Dear editors of the *Biogeosciences*

Revision for “Small spatial but large sporadic variability in methane emission measured from a patterned boreal bog” (manuscript no. bg-2017-443).

We want to thank the two Referees for their constructive comments that certainly improved the report. Accordingly, we have revised our manuscript following the suggestions made by the Referee #1 and the Referee #2 Tim Moore, or replied in detail why we have not followed their guidelines in some places. Here you will find the original statements of the referees and our responses to them.

Firstly, we would like to address the extreme high methane emissions that we reported in the manuscript having been measured sporadically in 2013 and 2014. After checking these high fluxes once more, we found nine highest fluxes measured in 2013 to result from a calculation error after all. Originally, we were quite skeptical about such high fluxes and checked a variety of potential sources of mistake, such as gas chromatograph data processing, typing errors, nonlinearity caused by ebullition and correctness of the flux calculation formula. What finally was the reason behind this very unfortunate calculation error was a wrong reference in the data processing sheet, which did not occur with most of the measurements, but only in these 9 cases. After correcting these cases, we also went carefully through the rest of the data to make sure that all the calculations are now correct and all the fluxes reported in the revised manuscript are true. The highest methane flux in the corrected data is now 1254 mg m^{-2} d^{-1} instead of the previously reported 17 000 mg m^{-2} d^{-1}. Consequently, we rerun the statistical analyses with the whole data set, as there was no need to exclude the highest fluxes from the analyses anymore. Our results remain generally the same as previously, but the statistically significant differences between the plant community types in 2013 changed a little. We reported previously that hummocks had higher methane fluxes than other plant community types that year. Now, our result is that hummocks and high lawns had higher fluxes than high hummocks and bare peat surfaces in 2013. Additionally, there were also higher methane fluxes from bare peat surfaces than from high hummocks in 2014. We have corrected the manuscript and the figures according to the new results of the analyses of the whole data set and excluded the incorrect report and discussion of the “extreme high fluxes”. We sincerely apologize for our mistake.

Referee #1:

Comment: Line 14: please add a name and location of the bog.

Response: We have added this information of the study site in the abstract.

Changes in manuscript: Line 14: we have added “situated in Siikaneva in southern Finland” to the sentence.

Comment: Line 17: add “species composition” to the list of variables that differ between the studied plant community types.

Response: We have added this as suggested (line 18 in the revised manuscript).

Changes in manuscript: Line 17 (line 18 in the revised manuscript): “species composition” has been added.

Comment: Line 36: Peatland can also be drained. Since here we are dealing with natural ecosystem, the term "mire" could be more correct.

Response: The Referee has a good point that “peatland” can also refer to a drained ecosystem. To be precise we have now changed the text in the beginning of introduction to “Mires or undrained peatlands”.

Changes in manuscript: Line 36: “Peatland” has been changed to “Mires and undrained peatlands”.

Comment: Line 111: How far weather station is from the bog?

Response: The Juupajoki-Hyytiälä weather station is located about 6.3 km east from the studied bog site in Siikaneva. We have now added this information (line 119 in the revised manuscript).

Changes in manuscript: Line 111 (line 119 in the revised manuscript): we have added “station that is located 6.3 km east from the bog site” to the sentence.

Comment: Line 114: "Bog pools" could be better term than “open water ponds”.

Response: We agree that “pool” would be better than “pond”. We have modified the sentence.

Changes in manuscript: Line 114 (line 123 in the revised manuscript): “open water ponds” has been changed to “open water pools”.

Comment: Line 114 about bare peat surfaces: ... or “mud bottom hollows". Since this term is used in figures and other studies please introduce it here as well.

Response: The Referee is correct that the term “mud bottom hollows” has been used in some other studies instead of the term “bare peat surfaces” that we are using in the manuscript, and the term “mud bottom” has accidentally remained in our manuscript in the caption of the figure 2 from a previous draft of the manuscript. We are now consistently using the term “bare peat surfaces”.

Changes in manuscript: No changes. The wrong term is corrected in the caption of the figure 2.

Comment: Line 121: To explain the differences in fluxes it is important to know the depth, type, degree of decomposition etc. of peat layer below measuring points.

Response: We agree. Unfortunately, we did not study the peat layers below the measuring points.

Changes in manuscript: No changes.

Comment: Line 125: add "bog microforms or ..."

Response: We have added this.

Changes in manuscript: Line 125 (line 135 in the revised manuscript): "or bog microforms" has been added to the sentence.

Comment: Line 149: Since sporadic ebullition is typical for bogs it is not correct to exclude them as likely errors.

Response: The Referee is correct that sporadic ebullition is typical for bogs and it should be taken into account. However, in here we focus only on diffusive gas flux, which we can reliable measure with our method. We are aware that in some previous studies the proportion of methane ebullition has been calculated based on non-linear chamber fluxes. Unfortunately, in our very wet measurement site, we were afraid that the ebullitive fluxes could be mixed up with artefacts caused by the measurement protocol. These artefacts can easily be differentiated from linear, diffusive fluxes, but not from ebullitive fluxes.

Changes in manuscript: No changes.

Comment: Lines 224–230: Table can give better overview of these data.

Response: We fully agree.

Changes in manuscript: The information on the lines 224–230 is now found in a newly added table (Table 1) and the text has been shortened accordingly (lines 229–231 in the revised manuscript).

Comment: Line 269; results that there were higher methane fluxes from hummocks than from the other plant community types in 2013: This is surprising finding and needs an explanation.

Response: After we had corrected the calculation error resulting in the very high fluxes and rerun the statistical analyses, we found that hummocks and high lawns had higher fluxes than high hummocks and bare peat surfaces. We fully agree, that this is a surprising finding, but we do not have an explanation. We would also like to draw attention to the very small differences among these plant community types.

Changes in manuscript: Line 270 (line 277 in the revised manuscript): we have added a sentence “This result in 2013 was surprising, but the differences between the plant community types were small.”

Comment: Line 273: Peat temperature response of methane flux where the response was assumed… “. Difficult to follow the meaning of this part of the sentence.

Response: We fully agree that this was confusing as part of the results. For this reason, we have now explained this in the methods more clearly than before and removed this part from the results.

Changes in manuscript: The sentence starting on the line 273 (line 279 in the revised manuscript) has been removed. See also the modifications in the 2.5 Analyses section starting on the line 212 (line 215 in the revised manuscript).

Comment: Line 280: “WT did not explain variation in methane fluxes…”. Interesting. Since WTD also directly influence the temperature of the top layer of anaerobic peat with most active methane production.

Response: Yes, indeed. This surprised us as well, but this is likely to be related to the general wetness of the whole site.

Changes in manuscript: No changes.

Comment: Line 299: High fluxes can be caused by the gas release from deeper peat layers therefore to compare fluxes from different locations one need to look on deeper peat as well.

Response: The high fluxes were caused by our unfortunate error, as explained in the beginning of the letter. We have now removed this part.

Changes in manuscript: This part has been removed.

Comment: Line 326: High WT, close to the surface, also mean higher temperature and these factors should be discussed in combination.

Response: This is an interesting point, but the combination of WT and peat temperature could not be studied, as WT did not significantly explain the variation in methane fluxes.

Changes in manuscript: No changes.

Comment: Line 333: Authors may add reference Karofeld, 2004 (The Holocene, 14 (1)) who studied mud-bottom hollows from this point of view.

Response: We have added this as suggested.

Changes in manuscript: line 333 (line 332 in the revised manuscript): Reference ‘Karofeld, 2004’ has been added as suggested.

Comment: Line 347: add ‘Frenzel & Karofeld, 2000’ to the reference list.

Response: We have added this as suggested.

Changes in manuscript: Line 347 (line 352 in the revised manuscript): Reference ‘Frenzel and Karofeld, 2000’ has been added as suggested.

Comment: Line 357: Please add also the effect of decreasing peat temperature in uppermost anaerobic layer caused by lowered WT and insulation by drier plants.

Response: This is an interesting point, but the combination of WT and peat temperature could not be studied, as WT did not significantly explain the variation in methane fluxes.

Changes in manuscript: No changes.

Comment: Line 376: See also Karofeld, 2004.

Response: We have not added this as a reference because we removed the two sentences from the discussion.

Changes in manuscript: The two sentences starting on the line 372 has been removed.

Comment: Line 381: add “thickness of” in front of “aerobic peat layer”.

Response: We agree that this clarifies the sentence.

Changes in manuscript: Line 381 (line 386 in the revised manuscript): “thickness of” has been added in front of “aerobic peat layer”.

Comment: Line 382: Please consider also the effect of temperature change in the top layer of anaerobic peat with lowering water table.

Response: Again, this is an interesting point, but the combination of WT and peat temperature could not be studied, as WT did not significantly explain the variation in methane fluxes.

Changes in manuscript: No changes.

Comment: Line 392: To explain such kind of not typical fluxes one have to look also deeper peat layers and sporadic gas release from there.

Response: This is a good point. Unfortunately, we did not study the peat layers below the measuring points and focused only on diffusive gas flux in this study.

Changes in manuscript: No changes.

Comment: Line 418: See also Karofeld & Tõnisson, 2014, Hydrological Processes 28 (3).

Response: The phenomenon to which this discussion was related was caused by our unfortunate error, as explained in the beginning of the letter. We have now removed this part of the discussion.

Changes in manuscript: The discussion about extreme high methane fluxes on lines 410–429 has been removed.

Comment: Line 423: Due to the hysteresis effect and depending from peat type and decomposition the effect of air pressure on gas release may take longer time to accumulate and then release.

Response: This is completely true and a good point. However, the phenomenon to which this was related was caused by our unfortunate error, as explained in the beginning of the letter.

Changes in manuscript: This part of the discussion has been removed.

Comment: Line 432: But why with EC maximum values measured with chambers (and likely caused by active bubble release) where not detected?

Response: Again, the phenomenon to which this discussion was related was caused by our unfortunate error, as explained in the beginning of the letter, and we have now removed this part of discussion

Changes in manuscript: This part of the discussion has been removed.

Comment: Line 437: This sounds more like Results and not Discussion.

Response: We fully agree and removed most of this part from the discussion and replaced it with "…and chamber fluxes were occasionally higher than the EC fluxes".

Changes in manuscript: Please see the modified text on lines 345–441 (line 425 in the revised manuscript).

Comment: Discussion is a bit too long but at the same time on explaining or discussing some important aspects (temperature effect combined with changes in WT, high emission from hummock).

Response: We shortened the discussion as suggested.

Changes in manuscript: The discussion has been shortened as mentioned in the previous replies above.

Referee #2 Tim Moore:

Comment: The authors express some surprise in the weak relationship between water table position and methane flux, anticipating a larger flux where there is a higher water table, as has been shown elsewhere. As with all relationships between a gradient of an environmental variable and the object of interest (in this case methane flux), the strength of the relationship depends on at least two things: one is the range of the variable, and another is how other variables interact along the gradient. Strong water table:methane flux relationships have been shown elsewhere, but they tend to occur over large water table gradients (50 or more cm, rather than the 25-30 cm encountered here) and when they are of a small scale, the relationship is not simple, for example Bellisario et al. (1999). Moreover, water tables are not static but rise and fall and that can create hysteresis so it is not at the highest water table that maximum emission is reached (e.g. Brown et al. 2014). While mean water table data are presented in Figure 1, was there much variation in water table position during the three seasons, and does this play a role in the observed temporal variability in flux?

Response: This is a good point. We were only focusing on the differences among the plant communities. As there were no differences in the seasonal trends among these communities and WT as such did not explain the fluxes, we did not go any further with this. We now have plotted the residuals of the model together with continuous WT data from the site for each year separately. Please see the corresponding graph below. Although, there seems to be some indication of hysteresis in 2012 spring, we do not see any general pattern when looking all the years. Therefore, we did not add this analysis to the manuscript.

Changes in manuscript: No changes.

Comment: The interaction between the influence of aerenchymous plants facilitating emission and the non-aerenchymous plants providing root exudate to stimulate methanogenesis, to partially explain the small spatial variability, is well presented, though no evidence is put forward to support the processes involved.

Response: Yes, this is truly only speculation, as we do not have measurement data to back this up.

Changes in manuscript: No changes.

Comment: Perhaps the most surprising result of the study is the occurrence of large positive or negative methane fluxes, which because of linearity in change of gas concentration in the chambers, could not be discounted (10% of the measurements were excluded because of non-linearity or other reasons). It would be interesting to see a graph depicting the magnitude:frequency of the observed fluxes (n = 516); it is not clear whether the extreme fluxes (2.5%) included both positive and negative fluxes (lines 190 to 195 could be clarified).

Response: As explained in the beginning of this letter, the extreme fluxes were after all a result of a very unfortunate error. For this reason, this part is no longer relevant.

Changes in manuscript: The result and discussion parts regarding extreme high positive methane fluxes have been removed.

Comment: These extreme fluxes are large by normal measurements, though it should be noted that they were observed over 35 minutes and then scaled up to a daily estimate: it is unlikely that the methane stored in the peat, or its generation, could sustain such a high flux for a day: what are rates of methane production for these systems (g/m2/day, or how much methane is stored in the peat profile?). There seems to be no strong attention to the reasons why a large methane emission could be observed: perhaps, given that these are 'real' fluxes, more information could be given on their spatial and temporal patterns (rather than 'random and sporadic'): this is hinted at in lines 293 to 299: where and when did the fluxes > 1 g/m2/d occur?

Response: Again**,** as explained in the beginning of this letter, the extreme fluxes were after all a result of a very unfortunate error. For this reason, this part is no longer relevant.

Changes in manuscript: The result and discussion parts regarding extreme high positive methane fluxes have been removed.

Comment: Perhaps more disconcerting is the occurrence of large uptake rates of methane, up to 300 mg/m2/d and it is difficult to conceive of a mechanism which would allow such large amounts of methane to be 'taken up' microbially, through methanotrophy. As noted, the largest methanotrophic potentials are usually observed around the position of the water table, which in these sites are close to the peat surface, so the diffusive pathway for methane consumption is fairly short. Nevertheless, it is somewhat surprising that these large consumption rates appear primarily on bare peat surfaces (line 291), whereas one might expect less microbial activity than where vegetation cover was denser (though the arenchymous R. alba occurs in the bare peat spots). Are these large consumption rates related to water table position (and hence largest potential rates of methane consumption)?

Response: We also found this rather surprising. Unfortunately, we did not find an explanation for this. The highest net uptake occurred in spring when the measurement plot was still frozen, but this was not the case during the other net uptake events. Of course, ice does not explain the net uptake of methane either. We would also like to note that together with all of the fluxes, we also inspected these again and found nothing wrong.

Changes in manuscript: No changes.

Comment: Line 15: add “with chamber exposure of 35 minutes”.

Response: We have added this to the sentence.

Changes in manuscript: Line 15 (line 16 in the revised manuscript): we have added “with chamber exposure of 35 minutes” to the sentence.

Comment: Line 15: change “for quantifying” to “to quantify”.

Response: We have corrected this.

Changes in manuscript: Line 15 (line 16 in the revised manuscript): “for quantifying” has been changed to “to quantify”.

Comment: Line 21: change “were higher…” to “was higher…”.

Response: We have corrected the sentence according to the new results of the statistical analyses of the whole data set.

Changes in manuscript: Starting on the line 21 (line 22 in the revised manuscript): “The only exception were higher fluxes from hummocks and high lawns than from high hummocks and bare peat surfaces in 2013 and from bare peat surfaces than from high hummocks in 2014.”

Comment: Line 38: change “water level” to “the water table”.

Response: We have changed this.

Changes in manuscript: Line 38: “water level” has been changed to “the water table”.

Comment: Line 41: change “methane” to “CH_4”. As you have defined this term, you should use it throughout.

Response: We have defined “methane” as the term “CH_4” as it is used in the figures. However, in the text we prefer “methane” as it in our opinion improves the readability and is not very much longer than “CH_4”.

Changes in manuscript: No changes.

Comment: Line 42: add “the” in front of the “water table”.

Response: We have corrected this.

Changes in manuscript: Line 42 (line 43 in the revised manuscript): "the" has been added to in front of the "water table".

Comment: Line 143: Do you have a continuous measurement of water table somewhere at the site, so that you can situate individual measurements in the dynamics of water table (see comment about hysteresis)?

Response: Please, see our response to the previous comment on this matter and the graphs in the end of this letter.

Changes in manuscript: No changes.

Comment: Line 171: add a space between "m" and "s^{-1}" in the unit of friction velocity.

Response: We have corrected this.

Changes in manuscript: Line 171 (line 186 in the revised manuscript): a space has been added between "m" and "s^{-1}" in the unit of friction velocity.

Comment: Line 194: A bit confusing why you would exclude the upper 2.5% and retain the lower 2.5%, as both groups were 'valid' measurements.

Response: This is not relevant any more, as explained before.

Changes in manuscript: Lines 186–199 have been removed.

Comment: Line 260: Would be nice to see a frequency:magnitude graph of all measurements, including the 'excluded' ones.

Response: Again, this is unfortunately not relevant any more, as explained before.

Changes in manuscript: No changes.

Comment: Line 286: add "a" in front of "high WT".

Response: We have corrected this.

Changes in manuscript: Line 286 (line 291 in the revised manuscript): "a" has been added in front of "high WT".

Comment: Line 287: about methane oxidation: well, you do not know it was 'oxidation', all we know is that the methane concentration in the chamber showed a rapid decline (from 1.8 to ?? ppm over 35 minutes) and you assume it was through microbial consumption/oxidation, though this would imply very high rates of methanotrophy. there maybe other reasons, such as advective effects, though there seems to be no support for an alternative.

Response: As pointed out we are not able to say if all the negative fluxes are due to net oxidation. Accordingly, when referring our results we now use term “negative net flux”.

Changes in manuscript: Throughout the manuscript, “oxidation” has been replaced with “negative net flux” when referring to our own results. In addition, we have added a sentence stating, that these negative fluxes may be linked to methane oxidation (line 393) (line 399 in the revised manuscript).

Comment: Line 301: add “an” in front of “ecosystem level”.

Response: We have corrected this.

Changes in manuscript: Line 301 (line 298 in the revised manuscript): “an” has been added in front of “ecosystem level”.

Comment: Line 304: maybe you could add “but real” to the sentence “as they were random and sporadic events” as defining the extreme methane fluxes.

Response: Unfortunately, this is not relevant any more, as explained before.

Changes in manuscript: This sentence has been removed.

Comment: Line 319: add “a” in front of “little higher”. In English 'a little higher' has a different meaning than 'little higher'. The former means it is higher, whereas the latter implies that they are the same. I think 96 vs 57 and 72 is in the former category.

Response: The Referee is correct that we meant “a little higher” in this case. We have corrected this.

Changes in manuscript: Line 319 (line 316 in the revised manuscript): “a” has been added in front of “little higher”.

Comment: Line 345: and whether you could ever explain the high rates of methane uptake..... on our discussion: “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.”

Response: We agree here, such study would also help to explain the reasons behind net methane uptake.

Changes in manuscript: A sentence has been added to line 345 (line 348 in the revised manuscript): **“**This could also clarify to what extent the high negative net fluxes are explained by microbial methane oxidation.”

Comment: Line 348: change “effect” to “affect”.

Response: We have corrected this.

Changes in manuscript: Line 348 (line 352 in the revised manuscript): “effect” has been corrected to “affect”.

Comment: Line 355: correct “boreal climate” to “boreal climates”.

Response: We have corrected this.

Changes in manuscript: Line 355 (line 361 in the revised manuscript): “boreal climate” has been corrected to “boreal climates”.

Comment: Line 356: add “the” in front of “WT”.

Response: We have added this.

Changes in manuscript: Line 356 (line 361 in the revised manuscript): “the” has been added in front of “WT”.

Comment: Line 356: change “enables” to “potentially creates”.

Response: We have changed this.

Changes in manuscript: Line 356 (line 362 in the revised manuscript): “enables” has been changed to “potentially creates”.

Comment: Line 365: add “a” in front of “positive correlation”.

Response: We have corrected this.

Changes in manuscript: Line 365 (line 372 in the revised manuscript): “a” has been added in front of “positive correlation”.

Comment: Line 375: a comment on the reference to Whiting and Chanton, 1993: careful, this study was driven by the rice outlier.......

Response: This is true. We removed the reference and the sentence completely.

Changes in manuscript: The two sentences on lines 372–375 have been removed.

We hope that the editors and the Referees find the quality of our revised manuscript sufficient to warrant publication in the *Biogeosciences*. We thank the Associate Editor and the Referees for their valuable and constructive comments.

On behalf of co-authors,
Sincerely yours,

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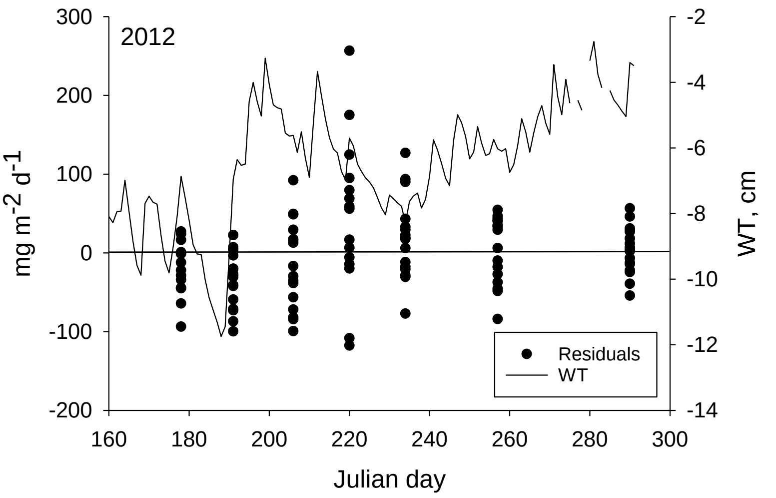

Figure 1. Residuals of the model plotted together with water table (WT) in 2012.

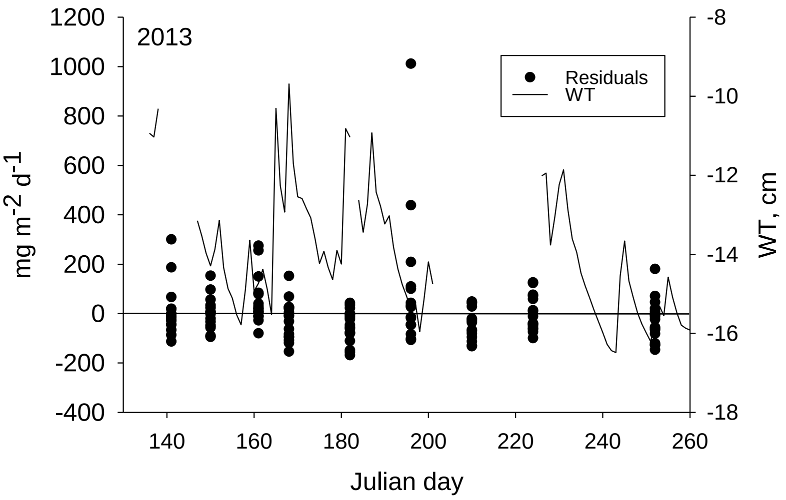

Figure 2. Residuals of the model plotted together with water table (WT) in 2013.

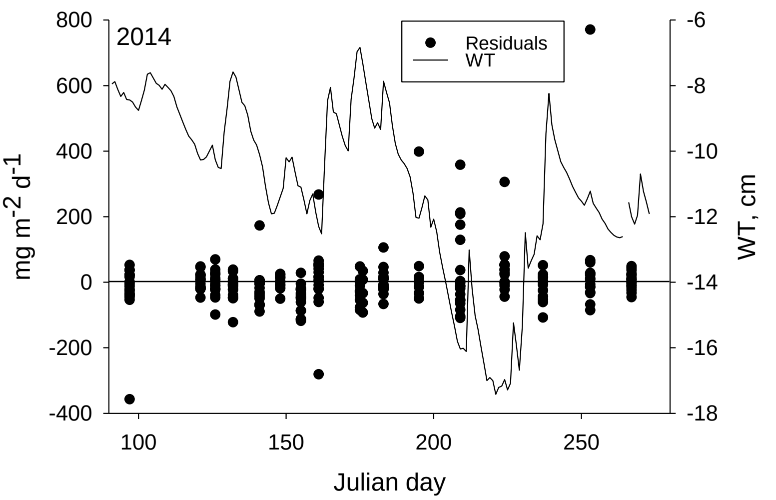

Figure 3. Residuals of the model plotted together with water table (WT) in 2014.

Small spatial 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 to quantify 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 aerenchymous plant species (LAI_{AER}). Methane emissions ranged from -309 to 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 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. 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 peatlands are wetland ecosystems where partly undecomposed organic material is stored as peat in anoxic conditions under the water 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 aerenchymous 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 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 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 of plant community types varies (Kotiaho et al., 2013). Sedges with aerenchymous tissue in their stems and roots, that allows transportation of oxygen to their roots, grow on the water-saturated surface types. Shrubs that lack aerenchymous 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 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 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 higher amount of aerenchymous 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. 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 aerenchymous vegetation (aerenchymous 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 aerenchymous 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 pools, 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 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. 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 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 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 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 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 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 aerenchymous plants (LAI_{AER}) for each sample plot was calculated based on the leaf area of the five aerenchymous 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 methane fluxes. The EC setup included an ultrasonic anemometer (USA-1, METEK GmbH, Germany) and an open-path methane 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 methane (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,

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

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, *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 methane flux model was then calculated using Eq. (1) and used to fill the gaps in the observed EC methane flux.

2.5 Analyses

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 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 temperature can be expected to have a nonlinear effect on methane flux, and therefore we mimicked the often-used exponential relation of methane flux to temperature by assumed peat temperature effect first to be constant until 10 °C degrees and then follow second degree polynomial. The 10 °C degrees' threshold was selected based on visual inspection. According to AIC-value 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, 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).

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 (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 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 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 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 differences between the plant community types were similar in each year.

Peat temperature did not differ between the plant community types in the warmest year 2013. In the coolest and wettest year 2012, 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 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 ranged from -90 to 387 mg $m^{-2}d^{-1}$, from -87 to 1254 mg $m^{-2}d^{-1}$ and from -309 to 910 mg $m^{-2}d^{-1}$ in 2012, 2013 and 2014, respectively (Fig 2). 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 methane 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, 483; p=0.0004), as there were higher methane fluxes from hummocks and high lawns than from 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 were small.

Methane emission increased with increasing peat temperature. 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 aerenchymous LAI, but also with the total LAI, even after the aerenchymous 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, 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 0.05. For the random effect 'plot cluster', standard deviation of the constant was 36.44 and standard deviation of residuals was 95.63 showing that the variation between clusters was smaller than the variation within clusters.

Although Siikaneva bog is a wet site with a high WT (see e.g. Moore et al., 2011) (Fig 1), negative flux values 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 to the soil ranged from ca. 4 to 309 mg m^{-2} d^{-1} (Fig 2). The highest net methane fluxes towards the soil were measured on bare peat surfaces in 2014 (185 and 309 mg m^{-2} d^{-1}).

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 upscaled monthly methane emissions for the whole ecosystem in July and August were 1.7 and 2.5 g m^{-2} mo^{-1} in 2012, 5.4 and 3.1 g m^{-2} mo^{-1} in 2013 and 4.9 and 3.5 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 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 in the middle of summer and decreasing towards autumn (Fig 5).

4 Discussion

The methane fluxes measured in this study ranged from -309 to 1254 mg m^{-2} d^{-1}. When 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 387 mg m^{-2} d^{-1}. They are, on average, of same magnitude as 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 ± 6 mg m^{-2} d^{-1}, which is a little higher than the mean fluxes in 2012 and 2014 (57 ±6 and 77 ± 7 mg m^{-2} d^{-1}) but lower than the mean flux in the warmest year 2013 (131 ± 12 mg m^{-2} d^{-1}) in this study. Similarly, another review (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 aerenchymous vegetation, as high WT reduces the thickness of aerobic peat layer and consequently methane consumption, while transport through aerenchymous 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 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 flux than high hummocks in 2014. 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 affects 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 aerenchymous 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 aerenchymous 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 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 aerenchymous 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. The effect of LAI_{TOT} on methane flux was about one third higher than the effect of 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 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 measured from wetter plant community type.

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 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-aerenchymous 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 flux rate can be straightly affected by a change in the abundance of aerenchymous 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.

Negative fluxes, i.e., net fluxes from the atmosphere to soil 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 flux was measured twice from one sample plot on a high hummock. This high hummock was the only sample plot that showed negative net 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 archaea. 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 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 net fluxes were also measured twice on waterlogged plant community types (HO and BP). This could be explained by plants with aerenchymous 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).

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. 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 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. 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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Tables

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

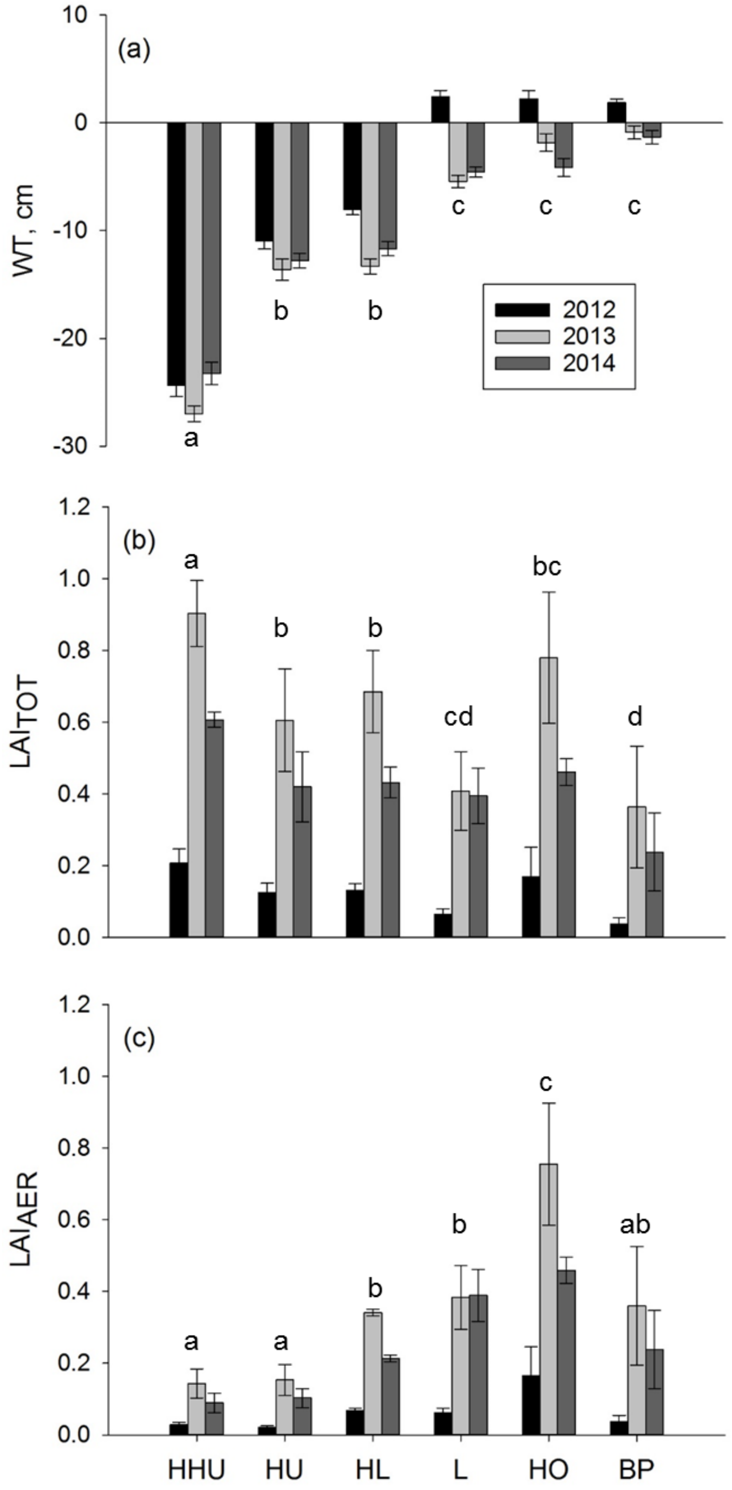

Figure 1. a) Mean water table and the mean of summer maximum of b) total leaf area (LAI_{TOT}) and c) leaf area of aerenchymous plant species (LAI_{AER}) in six plant community types: high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and bare peat surface (BP) in three subsequent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

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.

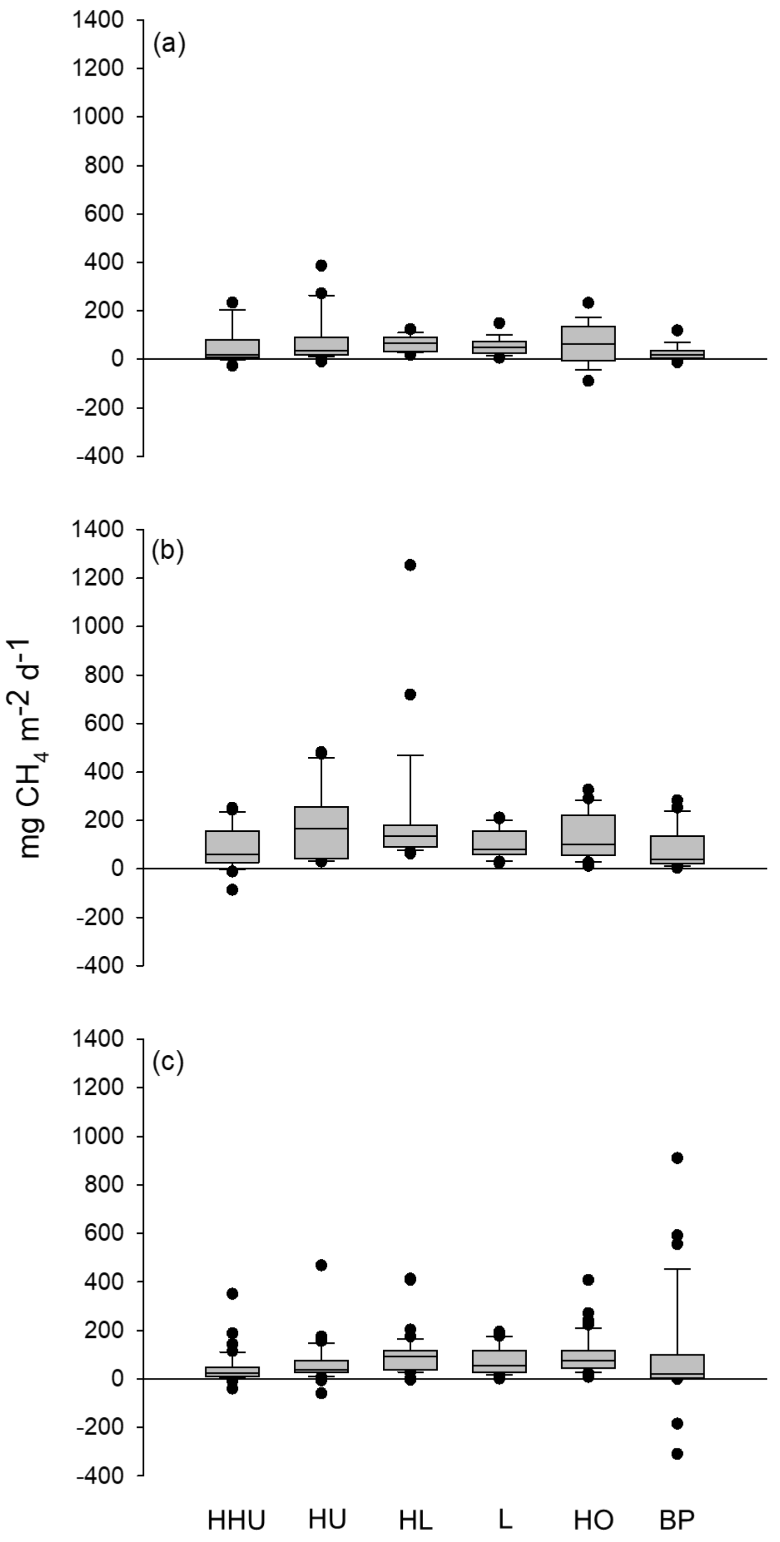

Figure 2. Methane fluxes in Siikaneva bog in three subsequent years a) 2012, b) 2013 and c) 2014 from six different plant community types: high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and bare peat surfaces (BP).

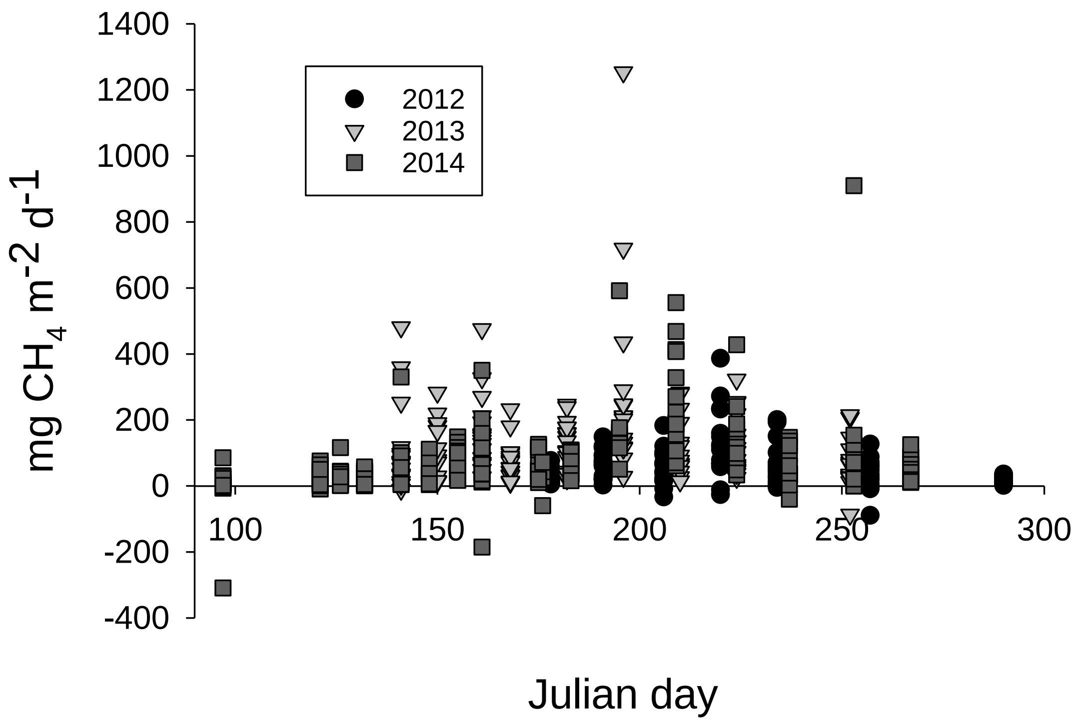

Figure 3. The measured methane fluxes in three subsequent years.

680

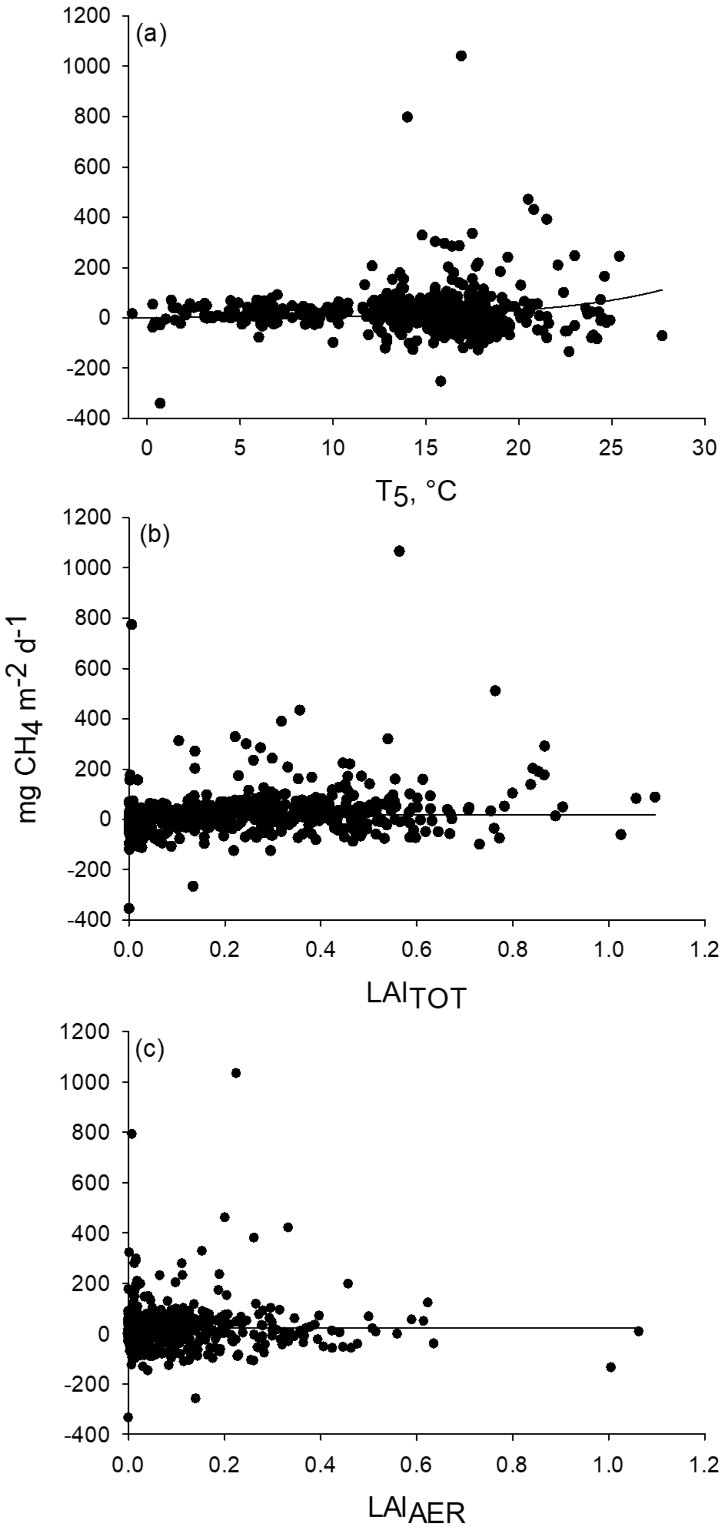

Figure 4. Response of methane flux to a) peat temperature in the depth of 5 cm, b) total leaf area (LAI_{TOT}) and c) leaf area of aerenchymous plant species (LAI_{AER}). Methane fluxes measured in 2012-2014 were adjusted to a) mean LAI_{TOT} (0.2661) and LAI_{AER} (0.1016), b)

mean peat temperature in the depth of 5 cm (14 °C) and mean LAI_{AER} (0.1016) and c) mean peat temperature in the depth of 5 cm (14 °C) and mean LAI_{TOT} (0.2661).

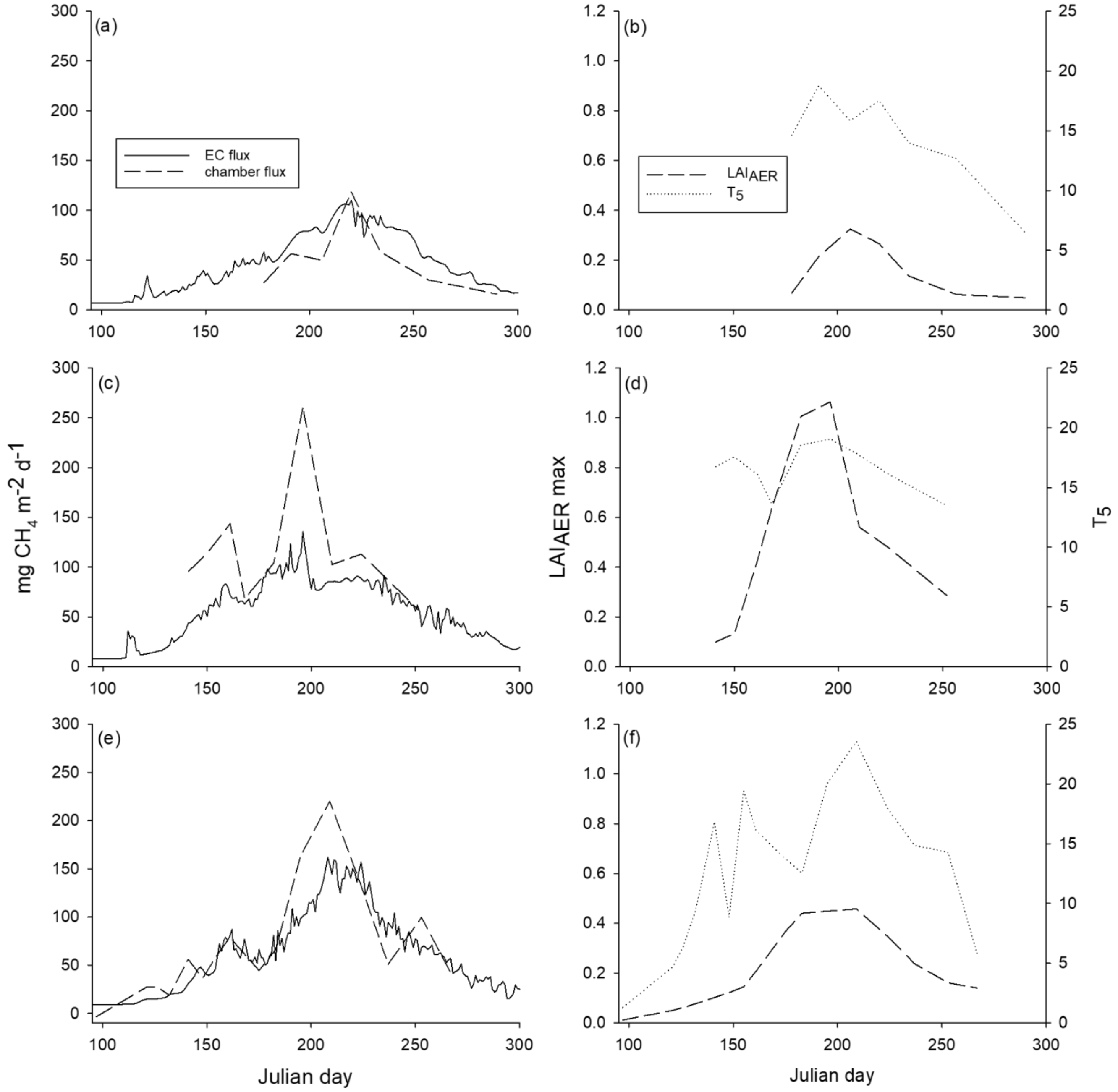

Figure 5. Ecosystem level methane fluxes measured with the eddy covariance (EC) technique and upscaled from chamber measurements (chamber flux) (left panel), and maximum leaf area index of aerenchymous plant species (LAI_{AER} max) and peat temperature in the depth of 5 cm (T_5) (right panel) over the growing seasons a-b) 2012, c-d) 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 aerenchymous 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	0.0000
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