the bog site, annual rainfall of the area is 707 mm, the annual cumulative temperature is 1318 degree days, the average annual temperature is 4.2 °C and the average temperatures in January and July are -7.2 °C and 17.1 °C. The bog site has a well-pronounced microtopography represented by open water pondspools, bare peat surfaces, hollows and higher and drier lawns and hummocks. The vegetation is dominated by *Sphagnum* mosses, except in the ponds and bare peat surfaces. *Sphagnum fuscum* and *S. rubellum* grow

130   on hummocks, where vascular plant vegetation is dominated by dwarf shrubs, such as *Andromeda polifolia*, *Calluna vulgaris* and *Empetrum nigrum*. *E. vaginatum* is also found on hummocks and it is common on lawns, where the moss layer is dominated by *Sphagnum magellanicum* and *S. rubellum*. *Sphagnum cuspidatum* and *S. majus*, in turn, are dominating wet hollows together with *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris*. *R.*
135   *alba* is often the only plant growing in the bare peat surfaces.

2.2 Sampling

To cover the spatial variation in vegetation and environmental conditions, sample plots were established to represent six different plant community types or bog microforms characteristic
140   to the site: high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and bare peat surfaces (BP). They were placed within the study site in three clusters of six plots each (18 sample plots in total).

The static chamber method (Alm et al., 2007) was used to measure the methane fluxes from the sample plots. Stainless steel collars of size 60 x 60 cm (surface area 3600 cm^2) were
145   installed around each plot for the measurements. The depth of the collars varied from 10 cm to 30 cm; the deepest ones in sample plots with deepest water table. In order to minimize the peat disturbance during the measurements, boardwalks supported by stilts driven to mineral soil underneath the peat were built next to the sample plots. During each measurement, an opaque aluminum chamber was placed in the groove on top of the collar, and water was poured into
150   the groove to make it airtight during the measurement. The chamber was then sealed with a rubber plug having a 1 mm diameter plastic tube with a three-way stopcock attached to it. A fan inside the chamber was used to mix the air in the chamber headspace. Four air samples of 20 ml were taken with a syringe from the headspace of the chamber at 5, 15, 25 and 35 minutes after the chamber was closed. The samples were placed in glass vials and kept in cold and dark
155   until their methane concentration was analyzed with an Agilent Technologies 7890A gas chromatograph and Gilson GX-271 liquid handler. Air temperature inside the chamber as well as peat temperatures at the moss surface and at the depths of 5 cm, 15 cm and 30 cm were measured during each methane measurement. Water level of the sample plot was measured relative to moss surface from a plastic tube installed into peat next to each sample plot. Each
160   tube had holes on their sides enabling water to settle inside them.

The chamber measurements were conducted seven times in 2012 (from 26 June to 16 October), nine times in 2013 (from 21 May to 9 September) and 16 times in 2014 (from 7 April to 24 September) over the growing season.

Methane flux during each measurement was calculated as the linear change in methane concentration in relation to time and taking into account the volume of and temperature in the chamber. Non-linear changes in methane concentration were considered to result from ebullition or leak in the chamber and excluded. In total, 10.4 % of the measurements were excluded as outliers. The resulting dataset consisted of 516 measurements in total.

2.3 Leaf area index

Leaf area of each sample plot was measured over the growing season following Wilson et al. (2007). An estimate for an average number of leaves per m^2 area for each vascular plant species was taken from leaf count conducted every third week from five sub-sample plots (8 x 8 cm) within each sample plot. For leaf size, samples of corresponding species were taken around the study site on each leaf area measurement day and the leaf area of each species was measured with a scanner. Leaf area index of all the vascular plant species (LAI_{TOT}) was then calculated by multiplying average leaf size with leaf number. Leaf area index of aerenchymatous plants (LAI_{AER}) for each sample plot was calculated based on the leaf area of the five aerenchymatous species growing on the site, *Carex limosa*, *Eriophorum vaginatum*, *Rhynchospora alba*, *Scheuchzeria palustris* and *Trichophorum cespitosum*.

2.4 Eddy covariance measurements

Eddy-covariance (EC) measurements were conducted at the site in 2012-2014, providing an independent ecosystem-scale estimate of CH_4 fluxes. The EC setup included an ultrasonic anemometer (USA-1, METEK GmbH, Germany) and an open-path CH_4 concentration analyzer (LI-7700, LI-COR Biosciences, USA). The measurement height was 2.4 m above the peat surface. EddyUH software was used to process the raw data and produce the 30 min average fluxes of latent heat, sensible heat and CH_4 (Mammarella et al., 2015). Standard EC data quality control (e.g., Aubinet et al., 2012) was performed by the software or manually; the EC flux data during calm periods (friction velocity $u_* < 0.1$ m s^{-1}) was excluded from the analysis.

The EC flux series missed a large fraction of data (65%) due to technical problems, flux quality filtering, or periods with insufficient turbulence. Therefore, gap-filling was necessary, which was done in the following way. First, a function was fit to all three years of data,

195     $$F_{CH_4mod} = a \cdot \exp(b \cdot T_{p20})$$ Eq. (1)

where F_{CH4mod} is the flux model (μmol m^{-2} s^{-1}) a and b the empirical parameters, and T_{p20} (°C) is the peat temperature at a 20 cm depth. T_{p20} was gapfilled with the equivalent data from the nearby fen station or using linear interpolation, and spline-smoothed to eliminate diurnal-scale variability. From that general fit, we established that b=0.167 (95% CI [0.163, 0.170]). Next,

200   a was determined for each year individually by fitting Eq. (1), now with b fixed at 0.167. This yielded a = [0.0049, 0.0056, 0.0062] for 2012, 2013 and 2014, respectively. The CH$_4$ flux model was then calculated using Eq. (1) and used to fill the gaps in the observed EC CH$_4$ flux.

2.5 Analyses

205   ~~Some sporadic, extremely high methane emissions were found in the data even after quality control. The measurements with extremely high emissions showed linearity of concentration change during chamber closure, and thus they could not be excluded as measurement errors or very infrequent large bubbles. The extreme emissions were not normally distributed, and, for that reason, the data were divided into two datasets: with and without these extreme emissions,~~

210   ~~the latter being used in statistical analysis. Based on 95 % confidence limits around the median, the group of extreme emissions consisted of the highest 2.5 % of all fluxes (altogether 13 values). The lowest 2.5 % of all fluxes were negative fluxes showing methane oxidation that had no valid reason to be excluded from statistical analysis. Therefore, only the highest 2.5 % of all fluxes were excluded leaving 97.5 % of measurements in the "normal" flux dataset. The~~

215   ~~resulting line between "normal" and extremely high emissions was between fluxes of 556 and 592 mg m^{-2}d^{-1}. In order to study the effect of air pressure on the extreme emissions, variation in air pressure (hPa) on the methane measurement days was calculated as the difference between the highest and the lowest air pressure values of each day. Graphical evaluation was then used to see whether the air pressure was decreasing or increasing on each day.~~

220   To address spatial variability, we used linear mixed-effects models to test whether the measured environmental variables (water table, LAI$_{TOT}$, LAI$_{AER}$ and peat temperature) differed between plant community types or years. These models were constructed with the whole

dataset, and each environmental variable was explained by potential fixed predictors of year and surface type as well as their interaction and by the random effects of measurement plot and plot cluster. To test, whether the seasonal pattern of the environmental variables differed among the plant community types, the models were then constructed separately for each year with potential fixed predictors of measurement day, plant community type and their interaction and with random effect of measurement plot cluster. Variation in methane flux was analyzed ~~with the "normal" dataset~~ by adding potential fixed predictors plant community type, year and their interaction, peat temperature at different depths, air temperature, LAI$_{TOT}$, LAI$_{AER}$ and water table to the model one by one. AIC-value (Akaike information criterion) and conditional F-test were used to evaluate whether an addition of a fixed predictor resulted in a significantly better model than the simpler one. Peat ~~As peat~~ temperature can be expected to have a nonlinear effect on methane flux, and ~~we~~ therefore we mimicked the ~~often used~~often-used exponential relation of methane flux to temperature by assumed ~~added it first as a linear and then as a second degree polynomial fixed predictor. In the third option,~~ peat temperature effect ~~was~~ first to be assumed constant until 10 °C degrees and then follow second degree polynomial ~~onwards~~. The 10 °C degrees' threshold was selected based on visual inspection. According to AIC-value ~~We then tested, which~~ this response shape explained the variation in the data better than a liner form. We tested also, which of the three peat temperature variables with the selected response form explained the variation in methane fluxes better. The measurement plot and plot cluster were included as random effects in all of the models. The data was analyzed with the function lme of the package nlme of R software (version 3.3.2). The residuals were normally distributed around mean of zero in all of the models. The fixed part of the model are reported in Appendix.

3 Results

3.1 Variation in environmental variables

Year 2012 was the coolest, ~~and~~ wettest and cloudiest of the three years studied, whereas year 2013 was the warmest. Year 2014 was intermediate in temperature and irradiation, but the driest of the three years (Table 1).

~~with temperature sum of the growing season 1172 degree days and annual rainfall 907 mm. Year 2013 was the warmest with temperature sum 1408 degree days and intermediate annual rainfall 615 mm, whereas 2014 was driest year with annual rainfall 579 and intermediate temperature sum 1349 degree days. Consistently, the cool and wet year 2012 was the cloudiest~~

255 ~~with cumulative photosynthetically active radiation (PAR) 68 296 µmol m⁻², while the warmest~~ ~~year 2013 was also the brightest with PAR 72 946 µmol m⁻². PAR of the driest year 2014 was~~ ~~70 800 µmol m⁻², respectively.~~

Reflecting our sampling strategy, there was a clear water table position gradient among the six plant community types that water tables (WT) divided into three statistically different groups 260 (degrees of freedom (DF)=5, 10; p<0.0001) (Fig 1). 1) High hummocks had the lowest WT, with the mean -25 cm, followed by 2) hummocks and high lawns, with mean the WT of -12 cm. 3) Lawns, hollows and bare peat surfaces had the highest WT with means close to the soil surface (Fig 1). The WT gradient was similar during all the three years, but the overall WT differed between the years. The year 2012 with the highest precipitation had a significantly 265 higher WT than 2013 or 2014 (Fig 1). The warmest year 2013 with intermediate precipitation and the lowest WT did not differ significantly from the year 2014 with the lowest precipitation and intermediate WT. There were no differences between the plant community types in the rhythm of the WT over the growing seasons.

LAI_{TOT} varied between the six plant community types (DF=5, 10; p<0.0001) (Fig. 1) forming 270 four groups. LAI_{TOT} was 1) highest on high hummocks, followed by 2) hummocks and high lawns, 3) hollows and 4) lawns and bare peat surfaces. The differences between the plant community types stayed similar over the three years. The summer maximum of LAI_{TOT} was lowest in the coolest and wettest year 2012 and highest in the warmest year 2013 (Fig. 1).

LAI_{AER} also varied between the six plant community types (DF=5, 10; p=0.0060) forming four 275 groups (Fig. 1). In contrast to LAI_{TOT}, 1) hollows had the highest LAI_{AER}. 2) High lawns and lawns had slightly higher LAI_{AER} than 3) bare peat surfaces, while 4) high hummocks and hummocks had the lowest LAI_{AER}. LAI_{AER} differed significantly between years (DF=2, 402; p<0.0001) (Fig 1). All the six plant community types had the highest LAI_{AER} in the warmest year 2013 and lowest LAI_{AER} in the coolest and wettest year 2012. Similar to LAI_{TOT}, the 280 differences between the plant community types were similar in each year.

~~In general, the p~~Peat temperature did not differ between the plant community types in the warmest year 2013. In t~~T~~he coolest and wettest year 2012~~, was an exception, as in that year~~ hollows and bare peat surfaces were significantly warmer than the other types (HO: 1.38 ± 0.33, DF=98, p=0.0001 and BP: 0.85 ± 0.32, DF=98, p=0.009). In the driest year 2014, bare 285 peat surfaces were significantly warmer than hummocks (0.61 ±0.31, DF=235, p=0.0485) and high lawns (0.77 ±0.31, DF=235, p=0.0154). Similarly to air temperature, the three years had

significantly different peat temperatures (DF=2, 483; p<0.0001) with the means of 14.1 °C, 16.5 °C and 12.6 °C in 2012, 2013 and 2014.

3.2. Variation in methane fluxes

Methane fluxes measured with chambers after exclusion of the sporadic extreme fluxes ranged from -90 to 387 mg m^{-2}d^{-1}, from -87 to ~~481~~ 1254 mg m^{-2}d^{-1} and from -309 to ~~556~~ 910 mg m^{-2}d^{-1} in 2012, 2013 and 2014, respectively (Fig 2). ~~Apart from the sporadically extreme fluxes,~~ ~~M~~methane fluxes were each year generally higher in the middle of the growing season than in spring or in autumn (Fig 3).

The variation in the ~~"~~normal~~"~~ methane fluxes ~~(the fluxes excluding 13 of the highest fluxes)~~ did not show any clear pattern between the plant community types (Fig. 2) and the classification did not explain the variation in the methane fluxes when plant community type was first used in the model as the only explanatory variable. The model where plant community type, year and their interaction were used as explanatory variables indicated a significant difference between the years, but contrary to expectations, no spatial variation related to plant community types common for the three growing seasons was found. However, a significant interaction term between the plant community type and year was detected (DF=10, ~~473~~483; p=0.0~~004~~004282), as there were higher methane fluxes from ~~hummocks~~ hummocks and high lawns than from ~~the other plant community types~~high hummocks and bare peat surfaces in 2013, as well as higher fluxes from bare peat surfaces than from high hummocks in 2014. This result in 2013 was surprising, but the differences between the plant community types are small.

Methane emission increased with increasing peat temperature. ~~As the measured peat temperature response of methane flux was not linear nor exponential, three different response forms were tested to find the best fitting model. Peat temperature response of methane flux where the response was assumed constant until 10 °C degrees and second degree polynomial onwards appeared to be superior over the other response forms tested to capture the measured pattern.~~ The peat temperature at the depth of 5 cm explained the variation in methane fluxes better than temperature in the depths of 15 and 30 cm. After the peat temperature in the depth of 5 cm was included in the model, the two other peat temperature variables and the chamber temperature made no effect on prediction. Methane flux was found to increase linearly with aerenchym~~at~~ous LAI, but also with the total LAI, even after the aerenchym~~at~~ous LAI was included in the model (Fig 4). WT did not explain variation in methane fluxes, as was found in

residual inspection and from the finding that WT was not able to improve the model. Therefore,
320 WT was not included as a fixed predictor in the final model (Table 1). Standard deviation of the constant for the random effect 'plot' was 3.50.05. For the random effect 'plot cluster', standard deviation of the constant was 30.836.44 and standard deviation of residuals was 69.895.63 showing that the variation between clusters was smaller than the variation within clusters.

325 Although Siikaneva bog is a wet site with a high WT (see e.g. Moore et al., 2011) (Fig 1), negative flux values, i.e. higher methane oxidation than production resulting in net fluxes from the atmosphere towards ecosystem were detected every year across the WT gradient. In 2013, negative fluxes were measured only on high hummocks, whereas in the other years those occurred on all the plant community types, except on lawns (Fig 2). Fluxes from the atmosphere
330 to the soil ranged from ca. 4 to 309 mg m^{-2} d^{-1} (Fig 2). The highest net methane oxidation fluxes towards the soil rates were measured on bare peat surfaces in 2014 (185 and 309 mg m^{-2} d^{-1}).

Exceptionally high methane fluxes, up to 17 000 mg m^{-2} d^{-1}, were observed sporadically throughout the growing season 2013 and twice from bare peat surfaces in 2014 (590 mg m^{-2} d^{-1} and 910 mg m^{-2} d^{-1}, respectively) (Fig 3). In 2013, high fluxes were measured from all plant
335 community types except from hummocks. Fluxes over 1000 mg m^{-2} d^{-1} were observed only in 2013. However, they were not detected among the ecosystem level flux measured with EC technique on the same days. The high fluxes did not correlate with WT, LAI$_{TOT}$, LAI$_{AER}$ or peat temperature. Furthermore, changes in air pressure during the measurement day could not explain the extremely high fluxes.

340 As the chamber measurement periods differed between the years, we compared the warmest period with highest fluxes, namely July and August, on an ecosystem level. As the measured fluxes were similar between the different plant community types, methane flux was interpolated to ecosystem level flux as a mean of all the 18 sample plots. The extreme methane fluxes (the highest 13 values) were excluded from the upscaling of the emissions in 2013 and
345 2014 as they were random and sporadic events. The upscaled monthly methane emissions for the whole ecosystem in July and August were 1.79 and 2.58 g m^{-2} mo^{-1} in 2012, 5.44.9 and 3.17 g m^{-2} mo^{-1} in 2013 and 4.9 and 3.59 g m^{-2} mo^{-1} in 2014. Cumulative EC methane fluxes for July and August amounted to 2.3 and 2.8 g m^{-2} mo^{-1} in 2012, 2.9 and 2.5 g m^{-2} mo^{-1} in 2013, and 3.4 and 3.7 g m^{-2} mo^{-1} in 2014, respectively. Methane emission peaks seen in EC fluxes
350 over the three growing seasons were also found in upscaled chamber fluxes (Fig 5). The

ecosystem level fluxes followed the seasonal pattern of peat temperature and LAI increasing in spring, having the highest peak the middle of summer and decreasing towards autumn (Fig 5).

355 **4 Discussion**

The ~~"normal"~~ methane fluxes measured in this study ~~that exclude 2.5 % of the highest measured fluxes,~~ ranged from -309 to ~~556~~ 1254 mg m^{-2} d^{-1}. When ~~also~~ the lowest and the highest 2.5 % of all the fluxes are excluded, the methane fluxes (95 % CI around the median) measured in this study range from -7 to ~~556~~ 387 mg m^{-2} d^{-1}. They are, on average, of same magnitude as
360 methane fluxes reported in previous studies of bog ecosystems (Crill et al., 1988, Waddington and Roulet, 1996, MacDonald et al., 1998, Laine et al., 2007). Turetsky et al. (2014) presented the mean methane flux of 15 bog sites as 96 $\pm$ 6 mg m^{-2} d^{-1}, which is a little higher than the mean fluxes in 2012 and 2014 (57 $\pm$6 and 7~~7~~2 $\pm$ 76 mg m^{-2} d^{-1}) but lower than the mean flux in the warmest year 2013 (1~~31~~22 $\pm$ 129 mg m^{-2} d^{-1}) in this study. Similarly, another review
365 (Wilson et al., 2016) that included wintertime fluxes calculated lower mean methane flux for boreal nutrient poor sites, 4 100 mg m^{-2} yr^{-1} with 95 % CI from 50 to 24 600 mg m^{-2} yr^{-1}.

Contrary to our hypothesis, the measured methane fluxes showed very little spatial variation in a highly heterogenous environment. We expected to find higher methane fluxes from wetter plant community types that have more aerenchym~~at~~ous vegetation, as high WT reduces the
370 thickness of aerobic peat layer and consequently methane consumption, while transport through aerenchym~~at~~ous plants facilitates methane emission from peat to the atmosphere. However, even though the plant community types differed in their WT, LAI$_{TOT}$ and LAI$_{AER}$, they generally had similar methane fluxes. This observation holds for each of the three growing seasons studied, which indicates that the spatial homogeneity of methane fluxes is not an
375 artifact but a characteristic property of the studied bog. The same site has been previously shown to have also spatially homogeneous biomass production and net ecosystem exchange rates, except on bare peat surfaces with little vegetation (Karofeld, 2004; Korrensalo, 2017). We found only small spatial variation, as hummocks and high lawns had higher methane flux than high hummocks and bare peat surfaces in 2013, and bare peat surfaces had higher methane
380 flux than high hummocks in 2014 ~~than the other plant community types~~. This result found in 2013 was opposite to previous studies that have found lower methane flux from hummocks than from hollows and lawns (Bubier et al., 1993, Waddington and Roulet, 1996, Saarnio et

al., 1997, MacDonald et al., 1998, Frenzel and Karofeld, 2000, Laine et al., 2007). Correspondingly, it is likely that the similarity of the methane fluxes between the plant community types results from underlying microbial processes of methane production and consumption. Methane oxidation partly regulates methane emissions, as potential methane oxidation is usually greater than potential methane production (Segers, 1998). Juottonen et al. (2015) showed that both methane producing and consuming microbe communities may have strong variation depending on site in boreal bogs. In addition, the effect of plant community type on activity of the microbe communities is not consistent and varies between bogs (Juottonen et al., 2015). Studying the microbial communities and their methane production and oxidation potentials in Siikaneva bog would be the next step to understand why methane fluxes are so similar over the different plant community types in the site. This could also clarify, to what extent the high negative net fluxes are explained by microbial methane oxidation.

As commonly found for biological processes, measured methane emissions increased with increasing peat temperature, similarly to previous studies (Kettunen et al., 1996, Daulat and Clymo, 1998, Frenzel and Karofeld, 2000; Laine et al., 2007). As temperature aeffects the activity of the methane producing microbes, rising temperature increases methane production until reaching the temperature optimum of the microbes around 20–30 °C (Dunfield et al., 1993). Increasing temperature may also enhance the methane transport through aerenchymatous plants (Große, 1996). For example, plant conductance for methane has been shown to correlate positively with soil temperature at the depth of 5 cm in rice plants (Hosono and Nouchi, 1997). As global warming will increase peat temperatures and prolong the growing season in boreal peatlands, more methane can be emitted through aerenchymatous plants. Methane producing microbial activity may also increase as long as there are anoxic conditions and available substrates. However, in boreal climates warming is predicted to lower the WT leading to thicker aerobic peat, which enables potentially creates a higher methane consumption rate layer (Yrjälä et al., 2011). Thus, changes in WT may compensate the effect of rising temperature under a warmer climate.

As expected, methane flux increased with higher LAI_{AER}. Plants with aerenchymatous tissues facilitate methane emissions by serving as conduits for methane from peat to the atmosphere that avoids the methane oxidation in aerobic peat layer. Frenzel and Karofeld (2000) measured highest methane fluxes from plots with *E. vaginatum* and *S. palustris* and showed that methane emission ceased when *S. palustris* was clipped below the WT. Interestingly, we found that methane flux increased also with LAI_{TOT}, even when LAI_{AER} was already taken into account.

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The effect of ~~LAI_AER~~ LAI_{TOT} on methane flux was ~~twice~~ about one third ~~as high~~higher ~~as~~ than the effect of ~~LAI_TOT~~LAI_{AER}. Previously, Marushchak et al. (2016) have found a positive correlation between LAI of vascular plants and methane emissions that explained most of the differences in methane fluxes among the fens and willow stands they measured. The positive

420   effect of LAI_{TOT} on methane flux can be explained by that it provides organic substrate for methanogenesis (Chanton et al., 1995). Although higher and drier plant community types had lower LAI_{AER} compared to wet plant community types, they had higher LAI_{TOT} that provides more substrate material than some wetter plant community types. This can partly explain our result that methane fluxes from drier plant community types were similar to the fluxes

425   measured from wetter plant community type. ~~Moreover, Korrensalo (2017) showed that biomass production rates on the same bog site are similar among the plant community types, except on bare peat surfaces that produce very little biomass~~ Karofeld 2004? ~~This can also partly explain our result, as methane emission has a positive correlation with primary production (Whiting and Chanton, 1993; Rinne et al., 2017).~~

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Both LAI_{TOT} and LAI_{AER} increased in the beginning of the growing season before reaching the maximum around July and subsequent decrease. A similar pattern could be seen in the measured methane fluxes that were generally higher in the middle of the growing season and had their peak around late July. This indicates that methane fluxes have a seasonal variation

435   following LAI_{TOT} and LAI_{AER}. As climate change is predicted to alter WT in peatlands, also their vegetation composition will change, potentially affecting the methane dynamics. Decreasing WT and increasing thickness of aerobic peat layer will enable non-aerenchym~~at~~ous plant species, such as shrubs, to grow on previously wetter sites. Because plant-mediated methane transport forms a significant part of the total methane flux (Bhullar et al., 2013), the

440   flux rate can be straightly affected by a change in the abundance of aerenchym~~at~~ous plant species. At the same time, a longer growing season and increasing primary production and substrate availability are able to increase methane emission. Our results show that it is important to take into account both LAI_{TOT} and LAI_{AER} in future models of peatland methane dynamics.

445   Negative fluxes, i.e., net fluxes from the atmosphere to soil ~~showing that net methane oxidation~~ took place on both dry and wet plant community types, and the highest fluxes towards ecosystem were in fact measured from bare peat surfaces. In 2013, negative net ~~methane~~

~~oxidation~~flux was measured twice from one sample plot on a high hummock. This high hummock was the only sample plot that showed negative net ~~methane oxidation~~fluxes each year. In 2012, negative fluxes were recorded from all plant community types except high lawns and lawns, and in 2013 from all plant community types but lawns, respectively. Generally, negative fluxes have been associated with higher methane oxidation by methanotrophic microbes than methane production by archea. Since methanotrophic microbes are aerobic, methane oxidation capacity is higher in drier plant community types that have a thicker aerobic peat layer (Sundh et al., 1995). This is typical for hummocks that can even serve as a sink for atmospheric methane (Frenzel and Karofeld, 2000). Methane oxidation activity is usually the highest near average WT, where methanotrophs have an optimal availability of both methane and oxygen (Sundh et al., 1995; Dedysh, 2002). Therefore, methane consumption takes place also in wetter plant community types that have WT close to the soil surface when they are not waterlogged. In this study, hollows and bare peat surfaces had WT mainly below the soil surface at the time they showed negative net ~~methane oxidation~~fluxes. For example, the two highest negative fluxes (-309 and -185 mg m^{-2} d^{-1}) were measured from the same bare peat surface of the first plot cluster in spring 2014, while its WT was below the soil surface and partly frozen. These fluxes are high compared to the highest negative fluxes measured previously from a boreal peatland (-48.5 mg m^{-2} d^{-1}), from a bog ecosystem (-19.5 mg m^{-2} d^{-1}), from drying peatlands (-15.7 mg m^{-2} d^{-1}) (Turetsky et al., 2014) and from mineral soil (ca. -4 mg m^{-2} d^{-1}) (Smith et al., 2000). Negative nett fluxes ~~methane oxidation was~~were also measured twice on waterlogged plant community types (HO and BP). This could be explained by plants with aerenchym~~at~~ous tissues that are typical for these community types and can transport oxygen to their rhizosphere enabling methane consumption. It is also possible that part of the methane oxidation has been anaerobic (Smemo and Yavitt, 2007).

~~Exceptionally high positive methane fluxes were measured from all the plant community types except from hummocks. These extremely high fluxes were sporadic and they did not correlate with WT, LAI_TOT, LAI_AER or peat temperature. The highest methane flux reported in the review article of Turetsky et al. (2014) from a bog or any peatland ecosystem is 5722.3 mg m^{-2} d^{-1}, which is higher than the two high fluxes that we measured in 2014. However, our highest eight fluxes measured in 2013 exceed that ranging from 5914 up to 17 224 mg m^{-2} d^{-1}. Despite the high rate of these fluxes, they were not detected by the EC technique that was used to measure ecosystem level methane flux rate on the same days. Changes in atmospheric pressure can cause rapid changes in methane flux rate, as falling atmospheric pressure can trigger methane~~

ebullition (Tokida et al., 2007). Although the apparent random large bubbles were excluded from the data, the magnitude of the high fluxes indicates that there is some sort of continuous background ebullition. We compared the measured methane fluxes against the change in air pressure on the measurement day but found no relation between them. Decrease in air pressure ranged from 2 to 6 hPa on the measurement days of high fluxes, and as the chamber closure lasted only 35 minutes, there was no rapid fall in air pressure during the measurement. Furthermore, some high fluxes were measured also when air pressure was increasing. While we are unable to explain these high fluxes, the fact that such fluxes were not detected in 2012 and that they were more common in 2013 than in 2014 suggests that there are significant annual differences in methane controlling factors in peatlands. Thus, long-term studies are important in order to detect inter-annual variation in methane dynamics. Automatic chambers would be needed to reveal the commonness of these abnormalities in measured fluxes that the EC technique was not able to capture.

Methane fluxes measured with the chamber technique (chamber fluxes) and upscaled to an ecosystem level for July and August were of the same magnitude as the corresponding monthly fluxes measured with the EC technique (EC fluxes). In the studied bog site, the source area (footprint) of EC measurements includes open pools and thus, the EC flux includes methane emitted via ebullition that is excluded from the chamber measurements. Therefore, the EC flux would be expected to be higher than the upscaled chamber flux. However, this was rarely the case, and chamber fluxes were occasionally higher than the EC fluxes. The monthly chamber fluxes agreed well with the EC fluxes in 2012. Both methods showed higher fluxes in August than in July. In 2013, upscaled chamber fluxes were higher than EC fluxes in both months, even as the extremely high methane fluxes were excluded from the upscaling. The upscaled chamber flux was much higher in July than in August, while the EC flux in July was only slightly higher than the EC flux in August. In 2014, the upscaled chamber flux was much higher than the EC flux in July but agreed well with it in August. The chamber flux was higher in July than in August, whereas the EC flux was little higher in August than in July. Higher chamber flux than EC flux could be explained by shifting of the EC footprint as it is affected by many factors, such as wind direction (Kormann and Meixner, 2001). While chamber measurements are always conducted on the same fixed sample plots, EC measurement footprint changes and thus its area of open pools that do not have vegetation serving as conduit for methane varies also. Overall, upscaling the chamber fluxes to ecosystem level appeared to be successful as it showed the same methane emission peaks that were detected with EC measurements over the

three growing seasons. This was seen even in 2012 when only few chamber measurement campaigns were conducted. In the future, regular measurements with automatic chambers through the growing season would make the upscaling of chamber fluxes more accurate and improve the comparison of the two methods as well as reveal the commonness of abnormalities measured only with chambers.

Conclusions

Highly different plant community types had generally similar methane flux rates over the three studied growing seasons. Methane fluxes increased with increasing peat temperature, LAI_{TOT} and LAI_{AER}, but were not affected by WT. Therefore, while the relation to LAI_{AER} shows the importance of plant-mediated methane transport from soil to the atmosphere, LAI_{TOT} further explains the methane flux rates, likely by indicating substrate availability for methanogenesis. However, LAI_{AER} and LAI_{TOT} explain only partly the lack of spatial variation in methane fluxes in the studied bog, which likely results from underlying microbial processes. We also found that negative net ~~methane oxidation~~fluxes took place occasionally every year and it was detected on both dry and wet plant community types. As both methane producing and oxidizing microbe communities have been shown to vary depending on the bog, studies of the microbial communities and their methane production and oxidation potentials in Siikaneva bog are needed to fully understand the methane dynamics of the site. ~~Furthermore, we report exceptionally high methane fluxes that were measured sporadically in 2013 and 2014 but not in 2012. These high fluxes remain unexplained, as they did not correlate with WT, peat temperature, LAI~~$_{TOT}$~~, LAI~~$_{AER}$~~ or changes in air pressure. Therefore, more long term studies with frequent sampling are required to detect and explain inter annual variation in methane fluxes from boreal peatlands.~~ Finally, the chamber fluxes were upscaled to ecosystem level and compared to the fluxes measured with EC technique. Upscaling appeared to be successful as the chamber fluxes and the EC fluxes were of the same magnitude, and as the same methane emission peaks could be seen in both fluxes in each growing season. However, upscaled chamber fluxes were often higher than EC fluxes, although they do not include methane ebullition from open pools as EC fluxes do. Regular measurements with automatic chambers would help to explain the differences and improve the comparison of the two methods in the future.

Data availability

Data is available upon request from the corresponding author.

Author contribution

EST came up with the idea and design. AK conducted the chamber measurements and processed the chamber and LAI data. Eddy covariance data was collected and analyzed by PA, TV, IM and JR. AK and EM fitted the mixed-effects models. The manuscript was written by EM, AK and EST and commented by all the other authors.

Competing interests

The authors declare that they have no conflict of interest.

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References

Ahti, T., Hämet-Ahti, L. and Jalas, J.: Vegetation zones and their sections in northwestern Europe, Ann. Bot. Fenn., 5, 169–211, 1968.

Alm, J., Shurpali, N. J., Tuittila, E-S., Laurila, T., Maljanen, M., Saarnio, S. and Minkkinen, K.: Methods for determining emission factors for the use of peat and peatlands –flux measurements and modelling, Boreal Environ. Res., 12, 85–100, 2007.

Aurela, M., Riutta, T., Laurila, T., Tuovinen, J-P., Vesala, T., Tuittila, E-S., Rinne, J., Haapanala, S. and Laine, J.: CO_2 exchange of a sedge fen in southern Finland –the impact of a drought period, Tellus, 59B, 826–837, 2007.

Bhullar, G. S., Edwards, P. E. and Venteriink, H. O.: Variation in the plant-mediated methane transport and its importance for methane emission from intact wetland peat mesocosm, J. Plant Ecol., doi: 10.1093/jpe/rts045, 2013.

Bosse, U. and Frenzel, P.: Activity and Distribution of Methane-Oxidizing Bacteria in

575   Flooded Rice Soil Microcosms and in Rice Plants (*Oryza sativa*), Appl. Environ. Microb., 63, 1199–1207, 1997.

Bubier, J., Costello, A., Moore, T. R., Roulet, N. T. and Savage, K.: Microtopography and methane flux in boreal peatlands, northern Ontario, Canada, Can. J. Botany, 71, 1056–1063, 1993.

580   Bubier, J.: The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands, J. Ecol., 83, 403–420, 1995.

Chanton, J. P., Bauer, J. E., Glaser, P. A., Siegel, D. I., Kelley, C. A., Tyler, S. C., Romanowicz, E. H. and Lazrus, A.: Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands, Geochim. Cosmochim. Acta, 59, 585   3663–3668, 1995.

Crill, P. M., Bartlett, K. B., Harris, R. C., Gorham, E., Verry, E. S., Sebacher, D. I., Madar, L. and Saner, W.: Methane flux from Minnesota peatlands, Global Biogeochem. Cy., 2, 371–384, 1988.

Daulat, W. E. and Clymo, R. S.: Effects of temperature and water table on the efflux of 590   methane from peatland surface cores, Atmos. Environ., 32, 3207–3218, 1998.

Dedysh, S. N.: Methanotrophic bacteria of acidic *Sphagnum* peat bogs, Microbiology, 71, 638-650, 2002.

Dise, N. B., Gorham, E. and Verry, E. S.: Environmental factors controlling methane emissions from peatlands in northern Minnesota, J. Geophys. Res., 98, 10 583-10 594, 1993.

595   Dunfield, P., Knowles, R., Dumont, R. and Moore, T. R.: Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH, Soil Biol. Biochem., 25, 321–326, 1993.

Frenzel, P. and Karofeld, E.: CH_4 emission from a hollow-ridge complex in a raised bog: The role on CH_4 production and oxidation, Biogeochemistry, 51, 91–112, 2000.

600   Frenzel, P. and Rudolph, J.: Methane emission from a wetland plant: the role of CH_4 oxidation in *Eriophorum,* Plant Soil, 202, 27–32, 1998.

Große, W.: The mechanism of thermal transpiration (=thermal osmosis), Aquat. Bot., 54, 101–110, 1996.

Hanson, R. S. and Hanson, T. E.: Methanotrophic Bacteria, Microbiol. Rev., 60, 439–471, 1996.

Hosono, T. and Nouchi, I.: The dependence of methane transport in rice plants on the root zone temperature, Plant Soil, 191, 233–240, 1997.

IPCC, Climate Change 2014: Synthesis Report, Contribution of Working Groups I, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp., 2014.

Joabsson, A., Christensen, T. R. and Wallén, B.: Vascular plant controls on methane emissions from northern peatforming wetlands, Trends Ecol. Evol., 14, 385–388, 1999.

Juottonen, H., Kotiaho, M., Robinson, D., Merilä, P., Fritze, H. and Tuittila, E-S.: Microform-related community patterns of methane-cycling microbes in boreal Sphagnum bogs are site specific, FEMS Microbiol. Ecol., 91, doi: 10.1093/femsec/fiv094, 2015.

Karofeld, E.: Mud-bottom hollows: exceptional features in carbon-accumulation bogs? The Holocene, 14, 119–124, 2004.

Kettunen, A., Kaitala, V., Alm, J., Silvola, J., Nykänen, H. and Martiakinen, P. J.: Cross-correlation analysis of the dynamics of methane emissions from a boreal peatland, Global Biogeochem. Cy., 10, 457–471, 1996.

Kirschke, S., Bousquet, P., Ciais, P., Saunois, M., Canadell, J. G., Dlugokencky, E. J., Bergamaschi, P., Bergmann, D., Blake, D. R., Bruhwiler, L., Cameron-Smith, P., Castaldi, S., Chevallier, F., Feng, L., Fraser, A., Heimann, M., Hodson, E. L., Houweling, S., Josse, B., Fraser, P. J., Krummel, P. B., Lamarque, J.-F., Langenfelds, R. L., Le Quéré, C., Naik, V., O'Doherty, S., Palmer, P. I., Pison, I., Plummer, D., Poulter, B., Prinn, R. G., Rigby, M., Ringeval, B., Santini, M., Schmidt, M., Shindell, D. T., Simpson, I. J., Spahni, R., Steele, L. P., Strode, S. A., Sudo, K., Szopa, S., van der Werf, G. R., Voulgarakis, A., van Weele, M., Weiss, R. F., Williams, J. E. and Zeng, G.: Three decades of global methane sources and sinks, Nature Geoscience, 6, 813–823, doi:10.1038/ngeo1955, 2013.

Korrensalo, A.: Behind the stability of boreal bog carbon sink: Compositional and functional variation of vegetation across temporal and spatial scales, Ph.D. thesis, School of Forest Sciences, University of eastern Finland, Finland, 2017.

Kormman, R. and Meixner, F. X.: An analytical footprint model for non-neutral stratification, Bound-Lay. Meteorol., DOI: 10.1023/A:1018991015119, 2001.

Kotiaho, M., Fritze, H., Merilä, P., Tuomivirta, T., Väliranta, M., Korhola, A., Karofeld, E. and Tuittila, E-S.: Actinobacteria community structure in the peat profile of boreal bogs follows a variation in the microtopographical gradient similar to vegetation, Plant Soil, 369, 103–114, 2013.

Larmola, T., Tuittla, E-S., Tiirola, M., Nykänen, H., Martikainen, P. J., Yrjälä, K., Tuomivirta, T. and Fritze, H.: The role of Sphanum mosses in the methane cycling of a boreal mire, Ecology, 91, 2356–2365, 2010.

Laine, A., Wilson, D., Kiely, G. and Byrne, K. A.: Methane flux dynamics in an Irish lowland blanket bog, Plant. Soil., 299, 181–193, DOI 10.1007/s11104-007-9374-6, 2007.

LeMer, J. and Roger, P.: Production, oxidation, emission and consumption of methane by soils: A review, Eur. J. Soil Biol., 37, 25–50, 2001.

Li, T., Raivonen, M., Alekseychik, P., Aurela, M., Lohila, A., Zheng, X., Zhang, Q., Wang, G., Mammarella, I., Rinne, J., Yu, L., Xie, B., Vesala, T. and Zhang, W.: Importance of vegetation classes in modelling CH_4 emissions from boreal and subarctic wetlands in Finland, Sci Total Environ., 572, 1111–1122, 2016.

MacDonald, J.A., Fowler, D., Harraves, K.J., Skiba, U., Leith, I.D. and Murray, B.: Methane emission rates from a northern wetland; response to temperature, water table and transport, Atmospheric Environment, 32, 3219–3227, 1998.

Mammarella, I., Peltola, O., Nordbo, A., Järvi, L., and Rannik, Ü.: Quantifying the uncertainty of eddy covariance fluxes due to the use of different software packages and combinations of processing steps in two contrasting ecosystems, Atmospheric Measurement Techniques, 9, 4915-4933, doi:10.5194/amt-9-4915-2016, 2016.

Marushchak, M. E., Friborg, T., Biasi, C., Herbst, M., Johansson, T., Kiepe, I., Liimatainen, M., Lind, S. E., Martikainen, P. J., Virtanen, T., Soegaard, H. and Shurpali, N. J.: Methane dynamics in the subarctic tundra: combining stable isotope analyses, plot- and ecosystem-scale flux measurements, Biogeosciences, 13, 597–608, 2016.

Melton, J. R., Wania, R., Hodson, E. L., Poulter, B., Ringeval, B., Spahni, R., Bohn, T., Avis, C. A., Beerling, D. J., Chen, G., Eliseev, A., Denisov, S. N., Hopcroft, P. O., Lettenmaier, D.

P., Riley, W. J., Singarayer, J. S., Subin, Z. M., Tian, H., Zürcher, S., Brovkin, V., van
Bodegom, P. M., Kleinen, T., Yu, Z. C. and Kaplan, J. O.: Present state of global wetland
extent and wetland methane modelling: conclusions from a model inter-comparison project
(WETCHIMP), Biogeosciences, 10, 753–788, 2013.

Moore, T. R., De Young, A., Bubier, J. L., Humphreys, E. R., Lafleur, P. M. and Roulet, N.
T.: A multi-year record of methane flux at the Mer Bleue bog, southern Canada, Ecosystems,
14, 646–657, DOI: 10.1007/s10021-011-9435-9, 2011.

Nisbet, E. G., Dlugokencky, E. J., Manning, M. R., Lowry, D., Fisher, R. E., France, J. L.,
Michel, S. E., Miller, J. B., White, J. W. C., Vaughn, B., Bousquet, P., Pyle, J. A., Warwick,
N. J., Cain, M., Brownlow, R., Zazzeri, G., Lanoisellé, M., Manning, A. C., Glooe, E.,
Worthy, D. E. J., Brunkle, E-G., Labuschagne, C., Wolff, E. W. and Ganesan, A. L.: Rising
atmospheric methane: 2007–2014 growth and isotopic shift, Global Biogeochem. Cycles, 30,
1356–1370, doi:10.1002/2016GB005406, 2016.

Raghoebarsing, A. A., Smolders, A. J., Schmid, M. C., Rijpstra, W. I. C., Wolters-Arts,
M., Derksen, J., Jetten, M.S., Schouten, S., Sinninghe Damsté, J.S., Lamers, L.P., Roelofs,
J.G., Op den Camp, H.J., and Strous, M.: Methanotrophic symbionts provide carbon for
photosynthesis in peat bogs, Nature, 436, 1153–1156, 2005.

Raivonen, M., Smolander, S., Backman, L., Susiluoto, J., Aalto, T., Markkanen, T., Mäkelä,
J., Rinne, J., Peltola, O., Aurela, M., Tomasic, M., Li, X., Larmola, T., Juutinen, S., Tuittila,
E-S., Heimann, M., Sevanto, S., Kleinen, T., Brovkin, V. and Vesala, T.: HIMMELI v1.0:
HelsinkI Model of MEthane buiLd-up and emIssion for peatlands, Geosci. Model. Dev.
Discuss., doi:10.5194/gmd-2017-52, 2017. Manuscript under review for journal Geosci. Model
Dev.

Riley, W. J., Subin, Z. M., Lawrence, D. M., Swenson, S. C., Torn, M. S., Meng, L., Mahowald,
N. M. and Hess, P.: Barriers to predicting changes in global terrestrial methane fluxes: analyses
using CLM4Me, a methane biogeochemistry model integrated in CESM, Biogeosciences, 8,
1925–1953, 2011.

Rinne, J., Riutta, T., Pihlatie, M., Aurela., M., Haapanala, S., Tuovinen, J-P., Tuittila, E-S. and
Vesala., T.: Annual cycle of methane emission from a boreal fen measured by the eddy
covariance technique, Tellus, 59B, 449–457, 2007.

Rinne, J., Tuittila, E-S., Peltola, O., Li, X., Raivonen, M., Alekseychik, P., Haapanala, S.,

Pihlatie, M., Aurela, M., Mammarella, I. and Vesala, T.: Temporal variation of ecosystem scale methane emission from a boreal fen in relation to temperature, water table position, and carbon dioxide fluxes, confidential manuscript submitted to Global Biogeochem. Cy., 2017.

Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M. and Tuittila, E-S.: Spatal variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem, Tellus, 59B, 838–852, 2007.

Rydin, H. and Jeglum, J.: The biology of peatlands, New York, NY: Oxford University Press Inc., 2006.

Saarnio, S., Alm, J., Silvola, J., Lohila, A., Nykänen, H. and Martikainen, P. J.: Seasonal variation in CH$_4$ emissions and production and oxidation potentials at microsites on an oligotrophic pine fen, Oecologia, 110, 414–422, 1997.

Segers, R.: Methane production and methane consumption: a review of processes underlying wetland methane fluxes, Biogeochemistry, 41, 23–51, 1998.

Smemo, K. A. and Yavitt, J. B.: Evidence for anaerobic CH$_4$ oxidation in freshwater peatlands, Geomicrobiol. J., 24, 583–597, 2007.

Smith, K. A., Dobbie, K. E., Ball, B. C., Bakken, L. R., Sitaula, B. K., Hansen, S., Brumme, R., Borken, W., Christensen, S., Priemé, A., Fowler, D., MacDonald, J. A., Skiba, U., Klemedtsson, L., Kasimir-Klemedtsson, A., Degórska, A. and Orlanski, P.: Oxidation of atmospheric methane in Northern European soils, comparison with other ecosystems, and uncertainties in the gobal terrestrial sink, Glob. Change Biol., 6, 791–803, 2000.

Ström, L., Ekberg, A., Mastepanov, M. and Christensen, T. R.: The effect of vascular plants on carbon turnover and methane emissions from tundra wetland, Glob. Change Biol., 9, 1185–1192, 2003.

Sundh, I., Mikkelä, C., Nilsson, M. and Svensson, B. H.: Potential aerobic methane oxidation in a Spahgnum-dominated peatland –controlling factors and relation to methane emission, Soil Biol. Biochem., 27, 829–837, 1995.

Tokida, T., Miyazaki, T., Mizoguchi, M., Nagata, O., Takakai, F., Kagemoto, A. and Hatano, R.: Falling atmospheric pressure as a trigger for methane ebullition from peatland, Global Biogeochem. Cy., 21, doi:10.1029/2006GB002790, 2007.

Turetsky, M. R., Kotowska, A., Bubier, J., Dise, N. B., Crill, P., Hornibrook, E. R. C.,
Minkkinen, K., Moore, T. R., Myers-Smith, I. H., Nykänen, H., Olefeldt, D. Rinne, J.,
Saarnio, S, Shurpali, N., Tuittila, E-S., Waddington, J. M., White, J. R., Wickland, K. P. and
Wilmking, M.: A synthesis of methane emissions from 71 northern, temperate, and
subtropical wetlands, Global Change Biol., doi: 10.1111, gcb.12580, 2014.

Turunen, J., Tomppo, E., Tolonen, K. and Reinikainen, A.: Estimating carbon accumulation
rates of undrained mires in Finland –application to boreal and subarctic regions, Holocene,
12, 69–80, 2002.

Waddington, J. M. and Roulet, N. T.: Atmosphere-wetland carbon exchanges: Scale
dependency of CO_2 and CH_4 exchange on the developmental topography of a peatland, Gobal
Biogeochem. Cy., 10, 233–245, 1996.

Waddington, J. M., Roulet, N. T. and Swanson, R. V.: Water table control of CH_4 emission
enhancement by vascular plants in boreal peatlands, J. Geophys. Res., 101, 22 775-22 785,
1996.

~~Whiting, G. J. and Chanton, J. P.: Priamry production control of methane emission from~~
~~wetlands, Nature, 364, 794–795, 1993.~~

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K. A., Farrell, E. P. and Tuittila, E-S.: A
high resolution green area index for modelling the seasonal dynamics of CO_2 exchange in
peatland vasvular plant communities, Plant Ecol., 190, 37–51, 2007.

Wilson D., Blain D., Couwenberg J., Evans C. D., Murdiyarso D., Page S. E., Renou-Wilson
F., Rieley J. O., Sirin A., Strack M. and Tuittila, E.-S.: Greenhouse gas emission factors
associated with rewetting of organic soils, Mires Peat, 17, 1–28, 2016.

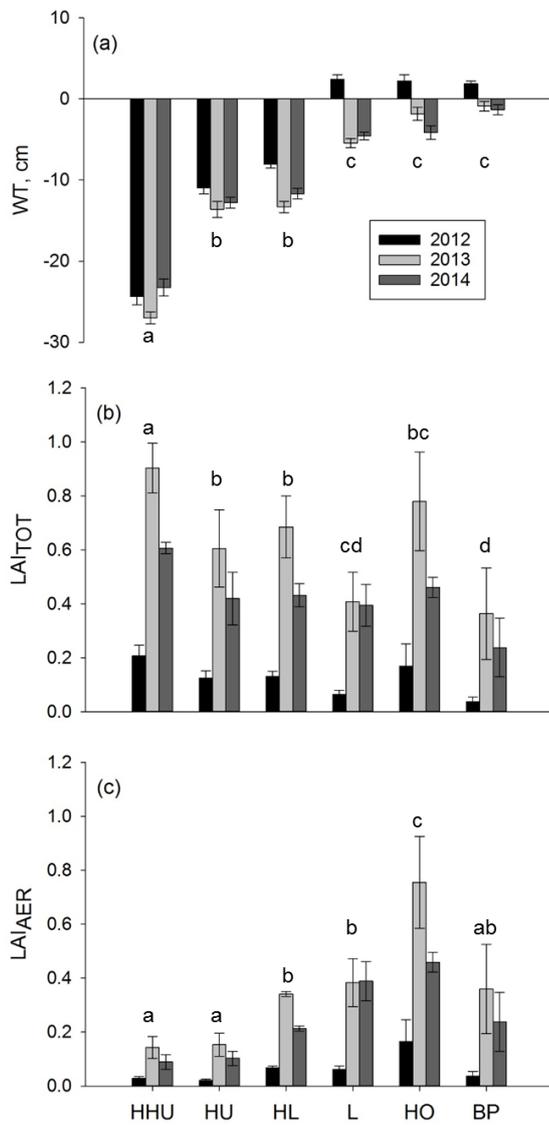
Yrjälä, K., Tuomivirta, T., Juottonen, H., Putkinen, A., Lappi, K., Tuittila, E-S., Penttilä, T.,
Minkkinen, K., Laine, J., Peltoniemi, K. and Fritze, H.: CH_4 production and oxidation
processes in a boreal fen ecosystem after long-term water table drawdown, Global Change
Biol., doi: 10.1111/j.1365-2486.2010.02290.x, 2011.

Yu, Z.: Holocene carbon flux histories of the world's peatlands: Global carbon-cycle
implications, Holocene, 21, 761–774, 2011.

Tables

755 Table 1. Temperature sum of the growing season, annual rainfall and the amount of photosynthetically active radiation (PAR) in the three studied years 2012–2014.

Year	Temp. sum degree days	Annual rainfall mm	PAR μmol m^{-2}
2012	1172	907	68 296
2013	1408	615	72 946
2014	1349	579	70 800

Figures

 Figure 1. a) Mean water table and the mean of summer maximum of b) total leaf area (LAI$_{TOT}$) and c) leaf area of aerenchymatous plant species (LAI$_{AER}$) in six plant community types: high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and bare peat surface (BP) in three subsequent years. The error bars show the standard error of the mean. The different letters (a-d) denote significant differences between the plant

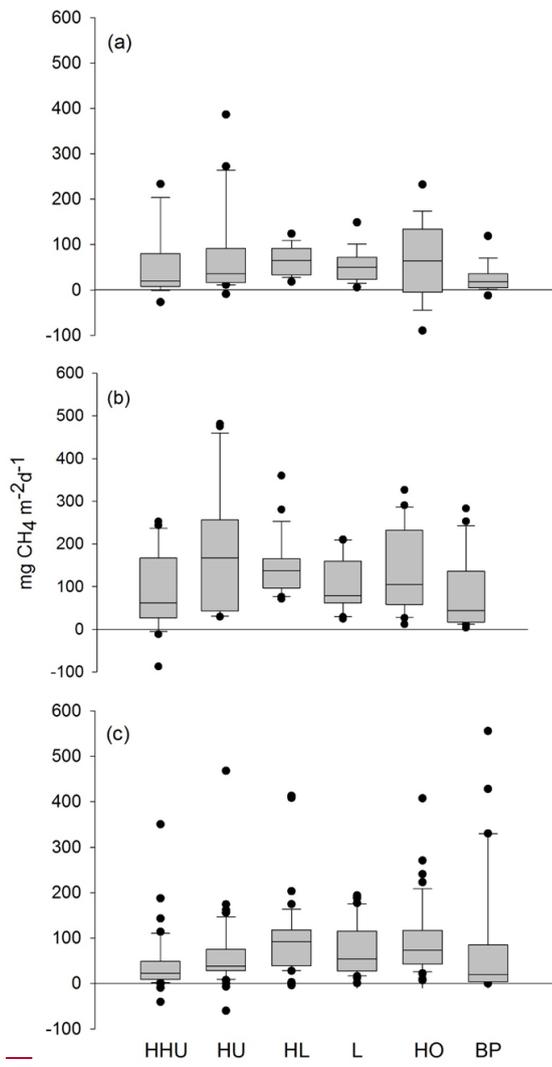
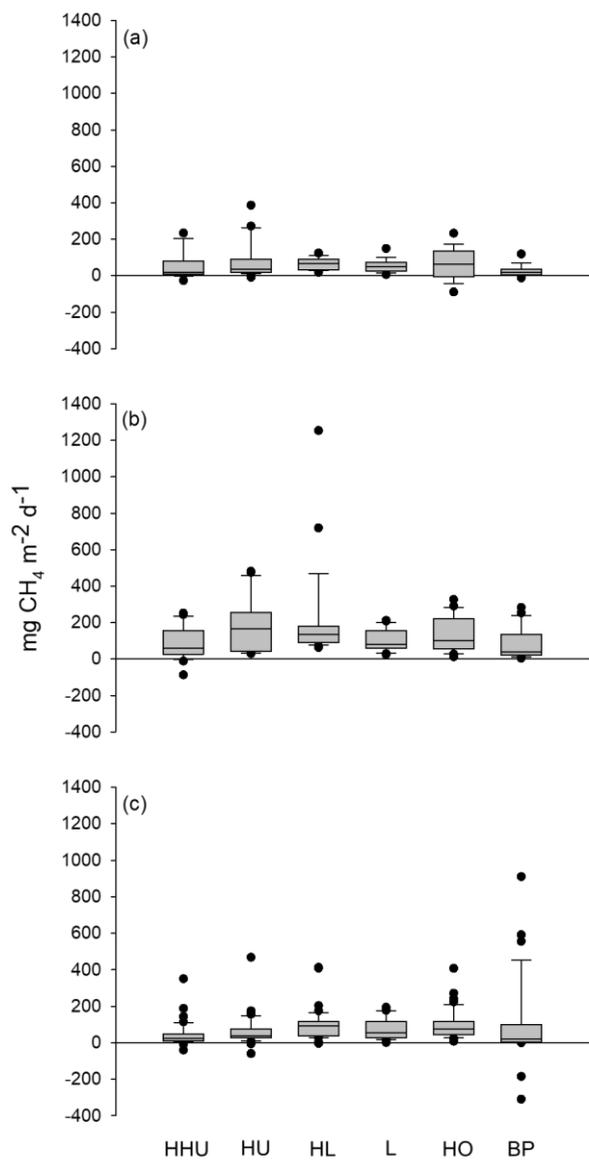
765 community types. Same letter above bars indicates that those plant community types do not differ statistically from each other. Note: statistical analyses for LAI have been conducted with mean LAI_{TOT} and LAI_{AER} instead of summer maximum.

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Figure 2. Methane fluxes in Siikaneva bog in three subsequent years a) 2012, b) 2013 and c) 2014 from six different plant community types: high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and ~~mud bottom (MB)~~bare peat surfaces (BP). ~~13 highest~~

fluxes and the two lowest fluxes from MB in 2014 (-309 and -185 mg CH_4 m^{-2} d^{-1}) have been
excluded from the figure in order to enable uniform scaling (see Fig. 3).

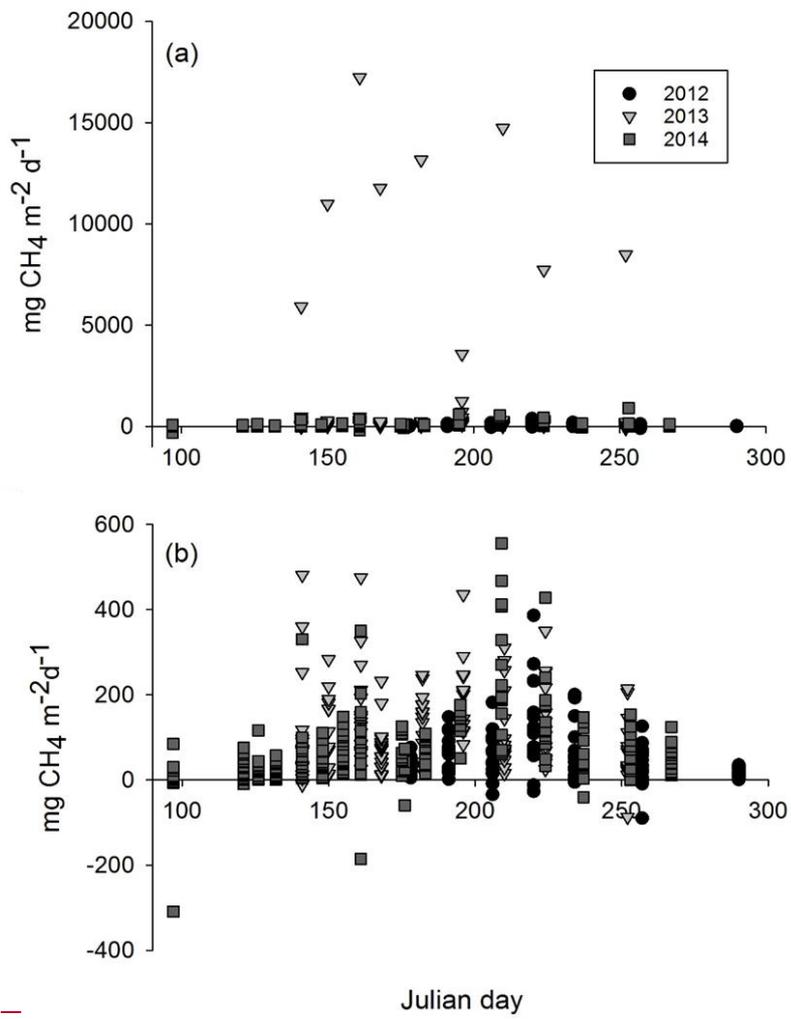
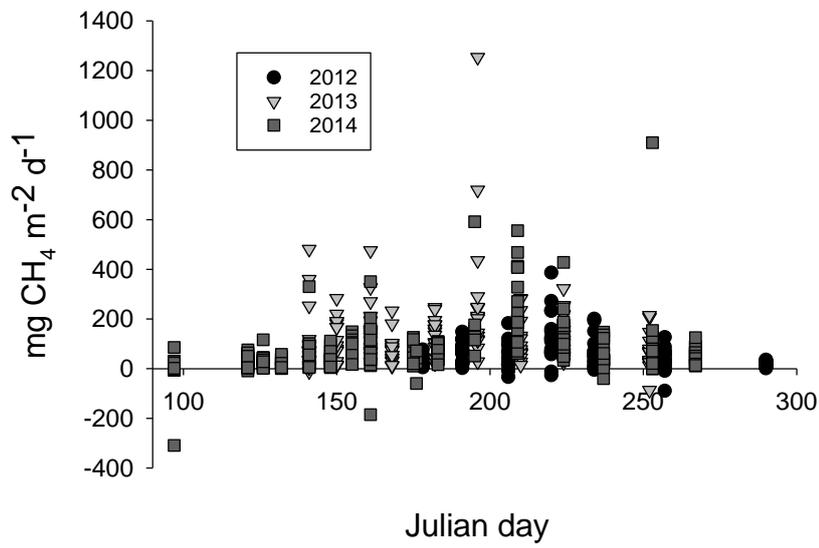



Figure 3. The measured methane fluxes in three subsequent years. shown for a) the whole
dataset and for b) the "normal" dataset excluding the 13 highest fluxes.

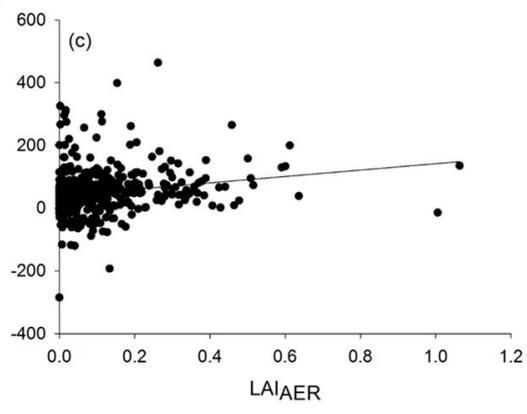
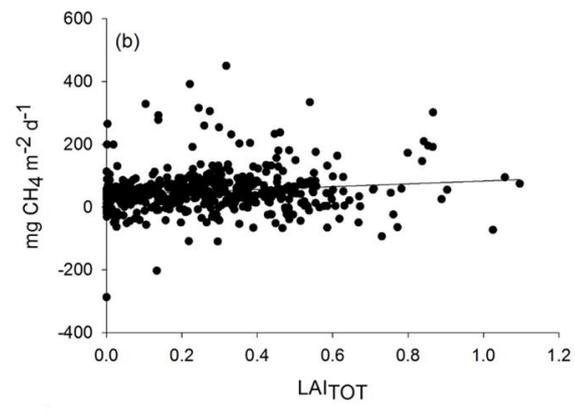
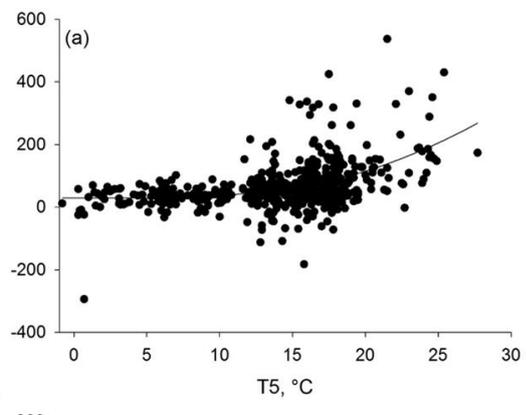
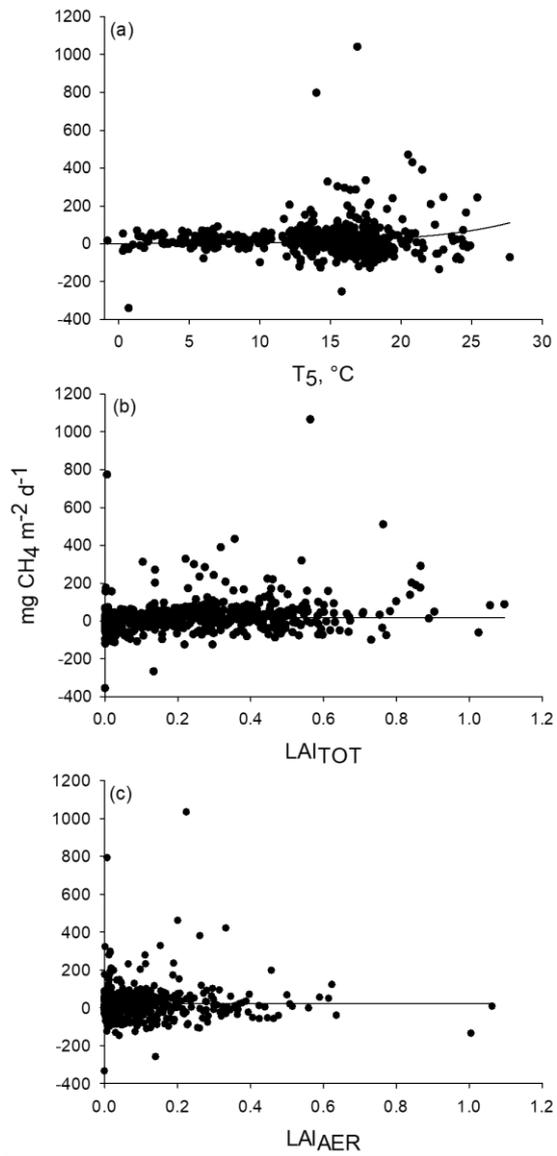



Figure 4. Response of methane flux to a) peat temperature in the depth of 5 cm, b) total leaf area (LAI_{TOT}) and c) leaf area of aerenchymatous plant species (LAI_{AER}). Methane fluxes measured in 2012-2014 were adjusted to a) mean LAI_{TOT} (0.~~2642~~2661) and LAI_{AER} (0.~~0984~~1016), b) mean peat temperature in the depth of 5 cm (~~13.9~~14 °C) and mean LAI_{AER}

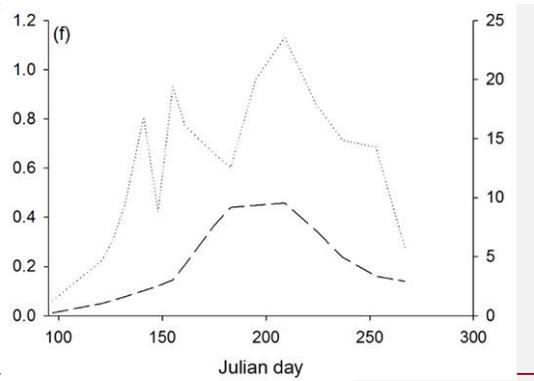
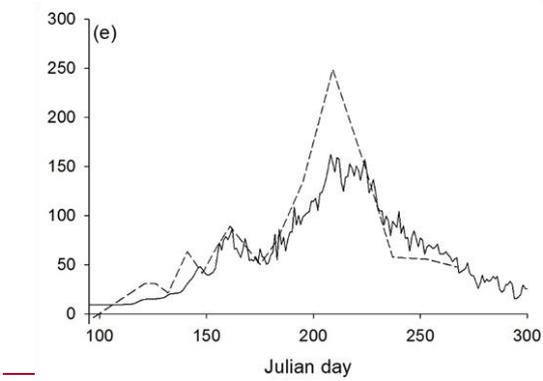
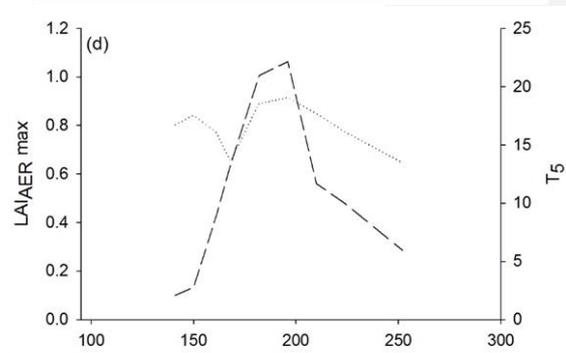
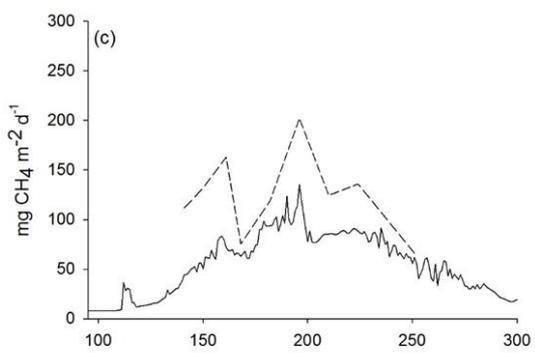
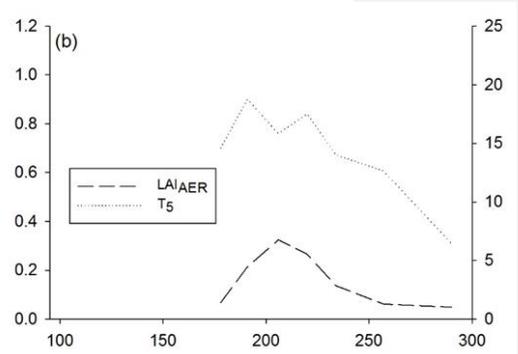
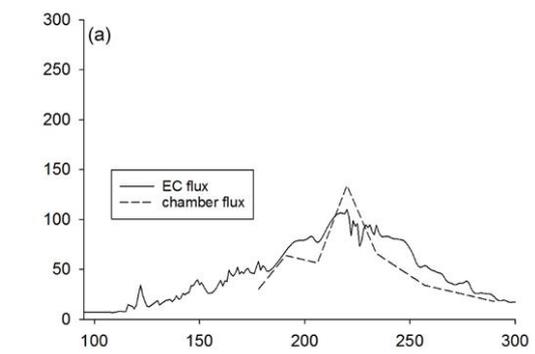
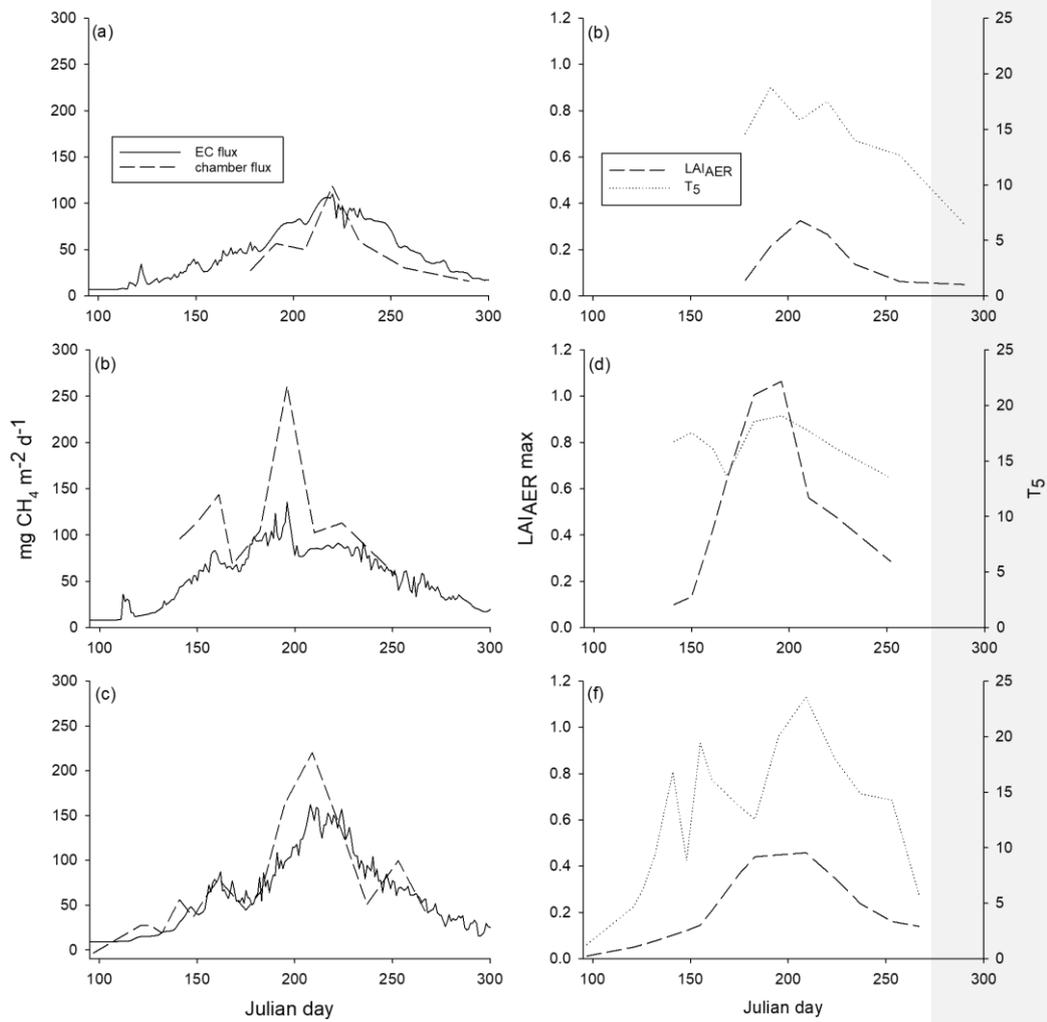
(0.~~0984~~1016) and c) mean peat temperature in the depth of 5 cm (~~13.9~~14 °C) and mean LAI$_{TOT}$ (0.~~2642~~2661).

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Figure 5. Ecosystem level methane fluxes measured with the eddie covariance (EC)
technique and upscaled from chamber measurements (chamber flux) (left panel), and
maximum leaf area index of aerenchymatous plant species (LAI$_{AER}$ max) and peat
temperature in the depth of 5 cm (T$_5$) (right panel) over the growing seasons a-b) 2012, c-d)
795   2013 and e-f) 2014.

Appendix A.

Table A1. Parameter estimates of the linear mixed-effects model for methane flux. Estimate value, standard error (SE), degrees of freedom (DF), and test statistics t- and p-values are given to the fixed predictors of the model as compared to high hummocks in 2012 (intercept). Fixed predictors are: plant community type divided into high hummocks, hummocks (HU), high lawns (HL), lawns (L), hollows (HO) and bare peat surfaces (BP), measurement year (2012–2014), interaction of plant community type and year (e.g. HU x 2013), peat temperature in the depth of 5 cm, leaf area index of all vegetation (LAI_{TOT}) and leaf area index of aerenchymatous plant species (LAI_{AER}).

Parameter	Value	SE	DF	t	p
(Intercept)	-14.79	38.88	483	-0.380	0.7038
HU	38.94	43.90	10	0.887	0.3959
HL	24.77	44.97	10	0.551	0.5938
L	29.22	47.74	10	0.612	0.5541
HO	10.57	46.55	10	0.227	0.825
BP	11.21	48.57	10	0.231	0.8222
2013	-2.49	30.25	483	-0.082	0.9343
2014	-14.99	27.66	483	-0.542	0.5881
Peat temperature	0.78	0.10	483	7.686	0
LAI_{TOT}	91.59	49.04	483	1.868	0.0624
LAI_{AER}	67.62	70.71	483	0.956	0.3395
HU × 2013	88.09	42.02	483	2.096	0.0366
HL × 2013	109.75	41.84	483	2.623	0.009
L × 2013	20.97	42.48	483	0.494	0.6218
HO × 2013	43.09	45.46	483	0.948	0.3437
BP × 2013	13.33	42.02	483	0.317	0.7511
HU × 2014	-5.35	36.96	483	-0.145	0.8849
HL × 2014	49.81	37.51	483	1.328	0.1848
L × 2014	26.15	37.66	483	0.694	0.4878
HO × 2014	65.10	38.48	483	1.692	0.0913
BP × 2014	84.55	38.34	483	2.205	0.0279
Parameter	Value	SE	DF	t	p
(Intercept)	8.45	30.00	470	0.282	0.7783
HU	30.07	34.47	10	0.873	0.4034
HL	14.16	35.21	10	0.402	0.696
L	10.77	37.16	10	0.290	0.7779
HO	-2.04	36.31	10	-0.056	0.9564
BP	-9.60	37.76	10	-0.254	0.8045
2013	-0.09	22.29	470	-0.004	0.9969
2014	-20.86	20.22	470	-1.032	0.3026
Peat temperature	0.77	0.07	470	10.351	0.0000

LAI~TOT~	45.02	36.47	470	1.235	0.2176
LAI~AER~	101.98	53.09	470	1.921	0.0553
HU × 2013	90.86	30.82	470	2.948	0.0034
HL × 2013	51.43	31.12	470	1.652	0.0991
L × 2013	14.12	31.96	470	0.442	0.6587
HO × 2013	41.58	33.55	470	1.239	0.2159
BP × 2013	17.38	31.03	470	0.560	0.5757
HU × 2014	-3.91	26.99	470	-0.145	0.8848
HL × 2014	50.31	27.39	470	1.837	0.0669
L × 2014	29.21	27.50	470	1.062	0.2887
HO × 2014	62.50	28.10	470	2.224	0.0266
BP × 2014	52.06	28.18	470	1.847	0.0653